Modelling of feeding behaviour, rumen load and the kinetics of digestion and passage of digesta in domestic and wild ruminants

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As the research supervisor, I agree to the submission of this thesis for examination.

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Name: Ignatius Verla Nsahlai (Professor of Animal Science)

Dedication

“In the hope of thereby preserving from decay the remembrance of what people have done”

This Thesis is dedicated to the entire Majola-Moyo clan;

To my late mother Thandiwe Moyo. It is so unfortunate that you could not live long to taste the sweet fruits that this thesis will reap in the future…

To my father Julius Moyo, to my aunt Ntombikayise Moyo who have both supported me thus far, to my brother Sikhumbuzo and sister Bokani, to my super cousin Hilington Dube, and all my cousins and to my late grandparents…

and lastly to my “future wife” who will read this thesis in a few years’ time
and to my “future kids” who will get the chance to read this work when I am an old man…

Numbers of good people are dwindling fast
Trying times need courage and resilience
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List of abbreviations

a – soluble fraction

ADF – acid detergent fibre

ADL – acid detergent lignin

AFRC – Agricultural Food and Research Council (United Kingdom)

APL – animal production level

AQLP – *Afzelia quanzensis* legume pods

b – slowly degradable fraction

BOAL – *Brassica oleraceae var. acephala* leaves

BW – body weight

c – rate of degradation of the slowly degradable fraction of fibre

CMLB – *Colophospermum mopane* leaves brown

CMLG – *Colophospermum mopane* leaves green

CMP – *Colophospermum mopane* pods

CP – crude protein

CPH – cowpea husks

CRP – cassava root peels

CSC – cottonseed cake

DB – diet subclass

DCP – dietary crude protein

DEB - duration of eating bouts

DH – *Diheteropogon hagerupii*

DL – days in lactation

DM – dry matter

DMD – dry matter disappearance

DMI – dry matter intake

DML – dry matter loss

DNDF – dietary neutral detergent fibre

DOM – degree of maturity

DP – days in pregnancy

DRB – duration of ruminating bouts

DS – diet class

DSTA – dietary starch

EC – *Eragrostis curvula*

ECB – Eragrostis curvula at bloom stage

ED – effective degradability

ET – *Eragrostis tremula*

FM – fish meal

FSG – functional specific gravity

GH – grass hay

GI – feeding management

GLM – general linear model

GNH – groundnut haulms

HEM – hemicellulose

iNDF – indigestible neutral detergent fibre

IRQ – improved roughage quality

k – fractional passage rate

KG - Kikuyu grass

k_l – rate of passage of liquid in the rumen

k_p – rate of passage of particles in the rumen

LH – lucerne hay

LSP – lespedeza

MB – millet bran

MBW – mature body weight

MCP – monocalcium phosphate

MD – mixed diets

MIS – millet stover

ML – maize leaves

MOC – Marula oil cake

MP – microbial protein

MPL – *Mucuna pruriens* leaves

MRT – mean retention time

MS – maize stover

MSD – maize stover at dry stage

MSM – maize stover at milk stage

MT – maize stalks

NDF – neutral detergent fibre

NDFI – neutral detergent fibre intake

NE – net energy

NEB – number of eating bouts

NE_f – net energies for fattening

NE_l – net energies for lactation

NE_m – net energies for maintenance

NLM – no lag model

NRB – number of ruminating bouts

NTLM – no time-lag model

OFR – outflow rate

OM – organic matter

PD – potential degradability

pdNDF – potentially degradable neutral detergent fibre

PFCC – protein-free cell contents

PRQ – poor roughage quality

PS – particle size

RDML – rumen dry matter load

REDIM – Repository of Intelligent Models

RLML – rumen liquid matter load

RMSE – root mean square error

RQ – roughage quality

RSD – residual standard deviation

RSE – residual standard error

RTDMI – rumination time per unit dry matter intake

RTNDFI – rumination time per unit neutral detergent fibre intake

RWML – rumen wet matter load

SBM – soya bean meal

SD – standard deviation

SE – Schizachyrium exile

SEM – standard error of the mean

SF – selectivity factor

SFC – sunflower cake

SFM – sunflower meal

SIL – feed type

SIRQ – semi-improved roughage quality
SNK – Student-Newman-Keuls
SS – sorghum stover
SSLS – sorghum stover leaves and sheath
SSS – sorghum stover stems
TAN – feed class
tL – time lag
TLM – time lag model
TNER – total net energy requirements
TS – time spent
TSC – time spent chewing
TSE – time spent eating
TSI – time spent idling
TSIL – time spent idling whilst lying
TSIS – time spent idling whilst standing
TSR – time spent ruminating
TT – *Themeda triandra*
UTCPH – urea treated cowpea husks
UTDH – urea treated *Diheteropogon hagerupii*
UTET – urea treated *Eragrostis tremula*
UTMS – urea treated maize stover
UTMIS – urea treated millet stover
UTSE – urea treated *Schizachyrium exile*
UTSS – urea treated sorghum stover
VGH – veld grass hay
VGHC – veld grass hay Camperdown
VGHD – veld grass hay from Dundee
VGHP1 – veld grass hay Pietermaritzburg area 1
VGHP2 – veld grass hay from the Pietermaritzburg area 2
WB – wheat bran
WS – wheat straw

Thesis outputs

Articles published in ISI Journals

1. Moyo M, Nsahlai IV. 2020. Consequences of increases in ambient temperature and effect of climate type on digestibility of forages by ruminants: a meta-analysis in relation to global warming. Animals 11(1):172.
2. Moyo M, Adebayo RA, Nsahlai IV. 2019. Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of goats and sheep under subtropical conditions. Asian Australas J Anim Sci 32(5):675-690.
3. Moyo M, Gueguim-Kana EB, Nsahlai IV. 2018. Prediction of solid digesta passage rate using liquid passage rate as one of the input variables in ruminants. S Afr J Anim Sci 48(4):758-769.

Book Chapters published

1. Moyo M, Bhiya ST, Masande K, Nsahlai IV. 2019. Evaluation and prediction of the nutritive value of underutilised forages as potential feeds for ruminants. In book: Forage Groups (Chapter: 6). Ricardo L. Edvan and Edson M. Santos (Editors). IntechOpen: London, United Kingdom. pp 87-106.
2. Moyo M, Nsahlai IV. 2018. Rate of passage of digesta in ruminants; Are goats different? In book: Goat Science (Chapter: 3). Sandor Kukovics (Editor). IntechOpen: London, United Kingdom. pp 39-74.

Conference proceedings and abstracts

1. Moyo M, Gueguim-Kana EB, Nsahlai IV. 2017. Influence of liquid passage rate on solid digesta passage rates for grazing and browsing domestic and wild ruminants. 50th South African Society for Animal Science Congress: “Golden Innovations for Sustainable Agriculture”. Port Elizabeth, Eastern Cape Province, South Africa (18th – 21st September, 2017) pp. 359-360. [Abstract].

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General Abstract

Roughage intake is affected by a collection of factors that include feeding behaviour, and the weight of rumen digesta which is a function of digesta clearance from the rumen as governed by the rates degradation and passage. Accurate prediction of intake depends on the ability to predict these factors. In literature, there are few models, if any, that can be used to estimate the weight of rumen digesta load, simulate feeding behaviour, predict passage rates of solid and liquid digesta, and degradability in the rumen of ruminants inhabiting environments with different diet qualities.The five main objectives of this study were to (1) investigate effects of diet and roughage quality on feeding behaviour; and to determine the main factors affecting and developing Random Forest models to estimate (2) time spent on diurnal feeding behaviours, (3) digestion of feeds in the rumen, (4) weight rumen digesta load and (5) rate of passage of digesta in the rumen.

The effects of diet and roughage quality on dry matter intake, duration and number of daytime and night-time eating bouts, and ruminating activities in small ruminants were investigated. 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). Daytime (06:00 to 18:00 h) and night-time (18:00 to 06:00 h) feeding behaviour activities were recorded. Roughage quality affected rumination index in Exp 1, but not in Exp 2, 3, and 5. Time spent eating and ruminating was affected by roughage quality (Exp 1, 3, and 4), period of day (all experiments) and their interaction (Exp 1). Period of day affected the duration of rumination sessions (Exp 1, 2, and 3); diet quality or roughage quality affected the duration of eating bouts (Exp 3) and rumination sessions (Exp 1 and 2). roughage quality had a significant effect on the duration eating sessions in Exp 3 only, whilst period of day affected this same behaviour in Exp 2 and 3.

To ascertain the influence of the period of the day, ambient temperature, climatic region, and ruminant feeding type on daytime and night-time feeding behaviour of ruminants a dataset was collected from studies that measured feeding behaviour. Studies that qualified for inclusion into the dataset should have (1) reported times spent eating (TSE), ruminating (TSR) and idling, number and duration of ruminating and eating sessions during a 12h day and 12h night period, and 24 h period (2) measured body weights of animals used, and (3) stated feeds or proportion of feeds in diets fed to or consumed by the animals. Diet properties, animal and environmental factors affecting feeding behaviour were identified in the studies. A mixed effects and

regression models captured the influence and response to the period of the day, ambient temperature, climatic region and ruminant feeding type of feeding behaviour. During the day, time spent ruminating and chewing became longer in large ruminants than at night. Predictions showed that time spent eating during the day and at night are expected to decline with an increase in ambient temperature, while times spent ruminating during the day will increase. Grazers and intermediate feeders spent more time eating during the day than at night, while browsers spent more time eating at night than during the day.

The influence on 24 h diurnal feeding behaviour patterns of ruminants in response to ambient temperature and ruminant feeding type were ascertained. Feeding behaviours scaled allometrically with body weight for all ruminant feeding types, except for TSE by browsers and intermediate feeders, and TSR by grazers. Times spent eating and TSR become shorter in large compared to small ruminants. Time spent ruminating became shorter in large browsers, while large intermediate feeders spent more TSR than their smaller counterparts. Browsers had less TSE, highest DEB and lowest number of eating bouts compared to grazers and intermediate feeders. Trends from this study showed that TSE, DEB, and idling are projected to increase with ambient temperature, while TSR is likely to decrease.

Models to predict TSE and TSR for grazing and browsing ruminants were developed. A dataset was created from studies that reported TSE and TSR, number of eating (NEB) and ruminating bouts (NRB), and the duration of ruminating (DRB) and eating bouts (DEB) over a 24h period. Factors affecting feeding behaviour were identified from each study and grouped into (1) diet properties, (2) animal and (3) environmental factors. These factors were used as input variables for the prediction of feeding behaviour. The dataset was randomly divided into two subsets: 70% for model training and 30% for model testing. Developed models accounted for 95% (TSE), 90% (TSR), 93% (DEB), 93% (DRB), 78% (NEB) and 90% (NRB) of the variation in prediction of feeding behaviour. The models attained 87% (TSE), 62% (TSR), 93% (DEB), 83% (DRB), 82% (NEB) and 77% (NRB) precision in prediction during testing using an independent dataset. This study developed good simulation models for feeding behaviour of ruminants.

The consequences of increases in ambient temperature and effect of climate type on digestibility of forages by ruminants using meta-analysis in relation to global warming were evaluated. A dataset on nylon bag degradability parameters bearing the chemical composition of roughages, grains, leaves, stems, fruits, concentrates, and diets given to animals, climate type, and ambient temperature were compiled. Data were analysed using mixed model regression and simple linear regression methodologies. Negative correlations between ambient temperature and degradability parameters were observed. Potential degradability was highest for studies carried out in cold and temperate climates compared to tropical and arid climates. A 1 °C increase in ambient temperature decreased PD by 0.39% (roughages), 0.76% (concentrates), and 2.41% (mixed diets), with an overall decrease of 0.55% for all feed types. The “b” fraction decreased by 0.1% (roughages), 1.1% (concentrates), 2.27% (mixed diets), and 0.35% (all feed types) for every 1 °C increase in ambient temperature. Increasing ambient temperature by 1 °C increased the neutral detergent fibre content of feeds by 0.4%. A test of slopes showed that the predicted decrease in rumen digestibility of feeds with ambient temperature would be most severe in tropical and arid regions compared to cold and temperate regions.

An evaluation and prediction of the nutritive and feeding value of underutilised forages that have a potential of being ruminant feeds was done. Underutilised forage legumes, leaves/trigs of forage trees and shrubs (non-leguminous), commonly used grass forages and concentrates were collected from various regions. The nylon bag method was used to determine degradability of the underutilised forage legumes, leaves/trigs of forage trees and shrubs (non-leguminous) in the rumen. A step-wise regression procedure was used to develop regression equations to predict degradability of forages in the rumen. Of the underutilised forages, the crude protein content tended to be double for *Brassica oleracea var. acephala* compared to *Colophospermum mopane* leaves and pods. Forage grasses (62.9±34 g/kgDM) tended to have very low crude protein contents compared to legumes (137.6±69 g/kgDM) and concentrates (177±39.9 g/kgDM). Underutilised *Brassica oleracea var. acephala* (305 g/kgDM) tended to have higher crude protein levels compared to commonly used protein sources (cotton seed cake = 222 g/kgDM). The regression model for predicting the soluble fraction accounted for 59% and 71% of the variation in model development and validation of predictions, respectively. The regression model for predicting the potential degradability accounted for 65% and 24% of the variation in model development and validation, respectively.

A dataset to enable prediction of degradation parameters in the rumen were collected from studies that (1) reported values for in-sacco degradability parameters viz. soluble fraction (a), slowly degradable fraction (b), potential degradability (PD) and rate of degradation (c) of roughages, grains, leaves, stems, fruits and concentrate formulations, and (2) stated the diets given to animals fed at ad-libitum. Two datasets were collated, one on studies that used the time-lag model and another on studies that used the no-time lag model in computing degradation parameters. Factors that affect degradability were identified in each of these studies and categorised into (i) diet properties (ii) feed sample properties (iii) ruminant feeding type and (iv) environmental factors. These factors were used as input variables to enable prediction of degradability. Each dataset was randomly divided into two subsets: 70% for training and 30% for testing. The no time-lag models attained 88% (“a”), 93% (“b”), 76% (“c”) and 90% (“PD”) precision in prediction during training and 58% (“a”), 52% (“b”), 48% (“c”) and 53% (“PD”) precision in testing. Time lag models accounted for 91% (“a”), 84% (“b”), 79% (“c”), 91% (“PD”) and 87% (lag) of the variation in prediction during training and 64% (“a”), 57% (“b”), 29% (“c”), 52% (“PD”) and 59% (lag) precision in testing. Both sets of models predicted “a”, “b”, PD, and lag with appreciable precision, but models for the prediction of the rate of degradation require improvement.

The influence of liquid passage rates on solid digesta passage rates and the possibilities of simultaneous prediction of solid and liquid passage rates in ruminants was examined. Artificial neural networks were used to develop models of solid and solid plus liquid passage rates. Studies that reported fractional passage rates, class and body mass of ruminants were included in the dataset. Factors affecting the rate of passage were identified from each study and grouped into (i) diet properties, (ii) animal, (iii) feed particle properties and (iv) environmental factors. Animal and feed factors that affect the rate of passage were identified in studies and used as input variables to estimate rate of passage in the rumen. The database was composed of observations of domestic and wild ruminants of variable body mass (1.5 to 1238 kg) from 74 (solid using predicted liquid passage rate) and 31 (solid using observed liquid passage rate) studies. Observations were randomly divided into 2 data subsets: 75% for training and 25% for validation. Developed models accounted for 76 and 77% of the variation in prediction of solid passage rates using predicted and observed liquid passage rate as inputs, respectively. Simultaneous prediction accounted for 83 and 89% of the variation of solid and liquid passage rates, respectively. On validation using an independent dataset, these models attained 45% (solid using predicted liquid), 66% (solid using observed liquid), 50% (solid predicted with liquid) and 69% (liquid predicted with solid) of precision in predicting passage rates. Simultaneous prediction of solid and liquid passage rate yielded better predictions (+7%) compared to independent predictions of solid passage rate.

Scaling relationships of rumen digesta load with body weight and the influence on ruminant digesta load in response to climatic region and ruminant feeding type were evaluated. A dataset on rumen digesta load (RDL) parameters bearing body weights of ruminants, proximate chemical composition of feeds and diets fed to or eaten by ruminants and climate type was created. Data were analysed using a linear regression and mixed model regression methodology. Grazers and intermediate feeders had hypoallometric scales of RDL with BW, while the scale was hyperallometric for browsers. Wet and liquid RDL of grazers and browsers scaled isometrically with BW. Intercepts of scaling relationships of RDL and BW were highest for intermediate feeders and lowest for browsers. For all RDL, body mass and animal production were both influential covariates. Ruminant species and ruminant feeding type ($p<0.05$) influenced all measures of RDL and was highest in grazers and lowest in browsers. The response of RDL to increases in ambient temperature where more linear than they were quadratic. Liquid and dry rumen digesta load were predicted to decrease in proportion by 0.02 ($p<0.0001$) for every 1°C increase in ambient temperature.

Models to estimate the weight of rumen digesta in ruminants were developed. A dataset was created from studies that (1) measured either the rumen dry matter load (RDML), rumen wet matter load (RWML) or rumen liquid matter load (RLML) by complete evacuation of the rumen through fistulas or after slaughtering, (2) reported body weights of animals and (3) stated the diets fed to or eaten by the animals. Factors affecting rumen digesta load were identified from each study and included animal (ruminant feeding type, body weight, degree of maturity, animal production level, days in lactation and pregnancy), diet composition (dry matter, neutral detergent fibre, crude protein, starch and ash content), management (grazing or fed-indoors) and environmental (climate type and ambient temperature) factors. These factors were used as input variables in predicting rumen digesta load. The dataset was divided into 2 subsets: 70% for model training and 30% for testing. The models accounted for 81% (scaled RDML) and 90% (unscaled RDML) of the variation in prediction of RDML. On testing, the models attained 59% (scaled RDML) and 84% (unscaled RDML) precision in prediction. Models attained high precision in prediction of RWML ($R^2 = 0.94$) and RLML ($R^2 = 0.94$) during training and testing of RWML ($R^2 = 0.85$) and RLML ($R^2 = 0.88$) using an independent dataset. In conclusion, the models gave good predictions of the weight of rumen digesta load. However, there is a need to correct for the effect of time delay from the point when feeding stops till when rumen digesta load is measured; this is quite cardinal in regressing in time to the exact rumen digesta load when the animal stopped eating.

In summary, results from this study showed that increases in ambient temperature will decrease rumen digestibility of forages and these will be more pronounced in arid regions. Small-sized ruminants adapted their feeding behaviour and rumen digesta load better than large-size ruminants. This implies that local breeds which are generally small in size can be better utilised to mitigate climate change by farmers in arid regions. High accuracy in prediction of feeding behaviour, rumen degradability, passage rate of digesta in the rumen and rumen digesta load would enable better prediction of dry matter intake by ruminants.

Chapter 1

General introduction

1.1 Background

Feed is the single most costly input into any livestock production enterprise. It is in the best interest of livestock farmers to develop feeding strategies to maximise feed use, for example, providing enough feed for animals to meet their requirements for maintenance, growth and production. This is achievable only when feed intake can be accurately estimated. Prediction of feed intake in ruminants is done using mathematical models (Seo et al. 2005; Seo et al. 2009). Such models may be used to accurately predict feed intake under the animal, environmental and feed factors in which they were developed. Nevertheless, application of these models should be carried out with caution since most models are empirical in nature rendering them situation specific. Feed intake is affected by a collation of factors and at any given time is a function of rumen digesta load, feeding behaviour, rates of digestion and particle breakdown, and rates of outflow of digesta from the rumen (Williams et al. 2014). It is imperative for intake prediction models to account for these factors in model development inorder to achieve realistic estimations of feed intake.

The appropriateness of the Illius and Gordon's (1991) model in prediction of feed intake in ruminants grazing on poor quality roughages in tropical regions was evaluated by Nsahlai and Apaloo (2007). The authors showed that the Illius and Gordon's (1991) mathematical model, though structurally adequate, underestimated roughage intake, and the weight of rumen digesta load for grazing ruminants fed on poor quality roughages in the tropics and sub-tropics. The unsuitability of the model to accurately predict intake was due to inaccurate calibrations used in estimating digesta passage rates and rumen digesta load.

The model of Illius and Gordon (1991), as with other models, estimates the weight of rumen digesta load and digesta passage rates as a function of body weight alone, which is erroneously insufficient. The passage rate models of Moyo et al. (2017) accounted for almost all dietary and animal factors affecting the rates of passage except for ambient temperature and climate type.

The critical role of feeding behaviour in influencing passage rates and feed intake has been overlooked. In the context of this study, feeding behaviour of ruminants refers to time spent on eating, ruminating, and idling (neither eating nor ruminating), and the duration and number of eating and ruminating bouts. Coleman et al. (2003) used feeding behaviour (ruminating time) to develop feed intake and digestibility prediction models, giving modest predictions. Most feeding behaviour prediction models have been developed for sheep and their performance in simulation of feeding behaviour for other ruminants remains unknown. There is poor simulation of digestibility of low-quality roughages which are commonly grazed and fed to ruminants in the tropics (Nsahlai and Apaloo 2007). Ambient temperature grossly affects digestibility of plant material through its influence in lignin deposition in plants. The magnitude of change in the rumen digestibility parameters of feeds as affected by changes in ambient temperature are not well documented.

A holistic approach that would enable accurate prediction of feed intake in ruminants involves the identification of the main factors affecting and the accurate prediction of feeding behaviour, feed degradation in the rumen, the rates of solid and liquid passage through the rumen, and rumen digesta load.

1.2 Problem statement

This study was proposed to address the following research problems: Little is known on the scaling relationships of feeding behaviour with body weight. The extent of decreases in digestibility of feeds by ruminants and rumen digesta load with increasing ambient temperature is unknown. There are few models, if any, that can be used to estimate the weight of rumen digesta load, simulate feeding behaviour, predict passage rates of solid and liquid digesta, and degradability in the rumen of ruminants inhabiting environments and feeding on different diet qualities.

1.3 Rationale

Simulation of feeding behaviour of ruminants (time spent eating, ruminating, chewing, and idling) across diverse climates and ambient temperatures allows scientists to predict the behavioural responses of ruminants to ecological changes. In the future, these models can be used as a baseline for detecting changes in feeding behaviour of ruminants considering the effects of global warming. Simulating feeding behaviour of ruminants that graze on rangelands is important to livestock feeding, especially in marginal environments where the available feed need to be maximised. Knowing how much time ruminants spend eating, ruminating, and idling when feeding would enable prediction of feed intake; enabling development of sustainable grazing management and practises to prevent depletion of farmland and natural grasslands as a result of overgrazing.

Modelling of fermentation processes provides easier methods of estimation of how much degradation of feed occurs in the rumen for use in prediction of feed intake. This would give a picture of the amount of nutrients that the animal obtains from feed. Also, this will reduce the cost of obtaining fistulated animals and use of invasive methods (fistulation) in rumen nutrition studies for determining digestibility of feeds in the rumen. Modelling of passage rate would enable easy calculation of digesta passage rates, limiting 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, rumen digesta load and more importantly feed intake. The ability to estimate rumen digesta load would provide easier methods of prediction of rumen digesta load for purposes of prediction of feed intake and simulation of feeding behaviour. Development of methods to predict the weight of rumen digesta load without having to completely evacuate the rumen will reduce the cost of cannulation of ruminants and avoid unnecessary slaughter of animals. Most importantly, estimations of rumen digesta load, degradation and the rate of passage of digesta in the rumen can be incooperated into development of models that seek to estimate feed intake and methane emissions from ruminants.

1.4 Aims and objectives

This study aims to estimate feeding behaviour, degradation of feeds in the rumen, the weight of rumen digesta and digesta passage rates in the rumen.

Aim 1 Feeding behaviour patterns of sheep and goats

1. To determine effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of sheep and goats

Aim 2 Modelling of feeding behaviour

1. To determine the how body size, ruminant feeding type and period of the day affects feeding behaviour in ruminants using Meta-Analyses.
2. To determine the main factors affecting feeding behaviour in ruminants using Meta-Analyses.
3. To develop Random Forest models for the prediction of total time spent on eating, ruminating, and idling of ruminants.

Aim 3 Modelling of degradation kinetics

1. To determine the effects of ambient temperature and climate type on rumen digestibility and chemical composition of forages using Meta-analysis.
2. To ascertain whether the nutrient composition of diets fed to ruminants affects

degradation, and to evaluate and predict rumen degradation of legume and grass forages, and *Brassica oleracea var. acephala* leaves.

3. To develop Random Forest model for the prediction of rapidly degradable fraction of fibre, slowly degradable fraction of fibre, time lag for fermentation to occur and the rate of degradation of fibre in the rumen.

Aim 4 Modelling of passage kinetics

1. To ascertain the influence of liquid passage rates on solid digesta passage rates in ruminants using modelling procedures.

Aim 5 Modelling of rumen digesta load

1. To determine the main factors affecting rumen digesta load in ruminants using Meta-Analyses.
2. To develop Random Forest models for the prediction of rumen digesta load.

1.5 Hypothesis

Hypothesis 1 Feeding behaviour patterns of sheep and goats

1. Diet quality and period of the day has an effect on diurnal feeding behaviour patterns of sheep and goats.

Hypothesis 2 Modelling of feeding behaviour

1. Ruminants adapt their feeding behaviour differently based on body size, feeding type and period of day.
2. Ruminant feeding type, body weight and ambient temperature are the main factors affecting feeding behaviour of ruminants.
3. Random Forest models predicted total time spent on eating, ruminating, and idling with high accuracy and precision.

Hypothesis 3 Modelling of degradation kinetics

1. Increases in ambient temperature would decrease forage quality and that climate type would have no effect forage quality.

2. The starch and neutral detergent fibre contents of the diets fed to ruminants affect degradability and that it is possible to predict the solubility and effective degradability of legume and grass forages, and *Brassica oleracea var. acephala* leaves.
3. Random Forest models predicted all degradation parameters, but the rate of degradation with high accuracy and precision.

Hypothesis 4 Modelling of passage kinetics

1. Liquid passage rates increase the accuracy of prediction of solid passage rates.

Hypothesis 5 Modelling of rumen digesta load

1. Degree of maturity, body weight and ambient temperature are the main factors affecting the weight of rumen digesta load.
2. Random Forest models predicted weight of rumen digesta load with high accuracy and precision.

Chapter 2

Review of literature [1]

Abstract

Fluid passage rates through the rumen influence digestion of soluble food nutrients, amount of short chain fatty acids absorbed in the rumen and that pass out of the rumen, the amount of by-pass protein of dietary origin and the amount of microbial protein available to the host as a protein source; making modelling of passage imperative. Current research on digesta passage rate should seek to incorporate various factors that affect rumen digesta load, and solid and liquid passage rates to develop intake and passage rate prediction models. The aim of this paper was to discuss factors that affect rates of passage of digesta in the rumen and rumen digesta load. Ambient temperature, animal physiological status and reproductive status, fermentation and diet quality are major factors affecting digesta passage rates. The animal's physiology also influences digesta passage rate. Computation of animal production level to account for all the physiological processes that affect passage rate is vital. 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. Corrected for diet properties, goats have similar passage rates to other ruminants.

Key words: diet selection, feeding behaviour, intermediate feeder, prediction model, ruminant

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[1] Moyo M, Nsahlai IV. 2018. Rate of passage of digesta in ruminants; Are goats different? In book: Goat Science (Chapter: 3). Sandor Kukovics (Editor). IntechOpen: London, United Kingdom. pp 39-74.

2.1 Introduction

Goats have become one of the most important livestock for resource limited farmers around the world because they can survive in harsh climatic conditions from cold temperate regions (in the Siberia) to hot arid deserts (in the Kalahari). Key to their ability to survive in diverse climatic regions is their ability to walk through tight, narrow places and their capability of efficiently utilising vast plant feed resources. Goats are important as a source of protein (milk and meat) and wealth. Given the increasing importance of goats among resource limited farmers in tropical and subtropical regions around the world, research on the physiological aspects of goat nutrition is vital for improved goat production. Feed availability and quality are the major factors affecting yields for and quality of chevon and milk in rural goat production systems. Enhanced milk and chevon productivity is largely dependent on feeding behaviour supported by improved nutritional status 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 rural communities around the world, especially in Africa and Asia. Hence, cost effective usage of these feeds is vital. Fundamental to cost effective concentrate supplementation for improved productivity of goat farming systems in the tropics relies on accurate and precise prediction of roughage intake. Accurate prediction of roughage intake would enable farmers to calculate precise quantities of concentrates to be fed to achieve a cost-effective level of production of good quality meat and milk.

One of the major challenges in developing sustainable and cost-effective feeding strategies for goats in rural production systems in Africa, Asia and other parts of the world is the inability to accurately predict roughage intake in goats. This is partly due to limited information on the critical factors that affect intake; digestion and passage rates of digesta, and rumen digesta load for goats. Nsahlai and Apaloo (2007) examined the appropriateness of Illius and Gordon’s (1991) model to predict the intake in ruminants grazing on poor quality roughages in tropical regions and showed that the model, though structurally adequate, underestimated roughage intake, partly due to poor estimates of gut fill and rate of passage. Similarly, other authors (Clauss et al. 1998; Clauss and Lechner-Doll 2001; 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. Nsahlai and Apaloo (2007) pointed out that the model of Illius and Gordon’s (1991) erroneously estimates rumen digesta load levels and passage rates as a function of body weight alone.

Given the role of fluid passage rates through the rumen in affecting by-pass proteins and fatty acids that are assimilated in the hindgut, passage of fluid would have a significant influence on milk protein and butterfat composition in dairy goats. This makes the study and modelling of digesta passage rate relatively important. Modelling of passage rates would necessitate prediction of roughage intake, microbial protein yield and milk composition in goats. Before any passage rate modelling exercise can be effectively carried out, factors that affect passage rates need to be reviewed and used to predict digesta passage rates.

Given the abundant literature on passage rates for cattle and sheep, and other ruminant feeding types, and limited data on goats, the paper (i) identifies the major factors that affect passage rates in ruminants (ii) explains the fundamental mechanisms by which each identified factor possibly affected rates of digesta passage from the rumen (iii) gives suggestions of the major factors that can be considered as critical input factors for developing passage rate prediction models distinguishing studies on goats (iv) determines whether or not goats are different with respect to other ruminants in terms of passage rates.

2.2 Rumen digesta load, gut capacity, and its estimation

Gut fill is referred to as rumen digesta load 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 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 digesta load 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 digesta load 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 digesta load 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) or slaughtering animals upon meal termination (Moyo et al. 2018). Rumen digesta load varies greatly with body weight and feeding habit. Rumen digesta load is approximated to be about 9% and 13% of body weight for browsers and grazers, respectively (Fuller et al. 2004). Interestingly, there is no apparent approximation of rumen digesta load based on body weight for intermediate feeders such as goats, although it may be assumed to fall within the range of 9-13% when grazers and browsers are regarded as extremes.

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 digesta load. Taweel et al. (2004) and Williams et al. (2014) reported scenarios whereby maximal rumen digesta load 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 digesta load after termination of morning feeding maybe misleading. However, Baumont et al. (1989) reported rumen digesta load to reach its first maximum after the main morning meals, with a daily maximal rumen digesta load being reached after the evening meal. Similar results were obtained by Thomson et al. (1985) where maximal rumen digesta load 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 digesta load levels which are time dependent, either before or after feeding bouts. These digesta load levels may be a function of the rate of emptying of rumen digesta after eating has stopped. At any given time, rumen digesta load levels are a function of the rate of feed intake, rates of digestion and particle breakdown, and rates of outflow (Williams et al. 2014). As such, rumen digesta load 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.

Based on rates of passage and digestion, estimation of rumen capacity using mathematical procedures gives variable but useable results. Estimated rumen pool size based on passage and degradation rates at the point of meal termination gave values which were even twice as large when compared to average observed values obtained from the literature (Nsahlai unpublished data). Failure of mathematical procedures to achieve tenable outcomes suggests that something uncertain takes place during the period after meal termination before evacuation.

2.3 Factors that affect rumen digesta load and rates of passage through the rumen

2.3.1 Animal species and feeding types

Ruminant livestock have different feeding habits (Clauss et al. 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 digesta load.

Sheep had lower mean retention times of solid in the rumen than cattle (58 vs. 65 h) (Bartocci et al. 1997). Lechner-Doll et al. (1991) added that selective retention of particles is more pronounced in cattle than in sheep suggesting that the 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) indicating different efficiencies in these ruminants. 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 digesta load 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 digesta load 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 phenomenon 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 less time re-chewing twigs than Merinos resulting in more intense rumen contractions that forced digesta out of the rumen quickly. Goats have a much similar feeding habit to these Dorper sheep as they utilise both grazing and browsing and are more selective of high-quality browse. It can be concluded that passage rate in ruminants is affected by interactions between diet, ruminant species, and their climatic environment.

Alcaide et al. (2000) observed no differences in particle passage rates in goats (intermediate feeder) and sheep (grazer) fed on various diets with average rates of 0.030 and 0.025 per hour, respectively. However, Clauss et al. (2006) suggested that smaller browsing species had much greater solid and fluid passage rates through the rumen than grazers of a much similar size. 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. 2006; Lechner et al. 2010). Surprisingly, intermediate feeders (such as goats) were not included in this comparison. 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 grazer’s 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, intermediate feeders and browsers exists.

Indirect evidence suggests that browsing ruminants have shorter mean retention times for liquid and solid digesta in the rumen compared to grazers. These include post ruminal absence of glucose transport mechanisms (GLUT transporters) in grazers which are present in browsers (Rowell 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 (Van Wieren 1996; Clauss and Lechner-Doll 2001) and lower total tract digestibility (Hadjigeorgiou et al. 2003) in browsers than grazers, 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). These differences are partly a result of faster fractional passage rates of fluid and solid through the rumen of browsers compared to grazers.

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. 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 polyphenolic compounds may increase the rate of passage of fluid. 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. Fluid from the interstitial spaces may be drawn into the rumen in an attempt to wash off these polyphenols (Silanikove et al. 2001) as a physiological response by the animal against them. 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 digesta load may be expected given that the passage rate is related to the amount of digesta in the rumen at any given time. Alcaide et al. (2000) showed that rumen digesta load 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 digesta load levels without noticeable rumen distension than sheep when fed medium quality diets. These results were not expected considering observations by Clauss et al. (2006) 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 digesta loads than sheep. 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 body weight (BW^x) 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 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 (Bartocci et al. 1997). Body weight cannot 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 in cattle 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 translated 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 digesta load (Silanikove et al. 1993). These findings indicated 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 digesta load data for goats adapted to subtropical and tropical climates in sub-Saharan African is limited, thus necessitating data on how climatic adaptation influences passage rates and rumen digesta load.

Rumen capacity and digesta load 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 suggested that Heidschnucken sheep have greater potentials in expanding their rumen capacity compared to Merino sheep. Black head sheep (cold climate or temperate breed) are unable to make such an adaptation relative to Heidschnucken sheep (Weyreter and Engelhardt 1984).

A new theory on passage rate is beginning to unfold based on anatomical features of the rumen in different ruminant feeding type. 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 characterised 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 caused entrapment of small particles in ridges of grazing ruminants than in browsers, causing longer retention times in grazers (Clauss et al. 2010).

2.3.2 Level of nutrition and feed intake

Plane of nutrition may be referred to as the level of feeding and animal production level. Level of feeding is defined as 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 (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 from feeding at maintenance level. Other authors (Varga and Prigge 1982; Lindberg 1988; Kovacs et al. 1998; Seo et al. 2001) 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 dry matter taking up space occupied by the fluid in the rumen thus exerting pressure on the rumen contents. With dry matter being bulkier (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 (1988) 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 elicits determination of maximal rumen digesta load levels in ruminants. 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 had high positive correlation to rumen capacity (Adams et al. 1987). Body weight alone is not a good indicator of maximal rumen digesta load; 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 digesta load or volume is more a function of various physiological states.

2.3.3 Roughage to concentrate ratio in diet

Supplementation of predominantly roughage-based diets has become a major practice in ruminant nutrition. Protein concentrate supplementation of ruminants grazed on pasture increases the nutritional status of ruminants (Salem and Smith 2008). Levels of concentrates added to predominantly roughage feed would affect the rate of passage of liquid and solid through the rumen. High roughage to concentrate ratio in the diet would lead to greater fluid and particulate passage rates from the rumen (Table 2.1). 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. Various authors (Evans 1981; Okeke et al. 1983; Merchen et al. 1986; Owens and Goetsch 1986; Poore et al. 1990) have reported that high proportions of concentrate in diets decreased the rates of fluid dilution and turnover in the rumen.

Table 2. 1 Effect of roughage to concentrate ratio in diet on rate of solid and fluid passage through the rumen of buffalo

Phase	Diet	R:C=87.5:12.5	F:C=75:25	F:C=62.5:37.5	F:C=50:50
	Parameter				
liquid	OFR (l/h)	3.47	3.16	2.76	2.41
liquid	RDL (l)	49.10	46.10	43.60	40.00
solid	k (%/h)	3.15	2.71	2.71	2.48

R:C, roughage to concentrate ratio; OFR, outflow rate; RDL, rumen digesta load; k, fractional passage rate. Adapted from Bartocci et al. (1997).

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 due to filling by saliva. Distension of the rumen wall results to contractions, emptying the rumen fluid and solid digesta to prevent it filling. These contractions squeeze solid and fluid digesta out of the rumen at an increased rate increasing the efficiency of microbial protein synthesis. 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.

Due to the bulky nature of forage, high roughage diets 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. 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 less bulk, concentrates would occupy far much less space in the rumen than forages, thus, high concentrate diets would induce low amplitude rumen contractions due to reduced tactile stimulation of the rumen wall. Low power of contractions would force less fluid out of the rumen per unit time compared to roughages leading to lower fluid and solid passage rates. Rumen digesta load was reported to be greater in diets that had higher proportion of roughage because roughages contribute to rumen digesta load 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 digesta load 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, thus, it passes out of the rumen at a much faster rate than roughage particles.

In the rumen, stratification occurs. 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 fine 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.

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, 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 et al. (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.

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. 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 liquid passage rate. However, ruminants that graze on grass that is at an earlier stage of development have high fluid passage rates through the rumen than those grazing on mature pasture. Previous works (Esteli and Galyean 1985;

McCollum and Galyean 1985; 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 lead 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 matter 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 fluid and reduces fluid outflow rate. This phenomenon is most likely to occur when high roughage diets are fed.

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 lesser the proportion that leaves the rumen thus the lower 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. Within a feed particle, 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. Plant particles undergoing fermentation produce gas, hence float and get entrapped in the floating fibre mat restricting their passage out of the rumen. 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 digesta load (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 digesta load 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 non-degradable fraction. This suggests that increased proportions of non-degradable fractions slowed down the rate of degradation of the degradable fractions, with overall effects of slowing down passage rate and increasing rumen digesta load. 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, as a result of high lignin content the rate of degradation is greatly reduced thus increasing retention time in the reticulorumen. 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 digesta load 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 digesta load exists. Using sheep fed on alfalfa hay and orchard grass hay, Baumont et al. (2000) 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 digesta load levels, suggesting a positive linear relationship between NDF content (x-axis) and rumen digesta load (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 digesta load. Boudon et al. (2009) stated that attainment of maximal rumen digesta load would limit feed intake in dairy cows grazed on highly digestible rye grass. Also, rumen digesta load 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 digesta load played a major role in regulation of feed intake with decreasing digestibility of a feed. Digestibility is negatively related to lignin content and high lignin content caused slow passage rate in the rumen (Dove 1996; Rinne et al. 2002). This actually suggests that passage rate of solid material was slower for low digestible feeds. Slower passage rates increased rumen digesta load 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 digesta load 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.

2.3.4 Ambient temperature

As ambient temperature fluctuates during the course of the year, or as the day progresses from sunrise to sunset; animals respond to these changes in varied ways and 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 panting, sweating, or licking own body which loses heat from body fluid via evaporation. Increasing plasma volume to increase heat dissipation (Chaiyabutr et al. 1987) possibly via radiation may occur. Under extremely high temperatures animals become reluctant to eat thus reducing dry matter intake (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 increasing 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 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 ambient 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 on exposure of animals to low ambient 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. 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 (Table 2.2). The observed increase in blood and plasma volumes indicated that animals responded to heat stress by dissipating heat via evaporation and radiation through the skin thus cooling their bodies using blood and water as medium. Water has a high specific heat capacity with reference to biological systems, and hence may be used to dissipate heat (Toole and Toole 2006) in most animals.

Table 2. 2 Effect of heat stress on blood volume, plasma volume and fluid passage rate through the rumen of Swamp buffalo

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

Adapted from Chaiyabutr et al. (1987).

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 would become high resulting in an increased flow of fluid through the rumen into the intestines (Chaiyabutr et al. 1987). Findings of Chaiyabutr et al. (1987) on the effect of high temperature on fluid passage rates make it appear as a special adaptation strategy of Swamp buffalo (*Bubalus bubalis*). Further research is needed to prove this theory.

Warren et al. (1974) observed increased levels of water intake with increasing ambient temperature. A study by Waybright and Varga (1991) showed increased fluid passage rates of up to 64% in water infused rumen. 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. 2006). The study by Warren et al. (1974) used Holstein cattle which are adapted to temperate climates; hence it is expected that a temperate breed would respond to high ambient temperatures of above 32°C to a great extent. Ruminants that are well adapted to high ambient 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. A change in passage rate as a result of fluctuations in ambient temperature is very high and the direction of change is unpredictable necessitating more research on the subject. Research needs to focus on the effects of differences in thermal resistance and/or thermal tolerance levels on passage rates in ruminant animals in the tropical regions. These suggest that studies need to consider season and place of study to index ambient temperature when modelling liquid passage rate to take into account the future effects of global warming on digesta passage kinetics. Research should account for the effect of ambient temperature on passage rate.

2.3.5 Stage of reproductive cycle and physiological state

The reproductive cycle can be subdivided into the lactational and non-lactational period, pregnancy stage, non-pregnancy stage and the number of days in gestation. 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 (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 2.3 and 2.4). 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 used 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. 3 Gut fill levels, and rumen liquid and solid passage rates in pregnant, non-pregnant, lactating, and non-lactating ewes

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

Adapted from Gunter et al. (1990).

Table 2. 4 Influence of gestation stage on rumen digesta load levels and fluid outflow rate in ewes

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

Adapted from Gunter et al. (1990).

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 ruminants 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 in accordance to Chaiyabutr et al. (1987)'s theory 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 digesta load 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 digesta load 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 digesta load 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 through the rumen increased by 20-36% between late pregnancy and lactation (Kaske and Groth 1997). Generally, rumen digesta load levels are expected to decrease with an increase in passage rates of solid and liquid digesta. Progressive increments in rumen digesta load 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 stalls (9.4% per hour). Animals that graze on rangelands spend more time chewing and eating than those confined to pens (Seo et al. 2006; Oshita et al. 2008). Cows have a greater frequency of rumen contractions during eating than during both rumination and rest (Okine and Mathison 1991). 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, 2.3/min during ruminating and 2.8/min during grazing (Frandson 1981) for cattle. It is therefore assumed that frequency of rumen contractions in goats and sheep are not documented. 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 digesta load. Earlier discussions we pointed out that high NDF content is associated with increased rumen digesta load levels.

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 digesta load. So far, a general trend in results showed higher fluid and solid passage rates in lactating than non-lactating ruminants (e.g., Kaske and Groth 1997). 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.

2.3.6 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 and functional specific gravity. 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 Mulligan 1989) observed a negative curvilinear relationship between functional specific gravity and particle size. 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, suggesting 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 functional specific gravity 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 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 whereby 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 2.5).

Table 2. 5 Effects of particle size and digestibility on mean retention time, rumen digesta load levels and rates of passage in the rumen

		Grass		Red clover	
Particle size	Parameter	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 particulate matter. Adapted from Bayat et al. (2010).

Although increased reticulorumen contractions have been shown to increase passage rates of both solid and liquid through 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 the effect 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 evidence that stratification does not occur in the rumen of browsing ruminants (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 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 be determined how and to what extent passage rates of fluid affect passage of small solids and vice-versa. Thus far, the selectivity factor (SF) is the only proposed measure of the relationship between mean retention times (MRT) of solid and liquid particles in the rumen ($SF = MRT_{solids} \div MRT_{liquids}$). The SF quotient values are used to describe ruminant ecological differences and find application in classification of ruminants into different feeding types (Clauss and Lechner-Doll 2001). Given that rumen retention time is a function of roughage quality, SF may be used to describe physiological differences in the degree of adaptation of ruminants to different roughages qualities. Nsahlai et al. (1999) proposed a relationship that took the form: $k_{liquids} = (k_{solids} – 0.0018) \div 0.360$. Both these relationships are mathematical in nature and do not give the clear biological relationships between passage rates of the two phases of rumen digesta. Given that both liquid and solid digesta phases exist intermingled together in the rumen, studies need to consider developing passage rate models that can be used to predict passage rates for both phases using one model.

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 digesta load (Allen 1996). Particle size reduction occurs during rumination or re-chewing of previously swallowed feed Kennedy (1985). Poppi et al. (1980), Dixon and Mulligan (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).

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 Midasch (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 fragility of particles. Now, inclusion of particle fragibility as a factor that influences passage rate and ultimately rumen digesta load 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) explained a faster passage rate of indigestible fibre components such as lignin using 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.

2.4 Are goats different in passage rates compared to other ruminants?

Generally, rates of passage of solid digesta are greatly dependent on the quality of diets ruminants consume. Botanical and nutritional preference of plant feed sources by ruminants varies greatly. Although goats are classified as intermediate feeders (Hofmann 1989), they are selective feeders. Goats demonstrate their botanical wisdom through a mastery of selecting high quality leafy parts on shrubs, trees and grass stalks that are of higher protein and lower cellulose contents compared to sheep and cattle. This wisdom allows goats to specifically select diets that are able to provide enough net energy and protein to meet their requirements for maintenance for which sheep seem to fail to achieve (Garcia et al. 1995). This implies that total tract digestibility and degradation rates of diets eaten by goats should be higher than diets eaten by sheep (Hadjigeorgiou et al. 2003) under similar feeding environments. Degradation rates of diets consumed by goats were found to be higher compared to diets consumed by sheep (Garcia et al. 1995), ensuring that goats maintain high intake levels to meet energy requirements (Table 2.6). Goats will spend more time eating per unit lucerne hay compared to sheep, due to their selective feeding behaviour (Domingue et al. 1991). This mastery in the art of selection of high-quality feeds is well documented in goats (Pfister and Malechek 1986; Domingue et al. 1991; Rutagwenda et al. 1990; Hadjigeorgiou et al. 2003) and is proposed to be one of the major reasons why goats have faster digesta passage rates compared to sheep and cattle. The art of botanical feed selection and preference differs between ruminants, with implications in differential passage rates in ruminants. Consequently, browsing ruminants have shorter mean retention times for liquid and solid digesta in the rumen compared to grazers largely because of increased diet quality. However, when stall-fed diet preference may be different due to type of diet allocated and hence affect diet selection.

Feed residues obtained from troughs used for feeding goats had high crude protein and low NDF content compared to those obtained from sheep (Domingue et al. 1991, Morand-Fehr et al. 1991; Hadjigeorgiou et al. 2003). These results may be interpreted in two ways. Firstly, it may be that trough fed goats select for low crude protein content and high NDF in feeds compared to sheep. However, sheep select plant feed materials of high cell wall content when compared to goats on pasture (Garcia et al. 1995). Goat selection for diets with low crude protein seems to be a phenomenon common to trough fed goats. Secondly, the use of feed residues during trough feeding of goats and sheep do not give clear results on diet and/or feed selection in these two ruminant species. Differential feeding behaviours occur in trough feeding of goats and sheep. When fed from troughs, goats eat feed from top to bottom whilst sheep eat from bottom to top. High crude protein, low NDF feed particles are finer than low crude protein, high NDF feed particles and are found at the bottom of feed troughs (Hadjigeorgiou et al. 2003). This implies that goats fed in troughs are more likely to consume low crude protein, high NDF diets. Differences in diet selection between goats and sheep fed in troughs warrants more research.

Botanical variation in diets consumed by goats and other ruminants are wide (Table 2.6 and 2.7) and dependent on seasonal availability of different classes and types of feeds in each climatic region. Although predominantly grazers, cattle consumed diets that contained 84 and 48% woody plants in the late wet season and early dry season (Moleele 1998). Number of plants selected by goats and sheep (25 plants) grazing in a semiarid thornbush savannah were similar, but lower in cattle (10 plants). Cattle tend to select monocotyledonous plants (90% of total eating time), goats consistently selected dicotyledonous plants (82% of total eating time), while total eating time was evenly shared between mono- and dicotyledonous plants in sheep across all seasons (Rutagwenda et al. 1990). Sheep diets contained lower lignin levels in the wet season compared to goats due to selection against browse by sheep (Pfister and Malechek 1986).

Table 2. 6 Botanical and chemical compositional characterisation of diets consumed by goat and sheep.

	Proportions (%)					
	I		II		III	
	Goats	Sheep	Goats	Sheep	Goats	Sheep
Grass	78	80.5	76.5	76.5	80.5	78.5
Shrubs	8	8.5	23.5	23.5	17	19.5
Trees	14	11	0	0	2.5	2
Rate of degradation (/h)	0.038	0.038	0.089	0.068	0.063	0.053
	NDF consumed (gNDF/kgDM)		Digestibility of DM		Digestibility of NDF	
L	662	658	0.495	0.524	0.471	0.521
M	677	671	0.475	0.522	0.466	0.533
S	660	656	0.480	0.493	0.446	0.475

I, April to May; II, May to June; III, June to July; DM, dry matter; L, long staple length; M, medium staple length; NDF, neutral detergent fibre; S, short staple length. Adapted from Garcia et al. (1995) and Hadjigeorgiou et al. (2003).

Table 2. 7 Botanical and crude protein of diets consumed by cattle, sheep and goats in different seasons

	Crude Protein consumed (g/kg DM)				Proportions (%)	
	cattle	sheep	goats		Goats	Sheep
DS	45±5	100±10	125±15	Grass	5.3	14.2
INT	70±10	115±15	125±15	Browse	45.3	40.2
GS	110±10	175±25	195±15	Forbes	44.1	41.5

DS, dry season; INT, intermediate season; GS, green season. Adapted from Pfister and Malechek (1986) and Rutagwenda et al. (1990).

The question on whether goats have faster passage rates than sheep, cattle, and other ruminants by virtue that they select less of fibrous plant material is debatable. Generally, goats had faster passage rate than sheep (0.069 vs 0.033 per h when fed as a group; 0.054 vs 0.029 per h when fed individually) when fed formulated diets meeting requirements for maintenance and lactation (Tsiplakou et al. 2011). Other workers have reported faster passage rates of solid digesta (Katoh et al. 1988; Garcia et al. 1995; Hadjigeorgiou et al. 2003, Schlecht et al. 2007; Tsiplakou et al. 2011), slower passage rates (Domingue et al. 1991) and similar passage rates (Alcaide et al. 2000) in goats compared to sheep fed on the same diets. Schlecht et al. (2007) observed faster passage rates in goats compared to cattle fed on the same diet (0.042 vs 0.033 per h when fed on bush hay; 0.053 vs 0.042 per h when fed on green feed).

Discussions on differences in passage rates between ruminant feeding types and species that do not consider effects of factors influencing digesta passage rates lacks descriptive and explanatory power. Given the large number of factors implicated in differential passage rates among goats and other ruminants, a digesta passage rate modelling exercise was used to test the null hypothesis that passage rates in goats are not different from other ruminants (grazers: cattle, sheep, buffalo, antelopes, mouflons, muskoxen, nilgai, blackbucks; browsers: moose, okapi, deer’s, dik-dik, duikers; intermediate feeders: goats, anoa, reindeer, gazelles, and ibex).

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 and included animal and feed factors. Quantification of factors that affected passage rates are described in Moyo et al. (2017). Process models developed as part of this study have been deposited into the Repository of Intelligent Models (REDIM) with accession number PRDA001762 and PRCN001814 for the estimation of solid and liquid passage rate respectively as indicated at http://www.redim.org.za/?search=PRDA001762 and http://www.redim.org.za/?search=PRCN001814.

After correcting for variation in 17 (liquid passage) and 23 (solid passage) factors that affect passage rates in the model, predicted liquid and solid passage rates for goats lay near the ideal prediction line and generally embedded with other ruminant feeding types (Fig 2.1 and 2.2).

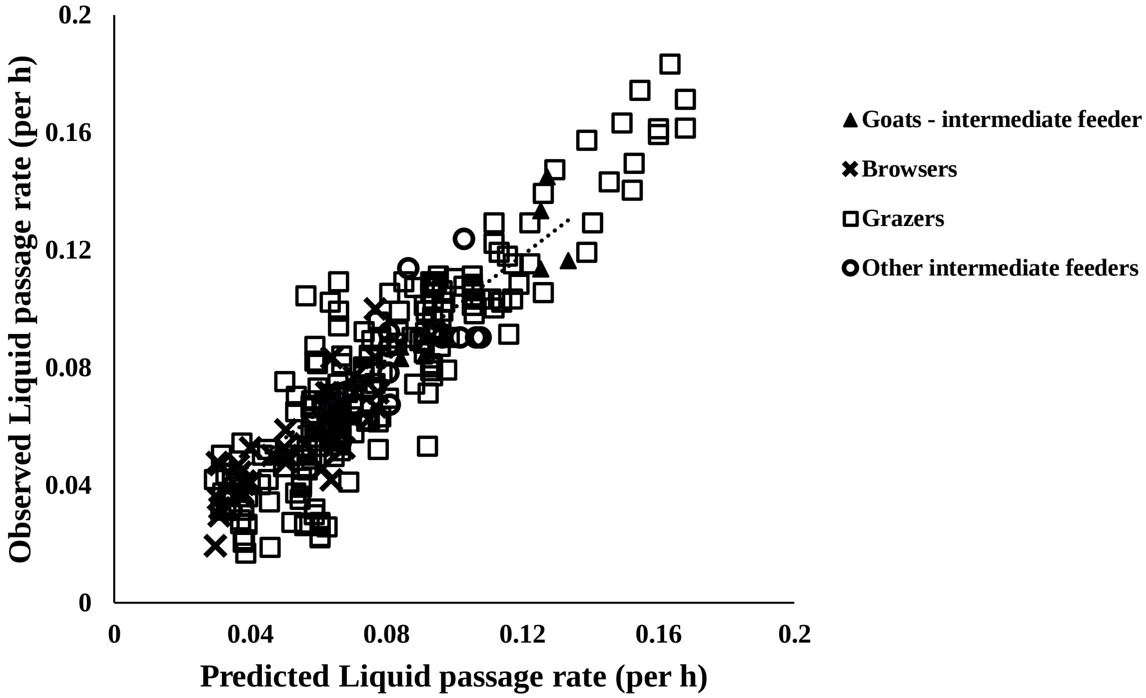

Fig. 2. 1 Relationship between observed and predicted liquid passage rates for goats and other ruminant feeding types

This sparse distribution and entanglement of passage rates for goats within that of other ruminants strengthens the view that goats cannot be easily distinguished from other ruminants based on digesta passage rates; so differences between goats and other ruminants are largely due to variation in diet quality.

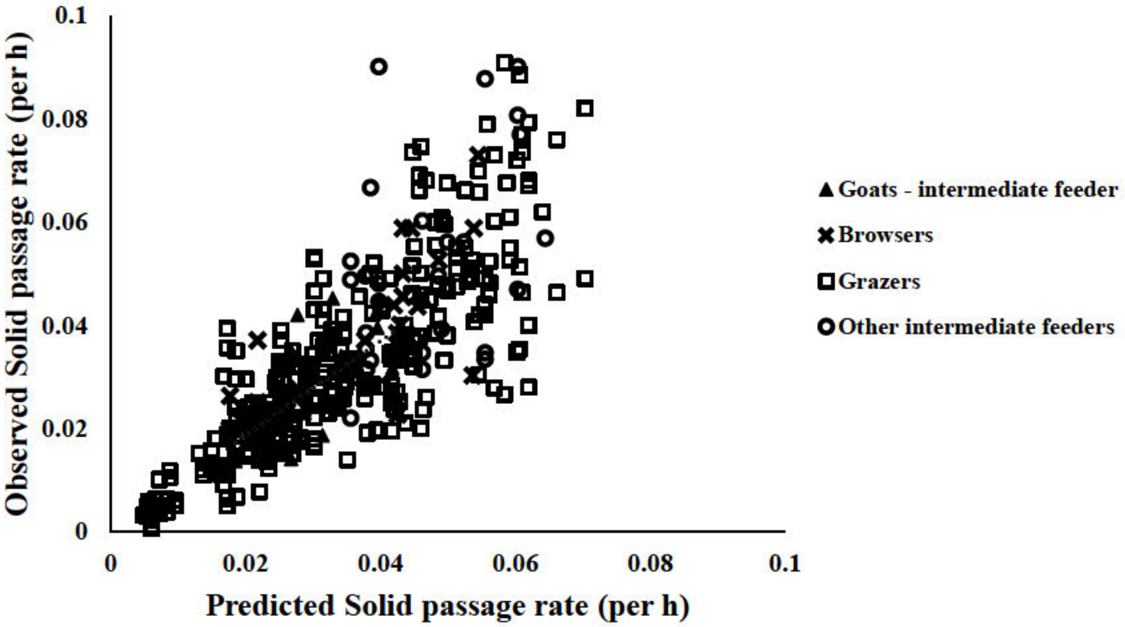

Fig. 2. 2 Relationship between observed and predicted solid passage rates for goats and other ruminant feeding types

After correcting for variation in factors that affect solid and liquid passage rates, goats are not different from other ruminants with respect to passage rates suggesting differences between goats and other ruminants are largely due to dietary quality. More studies should be carried to ascertain the dynamics of digesta kinetics after meal termination in goats.

2.5 Modelling in ruminant nutrition

In-vivo methods of measuring rumen digesta load and nylon-bag degradation of feeds in the rumen are complicated by the need to have rumen cannulated animals. In Africa, few veterinary facilities undertake this specialised surgical operation and animal welfare organisations such as the SPCA are campaigning against the use of invasive methods in animal research. The cost of cannulation and maintenance of fistulated animals is beyond the financial capacity of most research institutions in Africa. The scientific domain bears literature from studies that have documented important factors known to influence feeding behaviour, degradation, and passage of feeds in the rumen, and the weight of rumen digesta load. Current studies should take advantage of this information to build intelligent models to predict these parameters. Such models would provide easier means of estimation of these parameters with little reliance on cannulation of animals. Modelling will reduce the cost of cannulation of animals and the use of invasive methods (fistulation) in ruminant nutrition. Therefore, there is a need to develop rumen digesta load, degradation and passage rate prediction models using Machine Learning techniques.

2.5.1 Modelling of rumen digesta load and passage rate of digesta

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 by Nsahlai and Apaloo (2007). The authors showed that the Illius and Gordon’s (1991) mathematical model, though structurally adequate, underestimated roughage intake, and rumen digesta load levels for grazing ruminants fed on poor quality roughages in the tropics and sub-tropics. They concluded that the unsuitability of the model to accurately predict intake was due to calibrations used in estimating passage rates and rumen digesta load parameters which were largely inaccurate. Similarly, 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 digesta load levels and passage rates as a function of body weight, which is erroneously insufficient. Another reason for underestimation of roughage intake in grazing ruminants lies in longer mean retention times of roughages of poor quality in the rumen (Nsahlai and Apaloo 2007). Secondly, most 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 models have been limited to predicting passage rates for specific classes of ruminants such as dairy cattle (Seo et al. 2006), cattle from trials done in Europe and the United States alone (Krizsan et al. 2010) and goats (Tedeschi et al. 2012). These breeds are usually fed on good quality temperate roughages with access to protein and energy supplements. This limits the conditions to which their equations can be applied to arid and tropical conditions. The passage rate models of Moyo et al. (2017) accounted for almost all factors affecting the rates of passage except for ambient temperature and climate type. Such prediction models may be unsuitable for usage in prediction of roughage intake for ruminants reared in tropical and subtropical areas. It is important to determine rates of passage, rumen digesta load levels and rates of degradation in ruminants fed on non-supplemented poor-quality tropical grass species.

2.5.2 Modelling of feeding behaviour

The critical role of feeding behaviour in influencing passage rates and roughage intake has been overlooked. However, several studies including Sauvant et al. (1996) have simulated feeding behaviour in sheep kept indoors; while Coleman et al. (2003) used feeding behaviour (ruminating time) to develop intake and digestibility prediction models, both studies giving modest predictions. Few studies have considered simulation of all 3 major feeding behaviours (eating, ruminating, and idling) for use in prediction of intake and the models for simulation of feeding behaviour for all classes of ruminants; grazing and browsing wild and domesticated ruminants in different climatic regions are lacking. Simulation of feeding behaviour has been done by Sauvant et al. (1996), Coleman et al. (2003) and Baumont et al. (2004). Simulations of Baumont et al. (2004) gave good predictions on grazing and ruminating times for data reported by Penning et al. (1994), although predicted ruminating time was consistently higher than the observed ruminating time. Feeding behaviour simulation models by Sauvant et al. (1996) achieved good accuracy in prediction of grazing, eating, and chewing times for data reported by Baumont et al. (1989).

Most of these models have been developed for sheep and their performance in simulation of feeding behaviour for other ruminants remains unknown. Given the influence of plant nutritional composition and stage of maturity on eating and ruminating times, feeding behaviour simulation studies should account for these critical factors in simulation models. The limitations of most feeding behaviour simulation models are that there is need to adapt these models to simulation of behaviours of growing or lactating animals and to other types of diets.

2.5.3 Modelling of rumen digestibility

The amount of variation accounted for in observed against predicted digestibility relationships for simulations by Nsahlai and Apaloo (2007) were comparably higher than those reported in empirical studies by Kibon and Orskov (1993), Shem et al. (1995) and Umunna et al. (1995). There is poor simulation digestibility of low quality, low digestibility roughages which are commonly grazed and fed to ruminants in the tropics (Nsahlai and Apaloo 2007). Ambient temperature grossly affects digestibility of plant material through its influence in lignin deposition in plants. Studies should focus on development of digestibility models that account for variability in diet quality as brought about by ambient temperature and climate type.

2.6 Conclusion

Countless factors influence passage rates. Research has 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 digesta load levels and ultimately roughage intake should increase understanding of why part of the variation is not explained.

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.

Given that both liquid and solid digesta phases exist intermingled together in the rumen, studies need to consider developing passage rate models that can be used to predict passage rates for both phases using one model. Passage rate and rumen digesta load data for goats adapted to subtropical and tropical climates in sub-Saharan African is limited, thus necessitating data on how climatic adaptation influences passage rates and rumen digesta load. It can be concluded that passage rate in ruminants is affected by interactions between diet, ruminant species and their climatic environment.

Chapter 3

Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of sheep and goats under subtropical conditions [1]

Abstract

This study investigated the effect of diet and roughage 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 blocked by weight and randomly allocated to experimental diets. Daytime (06:00 to 18:00 h) and night-time (18:00 to 06:00 h) feeding behaviour activities were recorded. Roughage quality affected rumination index in Exp 1, but not in Exp 2, 3, and 5. Time spent eating and ruminating was affected by roughage quality (Exp 1, 3, and 4), period of day (all experiments) and their interaction (Exp 1). Intake rates (g/bout and g/min) were similar across diets. Period of day affected the duration of rumination sessions (Exp 1, 2, and 3); diet or roughage quality affected the duration of eating bouts (Exp 3) and rumination sessions (Exp 1 and 2). roughage quality had a significant effect on the duration eating sessions in Exp 3 only, whilst period of day affected this same behaviour in Exp 2 and 3. 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 crude protein and feed intake. Intake rates had strong positive correlations to intake. Time spent eating, ruminating, and chewing were affected by diet quality and time of the day. Improved feed quality increased eating time during the day but not at night. Reducing roughage quality tripled the difference in daytime chewing the curd at night.

Key words: Feeding behaviour, feed quality, goats, predation risk, sheep

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[1] Moyo M, Adebayo RA, Nsahlai IV. 2019. Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of goats and sheep under subtropical conditions. Asian Australas J Anim Sci 32(5):675-690.

3.1 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 (Salem and Smith 2008). The major constraint to ruminant livestock 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). It has been suggested that low levels of productivity in ruminants that graze on poor quality roughages may be a result of low feed intake. Due to the low nutrional value and bulkiness of tropical roughages, ruminants may 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 (neither eating nor ruminating), and the number of feeding and ruminating sessions ruminants 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 time of day (Emmans and Kyriazakis 2001). Predator-prey interactions between artiodactyls (grazing and browsing herbivores) and carnivorous animals in an ecosystem are manifested during feeding and thus changing feeding behaviour patterns of herbivores (Abdou et al. 2011). 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 ruminants.

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 low. 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 (Salem and Smith 2008). Urea treatment of poor-quality hay or crop residues has been shown to i) increase digestibility by up to 5% more than concentrate supplements, and ii) increase crude protein and energy values of forages, and generally improves the nutritional status of animals (Abdou et al. 2011).

Understanding feeding behaviour is crucial to increase accuracy of predicting intake of roughages, aiding in grazing management, developing feed budgets and in mitigation of droughts. Determination of how sheep and goats distribute time budgets for various feeding behaviours in response to different crude protein sources can be used as a tool to assess the acceptability of the feeds. Time budget on feeding behaviours is important as an indicator to detect feeds that can be easily utilised, especially in marginal environments where the available feed need to be maximised. 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 aim of this study was to determine i) how improvement of hay and diet quality influences feeding behaviour and intake in goats and sheep, ii) how daytime and night-time feeding behaviour patterns vary with diet and roughage quality, and iii) whether or not there is a link between feeding behaviour patterns and feed intake. This 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.

3.2 Materials and methods

3.2.1 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 700 m. 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°C 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.

3.2.2 Animals, housing, feeds, diets, and feeding

Five independent experiments were carried out to investigate how the improvement of the crude protein content of roughage-based diets by using urea treatment (Exp 1 and 2) and supplementation with lucerne hay (Exp 3), cottonseed meal and lespedeza (Exp 4), and fish and sunflower meal (Exp 5) would affect feeding behaviour of goats and sheep. In Exp 1, seven adult male 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% (w/w) 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 3.1). Sheep were randomly allocated to either IRQ (n = 4) or PRQ (n = 3) and given approximately 2 kg dry matter (DM) of either IRQ or PRQ veld hay at 10:00 h and 15:00 h daily for the whole duration of the trial. Chermiti et al. (1994) and Warly et al. (1994) used similar numbers of experimental animals. In Exp 2, eighteen Nguni goats were divided into two groups that comprised of nine light mass (average initial body mass of 16.94±2.51 kg) and nine 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% (w/w) urea for 20 days to give hay of IRQ, in the second treatment, veld hay was sprayed with 2.5% (w/w) urea before feeding to give semi-improved roughage quality (SIRQ), and the third treatment was untreated veld hay with PRQ (Table 5.1). Three goats from each group were randomly allocated to either IRQ, SIRQ, or PRQ. Each group was allocated to treatments (2 times) until there were six goats/feed type and given approximately 2 kg DM/d of either IRQ, SIRQ, or PRQ at 08:00 h and 15:00 h daily for the whole duration of the trial.

In Exp 3, twenty-five male Merino sheep (average initial body mass of 43.6±11.5 kg) were blocked by weight into five groups. Each group were randomly assigned to five dietary treatments in a completely randomised block design. These five diets were designed to provide a range of diet qualities that consisted of veld hay and Lucerne hay (LH) only, mixed in varying proportions (Table 3.1). Sheep were allocated approximately 2 kg DM of their diets twice (at 08:00 to 08:30 h and 15:00 to 15:30 h) daily for the whole duration of the trial. Final body mass was not determined because the trial duration was seven days only, hence body mass changes were not reported. In Exp 4, twelve male Damara sheep (average initial body mass of 27.54±3.68 kg) were randomly assigned to four different dietary treatments composed of varying levels of any one of three roughage sources: maize stover at milk stage (MSM), 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 (LSP) (Table 3.1) in a completely randomised design. In Exp 5, sixty-four 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 3.1). Concentrates were formulated to contain 160, 200, 240, and 280 g CP/kg and were based on either fish meal

(FM) or sunflower meal (SFM). The composition of these concentrates is given in Table 3.2. The concentrate portion of the diet was offered in two equal portions daily between 08:00 to 08:30 h and between 15:00 and 15:30 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 7 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, South Africa). 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 where intake and body weight changes were not determined due to the short duration of the trial. All experiments were not done concurrently.

3.2.3 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 06:00 to 18:00 h, and the night-time period from 18:00 to 06:00 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, recorded feeding behaviour without disturbing animals. 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.

3.2.4 Chemical analyses and design of experimental feeds and diets

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

3.2.5 Statistical analysis

Effects of roughage and diet quality on intake (except Exp 4) and feeding behaviour were statistically 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, BM = body mass and e_{ijkl} = experimental random error.

The Pearson correlation of all the continuous independent variables (CP, NDF, ADF, and hemicellulose) was used to select variables tested as covariates. The correlation between these variables was such that NDF and ADF could be use singly and CP and hemicellulose as a pair. Judging from the error term, the accepted model was the one with CP content.

Table 3. 1 Chemical composition and design of treatment diets

Items	Chemical composition (g/kg DM)						
	DM	CP	NDF	ADF	HEM	Ash	CF
Experiment 1							
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 5a							
Themeda triandra hay	931	61	733	440	293	40	12
TTH+16% FM concentrate	902	111	366	238	128	59	31
TTH+20% FM concentrate	903	134	365	237	128	68	29
TTH+24% FM concentrate	906	162	382	247	135	72	32
TTH+28% FM concentrate	907	183	383	247	136	76	36
Experiment 5b							
TTH+16% SFM concentrate	908	112	401	257	144	52	32
TTH+20% SFM concentrate	911	134	422	269	153	60	34
TTH+24% SFM concentrate	911	157	447	282	165	66	36
TTH+28% SFM concentrate	916	179	471	296	175	67	38

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

A meta-analyses of feeding behaviours from all 6 studies was done and data were analysed using the mixed model regression procedure (Sauvant et al. 2008). A model with discrete predictor variables (ruminant species, period of day and ruminant species×period of day interactions) and continuous predictor variables (CP content of diets) was used. These respective predictor variables were considered as fixed effects. Study×straw quality (whether roughages were treated with urea or not) interactions were considered as random effects. For the discrete predictor variable (ruminant species, period of day and ruminant species×period of day interactions), the following model was applied: $FB_{ijkm} = \mu+R_i+P_j+(R\times P)_{ij}+CP_k+SQ_l+e_{ijklm}$; where Y_{hijkm} = feeding behaviour (times spent eating and ruminating, number of eating and ruminating bouts, and duration of eating and ruminating bouts), μ = overall mean, SQ_l =

random effect of study×roughage quality, R_i = fixed effect of ruminant species (i = sheep; goats), P_j = fixed effect of period of the day (j = day; night), $(R\times P)_{ij}$ = fixed effect of ruminant species × period of day interactions, CP_k = fixed effect of crude protein content and e_{ijklm} = residual error. Data were weighted by the number of animals in each study and the standard errors of the mean (Sauvant et al. 2008). Least square means were used to compare the differences among means in the case of discrete predictor variables. The probability threshold for significance of random study effects was considered at $p<0.20$ as suggested by Sauvant et al. (2008).

Table 3. 2 Ingredient and chemical composition of sunflower meal and fish meal concentrates used in Exp 5a and 5b

Items	Concentrate composition							
	Fish meal				Sunflower meal			
	16%	20%	24%	28%	16%	20%	24%	28%
Ingredient composition								
Maize (g/kg)	848	784	714	649	747	615	484	353
FM or SFM (g/kg)	103.9	170.3	238.2	303.1	205.5	336.9	468.2	599.5
Vit and minerals (g/kg)	2.53	2.53	2.53	2.53	2.53	2.53	2.53	2.53
Limestone (g/kg)	20.2	20.2	20.2	20.2	20.2	20.2	20.2	20.2
MCP (g/kg)	20.2	20.2	20.2	20.2	20.2	20.2	20.2	20.2
NaCl (g/kg)	5	5	5	5	5	5	5	5
Chemical composition								
Dry matter (g/kg)	880	882	887	889	890	895	895	904
Organic matter (g/kg)	926	911	903	896	939	925	914	912
Crude protein (g/kg)	149.5	189.3	239.7	277.4	151.1	191.4	231.3	271.1
NDF (g/kg)	81.8	80.5	111.1	111.7	145.2	182	225.7	269.3
ADF (g/kg)	81.1	80.4	97.3	97.6	116.0	136.3	160.4	184.4
Crude fat (g/kg)	44.7	43.2	48.4	55	48.4	51.4	54.6	57.9

FM, fish meal; SFM, sunflower meal; Vit, vitamins; MCP, monocalcium phosphate; NaCl, sodium chloride; NDF, neutral detergent fibre; ADF, acid detergent fibre.

3.3 Results

In Exp 1, DM and NDF intake was higher for sheep fed on IRQ compared to sheep fed PRQ. Time spent ruminating per unit of dry matter and NDF intake were significantly higher for sheep fed PRQ compared to those fed IRQ, while average dry matter intake rates per unit time and feeding bout were similar for these two roughage qualities (Table 3.3). 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 3.4). There was great variation in daytime and night-time feeding behaviour patterns between and within each dietary treatment. Irrespective of roughage quality, sheep spent significantly more time eating during the day than at night, but less time ruminating during the day than at night. Ruminating sessions were longer at night than during the day.

Number of ruminating bouts were higher at night than during the day, while sheep visited feeding troughs 3 times more during the day than at night. Sheep spent more time idling whilst standing during the day than at night. Time spent idling whilst lying was greater at night than during the day. At night, sheep fed IRQ spent significantly more time idling whilst lying than sheep fed on PRQ. Sheep fed IRQ chewed less, however, sheep fed PRQ chewed more at night and less during the day than those fed on IRQ. Sheep fed PRQ lost 0.14 kg/d more than those fed on IRQ.

In Exp 2, unexpectedly, average dry matter intake, NDF intake, ruminating indices (dry matter and NDF), average dry matter intake rates per unit time and feeding bout were similar for all 3 roughage qualities in goats (Table 3.3). 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 3.5). Roughage quality had no effect ($p>0.05$) on all feeding behaviour parameters except for duration of ruminating bouts. Period of day significantly affected all feeding behaviour parameters except for time spent chewing. Goats spent more time eating and standing while idling during the day than at night, but spent more time ruminating at night than during the day. Number of eating bouts were greater during the day than at night ($p<0.05$), however, the number of ruminating bouts were greater during the night than during the day. Eating bouts were longer during the day than at night across all roughage qualities, with an opposing trend observed for the duration of ruminating bouts, which were longer at night than during the day. Goats spent more time lying at night than during the day. Goats fed PRQ lost 0.06 and 0.04 kg/d more than those on IRQ and SIRQ, respectively.

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 3.3). 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 (lucerne hay)) (Table 3.6). 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 and at night relative to 100% PRQ. Similarly, overall chewing times decreased during the day and at night 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 but increased gradually at night relative 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, but surprisingly, spent more time ruminating during the day than at night and less time idling while standing at night than during the day. Eating bouts were longer during the day than at night, and so were the number of eating bouts. Ruminating sessions were surprisingly longer during the day than at night, although the frequency of ruminating bouts was greater at night than during the day. Sheep spent more time lying at night than during the day.

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 (lespedeza)); 26% eating, 19% ruminating and 55% idling (60% SFM) and 32% eating, 23% ruminating and 45% idling (GH+40% SFM) (Table 3.7). Times spent eating were statistically similar for all diets, except for sheep fed on 40% LSP that ate longer than those fed on 60% SFM diet. Supplementation with 40% SFM compared to 40% LSP when MSM was the main roughage source decreased chewing time. Except for sheep fed MSM+LSP which spent more time eating per session compared to other dietary treatments, durations of eating bouts were similar across 3 diets ($p>0.05$). When MSM was the main roughage source, replacement of 40% SFM with 40% LSP increased duration of ruminating sessions.

In Exp 5a, diet quality had no effect on intake, rumination indices and intake rates (Table 3.3). On an average day, sheep spent 15% to 17% eating, 34% to 39% ruminating, 45% to 51% idling across all levels of FM supplementation (Table 3.8). Eating bouts were longer during the day than at night for sheep fed on 16%, 20%, 24%, and 28% FM supplement. However, ruminating sessions were longer at night than during the day, while the number of ruminating bouts were greater during the day than at night. Sheep supplemented with FM gained on average 0.185 kg/d in body mass.

Generally, sheep spent 15% to 16% eating, 32% to 33% ruminating, 50% to 52% 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 3.8). Period of day affected time spent ruminating and eating, duration of eating and ruminating sessions, and number of ruminating sessions. Eating sessions were longer during the day than at night, while ruminating bouts were longer at night than during the day. Unexpectedly, the number of ruminating bouts were greater during the day than at night. Also, sheep spent more time eating during the day than at night, and spent more time ruminating at night 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 0.136 kg/d in body weight. Overall, time spent eating between goats and sheep was similar, however, sheep spent more time eating during the day and at night compared to goats (Table 3.9). Both sheep and goats ruminated more at night than during the day, although sheep spent more time ruminating than goats irrespective of period of the day. Number of eating and ruminating bouts were similar for both sheep and goats. Sheep spent more time chewing than goats. Eating bouts were longer during the day than at night for both sheep and goats, while an opposing trend was observed where ruminating bouts were longer at night.

Dry matter intake was higher for sheep compared to goats (Table 3.10). Effects of variable CP in the diets seemed not to have an effect on intake, rumination indices and intake rates. Goats had lower overall intake rates (g/min) than sheep, while overall intake rates per feeding bout were similar for both ruminant species.

All feeding behaviours had significant positive correlations to intake (Table 3.11). Time spent chewing and ruminating have significant ($p<0.05$) correlations to intake ($r \approx 0.5$). There was a significant ($p<0.05$) correlation between time spent ruminating ($r = 0.89$) and eating ($r = 0.54$) to time spent chewing. Time spent eating was not ($r = 0.1$; $p>0.05$) correlated to time spent ruminating. Intake rates had a correlation to intake ($r>0.7$; $p<0.0001$). Surprisingly, the major feed attributes (NDF and ADF) though correlated between them had positive and significant ($p<0.005$) correlations to intake. The CP content had significant correlations to time spent eating and ruminating, and intake rates.

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

Items	Intake (kg/d)		Rumination time (/d)		DM intake rate		BMC
	DM	NDF	min/kg DMI	min/kg NDFI	g/min	g/bout	kg/d
Experiment 1							
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}
SEM	0.052	0.039	24.38	33.06	0.641	11.97	0.026
Significance	**	**	***	***	NS	NS	*
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}
SEM	0.111	0.101	59.85	65.07	0.4185	9.271	0.0094
Significance	NS	NS	NS	NS	NS	NS	***
Experiment 3							
100% PRQ	1.09^{a}	0.94^{a}	546^{a}	636^{a}	2.97^{a}	56.2^{a}	ND
75% PRQ+25% LH	1.25^{a}	1.04^{a}	492^{a}	592^{a}	3.90^{a}	72.7^{a}	ND
50% PRQ+50% LH	1.41^{a}	1.13^{a}	442^{a}	550^{a}	4.59^{a}	73.6^{a}	ND
25% PRQ+75% LH	1.37^{a}	1.06^{a}	502^{a}	648^{a}	5.42^{a}	76.3^{a}	ND
100% LH	1.59^{a}	1.19^{a}	370^{a}	496^{a}	6.20^{a}	90.6^{a}	ND
SEM	0.229	0.180	70.62	88.91	0.8707	13.76	ND
Significance	NS	NS	NS	NS	NS	NS	ND
Experiment 5a							
TT-hay+16% FM	0.91^{a}	0.37^{a}	546^{a}	1339^{a}	4.24^{a}	50.0^{a}	0.174^{a}
TT-hay+20% FM	0.92^{a}	0.37^{a}	619^{a}	1520^{a}	4.01^{a}	50.8^{a}	0.199^{a}
TT-hay+24% FM	0.92^{a}	0.39^{a}	527^{a}	1248^{a}	4.13^{a}	50.6^{a}	0.180^{a}
TT-hay+28% FM	0.89^{a}	0.37^{a}	624^{a}	1477^{a}	3.74^{a}	49.7^{a}	0.188^{a}
SEM	0.020	0.008	29.91	71.52	0.3104	1.908	0.021
Significance	NS	NS	NS	*	NS	NS	NS
Experiment 5b							
TT-hay+16% SFM	0.90^{a}	0.39^{b}	550^{a}	1253^{a}	4.12^{a}	49.7^{a}	0.163^{a}
TT-hay+20% SFM	0.92^{a}	0.42^{a}	522^{a}	1141^{a}	4.18^{a}	51.6^{a}	0.138^{a}
TT-hay+24% SFM	0.94^{a}	0.44^{a}	489^{a}	1043^{a}	4.65^{a}	52.1^{a}	0.145^{a}
TT-hay+28% SFM	0.90^{a}	0.45^{a}	531^{a}	1060^{a}	4.20^{a}	49.6^{a}	0.096^{b}
SEM	0.019	0.009	29.98	65.65	0.4476	1.790	0.015
Significance	NS	***	NS	NS	NS	NS	*

DM, dry matter; BMC, body mass change; NDF, neutral detergent fibre; DMI, dry matter intake; NDFI, neutral detergent fibre intake; IRQ, improved roughage quality; PRQ, poor roughage quality; SEM, standard error of the mean; NS, not significant; SIRQ, semi-improved roughage quality; ND, not determined; LH, lucerne hay; TT, Themeda triandra hay; FM, fish meal; SFM, sunflower meal.

^{a,b} Means in a row with different superscripts are significantly different ($p<0.05$).

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

Table 3. 4 Effect of improving veld hay quality on duration of day-time and night-time feeding behaviour patterns in Merino sheep (Exp 1)

Behaviour	Feeds						SEM	Significance of influence		
	IRQ			PRQ						
	Day	Night	24 h period	Day	Night	24 h period		Feed	Period	Feed×period
Time spent (min)										
Eating	222	52	274^a	140	47	187^b	12.56	*	***	*
Ruminating	188	305	493^b	230	424	654^a	5.131	***	***	***
Chewing	410	357	767^b	370	471	841^a	11.60	*	NS	***
Idling – standing[1)]	112	87	199^a	169	93	262^a	14.27	NS	**	NS
Idling – lying[1)]	198	277	475^a	185	152	338^b	24.32	*	NS	*
Duration of bouts (min)										
Eating	28	20	26^a	20	19	21^a	2.886	NS	NS	NS
Ruminating	20	23	22^b	25	37	32^a	1.763	***	***	*
Number of bouts										
Eating	8	3	11^a	7	2	9^a	0.695	NS	***	NS
Ruminating	10	13	23^a	10	12	22^a	1.016	NS	*	NS

IRQ, improved roughage quality; PRQ, poor roughage quality; SEM, standard error of the mean; NS, not significant.

[1)] 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

^{a,b} Means in a row with different superscripts are significantly different ($p<0.05$).

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

Table 3. 5 Effect of improving veld hay quality on duration of day-time and night-time feeding behaviour patterns in Nguni goats (Exp 2)

Behaviour	Feeds									SEM	Significance of influence		
	IRQ			SIRQ			PRQ						
	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h		Feed	Period	F×P
Time spent (min)													
Eating	216	76	292	237	58	295	193	56	249	16.29	NS	***	NS
Ruminating	112	291	403	89	269	358	70	227	297	26.95	NS	***	NS
Chewing	328	366	694	326	327	653	263	283	546	29.07	NS	NS	NS
Idling – standing[1)]	158	54	212	166	46	212	208	53	261	15.84	NS	***	NS
Idling – lying[1)]	231	300	531	225	347	572	246	384	630	32.21	NS	**	NS
Duration of bouts (min)													
Eating	22	18	21	26	18	25	22	19	21	1.306	NS	***	NS
Ruminating	24	29	27	23	27	26	16	25	23	2.00	*	**	NS
Number of bouts													
Eating	10	4	14	9	3	12	9	3	12	0.612	NS	***	NS
Ruminating	5	10	15	4	10	14	4	9	13	0.857	NS	***	NS

IRQ, improved roughage quality; SIRQ, semi-improved roughage quality; PRQ, poor roughage quality; F×P, feed×period interactions; SEM, standard error of the mean; NS, not significant.

1) 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

* p<0.05; ** p<0.01; *** p<0.001.

Table 3. 6 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)

Behaviour	Diets														SEM	Significance of influence		
	100% PRQ			75% PRQ + 25% LH			50% PRQ + 50% LH			25% PRQ + 75% LH			100% LH					
	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h	Day	Night	24 h	Day	Night		Diet	Period	D×P
TSE (min)	225	142	367	193	135	328	180	122	302	148	108	256	158	110	12.34	***	***	NS
TSR (min)	282	276	558	314	285	599	312	237	549	314	265	579	263	269	13.86	NS	**	*
TSC (min)	508	418	926	507	419	926	491	359	850	462	373	835	421	379	14.38	***	***	NS
TSIS (min)	82	54	136	73	55	128	98	68	166	120	83	203	143	94	12.70	***	***	NS
TSIL (min)	130	248	378	139	246	385	131	293	424	138	264	402	157	248	18.96	NS	***	NS
DEB (min)	22	15	19	23	16	19	19	13	16	15	13	13	15	14	1.431	***	***	NS
DRB (min)	26	23	24	29	24	27	26	20	23	27	23	24	22	23	1.3	*	***	*
NEB	10	9	19	9	8	17	10	9	19	10	9	19	10	8	0.67	NS	*	NS
NRB	11	12	23	11	12	22	12	12	24	12	12	24	12	12	0.6	NS	*	*

PRQ, poor roughage quality; LH, lucerne hay; SEM, standard error of the mean; D×P, diet×period interactions; TSE, time spent eating; NS, not significant; 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.

* p<0.05; ** p<0.01; *** p<0.001.

Table 3. 7 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	Diets				Significance	
	60% MSM + 40% SFM	60% MSM+ 40% LSP	40% MSD + 60% SFM	60% GH + 40% SFM	SEM	p value
Time spent (min)						
Eating	219^{ab}	290^{a}	156^{b}	189^{ab}	25.58	*
Ruminating	131^{a}	163^{a}	115^{a}	140^{a}	14.49	NS
Chewing	350^{b}	454^{a}	271^{c}	330^{b}	15.24	***
Idling – standing$^{1)}$	77^{ab}	43^{b}	139^{a}	78^{ab}	20.21	NS
Idling – lying$^{1)}$	174^{a}	104^{b}	190^{a}	193^{a}	16.34	*
Duration of bouts (min)						
Eating	11^{b}	15^{a}	9^{b}	11^{b}	0.75	**
Ruminating	6^{b}	9^{a}	6^{b}	7^{ab}	0.64	*
Number of bouts						
Eating	6^{a}	7^{a}	6^{a}	6^{a}	0.40	NS
Ruminating	6^{a}	6^{a}	6^{a}	7^{a}	0.58	NS

MSM, maize stover at milk stage; SFM, sunflower meal; LSP, lespedeza; MSD, maize stover at dry stage; GH, grass hay; SEM, standard error of the mean; NS, not significant.

$^{1)}$ 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.

^{a,b} Means in a row with different superscripts are significantly different ($p<0.05$).

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

Table 3. 8 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									
TT+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
TT+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
TT+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
TT+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	SEM	9.65	14.35	18.31	18.28	2.58	1.70	0.99	0.99
	Diet	NS	*	*	*	NS	NS	NS	NS
	Period	***	***	NS	NS	***	***	NS	***
	Diet×period	NS	NS	NS	NS	NS	NS	NS	NS
Experiment 5b									
TT+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
TT+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
TT+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
TT+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	SEM	11.91	14.81	18.95	18.92	2.26	1.27	1.025	0.99
	Diet	NS	NS	NS	NS	NS	NS	NS	NS
	Period	***	***	NS	NS	***	***	NS	***
	Diet×period	NS	NS	NS	NS	NS	NS	NS	NS

TSE, time spent eating; TSR, time spent ruminating; TSC, time spent chewing; TSI, time spent idling; DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts; TT, Themeda triandra hay; FM, fish meal; SEM, standard error of the mean; NS, not significant; SFM sunflower meal.

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

Table 3. 9 Effects of ruminant species, period of the day and their interactions on feeding behaviour (LSM±SEM) of sheep and goats fed varying roughage qualities in 6 different studies

Items	Feeding behaviour (min)						Significance				
	Goats			Sheep			Random effects	Fixed effects			
	D	N	Average	D	N	Average	ST×RQ	S	P	S×P	CP
TSE	206.4±24.9	54.4±24.9	130.4±22.0	179.2±13.0	82.6±13.2	130.9±12.6	*	NS	***	***	**
TSR	68.8±63.0	240.8±63.0	154.7±48.0	209.7±16.3	311.9±17.2	260.8±15.2	*	***	***	NS	**
TSC	269.7±77.1	289.3±77.1	279.5±56.2	408.6±17.5	309.3±19.4	359.0±13.5	NS	*	NS	NS	***
DEB	20.9±2.9	15.9±2.9	18.4±2.8	19.2±1.9	12.0±1.9	15.6±1.8	*	NS	***	NS	***
DRB	20.0±5.2	26.0±5.2	23.0±4.9	18.8±3.0	21.0±3.1	19.9±3.0	**	NS	***	NS	***
NEB	9.3±1.5	3.3±1.5	6.3±1.5	7.5±0.9	6.1±1.0	6.8±0.9	**	NS	***	***	NS
NRB	4.7±2.1	10.2±2.1	7.4±1.9	10.4±1.2	10.3±1.2	10.4±1.2	**	*	***	***	NS

LSM±SEM, least square means±standard error of the mean; D, day; N, night; ST×RQ, study by roughage quality interactions; S, species; P, period of day; S×P, species by period of day interactions; CP, crude protein; TSE, time spent eating; NS, not significant; TSR, time spent ruminating; DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts.

* p<0.05; ** p<0.01; *** p<0.001.

Table 3. 10 Effects of ruminant species on feeding behaviour (LSM±SEM) of sheep and goats fed varying diets and roughage qualities in 6 different studies

Items	Feeding behaviour		Significance		
	Ruminant species		Random effects	Fixed effects	
	Goats	Sheep	ST × RQ	S	CP
DMI (kg/d)	0.8±0.2	1.2±0.1	**	*	NS
NDFI (kg/d)	0.8±0.3	0.8±0.2	**	NS	NS
RTDMI (min/kg)	422.8±94.8	481.4±56.1	**	NS	NS
RTNDFI (min/kg)	441.1±234	879.5±174	*	*	NS
IR (g/min)	3.1±0.6	5.0±0.4	*	***	NS
IR (g/bout)	64.6±27.0	97.0±19.2	**	NS	NS

LSM±SEM, least square means±standard error of the mean; ST×RQ, study by roughage quality interactions; S, species; CP, crude protein; DMI, dry matter intake; NS, not significant; NDFI, neutral detergent fibre intake; RTDMI, rumination time per unit dry matter intake; RTNDFI, rumination time per unit neutral detergent fibre intake; IR, intake rate.

* p<0.05; ** p<0.01; *** p<0.001.

Table 3. 11 Pearson correlation of feed attributes and feeding behaviour parameters for all experimental data$^{1)}$

Items	TSR	TSE	TSC	IRgmin	IRgbout	DM	CP	NDF	ADF	HEM
DMI	0.47***	0.21*	0.50***	0.70***	0.77***	–0.11^{NS}	0.11^{NS}	0.33***	0.28**	–0.03^{NS}
TSR	-	0.10^{NS}	0.89***	0.32***	0.29**	–0.24**	0.25**	–0.07^{NS}	0.15^{NS}	0.25392**
TSE	-	-	0.54***	–0.50***	0.09^{NS}	0.09^{NS}	–0.28**	0.48***	0.48***	–0.22*
TSC	-	-	-	0.05^{NS}	0.29**	–0.16^{NS}	0.08^{NS}	0.16^{NS}	0.09^{NS}	0.11^{NS}
IRgmin	-	-	-	-	0.59***	–0.11^{NS}	0.27**	–0.01^{NS}	–0.08^{NS}	0.16^{NS}
IRgbout	-	-	-	-	-	0.30**	–0.21*	0.50***	0.38***	0.06^{NS}
DM	-	-	-	-	-	-	-0.56***	0.47***	0.25**	0.38***
CP	-	-	-	-	-	-	-	-0.64***	-0.61***	0.23*
NDF	-	-	-	-	-	-	-	-	0.94***	–0.34***
ADF	-	-	-	-	-	-	-	-	-	–0.62***
HEM	-	-	-	-	-	-	-	-	-	-

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; NS, not significant.

$^{1)}$ n = 114 and 22 diets.

* p<0.05; ** p<0.01; *** p<0.001.

3.4 Discussion

Diurnal feeding behaviour in ruminants 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 ruminants 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). 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. Goats are more likely to consume large proportions of leafy parts than sheep given their inclination to select. Sheep and goats are sensitive to the four primary tastes: sweet, salty, bitter, and sour [Baumont et al. 2000] and odoriferous compounds (Arnold 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, but not 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), respectively. 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 SFMs did not alter feed intake in sheep.

In this study, sheep and goats across all experiments maintained statistically similar intake rates (g/bout), thus differences in feed intake in any of the experiments would only be due to differences in bite frequency and bite mass/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). Rutter et al. (2002) experimenting on sheep fed on rye grass and clover, found that dry matter intake rates were similar between dietary treatments. This suggests that under any dietary condition intake rates are largely under the control of the animal’s physiological status in ruminants fed indoors. Under grazing conditions, intake rates are affected by feed factors such as leaf size and sward height (Prache 1997), and sward density, which are non-existent indoors.

Ruminants 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 of 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. 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. Factors influencing the adoption of any one of these intake control mechanisms 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 the 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 ruminants (Penning et al. 1995). Additionally, most studies, including the current study have failed to 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, 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 SFM, and were lower for SFM compared to FM (Exp 5). Given the high NDF content of SFM compared to FM, it was expected that sheep would spend more time ruminating per unit intake of SFM than FM. It could be that the size and fragility of fibre in sunflower facilitate rumen passage rate of these particles. 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 chewing 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/d. 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/d), Kaske and Groth (1997) in pregnant ewes (679 min/d) and Minervino et al. (2014) in sheep fed coast-cross hay (668 min/d). 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 (Nsahlai et al. 1996). 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 3.11) 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 (Moyo et al. 2018) 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. 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 increases CP levels slightly in grasses. Based on the positive relationship between CP content and intake rate (g/min) obtained in this study, CP may play a role in influencing feeding behaviour through intake rate. The generally low CP levels of mature tropical grasses led to goats maximising nutrient intake rates during the wet seasons when feeds of high nutritional quality (high CP levels) are abundant so as to build up enough reserves to survive the dry season (Sebata and Ndlovu 2012). It is possible an increment in the CP content and a decrease in NDF (Exp 3) would increase the intensity of microbial activity, depress the pH to 6 (Nsahlai and Umunna 1996) thus reducing the need for extended rumination times for optimal nutrient extraction. Effects of CP levels on feeding behaviour raised in the above discussion are strengthened based on the Pearson correlation of CP with time spent eating and ruminating, which are confounded by digestion rate and animal species, hence, more studies are needed to ascertain the extent to which different CP levels in feeds would 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 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 and palatability of the feed.

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). In this study, goats and sheep have distinct feeding behaviours when fed on poor quality roughages. Sheep spent more time chewing and tended to spend less time eating poor quality hay. On the other hand, goats are selective of leafy parts on grass stalks but sheep are less selective consuming more of the fibrous grass stalks. Leafy parts are more digestible than stalks, hence requiring less time ruminating in goats than in sheep. Selective feeding on poor quality roughages by goats extends the need for more time spent eating to achieve adequate intake to meet nutritional needs compared to sheep. Time spent eating at night accounts for approximately 10% to 15% of the total daily eating time (Gregorini 2012), which is fairly lower than 19% to 30% (Exp 1, 2, and 5) and 39% to 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. Domesticated ruminants exhibit feeding behavioural responses to a perceived fear of predation (Newman et al. 1995). The concept of predation and instinct may explain some of these adherences to strict circadian cycles. Risk of predation is greater during eating than ruminating because animals maintain poor levels of vigilance when eating as their heads are positioned downwards (Rutter et al. 2002). 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 perceived risk status of that 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, ruminants may have to spend more time idling whilst standing during the day than at night. Idling whilst standing during the day balances the total time of engaging in a behaviour that maintains good levels of vigilance during the day. Sheep (in Exp 3) displayed a unique way of reducing the perceived risk of predation. Ruminating time, number and duration of rumination sessions were greater during the day than at night and so were eating time, the number and duration of eating sessions. This suggests that it is in the sheeps blood to feel 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 5a 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). The concept on the role of idling behaviour in relation to maintenance of vigilance toward predation risk are still not well documented. 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. An 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 3.11). 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 (CP) 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. Consequently, back-fat reserves would have been 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 CP 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, chewing time, number of eating and ruminating session, and duration of eating bouts are physiologically controlled in small ruminants, though chewing time requires isometric scaling during modelling of intake. Goats and sheep fed on roughage alone ruminate at night and eat more during the day, but sheep fed a roughage and supplemented with Lucerne hay spent more time ruminating than eating. Time spent eating, ruminating, and chewing were affected by diet quality and time of the day. Improved feed quality increased eating time during the day but not at night. Reducing roughage quality tripled the difference in daytime chewing the curd at night.

3.5 Conclusion

Roughage intake is limited as a result of increased rumination time of low-quality roughages. Chewing time, number of eating and ruminating session, and duration of eating bouts are physiologically controlled in small ruminants, though chewing time requires isometric scaling during modelling of intake. The scaling relationship of feeding behaviour with body weight is important in understanding the adaptive feeding behaviours adopted by ruminants.

Chapter 4

The use of Random Forest models to estimate diurnal feeding behaviour of wild and domesticated ruminants [1]

Abstract

Few studies have considered simulating the major feeding behaviours of ruminants. This study developed models to predict time spent eating (TSE) and ruminating (TSR) for grazing and browsing ruminants. Data were collected from studies that reported TSE and TSR, number of eating (NEB) and ruminating bouts (NRB), and the duration of ruminating (DRB) and eating bouts (DEB) over a 24h period. Factors affecting feeding behaviour were identified from each study and grouped into (1) diet properties, (2) animal and (3) environmental factors. These factors were used as input variables for predicting feeding behaviour. Random Forest models were programmed on a 64-bit R version 3.6.2 (Dark and Stormy Night). Each dataset was randomly divided into two subsets: 70% for model training and 30% for model testing. Developed models accounted for 95% (TSE), 90% (TSR), 93% (DEB), 93% (DRB), 78% (NEB) and 90% (NRB) of the variation in prediction. On testing these models using independent datasets, models attained 87% (TSE), 62% (TSR), 93% (DEB), 83% (DRB), 82% (NEB) and 77% (NRB) precision in predictions. Time spent eating was over-predicted for red deer, while TSE was under-predicted for sheep. Models over-predicted TSR by cattle, blue duiker by 4-fold and sheep. The DEB were under-predicted by 2-fold for sheep, while DRB bouts by blue duikers were over predicted 6-fold. The NEB were both under- and over-predicted for cattle. Although there are over- and underpredictions from a few ruminants, the high coefficients of determination and low errors suggest that models can be recommended for use. Overall, this study developed good simulation models for feeding behaviour of ruminants from diverse nutritional and climatic environments.

Key words: grazing, prediction model, Random Forest model, rumination

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[1] Part of this chapter has been submitted to the journal Biology

4.1 Introduction

Time budget on feeding behaviour of wild and domesticated grazing ruminants is complicated by the influence of topography, risk of predation, large variability of feeds to choose from, presence of shepherds, occurrences of extreme unforeseen weather conditions such as snow, heavy rain and high wind speeds, ambient temperature, and changes in lengths of photo- and scotoperiods (Skogland 1984). Despite these, ruminants must be able to balance periods spent on eating, ruminating, and idling to maintain adequate feed intake for survival, rumination to improved digestion while getting enough rest. The effect of photo- and scotoperiods on times spent on eating and ruminating is confirmed in multiple studies. Some of these studies (Penning et al. 1993; Scheel 1993; Newman et al. 1995; Rook and Huckle 1997; Macmillan et al. 2018) have attributed differences in diurnal feeding behaviour to the ability of ruminants to maintain high levels of vigilance to perceived threat of predation. There are assumptions that domesticated animals have retained an evolved anti-predator behaviours and traits of alertness (Newman et al. 1995).

The proposed “concept of predation” is built on the idea that adoption of particular feeding behaviour in ruminants is related to the extent of vigilance the animal has to its surrounding when engaging on that feeding behaviour. In context, this concept assumes that: (i) when grazing ruminants eat, their heads are positioned downwards reducing their levels of vigilance to the surrounding thus, increasing chances of being preyed on, unlike browsers which may be facing up with their heads in their natural position when feeding (browsing) (Rutter et al. 2002) (ii) small ruminants are less-likely to be preyed on compared to large ruminants as they offer less reward according to the optimal foraging theory (Rodgers et al. 2015), (iii) the chance of ruminants being preyed on at night than during the day is high (Rook and Huckle 1997). Few studies have not considered exploring how different size ruminants of diverse feeding habits adapt their daytime and night-time feeding behaviour to the nutritionally and climatically diverse environments they inhabit.

The adaptive feeding behaviours adopted by grazing and browsing wild and domesticated ruminants under different diet and climatic conditions is unclear. Rumination efficiency (in g neutral detergent fibre ruminated per minute) scaled isometrically with body weight of adult ruminants (Van Soest 1994), following the Bell-Jarman principle. Animals eat to meet their requirements. Feed intake in mammal scales to approximately $BW^{0.7}$ and requirements to $BW^{0.75}$ (Geist 1974) so time spent eating per unit of body weight should scale to $BW^{-0.70 \text{ to } -0.75}$. Isometric scaling of chewing behaviour during modelling of intake, a scalar that needs to be explored.

A link between the “concept of predation” and results from allometric predictions of the relationship between feeding behaviour of different ruminant feeding types would invoke new hypothesis on the possible feeding behaviour adaptation strategies employed by ruminants. This study was designed to increase the current understanding of daytime and night-time feeding behaviour of ruminants.

Attempts have been made to simulate feeding behaviour and preference in ruminants. Several studies including Sauvant et al. (1996) have simulated feeding behaviour for ruminants kept indoors, while Gregorini et al. (2015) simulated foraging behaviour of grazing dairy cows. Fomum et al. (2015) and Wenninger and Shipley (2000) developed regression equations for predicting time spent browsing and ruminating from the cellulose content of diets eaten by ruminants. Studies that have considered simulating major feeding behaviours for diverse species of ruminants are scant. To the best of the author’s knowledge, few attempts have considered simulation of feeding behaviour for all classes of ruminants; grazing and browsing wild and domesticated ruminants in different climatic regions.

Knowledge on how much time ruminants spend eating, ruminating and idling would enable prediction of feed intake (Halachmi et al. 2015). Development of sustainable grazing management and practises to prevent depletion of natural grasslands as a result of overgrazing depends on simulated intake, diet selection and feeding behaviour of ruminants. Simulation models for feeding behaviours in ruminants would be useful as an animal welfare assessment tool with application in early prediction of bovine respiratory diseases in feedlots (Wolfger et al. 2015), and identification of cows at risk for metritis (Urton et al. 2005). Prediction of feeding behaviour responses using environmental factors such as ambient temperature is critical to understanding behavioural responses to ecological changes.

This study was designed to increase understanding of diurnal feeding behaviour in ruminants as a tool for ruminant diversification and reported findings of allometric analyses of diurnal feeding behaviour patterns with body weight and provides some evidence relating to adaptive feeding behaviour to nutritional and climatic diverse environments inhabited by ruminants. The aim of this study was to: (1) determine the effects ambient temperature, body size, feeding type and period of the day on daytime and night-time feeding behaviour of ruminants, and (2) develop Random Forest models to estimate total time spent on eating and ruminating for grazing and browsing wild and domestic ruminants from different climatic regions. The explicit assumptions tested were that: (1) browsing and grazing ruminants adapt their feeding behaviour differently based on body size, nutritional requirements, feeding type and period of day, diets they consume and climatic regions they inhabit corresponding to the digestive strategies they employ, and (2) it is possible to predict the time spent on eating and ruminating for ruminants of different feeding types and from different climatic regions.

4.2 Materials and methods

4.2.1 Creation of the dataset

A dataset was created using findings from 142 studies carried out worldwide. Studies included in the dataset met all of the following criteria: (1) studies should have reported times spent eating (TSE) and ruminating (TSR), number (NRB) and duration of ruminating (DRB) bouts, and number (NEB) and duration of eating (DEB) bouts over a 24h period, (2) studies that measured body weights of animals used and (3) studies that stated the feeds or the proportion of feeds in diets fed to or consumed by animals. A dataset was created containing feeding behaviour from wild and domesticated ruminants. Factors that affect feeding behaviour were identified in each of these studies and were categorised into three main groups: (i) diet properties, (ii) animal and (iii) environmental factors acoording to Fig. 4.1. Units of measurement for all quantitative factors are specified in various sections when mentioned. Qualitative factors that affect feeding behaviour were coded with numerical weightings, represented as numbers in parenthesis as (= 1, = 2, = 3 or = 4).

4.2.1.1 Animal factors

Animal related factors that affect feeding behaviour were either quantitative or qualitative. One qualitative factor affecting feeding behaviour was identified to be ruminant feeding type (RFT). To account for differences in selectivity during feeding, ruminants were classified into 3 feeding types according to Hofmann (1989). Ruminants classified as grazers or roughage selectors (= 1) included cattle (*Bos indicus* and *Bos taurus*), Mediterranean buffalo (*Bubalus bubalis*), sheep (*Ovis aries*) and swamp buffalo (*Bubalus bubalis carabanensis*); browsers or concentrate selectors (= 2) included blue duiker (*Philantomba monticola*), moose (*Alces alces*) and okapi (*Okapia johnstoni*) and intermediate feeders (= 3) included goats (*Capra hircus*), red deer (*Cervus elaphus*) reindeer (*Rangifer tarandus*), sable antelope (*Hippotragus niger*) and spotted deer (*Axis axis*). The quantitative factors included days in pregnancy (DP), days in lactation (DL), body weight (BW in kg), mature body weight (MBW in kg), degree of maturity (DOM) and animal production level (APL). The quotient of BW and MBW of these animals gave the DOM of animals used in each study. Mature body weights of each ruminant was looked up from publications (Frandsen 1992, Estes 1993, ADW 2014 and AWF 2016).

Animal production level was used to account for the motivation to eat to meet requirements for energy and to satisfy hunger (Sauvant et al. 1996; Baumont et al. 2004). Calculation of APL was done according to methods by AFRC (1993). To determine APL, the net energies for maintenance (NE_m), fattening (NE_f), lactation (NE_l), conception and production were calculated according to AFRC (1993). Since the AFRC (1993) formulae were developed for cattle, sheep, and goats only; wild ruminant animals in the dataset were assigned into either of the formulae for cattle, sheep and goats using their body weights or mature size and feeding types. Animals were assigned to the formulae for (1) cattle (cattle, Mediterranean buffalo, moose, okapi, red deer, reindeer, sable, spotted deer, and swamp buffalo), (2) sheep (sheep), or (3) goats (goats and blue duiker). Not all studies reported body weight changes or average daily gains of animals required to calculate NE_f. Animals used in studies that did not report average daily gains of animals were assumed to have been at maintenance level of feeding. Days in lactation for all lactating animals and days in pregnancy for all pregnant animals were used to account for the effects of physiological status on feeding behaviour. Not all studies reported days in milk and milk composition for all lactating animals required for calculation of NE_l. Days in milk for cows reported as early and late lactation were taken to be 60 and 290 days, respectively. The sum of these net energy values was used to calculate the total net energy requirements (TNER). Animal production level (APL) was calculated as $APL = TNER \div NE_m$.

4.2.1.2 Dietary factors

Diet properties that affect feeding behaviour identified in these studies were either qualitative or quantitative. Quantitative factors were mainly detergent and proximate chemical composition of feeds. These factors included dry matter (DM), crude protein (CP), neutral detergent fibre (NDF) and ash contents of diets offered to the animals all measured in g/kg DM. The proportion of concentrate (CON as a %) in roughage-based diets fed to animals was also included in the dataset. Studies in which feed composition were not reported but had the type of feed or diet reported, feed composition attributes were looked up in journal articles. These included Marinas et al. (2003), Hummel et al. (2006) and Feedipedia (2016).

Qualitative dietary factors that affect feeding behaviour included in the dataset were; feed class (TAN) and feed type (SIL). Discrete feed factors were categorised as follows; feed class classified feeds or diets wholly as or containing anti-nutrients as tannin rich (TAN = 1) or non-tannin (TAN = 0) containing. Feeds classified as tannin rich were millet, sorghum, sunflower meal, *Gliricidia sepium* leaves, Lespedeza’s, *Acacia karoo leaves*, *Grewia occidentalis leaves,* *Scurtis myrtinapacific* leaves, oak browse leaves, willow leaves, mimosa leaves, carob leaves, white and red clover leaves, dandelion leaves and browse leaves, while all other feeds were deemed to contain minute tannin levels. Feed type classified feeds as either a silage (SIL = 1) or non-silage (SIL = 0).

4.2.1.3 Environmental and management factors

The effect of activity on feeding behaviour was accounted for by identification of feeding management (GI) of animals in each study. Animals were managed as indoor zero grazing (GI = 0) or outdoor grazing (GI = 1). The effects of climate type (CT) on feeding behaviour were accounted for by identifying season and the location of where each study was done and classifying the climate of each study site using the updated Köppen-Geiger climate classification system (Peel et al 2007). Studies fell into 12 climatic regions namely; tropical monsoon (Am), tropical savannah climate (Aw), hot arid desert climate (BWh), hot arid steppe climate (BSh), cold arid steppe climate (BSk), dry temperate climate with hot summers (Csa), dry winter temperate climate with hot summer (Cwa), hot summer temperate climate without dry season (Cfa), warm summer temperate climate without dry season (Cfb), cold dry climate with warm summers (Dsb), cold climate with hot summers and no dry season (Dfa), and cold climate with warm summers and no dry season (Dfb). Studies were grouped into 4 climate types; tropical (= 1), arid (= 2), temperate (= 3) and cold (= 4) climates. Countries where and years when each study were done was obtained. Ambient temperature (AT) data for each of these study sites were obtained from Harris et al. (2014).

4.2.2 Meta-analysis of daytime and night-time, and diurnal feeding behaviour

Response variables (i.e. times spent eating, ruminating and idling, number and duration of ruminating and eating sessions over a 12h day and 12h night periods) were logarithmically transformed for purposes of estimating the scalar. Hereafter, each reference to a response variable will refer to the log10 of that response variable unless otherwise stated in the manuscript. Log_{10} transformation of body weight was done to meet assumptions of homogeneity. The response surface regression analysis of SAS 9.3 software (SAS Institute Inc., Cary, NC, USA) was used to determine whether the relationship between feeding behaviour measures and BW was linear or quadratic. The quadratic parameter was significant for times spent eating, ruminating, chewing and idling. A linear model with a log10 function was fitted to estimate the scaling relationships between body weight (BW) and scaled feeding behaviour (FB in min/d/kg BW) with the general equation: $\log_{10}$ (FB) = a + b $\log_{10}$ (BW) or FB = aBW^b; where 'a' is the intercept and 'b' is the slope of the line, also known as the allometric coefficient.

Because of the wide distribution of animal body weights reported in these studies, feeding behaviours were standardised by scaling to body weight (BW^b). A meta-analysis was done using the mixed model regression procedure according to St-Pierre (2001) and Sauvant et al. (2008) to determine the main effects of ruminant type, ruminant feeding type, period of day, climatic region and climate type on diurnal feeding behaviour. A model with discrete predictor variables (ruminant type, ruminant feeding type, period of day and climatic region, climate type) considered as fixed effects were used. The fixed effect of days in lactation, days in pregnancy, body weight, mature body weight, degree of maturity, animal production level, dry matter, neutral detergent fibre, ash and crude protein contents of diets fed to animals, whether diets fed to animals were tannin rich or non-tannin containing feeds, whether diets were silage or non-silage, whether animals were fed indoors or grazing outdoors, in-groups or individually, and ambient temperature were considered as covariates. Different studies were considered as random effects. Data were weighted by the standard error of mean according to Sauvant et al. (2008). Least square means were used to compare differences among means in the case of discrete predictor variables. The probability threshold for significance of fixed and random study effects for meta-analyses were considered at $p<0.05$.

A second model with discrete predictor variables considered as fixed effects was used to determine differences in chemical composition of feeds/diets fed to or consumed by ruminants based on ruminant type, feeding type and climatic region. Data were weighted by the standard error of mean according to Sauvant et al. (2008). Least square means were used to compare differences among means in the case of discrete predictor variables. The probability threshold for significance of fixed and random study effects for meta-analyses were considered at $p<0.05$.

Models were built to assess the influence of level of concentrate in the diets, days in lactation, days in pregnancy, body weight, mature body weight, degree of maturity, animal production level, dry matter, acid detergent fibre, neutral detergent fibre, ash and crude protein contents of diets fed to or eaten by animals, and ambient temperature, as well as combinations of these covariates on each response variable. The variance inflation factor (VIF) was used to assess multicollinearity among prediction variables according to Kaps and Lamberson (2017). Hemicellulose and ADF content were removed because of high multicollinearity (VIF > 10) with NDF. The model statistics of Akaike's information criterion (AIC) was applied in model selection to measure the relative goodness of fit of the statistical models. The value of Cp (smaller than the number of parameters in the model) and AIC (lower AIC is better model) were used to select an optimal model combination (Kaps and Lamberson 2017).

The Genmod procedure was used to determine the linear model with a natural log link function for the relative time spent of eating, ruminating, and chewing with the $\log_{10}$ transformed body weight. This model takes a linear form with a log link function, a function that associates the regressor with the response variable as: $\text{Ln TS}_y = \text{Ln TS}_0 + (\text{rate} \times \log_{10} \text{BW})$. This model was used to determine the rate of decrease of relative time spent eating, ruminating, and chewing with increasing $\log_{10}$ transformed body weight. The final model was: $\text{TS}_y = \text{TS}_0 \times e^r \times \log_{10} \text{BW}$, where TS_0 is the initial time spent on each activity (eating, ruminating, or chewing); TS, time spent on either eating, ruminating, or chewing; BW, body weight; and r, rate of decrease. The correlation procedure was used to establish the Pearson correlation coefficients of any two input predictor variables.

4.2.3 Prediction of diurnal feeding behaviour using Random Forest model

The input factors used in model development for prediction of feeding behaviour were CON, RFT, TAN, SIL, GI, DM, NDF, CP, ash, DP, DL, BW, DOM, APL, CT, and AT. Random Forest models were programmed on a 64-bit R version 3.6.2 (Dark and Stormy Night) to develop models to predict feeding behaviour. A Random Forest model was trained to predict feeding behaviour using diet, animal and environmental factors described above. The Random Forest algorithm intrinsically divided the dataset into 2 subsets: 70% of the dataset for model training and 30% for testing. The Random Forest was trained as a binary tree-based machine-learning method to predict feeding behaviour. The Random Forest algorithm was tuned for one parameter (i.e. “mtry”) using the “trainControl” option, and the search for the best “mtry” was randomly done. The “mtry” parameter represents the number of variables randomly sampled as candidates at each split. The most accurate value for “mtry” was selected for the combination that yielded the lowest error. During resampling the training data was cross-validated 10-fold 3 times. The best “mtry” values for each predicted variable were; TSE (“mtry” = 5, RMSE = 61.909, R^2 = 0.869 and MAE = 44.577), TSR (“mtry” = 5, RMSE = 79.870, R^2 = 0.657 and MAE = 56.325), DEB (“mtry” = 5, RMSE = 14.889, R^2 = 0.853 and MAE = 9.612), NEB (“mtry” = 12, RMSE = 3.825, R^2 = 0.775 and MAE = 2.228), DRB (“mtry” = 9, RMSE = 4.075, R^2 = 0.764 and MAE = 3.083) and NRB (“mtry” = 9, RMSE = 2.655, R^2 = 0.776 and MAE = 1.863). The number of decision trees (“ntree”) was set at 2000. After training the final models attained precision in prediction of 83.7% (TSE), 60.1% (TSR), 75.2% (DEB), 52.7% (NEB), 66.3% (DRB) and 68.9% (NRB).

After training and model development, the Random Forest models were used to predict the feeding behaviours using the training and testing datasets. Linear regressions of the observed against the predicted feeding behaviour was done and the coefficient of determination used to determine the precision of the Random Forest models in predicting feeding behaviour. Residual standard error (RSE) was used to determine accuracy of these models in predicting feeding behaviour. The linear and mean biases in model predictions were evaluated by regressing the residuals (observed minus predicted feeding behaviour) against predicted feeding behaviour using the training dataset. The intercept and slopes were tested against 0 to determine any linear or mean bias St-Pierre (2003).

4.3 Results

4.3.1 Meta-analysis of daytime and night feeding behaviour

4.3.1.1 Scaling of daytime and night-time feeding behaviour and body weight of ruminants

During the day, the number of eating bouts averaged 9 ± 7.38 at 46 ± 53.64 minutes per bout, while the 6 ± 2.88 eating bouts at night averaged 36 ± 37.41 minutes (Table 4.1). Frequency of rumination bouts was 9 ± 4.95 times during the day lasting 22 ± 11.09 minutes per bout, while the 10 ± 1.76 ruminating bouts at night averaged 28 ± 8.73 minutes. In all large ruminants, time spent ruminating and chewing became longer during the day than at night where time spent ruminating and chewing were similar for all sizes of ruminants (Table 4.2). Period of day did not affect allometric scalars between body weight and the duration of eating and ruminating bouts and number of eating bouts. Time spent ruminating and chewing at night scaled allometrically with body weight. All other daytime and night-time feeding behaviours scaled allometrically with body weight. There was an effect of period of day on allometric scales of body weight and time spent eating, ruminating, and chewing, but not with duration of eating and ruminating bouts.

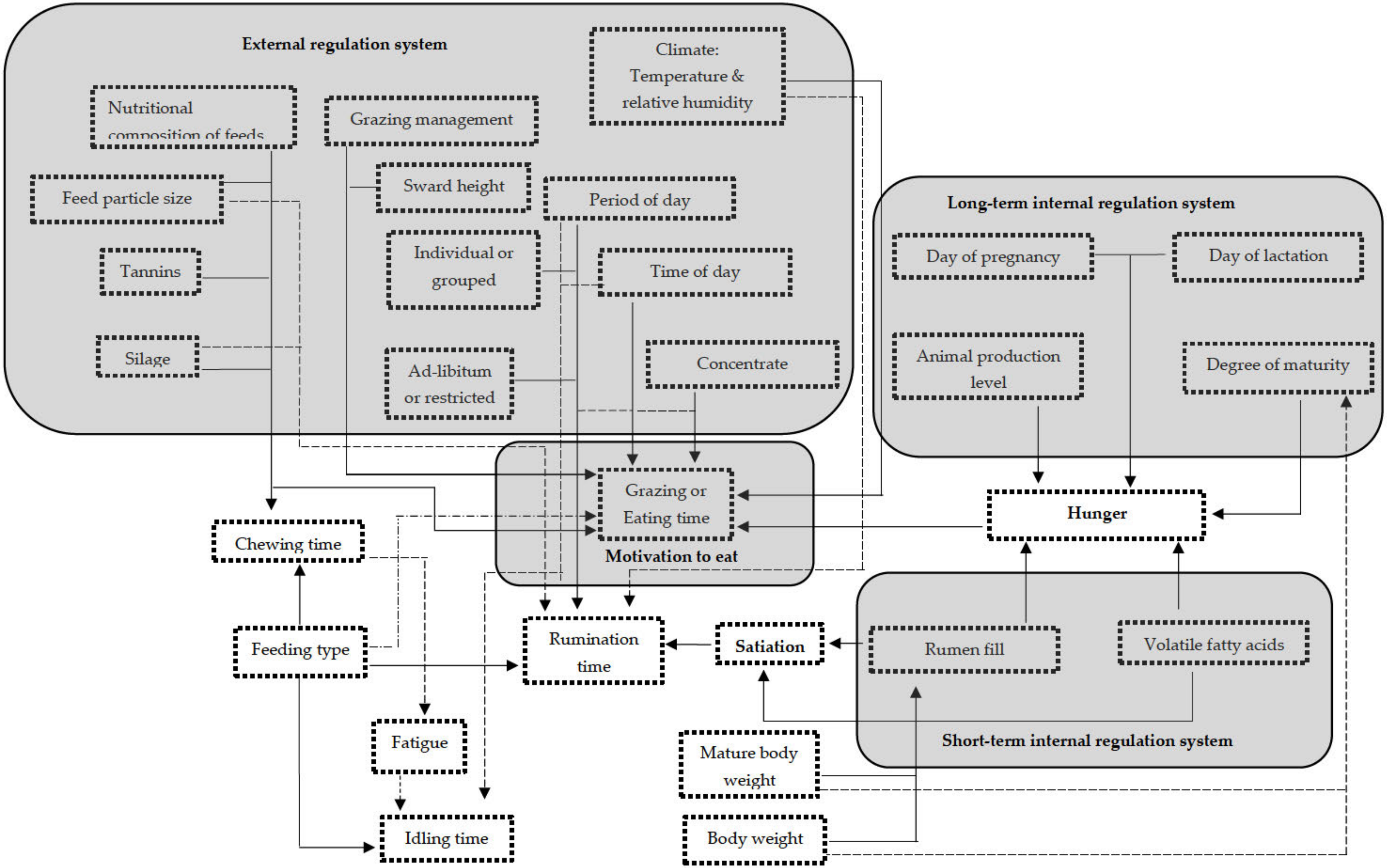


Fig. 4. 1 Factors affecting diurnal feeding behaviour of ruminants

4.3.1.2 Impact of animal, environmental and feed factors on daytime and night-time feeding behaviour

The Akaike's information criterion (AIC) showed that body weight and ambient temperature were the most influential factors affecting feeding behaviour (Table 4.3). Predictions from this meta-analysis showed that times spent eating during the day and at night are expected to decline with an increase in ambient temperature. Times spent ruminating during the day is expected to increase with ambient temperature, as time spent on eating decreases. Night-time duration of rumination bouts and time spent on rumination at night decreased with increasing in ambient temperature.

4.3.1.3 Effect of period of day and ruminant feeding type on daytime and night-time feeding behaviour

Period of day affected all feeding behaviour evaluated but the number and duration of eating bouts (Table 4.4). Time spent eating and chewing were longer during the day than at night, while time spent ruminating and idling, duration and number of ruminating sessions were higher during the night than the daytime. Duration and number of ruminating bouts in grazers were similar during the day and at night. Ruminant type had an effect on all daytime feeding behaviours evaluated but time spent chewing and duration of ruminating bouts; while night-time feeding behaviours were not affected by ruminant type except for number of eating bouts (Table 4.5). During the day, large ruminants (cattle and buffalo) spent 3 to 4-fold longer ruminating compared to their smaller ruminants (sheep and goats), but time spent ruminating at night increased in the smaller ruminants. During the day, goats and sheep had longer ruminating sessions than cattle. Time spent eating during daytime was similar for red deer (temperate climate), reindeer (cold climate) and sable antelope (arid to sub-tropical) all intermediate feeders and ruminants inhabiting different climatic regions.

Duration of eating bouts during the day was 3-fold longer in browsers compared to grazers and intermediate feeders, but similar at night. Frequency of eating bouts at night were higher in grazers and intermediate feeders than in browsers. Daytime and night-time duration of ruminating bouts was not affected by ruminant feeding type. Ruminant feeding type had no effect on time spent eating during the day and at night. Number of day-time ruminating bouts was higher for grazers than intermediate feeders, while number of night-time bouts were similar.

4.3.1.4 Effect of climate on daytime and night-time feeding behaviour in ruminants

Type of climate inhabited by ruminants had no effect on all daytime feeding behaviours evaluated but affected the number of eating bouts (Table 4.6). Climate type affected time spent eating and chewing at night. Ruminants from arid regions spent more time eating at night compared to ruminants inhabiting other climates.

4.3.2 Meta-analysis of diurnal feeding behaviour

4.3.2.1 Scaling of diurnal feeding behaviour and net energy requirements to body weight of ruminants

Ruminants have on average 13 ± 8.24 eating bouts per day lasting approximately 46 ± 39.07 minutes, 18 ± 5.604 rumination bouts of 26 ± 8.32 minutes in length on a full circadian cycle (Table 4.7). Total net energy requirements calculated according to AFRC (1993) scaled to $BW^{0.96}$ with the scalar different from the Bell-Jarman principle ($BW^{0.75}$) and 1 (Table 4.8). Time spent eating, ruminating, and chewing of browsers scaled isometrically with total net energy requirements. For the combined dataset, all feeding behaviours had a negative allometric scale that was different from the Bell-Jarman principle.

Feeding behaviours scaled allometrically with body weight for all ruminant feeding types. However, time spent eating and chewing by browsers and intermediate feeders, and time spent ruminating by grazers (Table 4.9) scaled isometrically with body weight. Time spent ruminating became shorter in large browsers, while large intermediate feeders spent more time ruminating than their smaller counterparts.

Relative time spent eating, ruminating, and chewing decreased exponentially with the $\log_{10}$ body weight (Figs 4.2-4.4). Per unit of body weight, small-size ruminants spent more time eating compared to their large counterparts. The exponential relationship between time spent eating (TSE in min/d/kg BW) and $\log_{10}$ BW (kg) was: $TSE = e^{4.93\ (\pm 0.033)} \times e^{[-1.80(\pm 0.022) \times \log(BW)]}$ ($n = 735$; $R^2 = 0.8094$) (Fig 4.2). The smallest ruminant by body weight (blue duiker) ruminated the longest per unit body weight. The relationship between time spent ruminating (TSR in min/d/kg BW) and $\log_{10}$ BW (kg) was: $TSR = e^{5.22\ (\pm 0.012)} \times e^{[-1.75(\pm 0.009) \times \log(BW)]}$ ($n = 566$; $R^2 = 0.8984$) (Fig 4.3). The relationship between time spent chewing (TSC in min/d/kg BW) and $\log_{10}$ BW (kg) was: $TSC = e^{6.39\ (\pm 0.017)} \times e^{[-2.18(\pm 0.012) \times \log(BW)]}$ ($n = 511$; $R^2 = 0.9326$) (Fig 4.4).

Table 4. 1 Descriptive statistics of diet, feed and climatic factors affecting degradation of feeds in the rumen

12h day period feeding behaviour	N	Max	Min	Mean ± SD	SEM
TSE (min/d)	122	662.40	15.67	321 ± 136.86	12.391
TSR (min/d)	82	365.15	15.00	167 ± 78.05	8.619
TSC (min/d)	76	670.68	109.80	429 ± 109.80	12.595
TSI (min/d)	72	461.70	90.00	279 ± 100.46	11.840
DEB (min/bout)	34	233.00	4.00	46 ± 53.64	9.200
DRB (min/bout)	35	53.86	6.00	22 ± 11.09	1.875
NEB (per 12h day)	35	41.70	1.40	9 ± 7.38	1.248
NRB (per 12h day)	36	16.70	0.80	9 ± 4.95	0.825
Animal factors					
BW (kg)	134	617.00	9.26	200 ± 204.96	17.706
MBW (kg)	134	850.00	25.00	303 ± 266.33	23.007
DOM	134	1.72	0.15	0.67 ± 0.36	0.031
DP (days)	134	237	0	12 ± 49.63	4.287
DL (days)	134	290	0	9 ± 50.15	4.333
APL	134	3.12	1.00	1 ± 0.57	0.049
Diet factors					
DM (g/kg)	134	926.00	140.00	618 ± 287.89	24.870
CP (g/kg)	134	259.00	20.00	144 ± 53.91	4.657
NDF (g/kg)	134	787.00	180.33	526 ± 125.71	10.860
ADF (g/kg)	134	632.00	58.62	326 ± 95.12	8.217
HEM (g/kg)	134	344.00	40.00	203 ± 63.96	5.526
Ash (g/kg)	134	187.00	10.76	83 ± 27.44	2.371
Con. (g/kg)	134	77.00	0.00	13 ± 22.14	1.913
Climatic factors					
AT (ºC)	134	31.16	-8.61	16.15 ± 7.66	0.662
12h night period feeding behaviour					
TSE (min/d)	61	372.00	19.84	138 ± 90.72	11.616
TSR (min/d)	56	438.60	138.84	292 ± 66.35	8.867
TSC (min/d)	52	618.00	95.50	416 ± 115.57	16.027
TSI (min/d)	48	511.66	102.00	324 ± 77.93	11.248
DEB (min/bout)	28	127.83	6.00	36 ± 37.41	7.069
DRB (min/bout)	29	49.30	18.00	28 ± 8.73	1.620
NEB (per 12h night)	29	10.00	1.60	6 ± 2.88	0.534
NRB (per 12h night)	30	13.00	4.68	10 ± 1.76	0.321
Animal factors					
BW (kg)	71	617.00	22.40	259 ± 237.58	28.196
MBW (kg)	71	680.00	50.00	363 ± 251.36	29.831
DOM	71	1.03	0.15	0.7 ± 0.31	0.037
DP (days)	71	237	0.00	20 ± 66.39	7.879
DL (days)	71	290	0.00	18 ± 68.04	8.075
APL	71	3.12	1.00	1.6 ± 0.66	0.078
Diet factors					
DM (g/kg)	71	926.00	140.00	613 ± 304.38	36.123
CP (g/kg)	71	259.00	20.00	149 ± 66.05	7.839
NDF (g/kg)	71	787.00	205.70	499 ± 146.40	17.374
ADF (g/kg)	71	632.00	149.38	316 ± 117.19	13.908
HEM (g/kg)	71	187.00	40.00	189 ± 72.34	8.585
Ash (g/kg)	71	187.00	41.30	88 ± 30.03	3.563
Con (g/kg)	71	77.00	0.00	18 ± 25.63	3.042
Climatic factors					
AT (ºC)	71	31.16	4.17	17 ± 6.82	0.809

ADF, acid detergent fibre; APL: animal production level; AT, ambient temperature; BW, body weight; Con, concentrate; CP, crude protein; DEB, duration of eating bouts; DL: days in lactation; DM: dry matter; DOM, degree of maturity; DP: days pregnant; DRB, duration of ruminating bouts; HEM, hemicellulose; MBM: mature body mass; NDF, neutral detergent fibre; NEB, number of eating bouts; NRB, number of ruminating bouts; SD, standard deviation; SEM, standard error of the mean; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

Table 4. 2 The regressions used to estimate the scaling relationships between body weight (BW) and feeding behaviour (FB) of browsing and grazing wild and domestic ruminants with general equation $\log_{10}(FB) = a + b \log_{10}(BW)$ or $FB = aBW^b$.

Feeding behaviour (min/d/kg BW)	Period	N	Intercept (a)	$P_{intercept}$	[A] Slope (b)	P_{slope}	RMSE	R^2	[B] Test
$\log_{10}$(TSE)	Day	122	2.16 ± 0.076	<0.0001	-0.85 ± 0.037^{b}	<0.0001	0.2153	0.8158	***
	Night	61	1.39 ± 0.136	<0.0001	-0.69 ± 0.063^{a}	<0.0001	0.2750	0.6694	***
$\log_{10}$(TSR)	Day	82	2.49 ± 0.092	<0.0001	-1.17 ± 0.047^{b}	<0.0001	0.2307	0.8865	***
	Night	56	2.47 ± 0.052	<0.0001	-1.01 ± 0.025^{a}	<0.0001	0.1039	0.9676	NS
$\log_{10}$(TSC)	Day	76	2.73 ± 0.058	<0.0001	-1.06 ± 0.025^{b}	<0.0001	0.1398	0.9448	*
	Night	52	2.58 ± 0.090	<0.0001	-0.99 ± 0.044^{a}	<0.0001	0.1722	0.9122	NS
$\log_{10}$(DEB)	Day	34	0.49 ± 0.172	0.0077	-0.45 ± 0.094^{a}	<0.0001	0.2954	0.4209	***
	Night	28	0.04 ± 0.122	0.7700	-0.29 ± 0.063^{a}	<0.0001	0.1802	0.4536	***
$\log_{10}$(DRB)	Day	35	0.90 ± 0.122	<0.0001	-0.78 ± 0.067^{a}	<0.0001	0.2070	0.8055	***
	Night	29	-1.17 ± 0.072	<0.0001	-0.86 ± 0.038^{a}	<0.0001	0.1059	0.9502	***
$\log_{10}$(NEB)	Day	35	1.42 ± 0.133	<0.0001	-0.31 ± 0.071^{a}	0.0001	0.2361	0.3672	***
	Night	29	1.16 ± 0.137	<0.0001	-0.23 ± 0.070^{a}	0.0023	0.2087	0.2950	***
$\log_{10}$(NRB)	Day	36	1.52 ± 0.135	<0.0001	-0.38 ± 0.073^{b}	<0.0001	0.2381	0.4447	***
	Night	30	1.09 ± 0.054	<0.0001	-0.06 ± 0.028^{a}	0.0458	0.0825	0.1350	***

* p<0.05; ** p<0.01; *** p<0.001; NS, not significant (p>0.05)

[A] The slope represents the scaling factor (b) based on the $\log_{10}$-transformed linear equation

[B] Test of slope against -1

DEB, duration of eating bouts; DRB, duration of ruminating bouts; N, number of data used; NEB, number of eating bouts; NRB, number of ruminating bouts; RMSE, root mean square error; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

Table 4. 3 Most influential factors affecting day-time and night-time feeding behaviour of wild and domestic ruminants using the Akaike's information criterion (AIC) and Cp statistic (C(p))

Model predictors	nPar	*C(p)*	*AIC*	R^2	RMSE	N	Relationships of feeding behaviour with model predictors
Daytime TSE							
Con, DM, BW, DOM, APL and AT	6+1	5.5709	-436.74	0.8996	0.1624	122	2.80 – 0.004×Con – 0.0003×DM – 0.97 $\log_{10}$ BW + 0.08×DOM – 0.12×APL – 0.004×AT
Con, DM, NDF, BW, DOM, APL and AT	7+1	6.8991	-435.46	0.9002	0.1626	122	2.70 – 0.004×Con – 0.0003×DM + 0.0001×NDF – 0.96 $\log_{10}$ BW + 0.08×DOM – 0.1×APL – 0.005×AT
Night-time TSE							
Ash, BW and AT	3+1	1.9096	-163.19	0.7269	0.2543	61	1.83 + 0.002×Ash – 0.87 $\log_{10}$ BW – 0.02×AT
CP, Ash, BW and AT	4+1	1.9166	-163.44	0.7369	0.2519	61	1.79 – 0.0008×CP + 0.003×Ash – 0.84 $\log_{10}$ BW – 0.01×AT
Daytime TSR							
DM, BW and AT	3+1	2.2290	-257.94	0.9147	0.2026	82	1.72 + 0.0005×DM – 0.98 $\log_{10}$ BW + 0.006×AT
DM, CP, BW and AT	4+1	2.4595	-257.87	0.9166	0.2015	82	1.77 + 0.0004×DM – 0.0006×CP – 0.96 $\log_{10}$ BW + 0.007×AT
Night-time TSR							
DM, BW and AT	3+1	0.3124	-261.93	0.9749	0.0932	56	2.87 – 0.0002×DM – 1.11 $\log_{10}$ BW – 0.006×AT
DM, CP, BW and AT	4+1	1.4575	-260.93	0.9754	0.0933	56	2.92 – 0.0002×DM – 0.0003×CP – 1.11 $\log_{10}$ BW – 0.005×AT
Daytime TSC							
Con, NDF, Ash, BW, DOM and APL	6+1	4.5160	-337.78	0.9720	0.1037	76	3.22 – 0.005×Con – 0.0005×NDF + 0.001×Ash – 1.19 $\log_{10}$ BW + 0.21×DOM – 0.09×APL
Con, DM, NDF, Ash, BW, DOM and APL	7+1	6.0190	-336.35	0.9722	0.1041	76	3.28 – 0.005×Con – 0.00004×DM – 0.0005×NDF + 0.001×Ash – 1.19 $\log_{10}$ BW + 0.20×DOM – 0.09×APL
Night-time TSC							
Con, DM, NDF, Ash, BW, DOM and AT	7+1	6.1390	-237.89	0.9767	0.0946	52	3.41 – 0.006×Con – 0.0003×DM – 0.0005×NDF + 0.001×Ash – 1.31 $\log_{10}$ BW + 0.24×DOM + 0.008×AT
Con, DM, NDF, BW, DOM and AT	6+1	6.4057	-237.17	0.9754	0.0961	52	3.56 – 0.006×Con – 0.0004×DM – 0.0005×NDF – 1.31 $\log_{10}$ BW + 0.25×DOM + 0.009×AT

Table 4.3 (continued)

Model predictors	nPar	*C(p)*	*AIC*	R^2	RMSE	N	
Daytime DEB							
Con and BW	2+1	-0.098	-81.40	0.4605	0.2896	34	$0.65 - 0.005\times\text{Con} - 0.50\log_{10}\text{BW}$
BW	1+1	-0.051	-80.99	0.4209	0.2953	34	$0.49 - 0.45\log_{10}\text{BW}$
Night-time DEB							
NDF, BW, DOM, APL and AT	5+1	5.7535	-147.26	0.9386	0.0657	28	$2.20 + 0.0007\times\text{NDF} - 1.15\log_{10}\text{BW} + 0.81\times\text{DOM} + 0.09\times\text{APL} - 0.09\times\text{AT}$
DM, NDF, Ash, BW, DOM and AT	6+1	5.7959	-147.90	0.9442	0.0641	28	$2.19 - 0.0003\times\text{DM} + 0.0005\times\text{NDF} + 0.002\times\text{Ash} - 1.16\log_{10}\text{BW} + 0.67\times\text{DOM} - 0.07\times\text{AT}$
Daytime DRB							
Con, DM, BW, APL and AT	5+1	5.2484	-144.33	0.9447	0.1177	35	$0.92 - 0.009\times\text{Con} + 0.001\times\text{DM} - 0.70\log_{10}\text{BW} + 0.16\times\text{APL} - 0.07\times\text{AT}$
Con, DM, BW, DOM, APL and AT	6+1	5.8184	-144.15	0.9475	0.1167	35	$1.30 - 0.009\times\text{Con} + 0.001\times\text{DM} - 0.87\log_{10}\text{BW} + 0.33\times\text{DOM} + 0.16\times\text{APL} - 0.09\times\text{AT}$
Night-time DRB							
Con, DM, NDF, CP, BW, APL and AT	7+1	7.4054	-163.39	0.9902	0.0533	29	$1.78 - 0.006\times\text{Con} + 0.0007\times\text{DM} + 0.0008\times\text{NDF} + 0.0008\times\text{CP} - 1.20\log_{10}\text{BW} + 0.29\times\text{APL} - 0.09\times\text{AT}$
Con, DM, NDF, CP, BW, DOM, APL and AT	8+1	8.2444	-163.09	0.9907	0.0531	29	$2.22 - 0.006\times\text{Con} + 0.0007\times\text{DM} + 0.0006\times\text{NDF} + 0.0007\times\text{CP} - 1.33\log_{10}\text{BW} + 0.29\times\text{DOM} + 0.25\times\text{APL} - 0.1\times\text{AT}$

nPar, number of parameters for each model is the number independent variables +1; nPar, number of parameters for each model is the number independent variables +1; APL: animal production level; AT, ambient temperature; BW, body weight; Con, concentrate; CP, crude protein; DEB, duration of eating bouts; DL: days in lactation; DM: dry matter; DOM, degree of maturity; DP: days pregnant; DRB, duration of ruminating bouts; NDF, neutral detergent fibre; RMSE, root mean square error; TSC, time spent chewing; TSE, time spent eating; TSR, time spent ruminating.

Table 4. 4 Effects of period of day and ruminant feeding type on diurnal feeding behaviour of browsing and grazing wild and domestic ruminants

Test of fixed effects		log$_{10}$ transformed feeding behaviour (min/d/kg BW)						log$_{10}$ transformed (/d)	
	Feeding type	TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Day	Grazers	0.37 ± 0.031	0.25 ± 0.056	0.67 ± 0.043	0.49 ± 0.016	-0.58 ± 0.200	-0.37 ± 0.159	1.01 ± 0.264	0.87 ± 0.059
	Browsers	0.20 ± 0.188	-	-	-	-	-	-0.41 ± 1.822	-
	Intermediate	0.38 ± 0.050	0.10 ± 0.110	0.68 ± 0.052	0.68 ± 0.056	-0.84 ± 0.602	-0.10 ± 0.265	0.58 ± 0.526	0.20 ± 0.456
Night	Grazers	0.10 ± 0.035	0.56 ± 0.059	0.65 ± 0.043	0.63 ± 0.016	-0.83 ± 0.199	-0.31 ± 0.159	0.95 ± 0.265	1.07 ± 0.060
	Browsers	0.39 ± 0.188	-	-	-	-	-	-0.12 ± 1.799	-
	Intermediate	-0.02 ± 0.123	0.39 ± 0.184	0.63 ± 0.061	0.68 ± 0.081	-0.94 ± 0.602	0.01 ± 0.265	0.13 ± 0.526	0.55 ± 0.456
Significance									
Period		*	**	*	*	NS	*	NS	**
Feeding type		NS	NS	NS	*	*	NS	NS	NS
P × F		*	NS	NS	*	NS	NS	***	NS

APL: animal production level; AT, ambient temperature; BW, body weight; Con, concentrate; CP, crude protein; DEB, duration of eating bouts; DL: days in lactation; DM: dry matter; DOM, degree of maturity; DP: days pregnant; DRB, duration of ruminating bouts; HEM, hemicellulose; MBM: mature body mass; NDF, neutral detergent fibre; NEB, number of eating bouts; NRB, number of ruminating bouts; P × F, period of day × feeding type interactions; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 4. 5 Effects of ruminant feeding type and ruminant type on day-time and night-time feeding behaviour of browsing and grazing wild and domestic ruminants

Day-time	$\log_{10}$ transformed feeding behaviour (min/d/kg BW)						$\log_{10}$ transformed (/d)	
Ruminant type	TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Grazers								
Cattle	0.92 ± 0.183	0.69 ± 0.494	0.49 ± 0.239	0.38 ± 0.312	-	-1.87 ± 0.633	1.24 ± 1.955	2.32 ± 0.590
Mediterranean buffalo	0.50 ± 0.147	0.45 ± 0.487	0.54 ± 0.312	0.78 ± 0.322	-	-	-	-
Sheep	0.21 ± 0.100	0.15 ± 0.299	0.88 ± 0.137	0.62 ± 0.148	-1.96 ± 1.299	0.42 ± 0.415	0.95 ± 0.874	0.21 ± 0.273
Intermediate feeders								
Goats	0.26 ± 0.108	-0.07 ± 0.311	0.90 ± 0.153	0.80 ± 0.155	-2.15 ± 1.723	0.83 ± 0.526	0.52 ± 1.188	-0.57 ± 0.493
Red deer	0.26 ± 0.073	-	-	-	-	-	0.26 ± 1.700	-
Reindeer	0.31 ± 0.108	-	-	-	-	-	-	-
Sable	0.30 ± 0.106	-	-	-	-	-	-	-
Significance	***	*	NS	***	*	*	NS	*
Night-time								
Grazers								
Cattle	-0.04 ± 0.436	0.37 ± 0.261	0.44 ± 0.280	0.94 ± 0.581	-1.38 ± 3.634	-0.10 ± 0.769	1.98 ± 2.666	1.74 ± 0.358
Mediterranean buffalo	0.01 ± 0.776	0.52 ± 0.293	0.76 ± 0.463	0.68 ± 0.818	-	-	-	-
Sheep	-0.03 ± 0.426	0.51 ± 0.236	0.71 ± 0.217	0.35 ± 0.355	-0.14 ± 1.875	-0.60 ± 0.420	0.26 ± 1.938	0.54 ± 0.209
Intermediate feeders								
Goats	-0.28 ± 0.538	0.39 ± 0.262	0.64 ± 0.273	0.33 ± 0.598	0.27 ± 2.432	-0.57 ± 0.757	-1.13 ± 1.951	0.09 ± 0.407
Red deer	0.23 ± 0.412	-	-		-0.97 ± 3.274	-	0.48 ± 3.125	-
Significance	NS	NS	NS	NS	NS	NS	***	NS
Day-time								
Feeding type								
Grazers	0.43 ± 0.022	0.35 ± 0.059	0.75 ± 0.044	0.57 ± 0.050	-0.43 ± 0.126	-0.42 ± 0.196	1.03 ± 0.200	0.93 ± 0.088
Browsers	0.23 ± 0.141	-	-	-	1.30 ± 0.668	-	0.09 ± 0.652	-
Intermediate feeders	0.44 ± 0.035	0.13 ± 0.085	0.74 ± 0.054	0.75 ± 0.058	-0.11 ± 0.185	-0.29 ± 0.230	0.64 ± 0.317	0.65 ± 0.150
Significance	NS	**	NS	***	*	NS	NS	*
Night-time								
Grazers	-0.04 ± 0.032	0.44 ± 0.015	0.62 ± 0.063	0.57 ± 0.060	-0.56 ± 0.123	-0.43 ± 0.021	0.98 ± 0.596	1.00 ± 0.110
Browsers	0.25 ± 0.199	-	-	-	-0.26 ± 0.916	-	-0.61 ± 1.165	-
Intermediate feeders	-0.28 ± 0.135	0.35 ± 0.062	0.54 ± 0.078	0.62 ± 0.148	-0.27 ± 0.330	-0.25 ± 0.136	-0.40 ± 0.607	0.91 ± 0.122
Significance	NS	NS	NS	NS	NS	NS	***	NS

DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating. * $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 4. 6 Effects climatic region on day-time and night-time feeding behaviour of browsing and grazing wild and domestic ruminants

Daytime	$\log_{10}$ transformed feeding behaviour (min/d/kg BW)						$\log_{10}$ transformed (/day)	
Climatic region	TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Tropical								
Aw	0.48 ± 0.295	0.21 ± 0.329	0.63 ± 0.196	0.55 ± 0.210	-	-	-	-
Arid								
BWh	0.10 ± 0.224	0.20 ± 0.389	0.72 ± 0.255	1.13 ± 0.290	-	-	-	-
Temperate								
Cfa	0.46 ± 0.176	0.61 ± 0.200	0.64 ± 0.100	0.22 ± 0.162	-0.94 ± 0.915	-0.01 ± 0.298	1.92 ± 0.470	1.56 ± 0.426
Cfb	0.46 ± 0.154	0.29 ± 0.169	0.88 ± 0.104	0.84 ± 0.144	-	-0.65 ± 0.469	0.48 ± 1.095	0.55 ± 0.371
Csb	0.31 ± 1.052	-	-	-	-	-		-
Cwa	0.39 ± 0.220	0.30 ± 0.344	0.78 ± 0.209	0.44 ± 0.218	0.23 ± 1.569	-0.42 ± 0.303	0.95 ± 0.529	0.96 ± 0.310
Cwb	0.46 ± 0.190	0.03 ± 0.292	0.76 ± 0.179	0.72 ± 0.196	-1.32 ± 3.410	-	-	-
Cold								
Dfb	0.57 ± 0.183	-	-	-	-	-	-	-
Dfc	0.48 ± 0.395	-	-	-	-	-	-	-
Significance	NS	NS	NS	NS	NS	NS	*	NS
Night-time								
Tropical								
Aw	-1.36 ± 0.454	0.17 ± 0.194	0.19 ± 0.266	0.55 ± 0.477	-	-	-	-
Arid								
BWh	0.06 ± 0.287	0.40 ± 0.177	0.41 ± 0.269	0.55 ± 0.444	-	-	-	-
Temperate								
Cfb	0.01 ± 0.071	0.48 ± 0.105	0.86 ± 0.114	0.57 ± 0.284	1.01 ± 1.019	-0.03 ± 0.309	1.64 ± 1.300	0.88 ± 0.219
Cwa	0.02 ± 0.108	0.42 ± 0.084	0.62 ± 0.081	0.33 ± 0.138	-1.35 ± 0.557	-0.64 ± 0.193	0.14 ± 0.816	1.04 ± 0.244
Cwb	0.37 ± 0.246	0.50 ± 0.289	0.24 ± 0.315	1.14 ± 0.521	-	-	-	-
Significance	*	NS	***	NS	NS	NS	NS	NS

Table 4.6 (continued)

Daytime Climatic region	$\log_{10}$ transformed feeding behaviour (min/d/kg BW) TSE	 TSR	 TSC	 TSI
Daytime				
Climatic region				
Tropical	0.45 ± 0.107	0.26 ± 0.261	0.68 ± 0.184	0.63 ± 0.169
Arid	0.30 ± 0.064	0.13 ± 0.309	0.75 ± 0.241	0.90 ± 0.245
Temperate	0.45 ± 0.026	0.34 ± 0.076	0.76 ± 0.058	0.55 ± 0.056
Cold	0.42 ± 0.056	-	-	-
Significance	NS	NS	NS	NS
Night-time				
Climatic region				
Tropical	-1.07 ± 0.413	0.21 ± 0.164	0.24 ± 0.414	0.61 ± 0.501
Arid	0.19 ± 0.277	0.45 ± 0.118	0.80 ± 0.359	0.60 ± 0.497
Temperate	0.01 ± 0.035	0.46 ±0.018	0.63 ± 0.088	0.57 ± 0.091
Significance	*	NS	NS	NS

DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

Aw, tropical savannah climate; BWh, hot arid desert climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season.

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 4. 7 Descriptive statistics of diet, feed and climatic factors affecting feeding behaviour in ruminants

24h feeding behaviour	N	Max	Min	Mean ± SD	SEM
Time spent eating (min/d)	741	849.60	40.46	377 ± 170.64	6.2688
Time spent ruminating (min/d)	573	754.56	0.00	417 ± 135.37	5.6553
Time spent chewing (min/d)	517	1384.00	149.70	770 ± 208.25	9.1590
Time spent idling (min/d)	517	1290.00	56.16	672 ± 211.48	9.3009
Duration of eating bouts (min/bout)	179	160.50	3.79	46 ± 39.07	2.9206
Duration of ruminating bouts (min/bout)	147	48.20	2.20	26 ± 8.32	0.6859
Number of eating bouts (per/d)	204	36.80	2.34	13 ± 8.24	0.5288
Number of ruminating bouts (per/d)	157	32.00	9.40	18 ± 5.604	0.4472
Animal factors					
Body weight (kg)	789	900	4.00	268 ± 234.87	8.3615
Mature body weight (kg)	789	1300	4.90	376 ± 290.13	10.329
Degree of maturity	789	2.30	0.06	0.69 ± 0.326	0.0116
Days in pregnancy (days)	789	237	0	4.71 ± 30.40	1.0821
Days in lactation (days)	789	312	0	24.02 ± 58.99	2.1001
Animal production level	789	3.79	0.78	1.50 ± 0.710	0.0252
Diet factors					
Dry matter (g/kg)	789	956.40	46.96	560 ± 284.52	10.129
Crude protein (g/kg)	789	751.00	2.94	149 ± 60.02	2.1368
Neutral detergent fibre (g/kg)	789	893.00	125.00	487 ± 140.01	4.9847
Acid detergent fibre (g/kg)	789	709.60	69.00	299 ± 102.08	3.6341
Hemicellulose (g/kg)	789	364.92	6.00	188 ± 68.02	2.4216
Ash (g/kg)	789	479.00	24.38	89 ± 42.45	1.5112
Concentrate (g/kg)	789	100.00	0.00	17 ± 24.28	0.8645
Climatic factors					
Ambient temperature (ºC)	789	35.95	-25.03	15 ± 9.23	0.3285

SD, standard deviation; SEM, standard error of the mean

4.3.2.2 Impact of animal, environmental and feed factors on diurnal feeding behaviour

The main factors that influence feeding behaviour were determined using the using Akaike's information criterion (AIC) (Table 4.10). Predictions from this meta-analysis showed that time spent eating and idling, and eating bouts are expected to increase with an increase in ambient temperature. Times spent ruminating and chewing are expected to decrease with increases ambient temperature. Level of concentrates in diets was inversely related to time spent ruminating, while eating and rumination time increased with the level of NDF in the feeds/diets. As a consequence of the increased ambient temperature, time spent eating and idling increased, while ruminating time decreased.

Ruminant type and feeding type affected all feeding behaviours evaluated (Table 4.11). Browsing ruminants showed distinct adaptive feeding behaviours compared to grazers and intermediate feeders. Browsers, grazers, and intermediate feeders spent similar times time eating, although browsers had the longest duration of eating bouts and lowest number of bouts while an opposite trend was observed for grazers and intermediate feeders. Time spent on rumination and duration of ruminating bouts were longer for grazer than browsers, but number of ruminating bouts were similar for both feeding types.

4.3.2.3 Effect of climate type on diurnal feeding behaviour in ruminants

Time spent eating in ruminants were similar across all climatic types and regions (Table 4.12). Time spent ruminating was highest for ruminants inhabiting tropical regions and lowest for ruminants in arid regions. Duration and number of ruminating sessions were highest in ruminants from tropical climates and lowest of those inhabiting very cold regions.

Table 4. 8 The regressions used to estimate the scaling relationships between total net energy requirements (TNER) and body weight (BW) and feeding behaviour (FB) of browsing and grazing wild and domestic ruminants with general equation $\log_{10}$ (FB) = a + b $\log_{10}$ (BW) or FB = aBW^{b}

Total requirements (MJ/d)	N	Intercept (a)	$P_{\text{intercept}}$	^{A} Slope (b)	P_{slope}	RMSE	R^2	^{B} Test	^{C} Test
log$_{10}$(TNE)				log$_{10}$ (BW) (kg					
Combined	993	-0.79 ± 0.02	<0.0001	0.96 ± 0.009	<0.0001	0.1574	0.9188	***	***
Feeding behaviour (min/d/kg BW)				log$_{10}$ (Total net energy requirements) (MJ/d)					
log$_{10}$(TSE)									
Grazers	792	1.30 ± 0.025	<0.0001	-0.78 ± 0.018	<0.0001	0.2911	0.7045	***	NS
Browsers	34	1.37 ± 0.424	0.0029	-0.84 ± 0.311	0.0109	0.3103	0.1858	NS	NS
Intermediate feeders	97	1.66 ± 0.078	<0.0001	-0.96 ± 0.076	<0.0001	0.2452	0.6241	NS	**
Combined	923	1.35 ± 0.024	<0.0001	-0.81 ± 0.018	<0.0001	0.2928	0.6994	***	***
log$_{10}$(TSR)									
Grazers	609	1.57 ± 0.023	<0.0001	-0.92 ± 0.017	<0.0001	0.2486	0.8341	***	***
Browsers	24	1.59 ± 0.164	<0.0001	-1.01 ± 0.124	<0.0001	0.3033	0.7507	NS	*
Intermediate feeders	77	1.57 ± 0.092	<0.0001	-0.87 ± 0.109	<0.0001	0.2768	0.4612	NS	NS
Combined	710	1.58 ± 0.021	<0.0001	-0.93 ± 0.016	<0.0001	0.2539	0.8231	***	***
log$_{10}$(TSC)									
Grazers	567	1.78 ± 0.020	<0.0001	-0.86 ± 0.015	<0.0001	0.2212	0.8514	***	***
Browsers	20	1.65 ± 0.355	0.0002	-0.81 ± 0.251	0.0045	0.2317	0.3687	NS	NS
Intermediate feeders	57	1.87 ± 0.068	<0.0001	-0.84 ± 0.075	<0.0001	0.1817	0.6954	***	NS
Combined	644	1.80 ± 0.019	<0.0001	-0.87 ± 0.015	<0.0001	0.2202	0.8473	***	***

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

^{A} The slope represents the scaling factor (b) based on the log$_{10}$-transformed linear equation

^{B} Test of slope against 1

^{C} Test of slope against Bell-Jarman principle

N, number of data used; RMSE, root mean square error; TNE, total net energy requirement; TSC, time spent chewing; TSE, time spent eating; TSR, time spent ruminating.

Table 4. 9 The regressions used to estimate the scaling relationships between body weight (BW) and feeding behaviour (FB) of browsing and grazing wild and domestic ruminants with general equation $\log_{10}(FB) = a + b \log_{10}(BW)$ or $FB = aBW^b$

Feeding behaviour (min/d/kg BW)	N	Intercept (a)	$P_{\text{intercept}}$	[A] Slope (b)	P_{slope}	RMSE	R^2	[B] Test
$\log_{10}$(TSE)				$\log_{10}$ (BW) (kg)				
Grazers	647	2.23 ± 0.038	<0.0001	-0.87 ± 0.016	<0.0001	0.2280	0.8133	***
Browsers	31	1.35 ± 0.781	0.0956	-0.48 ± 0.329	0.1587	0.3373	0.0673	NS
Intermediate feeders	63	2.48 ± 0.180	<0.0001	-1.00 ± 0.111	<0.0001	0.2020	0.5680	NS
Combined	741	2.25 ± 0.035	<0.0001	-0.88 ± 0.016	<0.0001	0.2317	0.8097	***
$\log_{10}$(TSR)								
Grazers	485	2.61 ± 0.029	<0.0001	-1.00 ± 0.013	<0.0001	0.1627	0.9247	NS
Browsers	24	2.15 ± 0.166	<0.0001	-0.79 ± 0.073	<0.0001	0.2237	0.8438	**
Intermediate feeders	63	3.04 ± 0.241	<0.0001	-1.37 ± 0.155	<0.0001	0.2671	0.5618	*
Combined	572	2.53 ± 0.029	<0.0001	-0.97 ± 0.014	<0.0001	0.1873	0.8990	*
$\log_{10}$(TSC)								
Grazers	453	2.78 ± 0.023	<0.0001	-0.96 ± 0.010	<0.0001	0.1277	0.9495	***
Browsers	21	2.25 ± 0.547	0.0006	-0.72 ± 0.225	0.0048	0.2164	0.3493	NS
Intermediate feeders	43	2.95 ± 0.151	0.0001	-1.11 ± 0.095	<0.0001	0.1575	0.7694	NS
Combined	518	2.78 ± 0.021	<0.0001	-0.95 ± 0.010	<0.0001	0.1294	0.9462	***
$\log_{10}$(DEB)	179	0.69 ± 0.103	<0.0001	-0.63 ± 0.045	<0.0001	0.3177	0.5308	***
$\log_{10}$(DRB)	147	1.03 ± 0.041	<0.0001	-0.83 ± 0.019	<0.0001	0.1304	0.9317	***
$\log_{10}$(NEB)	204	1.48 ± 0.070	<0.0001	-1.19 ± 0.030	<0.0001	0.2292	0.8869	***
$\log_{10}$(NRB)	157	1.58 ± 0.031	<0.0001	-1.16 ± 0.014	<0.0001	0.0984	0.9791	***

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

[A] The slope represents the scaling factor (b) based on the $\log_{10}$-transformed linear equation

[B] Test of slope against 1

DEB, duration of eating bouts; DRB, duration of ruminating bouts; N, number of data used; NEB, number of eating bouts; NRB, number of ruminating bouts; RMSE, root mean square error; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

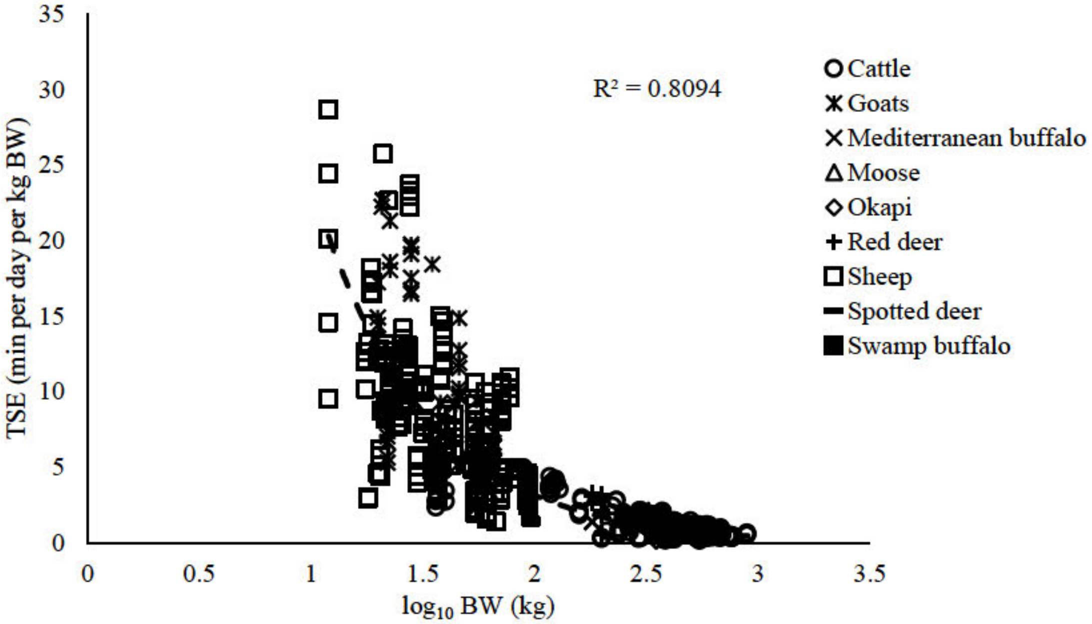


Fig. 4. 2 Relationship between scaled time spent eating and body weight in ruminants.

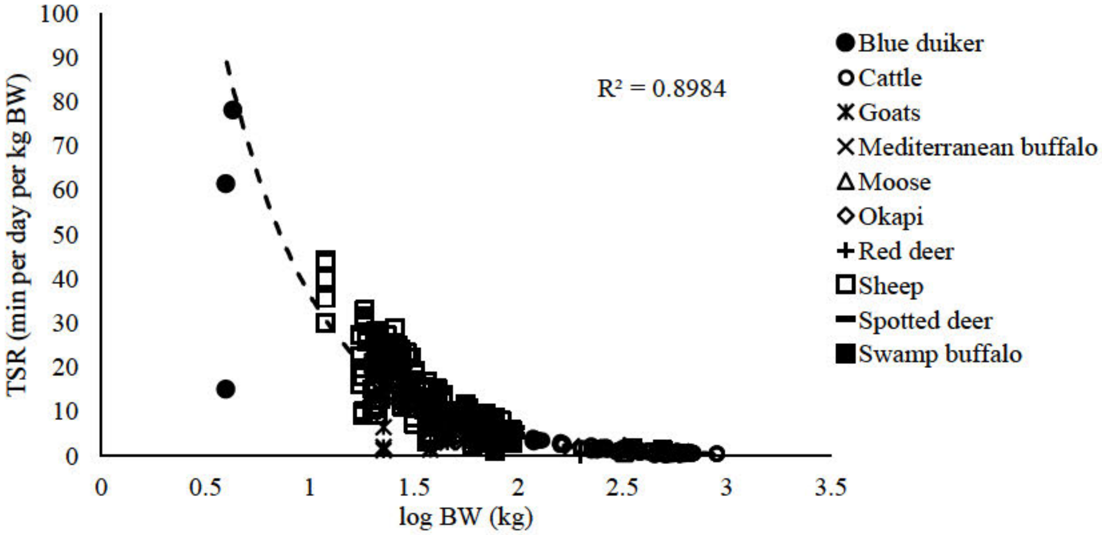


Fig. 4. 3 Relationship between scaled time spent ruminating and body weight in ruminants.

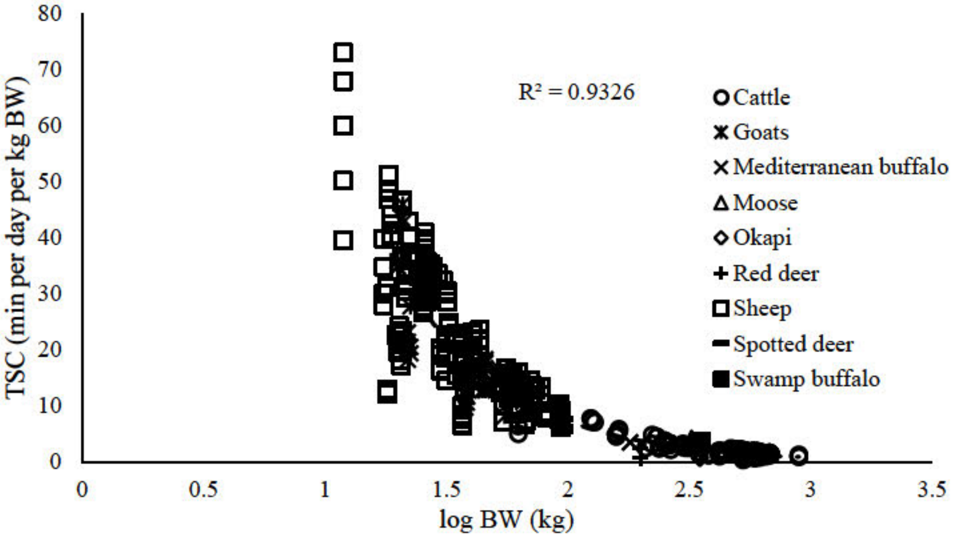


Fig. 4. 4 Relationship between scaled time spent chewing (eating + ruminating) and body weight in ruminants.

Table 4. 10 Assessment of the main factors influencing diurnal feeding behaviour using Akaike's information criterion (AIC) and Cp statistic (C(p)) behaviour of wild and domestic ruminants

Optimal model predictors	nPar	*C(p)*	*AIC*	R^2	N	Relationships of feeding behaviour with model predictors
TSE						
Con, DM, NDF, Ash, DL, BW, DOM and AT	8+1	8.0574	-2580.63	0.8935	741	$2.32 - 0.003\times Con - 0.0003\times DM + 0.0004\times NDF + 0.0003\times Ash + 0.0004\times DL - 0.95 \log_{10} BW + 0.05\times DOM + 0.002\times AT$
Con, DM, NDF, Ash, DP, DL, BW, DOM and AT	9+1	8.6927	-2580.02	0.8937	741	$2.32 - 0.003\times Con - 0.0003\times DM + 0.0004\times NDF + 0.0003\times Ash + 0.0003\times DP + 0.0004\times DL - 0.95 \log_{10} BW + 0.05\times DOM + 0.002\times AT$
Con, DM, NDF, Ash, DL, BW, DOM, APL and AT	9+1	9.0247	-2579.68	0.8937	741	$2.32 - 0.003\times Con - 0.0003\times DM + 0.0004\times NDF + 0.0003\times Ash + 0.0004\times DL - 0.95 \log_{10} BW + 0.05\times DOM + 0.01\times APL + 0.002\times AT$
TSR						
Con, DM, NDF, CP, Ash, DP, BW, DOM and AT	9+1	8.7632	-1971.69	0.9113	572	$2.30 + 0.002\times Con - 0.0005\times DM + 0.0003\times NDF - 0.0005\times CP + 0.0006\times Ash + 0.0005\times DP - 0.93 \log_{10} BW - 0.06\times DOM - 0.002\times AT$
Con, NDF, CP, Ash, DP, BW, DOM and AT	8+1	8.8775	-1971.54	0.9109	572	$2.30 + 0.002\times Con + 0.0004\times NDF - 0.0005\times CP + 0.0006\times Ash + 0.0004\times DP - 0.93 \log_{10} BW - 0.07\times DOM - 0.002\times AT$
Con, DM, NDF, CP, Ash, DP, BW, DOM, APL and AT	10+1	10.004	-1970.47	0.9114	572	$2.30 + 0.002\times Con - 0.00005\times DM + 0.0003\times NDF - 0.0005\times CP + 0.0006\times Ash + 0.0004\times DP - 0.93 \log_{10} BW - 0.06\times DOM + 0.01\times APL - 0.002\times AT$
TSC						
Con, DM, NDF, DP, DL, BW, DOM, APL and AT	9+1	9.4827	-2175.77	0.9539	517	$2.81 - 0.0006\times Con - 0.0002\times DM + 0.0003\times NDF + 0.0003\times DP + 0.0002\times DL - 0.99 \log_{10} BW - 0.03\times DOM + 0.01\times APL - 0.001\times AT$
TSI						
Con, DM, NDF, DP, BW, DOM and AT	7+1	5.2807	-2100.05	0.9590	517	$2.82 + 0.001\times Con + 0.0002\times DM - 0.0003\times NDF - 0.0003\times DP - 1.05 \log_{10} BW + 0.04\times DOM + 0.003\times AT$
Con, DM, NDF, BW, DOM and AT	6+1	6.3725	-2098.90	0.9587	517	$2.82 + 0.001\times Con + 0.0002\times DM - 0.0003\times NDF - 1.05 \log_{10} BW + 0.04\times DOM + 0.003\times AT$
Con, DM, NDF, DP, BW, DOM, APL and AT	8+1	6.6513	-2098.69	0.9590	517	$2.82 + 0.001\times Con + 0.0002\times DM - 0.0002\times NDF - 0.0003\times DP - 1.05 \log_{10} BW + 0.04\times DOM + 0.008\times APL + 0.003\times AT$
DEB						
Con, DM, NDF, CP, Ash, DP, DL, BW, DOM, APL and AT	10+1	11.054	-530.224	0.7850	179	$1.58 - 0.006\times Con - 0.0005\times DM - 0.0004\times NDF - 0.001\times CP + 0.004\times Ash - 0.0007\times DP - 0.0009\times DL - 0.80 \log_{10} BW - 0.19\times DOM + 0.06\times AT$
DRB						
Con, NDF, Ash, DL, BW and DOM	6+1	4.6815	-641.99	0.9531	147	$0.91 - 0.002\times Con + 0.0003\times NDF + 0.0003\times Ash - 0.0003\times DL - 0.78 \log_{10} BW + 0.15\times DOM$
Con, DM, NDF, Ash, DL, BW and DOM	7+1	5.0674	-641.92	0.9536	147	$0.87 - 0.002\times Con + 0.00006\times DM + 0.0002\times NDF + 0.0003\times Ash - 0.0003\times DL - 0.77 \log_{10} BW - 0.13\times DOM$
Con, NDF, Ash, BW and DOM	5+1	5.5397	-640.97	0.9521	147	$0.91 - 0.002\times Con + 0.0003\times NDF + 0.0003\times Ash - 0.80 \log_{10} BW - 0.16\times DOM$

nPar, number of parameters for each model is the number independent variables +1; APL: animal production level; AT, ambient temperature; BW, body weight; Con, concentrate; CP, crude protein; DEB, duration of eating bouts; DL: days in lactation; DM: dry matter; DOM, degree of maturity; DP: days pregnant; DRB, duration of ruminating bouts; NDF, neutral detergent fibre; NEB, number of eating bouts; NRB, number of ruminating bouts; RMSE, root mean square error; TSC, time spent chewing; TSE, time spent eating; TSR, time spent ruminating.

Table 4. 11 Effects of feeding type and ruminant type on diurnal feeding behaviour of browsing and grazing wild and domestic ruminants

Effect of ruminant type		$\log_{10}$ transformed feeding behaviour (min/d/kg BW)						$\log_{10}$ transformed (/d)	
Grazers	BW (kg)	TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Cattle	455	0.48 ± 0.048	0.37 ± 0.050	0.67 ± 0.027	0.84 ± 0.034	-0.88 ± 0.095	-0.55 ± 0.084	1.03 ± 0.077	1.25 ± 0.117
Mediterranean buffalo	513	0.35 ± 0.197	0.34 ± 0.147	0.67 ± 0.102	0.87 ± 0.109	-	-	1.10 ± 0.227	1.20 ± 0.183
Sheep	46.4	0.12 ± 0.057	0.71 ± 0.043	0.92 ± 0.024	0.64 ± 0.028	-0.60 ± 0.129	-0.85 ± 0.078	1.08 ± 0.123	1.22 ± 0.130
Swamp buffalo	426	0.39 ± 0.106	0.50 ± 0.062	0.68 ± 0.036	0.82 ± 0.042	-1.02 ± 0.119	-0.37 ± 0.125	0.96 ± 0.082	1.22 ± 0.134
Browsers									
Blue duiker		-	1.06 ± 0.205	-	-	-	-2.28 ± 0.221	-	1.02 ± 0.399
Moose	325	0.51 ± 0.213	0.69 ± 0.251	0.87 ± 0.118	0.45 ± 0.124	-	-	-	-
Okapi	350	-0.50 ± 0.23	0.23 ± 0.198	0.31 ± 0.119	1.08 ± 0.124	-	-	-	-
Intermediate feeders									
Goats	39.1	0.10 ± 0.062	0.65 ± 0.054	0.91 ± 0.029	0.69 ± 0.032	-0.48 ± 0.187	-0.97 ± 0.096	0.90 ± 0.181	0.93 ± 0.166
Red deer	192	0.24 ± 0.174	-0.47 ± 0.171	0.30 ± 0.160	1.03 ± 0.140	-0.49 ± 0.167	-	0.73 ± 0.183	-
Spotted deer	96.5	-0.40 ± 0.22	0.99 ± 0.218	1.02 ± 0.127	0.67 ± 0.142	-	-	-	-
Significance		***	***	***	***	NS	***	*	***
Effect of feeding type									
Grazers	297	0.32 ± 0.021	0.55 ± 0.018	0.80 ± 0.012	0.73 ± 0.012	-0.78 ± 0.037	-0.70 ± 0.018	1.05 ± 0.036	1.24 ± 0.027
Browsers	232	0.09 ± 0.110	0.53 ± 0.113	0.68 ± 0.070	0.79 ± 0.073	-0.05 ± 0.235	-1.97 ± 0.203	0.56 ± 0.206	1.23 ± 0.275
Intermediate feeders	42.3	0.29 ± 0.037	0.44 ± 0.041	0.78 ± 0.019	0.78 ± 0.017	-0.74 ± 0.076	-0.79 ± 0.059	0.90 ± 0.079	0.98 ± 0.047
Significance		NS	*	NS	**	**	***	*	***

BW, body weight; DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating.

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 4. 12 Effects climatic region on diurnal feeding behaviour of browsing and grazing wild and domestic ruminants

Effect of climatic type		$\log_{10}$ transformed feeding behaviour (min/d/kg BW)						$\log_{10}$ transformed (/d)	
Tropical climates	BW (kg)	TSE	TSR	TSC	TSI	DEB	DRB	NEB	NRB
Af	47.6	0.20 ± 0.107	0.71 ± 0.096	0.92 ± 0.046	0.54 ± 0.045	-0.84 ± 0.266	-0.40 ± 0.171	1.20 ± 0.211	1.31 ± 0.178
Am	68.3	0.25 ± 0.115	0.57 ± 0.093	0.81 ± 0.056	0.71 ± 0.058	-	-	-	-
Aw	202	0.39 ± 0.063	0.61 ± 0.051	0.90 ± 0.031	0.63 ± 0.032	-0.83 ± 0.138	-0.58 ± 0.081	1.27 ± 0.077	1.43 ± 0.056
Arid climates									
BSh	121	0.26 ± 0.084	0.32 ± 0.059	0.77 ± 0.042	0.76 ± 0.043	-0.90 ± 0.207	-	0.80 ± 0.157	-
BSk	620	0.43 ± 0.220	0.27 ± 0.172	0.64 ± 0.107	0.88 ± 0.115	-	-	-	-
BWh	242	0.38 ± 0.150	0.48 ± 0.168	0.78 ± 0.107	0.76 ± 0.111	-	-	1.14 ± 0.181	1.16 ± 0.122
Temperate climates									
Cfa	205	0.24 ± 0.051	0.54 ± 0.040	0.76 ± 0.025	0.77 ± 0.022	-0.67 ± 0.206	-0.71 ± 0.078	1.06 ± 0.146	1.05 ± 0.086
Cfb	354	0.36 ± 0.038	0.56 ± 0.030	0.78 ± 0.020	0.75 ± 0.019	-0.75 ± 0.120	-0.69 ± 0.037	1.00 ± 0.064	1.22 ± 0.046
Csa	231	0.35 ± 0.090	0.49 ± 0.087	0.77 ± 0.051	0.78 ± 0.051	-1.26 ± 0.203	-	1.01 ± 0.163	-
Csb	70.1	0.41 ± 0.162	0.47 ± 0.133	0.76 ± 0.106	0.75 ± 0.111	-	-1.48 ± 0.230	-	2.38 ± 0.023
Cwa	32.3	0.37 ± 0.125	0.61 ± 0.165	0.92 ± 0.105	0.72 ± 0.110	-	-0.60 ± 0.083	1.15 ± 0.183	1.30 ± 0.118
Cwb	609	0.17 ± 0.873	0.41 ± 0.216	0.74 ± 0.151	0.83 ± 0.152	0.13 ± 1.049	-0.77 ± 0.297	0.15 ± 0.349	1.00 ± 0.286
Cold climates									
Dfa	730	0.32 ± 0.165	0.50 ± 0.182	0.79 ± 0.109	0.76 ± 0.112	-0.87 ± 0.198	-	0.94 ± 0.132	-
Dfb	242	0.24 ± 0.064	0.56 ± 0.068	0.78 ± 0.041	0.75 ± 0.043	-0.74 ± 0.177	-1.04 ± 0.094	0.95 ± 0.124	1.10 ± 0.102
Dfc	74.7	0.26 ± 0.158	-	-	-	-	-	-	-
Dwa	96.5	-0.05 ± 0.219	0.65 ± 0.225	0.76 ± 0.123	0.81 ± 0.130	-	-	-	-
Significance		NS	*	*	***	NS	***	*	***
Effect of climatic region									
Tropical climates		0.33 ± 0.048	0.62 ± 0.041	0.89 ± 0.024	0.61 ± 0.024	-0.67 ± 0.094	-0.54 ± 0.076	1.21 ± 0.070	1.38 ± 0.038
Arid climates		0.29 ± 0.067	0.34 ± 0.051	0.76 ± 0.035	0.77 ± 0.036	-0.71 ± 0.158	-	0.87 ± 0.126	1.19 ± 0.085
Temperate climates		0.32 ± 0.027	0.54 ± 0.022	0.77 ± 0.014	0.77 ± 0.014	-0.76 ± 0.057	-0.70 ± 0.032	0.98 ± 0.048	1.20 ± 0.023
Cold climates		0.23 ± 0.052	0.55 ± 0.058	0.78 ± 0.036	0.76 ± 0.037	-0.81 ± 0.144	-1.16 ± 0.106	0.93 ± 0.085	1.17 ± 0.068
Significance		NS	***	***	***	NS	**	*	***

BW, body weight; DEB, duration of eating bouts; DRB, duration of ruminating bouts; NEB, number of eating bouts; NRB, number of ruminating bouts; TSC, time spent chewing; TSE, time spent eating; TSI, time spent idling; TSR, time spent ruminating, Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season; Dwa, cold climate with dry winter and hot summers (Dwa)

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

4.3.3 Modelling of diurnal feeding behaviour

Tables 4.13 and 4.14 give the animal, diet and environmental attributes used in model training and testing, respectively, for time spent eating and ruminating. The training dataset for TSE (Table 4.13) comprised of 518 observations of ruminants with variable physiological characteristics (TSE: 381.9 ± 169.01 min/d; BW: 272.5 ± 233.27 kg; DOM: 0.70 ± 0.322; APL: 1.5 ± 0.70), consuming diets of a wide range of qualities (DM: 547.7 ± 286.38 g/kg; NDF: 481.3 ± 136.22 g/kg; CP: 148.1 ± 56.91 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 15.2 ± 9.48°C). Observations used in testing the model to predict TSE comprised 223 observations of ruminants with variable physiological characteristics (TSE: 364.0 ± 174.12 min/d; BW: 274.3 ± 238.53 kg; DOM: 0.69 ± 0.322; APL: 1.6 ± 0.75), consuming diets of variable nutritional qualities (DM: 551.3 ± 279.78 g/kg; NDF: 478.0 ± 138.03 g/kg; CP: 155.7 ± 64.64 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 15.1 ± 8.99°C).

The training dataset for TSR (Table 4.14) comprised of 401 observations of ruminants with variable physiological characteristics (TSR: 415.1 ± 134.59 min/d; BW: 235.1 ± 239.78 kg; DOM: 0.65 ± 0.325; APL: 1.5 ± 0.76), consuming diets of a wide range of qualities (DM: 579.3 ± 273.69 g/kg; NDF: 500.9 ± 130.63 g/kg; CP: 145.3 ± 67.06 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 16.4 ± 8.85°C). Observations used in testing the model to predict TSR comprised of 172 observations of ruminants with variable physiological characteristics (TSR: 420.7 ± 137.51 min/d; BW: 252.0 ± 252.81 kg; DOM: 0.68 ± 0.357; APL: 1.5 ± 0.73), consuming diets of variable nutritional qualities (DM: 592.5 ± 286.35 g/kg; NDF: 491.1 ± 139.37 g/kg; CP: 148.8 ± 50.62 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 16.3 ± 9.14°C).

Developed models accounted for 95% (TSE), 90% (TSR), 93% (DEB), 93% (DRB), 78% (NEB) and 90% (NRB) of the variation in prediction of feeding behaviour (Table 6.3). On testing the model with an independent dataset, the models attained 87% (TSE), 62% (TSR), 93% (DEB), 83% (DRB), 82% (NEB) and 77% (NRB) precision in predicting feeding behaviour. There were a few outliers observed in prediction of feeding behaviours using both training and testing datasets. Time spent eating was over-predicted by 3-fold for Red deer, while TSE was under-predicted for sheep (Fig. 4.6). The Random Forest model over-predicted TSR by cattle (Fig. 4.7), blue duiker by 4-fold and sheep (Fig. 4.8). The DEB was under-predicted 2-fold for sheep (Fig. 4.9), while DRB by blue duikers was over-predicted 6-fold (Fig. 4.11). The number of eating bouts was both under- and over-predicted for cattle (Fig.

4.13).

A plot of residuals against the predicted TSE gave the equation: Y = -22 (± 4.5) + 0.1 (± 0.01) X (R^2 = 0.05; RSE = 38.7). The plot of residuals against the predicted TSR gave the equation: Y = -66 (± 8.4) + 0.2 (± 0.02) X (R^2 = 0.14; RSE = 43.22). The plot of residuals against the predicted DEB gave the equation: Y = -3.6 (± 1.49) + 0.1 (± 0.03) X (R2 = 0.04; RSE = 9.9). A plot of residuals against the predicted DRB gave the equation: Y = -3.1 (± 0.84) + 0.1 (± 0.03) X (R^2 = 0.12; RSE = 2.3). A plot of residuals against the predicted NRB gave the equation: Y = -1.5 (± 0.64) + 0.1 (± 0.03) X (R^2 = 0.04; RSE = 1.8). The intercepts and slopes of the residual plots for TSE, TSR, DEB, DRB and NRB were different ($P < 0.05$) from zero, showing that the models had a mean and linear bias.

A plot of residuals against the predicted NEB gave the equation: Y = -0.7 (± 0.67) + 0.04 (± 0.047) X (R^2 = 0.00; RSE = 3.9). The intercept (p = 0.339) and slope (p = 0.304) of the residual plot for NEB were not different from zero, showing that the model had no mean and linear bias.

Table 4. 13 Summary statistics of animal and feed attributes of animals used in training and testing the model for predicting time spent eating

		Training dataset for time spent eating (mean ± SD)						
Ruminant type	N	TSE (min/d)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	APL	BW (kg)	AT (°C)
Cattle	263	428 ± 167.5	477 ± 291.4	453 ± 142.6	154 ± 58.8	1.8 ± 0.80	456 ± 162.1	13 ± 8.2
Goats	53	366 ± 139.4	596 ± 230.0	453 ± 134.5	148 ± 43.9	1.4 ± 0.44	42 ± 16.4	18 ± 8.1
Mediterranean buffalo	7	246 ± 20.4	650 ± 42.9	530 ± 31.0	119 ± 14.7	1	486 ± 208.2	30 ± 1.0
Moose	10	594 ± 45.7	304	442	162	1	324.5	-13 ± 12.4
Okapi	2	102 ± 87.5	890	470	170	1	350	14.3
Red deer	6	532 ± 100.2	445 ± 219.0	509 ± 62.4	161 ± 24.8	1	190 ± 11.0	13 ± 6.9
Sheep	168	307 ± 144.7	653 ± 271.2	527 ± 119.9	142 ± 60.0	1.2 ± 0.36	46 ± 25.0	18 ± 8.1
Spotted deer	3	133 ± 11.3	478.5	432.8	149.0	1.2 ± 0.13	96.5	15 ± 11.8
Swamp buffalo	6	467 ± 210.3	564 ± 344.1	683 ± 44.2	68 ± 0.1	1.2 ± 0.21	426 ± 74.5	16 ± 7.7
		Testing dataset for time spent eating (mean ± SD)						
Cattle	112	389 ± 175.6	457 ± 269.0	443 ± 129.7	162 ± 52.0	1.9 ± 0.86	464 ± 168.3	13 ± 9.0
Goats	18	342 ± 154.3	596 ± 248.8	505 ± 157.6	150 ± 39.3	1.4 ± 0.50	42 ± 16.0	17 ± 7.8
Mediterranean buffalo	2	253 ± 9.6	625	512	128	1	608	29 ± 0.1
Moose	4	617 ± 64.8	304	442	162	1	324.5	-4 ± 13.7
Okapi	1	47	890	470	170	1	350	14.3
Red deer	6	474 ± 191.4	445 ± 219.0	509 ± 62.4	161 ± 24.8	1	193 ± 10.3	13 ± 6.9
Sheep	77	318 ± 157.1	694 ± 251.7	517 ± 143.0	150 ±86.5	1.2 ± 0.32	45 ± 23.7	19 ± 6.6
Spotted deer	1	135	479	433	149	2.2	96.5	7.1
Swamp buffalo	2	455 ±253.0	564 ± 444.2	683 ± 57.1	68 ± 0.1	1.2 ± 0.27	426 ± 96.2	16 ± 9.9

Table 4. 14 Summary statistics of animal and feed attributes of animals used in training and testing the model for predicting time spent ruminating

	Training dataset for time spent ruminating (mean ± SD)							
Ruminant type	N	TSR (min/d)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	APL	BW (kg)	AT (°C)
Blue duiker	2	291 ± 63.6	250 ± 71.4	399 ± 128.7	176 ± 14.1	1.0 ± 0.001	4 ± 0.2	7.5
Cattle	160	415 ± 105.9	459 ± 255.5	467 ± 122.5	151 ± 59.7	2.0 ± 0.10	469 ± 182.6	17 ± 7.09
Goats	58	320 ± 118.8	665 ± 238.3	524 ± 162.0	133 ± 51.3	1.2 ± 0.34	36 ± 14.4	16 ± 8.33
Mediterranean buffalo	5	465 ± 39.9	642 ± 39.3	524 ± 28.4	122 ± 13.5	1	523 ± 190.8	29 ± 0.37
Moose	11	530 ± 181.0	304	442	162	1	325	-9 ± 13.3
Okapi	2	290 ± 41.7	890	470	170	1	350	14.3
Red deer	2	75 ± 44.0	892	636	110	1	200	25 ± 0.1
Sheep	153	439.8699	688 ± 252.7	525 ± 123.0	146 ± 81.9	1.1 ± 0.27	46 ± 25.5	18 ± 7.7
Spotted deer	2	507	479	433	149	1.6 ± 0.82	97	13 ± 7.7
Swamp buffalo	6	622.32	564 ± 344.1	683 ± 44.2	68 ± 0.1	1.2 ± 0.21	426 ± 74.5	16 ± 7.7
	Testing dataset for time spent ruminating (mean ± SD)							
Blue duiker	1	60	230	125	63	1.0	4	7.5
Cattle	72	409 ± 115.5	480 ± 271.4	460 ± 130.2	163 ± 54.5	1.9 ± 0.88	490 ± 184.0	15 ± 7.32
Goats	14	359 ± 133.0	694 ± 264.9	532 ± 156.2	137 ± 54.2	1.1 ± 0.27	38 ± 15.5	15 ± 8.54
Mediterranean buffalo	4	437 ± 43.0	646 ± 44.0	528 ± 31.8	121 ± 15.1	1	501 ± 213.4	30 ± 1.28
Moose	3	593 ± 49.8	304	442	162	1	325	-19 ± 8.29
Okapi	1	179	890	470	170	1	350	14.3
Sheep	73	438 ± 148.9	698 ± 271.5	515 ± 141.1	141 ± 44.7	1.2 ± 0.37	43 ± 23.1	18.8 ± 7.35
Spotted deer	2	447 ± 20.5	479	433	149	1.3 ± 0.05	97	14 ± 16.26
Swamp buffalo	2	619 ± 68.6	564 ± 444.2	683 ± 57.1	68 ± 0.1	1.2 ± 0.27	426 ± 96.2	16 ± 9.90

Table 4. 15 Comparison of the equations for linear regression between observed (Y) and predicted (X) feeding behaviour for Random Forest model

		Parameter estimates					
Dataset	N	Intercept	$P_{\text{intercept}}$	Slope	P_{slope}	RSE	R^2 value
		Time spent eating (min/d)					
Training	518	39.38 ± 3.880	p<0.001	0.90 ± 0.009	p<0.001	35.71	0.9475
Testing	223	-13.77 ± 10.604	NS	1.03 ± 0.027	p<0.001	62.48	0.8712
Combined	741	-19.15 ± 4.519	p<0.001	1.05 ± 0.011	p<0.001	47.08	0.9240
		Time spent ruminating (min/d)					
Training	401	-66.20 ± 8.440	p<0.001	1.16 ± 0.020	p<0.001	43.22	0.8969
Testing	172	-53.57 ± 29.146	NS	1.14 ± 0.068	p<0.001	84.90	0.6188
Combined	573	-62.94 ± 9.975	p<0.001	1.16 ± 0.023	p<0.001	58.78	0.8118
		Duration of eating bouts (min/d)					
Training	125	-3.59 ±1.487	p=0.0171	1.06 ± 0.026	p<0.001	9.88	0.9314
Testing	55	-7.59 ± 2.662	p<0.001	1.18 ± 0.045	p=0.006	11.43	0.9271
Combined	180	-4.79 ± 1.325	p<0.001	1.10 ± 0.023	p<0.001	10.48	0.9280
		Duration of ruminating bouts (min/d)					
Training	102	-3.11 ± 0.839	p<0.001	1.12 ± 0.031	p<0.001	2.315	0.9268
Testing	45	-0.65 ± 1.868	NS	1.04 ± 0.070	p<0.001	3.200	0.8326
Combined	147	-2.41 ± 0.806	p<0.001	1.10 ± 0.030	p<0.001	2.618	0.9009
		No. of eating bouts (/d)					
Training	142	-0.67 ± 0.697	NS	1.05 ± 0.047	p<0.001	3.993	0.7798
Testing	62	0.55 ± 0.878	NS	0.94 ± 0.057	p<0.001	3.250	0.8187
Combined	204	-0.30 ± 0.554	NS	1.02 ± 0.037	p<0.001	3.783	0.7890
		No. of ruminating bouts (/d)					
Training	109	-1.45 ± 0.646	p<0.05	1.08 ± 0.034	p<0.001	1.815	0.9044
Testing	48	0.48 ± 1.424	NS	0.96 ± 0.077	p<0.001	2.400	0.7664
Combined	157	-0.98 ± 1.047	NS	1.05 ± 0.032	p<0.001	2.015	0.8707

NS: not significant; RSE: residual standard error

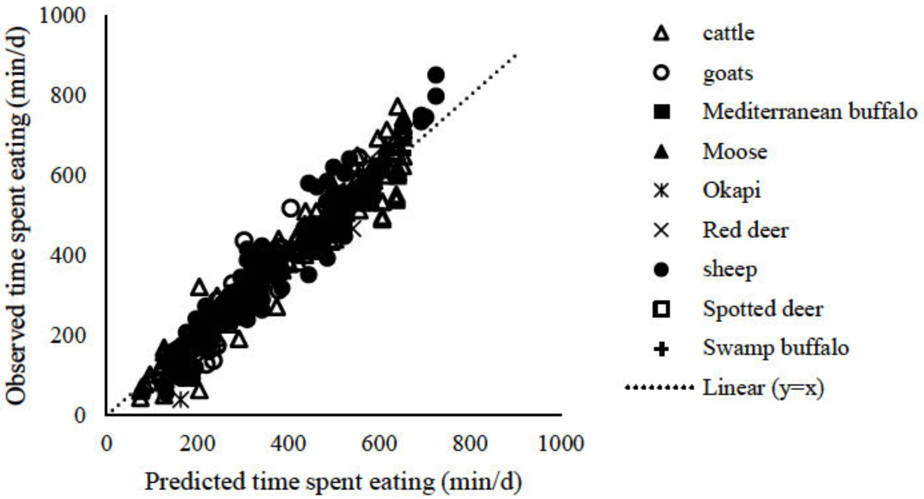


Fig. 4. 5 Relationship between the observed and predicted time spent eating during training of Random Forest model.

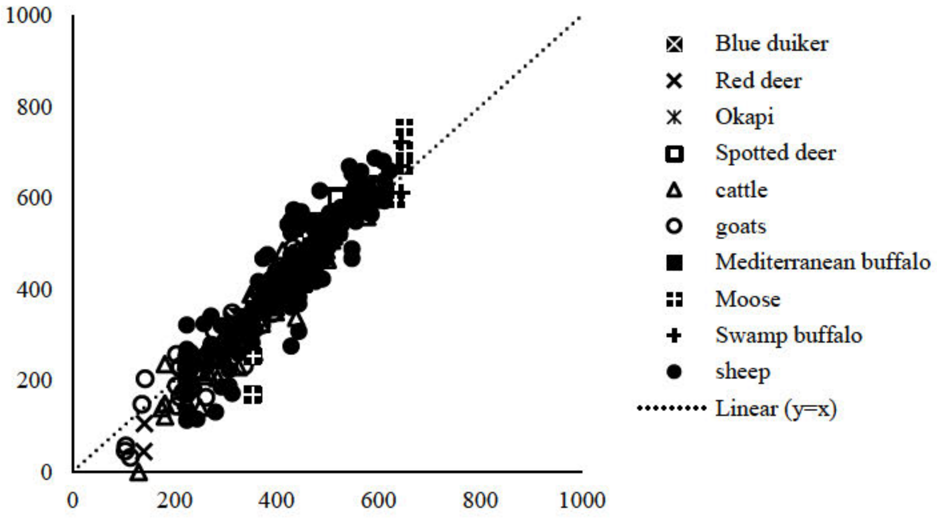


Fig. 4. 7 Relationship between the observed and predicted time spent ruminating during training of Random Forest model.

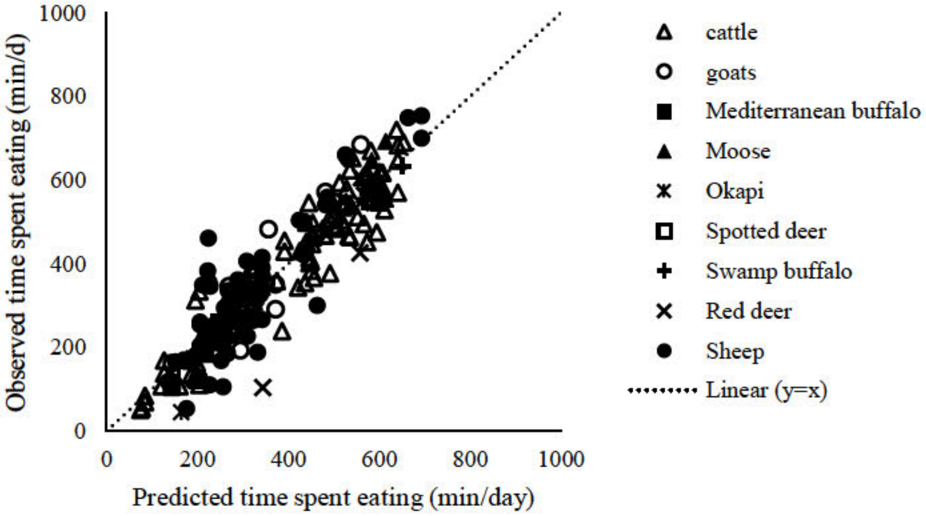


Fig. 4. 6 Relationship between the observed and predicted time spent eating during testing of Random Forest model.

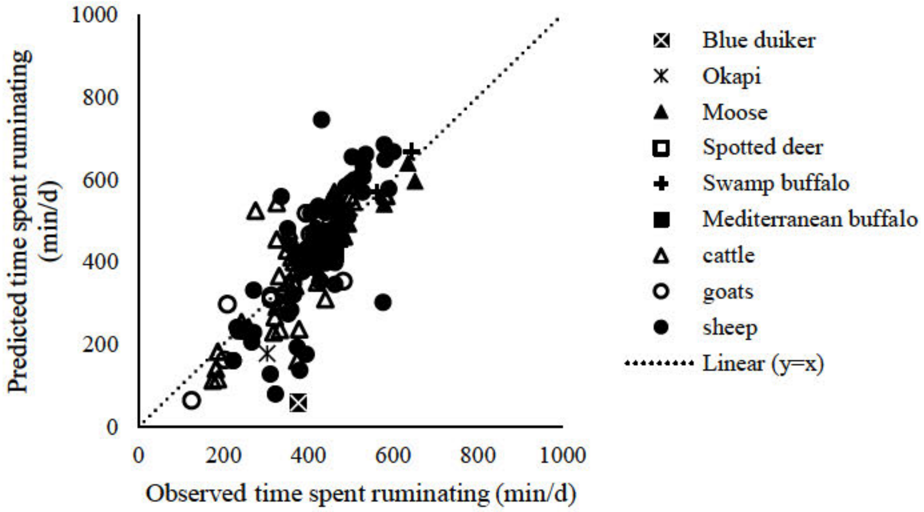


Fig. 4. 8 Relationship between the observed and predicted time spent ruminating during testing of Random Forest model.

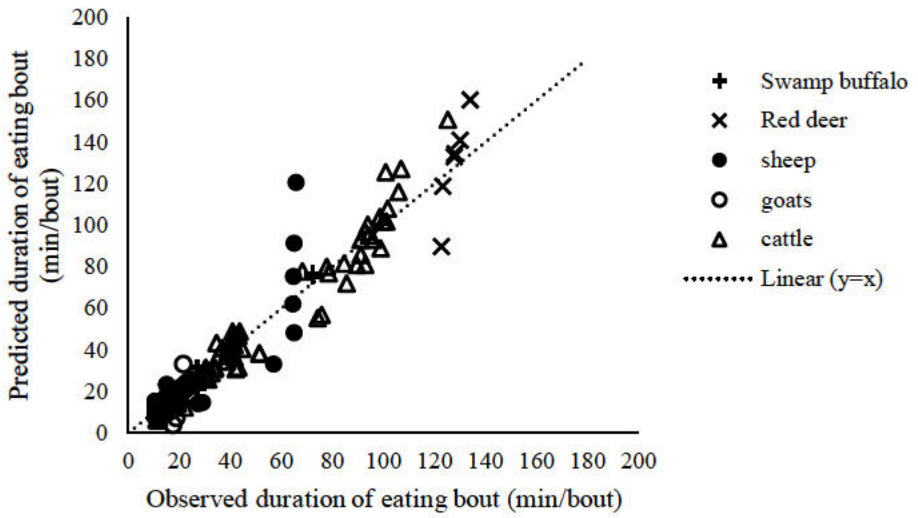


Fig. 4. 9 Relationship between the observed and predicted duration of eating bouts during training of Random Forest model.

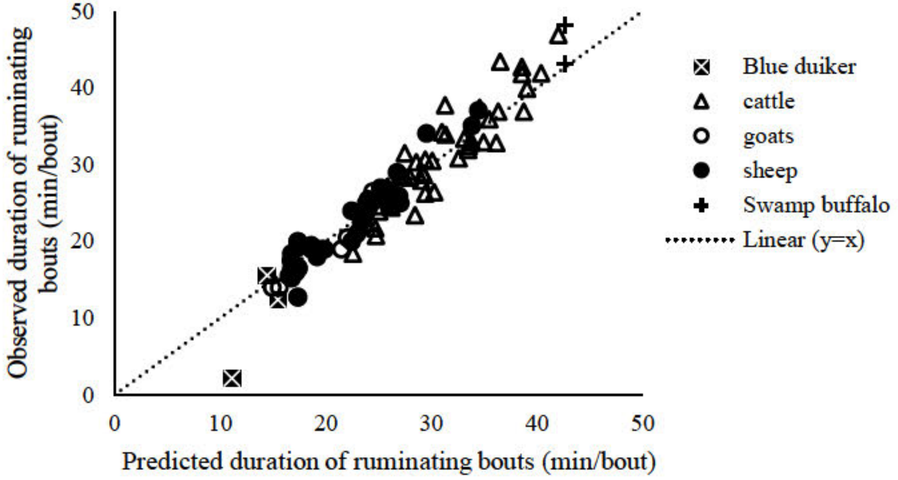


Fig. 4. 11 Relationship between the observed and predicted duration of ruminating bouts during training of Random Forest model.

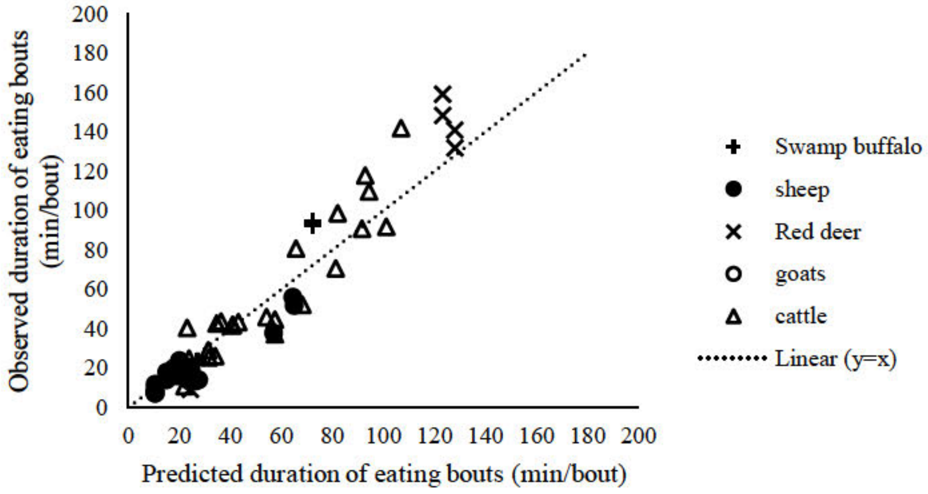


Fig. 4. 10 Relationship between the observed and predicted duration of eating bouts during testing of Random Forest model.

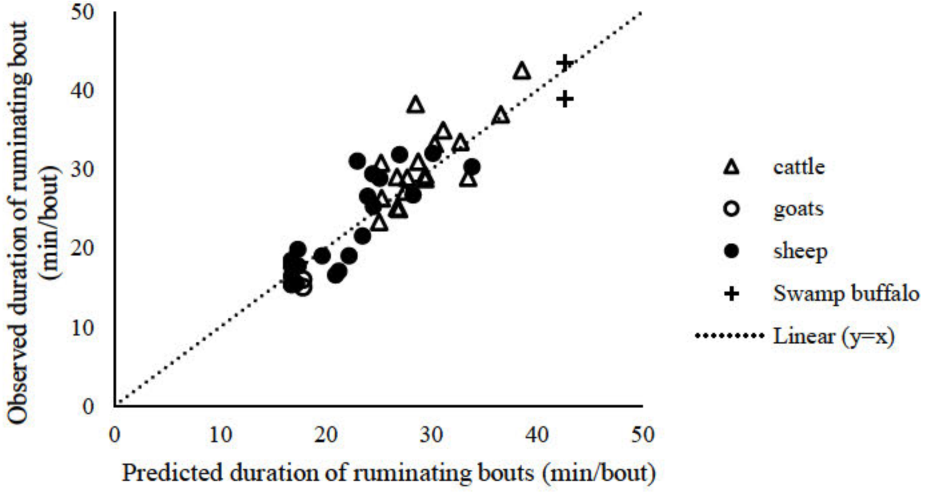


Fig. 4. 12 Relationship between the observed and predicted duration of ruminating bouts during testing of Random Forest model.

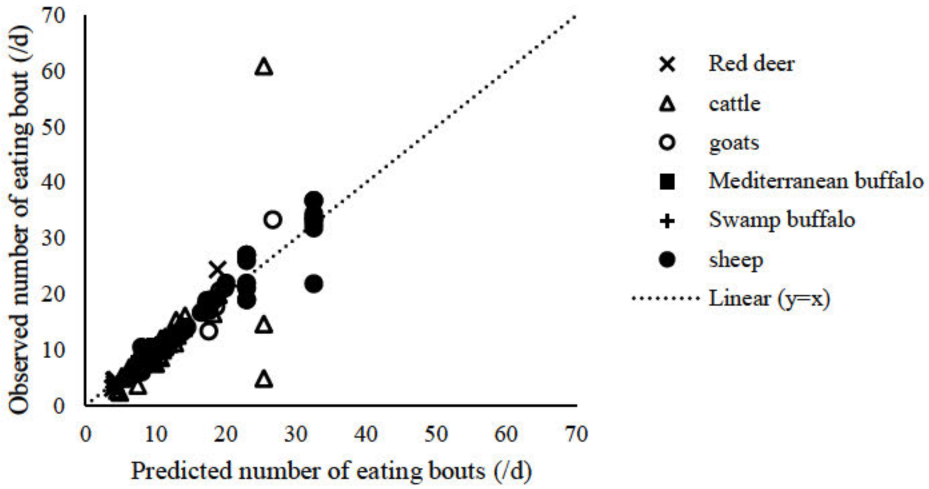


Fig. 4. 13 Relationship between the observed and predicted number of eating bouts during training of Random Forest model.

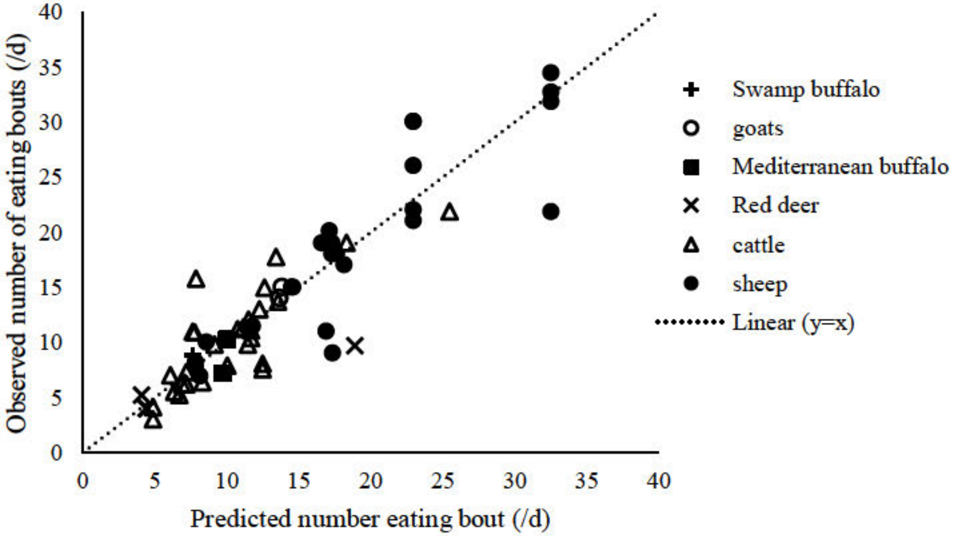


Fig. 4. 14 Relationship between the observed and predicted number of eating bouts during testing of Random Forest model.

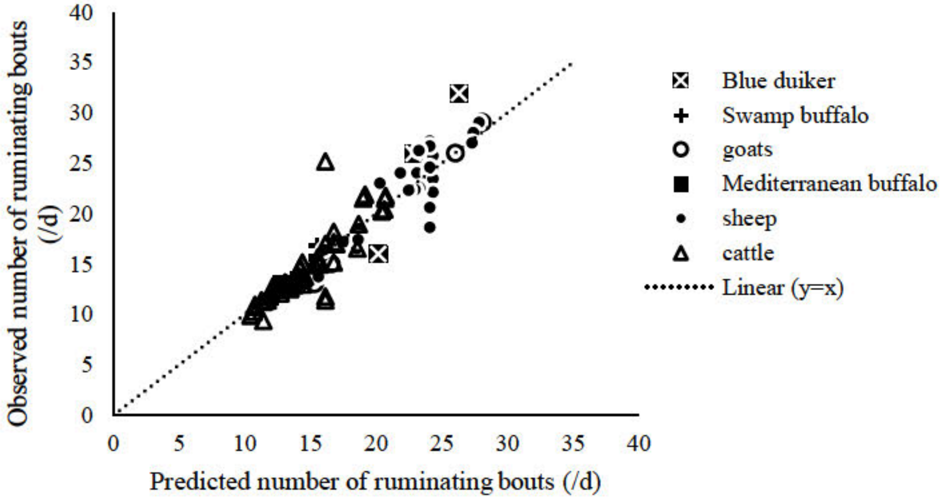


Fig. 4. 15 Relationship between the observed and predicted number of ruminating bouts during training of Random Forest model.

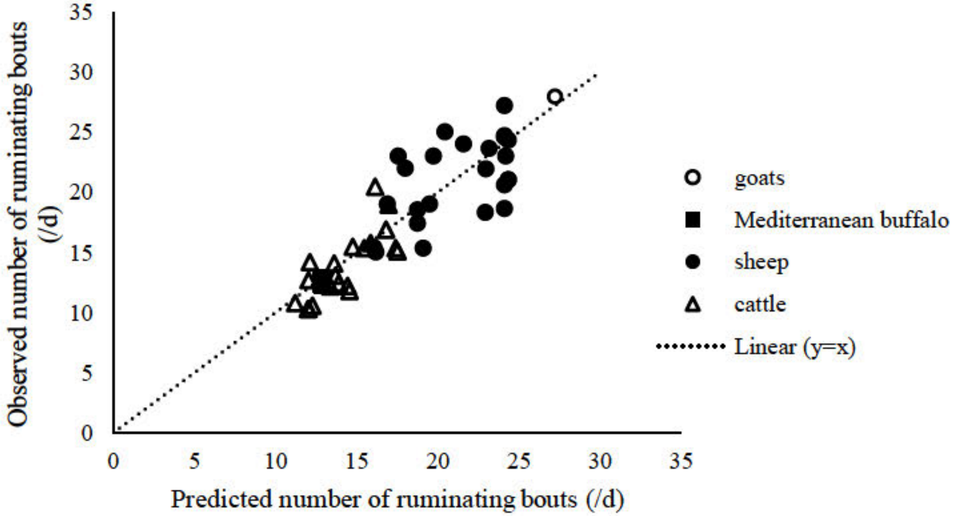


Fig. 4. 16 Relationship between the observed and predicted number of ruminating bouts during testing of Random Forest model.

4.4 Discussion

4.4.1 Daytime and night-time feeding behaviour patterns

The effect of photoperiod and scotoperiod on times spent on eating and ruminating is confirmed in multiple studies. Some of these studies (Rook and Huckle 1997; Macmillan et al. 2018) have attributed differences in diurnal feeding behaviour to the ability of ruminants to maintain high levels of vigilance to perceived threat of predation. The isometric scaling of digestive capacity with body weight and the allometric scaling of energy requirements scale allometrically to $BW^{0.75}$ (Geist 1974) puts small ruminants at a disadvantage relative to larger species (Van Soest 1996) in relation to digestive efficiency. Besides this disadvantage, it is plausible that small ruminants have developed adaptive strategies to overcome this disadvantage through modifications of their feeding behaviour and selection of predominantly nutritious aspects of herbage. Some inferences from findings of this meta-analyses will be partially explained using the above-mentioned concepts.

Grazing ruminants eat with their heads positioned downwards reducing their levels of vigilance to the surrounding and increasing their chances of being preyed upon (Rutter et al. 2002), while ruminating positions offer a better chance to increase vigilance. Differences in feeding behaviour brought about by period of day and size of ruminant may be partially explained using the optimal foraging theory. Effects of period of day on allometric scales revealed that the time spent eating became much shorter at night than during the day for large ruminants compared to small ruminants. The larger the ruminant, the more likely it will be preyed on compared to small ruminants based on predictions of the optimal foraging theory (Rodgers et al. 2015). Findings from the meta-analyses revealed that large ruminants prefer to spend less time eating at night probably to avoid partaking in a behaviour that compromises their levels of vigilance at a period of day when predation threat is highest.

It’s unclear why time spent ruminating and chewing became longer in large ruminants during the day than at night where time spent ruminating and chewing were similar for all sizes of ruminants. To improve levels of vigilance at night, it would be expected that large ruminants spend more time ruminating at night than small ruminants as an adaptive strategy. Rumination time during the day became longer in large ruminants than in small ruminants. This relationship supports the predictions according the Bell-Jarman principle that large ruminants because of their large rumen capacity that allow them to consume poor quality roughages are expected to spend more time ruminating. Although the duration and number of rumination bouts become longer in small ruminants during the day, it affirms that rumination efficiency is high in large ruminants.

Small ruminants have a high surface area to volume ratio meaning that they easily lose more heat than large ruminants. Ambient temperatures are normally high during the day than at night, and basal metabolic rates increase with increasing temperature. Although spending long periods of time eating during the day than at night might pose a disadvantage to small ruminants because of high rate of water evaporation, they are adapted to spend more time perceiving, selecting, and eating a better-quality diet than large ruminants during the day. To meet high demands for specific metabolic rates, small ruminants have high mass-specific feed intake rates (Clauss et al. 2013, Muller et al. 2013) compared to large ruminants. Hence, small ruminants would have to spend more time eating during the day compared to large ruminants at a period of the day where there is less threat of predation risk.

Increases in ambient temperature are predicted to decrease eating time in ruminants substantiating findings of Coffey et al. (1992) and Seman et al. (1997). High ambient temperatures above the thermoneutral zone have been implicated in reduced feed intake in ruminants probably to reduce heat increment of feeding (Pent et al. 2010). This trend is contrary to findings where feed intake was not affected by exposing sheep to ambient temperatures that caused heat stress (De et al. 2020), suggesting that sheep developed an adaptive mechanism to maintain intake of high-quality diets. The assumption of a positive relationship between feed intake and time spent eating is not appropriate as total intake is mainly controlled by intake rate, bite frequency and bite size (Pent et al. 2020). Any observed trend in relation to total time spent eating should be viewed as a strategy to counter or maintain adequate levels of intake. The observed negative response of time spent eating with increase in ambient temperature may suggest intake rates, bite size, bite mass and mass quality may increase with ambient temperature as a counter measure to maintain adequate levels of intake. Ketshabile et al. (2019) observed highest intake rates at mid-day when ambient temperatures are expected to be at their highest compared to earlier periods of the day in sheep and goats. High intake rates during the hottest period of the day may be an adaptive strategy to maximise intake, while reducing time spent eating. Our findings are supported by Veldhuis et al. (2020) who observed increased foraging behaviour in herbivores during the hottest periods of the day. These observations are contrary to the expected decreases in eating activities of ruminants exposed to high ambient temperatures that induce heat stress and reduce feed intake (De et al. 2020). At very high ambient temperatures, while the quality of meal increases, the time spent eating, bite frequency and bite size decrease causing overall decrease in feed intake of high-quality feeds.

Times spent ruminating during the day are expected to increase with ambient temperature, as time spent on eating decreases. Time spent ruminating during night-time, however, decreased with an increase in ambient temperature. Our predictions of increased rumination time during the day with increase in ambient temperature are contrary to findings of Gonyou et al. (1979) where cold exposure of cattle increased rumination time. Our prediction that rumination time at night would increase with exposure of ruminants to low ambient temperature are, however, similar to Gonyou et al. (1979) where rumination time increased 3-fold at -20°C compared to 20°C.

Inferences of this meta-analyses projects a negative response of duration of ruminating bouts during the day and at night with increasing ambient temperatures. While a positive response of time spent ruminating during the day was observed, this negative response of duration of rumination suggests the frequency of ruminating bouts are likely to increase with increasing ambient temperatures during the day to balance the total time spent ruminating. These findings show that as the daytime or night-time ambient temperature increases, the duration of rumination bouts are expected to decrease. This suggests that the number of ruminating sessions are expected to increase with ambient temperature and may be important in maintaining adequate rumination times at night. A high frequency of short ruminating sessions at night are likely to be a response to increasing ambient temperature more so for small ruminants.

It is generally accepted that increasing light period increases time spent eating in ruminants (Macmillan et al. 2018), while rumination would tend to occur at night (Gonyou et al. 1979. The response of differentially sized ruminant of varying feeding types to periods of day may be different. Grazers and intermediate feeders spent more time eating during the day than at night, while browsers spent more time eating at night than during the day. These findings suggest that because grazers and intermediate feeders are less vigilant during eating, they prefer to eat during the day when the risk of predation is low. At night when predation risk is high, grazers prefer to increase times spent ruminating and idling allowing high levels of vigilance. Browsers eat browse from trees allowing them to have their heads positioned straight or upwards. This eating posture may well be advantageous for browsers as it allows them to be vigilant during eating unlike grazers. In addition, browse synthesise tannins (astringent and bitter sensation), for which emission may be more during the daytime than at night. Consequently, with respect to browsers, time spent eating tended to be high at night than during the day to increase time spent on a feeding behaviour that improves levels of vigilance during a period when there is high risk of predation. Browsing ruminants eat browse feeds that are fermented faster than grass consumed by grazers, so it would be expected that the number of eating bouts be higher for browsers than grazers (Codron et al. 2019). High number of eating sessions would mean that browsers need to replace the ingesta lost in the rumen more frequently (Codron et al. 2019), which is contrary to our findings. Instead, grazers had high frequency of short duration meals compared to browsers. It is believed that frequency of eating bouts is more under control of period of day and partly of digestive physiology and other animal physiological factors. These findings also showed distinct differences between browsers and grazers in terms of durations of eating bouts, while intermediate feeders tended to fall on the extreme end as grazers. Based on predictions of this meta-analyses, there seems to be significant differences in adaptive feeding behaviour strategies employed by grazers and browsers to differences in period of day. Observations on daytime and night-time ruminating behaviour of browsers was lacking, making it impossible to understand effects of period of day and feeding type interactions on ruminating behaviour, warranting study on the subject.

Ruminants inhabiting arid climates are expected to spend more time eating at night compared to ruminants inhabiting other climates. The author is unaware of studies that have assessed how ruminants in different climatic regions adapt their feeding behaviours. During the day, large ruminants (cattle and buffalo) spent 3 to 4-fold longer ruminating compared to their smaller ruminants (sheep and goats), but time spent ruminating at night increased in smaller ruminants to match rumination times of their large counterparts. Most of the feeding behaviours were similar across climatic regions, except when considering daytime and night-time feeding behaviours in time spent eating and chewing, which may implicate the effect of ambient temperature, period of day and feed quality (selection and richness in tannins) on influencing feeding behaviour. It is recommended that in addition to increasing feeding behaviour variables, duration and number of eating and ruminating bouts should be included, even more of such studies should be done in cold climates for which there was a paucity of data.

4.4.2 Diurnal feeding behaviour patterns

Allometric predictions of the relationship between rumen capacity and body weight concluded that large-sized ruminant herbivores are able to better survive on poor quality roughages than small-size ruminants because of their greater digestive capacity and lower metabolic requirements per unit body weight (Muller et al. 2013). Predictions also suggested that small-sized ruminants can survive in areas where food material is scant because of their lower total metabolic needs and their ability to select nutritious components than large-size ruminants.

Digestive capacity encompasses size of the gut relative to body size and digestive efficiency. Digestive efficiency in ruminants is partly linked to the effectiveness of feed particle size reduction during eating and rumination, making feeding behaviour paramount in understanding digestive efficiency in ruminants. Ruminants can be classified into 2-distinct digestive types (viz. cattle-type and moose-type) (Clauss et al. 2010) and 3-distinct feeding types (viz. grazers, browsers and intermediate feeders) (Hofmann 1989). Studies have shown that differences in time spent on various feeding behaviours including eating and rumination exist amongst the digestion and feeding types (Rutagwenda et al. 1990). These differences may mean that ruminants of different feeding types adapt differently to the quality of diets (feeds) they consume and climatic regions they inhabit. To increase current understanding of adaptation of ruminants to different nutritional environments, allometric relationships of feeding behaviour for different feeding types is required. It is worth noting that short-term prediction of daily feeding behaviour cannot be validated due to variation brought about by diurnal patterns related to diet selection, feed preference, and limitations to digestion (Baumont et al. 2000). In addition, according to the proposed "concept of predation", adoption of particular feeding behaviour in ruminants is related to the extent of vigilance the animal has to its surrounding when engaging on that feeding behaviour. To contextualise this concept the authors suggest two explicit assumptions on the concept: (1) when grazing, ruminants' heads are positioned downwards reducing their levels of vigilance to the surrounding as such increasing chances of being preyed on, unlike browsers which may be facing up or their heads in their natural position when feeding off browse (Rutter et al. 2002) and (2) the smaller the ruminant, the less-likely that it is preyed on compared to large ruminants (Rodgers et al. 2015).

Geist (1974) scaled energy requirements of mammals including ruminants as a function of $BW^{0.75}$ according to the Bell-Jarman principle. Findings from this study showed that total net energy requirements calculated according to AFRC (1993) did not scale to $BW^{0.75}$ but to a higher scale of $BW^{0.96}$ which was not isometric. Inferences based on allometry showed that time spent eating became shorter in large grazers, while remaining similar in small and large browsers and intermediate feeders. Digestive capacity scaled isometric to body weight and energy requirements scaled allometrically to $BW^{0.75}$ (Geist 1974) meaning small ruminants are at a disadvantage relative to larger species (Van Soest 1996). This happens because the specific metabolic rate of small-sized ruminants coupled with their small gut capacity is higher than in large ruminants. This would mean that small ruminants would fail to eat to meet theuir energy requirements when consuming low nutrient dense diets unlike large ruminants; therefore, small ruminants should eat better quality diets to sustain high metabolic rates. To counter this disadvantage, longer times spent eating by small grazers suggests that small grazing ruminants are selective feeders compared to their large counterparts. Longer time spent eating would allow them more time to choose plant parts of better quality to improve nutrient supply. Selective feeding behaviour in small grazing ruminants has been reported from previous works (Pepeta 2019). Feed intake in mammal's scaled to approximately the range $BW^{0.7-0.75}$ (Clauss et al. 2013). Thus, small grazing ruminants must spend much more time eating than large ruminants. Based on the optimal forage theory, large grazing ruminants would prefer to spend less time eating probably to avoid partaking in a behaviour that compromises their levels of vigilance to a perceived threat of predation.

Large and small grazers spent similar times ruminating. Based on inferences of the Bell-Jarman principle, large grazers can better survive on poor quality roughages than small grazing ruminants (Clauss et al. 2013). This suggests that large grazing ruminants would spend more time ruminating poor quality roughage than small grazers. However, allometric findings on grazing and browsing ruminants but not of intermediate feeders seemed not to support this theory. Allometric findings showed that small sized browsing ruminants spent more time ruminating than their large counterparts. Tooth surface area in mammal's scaled to $BW^{0.67}$ (Shipley et al. 1994) implying that the efficiency of chewing during rumination increases with body weight. It would be expected that small browsing ruminants re-chew cud for longer periods to achieve comparative chewing efficiency compared to large browsers. Secondly, competition for feed resources is highest amongst small-size browsers because of their inability to reach good quality herbage compared to large browsers. As a result of competition for feed resources, small browsers may be forced to select and eat diets that are comparatively of lower quality. This would mean that small browsers would have to spend more time ruminating than their large counterparts to improve digestion. Empirical studies (Kaske et al. 2002) on feeding behaviour of domesticated ruminants show that sheep needed 10-fold more chews per unit of neutral detergent fibre intake to match the rumination efficiency of a large ruminant (cattle), partially supporting allometric findings on rumination times observed from this meta-analysis.

Depending on feed availability, intermediate feeders generally tend to be predominantly grazers than they are browsers and may consume diets that are of lower quality than browsers. Large intermediate feeders would be expected to have the capacity to eat large amounts of poor-quality feed relative to small intermediate feeders resulting in high rumen digesta load of dry and wet matter than small intermediate feeders. As an adaptive strategy, large intermediate feeders would be expected to spend more time ruminating than smaller intermediate feeders to improve nutrient extraction and survival from low quality roughages. It was anticipated that rumination time in grazers would follow a similar trend to that of intermediate feeders.

Regardless of feeding type, times spent eating, ruminating, and chewing, and the duration of eating and ruminating bouts become shorter in large ruminants compared to their small-sized counterparts. These findings support the generalisations by Clauss et al. (2013) that large herbivores (ruminants) do not digest feed better than smaller ruminants to increase digestive efficiency but eat more at low digestive efficiencies to make up for any deficits aided by large gut capacity. This is evident from extrapolations from the negative relationship between time spent ruminating and body weight obtained in the allometry performed in this study. The shorter time spent ruminating by large ruminants meant that the frequency of eating and ruminating bouts was high. The high frequency of eating and ruminating bouts, and large surface area for grinding of teeth in large ruminants are adaptations to ensure maximal digestive efficiency. Small ruminants have a better efficiency of digestion because of longer rumination periods than do large ruminants. These findings show that different sized ruminants adapt differently to diets they consume to maximise digestion.

Inferences from these allometric relationships point to the fact that small ruminants spend few but long eating sessions than do large ruminants. A similar inference may be deduced for rumination activities where time spent ruminating becomes shorter in large ruminants, with rumination bouts of high frequency and of short duration compared to smaller ruminants. Based on this study, predictions of the maximal time spent eating, ruminating and chewing was 656, 1024 and 871 min/d, respectively, for a largest extant ruminant with an average body weight of 1250 kg. Minimum time spent eating, ruminating and chewing by the smallest extant ruminant at 2 kg (supposedly the mouse deer based on body weight) were predicted to be 161, 218 and 618 min/d, respectively. Thus, it is proposed that the physiological daily limit for rumination be upgraded from Welch’s (1982) proposed 600 min per day to a maximum of 1024 min per day. Welch’s (1982) proposed limit failed to explain the occurrence of rumination times beyond 600 min/d based on findings by Deswysen and Ehrlein (1981) in sheep fed silage (607 and 653 min/d), Gherardi and Black (1989) in sheep fed wheaten hay-based diets (621, 638, 649, 659, 684, and 687 min/d), Renecker and Hudson (1989) in moose (632, 640, 672, 702, and 754 min/d), Pearson and Smith (1994) in buffalo fed barley straw (612, 668, 670 and 723 min/d), Kaske and Groth (1997) in pregnant ewes (667 and 679 min/d), Mawuenyegah et al. (1997) in sheep fed rice straw (631 min/d), Williams et al. (2000) in cows fed perennial rye grass (607 min/d), Phillips and Rind (2001) in cows fed grass-silage based diets (617 min/d), Hadjigeorgiou et al. (2003) in sheep fed grass hay (627 min/d), Pereira et al. (2013) in sheep fed grass silage-based diets (606 and 618 min/d), Minervino et al. (2014) in sheep fed coast cross hay (668 min/d). It seems that the majority of studies that reported rumination times in excess of 600 min/day were mostly on sheep. The comparison of trends for individual ruminant feeding types was not possible due to a small number of observations for ruminants classified as browsers. Our proposed prediction of a minimum rumination time of 218 min/d fails to explain the rumination time of 0 min/d observed by Bines and Dovey (1970) in cattle fed a 100% concentrate diet formulation which contained very minute levels of structural carbohydrates.

In this study times spent eating and idling are projected to increase, while times spent ruminating and chewing are likely to decrease with an increase in ambient temperature. Decreases in total time spent chewing with increasing ambient temperature suggests that the effect of ambient temperature is more pronounced on rumination than eating. Eating time was not affected by exposure of sheep to ambient temperatures that caused heat stress (De et al. 2020), although predictions of this study suggested that eating time would increase. These observations are contrary to the expectation of a decrease in the eating activity of ruminants exposed to high ambient temperatures that induced heat stress and reduce feed intake (De et al. 2020). It should be noted that the herbivore foraging ecology theory suggests that bite mass is the fundamental unit of intake (Gordon 2003) rather than time spent eating alone. The general consensus that high ambient temperature would decrease feed intake mainly applies to instantaneous increases in ambient temperatures but does not consider whether or not ruminants are adapted to high ambient temperatures. Reduced time spent eating makes sense when used to justify that animals respond to high ambient temperatures by reducing the heat increment of feeding. Although this response is biologically correct, if animals are exposed to long periods of heat stress, they should develop adaptive feeding behaviour strategies to maintain adequate feed intake. We hypothesise that ruminants may either increase time spent eating while reducing intake rates and bite mass (Ferreira et al. 2013) or reduce time spent eating and increase intake rates and bite mass. Based on the trend observed on time spent eating and ambient temperature, it is tempting to suggest that ruminants’ respond to increasing ambient temperature by increasing total time spent eating while reducing intake rates and bite mass to balance intake. Our assumption may be partially supported by findings of Miaron and Christopherson (1992) where feed intake of steers was similar when exposed to AT of -10, 10 and 28°C, meaning that steers in that study managed to balance time spent eating, intake rates and bite mass.

An increase in time spent eating does not necessarily mean that feed intake would increase, but a combination with intake rate, bite size and bite mass would balance intake (Pent et al. 2020). The ability of ruminants exposed to high ambient temperatures to increase time spent eating offers a possible means of increasing intake which may be viewed as a response to a short-term decrease in intake at high ambient temperatures. This increase in time spent eating should be viewed as an adaptive response to counter intake reduction at high ambient temperatures to maintain adequate intake. It appears that with an increase in AT, in order to increase intake, ruminants may reduce comminution through ruminative mastication per unit of intake in order to spend more time eating, similar to observations of Gibb et al. (1999) in lactating cows. This is partially supported by the negative relationship between AT and time spent ruminating, implying that most of comminution is done during eating. Ruminating times tended to be slightly longer for steers exposed to colder temperatures (-10°C and 10°C) compared to those exposed to warmer temperatures of 28°C (Miaron and Christopherson 1992). The negative relationship between AT and rumination time observed in simulations of this study are similar to other works (Miaron and Christopherson 1992; Acatincai et al. 2009; De et al. 2020). These findings suggest that when rumination time is shorter at high ambient temperatures, time spent eating would be expected to be longer at high ambient temperatures as the 2 behaviours are antagonistic, unless otherwise ruminants choose to idle instead of eating. Acatincai et al. (2009) observed a decrease in time spent ruminating (-102 min/day) when cattle were exposed to high ambient temperature of beyond 28°C, although the number of ruminating bouts remained similar.

The projected increases in ambient temperature due to climate change are likely to negatively impact digestive efficiency in ruminants by increasing lignin and NDF content of feed and decreasing potential rumen degradation of feeds (Deroche et al. 2020) and reducing time spent ruminating. There is a high likelihood that as global warming persists, digestive efficiency would be reduced as a result of an overall decrease in time spent chewing and ruminating coupled with a reduction in quality of feeds consumed by ruminants. Time and energy spent eating/chewing will increase but may decrease intake rates and bite size with serious negative consequences on feed intake and productive performance of ruminant livestock. To counter these negative effects, ruminants would need to either become more selective during eating to select better quality plant parts, and increase bite mass, bite frequency and have high frequency of long meals to maintain adequate levels of intake as adaptive feeding behaviours. Small ruminants have lower absolute intake requirements and better water retention efficiency than large ruminants. In this regard, small browsing and grazing ruminants would become more important than large counterparts in areas where global warming is likely to decrease forage quality and quantity. Our findings that small-sized ruminants spent more time eating than their large counterparts, makes small ruminants better adapted to conditions of increasing ambient temperature.

Browsing ruminants showed distinct adaptive feeding behaviours compared to grazers and intermediate feeders. Browsers had the highest duration of eating bouts and lowest number of bouts while an opposite trend was observed for grazers and intermediate feeders. These findings reveal that as a feeding strategy that to balance total time spent eating, browsers adopt to long but few eating bouts, while grazers adopt to high frequency of short eating bouts. Time spent on rumination and duration of ruminating bouts were higher for grazer than browsers, but the number of ruminating bouts were similar for both feeding types. Grazers generally tend to consume feeds or diets with high structural carbohydrate content; hence, they are expected to ruminate for long periods compared to browsers. Browsing ruminants eat browse and select better quality diets that are fermented faster than grass consumed by grazers, so it is expected that the number of eating bouts would be higher for browsers than grazers (Codron et al. 2019). High number of eating sessions would mean that browsers need to replace the feed lost in the rumen more frequently (Codron et al. 2019). Consistent with our prediction, Fomum et al. (2015) observed increased time spent eating and ruminating on high cellulose diets seen in positive relationship between percentage cellulose content of browses and mean browsing time of Nguni goats in the rainy season. Browsers adopt long but few eating bouts, while grazers adopt high frequency of short eating bouts. Instead grazers had high frequency of short duration meals compared to browsers. This study showed distinct difference between browsers and grazers in terms of durations and frequency of eating bouts, while intermediate feeders tended to fall on the extreme end as grazers.

Ruminants inhabiting tropical regions had the longest total length of rumination while it was lowest for ruminants in arid regions. Frequency of ruminating sessions was highest in ruminants from tropical climates and lowest for those inhabiting very cold regions. These findings reveal that ruminants in cold regions spent more hours idling per day evading the cold by being idle or hibernating, or perhaps because their diets are more digestible and do not need to spend more time ruminanting. The high frequency of eating bouts in ruminants inhabiting tropical climates was responsible for the longer eating times in tropical ruminants compared to cold climate ruminants. Feed resources in cold climates is generally scant and sub-zero ambient temperatures make it physiologically challenging for these ruminants to spend long times eating. We recommend that in addition to increasing feeding behaviour variables to include duration and number of eating and ruminating bouts, even more of such studies should be done on browsing ruminants and in arid and cold climates for which there was a paucity of data.

4.4.3 Modelling of diurnal feeding behaviour

Numerous studies have shown that feed properties including CP, NDF and sward height (Fomum et al. 2015; Xiao et al. 2020), plant morphology (Sebata and Ndlovu 2010), animal factors such as metabolisable energy requirements (Xiao et al. 2020), stage of pregnancy and lactation (Kaske and Groth 1997), milk yield and body weight (Brumby 1959), ambient temperature, ruminant type and season (Rutagwenda et al. 1990; Safari et al. 2011) affect feeding behaviour of ruminants. In the current work, 16 variables classified as animal, feed and environmental factors were identified from literature listed above and used as input variables to predict feeding behaviour for ruminants.

4.4.3.1 Performance of Random Forest models in prediction

A performance test on the capability of the Random Forest models in prediction was done using the training and test datasets. A couple of outliers were observed in prediction of feeding behaviours on both datasets. Time spent eating was over-predicted for red deer that inhabited much warmer semi-arid climates in the study of Vasquez et al. (1994) and their observed TSE was shorter compared to observations of red deer from temperate climates. Predictions of TSE for their red deer counterparts inhabiting much cooler temperate climates were more precise. This suggests that the red deer inhabiting semi-arid climates spent less time eating than normal owing to their low tolerance to warm climates. An over-prediction was seen on rumination processes of blue duiker fed on figs (Wenninger and Shipley 2000), sheep grazing on highly digestible white clover pasture (Penning et al. 1995) and cattle that were fed a roughage free diet (Bines and Dovey 1970). The low content of structural carbohydrates in the diet contributed to the observed short time spent on ruminating processes. The predictions show that the model could not capture this variation due to few studies reporting findings on feeding behaviour of ruminants fed concentrate-only and highly digestible diets. The desire to eat is correlated to the frequency of eating bouts. The quantity of rumen digesta load influences the desire to eat (Allen 1996). Cows that had their NEB under-predicted (Lindstrom and Redbo 2000) had their rumen content regulated to stay at 75% of normal feed allotment. The extremely high observed NEB may have been a result of cow’s desire to eat pushed by the increased sensation of hunger forcing them to feed more frequently. Rumen digesta load was not accounted for in model development due to lack of information.

4.4.3.2 Comparison of Random Forests with published models

Quantitative physical features of feeds have been used to develop feeding behaviour prediction equations. Benvenutti et al. (2017) developed non-linear regressions to simulate time spent grazing ($R^2 = 0.64$) and ruminating ($R^2 = 0.52$) by sheep using residual sugarcane height. Sward surface height accounted for 58% of the variation in the daily proportion of TSE and accounted for only 37% of the variation for the proportion of TSR (Penning et al. 1997). Simulations of Baumont et al. (2004) gave good predictions of time spent grazing ($R^2 = 0.98$; standard deviation = 8.9 min; n=4) and ruminating ($R^2 = 0.75$; standard deviation = 61.2 min; n=4) for data reported by Penning et al. (1994), although predicted ruminating time was consistently higher than the observed ruminating time. Feeding behaviour simulation models by Sauvant et al. (1996) accuracy predicted time spent eating (standard deviation = 21.0 min; n=3) and ruminating (standard deviation = 20.03 min; n=3). Models of Penning et al. (1997) and Baumont et al. (2004) provide realistic simulations of feeding behaviour for various types of sheep grazing different types of vegetative swards under continuous and rotational grazing systems.

Numerous attempts have been made to develop prediction models for feeding behaviour using animal factors. The relationship between predicted proportion of time spent feeding on grasses in relation to the observed time using the energy maximising strategy ($R^2 = 0.73$) and sodium maximizing strategy ($R^2 = 0.80$) during feeding gave reasonable predictions, except for the time minimizing strategy ($R^2 = 0.19$) which gave poor predictions (Forchhammer and Boomsma 1995). The accuracy of the Random Forest models was 7% and 14% better than the sodium and energy maximizing strategy models of Forchhammer and Boomsma (1995). Linear regressions of Gregorini et al. (2007) predicted a linear decrease in proportion of time spent eating with increase in rumen digesta load (SEM = 0.0056; $p<0.001$) in cattle. Regression models developed by Brumby (1959) took the form: TSE = 473 – 0.07(BW) + 0.15(Fat corrected milk) (n = 19, mean square = 1798) and TSR = 262 + 0.12(BW) + 0.04(Fat corrected milk) (n = 19, mean square = 936) for prediction of feeding behaviour of Holstein and Jersey cows. Dry matter intake predicted the number of eating ($R^2 = 0.005 – 0.33$) and ruminating ($R^2 = 0.05 – 0.09$) bouts, and duration of ruminating bouts ($R^2 = 0.05 – 0.28$) with lower precision (Kammes and Allen 2012) than the RF models developed in this study.

Simple linear regression equations have been used to predict feeding behaviour using proximate chemical composition of diets eaten by ruminants. Feeding behaviour of sheep predicted from physical effectiveness of NDF and, unfragile dry matter and NDF fractions accounted for 66% – 93% (TSE) and 46% – 78% (TSR) of the variation in prediction of feeding behaviour (Zali et al. 2015). Simple linear equations accounted for 77% of the variation in prediction of time spent browsing by Nguni goats from the percentage cellulose content of browse (Fomum et al. 2015). Rumination time of blue duiker was predicted with an accuracy of 92% using the NDF content of diets fed to duikers (Wenninger and Shipley 2000). The relationship of time spent eating and ruminating with the total energy content of feeds infused in the rumen accounted for 74% and 50% of the variation (Gherardi and Black 1989).

Other studies (Pinho et al. 2016; Almeida et al. 2014) have developed simple linear and non-linear equations to predict feeding behaviour using inclusion levels of diet supplements fed to ruminants. Accuracy of linear and quadratic relationships of feed inclusion levels in predicting TSE ($R^2 = 0.63$) and TSR ($R^2 = 0.71$) by sheep (Pinho et al. 2016) was lower than the accuracy achieved by the random forest models. Inclusion levels of glycerine in heifer diets predicted grazing time ($R^2 = 0.75$), ruminating time $R^2 = 0.99$, eating time at trough ($R^2 = 0.64$), duration of grazing bouts ($R^2 = 0.87$) and duration of eating bout at trough ($R^2 = 0.94$) with high precision (Almeida et al. 2014). The number of grazing bouts and, NRB and DRB could not be predicted from glycine inclusion levels (Almeida et al. 2014). The success of yielding linear and non-linear prediction models of feeding behaviour from feed inclusion levels has been unsuccessful for some studies (Almeida et al. 2014; Nicory et al. 2015; Conceicao et al. 2016).

The models from the studies discussed above give good predictions of feeding behaviour. Because most of the models were developed to make predictions of feeding behaviour for cattle and sheep, their performance in simulation of feeding behaviour for other ruminants remains unknown. Critical roles of the effects of ambient temperature fluctuations and climate type on observed feeding behaviour of ruminants is neglected in most empirical studies. These models and equations should be used with caution especially for prediction of feeding behaviour of ruminant species not included in their range, limiting their use. This study developed models for prediction of time spent eating and ruminating for 10 ruminant species with high accuracy and precision.

4.5 Conclusion

Our study confirmed significant differences in adaptive feeding behaviour strategies employed by grazers and browsers to differences in period of the day. There were distinct differences between browsers and grazers in terms of durations and frequency of eating bouts, while intermediate feeders tended to fall on the extreme end as grazers. We recommend that more studies in understanding daytime and night-time feeding behaviours of ruminants be done for browsers inhabiting cold climates for which there was a paucity of data.

Trends from this study showed that time spent eating and idling are projected to increase, while time spent ruminating and chewing are likely to decrease with increasing ambient temperature. Small-sized ruminants spent more time eating than their large counterparts, making small ruminants better adapted to conditions of increasing ambient temperature. Small browsing and grazing ruminants would become more important than large counterparts in areas where global warming is likely to decrease forage quality and quantity. Browsers spent less time eating, had the highest duration of eating bouts and lowest number of bouts while an opposite trend was observed for grazers and intermediate feeders. Times spent eating, ruminating and chewing, and the duration of eating and ruminating bouts become shorter in large ruminants compared to their small-sized counterparts.

Models in this study accounted for the effects of climate type and ambient temperature in predictions which most studies have not considered. We strongly recommend use of the Random Forest models developed in this study for simulation of feeding behaviour of ruminants.

Chapter 5

Estimation of rumen digestion of forages by ruminants using Random Forests [1, 2]

Abstract

This study developed models to predict degradation parameters in the rumen. Datasets were collected from studies that (1) reported values for in-sacco degradability parameters viz. soluble fraction (a), slowly degradable fraction (b), potential degradability (PD) and rate of degradation (c) of roughages, grains, leaves, stems, fruits and concentrate formulations, and (2) stated diets given to animals fed at ad-libitum. Two datasets were collated, one on studies that used the time-lag model and another on studies that used the no-time lag model in computing degradation parameters. Factors that affect degradability were identified in each of these studies and categorised into (i) diet properties (ii) feed sample properties (iii) ruminant feeding type and (iv) environmental factors. These factors were used as input variables to enable prediction of degradability. Random Forest models were programmed on a 64-bit R version 3.6.2 (Dark and Stormy Night). Each dataset was randomly divided into two subsets: 70% for training and 30% for testing. The no time-lag models attained 88% ("a"), 93% ("b"), 76% ("c") and 90% ("PD") precision in prediction during training. On testing, these models attained 58% ("a"), 52% ("b"), 48% ("c") and 53% ("PD") precision in prediction. Time lag models accounted for 91% ("a"), 84% ("b"), 79% ("c"), 91% ("PD") and 87% (lag) of the variation in prediction during training. On testing, these models attained 64% ("a"), 57% ("b"), 29% ("c"), 52% ("PD") and 59% (lag) precision in prediction. Both sets of models predicted "a", "b", PD and lag with appreciable precision. However, models for prediction of the rate of degradation require improvement.

Key words: Degradability, Fermentation kinetics, nylon bag technique, prediction model, roughages, concentrates

[1] Moyo M, Bhiya ST, Masande K, Nsahlai IV. 2019. Evaluation and prediction of the nutritive value of underutilised forages as potential feeds for ruminants. In book: Forage Groups (Chapter: 6). Ricardo L. Edvan and Edson M. Santos (Editors). IntechOpen: London, United Kingdom. pp 87-106.

[2] Moyo M, Nsahlai IV. 2020. Consequences of increases in ambient temperature and effect of climate type on digestibility of forages by ruminants: a meta-analysis in relation to global warming. Animals, 11(1):172.

5.1 Introduction

Rumen degradation of feeds is vital in determining the digestibility of feeds (Fonseca et al. 1998) and intake (Kibont and Orskov 1993) by ruminants. Extents of rumen fermentation of feedstuff determine the amounts of microbial protein synthesis and by-pass nutrients of dietary origin available for assimilation in the small intestines. The ability to estimate degradation of feeds is an important facet in planning and implementing sustainable feeding strategies to improve the productivity of livestock. The nylon bag procedure (Orskov et al. 1980) is principally used to determine the digestibility of feedstuff in the rumen. Although easy to implement, the nylon bag technique requires rumen fistulation of animals. Availability of experienced veterinarians to carryout fistulation, the prohibitive cost of the fistulation procedure and long-term maintenance of fistulated animals is beyond the financial capacity of most research institutions in developing countries.

The extent of degradation of roughages in the rumen partly depends on rumen ecology, which is mainly determined by the diet fed to animals. Notable previous works (Kibont and Orskov 1993; Shem et al. 1995; Cone et al. 1998; Karsli and Russell 2002) have failed to account for effects of rumen ecology and environmental factors in rumen degradability prediction models. Equations for predicting degradation parameters mainly use properties of feed being degraded as major prediction variables. It is known that the degradation of roughage diets depends on the composition of microbes (bacteria, protozoa and fungi) in the rumen (Bach et al. 2005). Therefore, the potential extent of degradation of roughages in the rumen partly depends on rumen ecology as determined by diets fed to animals and outflow rates of liquid and solid in the rumen (Bach et al. 2005). The duration for incubating feeds in the rumen in degradation studies vary between temperate and tropical regions, suggesting that potential degradability of feeds may be influenced by climate and ambient temperature.

Global temperatures are expected to increase by just over 1 °C per annum, and global warming is projected to reduce forage quality by lowering digestibility and crude protein content of feeds (Polley et al. 2013; Rojas-Downing et al. 2017). Few studies (Christopherson 1976; Kennedy et al. 1976; 1982; Kennedy and Mulligan 1978; Christopherson and Kennedy 1983) have documented the extent to which a unit increase in ambient temperature would decrease forage digestibility. Studies need to simulate how forage quality would respond under future climate change scenarios. The ability to predict how digestibility would be affected by ambient temperature can be a useful tool in planning and implementing strategies of improving feed quality and feeding management to ensure improved growth response of ruminants.

The magnitude of change in the rumen digestibility parameters of feeds as affected by changes in ambient temperature are not well documented. Despite the large number of research publications on the degradation of feeds in the rumen, few attempts have been made to synthesize a global view of the main determinants of degradation. Most studies that have predicted degradability of feedstuffs in the rumen have considered effects of feed properties of the material being degraded in nylon bags on the extent of fermentation. Little emphasis has been made towards considering the effects of diets fed to animals and animal factors on the extent of degradation, which determine the rumen environment. The advent of machine learning techniques provides new ways of developing novel methods to estimate the extents of degradation of feeds in ruminants. This would reduce the use of invasive methods in ruminant nutrition. Modelling of degradation parameters would provide more convenient methods of predicting degradation parameters of feeds for use in predicting total tract digestibility and feed intake.

This study summarized findings across published studies to establish the main determinants of degradation of feeds in the rumen using meta-analysis methodology. The aim of this study was to: (1) evaluate rumen degradation of legume forages (*Colophospermum mopane* leaf meal and pods, Cowpea haulms, *Mucuna pruriens*, cassava peels and *Afzelia quanzensis* legume pods) and *Brassica oleracea var. acephala*, (2) determine the effects of ambient temperature and climate type on rumen digestibility and chemical composition of forages, and (3) to estimate rumen degradation parameters of forages using the Random Forests Model. The explicit hypothesis tested were that: (1) *Brassica oleracea var. acephala* leaves would have higher potential degradability in the rumen than *Colophospermum mopane* leaf meal and pods, Cowpea haulms, *Mucuna pruriens*, cassava peels and *Afzelia quanzensis* legume pods, (2) increases in ambient temperature would decrease forage quality and that climate type would have no effect forage quality, and (3) it is possible to estimate rumen degradation of forages using Random Forest models.

5.2 Materials and methods

5.2.1 Evaluation of the nutritional value of underutilised forages and roughages

Underutilised forage legumes and, forage trees and shrubs (non-leguminous) were collected from various regions. These forages included *Colophospermum mopane* leaves and pods (Mangwe district; 20°36'57.5"S 27°45'39.7"E), and *Brassica oleracea var. acephala* leaves (Bulawayo; 20°09'52.1"S 28°35'00.4"E) harvested in South-western Zimbabwe, and *Afzelia quanzensis* legume pods (Pietermaritzburg; 29°39'45.6"S 30°24'17.9"E) harvested in South Africa.

Eleven commonly used forages (10 forage grasses and 1 legume forage) were collected in KwaZulu-Natal, South Africa. These roughages included cowpea leaves and stems (*Mucuna pruriens*), maize stover, maize leaves, maize stalks (*Zea mays*), wheat straw (*Tritium aestivum*), kikuyu grass (*Pennisetum clandenstinum*), weeping love grass at mature and bloom stages (*Erograstis curvula*), bean straw, veld grass hay (Pietermaritzburg; 29°39'45.6"S 30°24'17.9"E), veld grass hay (Dundee; 28°09'17.2"S 30°12'42.8"E) and veld grass hay (Camperdown; 29°43'40.4"S 30°31'34.9"E). The forage hays were air-dried under a shade at ambient temperature and stored.

Moisture, dry matter (Method 934.01), organic matter and ash content (Method 942.05) of these forages and roughages were analysed using the procedures described by the Association of Official Analytical Chemists (2000). 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 fibre, acid detergent fibre and acid detergent lignin were analysed using ANKOM A220 fibre analyser (ANKOM Technology, New York, USA). Hemicellulose content was calculated as the difference between neutral detergent fibre and acid detergent fibre content (Hemicellulose = neutral detergent fibre – acid detergent fibre). The cellulose and acid detergent lignin content were determined using the method of Van Soest and Wine (1968).

The nylon bag technique (Orskov et al. 1980) was used to determine the degradability of forages and roughages in the rumen. Dried forages were milled to pass through a 2-mm screen using a hammer mill (Scientec hammer mill 400, Lab World Pty Ltd, Johannesburg, South Africa). Approximately 4 g of each ground forage sample was weighed into ANKOM nylon bags (ANKOM Co, Fairport, New York, USA; internal dimensions: 5 cm × 9 cm; pore size 50 μm) and sequentially incubated (in triplicates per time interval) in the rumen for 120, 96, 72, 48, 24, 9, 6, and 3 hours using 4 non-lactating Jersey cows (body weight = 330 ± 19.97). The cows were fed on veld hay (*Themeda triandra*) and supplemented with 2 kg Lucerne hay per day (Table 8.1) at Ukulinga Research Farm, Pietermaritzburg, South Africa (29°39'45.6"S 30°24'17.9"E). Incubated bags were removed and washed together with the un-incubated (zero hour) bags for 30 minutes (6 cycles each lasting 5 minutes) using a semi-automatic washing machine. Washed bags were oven dried for 48 hours at 80°C and weighed.

Degradability of forages was determined using dry matter loss (DML) in nylon bags. A curve for DML against incubation time was plotted and used to inspect for outliers. The model of McDonald (1981) was fitted on Statistical Analysis System 9.3 (SAS Institute Inc., Cary, NC, USA) to generate degradation parameters of the forages. The model used was: $Y = a+b(1–e^{–c(t–L)})$, where: Y, degradability at time (t); a, intercept; b, potentially degradable fraction; c, rate of degradation of b; and L, lag time. Effective degradability (ED) was calculated using a predicted passage rates for each forage. The passage rate of solid was predicted using models developed by Moyo et al. (2017).

5.2.2 Creation of datasets

This dataset was created from studies that met all of the following criteria: (1) studies were published in peer-reviewed journals, (2) in-sacco degradability was done using the nylon-bag technique, (3) studies reported the degradability of dry matter in the rumen, (4) studies reported the degradability of any feed including roughages, grains, leaves, stems, fruits, concentrates and diet formulations, and (5) studies stated the feeds or diets and any supplementary feeds fed to the animals, (6) animals were fed ad libitum. Observations on the degradability of organic matter and neutral detergent fibre were not included in the dataset.

Degradation models used in computing dry matter loss (DML) from each study were identified. Studies that reported negative values for time lag (L) were taken to be zero as negative times do not have biological meaning. Studies reported degradability parameters computed using either the (i) no time lag model: $DML=a+b \times[1-exp^{(-c \times t)}]$ or the (ii) model accounting for time lag: $DML=a+b \times[1-exp^{-c(t-L)}]$. Thus, two datasets were collated, one from studies that used the time-lag model and another from studies that used the no-time lag model in computing degradation parameters.

Factors that affect degradability identified in each of these studies were categorised into four groups: (i) properties of diets fed to the ruminants (ii) properties of feed samples incubated in the rumen (iii) effects of ruminant feeding type and (iv) environment factors according to Fig. 5.1. Potential degradability (PD) was calculated in studies that did not report it using the formulae: PD = a + b. Factors that affect degradation of feeds identified in these studies were both quantitative and qualitative. Units used in quantifying all quantitative factors are specified in various sections when mentioned. Qualitative factors that affect degradation parameters were coded with numerical weightings, represented as numbers in parenthesis as (= 1, = 2, = 3 or = 4).

5.2.2.1 Diet properties

Diet properties were used to account for the effect of rumen ecology on degradation. Nutritional attributes of diets fed to ruminants included in the dataset were dietary neutral detergent fibre (DNDF), dietary starch (DSTA) including sugars, vitamins, pectins, fats and minerals, and dietary crude protein (DCP) contents of entire diet (all in g/kg). Starch content of diets fed to animals was calculated using the general formula: DSTA = 1000 – (DNDF + DCP). Discrete dietary properties that affect degradation parameters included in the dataset were diet class and diet subclass. Discrete dietary factors were categorised as follows: diet class (DS) classified diets either as silage (= 1) or non-silage (= 0) and diet subclass (DB) classified diets either as a browse (= 1) or non-browse (= 0). Thus, diet properties included in the dataset were DNDF, DSTA, DCP, DS and DB.

5.2.2.2 Feed sample properties

The incubated feed sample properties included in the dataset were particle size (PS), feed class (FS), feed subclass (FUT), feed type (FT) and feed proximate compositional attributes viz. dry matter (DM), crude protein (CP), neutral detergent fibre (NDF) and ash (all in g/kg). Particle size (mm) of degradation samples were determined from the screen size used to grind the samples for incubation.

Discrete feed factors that affect degradation parameters included in the dataset were FS, FUT and FT. Discrete feed factors were categorised as follows; FS classified feeds either as a silage (= 1) or non-silage (= 0); FUT classified feeds either as urea-treated (=1) or untreated (=0); and FT classified feeds either as a roughage (= 1), concentrate (= 2) or mixed diet (= 3). Feed type classified feeds into 3 groups as roughages (any part of a plant that is not a fruit or grain), concentrates (parts of a plant that constitutes a grain or fruit), and mixed diet (mixture of roughages and concentrates). Thus, feed properties included in the dataset were DM, CP, NDF, ash, PS, FS, FUT and FT.

5.2.2.3 Ruminant species and experimental factors

To account for the effect of ruminant species feeding type (RFT), ruminants were grouped into 2 feeding types based on the classification by Hofmann (1989) as; grazers or roughage selectors (buffalo, cattle and sheep = 1) and intermediate feeders (goats = 2). The effect of the length of incubation (IC) in hours on PD and the effect of feeding system (GI) were included in the dataset. The only qualitative experimental factor included in the dataset was the feeding system which classified animals as either grazing (GI = 1) or as fed indoors (GI = 0).

5.2.2.4 Climate and ambient temperature

Effects of climate type (CT) was accounted for by identifying the location of the study site and classifying the climate of the site using the updated Köppen-Geiger climate classification system according to Peel et al. (2007). Studies fell into 15 climatic regions namely; tropical rain forest (Af), tropical savannah climate (Aw), hot arid desert climate (BWh), hot arid steppe climate (BSh), cold arid steppe climate (BSk), dry temperate climate with hot summers (Csa), dry temperate climate with warm summers (Csb), dry winter temperate climate with hot summer (Cwa), dry winter temperate climate with warm summers (Cwb), hot summer temperate climate without dry season (Cfa), warm summer temperate climate without dry season (Cfb), cold dry climate with warm summers (Dsb), cold climate with hot summers and no dry season (Dfa), cold climate with warm summers and no dry season (Dfb), and cold climate with warm summers and no dry season (Dfc). The effect of climate type was done by allocating each climatic region into either belonging to tropical (= 1), arid (= 2), temperate (= 3) or cold (= 4) climates. The countries where and years when, each study was done were obtained and the ambient temperature (AT) data for each of these sites estimated from data by Harris et al. (2014).

5.2.3 Creation of modelling datasets for linear regression

Data were collected from studies that reported at least average values for in-sacco (nylon bag technique) degradability parameters (a, soluble fraction; b, slowly degradable fraction and c, rate of degradation) of roughages and stated the diet, feeds and feed supplements given to animals. A dataset was created bearing degradability parameters from wild and domesticated ruminants from 40 studies. Factors affecting degradability were identified in each of these studies and were categorised into two main groups: (1) diet properties (i.e. fed to the animal) and (2) feed sample properties (i.e. incubated in the rumen). Diet properties were used to account for the effects of rumen ecology on fermentation and included neutral detergent fibre (NDF), protein-free cell contents (PFCC) which include starch, sugars, vitamins, pectins, fats and minerals, and crude protein (CP) contents of entire diet (all in g/kg), level of concentrate supplementation (%) and provision of a urea supplement in the form of a lick (presence=1, absence=0). Feed sample properties included urea treatment (%) of sample and feed compositional attributes (DM, dry matter; CP, crude protein; NDF, neutral detergent fibre, ADF, acid detergent fibre; HEM, hemicellulose and ash all in g/kg). Protein-free cell contents of the diet fed to animals was calculated using the formula: PFCC = 1000 – (NDF + CP). Potential degradability (PD) and hemicellulose (HEM) content were calculated in studies that did not report them using the formulae: PD = a + b; and HEM = NDF – ADF, respectively. Studies that did not report dietary composition of feeds but mentioned names of feeds used had their composition looked up in studies that reported them. These factors were used as input parameters to develop regression models for predicting degradability of feeds in the rumen.

5.2.4 Meta-analysis of the rumen degradation of feeds

Data were normalized to meet assumptions of homogeneity of variance using the logarithmic transformation. A meta-analysis was done using the mixed model regression procedure of SAS 9.3 software (SAS Institute Inc., Cary, NC, USA) according to St-Pierre (2001) and Sauvant et al. (2008) to determine the main effects of feed type, ruminant type, ruminant feeding type, and climate on rumen degradation of feeds. A model with discrete predictor variables (feed type, ruminant type, ruminant feeding type and climate) considered as fixed effects were used. The fixed effects of dry matter, ash, and crude protein contents of feed samples, particle size of feed samples, whether feed samples were silage or non-silage, treated with urea or untreated, crude protein, and PFCC contents of diets fed to animals, whether the diet was a silage or non-silage, browse or non-browse, whether animals were fed indoors or grazing outdoors, and ambient temperature were considered as covariates. Study × incubation time interactions from different studies were considered as random effects. Data were weighted by the number of animals in each study and the standard errors of the mean (Sauvant et al. 2008).

A second model with discrete predictor variables (feed type and climate) considered as fixed effects were used to determine the main effects of feed type and climate on chemical composition of feeds/diets incubated for rumen degradation. The fixed effects of whether or not feed samples were a silage or non-silage and whether or not feed samples were treated with urea or untreated and ambient temperature were considered as covariates. Study × incubation time interactions from different studies were considered as random effects. Data were weighted by the number of animals in each study. Least square means were used to compare differences among means in the case of discrete predictor variable. The probability threshold for significance of fixed and random study effects for meta-analyses were considered at $p < 0.05$. The correlation procedure was used to establish the Pearson correlation coefficients of any two input predictor variables.

5.2.5 Development of linear regression models

A step-wise regression procedure on the Statistical Analysis System 9.3 (SAS Institute Inc., Cary, NC, USA) was used to select parameters that qualified to develop regression equations to predict (1) rapidly degradable fraction of fibre (a); (2) potential degradability (PD); (3) time lag for fermentation to occur (tL); and (4) rate of degradation (c) in the rumen. One parameter from a pair of correlated parameters was dropped in model development when both correlated parameters significantly influence degradation parameters. Those parameters that qualified for model development were CP and NDF content of feed sample (model for soluble fraction of fibre); ADF content of feed sample and PFCC content of diet (model for potential degradability); ADF, CP and ash content of feed sample, and PFCC content of diet (model for time-lag); NDF and CP content of feed sample, and, PFCC and DNDF content of diet (model for degradation rate).

Regression models were used to simulate the rumen degradability of *Colophospermum mopane* leaves and pods, *Diheteropogon hagerupii*, *Eragrostis tremula*, *Mucuna pruriens* leaves, Marula oil cake, *Afzelia quanzensis* legume pods, *Brassica oleraceae var. acephala* leaves, maize stover, leaves and stalks, millet stover, wheat straw, *Eragrostis curvula*, Kikuyu grass, *Schizachyrium exile*, veld grass hay, cowpea husks, cassava root peels, groundnut haulms, *Eragrostis tremula*, sorghum stover, leaves and sheath, and stems, millet bran, wheat bran, and cottonseed cake. The effective degradability of these forages was calculated using the model of McDonald (1981).

5.2.6 Development of Random Forest models

Random Forest models were programmed on a 64-bit R version 3.6.2 (Dark and Stormy Night) to predict degradability of feeds in the rumen. Random Forest models were trained to predict degradability of feeds in the rumen using diet, feed, animal and environmental factors described previously. Since different variables span over wide ranges, normalisation (within the interval (0, 1)) of input and output data was done. The Random Forest algorithm intrinsically divided the dataset into 2 subsets: 70% of the dataset was used for model training and 30% for testing. The Random Forest was trained as a binary tree-based machine-learning method to predict degradability of feeds in the rumen. The Random Forest algorithm was tuned for one parameter (i.e. “mtry”) using the “trainControl” option, and the search for the best “mtry” was randomly done. The “mtry” parameter represents the number of variables randomly sampled as candidates at each split. The most accurate value for “mtry” was selected from the combination that yielded the lowest error. During resampling, training data were cross-validated 10-fold 3 times.

5.2.6.1 No lag dataset

The number of decision trees ("ntree") was set at 2000. The best "mtry" values for each predicted variable were: soluble fraction ("mtry" = 3, RMSE = 63.721, R^2 = 0.602 and MAE = 42.489), slowly degradable fraction ("mtry" = 9, RMSE = 87.170, R^2 = 0.659 and MAE = 59.832), rate of degradation ("mtry" = 3, RMSE = 0.024, R^2 = 0.488 and MAE = 0.014) and potential degradability ("mtry" = 12, RMSE = 95.653, R^2 = 0.602 and MAE = 66.223). After training the final models attained precision in prediction of 53.23% (soluble fraction), 67.5% (slowly degradable fraction), 43.7% (rate of degradation) and 53.96% (potential degradability).

5.2.6.2 Time lag dataset

The number of decision trees ("ntree") was set at 2000. The best "mtry" values for each predicted variable were: soluble fraction ("mtry" = 5, RMSE = 77.663, R^2 = 0.702 and MAE = 51.623), slowly degradable fraction ("mtry" = 3, RMSE = 99.640, R^2 = 0.569 and MAE = 68.726), rate of degradation ("mtry" = 3, RMSE = 0.089, R^2 = 0.456 and MAE = 0.028), potential degradability ("mtry" = 5, RMSE = 86.937, R^2 = 0.625 and MAE = 57.784) and lag ("mtry" = 3, RMSE = 1.848, R^2 = 0.558 and MAE = 1.210). After training the final models attained precision in prediction of 66.62% (soluble fraction), 46.61% (slowly degradable fraction), 5.21% (rate of degradation), 58.67% (potential degradability) and 51.88% (lag).

5.2.6.3 Statistical analysis

Regression analyses of observed against predicted degradability parameters were done using the linear regression procedure. Coefficients of determination were used to access the precision of regression lines in approximating real data points. Residual standard error (RSE) was used to determine accuracy of these models. The linear and mean biases in model predictions were evaluated by regressing the residuals (observed minus predicted degradability parameters) against predicted degradability parameters using the training dataset. The intercept and slopes were tested against 0 to determine any linear or mean bias St-Pierre (2003).

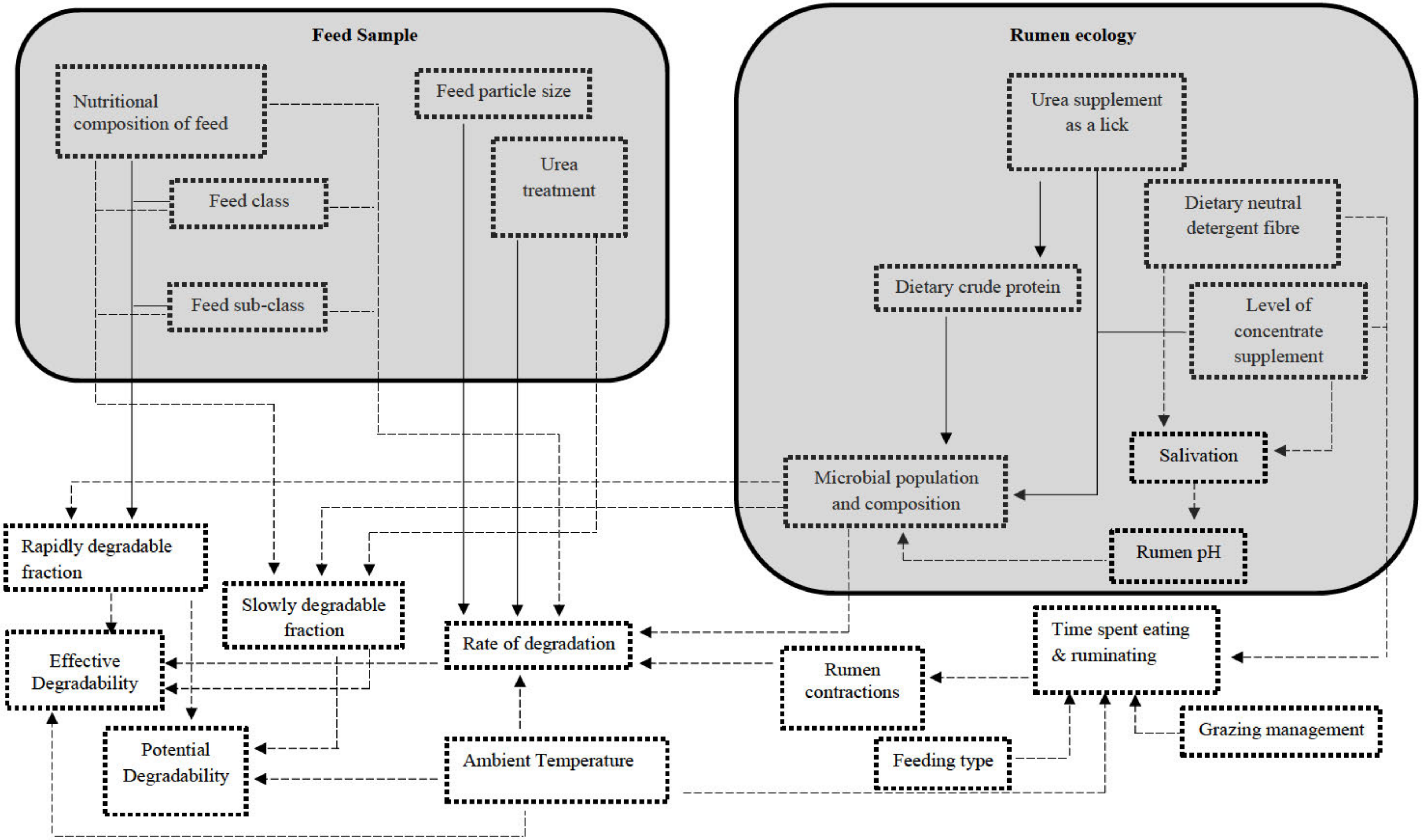


Fig. 5. 1 Factors affecting degradation of forages in the rumen

5.3 Results

5.3.1 Description of the nutritional value of underutilised forages and roughages

Of the underutilised forages, the crude protein content tended to be double as much for *Brassica oleracea var. acephala* compared to *Colophospermum mopane* leaves and pods (Table 5.2). Forage grasses (62.9±34 g/kgDM) tended to have very low crude protein contents compared to legumes (137.6±69) and concentrates (177±39.9). Underutilised *Brassica oleracea var. acephala* (305 g/kgDM) tended to have higher crude protein levels compared to commonly used protein sources (CSC = 222 g/kgDM).

The potential degradability of forage grasses (651±111 g/kgDM), cotton seed cake concentrate (756±95.4 g/kgDM) and, forage legumes, trees and shrubs (745±110.2 g/kgDM) are presented on Tables 5.3 – 5.5.

Table 5. 1 Chemical composition of experimental feeds and diets fed to cows during nylon bag degradability.

Diets	Chemical composition of feeds and diets fed to cows (g/kg DM)							
Forages	DM	OM	CP	NDF	ADF	ADL	HEM	CEL
IPR	727	922	89	745	415	-	330	-
LH	906	911	136	524	361	-	163	-
[#] Roughages								
Diet 1 (VGH)	933	867	69	795	603	190	192	413
LH	895	564	165	487	356	77	131	279
Diet 2 (VGH + 33% LH)	920	767	101	693	521	153	172	369
Diet 3 (VGH + 50% LH)	914	716	117	641	480	134	162	346

[#] Data adapted from Katamzi (2015).

DM, Dry matter; OM, Organic matter; N, Nitrogen; NDF, Neutral detergent fibre; ADF, Acid detergent; ADL, Acid detergent lignin; HEM, Hemicellulose; CEL, Cellulose; VGH, Veld grass hay; LH, lucerne hay.

Table 5. 2 Chemical composition of incubated forages.

Group	Chemical composition of incubated feeds (g/kg DM)							
Forage legumes, trees and shrubs	DM	OM	CP	NDF	ADF	ADL	HEM	CEL
CPH	944	935	85	617	428	102	189	328
UTCPH	627	928	141	615	422	105	193	312
GNH	932	889	109	495	386	116	110	265
CMLB	906	941	132	407	199	-	208	-
CMLG	918	931	144	470	175	-	295	-
CMP	916	946	195	477	197	-	280	-
MPL	917	942	118	607	233	-	374	-
CRP	896	953	78	489	98	-	391	-
AQLP	956	978	70	628	220	-	408	-
BOAL	908	746	305	363	137	-	226	-
$^{\#}$ Forage grasses								
MS	930	828	96	718	614	118	104	496
ML	925	660	102	645	559	100	86	459
WS	878	800	42	764	691	175	73	516
EC	931	836	107	815	503	130	312	373
ECB	925	890	128	874	615	171	259	444
KG	919	833	99	778	666	189	112	477
VGHD	932	887	41	885	629	159	256	470
VGHC	929	866	41	834	564	110	270	454
VGHP$_1$	932	877	51	849	619	189	230	430
VGHP$_2$	936	882	37	876	609	142	267	467
DH	970	959	20	880	565	78	316	485
UTDH	617	968	36	876	566	88	310	476
ET	969	976	21	796	465	67	330	397
UTET	613	971	47	829	485	72	344	414
SE	949	954	22	813	518	49	295	447
UTSE	626	956	49	812	541	90	270	450
MIS	954	913	39	816	518	130	298	394
UTMIS	619	911	46	799	523	118	276	406
SS (whole)	964	845	23	791	535	198	257	296
UTSS (whole)	624	843	45	773	514	189	259	331
SSLS	973	809	40	725	440	145	285	289
SSS	962	906	22	731	438	100	293	332
$^{\#}$ Concentrates								
MB	919	897	146	513	122	63	391	61
WB	953	951	163	477	125	35	352	86
CSC	980	948	222	570	437	101	133	339

$^{\#}$ Data adapted from Katamzi (2014) and Abdou et al. (2017).

ADL, acid detergent lignin; DM, dry matter; OM, organic matter; NDF, neutral detergent fibre; ADF, acid detergent fibre; HEM, hemicellulose; CP, crude protein; CEL, cellulose; CMLB, *Colophospermum mopane* leaves brown; CMLG, *Colophospermum mopane* leaves green CMP, *Colophospermum mopane* pods; DH, *Diheteropogon hagerupii*; ET, *Eragrostis tremula*; MPL, *Mucuna pruriens* leaves; AQLP, *Afzelia quanzensis* legume pods; BOAL, Brassica oleraceae var. acephala leaves; MS, Maize stover; ML, Maize leaves; MT, Maize stalks; MIS, Millet stover; UTMIS, urea treated millet stover; WS, Wheat straw; EC, Eragrostis curvula; ECB, *Eragrostis curvula* at bloom stage; KG, Kikuyu grass; SE, *Schizachyrium exile*; VGHD, Veld grass hay from Dundee; VGHC, Veld grass hay Camperdown; VGHP$_1$, Veld grass hay Pietermaritzburg area 1; VGHP$_2$, Veld grass hay from the Pietermaritzburg area 2; CPH, cowpea husks; CRP, cassava root peels; GNH, groundnut haulms; UTCPH, urea treated cowpea husks; UTDH, urea treated *Diheteropogon hagerupii*; UTET, urea treated *Eragrostis tremula*; UTSE, urea treated *Schizachyrium exile*; UTMIS, urea treated maize stover; SS, Sorghum stover; UTSS, urea treated sorghum stover; SSLS, Sorghum stover leaves and sheath; SSS, Sorghum stover stems; MB, Millet bran; WB, Wheat bran; CSC, Cottonseed cake.

Table 5. 3 Nylon bag degradation of forage legumes, forage trees and shrubs (non-leguminous), and concentrates.

	Rumen degradation of feeds						
	CPH	UTCPH	GNH	CMLB	CMLG	CMP	
a (g/kg)	234	236	305	519	358	398	
b (g/kg)	466	483	457	224	361	286	
c (h^{-1})	0.15	0.08	0.14	0.06	0.07	0.11	
PD (g/kg)	700	719	762	743	719	684	
ED (g/kg)	556	505	621	668	611	623	
tL (h)	-	-	-	7.1	0	1.9	
	MPL	CRP	AQLP	BOAL	CSC	MB	WB
a (g/kg)	178	293	278	351	276	449	457
b (g/kg)	550	600	274	600	371	374	342
c (h^{-1})	0.08	0.22	0.05	0.15	0.05	0.29	0.22
PD (g/kg)	728	893	552	951	647	823	799
ED (g/kg)	578	821	449	851	439	755	722
tL (h)	0	0	2.0	0	-	-	-

CMLB, *Colophospermum mopane* leaves - brown; CMLG, *Colophospermum mopane* leaves - green; CMPG, *Colophospermum mopane* pods; CPH, cowpea husks; CRP, cassava root peels; GNH, groundnut haulms; MPL, *Mucuna pruriens* leaves; AQLP, *Afzelia quanzensis* legume pods; BOAL, *Brassica oleraceae var. acephala* leaves; UTCPH, urea treated cowpea husks; MB, Millet bran; WB, Wheat bran; CSC, Cottonseed cake; a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; PD, potential degradability; ED, effective degradability (calculated at kp: rate of passage of particles in the rumen = 0.03 per h).

Table 5. 4 Nylon bag degradability of forage grasses (roughages) in cows fed 3 different diets[#].

	Diet 1 (100% veld hay)									
	MS	ML	WS	ECM	ECB	KG	GHD	GHC	GHP_1	GHP_2
a (g/kg)	194	158	17	86	43	76	53	44	39	174
b (g/kg)	445	454	373	518	491	430	475	400	446	439
c (h^{-1})	0.049	0.049	0.033	0.048	0.037	0.047	0.027	0.032	0.026	0.029
PD (g/kg)	639	612	391	604	534	506	499	445	486	613
ED (g/kg)	645	637	351	622	454	339	405	398	385	351
	Diet 2 (67% veld hay: 33% lucerne hay)									
a (g/kg)	194	158	16	87	44	76	24	43	51	28
b (g/kg)	592	623	534	726	818	577	869	622	521	647
c (h^{-1})	0.039	0.043	0.016	0.033	0.017	0.017	0.008	0.018	0.029	0.017
PD (g/kg)	786	780	556	813	819	652	894	665	572	676
ED (g/kg)	531	524	201	467	289	272	212	258	285	265
	Diet 2 (50% veld hay: 50% lucerne hay)									
a (g/kg)	194	158	16	87	44	76	24	43	40	173
b (g/kg)	607	659	489	727	647	507	593	591	543	428
c (h^{-1})	0.052	0.051	0.033	0.042	0.029	0.03	0.019	0.024	0.025	0.03
PD (g/kg)	801	817	505	814	691	582	616	634	583	600
ED (g/kg)	579	572	269	512	365	329	256	299	285	387

[#] Data adapted from Katamzi (2014)

MS, Maize stover; ML, Maize leaves; MT, Maize stalks; WS, Wheat straw; EC, Erograstis curvula; ECB, Erograstis curvula at bloom stage; KG, Kikuyu grass; VGHD, Veld grass hay from Dundee; VGHC, Veld grass hay Camperdown; VGHP1, Veld grass hay Pietermaritzburg area 1; VGHP2, Veld grass hay from the Pietermaritzburg area 2; kp, rate of passage of particles in the rumen; a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; PD, potential degradability; ED, effective degradability (calculated at kp: rate of passage of particles in the rumen = 0.03 per h).

Table 5. 5 Nylon bag degradability of urea treated and untreated forage grasses (roughages) in cows fed Kikuyu pasture[#].

	Rumen degradation of feeds					
	DH	UTDH	ET	UTET	SE	UTSE
a (g/kg)	99	129	136	165	91	157
b (g/kg)	572	529	521	538	564	525
c (h^{-1})	0.02	0.02	0.02	0.02	0.02	0.03
PD (g/kg)	671	658	657	703	655	682
ED (g/kg)	224	248	267	271	238	307
	MS	UTMS	SS (whole)	UTSS (whole)	SSLS	SSS
a (g/kg)	131	182	223	251	217	206
b (g/kg)	552	437	507	470	548	421
c (h^{-1})	0.01	0.02	0.02	0.02	0.03	0.02
PD (g/kg)	683	619	730	721	765	627
ED (g/kg)	214	298	330	362	376	313

[#] Data adapted from Abdou et al. (2017).

MS, Maize stover; ML, Maize leaves; MT, Maize stalks; WS, Wheat straw; EC, Erograstis curvula; ECB, Erograstis curvula at bloom stage; KG, Kikuyu grass; VGHD, Veld grass hay; a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; PD, potential degradability; ED, effective degradability (calculated at kp: rate of passage of particles in the rumen = 0.03 per h)

5.3.2 Meta-analysis of the rumen degradation of feeds

In some studies, not all the variables of interest were reported, therefore, the number of observations across variables was not uniform (Table 5.6). There were large differences between minimum and maximum values in the dataset for degradability parameters, proximate composition of diets (DCP, DNDF and PFCC) fed to animals and feed samples (DM, CP, NDF, ADF, HEM, and ash) degraded in the rumen. The variability in ambient temperatures (CV = 45.66%) of regions where these studies were done and incubation times of feeds in the rumen among studies was high.

Table 5. 6 Descriptive statistics of diet, feed and climatic factors affecting degradation of feeds in the rumen.

Diet	N	Max	Min	Mean ± SD	SEM	CV (%)
Crude protein (g/kg)	1006	311	20	124 ± 44.5	1.41	35.98
Neutral detergent fibre (g/kg)	1006	913	129	565 ± 124.4	3.92	22.04
Protein-free cell contents (g/kg)	1006	740	48	311 ± 109.5	3.45	35.24
Feed sample						
Dry matter (g/kg)	1015	992	70	713 ± 302.8	9.51	42.47
Crude protein (g/kg)	1009	519	19	119 ± 75.6	2.38	63.67
Neutral detergent fibre (g/kg)	1006	919	69.3	558 ± 193.7	6.14	35.01
Acid detergent fibre (g/kg)	1006	715	29	357 ± 136.2	4.31	38.48
Hemicellulose (g/kg)	1006	524	5.8	202 ± 100.4	3.17	50.04
Ash (g/kg)	1009	330	11	87 ± 39.9	1.25	45.91
Particle size (mm)	1015	100	0.5	3.3 ± 6.72	0.21	206.4
Soluble fraction (g/kg)	945	751	27	214 ± 119.3	3.89	55.81
Slowly degradable fraction (g/kg)	947	984	64	502 ± 149.9	4.87	29.86
Rate of degradation (per h)	997	2.148	0.007	0.050 ± 0.085	0.003	170.5
Potential degradability (g/kg)	974	1000	31	711 ± 151.1	4.84	21.22
Lag (h)	375	17.90	0.00	2.24 ± 2.763	0.143	123.4
Climate						
Ambient temperature (°C)	1015	28.2	−5.9	17.8 ± 8.14	0.26	45.66
Experimental factors						
Incubation time (h)	1015	336	36	117 ± 79.3	2.49	67.58
No. of replicates used	977	12	1	3.7 ± 1.7	-	46.28

CV, coefficient of variation; SEM, standard error of the mean; SD, standard deviation.

Table 5. 7 Pearson correlations between diet, feed and climatic factors affecting degradation of feeds in the rumen.

	Diet Attributes			Feed Sample Attributes						Environmental factors		Degradability Parameters				
	DCP	**DNDF**	**PFCC**	**DM**	**CP**	**Ash**	**NDF**	**ADF**	**HEM**	**AT**	**IT**	**a**	**b**	**c**	**PD**	**Lag**
DCP	-	-0.50 ***	0.15 ***	-0.17 ***	0.19 ***	0.02 ^{NS}	-0.01 ^{NS}	-0.08 *	0.08 **	-0.24 ***	0.26 ***	0.07 *	0.09 **	0.05 ^{NS}	0.15 ***	0.15 **
DNDF		-	-0.94 ***	-0.03 ^{NS}	-0.11 ***	0.16 ***	0 27 ***	0.22 ***	0 23 ***	0.44 ***	-0.09 **	-0.09 **	-0.04 ^{NS}	-0.08 *	-0 11 ***	0.02 ^{NS}
PFCC			-	0.10 **	0.05 ^{NS}	-0.19 ***	-0.31 ***	-0.22 ***	-0.30 ***	-0.40 ***	-0.01 ^{NS}	0.07 *	0.01 ^{NS}	0.07 *	0.07 *	-0.07 ^{NS}
DM				-	-0.17 ***	-0.24 ***	0 13 ***	0.20 ***	-0.03 ^{NS}	0.09 **	-0.27 ***	-0.25 ***	0.04 ^{NS}	0.02 ^{NS}	-0 16 ***	-0.22 ***
CP					-	0.18 ***	-0.56 ***	-0.50 ***	-0.41 ***	-0.08 **	0.18 ***	0.23 ***	0.07 *	0.26 ***	0.25 ***	-0.10 *
Ash						-	-0.01 ^{NS}	0.04 ^{NS}	-0.08 *	0.19 ***	0.12 ***	-0.01 ^{NS}	0.04 ^{NS}	-0.03 ^{NS}	-0.02 ^{NS}	0.21 ***
NDF							-	0.87 ***	0.75 ***	0.16 ***	0.01 ^{NS}	-0.38 ***	-0.01 ^{NS}	-0.21 ***	-0 32 ***	0.29 ***
ADF								-	0 33 ***	0.20 ***	-0.02 ^{NS}	-0.39 ***	-0.09 **	-0.18 ***	-0.41 ***	0.38 ***
HEM									-	0.04 ^{NS}	0.03 ^{NS}	-0.21 ***	0.12 ***	-0.15 ***	-0.07 *	0.14 **
AT										-	-0.13 ***	-0.13 ***	-0.19 ***	-0.11 ***	-0 30 ***	0.14 **
IT											-	-0.07 *	0.19 ***	-0.01 ^{NS}	0.15 ***	0.23 ***
a												-	-0.43 ***	0.08 *	0.38 ***	-0.02 ^{NS}
b													-	-0.08 *	0.67 ***	-0.18 ***
c														-	-0.01 ^{NS}	-0.08 ^{NS}
PD															-	-0.20 ***
tL																-

DCP, dietary crude protein; DNDF, dietary neutral detergent fibre; DM, dry matter; CP, crude protein, NDF, neutral detergent fibre; ADF, acid detergent fibre; HEM, hemicellulose; PFCC, protein-free cell contents; AT, ambient temperature; IT, incubation time; a, soluble fraction; b, slowly degradable fraction; PD, potential degradability and c, rate of degradation; tL, time lag.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant ($p > 0.05$).

There were significant positive correlations between DCP and PD (r < 0.15; $p < 0.05$), and length of incubation and PD (r < 0.15; $p < 0.05$) (Table 5.7). Significant negative correlations ($p < 0.05$) between AT and degradability parameters (a, b, c, and PD) were observed. Correlations between CP and degradability parameters (a, b, c, and PD) were positive and significant. There were significant negative correlations between ADF and degradability parameters (a, b, c, and PD).

Concentrates had the highest solubility compared to roughages and mixed diets, while the potential degradability and the slowly degradable fraction were higher for concentrates and mixed diets compared to roughages (Table 5.8). Ruminants classified as grazers had faster rates of degradation compared to intermediate feeders. Ruminant type had no effect on all degradation parameters but the rate of degradation of feeds in the rumen. The rate of degradation in small ruminants (goats and sheep) was lower than in large ruminants (buffalo and cattle). The PD was highest for studies carried out in cold and temperate climates compared to tropical and arid climates.

Rumen ecology as influenced by diet properties fed to animals affected the rate of degradation and PD of feeds in the rumen (Table 5.9). Animals fed on diets classified as browse had similar PD (466 ± 168.6 g/kg) with those fed on non-browse (671.9 ± 64.93 g/kg) diets. Silage diets had similar PD (609 ± 105.04 g/kg) to non-silage (529 ± 94.62 g/kg) diets. The solubility of feeds was higher for animals fed non-silage diets (224.7 ± 181.49 g/kg) compared to those fed on silage diets (6.3 ± 191.65 g/kg).

Table 5. 8 Effects of feed sample and diet properties, ambient temperature, ruminant type, feeding type, and climatic region on rumen degradation of feeds.

Test of Fixed Effects	Degradation Parameter Estimates (Mean ± SE)				
Effect of Feed Type	**a (g/kg)**	**b (g/kg)**	**c (per h)**	**PD (g/kg)**	**Lag (h)**
Roughages	212 ± 53.68	491 ± 99.24	0.046 ± 0.0072	697 ± 56.9	2.78 ± 4.311
Concentrates	237 ± 60.57	538 ± 99.84	0.080 ± 0.0088	780 ± 60.4	0.96 ± 4.411
Mixed diets	199 ± 103.76	634 ± 190.80	0.051 ± 0.0154	833 ± 103.2	0.00 ± 6.62
Significance	***	***	*	**	NS
Effect of climatic region					
Tropical climates					
Af	92 ± 326.81	619 ± 731.79	0.029 ± 0.0281	643 ± 128.8	6.07 ± 6.098
Aw	200 ± 90.55	466 ± 195.93	0.039 ± 0.0161	666 ± 87.1	1.54 ± 5.57
Arid climates					
BSh	176 ± 96.07	404 ± 201.34	0.037 ± 0.0180	581 ± 102.2	-
BSk	160 ± 95.27	537 ± 196.73	0.068 ± 0.0210	697 ± 93.7	5.13 ± 5.593
BWh	151 ± 484.22	358 ± 718.25	0.052 ± 0.0444	606 ± 203.4	-
Temperate climates					
Cfa	266 ± 92.72	476 ± 223.75	0.051 ± 0.0154	697 ± 87.5	0.62 ± 5.253
Cfb	258 ± 70.82	535 ± 162.21	0.052 ± 0.0143	792 ± 77.9	2.79 ± 6.03
Csa	288 ± 89.65	437 ± 176.15	0.055 ± 0.0189	725 ± 94.1	2.60 ± 5.723
Csb	231 ± 135.18	491 ± 274.70	0.056 ± 0.0319	722 ± 121.6	-
Cwa	247 ± 103.03	476 ± 240.21	0.064 ± 0.0207	722 ± 117.8	0.58 ± 5.828
Cwb	185 ± 82.56	533 ± 159.05	0.036 ± 0.0134	715 ± 77.7	2.71 ± 5.60
Cold climates					
Dfa	241 ± 183.70	447 ± 266.03	0.080 ± 0.0271	688 ± 112.7	1.31 ± 5.956
Dfb	120 ± 141.29	615 ± 478.79	0.234 ± 0.0511	735 ± 115.0	2.03 ± 5.840
Dfc	98 ± 333.95	624 ± 609.91	0.027 ± 0.0426	722 ± 210.8	-
Dsb	213 ± 100.76	478 ± 233.82	0.032 ± 0.0274	691 ± 150.8	-
Significance	NS	NS	NS	NS	***
Effect of climate type					
Tropical	193 ± 63.90	476 ± 147.93	0.038 ± 0.0113	664 ± 54.105	2.62 ± 1.828
Arid	166 ± 55.52	439 ± 133.61	0.050 ± 0.0128	621 ± 55.482	3.14 ± 3.200
Temperate	237 ± 27.98	515 ± 69.991	0.048 ± 0.0054	745 ± 25.097	2.19 ± 0.684
Cold	152 ± 64.35	562 ± 164.32	0.103 ± 0.0167	715 ± 62.092	1.85 ± 1.914
Significance	NS	NS	NS	***	NS
Effect of feeding type					
Grazers	310 ± 57.92	506 ± 107.95	0.050 ± 0.0084	711 ± 38.1	2.34 ± 2.112
Intermediate feeders	209 ± 67.14	413 ± 113.16	0.045 ± 0.0084	723 ± 104.0	0.65 ± 9.708
Significance	NS	NS	***	NS	NS
Effect of ruminant type					
Buffalo	140 ± 163.43	519 ± 275.95	0.050 ± 0.0175	649 ± 95.64	3.33 ± 2.80
Cattle	140 ± 65.50	520 ± 124.65	0.052 ± 0.0093	726 ± 43.36	1.86 ± 2.487
Goats	307 ±75.71	414 ± 137.50	0.046 ± 0.0098	722 ± 105.98	0.65 ± 9.789
Sheep	218 ± 68.19	492 ± 133.48	0.048 ± 0.0098	703 ± 48.64	2.67 ± 2.472
Significance	NS	NS	***	NS	*

a, soluble fraction; b, slowly degradable fraction; PD, potential degradability and c, rate of degradation; Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant ($p > 0.05$).

Table 5. 9 Covariate effects of feed sample and diet properties, ambient temperature and climatic region on rumen degradation of feeds.

Covariate Fixed Effects	a (g/kg)		b (g/kg)		c (per h)		PD (g/kg)		Lag (h)	
	F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Diet										
Browse	0.02	NS	0.20	NS	0.95	NS	1.50	NS	-	-
Silage	7.20	**	0.56	NS	0.20	NS	2.08	NS	5.68	*
CP (g/kg)	0.01	NS	1.05	NS	10.6	**	2.12	NS	0.07	NS
PFCC (g/kg)	0.23	NS	2.98	*	13.6	***	0.00	NS	0.89	NS
Feed sample										
DM (g/kg)	3.61	*	19.4	***	0.31	NS	1.46	NS	10.27	**
CP (g/kg)	27.3	***	311	***	6834	***	47.1	***	26.46	***
Ash (g/kg)	0.03	NS	60.1	***	114	***	27.3	***	0.04	NS
Silage	1.66	NS	0.05	NS	0.11	NS	0.98	NS	6.63	**
UT	0.00	NS	0.06	NS	5.18	*	0.02	NS	0.19	NS
PS (mm)	1.22	NS	0.47	NS	0.33	NS	0.01	NS	NS	0.08
Environment										
AT (°C)	0.02	NS	3.55	*	0.89	NS	8.09	***	1.31	NS
GR or IN	0.01	NS	0.00	NS	4.11	*	0.72	NS	-	-
Random effects										
S × I		**		**		***		***		NS

a, soluble fraction; b, slowly degradable fraction; c, rate of degradation; PD, potential degradability; S×I, Study×incubation time interactions; DM, dry matter; CP, crude protein; PFCC, protein-free cell contents; GR, grazing; IN, indoors; UT, urea treatment; PS, particle size. *P*, *p*-value; *F*, F-statistic; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant ($p > 0.05$).

Relationships between PD and AT were more linear ($p < 0.0001$) than they were quadratic ($p = 0.0137$). Significant negative linear relationships were observed between ambient temperature (AT) and the slowly degradable fraction of fibre (b) and potentially degradability (PD) as shown on Table 5.10. A 1 °C increase in AT decreased PD by 0.39% (roughages), 0.76% (concentrates) and 2.41% (mixed diets). The “b”-fraction decreased by 0.1% (roughages), 1.1% (concentrates), and 2.27% (mixed diets) for every 1 °C increase in AT. Regression equations demonstrated that the PD and b decreased by approximately 0.55% and 0.35% for every 1 °C increase in AT. A significant positive linear relationship was observed between PD and dietary crude protein (DCP). Large differences were found for slopes of regression equations among all three feed types. Negative effects of increasing AT on PD and b were more pronounced in mixed diets, followed by concentrates and less on roughages. Regression analysis showed that a unit increase in DCP content improved PD of mixed diets six times more than roughages. The PD increased slightly by approximately 0.05% for every unit increase in DCP content for all feed samples.

Significant positive linear relationships were observed between ambient temperature (AT), the dry matter (DM), and neutral detergent fibre contents of feeds, as shown in Table 5.11. Regression equations demonstrated that DM gradually increased by 7% (mixed diets) and 0.4% (roughages) for every 1 °C increase in AT. Increasing ambient temperature by 1 °C increased neutral detergent fibre content of feeds by 0.4%. Test of slopes showed DM content of mixed diets increased by 15 times more compared to roughages for every 1 °C increase in AT. The rates of degradation calculated using the no time-lag tended to be higher than the rates of degradation estimated from the model that accounts for time lag (Table 5.12). The Lag time was longer for roughages compared to concentrates. Ruminant type and feeding type affected estimation of rates of degradation using the no time-lag model. Roughages had low CP and high NDF contents compared to concentrates and mixed diets (Table 5.13).

5.3.3 Linear regression models

From the step-wise regression procedure for all prediction models, level of concentrate supplementation, provision of a urea supplement in the form of a lick and urea treatment of feed sample were rejected in model development. The regression model for predicting the soluble fraction (a) was $a = 558.12(\pm 62.45) + 0.27(\pm 0.133)\ CP - 0.57(\pm 0.07)\ NDF$ ($n = 113$, SEM = 6.86), accounting for 59% of the variation in development. The regression model for predicting the potential degradability (PD) was $PD = 1025.96(\pm 66.64) - 0.91(\pm 0.10)\ ADF + 0.32(\pm 0.08)\ PFCC$ ($n = 113$, SEM = 9.27), accounting for 65% of the variation in development.

The regression model for predicting the time-lag (tL) was $tL = -11.33(\pm 1.89) + 0.030(\pm 0.002)\ ADF + 0.01(\pm 0.003)\ CP - 0.006(\pm 0.001)\ PFCC + 0.02(\pm 0.007)\ ASH$ ($n = 113$, SEM = 0.17), accounting for 77% of the variation in development. The regression model for predicting the rate of degradation (c) was $c = 0.12(\pm 0.05) + 0.00013(\pm 0.00002)\ CP - 0.00012(\pm 0.00006)\ PFCC - 0.00002(\pm 0.00001)\ NDF - 0.00008(\pm 0.00005)\ DNDF$ ($n = 113$, SEM = 0.0009), accounting for 55% of the variation in development.

Table 5. 10 Equations for linear regression between ambient temperature and dietary crude protein (independent variables) and slowly degradable fraction of fibre and potential degradability in the rumen.

Independent		Parameter Estimates						R^2
Variables	**Feed Type**	**N**	**Intercept**	**$p_{intercept}$**	**Slope**	**p_{slope}**	**RMSE**	
				Slowly Degradable Fraction (g/kg)				
AT (°C)	R	806	507.9 ± 13.62	<0.0001	−0.87 ^{a} ± 0.66	0.1890	144.2	0.002
	C	102	685.0 ± 24.23	<0.0001	−11.4 ^{c} ± 1.52	<0.0001	143.8	0.359
	MD	39	889.8 ± 34.47	<0.0001	−22.7 ^{d} ± 2.94	<0.0001	59.27	0.616
	All feeds	947	564.8 ± 11.71	<0.0001	−3.45 ^{b} ± 0.589	<0.0001	147.4	0.035
				Potential Degradability (g/kg)				
AT (°C)	R	830	771.2 ± 12.91	<0.0001	−3.90 ^{a} ± 0.629	<0.0001	140.0	0.044
	C	105	876.7 ± 28.73	<0.0001	−7.60 ^{b} ± 1.83	<0.0001	173.2	0.144
	MD	39	1104 ± 31.27	<0.0001	−24.1 ^{c} ± 2.67	<0.0001	53.76	0.688
	All feeds	974	810.2 ± 11.24	<0.0001	−5.48 ^{b} ± 0.568	<0.0001	144.3	0.087
DCP (g/kg)	R	821	672.9 ± 14.76	<0.0001	0.23 ^{c} ± 0.117	0.0523	140.8	0.005
	C	105	800.1 ± 88.08	<0.0001	−0.16 ^{b} ± 0.687	0.8175	187.2	0.000
	MD	39	525.4 ± 26.25	<0.0001	1.52 ^{a} ± 0.125	<0.0001	43.07	0.799
	All feeds	965	653.6 ± 13.98	<0.0001	0.49 ^{b} ± 0.107	<0.0001	147.6	0.022
				Rate of Degradation (per h)				
AT (°C)	R	847	0.05 ± 0.0031	<0.0001	−0.001 ^{a} ± 0.0002	0.0006	0.034	0.014
	C	108	0.07 ± 0.0086	<0.0001	0.002 ^{a} ± 0.0006	0.7093	0.053	0.003
	MD	39	0.06 ± 0.0086	<0.0001	−0.0005 ^{a} ± 0.0007	0.461	0.015	0.015
	All feeds	994	0.06 ± 0.0028	<0.0001	−0.0006 ^{a} ± 0.0001	<0.0001	0.037	0.019
AT (°C)	TLM	363	0.08 ± 0.0153	<0.0001	−0.001 ^{a} ± 0.00095	NS	0.134	0.060
	NTLM	634	0.06 ± 0.0035	<0.0001	−0.001 ^{a} ± 0.00016	<0.0001	0.033	0.035

^{a,b,c,d} Means in a column with different superscripts are significantly different ($p < 0.05$).DCP, dietary crude protein; AT, ambient temperature; N, number of data used; NTLM, no time-lag model; TLM, time lag model; R, roughages; C, concentrates; MD, mixed diets.

Table 5. 11 Equations for linear regression between chemical composition of feeds degraded in the rumen and ambient temperature.

Independent	Parameter Estimates							R^2
Variables	**Feed Type**	**N**	**Intercept**	$p_{\text{intercept}}$	**Slope**	p_{slope}	**RMSE**	
				Dry Matter (g/kg DM)				
AT (°C)	R	866	632.8 ± 26.829	<0.0001	4.04 ^{b} ± 1.321	0.0023	301.1	0.011
	C	109	896.3 ± 15.045	<0.0001	−1.04 ^{c} ± 0.972	0.287	92.88	0.011
	MD	39	−458.6 ± 130.3	0.0012	69.7 ^{a} ± 11.11	<0.0001	223.9	0.515
	All feeds	1014	653.1 ± 22.82	<0.0001	3.35 ^{b} ± 1.165	0.0042	301.8	0.008
				Neutral Detergent Fibre (g/kg DM)				
AT (°C)	R	860	597.3 ± 15.73	<0.0001	−0.36 ^{c} ± 0.775	0.642	176.5	0.029
	C	107	173.9 ± 23.71	<0.0001	11.5 ^{a} ± 1.554	<0.0001	146.1	0.341
	MD	39	394.8 ± 38.97	<0.0001	10.5 ^{a} ± 3.325	0.0031	67.0	0.213
	All feeds	1006	486.6 ± 14.44	<0.0001	4.03 ^{b} ± 0.739	<0.0001	191	0.029
				Crude Protein Content (g/kg DM)				
AT (°C)	R	860	107.2 ± 5.654	<0.0001	−0.014 ^{b} ± 0.28	0.9593	75.32	0.000
	C	109	148.6 ± 17.91	<0.0001	2.51 ^{a} ± 1.157	0.0325	110.6	0.042
	MD	39	342.1 ± 14.18	<0.0001	−11.8 ^{d} ± 1.210	<0.0001	24.39	0.720
	All feeds	1008	132.2 ± 5.695	<0.0001	−0.76 ^{c} ± 0.291	0.0094	75.32	0.007

^{a,b,c,d} Means in a column with different superscripts are significantly different ($p < 0.05$). AT, ambient temperature; R, roughages; C, concentrates; MD, mixed diets; N, number of data used.

Table 5. 12 Effects of feed sample and diet properties, ambient temperature, ruminant type and feeding type, and climatic region on rumen degradation of feeds.

Test of Fixed Effects	Lag Time Model		No Lag Time Model
Effect of Feed Type	**c (per h)**	**Lag (h)**	**c (per h)**
Roughages	0.048 ± 0.0098	2.773 ± 4.3112	0.045 ± 0.0182
Concentrates	0.079 ± 0.0101	0.960 ± 4.4111	-
Mixed diets	0.068 ± 0.1997	-	0.051 ± 0.0235
Significance	NS	***	NS
Effect of climatic region			
Tropical climates			
Af	-	6.067 ± 6.0983	0.029 ± 0.0304
Aw	0.032 ± 0.0700	1.540 ± 5.5654	0.040 ± 0.0197
Arid climates			
BSh	0.041 ± 0.0722	-	0.037 ± 0.0203
BSk	0.089 ± 0.0687	5.134 ± 5.5930	0.052 ± 0.0284
BWh	0.054 ± 0.0771	-	0.051 ± 0.0527
Temperate climates			
Cfa	0.054 ± 0.0674	0.619 ± 5.2530	0.045 ± 0.0220
Cfb	0.045 ± 0.0677	2.791 ± 6.0284	0.059 ± 0.0226
Csa	0.059 ± 0.0689	2.599 ± 5.7277	0.054 ± 0.0237
Csb	-	-	0.056 ± 0.0346
Cwa	0.057 ± 0.0684	0.579 ± 5.8280	0.127 ± 0.2257
Cwb	0.037 ± 0.0693	2.741 ± 5.5972	0.034 ± 0.0162
Cold climates			
Dfa	0.054 ± 0.0701	1.313 ± 5.9558	0.104 ± 0.0434
Dfb	0.234 ± 0.0805	2.033 ± 5.8402	-
Dfc	-	-	0.027 ± 0.0521
Dsb	-	-	0.032 ± 0.0313
Significance	NS	***	NS
Effect of climate type			
Tropical	0.032 ± 0.0145	2.626 ± 1.7446	0.039 ± 0.0133
Arid	0.073 ± 0.0137	3.137 ± 1.7201	0.044 ± 0.0154
Temperate	0.046 ± 0.0043	2.194 ± 0.5132	0.051 ± 0.0079
Cold	0.184 ± 0.0158	1.853 ± 1.9538	0.045 ± 0.0234
Significance	NS	NS	NS
Effect of feeding type			
Grazers	0.059 ± 0.0668	2.342 ± 2.112	0.045 ± 0.0195
Intermediate feeders	0.031 ± 0.0678	0.654 ± 9.708	0.064 ± 0.0195
Significance	NS	NS	***
Effect of ruminant type			
Buffalo	0.111 ± 0.0715	3.331 ± 2.7980	0.033 ± 0.0261
Cattle	0.058 ± 0.0681	1.865 ± 2.4869	0.049 ± 0.0203
Goats	0.031 ± 0.0699	0.654 ± 9.7886	0.064 ± 0.0202
Sheep	0.058 ± 0.0680	2.672 ± 2.4723	0.042 ± 0.0201
Significance	NS	*	***

Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season. * $p < 0.05$; *** $p < 0.001$; NS, not significant ($p > 0.05$).

Table 5. 13 Effects of feed type, climatic region and ambient temperature on chemical composition of feed samples incubated in the rumen.

Test of Fixed Effects	Chemical Composition Estimates (g/kg DM) (Mean ± SE)					
Effect of Feed Type	**DM**	**CP**	**NDF**	**ADF**	**HEM**	**Ash**
Roughages	822.5 ± 31.30	109.6 ± 8.42	606.5 ± 21.19	395 ± 14.23	211 ± 11.94	90.5 ± 4.58
Concentrates	878.8 ± 38.39	166.7 ± 11.04	355.7 ± 26.32	209 ± 18.15	147 ± 15.06	68.0 ± 5.88
Mixed diets	803.0 ± 63.28	131.9 ± 19.42	590.7 ± 43.67	367 ± 30.96	222 ± 25.39	95.1 ± 10.16
Significance	NS	***	***	***	***	***
Effect of climatic region						
Tropical climates						
Af	806 ± 159.02	83.3 ± 42.56	609 ± 107.82	365 ± 72.17	241 ± 60.67	122.9 ± 23.20
Aw	565 ± 70.91	133.2 ± 19.50	466.0 ± 48.31	297 ± 32.68	168 ± 27.35	88.5 ± 10.54
Arid climates						
BSh	895.5 ± 93.97	112.5 ± 25.69	560.1 ± 63.86	406 ± 43.11	154 ± 36.11	73.4 ± 13.91
BSk	888.4 ± 84.04	85.8 ± 23.87	660.9 ± 57.39	416 ± 39.39	232 ± 32.76	95.9 ± 12.78
BWh	865 ± 129.37	145.1 ± 35.01	481.2 ± 87.81	374 ± 59.04	107 ± 49.53	61.8 ± 19.01
Temperate climates						
Cfa	669.9 ± 72.04	188.1 ± 19.88	517.5 ± 48.96	310 ± 33.19	208 ± 27.75	99.3 ± 10.73
Cfb	781.3 ± 66.44	136.0 ± 18.27	491.6 ± 45.10	300 ± 30.55	193 ± 25.55	68.9 ± 9.87
Csa	772.2 ± 86.29	135.6 ± 23.56	419.7 ± 58.62	275 ± 39.56	144 ± 33.14	91.9 ± 12.76
Csb	493 ± 131.79	153.0 ± 36.01	400.4 ± 90.22	222 ± 60.67	177 ± 50.91	101.7 ± 19.55
Cwa	921 ± 91.90	123.7 ± 24.97	531.0 ± 62.41	315 ± 42.02	215 ± 35.23	70.8 ± 13.54
Cwb	835.3 ± 62.35	126.3 ± 17.13	509.6 ± 42.48	307 ± 28.73	206 ± 24.04	85.4 ± 9.26
Cold climates						
Dfa	884 ± 137.52	201.4 ± 37.25	420.8 ± 93.28	247 ± 62.76	176 ± 52.64	72.4 ± 20.22
Dfb	913 ± 137.48	187.5 ± 37.09	507.0 ± 93.19	273 ± 62.60	235 ± 52.54	48.9 ± 20.16
Dfc	890 ± 232.82	89.7 ± 62.30	657.0 ± 157.7	428 ± 105.6	231 ± 88.77	109.6 ± 33.96
Dsb	928 ± 158.12	139.8 ± 42.50	533 ± 107.19	321 ± 71.88	214 ± 60.38	76.7 ± 23.13
Significance	**	NS	NS	NS	NS	NS
Effect of covariates						
Feed sample						
Silage	***	NS	*	NS	***	*
Urea treatment	NS	NS	NS	*	*	NS
Environmental factors						
Ambient temperature	*	NS	NS	NS	NS	NS
Test of random effects						
Study×incubation time	***	***	***	***	***	***

DM, dry matter; CP, crude protein, NDF, neutral detergent fibre; ADF, acid detergent fibre; HEM, hemicellulose; Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant ($p > 0.05$).

5.3.3.1 Model predictions

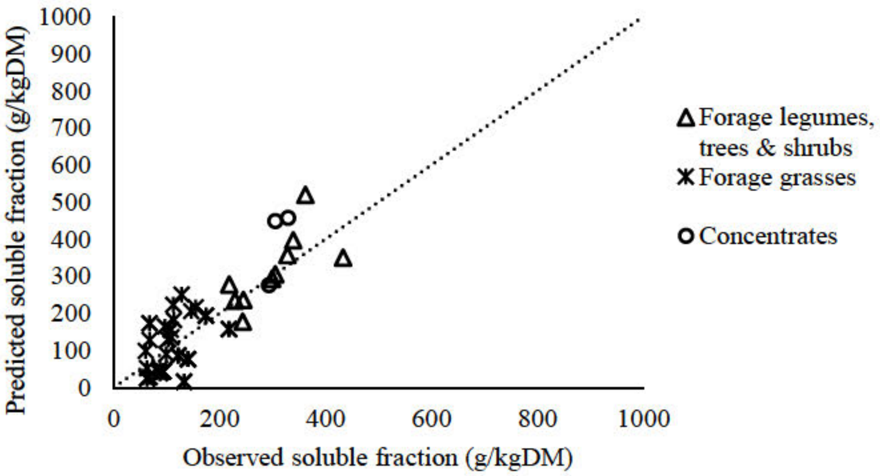


Fig. 5. 2 Relationship between observed and predicted degradability of soluble fraction

The regression model for predicting the soluble fraction of feeds accounted for 70% of the variation in prediction for forage legumes, trees and shrubs, forage grasses and concentrates (Fig. 5.2).

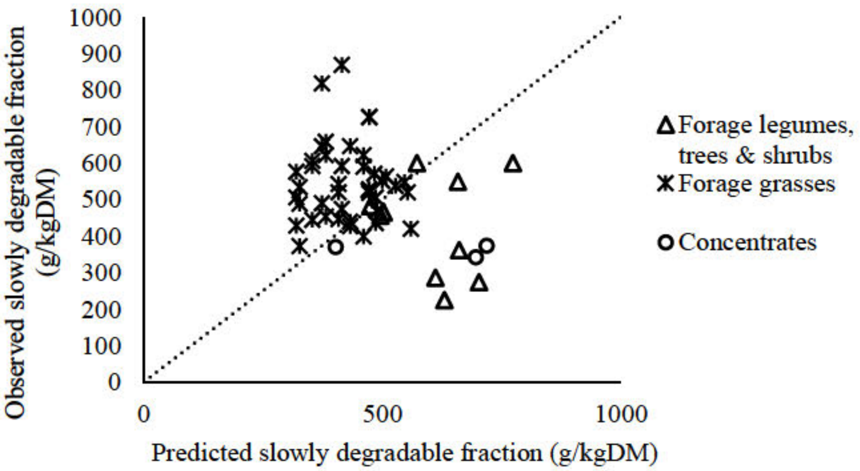


Fig. 5. 3 Relationship between observed and predicted degradability of slowly degradable fraction

The regression model for predicting the slowly degradable fraction of feeds for forage legumes, trees and shrubs, forage grasses and concentrates (Fig. 5.3).

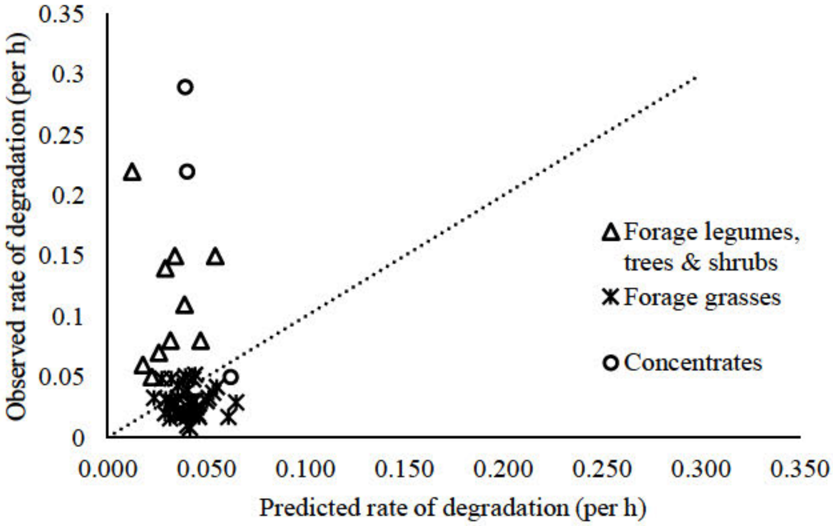


Fig. 5. 4 Relationship between observed and predicted rates of degradation

The regression model for predicting the rate of degradation accounted for 4% of the variation in prediction for forage legumes, trees and shrubs, forage grasses and concentrates (Fig. 5.4).

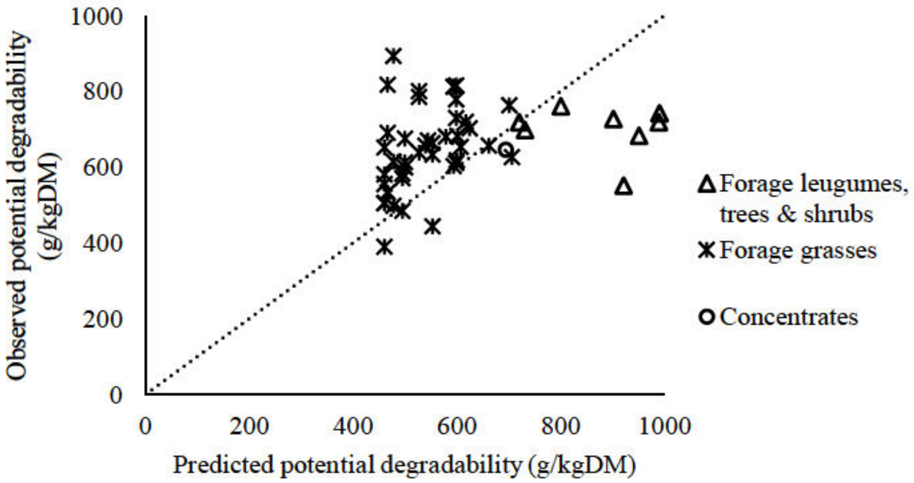


Fig. 5. 5 Relationship between observed and predicted potential degradability

The regression model for predicting the potential degradability accounted for 24% of the variation in prediction for forage legumes, trees and shrubs, forage grasses and concentrates (Fig. 5.5).

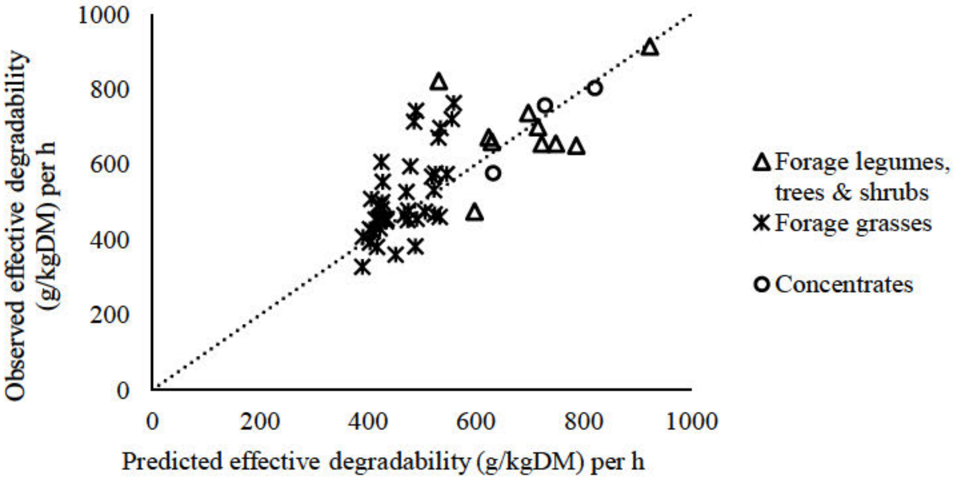


Fig. 5. 6 Relationship between observed and predicted effective degradability

The regression model for predicting the effective degradability of feeds accounted for 57% of the variation in prediction for forage legumes, trees and shrubs, forage grasses and concentrates (Fig. 5.6).

5.3.4 Random Forest models

5.3.4.1 No-lag model

The training and testing datasets for degradability parameters (Tables 5.14 and 5.15) comprised observations from roughages and mixed diets of varying qualities, from 4 climate types of variable ambient temperatures. The models developed in the current work using the lag-time dataset accounted for 88% ("a"), 93% ("b"), 76% ("c") and 90% ("PD") of variation in degradability parameters (Table 5.14). On testing the model with an independent dataset, these models attained 58% ("a"), 52% ("b"), 48% ("c") and 53% ("PD") of variation in predicting degradability parameters (Table 5.15). A few over- and under-predictions of the soluble fraction (Fig. 5.7 a), slowly degradable fraction (Fig. 5.8 b), rates of degradation (Fig. 5.9 b) and potential degradability (Fig. 5.10 b) of roughages were obtained.

A plot of residuals against the predicted solubility fraction gave the equation: Y = -42 (± 4.9) + 0.2 (± 0.02) X ($R^2 = 0.19$; RSE = 35.3). The plot of residuals against the predicted slowly degradable fraction gave the equation: Y = -59 (± 8.1) +0.1 (± 0.02) X ($R^2 = 0.12$; RSE = 41.0). The plot of residuals against the predicted rate of degradation gave the equation: Y = -0.01 (± 0.002) + 0.2 (± 0.03) X ($R^2 = 0.09$; RSE = 0.02). A plot of residuals against the predicted potential degradability gave the equation: Y = -110 (± 13.6) + 0.2 (± 0.02) X (R^2 = 0.14; RSE = 48.3). Intercepts and slopes of the residual plots for all variables were different (P <0.001) from zero, showing that the models had a mean and linear bias.

5.3.4.2 Time lag dataset

The training and testing datasets for degradability parameters (Tables 5.16 and 5.17) comprised observations from roughages and concentrates of varying qualities, from 4 climate types of variable ambient temperatures. Models developed in the current work using the lag-time dataset accounted for 91% ("a"), 84% ("b"), 79% ("c"), 91% ("PD") and 87% (lag) of variation in degradability parameters (Table 9.4). On testing the model with an independent dataset, these models attained 64% ("a"), 57% ("b"), 29% ("c"), 52% ("PD") and 59% (lag) of variation in degradability parameters (Table 5.17). A few over- and under-predictions of the soluble fraction for concentrates (Fig. 5.11), slowly degradable fraction for concentrates and roughages (Fig. 5.12 b), rates of degradation for concentrates, roughages and mixed diets (Fig. 5.13 a and b) and the potential degradability of roughages and concentrates (Fig. 5.14 b) were obtained.

A plot of residuals against the predicted solubility fraction gave the equation: Y = -28 (± 5.9) + 0.1 (± 0.02) X (R^2 = 0.09; RSE = 42.5). The plot of residuals against the predicted slowly degradable fraction gave the equation: Y = -92 (± 16.2) +0.2 (± 0.03) X (R^2 = 0.11; RSE = 59.2). The plot of residuals against the predicted rate of degradation gave the equation: Y = -0.04 (± 0.005) + 0.6 (± 0.05) X (R^2 = 0.33; RSE = 0.07). A plot of residuals against the predicted potential degradability gave the equation: Y = -102 (± 16.8) + 0.1 (± 0.02) X (R^2 = 0.13; RSE = 43.6). A plot of residuals against the predicted time lag gave the equation: Y = -42 (± 4.9) + 0.2 (± 0.02) X (R^2 = 0.19; RSE = 35.3). All intercepts and slopes of the residual plots for all variables were different (P <0.001) from zero, showing that the models had a mean and linear bias.

The capability of the models in predicting degradation of underutilised feeds from plant species not represented in the datasets collected is shown in Table 5.20. The no-lag model gave good predictions of the rates of degradation of all under-utilised feeds, except for *Brassica oleraceae var. acephala* leaves and cassava root peels. The rate of degradation of *Brassica oleraceae var. acephala* leaves was better predicted using the time-lag model.

Table 5. 14 Summary statistics of diet properties, feed sample attributes and animals used in training of Random Forest model for degradation parameters predicted using the no lag model

		Training dataset for degradation parameters (mean ± SD)								
Feed sample type	N	a (g/kg)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	DCP (g/kg)	DNDF (g/kg)	AT (°C)	DSTA (g/kg)	PS (mm)
Roughages	374	201 ± 104.6	739 ± 286.0	572 ± 178.3	113 ± 63.7	110 ± 39.0	590 ± 110.9	21 ± 7.6	299 ± 95.5	2.5 ± 2.82
Mixed diets	22	199 ± 32.6	314 ± 304.1	506 ± 72.4	213 ± 38.0	205 ± 53.6	506 ± 72.4	11 ± 1.9	289 ± 62.4	8.3 ± 3.17
		b (g/kg)								
Roughages	374	496 ± 152.1	745 ± 281.1	576 ± 174.8	112 ± 61.7	110 ± 40.0	589 ± 114.3	21 ± 7.7	300 ± 99.7	2.6 ± 3.72
Mixed diets	22	645 ± 93.1	331 ± 517.3	517 ± 74.2	210 ± 45.5	202 ± 58.7	517 ± 74.2	11 ± 2.7	281 ± 40.3	8.4 ± 2.97
		c (g/kg)								
Roughages	432	0.05 ± 0.037	700 ± 302.7	577 ± 173.7	113 ± 62.9	116 ± 41.5	579 ± 116.4	20 ± 7.7	305 ± 97.5	2.5 ± 2.60
Mixed diets	30	0.05 ± 0.014	297 ± 295.8	512 ± 71.9	213 ± 41.0	208 ± 52.1	512 ± 71.9	11 ± 2.7	280 ± 55.8	8.5 ± 2.98
		PD (g/kg)								
Roughages	386	687 ± 151.3	740 ± 284.1	578 ± 176.9	109 ± 60.8	112 ± 39.7	582 ± 119.3	20 ± 7.8	299 ± 95.5	2.5 ± 2.82
Mixed diets	24	836 ± 89.1	334 ± 321.5	512 ± 76.5	208 ± 45.0	201 ± 57.2	512 ± 76.0	11 ± 3.0	289 ± 62.4	8.3 ± 3.17

a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; DCP, dietary crude protein; DNDF, dietary neutral detergent fibre; AT, ambient temperature; DSTA, dietary starch; PS, particle size; PD: potential degradability.

Table 5. 15 Summary statistics of diet properties, feed sample attributes and animals used in testing of Random Forest model for degradation parameters predicted using the no lag model

		Testing dataset for degradation parameters (mean ± SD)								
Feed sample type	N	a (g/kg)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	DCP (g/kg)	DNDF (g/kg)	AT (°C)	DSTA (g/kg)	PS (mm)
Roughages	154	204 ± 99.9	744 ± 287.8	569 ± 193.3	116 ± 59.7	113 ± 41.1	584 ± 129.8	20 ± 7.9	303 ± 110.4	2.7 ± 4.02
Mixed diets	16	189 ± 37.8	307 ± 318.1	522 ± 81.0	209 ± 52.7	206 ± 57.7	522 ± 81.0	12 ± 4.2	272 ± 31.0	8.6 ± 3.11
		b (g/kg)								
Roughages	154	506 ± 140.1	730 ± 298.4	558 ± 200.2	117 ± 64.5	113 ± 38.6	587 ± 122.0	21 ± 7.7	300 ± 100.7	2.5 ± 1.35
Mixed diets	16	635 ± 79.9	285 ± 276.5	507± 79.3	214 ± 43.6	210 ± 49.8	507 ± 79.8	11 ± 3.7	282 ± 65.6	8.4 ± 3.38
		c (g/kg)								
Roughages	148	0.04 ± 0.021	769 ± 268.4	551 ± 189.7	117 ± 60.4	106 ± 39.3	580 ± 137.5	20 ± 8.2	313 ± 119.0	2.7 ± 4.15
Mixed diets	8	0.05 ± 0.017	365 ± 357.4	516 ± 93.2	203 ± 56.8	197 ± 66.1	516 ± 93.2	12 ± 4.4	287 ± 34.0	8.0 ± 3.72
		PD (g/kg)								
Roughages	163	702 ± 147.1	739 ± 292.0	564 ± 191.8	123 ± 66.0	112 ± 40.7	590 ± 124.9	21 ± 7.6	298 ± 103.3	2.5 ± 1.57
Mixed diets	14	836 ± 106.5	272 ± 284.1	514 ± 76.7	216 ± 43.8	213 ± 51.0	514 ± 76.7	11 ± 3.4	273 ± 41.7	9.0 ± 2.52

a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; DCP, dietary crude protein; DNDF, dietary neutral detergent fibre; AT, ambient temperature; DSTA, dietary starch; PS, particle size; PD: potential degradability.

Table 5. 16 Summary statistics of diet properties, feed sample attributes and animals used in training Random Forest model for degradation parameters predicted using the time lag model

		Training dataset for degradation parameters (mean ± SD)								
Feed sample type	N	a (g/kg)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	DCP (g/kg)	DNDF (g/kg)	AT (°C)	DSTA (g/kg)	PS (mm)
Roughages	188	241 ± 136.3	696 ± 316.1	638 ± 162.8	90 ± 65.1	133 ± 43.0	591 ± 116.2	16 ± 6.6	275 ± 103.0	4.8 ± 14.12
Concentrates	64	221 ± 157.9	874 ± 116.8	337 ± 180.6	186 ± 116.4	122 ± 23.0	502 ± 97.9	12 ± 10.1	375 ± 99.5	2.3 ± 1.12
Mixed diets	1	329.4	927.4	520	130	109.6	386.7	18.2	503.7	2
		b (g/kg)								
Roughages	188	472 ± 134.6	696 ± 316.1	638 ± 162.8	90 ± 65.1	133 ± 43.0	591 ± 116.2	16 ± 6.6	275 ± 103.0	4.8 ± 14.12
Concentrates	64	545 ± 178.4	874 ± 116.8	337 ± 180.6	186 ± 116.4	122 ± 23.0	502 ± 97.9	12 ± 10.1	375 ± 99.5	2.3 ± 1.12
Mixed diets	1	393.5	927.4	520	130	109.6	386.7	18.2	503.7	2
		c (g/kg)								
Roughages	188	0.05 ± 0.159	662 ± 328.3	621 ± 167.0	95 ± 65.4	133 ± 43.4	586 ± 113.6	15 ± 6.4	281 ± 99.3	4.8 ± 14.12
Concentrates	83	0.09 ± 01427	878 ± 104.0	317 ± 177.9	183 ± 115.7	124 ± 26.2	480 ± 121.7	13 ± 8.7	396 ± 126.0	2.3 ± 1.12
Mixed diets	1	0.068	927.4	520	130	109.6	386.7	18.2	503.7	2
		PD (g/kg)								
Roughages	187	715 ± 114.7	682 ± 320.7	623 ± 165.5	93 ± 67.3	134 ± 43.0	581 ± 115.1	15 ± 6.6	285 ± 100.8	4.0 ± 10.23
Concentrates	70	767 ± 196.9	882 ± 102.6	336 ± 187.6	184 ± 119.5	124 ± 27.4	486 ± 121.3	13 ± 8.9	389 ± 125.3	2.3 ± 1.15
Mixed diets	1	722.9	927.4	520	130	109.6	386.7	18.2	503.7	2
		Lag (g/kg)								
Roughages	211	3 ± 2.6	678 ± 322.1	619 ± 167.7	92 ± 64.9	131 ± 41.2	575 ± 117.7	15 ± 6.7	294 ± 103.1	4.4 ± 11.69
Concentrates	73	1.0 ± 3.21	871 ± 108.6	305 ± 183.5	165 ± 105.4	121 ± 23.5	467 ± 127.8	12 ± 9.4	411 ± 129.9	2.4 ± 1.06
Mixed diets	1	0	927.4	520	130	109.6	386.7	18.2	503.7	2

a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; DCP, dietary crude protein; DNDF, dietary neutral detergent fibre; AT, ambient temperature; DSTA, dietary starch; PS, particle size; PD: potential degradability.

Table 5. 17 Summary statistics of diet properties, feed sample attributes and animals used in testing Random Forest model of degradation parameters predicted using the time lag model.

		Testing dataset for degradation parameters (mean ± SD)								
Sample type	N	a (g/kg)	DM (g/kg)	NDF (g/kg)	CP (g/kg)	DCP (g/kg)	DNDF (g/kg)	AT (°C)	DSTA (g/kg)	PS (mm)
Roughages	73	220 ± 114.0	714 ± 307.5	604 ± 182.6	94 ± 65.5	130 ± 41.2	562 ± 120.9	15 ± 6.6	308 ± 101.1	2.7 ± 1.16
Concentrates	36	270 ± 184.3	901 ± 30.3	310 ± 174.5	175 ± 107.4	131 ± 33.2	463 ± 131.8	13 ± 8.0	405 ± 137.1	2.6 ± 1.14
		b (g/kg)								
Roughages	73	508 ± 136.5	714 ± 307.5	604 ± 182.6	94 ± 65.5	130 ± 41.2	562 ± 120.9	15 ± 6.6	308 ± 101.1	2.7 ± 1.16
Concentrates	36	534 ± 183.5	901 ± 30.3	310 ± 174.5	175 ± 107.4	131 ± 33.2	463 ± 131.8	13 ± 8.0	405 ± 137.1	2.6 ± 1.14
		c (g/kg)								
Roughages	61	0.03 ± 0.015	768 ± 274.2	624 ± 176.5	87 ± 66.7	135 ± 34.4	564 ± 124.6	16 ± 6.4	300 ± 110.8	3.3 ± 2.50
Concentrates	23	0.06 ± 0.024	894 ± 36.2	298 ± 187.5	151 ± 92.2	129 ± 28.0	432 ± 112.1	10 ± 10.7	439 ± 117.8	2.5 ± 1.02
		PD (g/kg)								
Roughages	78	725 ± 124.3	723 ± 305.2	637 ± 175.4	86.9 ± 58.9	128 ± 40.1	585 ± 124.0	16 ± 6.6	287 ± 108.3	5.3 ± 15.50
Concentrates	33	822 ± 154.3	882 ± 77.8	295 ± 152.3	171 ± 94.5	129 ± 26.1	472 ± 109.6	11 ± 9.9	400 ± 107.5	2.6 ± 1.04
		Lag (g/kg)								
Roughages	54	3 ± 2.1	755 ± 286.6	659 ± 168. 2	88 ± 65.6	137 ± 46.0	611 ± 113.5	16 ± 6.5	252 ± 95.8	4.4 ± 13.28
Concentrates	34	1 ± 2.4	905 ± 35.9	334 ± 170.4	203 ± 119.7	133 ± 31.2	484 ± 118.7	13 ± 8.6	383 ± 122.6	2.3 ± 1.21

a, rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; DCP, dietary crude protein; DNDF, dietary neutral detergent fibre; AT, ambient temperature; DSTA, dietary starch; PS, particle size; PD: potential degradability.

Table 5. 18 Comparison of the equations for linear regression between observed (Y) and predicted (X) degradability of Random Forest model using training, testing and entire data for the no-lag model dataset

Dataset	N	Intercept	$P_{\text{intercept}}$	Slope	P_{slope}	RSE	R^2
	Soluble fraction (g/kgDM) (mean ± SD)						
Training	396	55 ± 3.0	$P<0.001$	0.7 ± 0.01	$P<0.001$	27.3	0.88
Testing	170	98 ± 7.9	$P<0.001$	0.5 ± 0.04	$P<0.001$	43.9	0.58
	Slowly degradable fraction (g/kgDM) (mean ± SD)						
Training	396	86 ± 6.1	$P<0.001$	0.8 ± 0.01	$P<0.001$	35.4	0.93
Testing	170	218 ± 22.8	$P<0.001$	0.6 ± 0.04	$P<0.001$	78.0	0.52
	Rate of degradation (per h) (mean ± SD)						
Training	462	0.02 ± 0.001	$P<0.001$	0.6 ± 0.02	$P<0.001$	0.01	0.76
Testing	156	0.02 ± 0.002	$P<0.001$	0.5 ± 0.04	$P<0.001$	0.01	0.48
	Potential degradability (g/kgDM) (mean ± SD)						
Training	410	156 ± 9.1	$P<0.001$	0.8 ± 0.01	$P<0.001$	39.5	0.90
Testing	177	310 ± 28.9	$P<0.001$	0.6 ± 0.04	$P<0.001$	78.3	0.53

NS: not significant; RSE: residual standard error

Table 5. 19 Comparison of the equations for linear regression between observed (Y) and predicted (X) degradability of Random Forest model using training, testing and entire data for the lag model

	N	Intercept	$P_{\text{intercept}}$	Slope	P_{slope}	RSE	R^2
		Soluble fraction (g/kgDM) (mean ± SD)					
Training	253	-28 ± 5.9	$P<0.001$	1.1 ± 0.02	$P<0.001$	42.5	0.91
Testing	109	-28 ± 20.8	NS	1.1 ± 0.09	$P<0.001$	85.6	0.64
		Slowly degradable fraction (g/kgDM) (mean ± SD)					
Training	253	-93 ± 16.2	$P<0.001$	1.2 ± 0.03	$P<0.001$	59.2	0.84
Testing	109	-35 ± 47.1	*NS*	1.1 ± 0.09	$P<0.001$	100.7	0.57
		Rate of degradation (per h) (mean ± SD)					
Training	272	-0.04 ± 0.005	P<0.001	1.6 ± 0.05	$P<0.001$	0.070	0.79
Testing	84	0.02 ± 0.005	p<0.001	0.5 ± 0.09	$P<0.001$	0.018	0.29
		Potential degradability (g/kgDM) (mean ± SD)					
Training	258	-102 ± 16.8	$P<0.001$	1.1 ± 0.02	$P<0.001$	43.6	0.91
Testing	111	21 ± 67.8	*NS*	1.0 ± 0.09	$P<0.001$	97.7	0.52
		Time lag (h) (mean ± SD)					
Training	284	-0.6 ± 0.09	$P<0.001$	1.3 ± 0.03	$P<0.001$	1.05	0.87
Testing	88	-0.1 ± 0.25	*NS*	1.1 ± 0.10	$P<0.001$	1.50	0.59

NS: not significant; RSE: residual standard error

Table 5. 20 Comparison of the time lag and no-lag models in prediction of degradation of underutilised feeds of plant species not represented in the datasets used in model development

Feeds		a (g/kg)	b (g/kg)	c (per h)	PD (g/kg)
Brown *Colophospermum mopane* leaves	Observed	519	224	0.060	743
	Predicted – NLM	268	462	0.072	703
	Predicted – TLM	289	460	0.052	752
Green *Colophospermum mopane* leaves	Observed	358	361	0.070	719
	Predicted – NLM	279	472	0.074	738
	Predicted – TLM	238	467	0.053	706
Colophospermum mopane pods	Observed	398	286	0.110	684
	Predicted – NLM	282	471	0.073	738
	Predicted – TLM	245	443	0.068	677
Mucuna pruriens leaves	Observed	178	550	0.080	728
	Predicted – NLM	267	473	0.064	719
	Predicted – TLM	234	449	0.036	681
Manihot esculenta root peels	Observed	293	600	0.220	893
	Predicted – NLM	280	452	0.065	672
	Predicted – TLM	226	450	0.041	680
Afzelia quanzensis pods	Observed	278	274	0.050	552
	Predicted – NLM	280	474	0.044	714
	Predicted – TLM	167	516	0.097	640
Brassica oleraceae var. acephala leaves	Observed	351	600	0.150	951
	Predicted – NLM	246	603	0.093	708
	Predicted – TLM	293	482	0.117	758

a: rapidly degradable fraction; b, slowly degradable fraction; c, rate of degradation; PD: potential degradability; NLM: no lag model; TLM: time lag model.

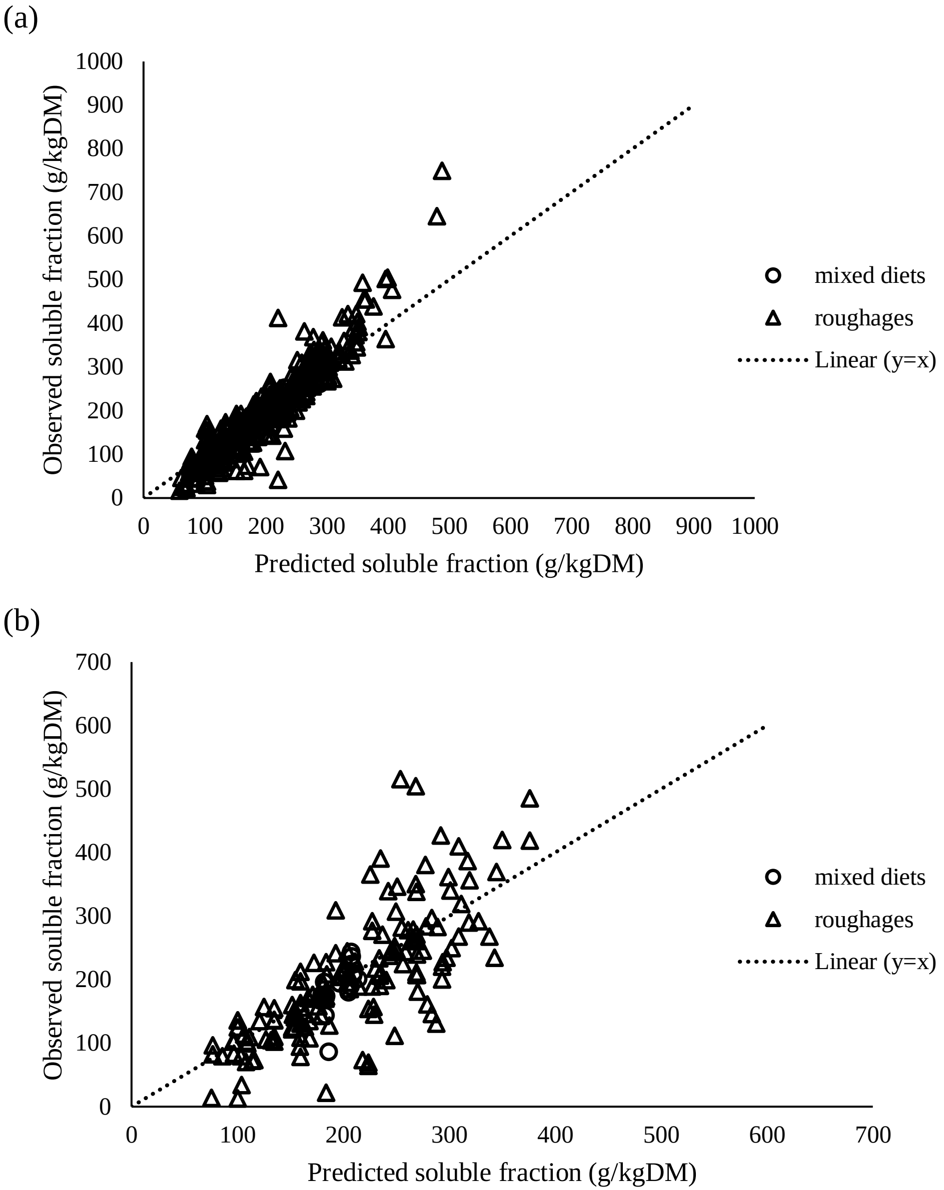


Fig. 5. 7 Relationship between the observed and predicted soluble fraction in (a) training and (b) testing of no time lag Random Forest model.

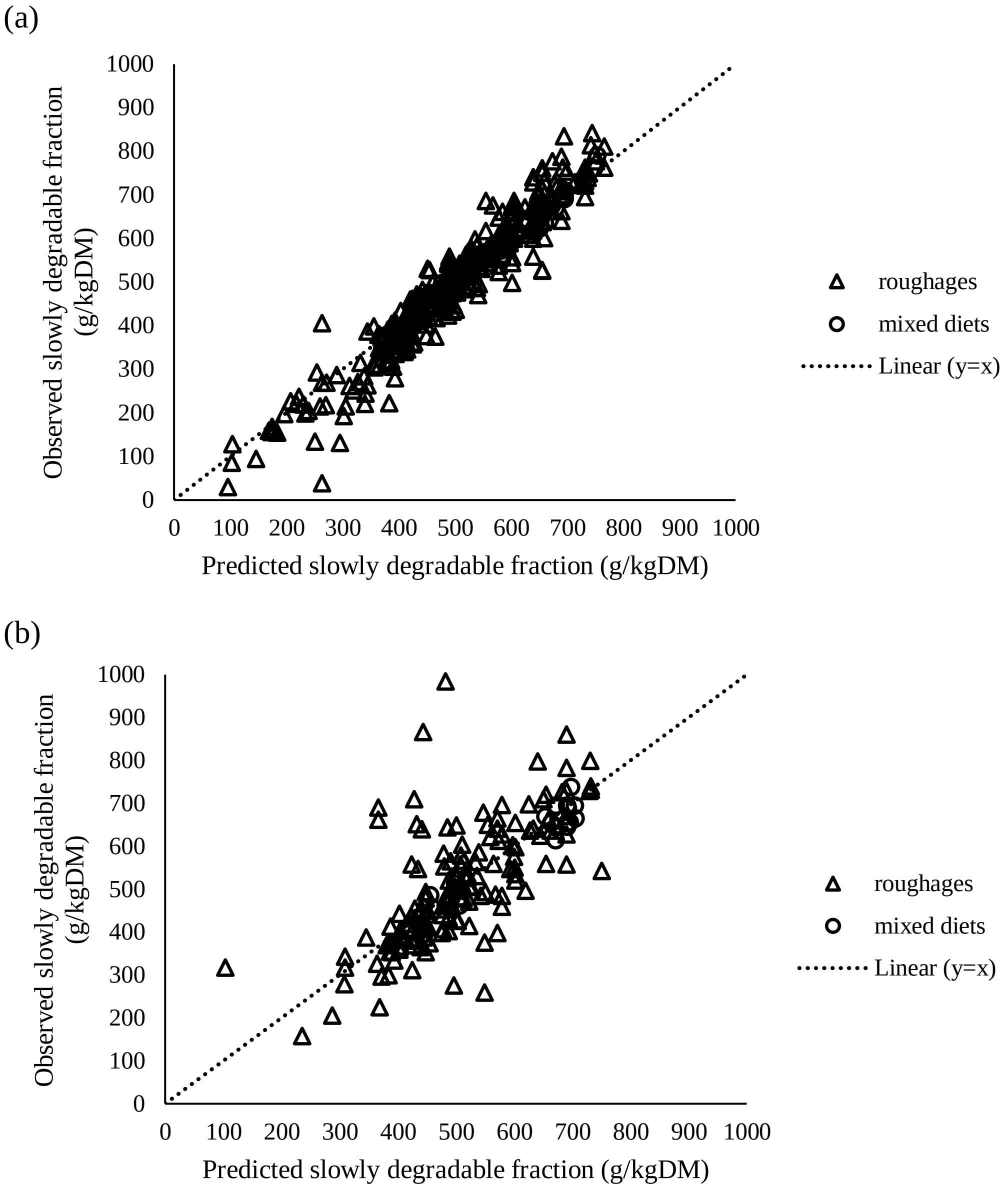


Fig. 5. 8 Relationship between the observed and predicted slowly degradable fraction in (a) training and (b) testing of no time lag Random Forest model.

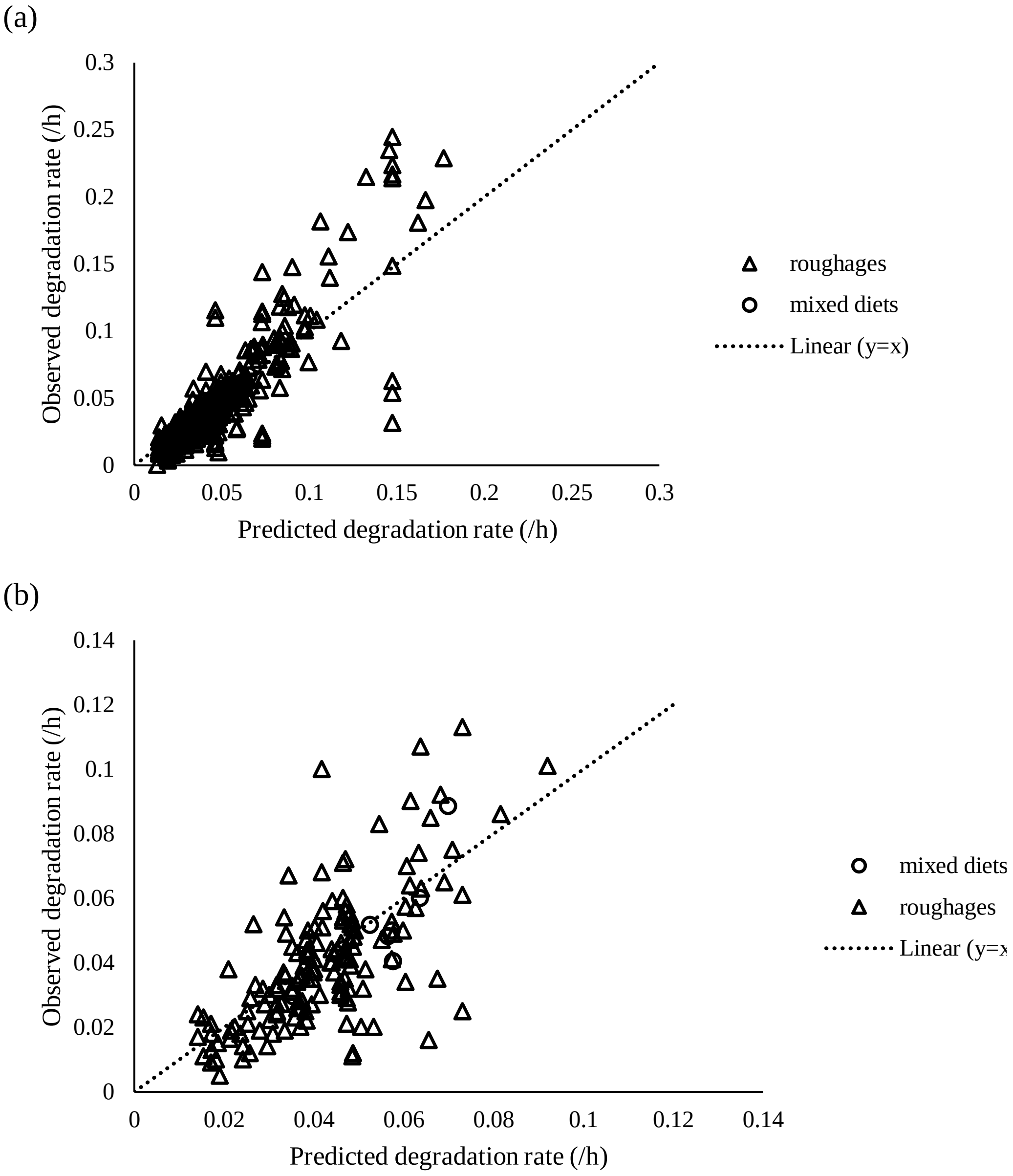


Fig. 5. 9 Relationship between the observed and predicted degradation rates in (a) training and (b) testing of no time lag Random Forest model.

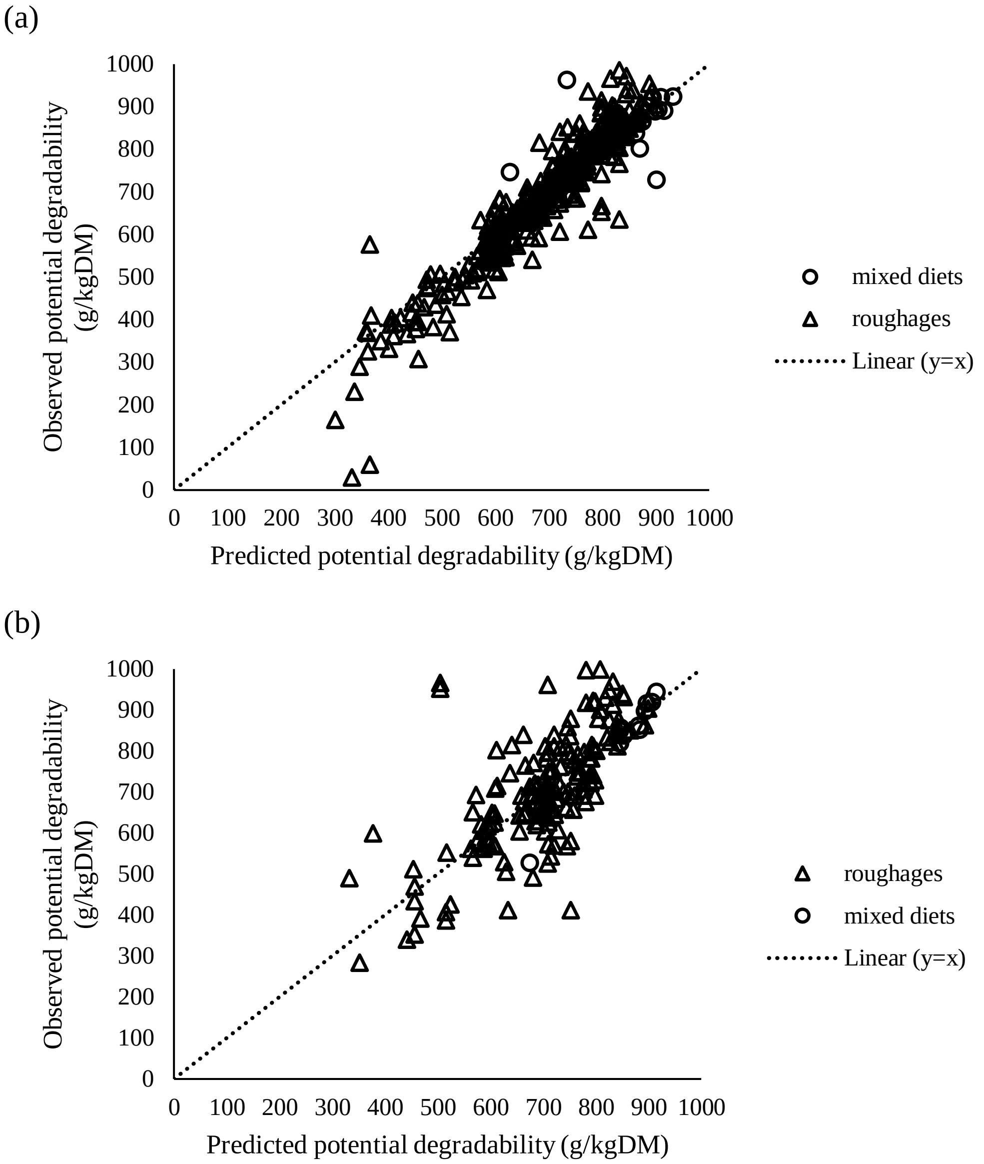


Fig. 5. 10 Relationship between the observed and predicted potential degradability in (a) training and (b) testing of no time lag Random Forest model.

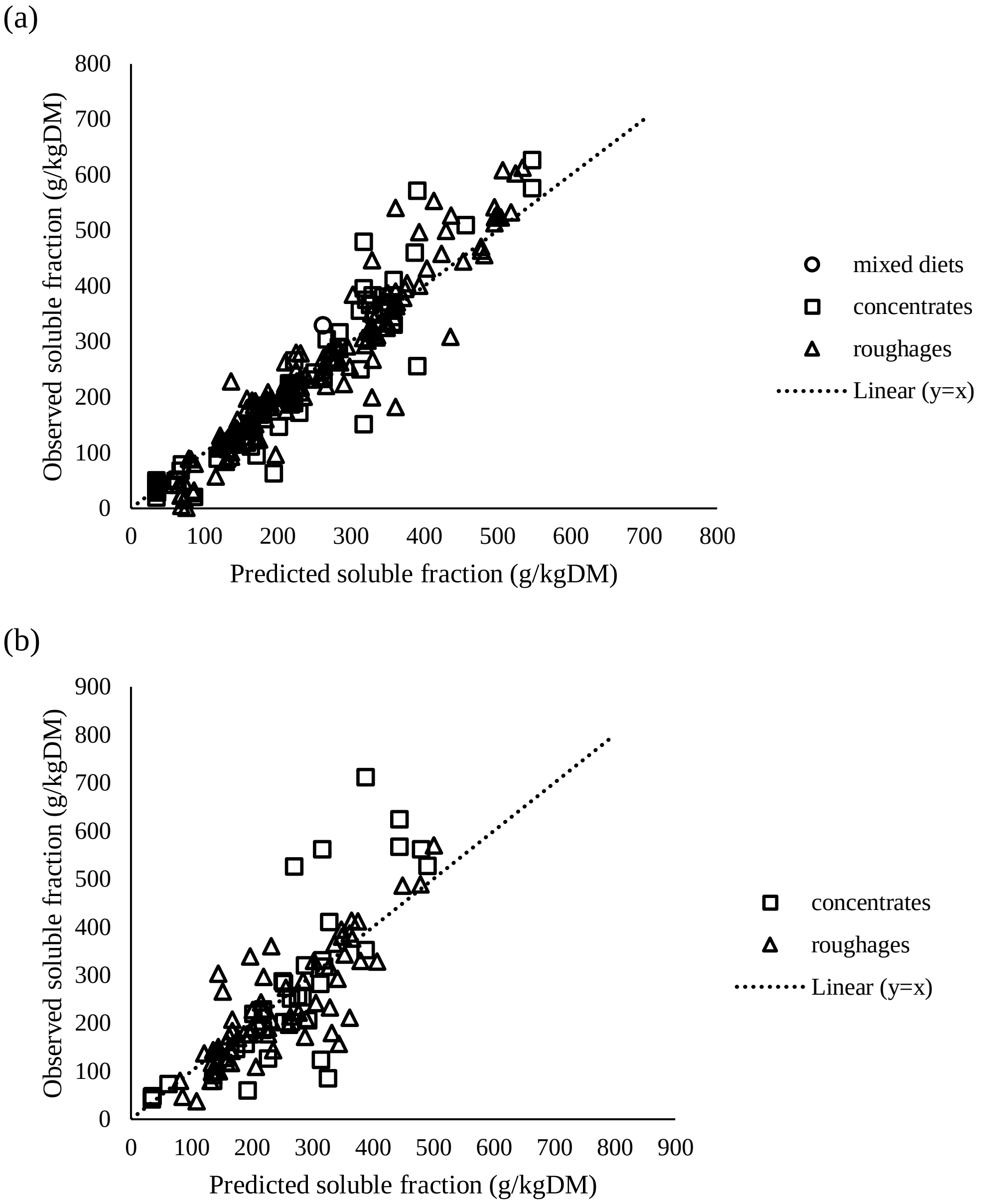


Fig. 5. 11 Relationship between the observed and predicted soluble fraction in (a) training and (b) testing of the time lag Random Forest model.

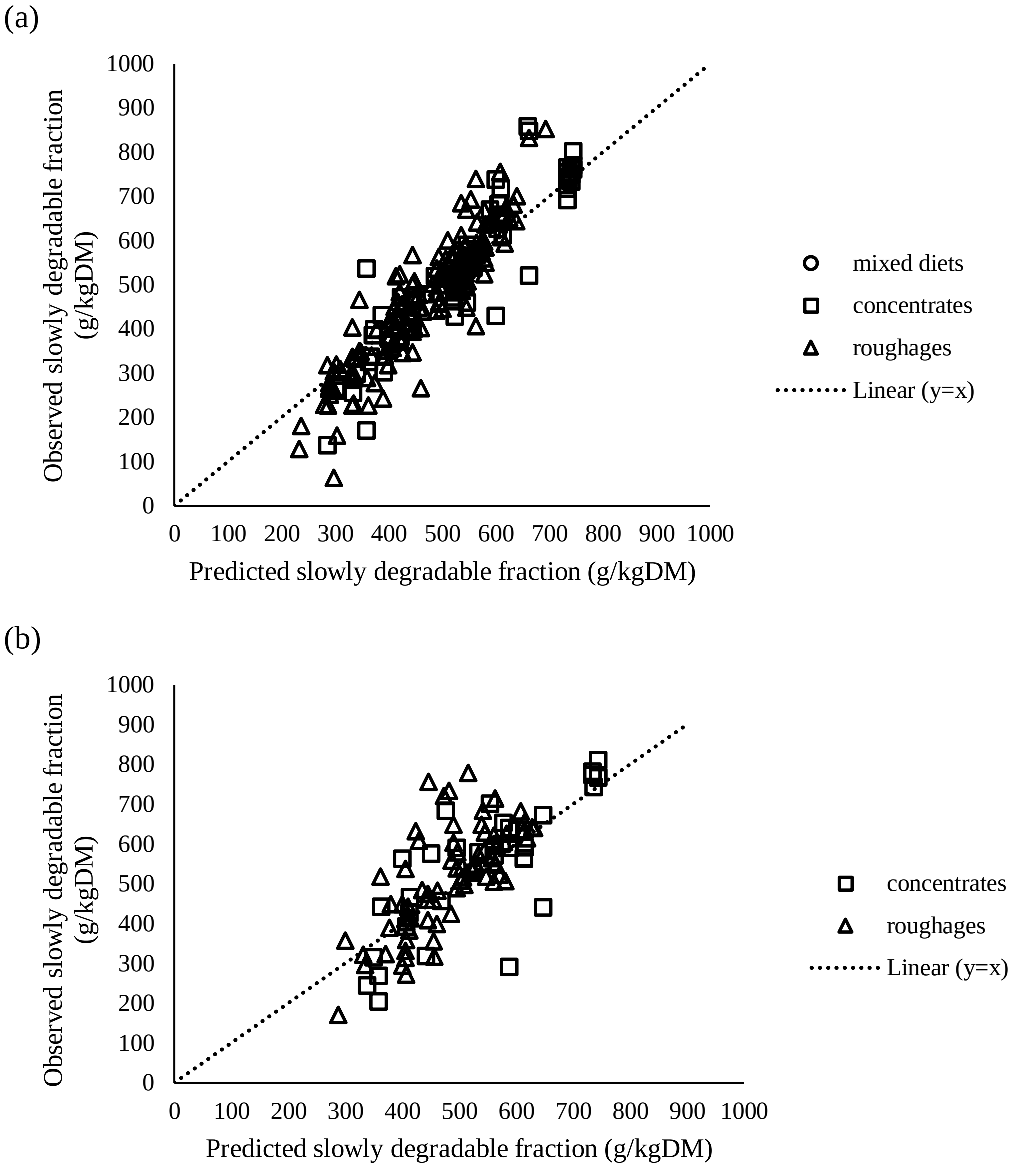


Fig. 5. 12 Relationship between the observed and predicted slowly degradable fraction in (a) training and (b) testing of the time lag Random Forest model.

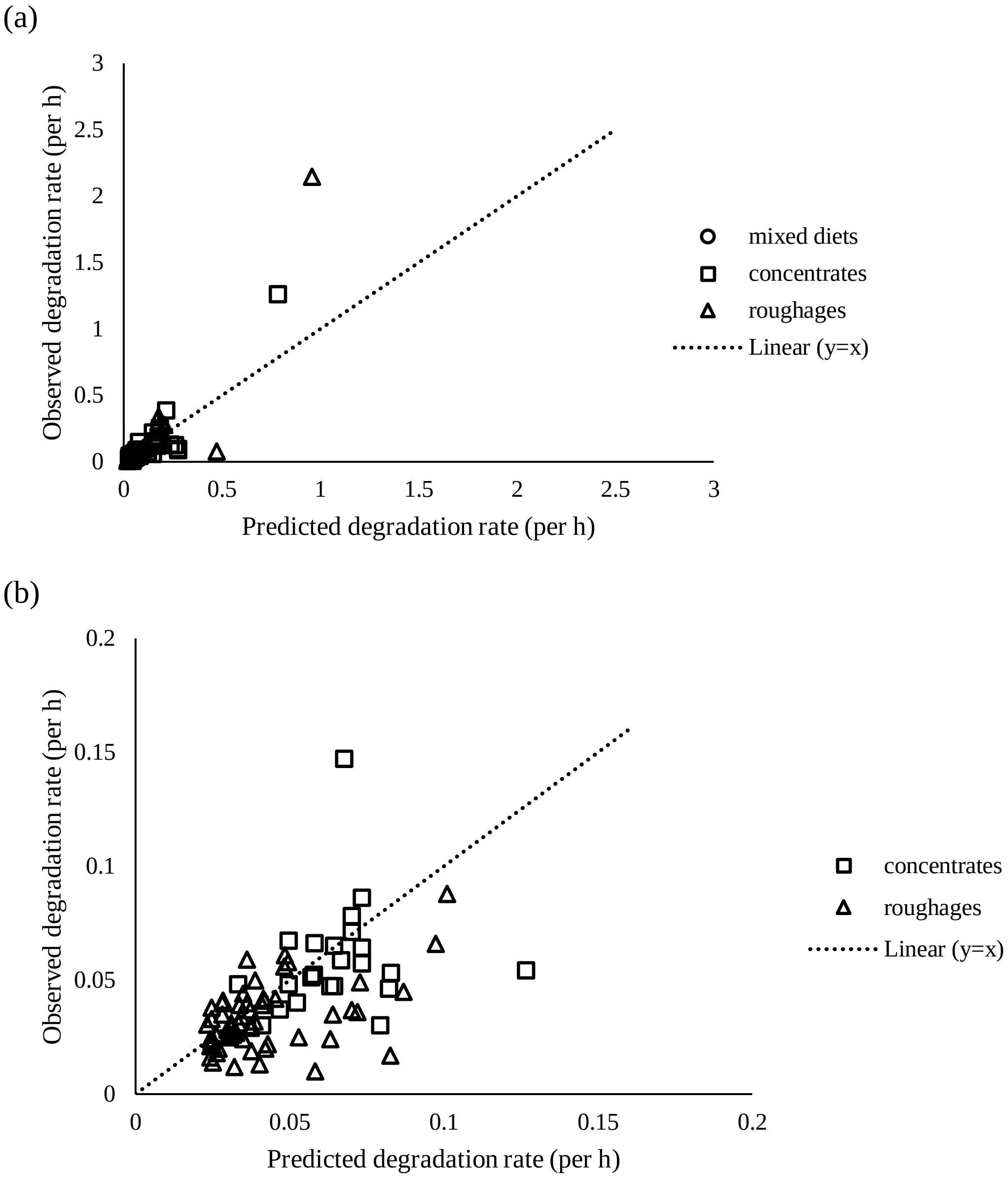


Fig. 5. 13 Relationship between the observed and predicted degradation rates in (a) training and (b) testing of the time lag Random Forest model.

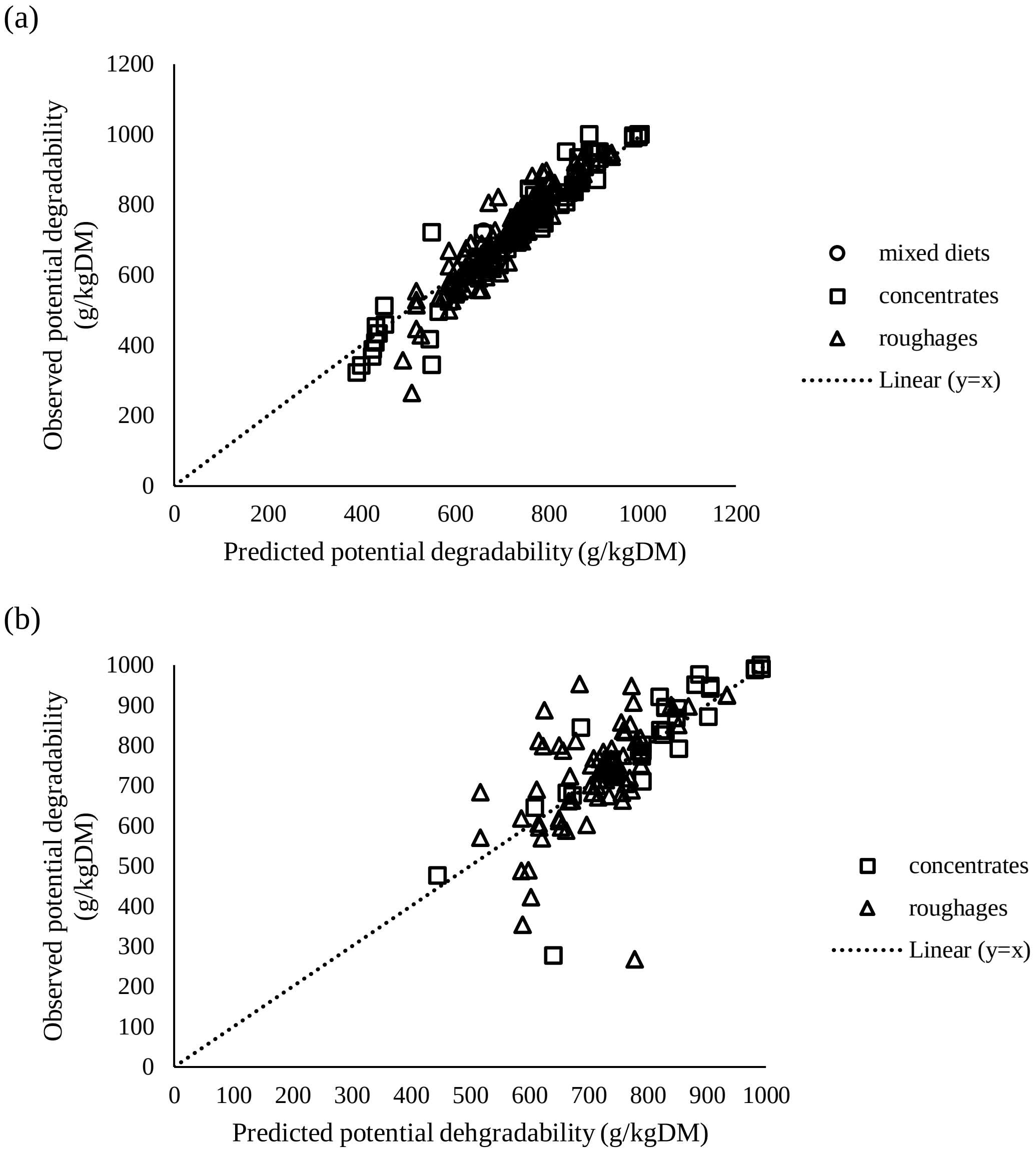
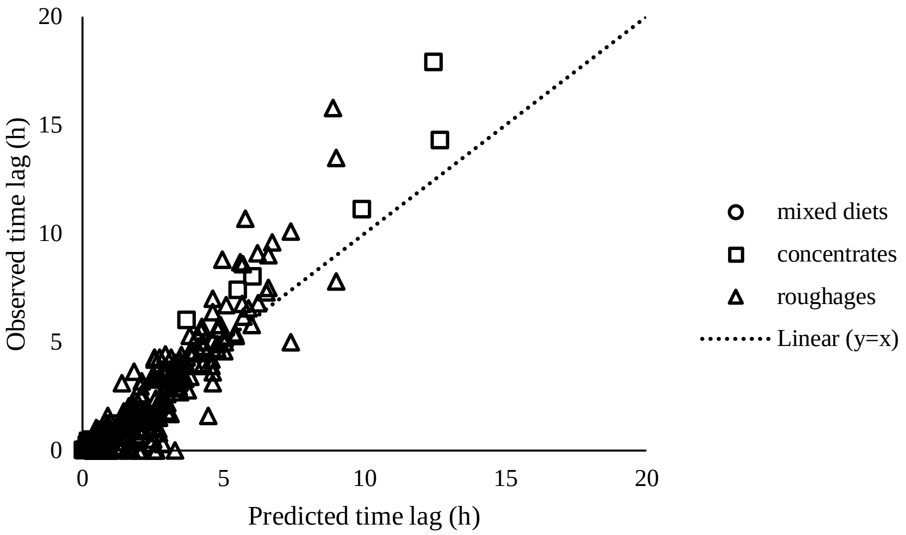


Fig. 5. 14 Relationship between the observed and predicted potential degradability in (a) training and (b) testing of the time lag Random Forest model.

(a)



(b)

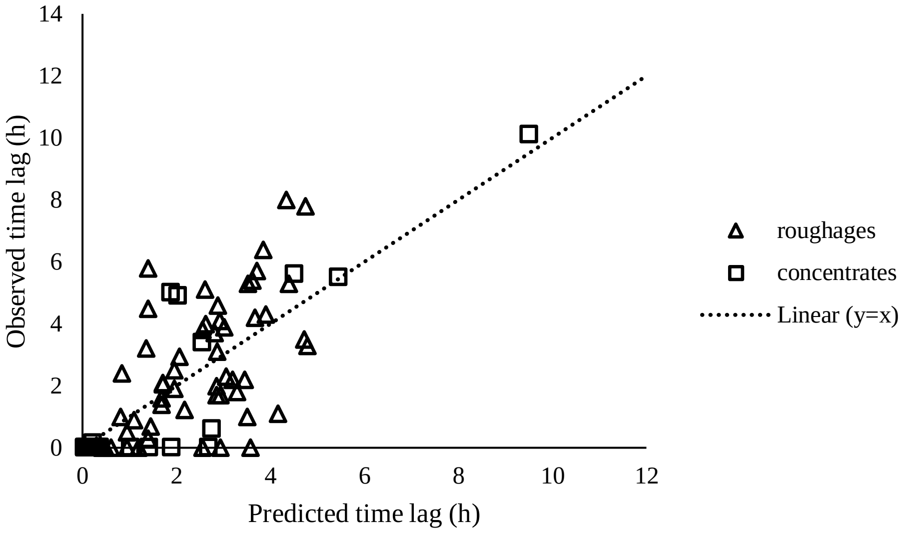


Fig. 5. 15 Relationship between the observed and predicted time lag in (a) training and (b) testing of the Random Forest model.

5.4 Discussion

5.4.1 Evaluation of the nutritional value of underutilised forages and roughages

Among the forage legumes, trees and shrubs, *Brassica oleracea var. acephala* leaves had a superior crude protein content and the lowest neutral and acid detergent fibre contents. The CP content of *Brassica oleracea var. acephala* is slightly higher than those reported by McDonald et al. (1981) and Barry et al. (1984). The rate of degradation of *Colophospermum mopane* pods was similar to that of *Brassica oleracea var. acephala*. High levels of degradability of these feeds were partly due to high levels of crude protein which could help in the proliferation of microbial populations in the rumen, increasing ED and rate of degradation of these forages. Faster rates of degradation may suggest faster rates of passage of these feeds in the rumen, which could increase microbial protein supply for host animals in the hindgut, improving animal's nutritional status. The CP level in *Colophospermum mopane* leaves was similar to, while NDF contents tended to be comparably higher than those reported by other authors (Halimani et al. 2005, Lukhele and Van Ryssen 2005).

5.4.2 Meta-analysis of the rumen degradation of feeds

Changing climatic conditions towards global warming are projected to reduce forage quality, but little is known concerning the extent of reduction in a parameter such as the digestibility of feeds. Determining the extent of the overall effects of climates and global warming on feed nutritional composition and in-vivo digestibility using controlled experiments is challenging because of the need for replication of a wide range of ambient temperature treatments and other environmental factors. A meta-analysis evaluation would help us to infer on the effect of ambient temperature on digestibility and how forages (feeds) would respond under future climate change scenarios. The main motive for this study was to simulate how forage quality and digestibility would respond under future climate change scenarios. It is worth noting that, in the estimation of degradation parameters, different mathematical models give rise to a variation in these estimates and discrepancies are highlighted in various sections of this discussion.

5.4.2.1 Implications of Using the no Time-Lag and Time-Lag Models on the Rate of Degradation

Degradability parameters (a, b, c and PD) are generally predicted by fitting dry matter loss from nylon bags using 2 types of models, one that accounts for and another that does not account for the time-lag. The no lag model by Orskov and McDonald (1979) takes the form $Y = a + b\ (1 - e^{-ct})$ and is suitable for feeds with low fiber content; and the model that accounts for the time-lag by McDonald (1981) takes the form $Y = a + b\ (1 - e^{-c(t - L)})$ and is suitable for fibrous feeds; where: Y = degradability at time (t), a = intercept (rapidly soluble fraction or solubility), b = slowly degradable fraction, c = rate of degradation of the slowly degradable fraction (b) and L = lag time. The time-lag is the period of colonization occurring between the washing away of solubles and the initial commencement of fermentation of feed by bacteria. Quantification of this time lag is crucial in determining the exact rate of degradation of a feed particle in the rumen. Not accounting for time-lag can either depress (for roughages) or inflate (for all feed types) the rate of degradation and gives erroneous estimates because there is time required for feed particles to be colonized before degradation commences. Hence, the model that does not account for time-lag can underestimate the rate of degradation of the slowly degradable fraction. For reporting purposes, workers should consider predicting degradation parameters using the model that accounts for the time-lag.

An option for workers that prefer using the model that does not account for time-lag, an additional parameter called the “wash-loss” should be reported instead for example Navatne and Ibrahim (1988) and Umunna et al. (1995). The wash-loss value can be used to re-calculate the rate of degradation. The sigmoid shaped degradability curve (using the no-time lag model) can be reconstructed and plotted together with the linear wash-loss curve. The two curves intersect at the coordinates (Lag time; wash-loss value). The lag time for degradation to occur can be determined from the points of intersection of these two curves. The rates of degradation and time lag preceding degradation in studies that use the no time lag model can then be recalculated. The new rates of degradation (‘c’) can be calculated using the time lag model at the point of inflection where the rate change was fastest normally assumed to occur at an approximate range of 9-24 h of incubation for most feed types.

Computation of the rates of degradation using the time-lag model may result in negative values for time lag being reported and these negative lag times have no biological meaning. It is more appropriate to assume all negative lag-times for degradation to commence at 0 h, especially feeds classified as concentrates. Studies that seek to predict or simulate degradation rates should separate datasets based on which of the two models were used to estimate degradation rates to avoid under predicting the rate of degradation, in a similar way to the meta-analysis of Busanello et al. (2017).

5.4.2.2 Effects of Climate and Ambient Temperature on Degradation of Forages

Expectedly, the potential degradability and the rate of degradation of roughages were lower than that of concentrates, while feeds from cold and temperate climates were digested faster than feeds from tropical and arid climates. The effect of climatic region on digestibility of roughages was evident from a study by Nsahlai and Apaloo (2007). In their evaluation of temperate roughage-based digestibility models, Illius and Gordon (1991) predicted the digestibility of tropical roughages, whereby the overall trend between the observed and the predicted digestibility was positive, achieving accuracies of 36-52%. Nsahlai and Apaloo′s (2007) evaluations using tropical roughages did not compare well with accuracies of approximately 70% obtained from model evaluation using temperate roughages. These low levels of accuracy of simulating the digestibility of low-quality roughages commonly grazed and fed to ruminants in the tropics may have been due to the effect of ambient temperature on digestibility of plant material (Nsahlai and Apaloo 2007), for which the effect has been indexed. The effects of AT on degradability of feeds in the rumen may occur in two ways: firstly, through changing the chemical composition of feed sample and secondly by possibly altering rumen physiological processes.

There are suggestions that increases in AT would affect the degradability of feeds in the rumen by increasing the lignin and NDF (Sanz-Saez et al. 2012) and decreasing the CP content of feeds, thereby lowering the rate of degradation and PD of feeds (Polley et al. 2013). Elevated levels of AT increase NDF, but decrease the CP content of feeds, lowering feed quality (Rojas-Downing et al. 2017). In this study, gradual increases in ambient temperate had a negative linear effect on the PD and b-fraction. This observation can be partially supported by the positive relationship between NDF and AT, which increases NDF content of feeds with increases in AT, lowering PD of feeds. Miaron and Christopherson (1992) observed a quadratic relationship between apparent digestibility (Y) and temperature (X) that took the form $Y = 69 - 0.188x - 0.017x^2$. Findings from this meta-analysis suggest that, with global warming, the quality of feeds, based on rumen degradability would most likely decrease by 0.6% for every 1 °C increase in ambient temperature. A favourable increase in rumen degradability, PD, would be expected in regions where temperatures are predicted to decrease due to climate change.

Contrary to trends observed in this study, a decrease in AT from 21 °C to 0 °C did not significantly affect nylon bag degradability of cell wall constituents, although feed form × ambient temperature interactions affected the rate of degradation of cell wall constituents (Kennedy 1985). Again, prolonged exposure of sheep and steers to cold temperature of approximately 2 to 5 °C would cause a depression in apparent dry matter digestibility of 0.2% and 0.08% per degree Celsius compared to sheep and steers exposed to temperatures of 22 to 25 °C, respectively. The decrease in digestibility at low ambient temperatures can be attributed to increases in the rate of passage of digesta in through the rumen (Christopherson 1976), limiting time taken for fermentation to occur. Apparent digestibility of dry and organic matter on average were 17% higher at 28 °C than at 10 °C in steers (Miaron and Christopherson 1992). The regression of pooled data from 16 studies showed a positive trend between digestibility and ambient temperature (Christopherson and Kennedy 1983), contrary to the trend from this study where rumen digestibility decreased with an increase in AT.

Kennedy et al. (1976) reported a decrease in digestibility of organic matter in the rumen (F) with exposure of sheep to AT of −1 to 1 °C and 18 to 21 °C, and was highly correlated to solid digesta passage rate (kp) in the rumen ($F = 14.57\ kp + 239$; $R^2 = 0.90$, $SE = 32.6$).

Low AT (−1 to 1 °C) caused faster liquid and solid digesta passage rates in sheep compared to high AT (18–21 °C) (Kennedy et al. 1976; 1982; Kennedy and Mulligan 1978), but did not have an effect on digesta passage rates (Kennedy 1985), while high AT (41 °C) caused faster liquid passage rates compared to low AT (26 °C) in swamp buffalo (Chaiyabutr et al. 1987). Theoretically, degradability of DM in the rumen is expected to decrease with an increase in AT, due principally to deceased rate of digestion consequent upon higher lignification and faster rates of passage of digesta in the rumen at low AT. Fast passage rates of digesta in the rumen decreases the maintenance energy requirements and mean age of microbial population causing an abundance of young microbial cells with high growth potential which is lacking in old bacterial cells (Isaacson et al. 1975). Abundance of young bacterial cells in the rumen translates to increased rate of degradation and high PD in the rumen. Findings of this study that showed a linear decrease in PD with increasing AT are supported by this theory. Another point of contention would be that an increase in passage rate of solid digesta in the rumen would reduce mean retention time of feed in the rumen for microbial fermentation. Low mean retention times as a result of sheep exposure to low AT (−1 to 1 °C) would be expected to reduce digestibility of feed in the rumen compared to sheep exposed to high AT (18 to 21 °C), consistent with findings of Kennedy et al. (1976; 1982) and Kennedy and Mulligan (1978). Empirical findings available on the nature of the relationship between AT and digestion gave a different trend to those obtained from this study. These may be attributed to that most published studies have evaluated relatively narrow ranges of ambient temperatures and at the very best compared two or three temperature treatments (Christopherson and Kennedy 1983; Miaron and Christopherson 1992). Increases in AT have an overall effect of increasing lignin and ultimately NDF content of feeds (Sanz-Saez et al. 2012; Polley et al. 2013). The overall positive linear trend between NDF content of feeds and AT, and a significant negative correlation between NDF content of feeds and PD observed in this study, strongly support the theory that increases in AT would most likely cause a decrease in PD of feeds in the rumen.

Predictions from this study showed a sharp decrease in PD of concentrates compared to roughages. The rate of decrease of degradability of the slowly degradable fraction per unit increase in AT followed the trend: mixed diets > concentrates > roughages. Roughages had the least negative response in PD to increases in AT. High NDF and ADF contents of feeds reduce dry matter digestibility (Riaz et al. 2014). Because roughages had high NDF content compared to concentrates, it was expected that concentrates would have a much greater rate of decrease in PD per unit increase of AT. The digestibility of concentrates was more susceptible to influences of ambient temperature, contrary to Christopherson and Kennedy

(1983) where digestibility of slowly degradable forages appeared to be more susceptible to influence by ambient temperature induced changes compared to rapidly degradable forages. The higher the ambient temperature, the lower the CP of feeds, as evidenced by the significant negative correlation between these two variables. This would most likely decrease the PD of feeds in the rumen.

Trends observed in this study suggested that average crude protein content of feeds incubated in the rumen was highest for cold climates, followed by temperate climate, then arid climates and lowest for tropical climates. Feeds from arid desert climates characterised by low erratic rainfall had similar crude protein content to feeds in high rain fall tropical rain forest climates. This may be because plants from arid desert climates grow fast and reach maturity quickly when water is available and deposit less lignin making the resultant feeds to be of good quality with relatively high CP and low NDF. The potential degradability of feeds in cold climates (Dfa and Dfb) was lowest compared to tropical, arid and temperate climates, although feeds from cold climates had one of the highest crude protein contents.

5.4.2.3 Effects of Diet and Feed Sample Chemical Content on Degradation

There was a significant positive relationship between PD and dietary crude protein. Increasing crude protein content of diets fed to ruminants increased PD of feeds in the rumen. Riaz et al. (2014) also reported a positive influence of dietary crude protein on dry matter digestibility in buffaloes, cattle, sheep and goats. Bonsi et al. (1994) showed that graded levels of *Sesbania sesban*, which were used to gradually increase dietary crude protein content, tended to increase the rate of degradation. A constant supply of energy and crude protein from the diet is required for bacterial population growth and proliferation responsible for most degradation in the rumen. Thus, an increase in dietary crude protein is expected to increase the PD of feeds. This trend is substantiated by the significant positive correlation between dietary crude protein content and degradation parameters (a, b, and PD) observed in this study. The response of degradation of mixed diets to increased dietary crude protein levels was higher than for roughages. This is because roughages generally tend to be of lower quality (high NDF and low crude protein contents) than mixed diets, lowering the response of rate of increase of degradation of roughages to incremental levels of dietary crude protein.

The PD for roughages was lower than that of concentrates and mixed diets. Due to better proximate nutritional composition, it is expected that the digestion of concentrates would be higher than that of roughages. The faster rates of digestion and high digestibility of concentrates (grain meals, seeds and fruits) compared to roughages (Asizua et al. 2018), concentrates are incubated for much shorter periods compared roughages. The high PD of concentrates compared to roughages may be linked to lower average duration of incubation times observed in studies that measured degradation of concentrates (48–70 h) compared to roughages (117 h) and mixed diets (275 h). The average incubation time of feeds in all studies in the dataset was approximately 120 h, showing that concentrates reach their PD relatively earlier (48 h).

Potential degradability is a feed property that is affected by the rumen ecology because of degradation rate and length of incubation of fibrous feeds (Krizsan and Huhtanen 2013), where shorter durations of incubations point to imprecise estimates. A shorter incubation time of feeds in the rumen can bring about erroneous estimates of PD by either depressing the PD for roughages or inflating the PD when the degradation curve is terminated at a point where the curve is still rising before it reaches a horizontal asymptote. Although not tested in their study, findings of Tolera and Sundstøl (2013) showed increased dry matter disappearance (DMD) with increasing incubation time for maize stover (DMD4h = 18.5%, DMD24h = 36%, DMD48h = 51%, and DMD96h = 66%) and *Desmodium intortum* hay (DMD4h = 29.1%, DMD24h = 54.4%, DMD48h = 65.1%, and DMD96h = 67.2%). This trend is consistent with the positive significant correlation between incubation time and PD observed in this study. A meta-analysis finding by Busanello et al. (2017) showed that the degradation of dry matter was similar for meals (oil cakes) and grains (concentrates).

Climatic region did not affect rates of degradation of feeds in the rumen. This may have been due to the similar neutral detergent fibre content of feeds from all climatic regions. Feeds of high ash content had better PD in the rumen, probably facilitated by the catalytic effects of ash on bacteria in the rumen. Contrary to our findings, ensilage of feeds tended to increase the effective degradation of dry matter and acid detergent fibre in the rumen compared to fresh feed samples (Cushnahan et al. 2013).

The negative effects of ambient temperature on forage quality have major implications to small ruminant feeding. Small ruminants possess a small rumen fermentation capacity with respect to their high metabolic requirements and, consequently, select and consume a better-quality diet, which is retained and digested for short periods rendering reduced potential for maximal degradation of low-quality roughages (Demment 1982; Demment and Van Soest 1985). Under future climate change scenarios where increases in AT are anticipated, the observed trend in the decrease in digestibility of feeds with increases in AT in this study cannot be overlooked. Although the 0.6% decrease in PD per 1 °C increase in AT (−5.9 to 28.2 °C) may seem small, it may have dire consequences to ruminant livestock performance. The predicted decrease in PD would be most severe in tropical areas where most grass species are generally of low quality compared to temperate grasses. Findings from this study predicted a sharp decrease in PD of concentrates (−0.7%), in which concentrates had the sharpest decline compared to roughages and mixed diets. Cereal grain concentrates are mainly used to supplement ruminant livestock in tropical areas, where ambient temperatures are generally high, suggesting that most cereal grains will decrease in digestibility. The implications for ruminant livestock would be a decrease in their performance attribute. Alternative feeding strategies, such as urea supplementation and treatment of poor-quality roughages would need to be adopted to improve the nutritional status of ruminant livestock (Salem and Smith 2008; Rust and Rust 2013). The adoption of drought-tolerant ruminant livestock species and/or breeds that are capable of efficiently utilising poor-quality roughages needs to be undertaken. This would entail exploiting local or indigenous breeds of cattle, sheep, and goats.

5.4.3 Performance of linear regression in prediction of rumen degradation of feeds

Relationships between two variables is said to be ideal when the coefficient of determination (R^2) is unity; any deviation from unity degree indicates the degree of imperfection. The above parameter were used to determine the effective degradability (ED): (ED=a + (PD - a) x c/(c + kp); where ‘a’ is soluble fraction, PD is the potential degradability, ‘c’ is the rate of degradation and kp is the rate of passage of particles through the rumen. Effective degradability is equivalent to digestibility in the rumen. The predicted effective degradability indicated in Fig. 5.6 followed the expected trends, suggesting that these models (for predicting ‘a’, PD, and ‘c’) in the meantime can be used for this purpose. The overall trend between the observed and the predicted digestibility is positive, though accounting for just 36-52% of the total variation (Nsahlai and Apaloo 2007), which does not compare favorably with R^2 of 70% obtained with the application of the simulation model to temperate roughages (Illius and Gordon 1991) and those from this study. The amount of variation accounted for in observed against predicted digestibility for simulations by Nsahlai and Apaloo (2007) were comparably higher than those reported in empirical studies by Shem et al. (1995), Kibon and Orskov (1993) and Umunna et al. (1995).

The rather low precision in predicting the rate of degradation (mainly for concentrates, legume forages, trees and shrubs) and the potential degradability (concentrates) of feeds in this study may have been due to the fact that the studies that were used in model development reported data on degradation of roughages grasses only, which are generally of low quality, and did not use data on concentrates, legume forages, trees and shrubs. Despite this, simulations of solubility and effective degradability were good, suggesting that slight modification of model parameters may give better prediction of all degradability (nutritive value) of a large number and classes of forage crops. Generally, there is poor simulation of digestibility for low quality roughages, which are commonly grazed and fed to ruminants in the tropics. Ambient temperature grossly affects the digestibility of plant material through its influence on lignin deposition in plants. Studies should focus on development of digestibility models that account for variability in diet quality as brought about by ambient temperature. Future studies may need to account for the type of model used in computation of degradation parameters.

5.4.4 Random Forest models for rumen degradation of feeds

Numerous studies have shown that feed properties including CP, ADF and NDF (van Vuuren et al. 1991; Tovar-Gomez et al. 1997; Ramirez et al. 2000; Zhao et al. 2015), ambient temperature, feed processing (Rahal et al. 1997; Shen et al. 1998; Zhao et al. 2015), ruminant type, length of incubation time (Lanyasunya et al. 2006), particle size (Zali et al. 2015; Zhao et al. 2015) and season (Rutagwenda et al. 1990; Yayota et al. 2009; Tang et al. 2011) affect degradation of feeds in the rumen. The current work used 17 animal, feed, and environmental factors to develop models to predict rumen digestibility of feeds for ruminants inhabiting a wide range of nutritional and climatic environments.

5.4.4.1 Performance of no lag Random Forest models in prediction

The performance of the Random Forest models in prediction was validated using the training and test datasets. A couple of sporadic outliers were observed in prediction of degradability parameters on the testing dataset. The solubility fraction was overpredicted for roughages (Shen et al. 1998; Alcaide et al. 2000; Bogoro et al. 2006). The observed solubilities (13 – 65 g/kg DM) of the roughages in these studies was very low compared to the average of the data set. The observed low solubility from Shen et al. (1998) may have been a result of the loss of the soluble fractions during the process of urea treatment of rice straw, which had implications in predictions in this study. Solubility was under-predicted for *Acacia nubica* (Abdulrazak et al. 2000) and *Ficus exasperata* leaves (Ikhimioya et al. 2005) both of which had observed solubility above the range of solubilities used in model development. The variation brought about by these samples were not entirely captured in model development. This is evident from the poor performance in predictions for these samples.

Notable under-predictions of the slowly degradable fraction were on *Ekebergia capenesis* leaves (Belachew et al. 2013) and broken rice (Chumpawadee et al. 2005). The observed high slowly degradable fraction (Chumpawadee et al. 2005) was evident from the short incubation period (48 h) causing early termination of the degradation curve. The average incubation time of roughages in the rumen is about 120 h, and early termination of degradation curve causes imprecise estimates of the slowly degradable fraction and PD. Feeds that had the rate of degradation over-predicted were rice pollard (Chumpawadee et al. 2005), grass silage (Bruining et al. 1998) and sorghum stover placed in the dorsal rumen (Bogoro et al. 2006). The under-estimated rates of degradation were for small particles (0.04 – 1.25 mm) of the rapidly degradable portion of grass silage (Bruining et al. 1998), lucerne hay (Moore et al. 1990) and early bloom Persian clover hay (Khazaal et al. 1993b). Evident from the under predictions is that feeds samples were small particles of highly fermentable fractions and feeds that are generally highly fermentable in the rumen. The models in this study could not account for various fractions of feed samples due to the complexities associated with indexing for such fractions. Potential degradability was over predicted for cottonseed hulls (Moore et al. 1990) while PD was under-estimated for groundnut haulms deposited in the dorsal rumen (Bogoro et al. 2006).

5.4.4.2 Performance of lag Random Forest models in prediction

The solubility of leaves from *Maesa lanceolata* (Belachew et al. 2003) and cotton seed meal (Chakeredza et al. 2002) were over-estimated. Cowpeas (Nsahlai and Umunna 1996) and, the dent from ensiled and flint from un-ensiled ground corn (Philippeau and Michalet-Doreau 1998) had their solubilities under-estimated. The slowly degradable fraction of dent from ensiled and flint from un-ensiled ground corn (Philippeau and Michalet-Doreau 1998) was over-predicted. *Desmodium uncinatum* (Nsahlai and Umunna 1996) and maize stover (Ngwa et al. 2001) had their slowly degradable fraction under-estimated.

Under-predictions of the rates of degradation from the training dataset were on Cuban *Leucaena leucocephala* leaves and full-fat peanuts, while the rate of degradation of Nigerian *Leucaena leucocephala* leaves were over-predicted (Gralek et al. 1997). From the test dataset, rates of degradation were over-estimated for *Desmodium uncinatum* and *Leucaena leucocephala* (Nsahlai and Umunna 1996), maize stover (Chakeredza et al. 2002), sorghum straw (Salcedo-Meza et al. 2004) and fish meal (Abate and Kiflewahia 1992), but under-estimated for a concentrate feed (Yanez-Ruiz et al. 2004). Fresh dwarf bamboo (Yayota et al. 2009), *Rhus glutinosa* fruit (Belachew et al. 2013), and barley straw and bromegrass (Ndlovu and Buchanan-Smith 1985) were over predicted. There was an over-prediction of the potential degradability of *Desmodium uncinatum* (Nsahlai and Umunna 1996). The over-prediction of dwarf bamboo may have been a result of the large particle size (100 mm) of the incubated samples.

5.4.4.3 Comparison of Random Forest models with existing models

A handful of studies (Nsahlai et al. 1999; Karsli and Russell 2002) have developed simple linear and non-linear equations to predict rumen degradability from the proximate chemical composition of feed samples. Neutral detergent fibre predicted solubility (R^2 = 0.63) and PD (R^2 = 0.64) (Tang et al. 2011), and PD (R^2 = 0.71) (Umunna et al. 1995) with high accuracy. Acid and neutral detergent fibre content of feeds accounted for 73% and 50% of the variation in prediction of rumen organic matter digestibility (Karsli and Russell 2002). The rate of degradation was accurately predicted (R^2 = 0.89) from the lignin-cellulose ratio and rumen degradable nitrogen (Nsahlai et al. 1999). Potential degradability was predicted from nitrogen levels with an accuracy of 91% (Umunna et al. 1995). The soluble fraction predicted from sugar and protein content, respectively, achieved accuracies of 86% and 91% (Cone et al. 1998).

Few linear prediction equations for degradation parameters from animal factors exist. Liquid digesta passage rates predicted rates of degradation (R^2 = 0.79, RSD = 0.004) and 48 h degradability (R^2 = 0.86, RSD = 33.01) with high accuracy and precision (Shem et al. 1995). Other studies (Zhao et al. 2015; Yansari 2017b) have used physical properties of feed samples to predict degradation parameters in the rumen. Linear relationships between water holding capacity ("a": R^2 = 0.54; "b": R^2 = 0.31; "c": R^2 = 0.52), initial functional specific gravity ("a": R^2 = 0.87; "b": R^2 = 0.62; "c": R^2 = 0.99) and final functional specific gravity ("a": R^2 = 0.80; "b": R^2 = 0.63; "c": R^2 = 0.93) gave good predictions of the rate of degradation and, soluble and slowly degradable fractions (Yansari 2017b). The predictions of degradation parameters from hydration rate ("a": R^2 = 0.027; "b": R^2 = 0.022; "c": R^2 = 0.031) were poor (Yansari 2017b). The accuracy in prediction of the rate of degradation of feed particle sizes retained on 3.35- and 1.18-mm sieves was 54% – 57% (Zhao et al. 2015).

Simple linear regression equations have been used to predict in situ degradation parameters from estimated parameters from in vitro gas production (Kibont and Orskov, 1993; Siaw et al. 1993; Habib et al. 1997; Kamalak et al. 2005) and fermentation products (Khazaal et al. 1995). In-vitro gas production explained 58 – 95% (Kibon and Orskov 1993; Kamalak et al. 2005) of variation of dry matter disappearance in the rumen. The linear regression equation (Kamalak et al. 2005) for calculating PD at 96h of incubation took the form: PD = 40.3 + 0.443gas96h (R^2 = 0.97), while Kibon and Orskov's (1993) best model achieved an accuracy of 90% from 48h in-vitro gas production. Gas production from the soluble (a) and insoluble fraction (b) alone could only explain 1% – 20% of the variation for both in situ predictions of "a" and "b", while the rate of degradation from gas production could not explain any variation in *in-situ* rates of degradation (Siaw et al. 1993; Cone et al.

1998; Kamalak et al. 2005). Short chain fatty acid concentration after 96h of incubation were strongly related to nylon bag degradability ($R^2 = 0.90$) suggesting the potential use of short chain fatty acid concentrations to predict rumen degradation (Khazaal et al. 1995). The linear relationship of in vitro digestibility and in sacco rate of degradation in wheat straw accounted for 71% of the variation in prediction (Habib et al. 1997).

5.5 Conclusion

The nutritive value of underutilised forages; *Brassica oleracea var. acephala* and, *Colophospermum mopane* leaf meal and pods was good with high levels of crude protein and potential degradability in the rumen; suggesting their potential use as ruminant feeds during the dry season. Predicted solubility and effective degradability lay near the ideal prediction line; giving good predictions for these parameters. However, some adjustments in the inputs for prediction of potential degradability and rate of degradation are needed to improve predictions.

Increases in ambient temperature would increase the neutral detergent fibre content of feeds, lowering the potential degradability of dry matter in the rumen. A 1 °C increase in AT decreased PD by 0.39% (for roughages), 0.76% (for concentrates), and 2.41% (for mixed diets). The slowly degradable fraction decreased by 0.1% (for roughages), 1.1% (for concentrates), and 2.27% (for mixed diets) for every 1 °C increase in AT. Overall, a 1 °C increase in AT decreased PD and “b” by 0.55% and 0.35%, respectively. Increasing ambient temperature by 1 °C increased neutral detergent fibre content of feeds by 0.4%. The predicted decrease in rumen digestibility of feeds with ambient temperature would be most severe in tropical and arid regions compared to cold and temperate regions. A sharp decrease in the potential degradability of concentrates (-0.7%) was predicted, in which concentrates had the sharpest decline compared to roughages. Findings from this study can be incorporated into the initial mitigating measures aimed at improving the feeding value of poor-quality roughages, especially crop residues such as straws and stovers. The effect ambient temperature on potential degradability in the rumen provides strong evidence of why ambient temperature should be accounted for in models that seek to predict digestibility in the rumen.

From studies discussed above, the chemical composition of feeds, physical properties of feed particles and animal factors gave fairly good estimates for degradation in the rumen comparable to the accuracies of models in this study. However, the performance of these models in estimating rumen degradation using an independent dataset is lacking. The current work used 17 animals, feed and environmental factors to develop models to estimate rumen degradation of feeds for ruminants inhabiting a wide range of nutritional and climatic environments. Cautious use of models developed in this study is recommended, pending fine-tuning of the model for prediction of rates of degradation of feeds to achieve better accuracy.

Chapter 6

Prediction of solid digesta passage rate using liquid passage rate as one of the input variables in ruminants [1]

Abstract

This study investigated the influence of liquid passage rates on solid digesta passage rates and the possibilities of simultaneous prediction of solid and liquid passage rates in ruminants. Artificial neural networks were used to develop models of solid and solid plus liquid passage rates. Studies that reported fractional passage rates, class and body mass of ruminants were included in the dataset. Animal and feed factors that affect the rate of passage were identified in studies. The database was composed of observations of domestic and wild ruminants of variable body mass (1.5 to 1238 kg) from 74 (solid using predicted liquid passage rate) and 31 (solid using observed liquid passage rate) studies, and 15 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 76 and 77% of the variation in prediction of solid passage rates using predicted and observed liquid passage rate as inputs, respectively. Simultaneous prediction accounted for 83 and 89% of the variation of solid and liquid passage rates, respectively. On validation using an independent dataset, these models attained 45% (solid using predicted liquid), 66% (solid using observed liquid), 50% (solid predicted with liquid) and 69% (liquid predicted with solid) of precision in predicting passage rates. Simultaneous prediction of solid and liquid passage rate yielded better predictions (+7%) compared to independent predictions of solid passage rate. Predicting solid passage rates simultaneously with liquid passage rate accounted for more variation compared to independent predictions of solid rates. Inclusion of liquid passage rate as an input variable gave better predictions of solid passage rates.

Key words: fractional passage rate, simultaneous predictions, prediction model, ruminants

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[1] Moyo M, Gueguim-Kana EB, Nsahlai IV. 2018. Prediction of solid digesta passage rate using liquid passage rate as one of the input variables in ruminants. S Afr J Anim Sci 48(4):758-769.

6.1 Introduction

Solid and liquid digesta in the rumen exists intermingled together. Solid digesta is suspended on the fluid phase, with products of fermentation present in solution. Passage of fluid greatly influences 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). There is a possibility that the rate of passage of liquid in the rumen may influence the rate of movement of solid digesta out of the rumen. The role of liquid passage rates in influencing the passage of particulate matter is still not well understood. Previous works of Ellis et al. (1982), Faichney and White (1988) and Faichney et al. (1989) have demonstrated that very small particles and microbial matter move along the digestive tract at a rate very close to that of water and solutes; Aharoni et al. (1999) used this concept. However, passage rate modelling exercises have developed models that are used to predict solid and liquid passage rates separately, although these processes may be mutually inclusive Faichney (1980). Given that both phases exist intermingled together current studies need to consider predicting both solid and liquid passage rates using interacting phases. Simultaneous prediction of solid and liquid passage rates is possible using feed compositions, animal factors and, environmental and management conditions.

It is still unclear why few studies, if any, have failed to exploit the effects of liquid passage rate in predicting the rate of particulate passage in the rumen. This study investigated the influence of liquid passage rates on solid digesta passage rates in ruminants. The objectives of this study were to (1) develop solid passage rate prediction model(s) using liquid passage rate as one of the input variables (2) develop a single model that simultaneously predicts solid and liquid passage rates. The study tested the hypothesis that inclusion of liquid passage rate improves the precision and accuracy of predicting solid passage rate.

6.2 Materials and methods

6.2.1 Creation of dataset

A dataset was created following the methods described by Moyo et al. (2017). Modelling was carried out from studies that met all of the following criteria: (1) studies should have reported the rate of passage or mean retention time (MRT_R) of solid alone or both solid and liquid digesta in the rumen, (2) studies that measured body weights of animals used and (3) studies that stated the feeds or the proportion of feeds in diets fed to or consumed by animals. Passage rates reported as mean retention time in the rumen were converted to fractional passage rate (FPR) by taking the inverse of mean retention time in the rumen (FPR = 1 ÷

MRT_R). Studies that did not specify the animal species were not included in the dataset. A dataset was created containing digesta passage rates from wild and domesticated ruminants. Factors that affect rate of passage of digesta were identified in each of these studies and were categorised into four main groups: (i) diet properties, (ii) animal, (iii) feed particle properties and (iv) environmental factors. Units of measurement for all quantitative factors are specified in various sections when mentioned. Qualitative factors that affect digesta passage rates were coded with numerical weightings, represented as numbers in parenthesis as (= 1, = 2, = 3 or = 4).

6.2.2 Animal factors

Animal related factors that affect rates of passage were either quantitative or qualitative. One qualitative factor affecting passage rates was identified to be ruminant feeding type (RFT). To account for differences in selectivity during feeding, ruminants were classified into 3 feeding types according to Hofmann (1989). Ruminants classified as grazers or roughage selectors (= 1) included cattle (*Bos taurus* and *Bos indicus*), addax (*Addax nasomaculatus*), Swamp buffalo (*Bubalus bubalis*), mouflon (*Ovis gmelini*), muskoxen (*Ovibos moschatus*), nilgai (*Boselaphus tragocamelus*), sheep (*Ovis aries*) and blackbuck (*Antilope cervicapra*); browsers or concentrate selectors (= 2) included moose (*Alces alces*), okapi (*Okapia johnstoni*), roe deer (*Capreolus capreolus*), Kirk’s dik-dik (*Madoqua kirkii*), Blue duiker (*Philantomba monticola*) and mouse deer (*Tragulus javanicus*) and intermediate feeders (= 3) included goats (*Capra hircus*), anoa (*Bubalus quarlesi*), reindeer (*Rangifer tarandus*), Thompson’s gazelle (*Eudorcas thomsonii*) and ibex (*Eudorcas thomsonii*). The quantitative factors included days in pregnancy (DP), days in lactation (DL), body weight (BW in kg), mature body weight (MBW in kg), physiological age (PA) and animal production level (APL). The degree of maturity, which is correlated with the physiological age (PA), was calculated as the quotient of BW and MBW of these animals (PA = BW ÷ MBW). Mature body weights of each ruminant was looked up from publications. 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).

The effects of energy requirements on the rate of passage of digesta particles in the rumen was accounted for using animal production level. Calculation of APL was done according to methods by AFRC (1993). To determine APL, the net energies for maintenance (NE_m), fattening (NE_f), lactation (NE_l), conception and production were calculated according to AFRC (1993). Since the AFRC (1993) formulae were developed for cattle, sheep and goats only; wild ruminant animals in the dataset were assigned into either of the formulae for cattle, sheep and goats using their body weights or mature size and feeding types. Animals were assigned to the formulae for (1) cattle (cattle, muskoxen, anoa, antelope-addax, buffaloes, moose, mouflon, nilgai, okapi, reindeer and roe deer), (2) sheep (sheep, blackbucks, and gazelles), or (3) goats (goats, dik-dik, duikers, mouse deer and ibex).

Not all studies reported body weight changes or average daily gains of animals required to calculate NE_f. Animals used in studies that did not report average daily gains of animals were assumed to have been at maintenance level of feeding. Days in lactation for all lactating animals and days in pregnancy for all pregnant animals were used to account for the effects of physiological status on passage rates of digesta. Not all studies reported days in milk and milk composition for all lactating animals required for calculation of NE_l. Days in milk for cows reported as early and late lactation were taken to be 60 and 290 days, respectively. Three studies did not report the milk composition for sheep, ibex, and cows. Thus, to calculate the energy value for milk, an average butter fat content for milk of sheep, ibex (Raynal-Ljutovac et al. 2008), and cows (Lock and Garnsworthy 2003) of 3.2, 3.5, and 3.8%, respectively, was used. Milk content for ibex was assumed to be equivalent to that of goats. The sum of these net energy values was used to calculate the total net energy requirements (TNER). Animal production level (APL) was calculated as APL = TNER ÷ NE_m.

6.2.3 Dietary factors

The properties of diets fed to animals that affect rate of passage of digesta in these studies were either qualitative or quantitative. Quantitative factors were mainly detergent and proximate chemical composition of feeds. These factors included dry matter (DM), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), ash and urea contents of diets offered to the animals all measured in g/kg DM. Studies in which feed composition were not reported but had the type of feed or diet reported, feed composition attributes 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 diets that did not have 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 (± 11.420) + 0.551 (± 0.02086) X (n = 360, Root Mean Square Error = 61.55, $R^2 = 0.66$, CV = 18.9%).

Qualitative dietary factors that affect rate of passage included in the dataset were; feed class (TAN) and feed type (SIL). Discrete feed factors were categorised as follows; feed class classified feeds or diets wholly as or containing anti-nutrients as tannin rich (TAN = 1) or non-tannin (TAN = 0) containing. Feeds classified as tannin rich were millet, sorghum, carob leaves, red clover leaves and browse leaves, while all other feeds were deemed to contain minute tannin levels. Feed type classified feeds as either a silage (SIL = 1) or non-silage (SIL = 0).

6.2.4 Feed particle factors

The *in-sacco* degradability parameters were used to account for the effect of particle fermentation and buoyancy on the rate of passage of solid particles. The effects of fermentation processes on rate of passage was accounted for using soluble fraction (a), slowly degradable fraction (b), rate of degradation (c), potential degradability (PD) and particle size (PS). 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 effect of particle size was indexed based on diameter as small = 1, medium = 2, large = 3, mixed sizes = 0. Studies in which degradation parameters of feed particles in the rumen were not reported but had the type of feed or diet reported, degradation parameters were looked up in journal articles. These included Tesfayohannes et al. (2013), Katamzi (2015) and Abdou (2016).

The potential degradability at half-life ($\mathrm{PD}\frac{1}{2}\mathrm{life}$) was used to account for the effects of particle buoyancy. The half-life of solid matter in the rumen was calculated using rates of degradation (c) according to Grovum and Phillips (1973), where: $\mathrm{t}\frac{1}{2}\ \mathrm{life} = (0.693\ \div \mathrm{c})$. Degradation models used in computing dry matter loss from each study were identified and the $\mathrm{PD}\frac{1}{2}\mathrm{life}$ was calculated using the following formulae: $\mathrm{PD}\frac{1}{2}\mathrm{life}\ = \mathrm{a} + \mathrm{b}\ \times [1 - \exp(-\mathrm{c}\ \times \mathrm{t}\frac{1}{2}\mathrm{life})]$ (no time lag model) or $\mathrm{PD}\frac{1}{2}\mathrm{life}\ = \mathrm{a} + \mathrm{b}\ \times [1 - \exp -\mathrm{c}(\mathrm{t}\frac{1}{2}\mathrm{life} - \mathrm{L})]$ (model accounting for time lag, where L: lag).

6.2.5 Environmental and management factors

The effect of activity on rate of passage were accounted for by identification of feeding management (GI) and feeding regime (FR) of animals in each study. Animals were managed as indoor zero grazing (GI = 0) or outdoor grazing (GI = 1) and fed ad-libitum (FR = 1) or restricted (FR = 0).

6.2.2 The datasets

Most studies that reported solid passage rates did not measure liquid passage rates, and vice-versa. Therefore, two datasets were collated, one for solid passage rate that did not report liquid passage rates; and another for solid passage rates with observed liquid passage rates.

Input variables in studies that reported solid passage rate alone were entered into the liquid passage prediction model by Moyo et al. (2017) so as to estimate probable (predicted) liquid passage rates. After prediction of liquid passage rates, two final datasets for solid passage rate with observed and predicted liquid passage rates were created. These two data sets were used to develop solid passage rate prediction models that included the predicted (model 1) and observed (model 2) liquid passage rates as input variables. A third model (model 3) used data that reported both solid and liquid passage rate to simultaneously predict solid and liquid passage rates. Although publications collected for creating these datasets might not include all published literature, studies used to build these datasets were readily available to authors and sourced as in Moyo et al. (2017).

The number of observations in these datasets were unevenly distributed among ruminant feeding types for solid prediction using observed liquid passage rate and for simultaneous predictions of solid and liquid passage rates (70% were grazers, 19% were browsers and 11% were intermediate feeders), and predicted liquid passage rate (72% were grazers, 8% were browsers and 20% were intermediate feeders). In predicting the solid passage rate using observed liquid passage rate as an input variable, 16 observations were on pregnant and lactating animals (4 pregnant cattle, 4 lactating cattle, 4 lactating sheep and 4 pregnant sheep). Only four (4) observations on pregnant and lactating (4 pregnant sheep) were used for validation. All other classes of ruminants were neither lactating nor pregnant. In predicting solid passage rates where input included predicted liquid passage rate, 113 observations were on pregnant and lactating animals (6 pregnant cattle, 92 lactating cattle, 4 lactating sheep, 7 pregnant sheep and 4 lactating ibex). Twenty-three (23) observations on pregnant and lactating animals (2 pregnant cattle, 16 lactating cattle, 4 lactating ibex and 1 pregnant sheep) were used for validation. All other classes of ruminants were neither lactating nor pregnant.

In predicting both solid and liquid passage rate, 14 observations were on pregnant and lactating animals (3 pregnant cattle, 2 lactating cattle, 2 lactating sheep and 7 pregnant sheep). Six (6) observations on pregnant and lactating animals (1 pregnant cow, 2 lactating cattle, 1 pregnant sheep and 2 lactating sheep) were used for validation. All other classes of ruminants were neither lactating nor pregnant. Tables 6.1-6.3 give the animal and diet compositional attributes used in model development.

6.2.3 Development of Artificial Neural Network model

In the present work, Artificial Neural Network models were programmed on the 32-bit Visual Basic Ver 6.0 to develop three process models to predict solid passage rates using predicted liquid passage rate as an input (model 1), to predict solid passage rates using observed liquid passage rate as an input (model 2) and to simultaneously predict both liquid and solid passage rates (model 3). Datasets included data from studies that reported solid passage rates alone with liquid passage rates predicted using models of Moyo et al. (2017) (models 1) and that reported both solid and liquid passage rates (model 2 and 3). These models were developed using 2 separate datasets. Each dataset was divided into 2 subsets of 75% data used for model training and the remaining 25% was used 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. The network topologies consisted of 24-13-1, 24-13-1 and 24-13-2 corresponding to the numbers of neurons of input, hidden and output layers for model 1, model 2 and model 3, respectively. Training was carried out using back-propagation algorithm. These models were trained for 2700 (model 1), 2300 (model 2) and 3000 (model 3) epochs at learning rate of 0.05, momentum of 0.8 and the net errors were reduced to 0.018 (model 1), 0.015 (model 2) and 0.013 (model 3) on training data.

6.2.4 Statistical analysis

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 variables, are reported in Moyo et al. (2017). 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 to determine any linear or mean bias St-Pierre (2003). Process models developed in this study have been deposited in the Repository of Intelligent Models with accession numbers PRQG001771, PRSQ001583 and PRNG000922 for model 1, model 2 and model 3, respectively, as indicated at http://www.redim.org.za/?search=PRQG001771, http://www.redim.org.za/?search=PRSQ001583 and http://www.redim.org.za/?search=PRNG000922 .

Table 6. 1 Species and feeding attributes of animals used in training to predict and validate solid passage rates

	Solid using observed liquid passage rate				Solid using predicted liquid passage rate			
	Prediction	Validation	Solid passage rate (per h)	Liquid passage rate (per h)	Prediction	Validation	Solid passage rate (per h)	Liquid passage rate (per h)
Species	14	12			15	14		
Mass (kg)	1.5–1238	1.5–1238			1.5–1238	1.5–1238		
Grazers	121	41			312	98		
Cattle	47	18	0.031 ± 0.015	0.078 ± 0.031	208	56	0.031 ± 0.020	0.098 ± 0.052
Sheep	57	21	0.035 ± 0.014	0.077 ± 0.025	89	36	0.036 ± 0.015	0.072 ± 0.022
Buffaloes	2	0	0.024 ± 0.000	0.048 ± 0.030	2	0	0.024 ± 0.000	0.059 ± 0.010
Antelopes	8	0	0.024 ± 0.004	0.056 ± 0.018	4	4	0.024 ± 0.004	0.033 ± 0.001
Muskoxen	7	2	0.037 ± 0.033	0.057 ± 0.037	9	2	0.032 ± 0.031	0.043 ± 0.017
Browsers	34	10			33	15		
Moose	6	3	0.022 ± 0.007	0.028 ± 0.008	6	6	0.022 ± 0.006	0.030 ± 0.000
Okapi	13	3	0.045 ± 0.010	0.062 ± 0.014	14	2	0.045 ± 0.010	0.054 ± 0.009
Dik-dik	7	3	0.040 ± 0.016	0.076 ± 0.014	7	3	0.040 ± 0.016	0.043 ± 0.000
Duikers	4	1	0.039 ± 0.008	0.048 ± 0.010	2	3	0.039 ± 0.008	0.058 ± 0.002
Mouse deer	4	0	0.046 ± 0.004	0.051 ± 0.006	4	1	0.046 ± 0.004	0.053 ± 0.011
Intermediate feeder	20	7			79	30		
Anoa	3	1	0.039 ± 0.008	0.081 ± 0.011	3	1	0.039 ± 0.008	0.081 ± 0.039
Reindeer	1	2	0.020 ± 0.000	0.036 ± 0.000	2	2	0.020 ± 0.000	0.033 ± 0.000
Gazelles	5	1	0.056 ± 0.012	0.099 ± 0.014	3	3	0.056 ± 0.012	0.099 ± 0.008
Goats	11	3	0.027 ± 0.003	0.122 ± 0.017	56	15	0.027 ± 0.007	0.091 ± 0.031
Ibex	0	0	-	-	15	9	0.054 ± 0.021	0.096 ± 0.032

Table 6. 2 Species and feeding attributes of animals used in prediction and validation data sets of passage rates in simultaneous prediction of liquid and solid passage rates

	Solid and liquid passage predicted simultaneously			
	Prediction	Validation	Solid passage rate (per h)	Liquid passage rate (per h)
Species	14	10		
Mass (kg)	1.5–1238	1.5–1238		
Grazers	118	44		
Cattle	48	17	0.031 ± 0.015	0.078 ± 0.031
Sheep	57	21	0.035 ± 0.014	0.077 ± 0.025
Buffaloes	2	0	0.024 ± 0.000	0.048 ± 0.030
Antelopes	5	3	0.024 ± 0.004	0.056 ± 0.018
Muskoxen	6	3	0.037 ± 0.033	0.057 ± 0.037
Browsers	34	10		
Moose	7	2	0.022 ± 0.007	0.028 ± 0.008
Okapi	11	5	0.045 ± 0.010	0.062 ± 0.014
Dik-dik	7	3	0.040 ± 0.016	0.076 ± 0.014
Duikers	5	0	0.039 ± 0.008	0.048 ± 0.010
Mouse deer	4	0	0.046 ± 0.004	0.051 ± 0.006
Intermediate feeder	23	4		
Anoa	2	2	0.039 ± 0.008	0.081 ± 0.011
Reindeer	3	0	0.020 ± 0.000	0.036 ± 0.000
Gazelles	5	1	0.056 ± 0.012	0.099 ± 0.014
Goats	13	1	0.027 ± 0.003	0.122 ± 0.017

Table 6. 3 Summary statistics of feed and animal attributes used in both prediction and validation of passage rates

	Solid using observed liquid passage rate model				
	N	Max	Min	Mean	SD
Urea (g/kg)	233	7.065	0	0.200	1.032
Dry Matter (g/kg)	233	957	171	778	239
Neutral Detergent Fibre (g/kg)	233	910	110	505	174
Acid Detergent Fibre (g/kg)	233	603	55	316	109
Crude Protein (g/kg)	233	295	25.700	147	65.159
Ash (g/kg)	233	138	25	78.478	18.413
Days in pregnancy (days)	233	138	0	3.768	18.739
Days in lactation(days)	233	45	0	1.043	5.761
Mature body mass (kg)	233	1100	2	300	268
Physiological age	233	1.515	0.169	0.623	0.292
Animal production level	233	1.827	0.875	1.065	0.182
Fractional passage rate (per h)	233	0.081	0.007	0.034	0.015
a (g/kg)	233	498	53	211	106
b (g/kg)	233	796	298	544	96.66
c (per h)	233	0.174	0.010	0.053	0.026
Potential degradability at half-life (g/kg)	233	701	308.5	467	0.73
Potential degradability (g/kg)	233	964	413	711	123.4

a, rapidly degradable water-soluble fraction of fibre; b, slowly degradable fraction of the insoluble fraction of fibre; c, rate of degradation.

6.3 Results

Input inclusive of observed liquid passage rate: The regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) was Y = 0.0008 (± 0.00148) + 0.921

(± 0.03786) X (n = 175, RMSE = 0.00704), accounting for 77% of the variation in prediction. The intercept was not different from 0 (P = 0.5697), but the slope was less than 1 (P = 0.039) (Fig 6.1). A plot of residuals (predicted-observed solid passage rates) against predicted solid passage rate followed the pattern (Fig 6.2) in this equation: Y = 0.0008 (± 0.00148) – 0.079 (± 0.0379) X (R^2 = 0.024; RMSE = 0.00704). The intercept of the residual plot was not different (P = 0.5697) from zero, but the slope was different (P = 0.0391) from zero, showing that the model had no mean bias, but had a linear bias. With the exception of 2 outliers (sheep), it can be observed from the plot that residuals did not form a defined pattern on the horizontal axis. A plot of residual solid passage rate against observed solid passage rate was used to assess the goodness of predictions (Fig 6.3). It can be observed from the plot that residual solid passage rate increased with increasing solid passage rates. Using validation data, the regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) was Y = -0.0028 (± 0.00368) + 1.062 (± 0.1013) X (n = 58, RMSE = 0.010), which accounted for 66% of the variation in unseen data. The intercept and slope were not significantly different from 0 (P = 0.449) and unity (P = 0.543), respectively (Fig 6.4).

Input inclusive of predicted liquid passage rate: The regression relationship between the observed (Y) and predicted (X) solid passage rate (per h) was Y = -0.0006 (± 0.00103) + 1.079 (± 0.02929) X (n = 424, RMSE = 0.009), which accounted for 76% of the variation in prediction. The intercept was not different from zero (P = 0.5453), but the slope was different from 1 (P = 0.007) (Fig 6.5). A plot of residual solid passage rate against predicted solid passage rate assessing the mean bias (intercept) and linear bias (slope) (Fig 6.6) gave the equation Y = -0.0006 (± 0.00103) + 0.079 (± 0.0293) X (R^2 = 0.0169; RMSE = 0.00902). The intercept of this equation was not different from zero (P = 0.5453), but the slope was different from zero (P = 0.0073), showing that the model had no mean bias, but had a linear bias. It can be observed from the plot that residuals did not form a defined pattern on the horizontal axis. A plot of residual solid passage rate against observed solid passage rate assessing the goodness of the prediction (Fig 6.7) showed that the residual solid passage rate increased with increasing solid passage rates. The regression relationship between the observed (Y) and predicted (X) liquid passage rates (per h) was Y = 0.00797 (± 0.00241) + 0.7566 (± 0.070) X (n = 142, RMSE = 0.0123), accounting for only 45% of the variation in unseen data. The intercept and slope were significantly different from zero (P = 0.0012) and unity (P = 0.001), respectively (Fig 6.8).

Simultaneous predictions: The regression relationship between the observed (Y) and predicted (X) liquid passage rates when predicted simultaneously with solid passage rates (per h) was Y = -0.00018 (± 0.0022) + 1.006 (± 0.027) X (n = 175, RMSE = 0.010452), accounting for 89% of the variation in prediction. The intercept (P = 0.9323) and slope (P = 0.8374) were not different from 0 and 1, respectively (Fig 6.9). A plot of residual liquid passage rate against predicted liquid passage rate assessing the mean bias (intercept) and linear bias (slope) (Fig 6.10) gave the equation Y = 0.00003 (±0.00218) + 0.00359 (±0.0274) X (R^2 = 0.0001, RMSE = 0.0104). The intercept (P = 0.9883) and slope (P = 0.8959) from the residual plot were not different from zero. It was observed that residuals showed no obvious pattern on the horizontal axis. A plot of residual liquid passage rate against observed liquid passage rate was used to assess the goodness of predictions (Fig 6.11) and how far predictions are from reality; the plot indicated that residual liquid passage rate increased with increasing liquid passage rates when simultaneously predicted with solid passage rates. The regression relationship between the observed (Y) and predicted (X) liquid passage rates (per h) using the validation data was Y = 0.0127 (± 0.00586) + 0.8697 (± 0.0781) X (n = 58, RMSE = 0.0153), accounting for 69% of the variation in unseen data. The intercept was different from 0 (P = 0.0351) and slope were not different from unity (P = 0.1011) (Fig 6.12).

The regression relationship between the observed (Y) and predicted (X) solid passage rate when predicted simultaneously with liquid passage rates (per h) was Y = 0.00153 (± 0.00125) + 1.036 (± 0.0357) X (n = 175, RMSE = 0.00648), accounting for 83% of the variation in prediction. The intercept (p = 0.2231) and slope (p = 0.2816) were not different from 0 and 1, respectively (Fig 6.13). A plot of residual against predicted solid passage rate assessing the mean bias (intercept) and linear bias (slope) (Fig 6.14) gave the equation: Y = 0.00153 (±0.00125) + 0.03855 (±0.0357) X (R^2 = 0.0067, RMSE = 0.00648). The intercept (P = 0.2231) and slope (P = 0.2816) from the residual plot were not different from zero. It can be observed from the plot that residuals showed no obvious pattern on the horizontal axis. A plot of residual solid passage rate against observed solid passage rate was used to assess the goodness of predictions (Fig 6.15) and how far these predictions were from reality. It can be observed from the plot that residual solid passage rate increased with increased solid passage rates when concurrently predicted with liquid passage. The regression relationship between the observed (Y) and predicted (X) solid passage rates (per h) was Y = 0.0073 (± 0.0035) + 0.775 (± 0.1026) X (n = 58, RMSE = 0.0100), accounting for 50% of the variation in unseen data. The intercept and slope were different from 0 (P = 0.0447) and 1 (P = 0.0323), respectively (Fig 6.16).

Predicting solid passage rates simultaneously with liquid passage rate accounted for more variation compared to using observed (+6%) and predicted (+7%) liquid passage rates as input variables for prediction of solid passage rate. In model validation, the method simultaneously predicting both rates explained +5% more variation compared to validation where liquid passage rate was an input. However, validation of solid passage rate when simultaneously predicted with liquid passage rates explained -16% less variation compared to validation of the solid using observed liquid model.

6.4 Discussion

The critical role of liquid passage rate in determining passage of particulate matter is undermined to the extent that solid and liquid passage rates are normally predicted separately. It is only recently that liquid passage rate prediction equations have accurately predicted liquid passage rates, accounted for 82-94% of the variation in prediction (Seo et al. 2006; 2007; Moyo et al. 2017). Previously, inclusion of liquid passage rate as an input variable for predicting solid passage rate may have been hindered by the failure to accurately predict liquid passage rates. Passage rate of particulate matter through the rumen partly depends on how much material passes out using liquid as a medium and how much gets hindered by the reticulo-omasal orifice. This makes simultaneous prediction of liquid and solid phases relatively important. Normally, passage rate prediction models have been developed for specific ruminants; buffalo, cattle, sheep and goats (Cannas and Van Soest 2000; Seo et al. 2009).

Prediction models developed in this study accounted for a large amount of variation in unseen observations. Models achieved high precision in predicting solid passage rates using observed and predicted liquid passage rates as input factors for 15 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 clustered along the ideal prediction line. Some sporadic outliers in prediction of solid passage rates using observed liquid passage rate for sheep are identifiable, where passage rates were underestimated (high residuals; Fig 6.1). These data included Blackhead sheep that inhabit the temperate climate. These findings support the suggestions that accounting for variations in ambient temperature between studies may improve accuracy in predicting solid passage rates (Warren et al. 1974; Chaiyabutr et al. 1987). Inclusion of liquid passage rate as an input variable yielded better models for predicting of particulate passage rates in the rumen. The solid passage rate prediction models developed in this study accounted for +10% (using predicted) and +11% (using observed) more variation, but lowered RMSE by -52 (observed liquid) and -39% (predicted liquid) in prediction of solid passage rates compared to the solid passage rate prediction model by Moyo et al. (2017). On evaluation (validation) using independent datasets, models gave improved R^2 values by +24 (observed liquid) and +3% (predicted liquid) compared to the solid passage rate model of Moyo et al. (2017).

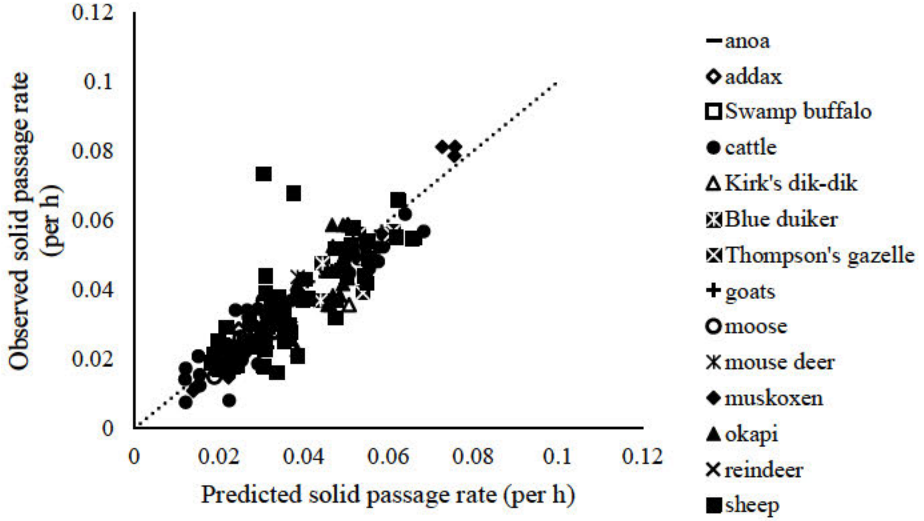


Fig. 6. 1 Relationship between the observed and predicted solid passage rates using observed liquid passage as an input variable for model development.

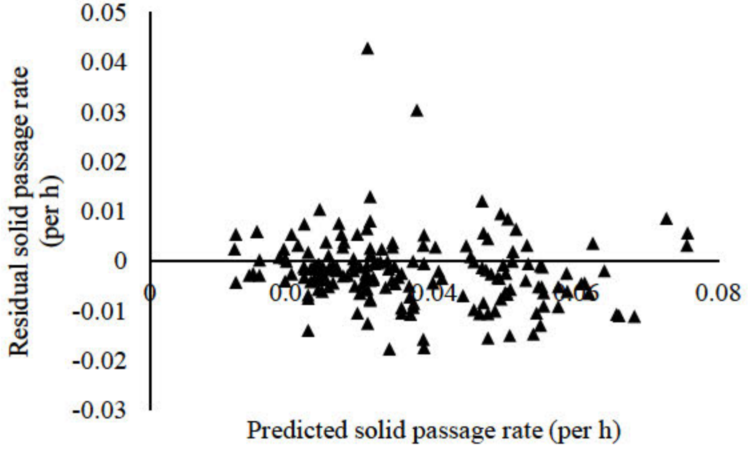


Fig. 6. 2 Residual plot (Observed – Predicted) against predicted solid passage using observed passage rate as an input variable to test model bias in prediction.

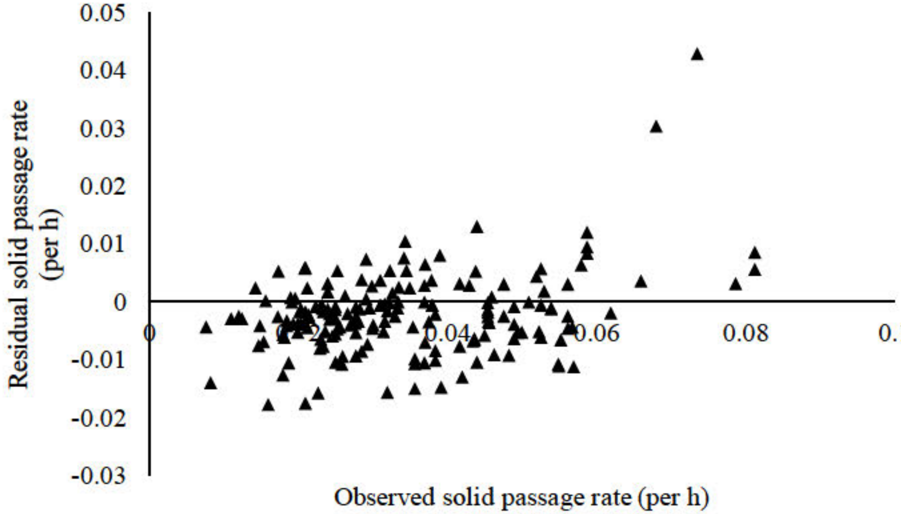


Fig. 6. 3 Residual plot (Observed – Predicted) against observed solid passage rate.

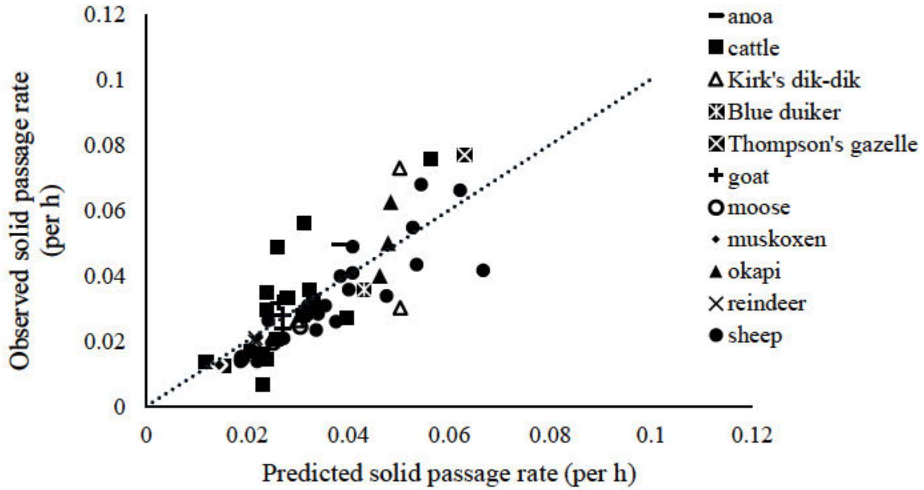


Fig. 6. 4 Relationship between the observed and predicted solid passage rates using observed liquid passage as part of input variables for model validation.

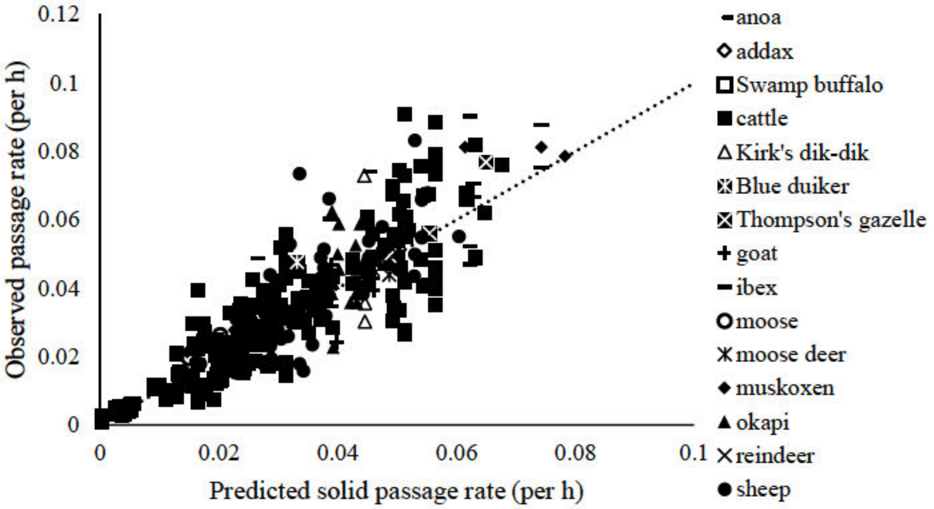


Fig. 6. 5 Relationship between the observed and predicted solid passage rates using predicted liquid passage as an input variable for model development.

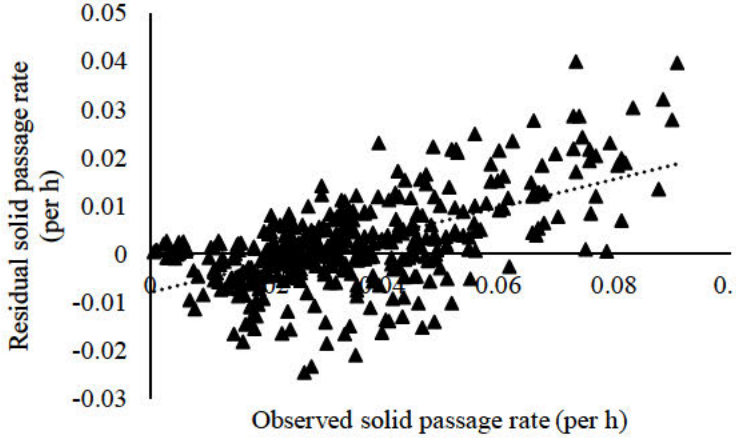


Fig. 6. 6 Residual plot (Observed – Predicted) against predicted solid passage rate using predicted liquid passage rate as an input variable to test model bias in prediction.

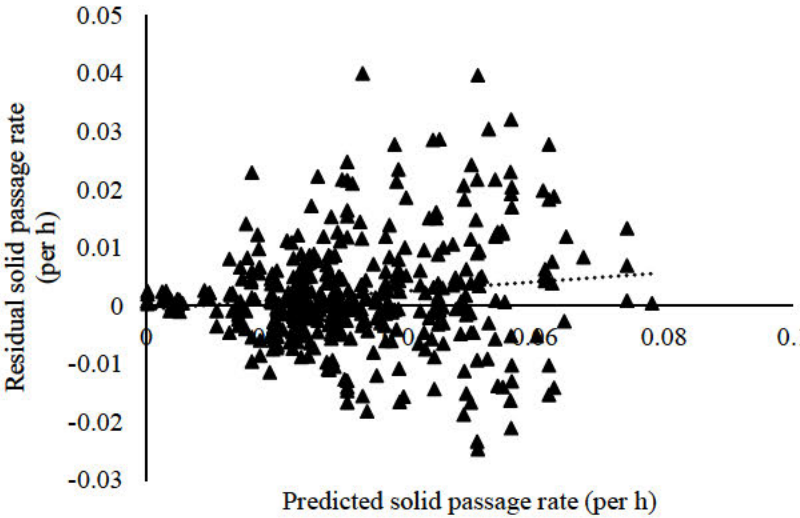


Fig. 6. 7 Residual plot (Observed – Predicted) against observed solid passage rate.

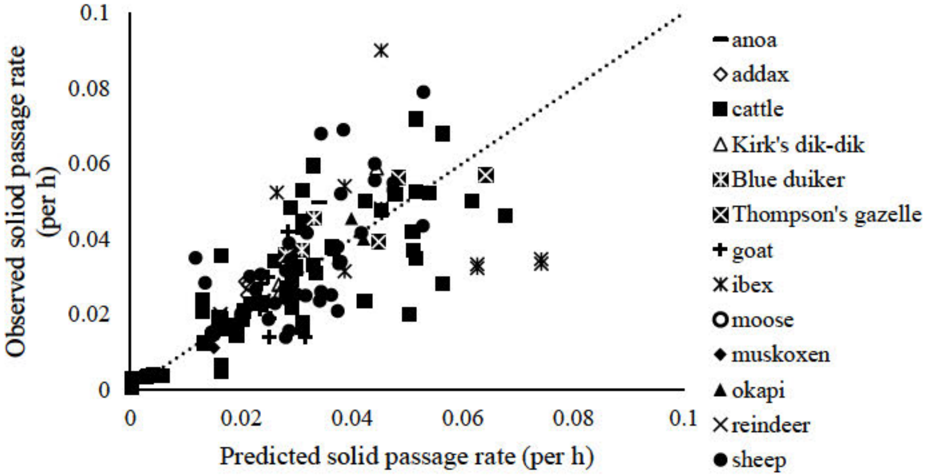


Fig. 6. 8 Relationship between the observed and predicted solid passage rates using predicted liquid passage as an input variable for model validation

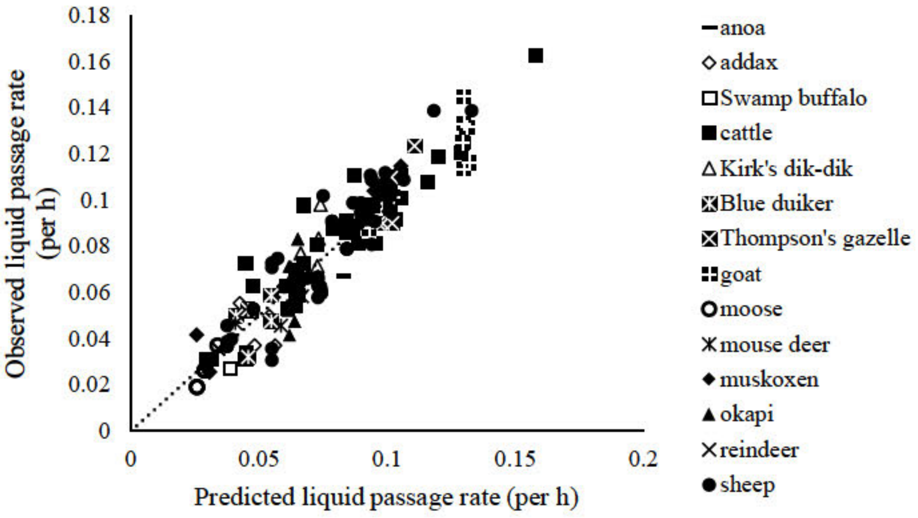


Fig. 6. 9 Relationship between the observed and predicted liquid passage rates when both liquid and solid are predicted together in model development.

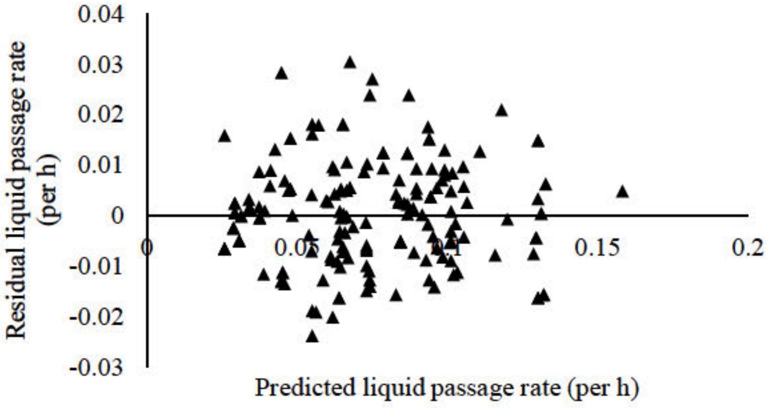


Fig. 6. 10 Residual plot (Observed – Predicted) against predicted liquid passage rate when both liquid and solid are predicted together to test model bias in prediction.

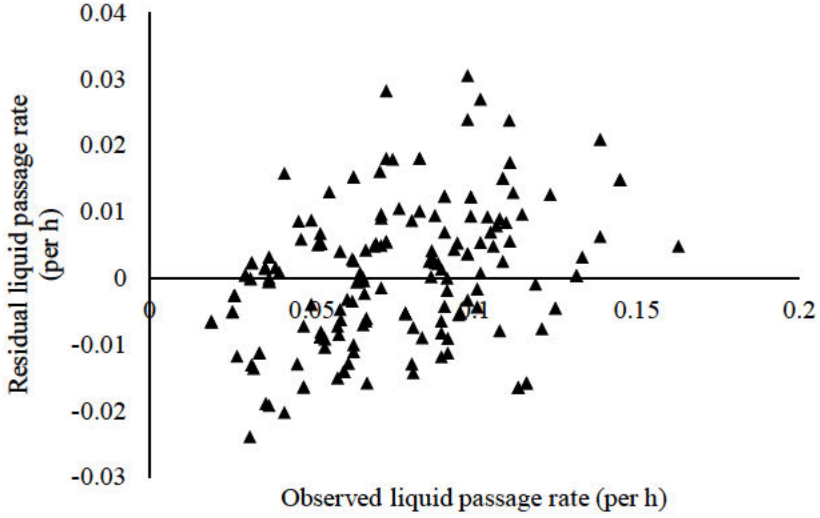


Fig. 6. 11 Residual plot (Observed – Predicted) against observed liquid passage when both liquid and solid are predicted together.

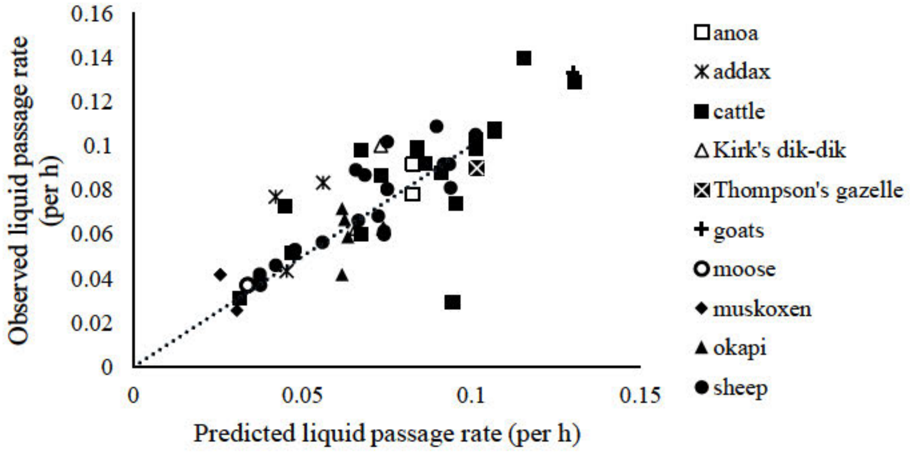


Fig. 6. 12 Relationship between the observed and predicted liquid passage rates when both liquid and solid are predicted together for model validation

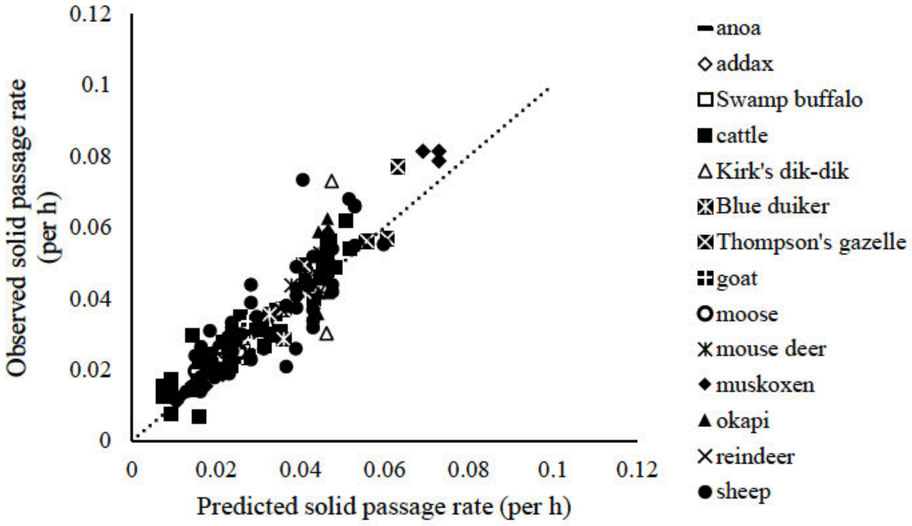


Fig. 6. 13 Relationship between the observed and predicted solid passage rates when both liquid and solid are predicted together for model development.

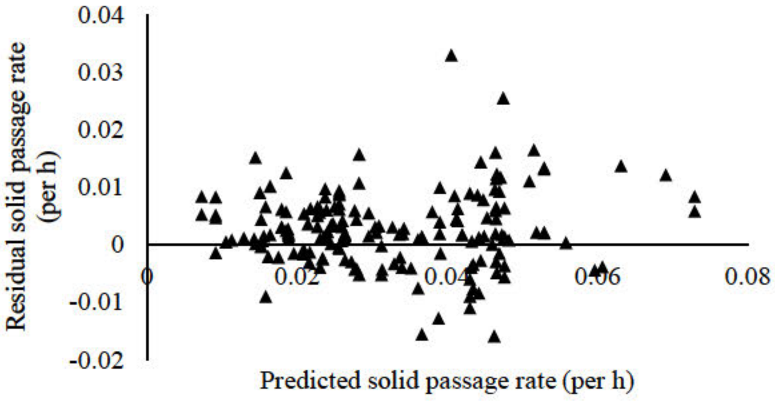


Fig. 6. 14 Residual plot (Observed – Predicted) against predicted solid passage rate when both liquid and solid are predicted together to test model bias in prediction.

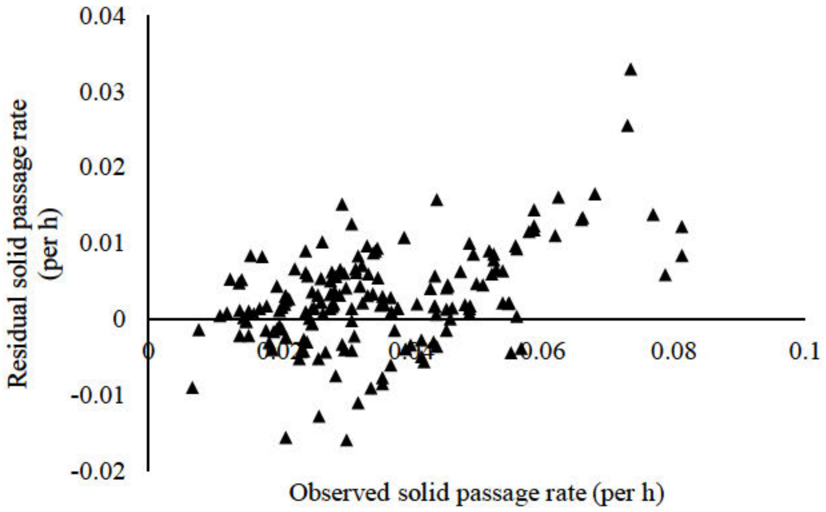


Fig. 6. 15 Residual plot (Observed – Predicted) against observed solid passage rate when both liquid and solid are predicted together.

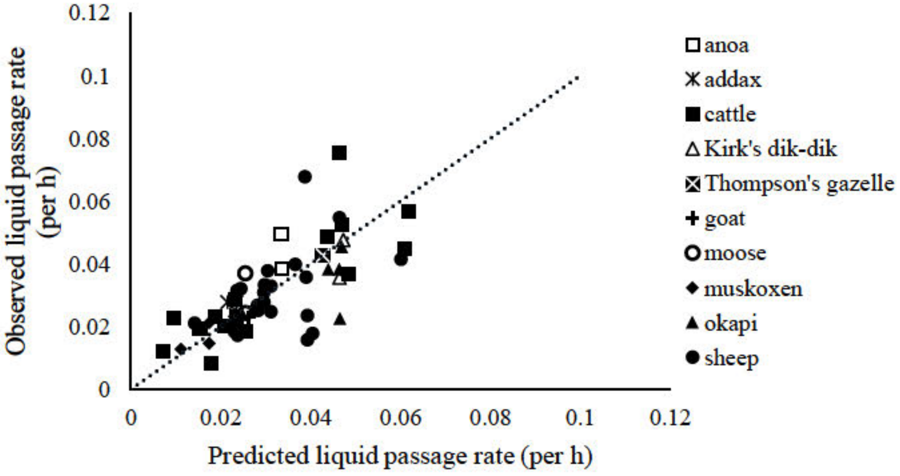


Fig. 6. 16 Relationship between the observed and predicted solid passage rates when both liquid and solid are predicted together for model validation.

These agree with suggestions made by previous workers that fine particles move along the digestive tract at a rate closer to that of water and solutes (Ellis et al. 1982; Faichney and White 1988; Faichney et al. 1989; Aharoni et al. 1999). Better predictions that accounted for 86% (Seo et al. 2009) and, 87 and 95% (Seo et al. 2006) of the variation for solid passage rates have been reported. However, these predictions were limited to beef cattle or to dairy cows and included intake as a major input variable unlike those from this study.

Previously published equations attained modest R^2 values in predictions of 15-66% for rates of passage of particulate matter (Cannas and Van Soest 2000). An improved R^2 value for the particle passage rate model because of including liquid passage rate as an input variable authenticates the importance of fluid passage in influencing particulate digesta movement (Aharoni et al. 1999; Faichney 1980). Simultaneous prediction of solid and liquid passage rates generally improved coefficients determination but reduced RMSE compared to independent predictions of solid passage rates reported in this study and those of Moyo et al. (2017). Using simultaneous method, the amount of variation accounted for in the prediction of liquid passage rate was +7% greater compared to prediction of liquid passage rate alone by Moyo et al. (2017). Similarly, the simultaneous method improved the explained variation in solid passage rate (observed vs predicted) by +17% compared to prediction of solid passage rate alone by Moyo et al. (2017).

Mathematical relationships between the passage rates of liquid ($\mathrm{k_l}$) and solid ($\mathrm{k_p}$) matter have been proposed. The ones of Nsahlai et al. (1999) take the form: $\mathrm{k_l} = (\mathrm{k_p} - 0.0018) \div 0.360$ and $\mathrm{k_l} = (\mathrm{k_p} - 0.0148) \div 0.163$. Similarly, the selectivity factor which is a quotient of the mean retention time of liquid to solid in the rumen have been proposed by Clauss and Lechner-Doll (2001). The model developed to predict solid passage rate using observed liquid passage rate took advantage of the influence of fluid in the movement of solid in the rumen to develop improved solid passage rate prediction models. However, the disadvantage of this model is that the passage rate of liquid has to be known prior to prediction. To overcome this disadvantage, a model that uses predicted liquid passage rate to predict the passage rate of solid matter was developed. It helps to predict solid passage rate without having to measure liquid passage rate prior to prediction. Although using predicted liquid comes with an error of prediction, its predictive potential was shown to be equal to that of using observed liquid passage rate. This suggests that the added neurons in the typology ([24-13-1] and [24-13-2] vs [17-17-1]) and/or the passage of liquid would help to modulate particulate passage rate.

Given that solid and liquid phases are intermingled in the rumen, simultaneously predicting passage rates for both phases remove the error incurred to predict and use liquid passage rate as an input when estimating the solid passage rate. Better predictions of solid and liquid passage rate were obtained when both phases were simultaneously predicted compared to individual predictions of solid and liquid passage rates. The reason why the validation of solid passage rate using simultaneous prediction models could explain only 50% of the variation is not known but may be due in part to variation and interaction due to changes in ambient temperature and type of animal. The influence of liquid passage rate on particulate passage rate is important to increase the accuracy of predictions.

6.5 Conclusion

Inclusion of liquid passage rate as an input variable gave better predictions of solid passage rates. Liquid passage rates play an important role in facilitating passage of particulate matter out of the rumen. Liquid passage rates should be taken as a critical factor in development of particulate passage rate models.

Chapter 7

Estimation of rumen digesta load of wild and domesticated ruminants

Abstract

This study was performed to (1) investigate scaling relationships of rumen digesta load with body weight and evaluate the influence on ruminant digesta load in response to climatic region and ruminant feeding type, and (2) to estimate the weight of rumen digesta in ruminants. A dataset was created from studies that (1) measured either the rumen dry matter load (RDML), rumen wet matter load (RWML) or rumen liquid matter load (RLML) by complete evacuation of the rumen through fistulas or after slaughtering, (2) reported bodyweights of animals and (3) stated the diets fed to or eaten by animals. Factors affecting rumen digesta load were identified and used as input variables in predicting rumen digesta load. Data were analysed using a linear regression and mixed model regression methodology. Rumen digesta load prediction models were programmed on a 64-bit R 3.6.2 version (Dark and Stormy Night). The RF algorithm intrinsically divided the dataset into 2 subsets: 70% for model training and 30% for testing. Grazers and intermediate feeders had hypoallometric scales of RDL with BW, while the scale was hyperallometric for browsers. Wet and liquid RDL of grazers and browsers scaled isometrically with BW. Climatic type ($p<0.05$) and region ($p<0.15$) influenced RDL and was highest for ruminants inhabiting tropical regions, followed by cold, temperate, and lowest in arid climates. Ruminant species and ruminant feeding type ($p<0.05$) influenced all measures of RDL, was highest in grazers and lowest in browsers. Liquid and dry rumen digesta load were predicted to decrease in proportion by 0.02 ($p<0.0001$) for every 1°C increase in ambient temperature. The models developed in this work accounted for 81% (scaled RDML) and 90% (unscaled RDML) of the variation in prediction of RDML. On testing, the models attained 59% (scaled RDML) and 84% (unscaled RDML) precision in prediction. Models attained high precision in prediction of RWML ($R^2 = 0.94$) and RLML ($R^2 = 0.94$) during training and testing of RWML ($R^2 = 0.85$) and RLML ($R^2 = 0.88$) using an independent dataset. In conclusion, RDL scaled allometrically to body weight, did not scale according to the Bell-Jarman principle. It was predicted that increases in ambient temperature will decrease rumen digesta load.

Key words: Allometry, ambient temperature, Random Forests, rumen digesta load, ruminants

7.1 Introduction

Theoretically, ruminants eat to meet their requirements for maintenance, growth and production unless constrained by factors such as rumen capacity, ambient temperature, feed quality and availability. Frequently, ruminants face a conundrum of balancing between selection of high-quality diets and maintaining adequate intake without negatively affecting digestive efficiency (Hume 2005). Key to evasion of this challenge is the evolution of adaptations strategies peculiar to ruminants, such as rumination and prolonged retention of digesta in the rumen to maximise nutrient extraction (Clauss and Hummel 2017). The quantity of digesta in the rumen is regulated through intake-passage rate interactions (Clauss et al. 2007) and the rate of degradation of digesta in the rumen is determined by the quality of diet consumed (Nsahlai and Apaloo 2008). Among ruminant species and feeding types of similar size, there appears to be differences in rumen digesta load. Studies that seek to predict rumen digesta loads need to first determine accurate scaling factors to standardise rumen digesta load across ruminant species. The Bell-Jarman principle (Geist 1974) suggests isometric scaling relationship of rumen digesta load with body weight. Rumen digesta load scales positive and linear with body weight as repeatedly proposed (Illius and Gordon 1992, Nsahlai and Apaloo 2008, Clauss et al. 2003, 2007).

There is overwhelming body of evidence showing that animal physiological status affects dry matter intake of roughage diets (Helander et al. 2014; Nsahlai and Apaloo 2007) by ruminants ultimately affecting rumen digesta load. For instance, lactating ruminants consume more feed (Hartnell and Satter 1979) than their non-lactating counterparts, while late pregnancy ruminants exhibit a low feed intake. Allometric scaling of digestive physiology measures along a degree of maturity (Illius and Gordon 1991) and animal production level gradient have been explored (Adebayo et al. [accepted]) and would widen understanding underlying dynamics of rumen digesta load. Rumen digesta load is one of the main regulators of roughage intake in ruminants. Global warming for which the main culprit chemicals are over production of carbon dioxide, methane and nitrous oxide would affect ruminant production. In the tropics, anticipated responses of feeds to climate change are increase lignification, high neutral detergent fiber and reduced crude protein, all of which would surely dampen animal production. The projected negative effects of global warming on intake (Rojas-Downing et al. 2017) necessitates determination of the responses of rumen digesta load to climate variables. This would deepen our current understanding of responses of rumen physiology to variable ambient temperature and how they are likely to affect intake.

Some models for predicting rumen digesta load are a function of body weight (Illius and

Gordon 1991; Illius and Gordon 1992) and feed intake (Sekine et al. 1991) alone. Studies (Nsahlai and Apaloo 2007) have shown that roughage quality may have a profound effect on rumen digesta load. As a result, Adebayo et al. [in-press] used diet quality and animal factors in predicting rumen digesta load for cattle and sheep. Existing models are structurally inadequate for rumen digesta load predictions for ruminants inhabiting environments of diverse nutritional and climatic factors.

This study was designed to increase the current understanding of rumen digesta load dynamics of ruminants living in different nutritional environments and climatic regions. The objective of this study was to: (1) determine how rumen digesta load scales with body weight, animal production level and degree of maturity, (2) investigate the influence on ruminant digesta load of wild and domestic ruminant species in response to ambient temperature, climatic region, and ruminant feeding type, and (3) to develop Random Forest models to estimate the rumen digesta load of ruminants. It was hypothesized that: (1) ruminants with small body weight would have high rumen digesta load than their larger counterparts, with an allometric scaling relationship between rumen digesta load and body weight, (2) climatic region and ambient temperature would affect rumen digesta load and that grazing ruminants would have higher rumen digesta load than browsing ruminants, and (3) it is possible to estimate rumen digesta loadusing Random Forest models.

7.2 Materials and methods

7.2.1 Creation of dataset

Data were collected from 72 studies carried out worldwide between 1945 and 2016, and that reported at least average values or ranges for bodyweights of animals, measured rumen digesta load and stated the feeds and/or proportion of feeds in diets fed. This work was carried out from studies that met all of the following criteria: (1) studies were published in peer-reviewed journals, (2) studies that reported bodyweights of animals (3) studies that measured either the rumen dry matter load (RDML), rumen wet matter load (RWML) or rumen liquid matter load (RLML) by complete evacuation of rumen through the fistulas or after slaughtering and (4) stated feeds or the proportion of each feed in the diet fed to animals. A dataset was created containing observations from wild and domesticated ruminants. Qualitative and quantitative factors that affect rumen digesta load were identified from each study and, these included animal, diet, management and environmental factors according to Fig. 7.1. Qualitative factors that affect rumen digesta load were coded with numerical weightings, represented as numbers in parenthesis as (= 1, = 2, = 3 or = 4). Although publications collected for creating these datasets might not include all published literature, studies used to build these datasets were readily accessible and available.

7.2.2.1 Animal factors

Animal related factors that affect rumen digesta load were either quantitative or qualitative. Qualitative factors affecting rumen digesta load were identified to be ruminant feeding type (RFT), while the quantitative factors were body weight (BW), mature body weight (MBW), degree of maturity (DOM), days in lactation (DL), days in pregnancy (DP) and animal production level (APL).

7.2.2.1.1 BODY WEIGHT, DEGREE OF MATURITY AND ANIMAL PRODUCTION LEVEL

Quantitative factors included body weight (BW), mature body weight (MBW), degree of maturity (DOM) and animal production level (APL). The quotient of BW and MBW of animals gave DOM of animals used in each study. Calculation of APL was done according to AFRC (1993). Mature body weights of ruminants were looked up from publications (Frandsen 1992, Estes 1993, ADW 2014 and AWF 2016). To determine APL, the net energies for maintenance (NE_m), fattening (NE_f), lactation (NE_l) and conception and production were calculated according to AFRC (1993). Since the AFRC (1993) formulae were developed for cattle, sheep and goats only; wild ruminant animals in the dataset were assigned into either of the formulae for cattle, sheep and goats using their body weights or mature size. Animals assigned to the formulae for cattle were cattle (*Bos taurus* and *Bos indicus*), addax (*Addax nasomaculatus*), African buffalo (*Syncerus caffer*), muskoxen (*Ovibos moschatus*), waterbuck (*Kobus ellipsiprymnus*), gemsbok (*Oryx gazella*), black wildebeest (*Connochaetes gnou*), blue wildebeest (*Connochaetes taurinus*), moose (*Alces alces*), giraffe (*Giraffa camelopardalis*), gerenuk (*Litocranius walleri*), tsessebe (*Damaliscus lunatus*), hartebeest (*Alcelaphus buselaphus*), red deer (*Cervus elaphus*), spotted deer (*Axis axis*), sika deer (*Cervus nippon*), topi (*Damaliscus lunatus jimela*), kudu (*Tragelaphus strepsiceros*) and eland (*Taurotragus oryx*); the formulae for sheep were sheep (*Ovis aries*), bushbuck (*Tragelaphus sylvaticus*), impala (*Aepyceros melampus*), Grant’s gazelle (*Nanger granti*), mountain reedbuck (*Redunca fulvorufula*), mule deer (*Odocoileus hemionus*) and fallow deer (*Dama dama*); and the formulae for goats were goats (*Capra hircus*), Suni (*Neotragus moschatus*), Kirk’s dik-dik (*Madoqua kirkii*), steenbok (*Raphicerus campestris*), bush duiker (*Sylvicapra grimmia*), Thompson’s gazelle (*Eudorcas thomsonii*), roe deer (*Capreolus capreolus*), springbok (*Antidorcas marsupialis*), reindeer (*Rangifer tarandus*) and white-tailed deer (*Odocoileus* *virginianus*). Not all studies reported body weight changes or average daily gains of animals required to calculate NE_f. Animals used in studies that did not report average daily gains of animals were assumed to have been at maintenance. Days in lactation for all lactating animals and days in pregnancy for all pregnant animals were used to account for the effects of physiological status on rumen digesta load. Days in milk for cows reported as early and late lactation were taken to be 60 and 290 days, respectively. The sum of these NE values was used to calculate the total net energy requirements (TNER). Animal production level (APL) was calculated as APL = TNER ÷ NE_m.

7.2.2.1.2 RUMINANT FEEDING TYPE

Ruminants were separated into 3 main feeding types according to the classification by Hofmann (1989). Animals classified as grazers or roughage selectors (= 1) were addax, African buffalo, black wildebeest, blue wildebeest, bushbuck, cattle, hartebeest, mountain reedbuck, muskoxen, gemsbok, sheep, swamp buffalo, topi, tsessebe, and waterbuck; browsers or concentrate selectors (= 2) included bush duiker, gerenuk, giraffe, Kirk's dik-dik, kudu, moose, mule deer, roe deer, springbok, and suni; while intermediate feeders (= 3) included Grant's gazelle, eland, fallow deer, goats, impala, red deer, reindeer, sika deer, spotted deer, steenbok, Thomson's gazelle, and white-tailed deer.

7.2.2.2 Dietary factors

Diet properties that affect rumen digesta load were mainly proximate chemical composition of feeds. These factors included dry matter (DM), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose (HEM), ash, and protein-free cell contents (PFCC) of diets offered to the animals. The hemicellulose content was calculated in studies that did not report it using the formulae: HEM = NDF – ADF. Protein-free cell contents (PFCC) which include starch, sugars, vitamins, pectins, fats and minerals was calculated using the formula: PFCC = 1000 − (NDF + CP). If studies did not report all dietary composition of feeds fed to animals but mentioned names of feeds used, their composition was looked up from available sources. These sources included Halimani et al. (2005), Feedipedia (2019), Suksombat and Junpanichcharoen (2005), Krizsan et al. (2018), Demment and Van Soest (1985), and Condron et al. (2007). Identification of natural diets for African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), waterbuck (*Kobus defassa*), gemsbok (*Oryx beisa*) and gerenuk (*Litocranius walleri*) was based on Hall-Martin et al. (1974), Demment and Van Soest (1985), and Hofmann (1973).

7.2.2.3 Environmental and management factors

The effect of activity on frequency of rumen contractions and rumen digesta load were accounted for by identifying of feeding management (GI) of animals in each study. Animals were managed as fed indoor (= 0) or outdoor grazing (= 1). Effects of climate type (CT) on rumen digesta load were accounted for by identifying season and the location of where each study was done and classifying the climate of each study site using the updated Köppen-Geiger climate classification system (Peel et al. 2007). The effect of climate type was done by allocation of each climatic region into either tropical (= 1), arid (= 2), temperate (= 3) and cold (= 4) climate types according to the Köppen-Geiger climate classification system. To account for the effect of ambient temperature (AT), countries where and years when each study were done was identified and AT data for each study site was obtained from Harris et al. (2014).

Studies fell into 12 climatic regions namely; tropical monsoon (Am), tropical savannah climate (Aw), hot arid desert climate (BWh), hot arid steppe climate (BSh), cold arid steppe climate (BSk), dry temperate climate with hot summers (Csa), dry winter temperate climate with hot summer (Cwa), hot summer temperate climate without dry season (Cfa), warm summer temperate climate without dry season (Cfb), cold dry climate with warm summers (Dsb), cold climate with hot summers and no dry season (Dfa), and cold climate with warm summers and no dry season (Dfb). The country where and years when each study was done were obtained.

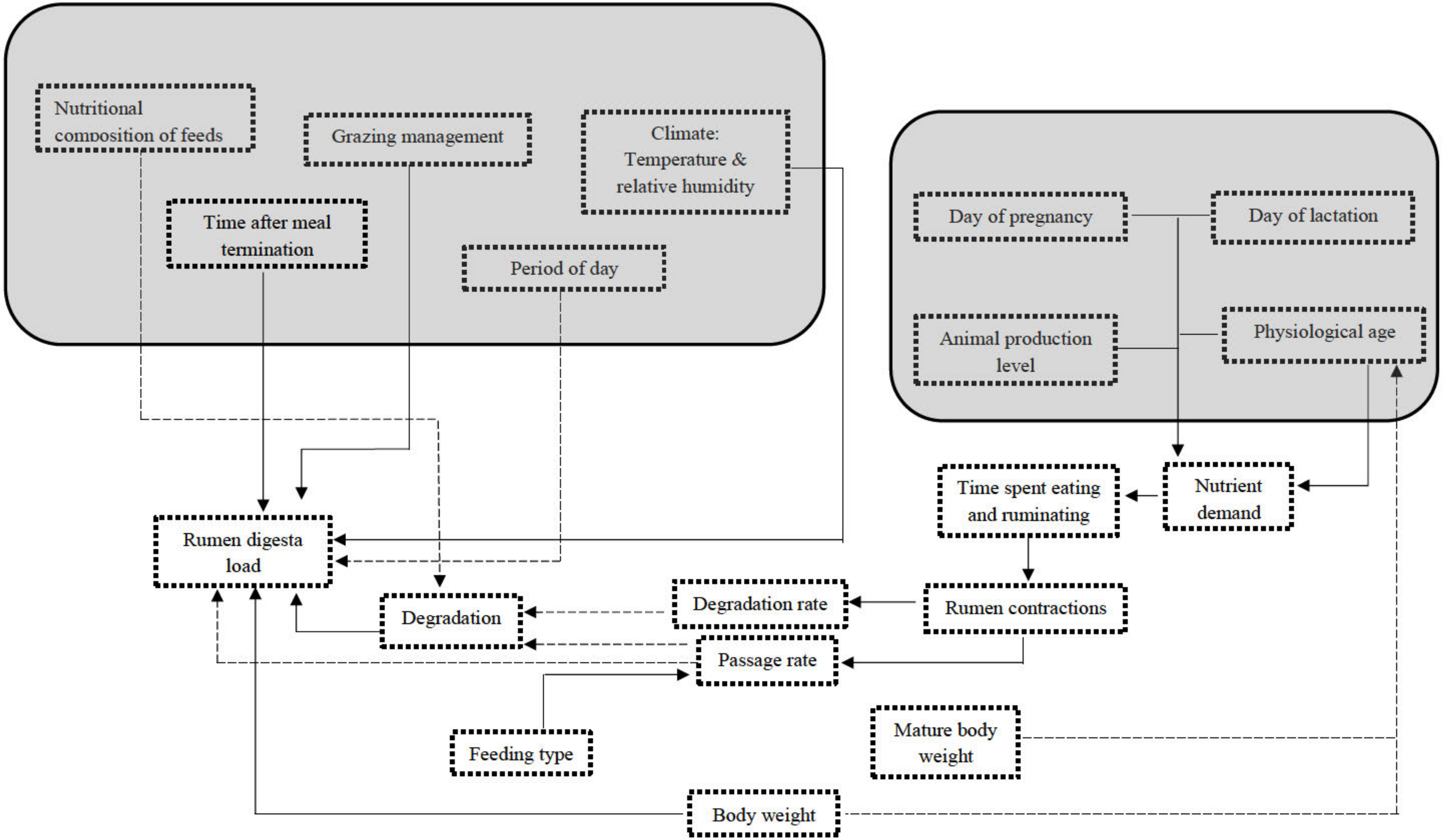


Fig. 7. 1 Factors affecting rumen digesta load of grazing and browsing ruminants

7.2.2 Meta-analysis of rumen digesta load

Response variables (i.e. wet, dry and liquid mass of rumen digesta loads) were logarithmically transformed for purposes of estimating the scalar. Hereafter, each reference to a response variable will refer to the $\log_{10}$ of that response variable unless otherwise stated in the manuscript. Log_{10} transformation of body weight (BW) was done to meet assumptions of homogeneity of variance and maintain consistency with previous studies that estimated scaling relationships of gut digesta load (Ramzinski and Weckerly 2007; Weckerly 2010; Luna et al. 2012; Muller et al. 2013). The response surface regression analysis of SAS 9.3 software (SAS Institute Inc., Cary, NC, USA) was used to determine whether the relationship between rumen digesta load (RDL) and BW was linear or quadratic. The quadratic parameter was not significant. A linear model with a $\log_{10}$ function was fitted to estimate the scaling relationships between body weight (BW) and rumen digesta load (RDL) with the general equation: $\log_{10}$ (RDL) = a + b $\log_{10}$ (BW) or RDL = aBW^b; where ‘a’ is the intercept and ‘b’ is the slope of the line, also known as the allometric coefficient.

Because of the wide distribution of animal body weights reported in these studies, rumen digesta loads was standardised using the allometric scaling factors obtained from the dataset. Rumen digesta load was scaled to body weight (BW^b). A meta-analysis was done using the mixed model regression procedure according to St-Pierre (2001) and Sauvant et al (2008) to determine the main effects of ruminant type, ruminant feeding type and climate on rumen digesta load. A model with discrete predictor variables (ruminant type, ruminant feeding type and climate) considered as fixed effects were used. The fixed effect of days in lactation, days in pregnancy, body weight, mature body weight, degree of maturity, animal production level, dry matter, neutral detergent fibre, ash and crude protein contents of diets fed to animals, whether animals were fed indoors or grazing outdoors and ambient temperature were considered as covariates. Different studies were considered as random effects.

A second model with discrete predictor variables considered as fixed effects was used to determine the main effects of ruminant type, ruminant feeding type and climate on chemical composition of feeds/diets fed to or consumed by ruminants. Data were weighted by the number of animals in each study and the standard error of mean according to Sauvant et al. (2008). Least square means were used to compare differences among means in the case of discrete predictor variables. The probability threshold for significance of fixed and random study effects for meta-analyses were considered at $p<0.05$ (Sauvant et al. 2008).

Models were built to assess the influence of days in lactation, days in pregnancy, body weight, mature body weight, degree of maturity, animal production level, dry matter, acid detergent fibre, neutral detergent fibre, ash and crude protein contents of diets fed to or eaten by animals, and ambient temperature, as well as combinations of these covariates on each response variable. The variance inflation factor (VIF) was used to assess multicollinearity among prediction variables according to Kaps and Lamberson (2017). Starch and acid detergent fibre content were removed because of high multicollinearity (VIF > 10) with NDF. The model statistics of Akaike's information criterion (AIC) was applied in model selection to measure the relative goodness of fit of the statistical models. The value of *Cp* (smaller than the number of parameters in the model) and AIC (lower AIC is better model) were used to select an optimal model (Kaps and Lamberson 2017). The correlation procedure was used to establish the Pearson correlation coefficients of any two input predictor variables.

7.2.3 Development of random forest model

Factors used as input variables for predicting rumen digesta load were RFT, BW, DOM, DP, DL, APL, DM, NDF, CP, STA, ash, GI, CT and AT. Random Forest models were programmed on a 64-bit R version 3.6.2 (Dark and Stormy Night) to predict rumen digesta load. A random forest model was trained to predict rumen digesta load using diet, feed, animal and environmental factors described previously. Since different variables span over wide ranges, normalisation (within the interval (0, 1)) of input and output variables was done. The Random Forest algorithm intrinsically divided the dataset into 2 subsets: 70% of the dataset for model training and 30% for testing. The random forest was trained as a binary tree-based machine-learning method to predict rumen digesta load. The Random Forest algorithm was tuned for one parameter (i.e. "mtry") using the "trainControl" option, and the search for the best "mtry" was randomly done. The "mtry" parameter represents the number of variables randomly sampled as candidates at each split. The most accurate value for "mtry" was selected for the combination that yielded the lowest error. During resampling the training data was cross-validated 10-fold 3 times. The best "mtry" values for each predicted variable were; scaled RDML ("mtry" = 3, RMSE = 0.019, R^2 = 0.617 and MAE = 0.014), unscaled RDML ("mtry" = 5, RMSE = 1.89, R^2 = 0.81 and MAE = 1.241), RWML ("mtry" = 3, RMSE = 13.256, R^2 = 0.874 and MAE = 8.827) and RLML ("mtry" = 5, RMSE = 10.919, R^2 = 0.885 and MAE = 7.468). The number of decision trees ("ntree") was set at 2000. After training the final models attained precision in prediction of 60.9% (scaled RDML), 81% (unscaled RDML), 86.58% (RWML) and 87.69% (RLML).

Regression analyses of observed against predicted rumen digesta load 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. Residual standard error (RSE) was used to determine accuracy of these models. The linear and mean biases in model predictions were evaluated by regressing the residuals (observed minus predicted rumen digesta load) against predicted rumen digesta load using the training dataset. The intercept and slopes were tested against 0 to determine any linear or mean bias St-Pierre (2003)

Table 7. 1 Descriptive statistics of animal, diet, feed and climatic factors affecting degradation of feeds in the rumen

Animal factors	N	Max	Min	Mean ± SD	SEM	CV (%)
RL (kg)	428	128.1	0.251	43.45 ± 32.315	1.56	74.89
RDML (kg)	527	23.00	0.0315	6.05 ± 4.663	0.203	77.11
RWML (kg)	484	146.6	0.30	44.34 ± 37.015	1.682	83.48
BW (kg)	583	875	3.6	353 ± 246.2	10.196	69.79
MBW (kg)	583	1200	6.1	455 ± 301.9	12.51	66.41
DOM	583	1.602	0.15	0.79 ± 0.394	0.016	50.15
DP (days)	583	274	0.00	8.18 ± 31.987	1.325	391.2
DL (days)	583	312	0.00	36.8 ± 77.092	3.193	209.4
APL	583	3.73	1.00	1.42 ± 0.708	0.029	49.92
Diet factors						
DM (g/kg)	583	943	121	564 ± 311.77	12.91	55.27
CP (g/kg)	583	340	16.50	153 ± 62.972	2.61	41.13
NDF (g/kg)	583	873	129	517 ± 144.71	5.99	27.99
ADF (g/kg)	583	654	38.00	313 ± 91.99	3.81	29.42
HEM (g/kg)	583	444	6.0.0	208 ± 87.01	3.60	42.83
Ash (g/kg)	583	322	22.96	91.29 ± 51.107	2.117	55.98
PFCC (g/kg)	583	740	44.00	330 ± 116.39	4.82	35.28
Climatic factors						
AT (ºC)	583	30	-8.0	12.83 ± 7.380	0.306	57.53

ADF, acid detergent fibre; APL, animal production level; DL, days in lactation; DM, dry matter; DP, days pregnant; BW, body weight; MBM, mature body mass; NDF, neutral detergent fibre; CP, crude protein; NDF, neutral detergent fibre; PS, particle size; PFCC, protein-free cell contents; AT, ambient temperature; CV, coefficient of variation; SEM, standard error of the mean; RDL, rumen digesta load; DOM, degree of maturity.

7.3 Results

7.3.1 Meta-analysis of rumen digesta load

Dry rumen digesta load scaled allometrically with BW for all ruminant feeding types (Table 7.2). Grazers and intermediate feeders had allometric scaling factors of < 1, while the allometric scale was > 1 for browsers. Wet and liquid rumen digesta load of grazers and browsers scaled isometrically with BW, while an allometric relationship was observed with intermediate feeders. Scaling factors for dry rumen load (grazers, browsers and combined feeding types), and both wet and liquid rumen load (grazers and combined feeding types) were higher than the scaling factors of the Bell-Jarman principle of $BW^{0.75}$.

Intercepts of scaling relationships of dry rumen load and BW were highest for intermediate feeders, then grazers and lowest for browsers. Intercepts of scaling relationships of wet and liquid rumen digesta load and BW were higher ($p<0.05$) for intermediate feeders compared to grazers and browsers with the latter 2 feeding types having similar intercepts ($p>0.05$). Rumen digesta load scaled isometrically with degree of maturity ($DOM^{0.85 – 1.01}$), while animal production level ($APL^{1.37 – 1.62}$) scaled allometrically.

The response of rumen digesta load to increases in ambient temperature where more linear than they were quadratic (Table 7.3). The overall response of rumen digesta load to an increase in ambient temperature showed a gradual decrease. Liquid and dry rumen digesta load were predicted to decrease in proportion by 0.02 ($p<0.0001$) for every 1°C increase in ambient temperature. Dry rumen digesta load was predicted to decrease by a proportion of 0.05 for every 1°C increase in ambient temperature in ruminants kept in tropical climates, while there was a predicted increase in rumen digesta load for ruminants in cold climates. Estimation of scaling relationships of rumen digesta load and body weight using the classical log-log linear regressions (Table 7.2) gave similar predictions of scaling factors as the 6-best models for each response variable that were developed using Akaike's information criterion (AIC) (Table 7.4).

Climate type ($p<0.05$) and climatic region ($p<0.15$) influenced dry, wet and liquid rumen loads (Table 7.4 and 7.5). Dry, wet, and liquid rumen digesta load were highest for ruminants inhabiting tropical regions, followed by cold, temperate, and lowest in arid climates. Influential covariates on rumen dry digesta weight were body weight, mature body weight, degree of maturity and animal production level. Wet mass of digesta was influenced by body weight, mature body weight, animal production level and days in pregnancy, while the weight of liquid matter was not influenced by mature body weight.

Ruminant species ($p<0.05$) and ruminant feeding type ($p<0.05$) affected all measures of rumen digesta load (Table 7.4 and 7.6). Grazers (0.055 kg) had the heaviest dry rumen loads, followed by intermediate feeders (0.035 kg) with browsers (0.025 kg) having the lightest rumen loads. Wet and liquid rumen loads were lowest for intermediate feeders (wet = 0.079 kg and liquid = 0.081 kg), followed by browsers (wet = 0.089 kg and liquid = 0.091 kg) and highest for grazers (wet = 0.107 kg and liquid = 0.105 kg).

Table 7. 2 Estimates of the scaling relationships between body weight (BW) and rumen digesta load (RDL) of browsing and grazing wild and domestic ruminants with general equation of: $\log_{10}(RDL) = a + b \log_{10}(BW)$ or $RDL = aBW^{b}$.

Rumen digesta load	N	Intercept (a)	$P_{\text{intercept}}$	[A] Slope (b)	P_{slope}	RMSE	R^2	[B] Test	[C] Test
$\log_{10}$(RDML)		$\log_{10}$ (BW) (kg)							
Grazers	473	$-1.72^{b} \pm 0.055$	<0.0001	$0.95^{b} \pm 0.022$	<0.0001	0.1956	0.8009	*	***
Browsers	15	$-2.09^{c} \pm 0.088$	<0.0001	$1.13^{a} \pm 0.053$	<0.0001	0.1429	0.9716	*	***
Intermediate feeders	39	$-1.37^{a} \pm 0.144$	<0.0001	$0.79^{c} \pm 0.087$	<0.0001	0.2127	0.6882	*	NS
Combined	527	$-1.70^{b} \pm 0.042$	<0.0001	$0.95^{b} \pm 0.017$	<0.0001	0.1987	0.8519	**	***
$\log_{10}$(RWML)									
Grazers	384	$-0.81^{b} \pm 0.057$	<0.0001	$0.97^{a} \pm 0.023$	<0.0001	0.1921	0.8220	NS	***
Browsers	24	$-0.75^{a, b} \pm 0.23$	<0.0001	$0.89^{a, b} \pm 0.13$	<0.0001	0.3717	0.7009	NS	NS
Intermediate feeders	76	$-0.52^{a} \pm 0.146$	<0.0001	$0.74^{b} \pm 0.083$	<0.0001	0.230	0.5193	**	NS
Combined	484	$-0.90^{b} \pm 0.045$	<0.0001	$1.00^{a} \pm 0.019$	<0.0001	0.2155	0.8469	NS	***
$\log_{10}$(RLL)									
Grazers	382	$-0.93^{b} \pm 0.053$	<0.0001	$1.00^{a} \pm 0.021$	<0.0001	0.178	0.8522	NS	***
Browsers	11	$-1.23^{b} \pm 0.423$	0.0175	$1.13^{a} \pm 0.230$	0.0008	0.506	0.7300	NS	NS
Intermediate feeders	35	$-0.57^{a} \pm 0.131$	0.0001	$0.79^{b} \pm 0.078$	<0.0001	0.1826	0.7562	**	NS
Combined	428	$-0.91^{b} \pm 0.045$	<0.0001	$0.99^{a} \pm 0.019$	<0.0001	0.1919	0.8678	NS	***
		$\log_{10}$ (DOM)							
$\log_{10}$(RDML)	484	0.71 ± 0.026	<0.0001	1.01 ± 0.115	<0.0001	0.4823	0.1277	NS	*
$\log_{10}$(RWML)	484	1.53 ± 0.0310	<0.0001	0.85 ± 0.126	<0.0001	0.5268	0.0848	NS	NS
$\log_{10}$(RLL)	428	1.55 ± 0.0311	<0.0001	0.86 ± 0.129	<0.0001	0.5027	0.0935	NS	NS
		$\log_{10}$ (APL)							
$\log_{10}$(RDML)	484	0.40 ± 0.0235	<0.0001	1.37 ± 0.107	<0.0001	0.4504	0.2407	***	***
$\log_{10}$(RWML)	484	1.27 ± 0.0250	<0.0001	1.62 ± 0.143	<0.0001	0.4896	0.2111	***	***
$\log_{10}$(RLL)	428	1.29 ± 0.0262	<0.0001	1.42 ± 0.140	<0.0001	0.4739	0.1943	**	***

[A] The slope represents the scaling factor (b) based on the $\log_{10}$-transformed linear equation

[B] Test of slope against 1

[C] Test of scaling factor against Bell-Jarman principle of $BW^{0\ 75}$

APL, animal production level; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load; DOM, degree of maturity; RMSE, root mean square error; N, number of data used.

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 7. 3 Equations for linear regression between rumen digesta load and ambient temperature of browsing and grazing wild and domestic ruminants

Rumen digesta load	N	Intercept (a)	$P_{\text{intercept}}$	[A] Slope (b)	P_{slope}	RMSE	R^2	*L*	*Q*
$\log_{10}$(RDML)		Ambient temperature (°C)							
Grazers	473	0.811 ± 0.044	<0.0001	-0.01 ± 0.003	<0.0001	0.4313	0.032	***	*
Browsers	15	-0.08 ± 0.753	0.9119	-0.01 ± 0.035	0.6796	0.8423	0.014	NS	NS
Intermediate feeders	39	0.22 ± 0.174	0.2114	-0.02 ± 0.008	0.0546	0.3621	0.096	*	NS
Combined	527	0.88 ± 0.0477	<0.0001	-0.02 ± 0.003	<0.0001	0.4921	0.092		
$\log_{10}$(RWML)									
Grazers	384	1.73 ± 0.052	<0.0001	-0.013 ± 0.004	0.0003	0.4476	0.034	***	NS
Browsers	24	0.77 ± 0.183	0.0004	0.005 ± 0.013	0.7182	0.6777	0.006	NS	NS
Intermediate feeders	76	0.78 ± 0.060	<0.0001	-0.002 ± 0.004	0.6114	0.3310	0.005	NS	NS
Combined	484	1.44 ± 0.050	<0.0001	-0.004 ± 0.003	0.3037	0.5507	0.002		
$\log_{10}$(RLL)									
Grazers	382	1.66 ± 0.052	<0.0001	-0.01 ± 0.004	0.0010	0.4539	0.028	***	NS
Browsers	11	0.09 ± 0.867	0.9165	0.03 ± 0.043	0.4659	0.9437	0.060	NS	NS
Intermediate feeders	35	0.99 ± 0.172	<0.0001	-0.01 ± 0.008	0.1030	0.3543	0.079	NS	NS
Combined	428	1.70 ± 0.056	<0.0001	-0.02 ± 0.004	<0.0001	0.5097	0.066		
$\log_{10}$(RDML)									
Tropical	13	1.74 ± 0.198	<0.0001	-0.051 ± 0.010	0.0004	0.2469	0.693	***	***
Arid	26	0.37 ± 0.199	0.0752	-0.011 ± 0.014	0.4103	0.5497	0.028	NS	NS
Cold	89	0.83 ± 0.029	<0.0001	0.009 ± 0.003	0.0035	0.1886	0.094	**	*
Temperate	399	0.92 ± 0.070	<0.0001	-0.027 ± 0.004	<0.0001	0.5083	0.090	***	***
$\log_{10}$(RWML)									
Tropical	8	1.63 ± 0.016	<0.0001	0.033 ± 0.001	<0.0001	0.0090	0.992	***	NS
Arid	22	1.08 ± 0.255	0.0004	-0.007 ± 0.016	0.6546	0.6379	0.010	NS	NS
Cold	79	1.55 ± 0.050	<0.0001	0.015 ± 0.005	0.0042	0.3319	0.101	**	NS
Temperate	375	1.36 ± 0.066	<0.0001	-0.0003 ± 0.004	0.9402	0.5567	0.000	NS	***
$\log_{10}$(RLL)									
Tropical	8	1.60 ± 0.017	<0.0001	0.03 ± 0.001	<0.0001	0.0096	0.990	*	NS
Arid	22	1.01 ± 0.262	0.0010	-0.008 ± 0.017	0.6560	0.6544	0.010	NS	NS
Cold	64	1.71 ± 0.024	<0.0001	0.004 ± 0.002	0.0425	0.1343	0.065	*	NS
Temperate	334	1.72 ± 0.075	<0.0001	-0.02 ± 0.005	<0.0001	0.5103	0.069	***	NS

[A] The slope represents the scaling factor (b) based on the $\log_{10}$-transformed linear equation

[B] Test of slope against 1

[C] Test of scaling factor against Bell-Jarman principle of BW$^{0\ 75}$

L, linear; Q, quadratic; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load; RMSE, root mean square error; N, number of data used.

* p<0.05; ** p<0.01; *** p<0.001; NS, not significant (p>0.05)

Table 7. 4 Models analysed using Akaike's information criterion (AIC) and Cp statistic (C(p)) for estimating the scaling relationships between body weight and rumen dry, wet and liquid loads of wild and domestic ruminants

	nPar	*C(p)*	*AIC*	R^2	Models
Model predictors					$\log_{10}$ RDML
DOM, DL, BW, Ash and NDF	5+1	3.3744	-1748.25	0.8669	-1.76 – 0.14×DOM + 0.0007×DL + 0.95 $\log_{10}$ BW – 0.0006×Ash + 0.0003×NDF
DOM, DL, BW, Ash, NDF and AT	6+1	4.7969	-1746.84	0.8670	-1.76 – 0.14×DOM + 0.0006×DL + 0.96 $\log_{10}$ BW – 0.0006×Ash + 0.0003×NDF + 0.01×AT
DOM, DL, BW, CP, Ash and NDF	6+1	4.8397	-1746.79	0.8670	-1.72 – 0.14×DOM + 0.0007×DL + 0.95 $\log_{10}$ BW – 0.0001×CP – 0.0005×Ash + 0.0003×NDF
DOM, DP, DL, BW, Ash and NDF	6+1	5.2567	-1746.37	0.8669	-1.75 – 0.14×DOM + 0.00009×DP + 0.0007×DL + 0.95 $\log_{10}$ BW – 0.0006×Ash + 0.0003×NDF
DOM, DL, BW, DM, Ash and NDF	6+1	5.3742	-1746.25	0.8669	-1.76 – 0.14×DOM + 0.0007×DL + 0.95 $\log_{10}$ BW – 0.0006×Ash + 0.0003×NDF
					$\log_{10}$ RWML
DOM, DL, BW and CP	4+1	4.4457	-1517.51	0.8593	-0.69 – 0.18×DOM + 0.0006×DL + 0.99 $\log_{10}$ BW – 0.0006×CP
DOM, DL, BW, DM and CP	5+1	4.6556	-1517.33	0.8598	-0.74 – 0.18×DOM + 0.0006×DL + 1.00 $\log_{10}$ BW + 0.00004×DM – 0.0005×CP
DOM, DP, DL, BW and CP	5+1	5.2809	-1516.69	0.8596	-0.68 – 0.19×DOM + 0.0003×DP + 0.0006×DL + 0.99 $\log_{10}$ BW – 0.0006×CP
DOM, DP, DL, BW, DM and CP	6+1	5.3739	-1516.63	0.8602	-0.73 – 0.19×DOM + 0.0003×DP + 0.0006×DL + 1.00 $\log_{10}$ BW + 0.00005×DM – 0.0006×CP
DOM, DL, BW, CP and Ash	5+1	5.5151	-1516.46	0.8595	-0.65 – 0.19×DOM + 0.0007×DL + 0.99 $\log_{10}$ BW – 0.0005×CP – 0.0004×Ash
					$\log_{10}$ RLL
DOM, DL, BW, DM, Ash and NDF	6+1	5.3597	-1446.31	0.8811	-0.71 – 0.18×DOM + 0.0007×DL + 0.97 $\log_{10}$ BW – 0.00007×DM – 0.001×Ash + 0.0002×NDF
DOM, DP, DL, BW, DM, Ash and NDF	7+1	6.2425	-1445.45	0.8814	-0.70 – 0.19×DOM + 0.0003×DP + 0.0007×DL + 0.97 $\log_{10}$ BW – 0.00007×DM – 0.001×Ash + 0.0002×NDF
DOM, DL, BW, DM, CP, Ash and NDF	7+1	7.0350	-1444.64	0.8812	-0.74 – 0.18×DOM + 0.0007×DL + 0.97 $\log_{10}$ BW – 0.00007×DM + 0.0001×CP – 0.001×Ash + 0.0002×NDF
DOM, DL, BW, DM, Ash, NDF and AT	7+1	7.3594	-1444.31	0.8811	-0.71 – 0.18×DOM + 0.0007×DL + 0.97 $\log_{10}$ BW – 0.00007×DM – 0.001×Ash + 0.0002×NDF – 0.00002×AT
DOM, DP, DL, BW, DM, CP, Ash and NDF	8+1	8.0158	-1443.68	0.8815	-0.72 – 0.18×DOM + 0.0003×DP + 0.0007×DL + 0.97 $\log_{10}$ BW – 0.00007×DM + 0.0001×CP – 0.001×Ash + 0.0002×NDF
					Models with $\log_{10}$ BW dropped from development
					$\log_{10}$ RDML
DOM, DL, DM, Ash, NDF and AT	6+1	5.3423	-913.30	0.3533	1.01 + 0.47 $\log_{10}$ DOM + 0.002×DL – 0.0003×DM – 0.002×Ash + 0.0003×NDF – 0.02×AT
DOM, DL, DM, CP, Ash, NDF and AT	7+1	7.1299	-911.51	0.3536	0.96 + 0.48 $\log_{10}$ DOM + 0.002×DL – 0.0003×DM + 0.0002×CP – 0.002×Ash + 0.0004×NDF – 0.02×AT
					$\log_{10}$ RWML
DOM, DL, CP and AT	4+1	2.2209	-701.34	0.2400	1.62 + 0.50 $\log_{10}$ DOM + 0.003×DL – 0.0008×CP – 0.01×AT
DOM, DP, DL, CP and AT	5+1	3.5598	-700.01	0.2411	1.61 + 0.48 $\log_{10}$ DOM + 0.0005×DP + 0.003×DL – 0.0008×CP – 0.009×AT
					$\log_{10}$ RLL
DOM, DL, DM, CP, Ash, NDF and AT	7+1	7.6306	-715.67	0.3477	1.72 + 0.40 $\log_{10}$ DOM + 0.003×DL – 0.0004×DM + 0.0009×CP – 0.003×Ash + 0.0005×NDF – 0.02×AT
DOM, DP, DL, DM, CP, Ash, NDF and AT	8+1	9.0000	-714.31	0.3487	1.72 + 0.39 $\log_{10}$ DOM + 0.0005×DP + 0.002×DL – 0.0004×DM + 0.0009×CP – 0.003×Ash + 0.0005×NDF – 0.02×AT

nPar, number of parameters for each model is the number independent variables +1; DL: days in lactation; DM: dry matter; DP: days pregnant; BW, body weight; NDF: neutral detergent fibre; CP, crude protein; AT, ambient temperature; CV, coefficient of variation; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load; DOM, degree of maturity.

Table 7. 5 Effects climatic region and ambient temperature on scaled and unscaled (actual) rumen digesta load of browsing and grazing wild and domestic ruminants

Effect of climatic region		BW (kg)	log$_{10}$ scaled rumen digesta load (LSM±SE) (kg)			log$_{10}$ actual rumen digesta load (LSM±SE) (kg)		
Tropical climates	N		RDML ($BW^{0\ 95}$)	RWML ($BW^{1\ 0}$)	RLL ($BW^{0\ 99}$)	RDML	RWML	RLL
Am	5	160.00	-1.52 ± 0.187	-	-	0.17 ± 0.226	-	-
Aw	8	680.00	-1.34 ± 0.179	-0.71 ± 0.239	-0.85 ± 0.199	0.31 ± 0.217	1.53 ± 0.406	1.28 ± 0.284
Arid climates								
BSh	20	350.95	-1.57 ± 0.135	-0.93 ± 0.150	-1.01 ± 0.115	0.14 ± 0.157	1.34 ± 0.262	1.33 ± 0.173
BSk	4	53.300	-1.66 ± 0.172	-1.89 ± 0.219	-1.77 ± 0.171	-0.13 ± 0.210	-0.06 ± 0.382	0.43 ± 0.256
BWh	2	89.750	-1.76 ± 0.215	-1.55 ± 0.391	-1.23 ± 0.337	-0.04 ± 0.249	0.70 ± 0.549	1.08 ± 0.429
Temperate climates								
Cfa	55	231.09	-1.44 ± 0.070	-1.04 ± 0.073	-1.08 ± 0.064	0.15 ± 0.082	1.02 ± 0.121	1.06 ± 0.094
Cfb	359	374.12	-1.41 ± 0.037	-0.91 ± 0.049	-0.95 ± 0.037	0.26 ± 0.044	1.28 ± 0.082	1.25 ± 0.055
Csa	23	171.11	-1.34 ± 0.116	-1.08 ± 0.143	-1.03 ± 0.103	0.25 ± 0.142	0.97 ± 0.240	1.20 ± 0.152
Cwa	12	30.870	-1.36 ± 0.829	-0.97 ± 0.235	-0.89 ± 0.187	0.20 ± 0.843	0.91 ± 0.396	1.09 ± 0.272
Cold climates								
Dfa	32	542.50	-1.35 ± 0.102	-0.75 ± 0.144	-0.86 ± 0.097	0.40 ± 0.120	1.62 ± 0.238	1.40 ± 0.147
Dfb	53	363.05	-1.46 ± 0.083	-0.93 ± 0.098	-0.97 ± 0.083	0.18 ± 0.010	1.19 ± 0.160	1.23 ± 0.120
Dsb	10	464.00	-1.05 ± 0.161	-0.67 ± 0.216	-0.77 ± 0.171	0.71 ± 0.201	1.61 ± 0.380	1.47 ± 0.255
Significance			NS	**	**	NS	*	NS
Effect of feeding type								
Grazers	475	413.33	-1.26 ± 0.079	-0.97 ± 0.062	-0.98 ± 0.049	0.56 ± 0.084	1.41 ± 0.099	1.41 ± 0.068
Browsers	28	121.53	-1.60 ± 0.084	-1.05 ± 0.065	-1.04 ± 0.055	-0.11 ± 0.099	0.97 ± 0.102	1.16 ± 0.075
Intermediate feeders	80	73.832	-1.46 ± 0.088	-1.10 ± 0.066	-1.09 ± 0.058	0.21 ± 0.094	0.92 ± 0.103	0.92 ± 0.078
Significance			***	***	**	***	***	***
Covariate fixed effects								
Animal factors								
BW (kg)			***	***	*	***	*	***
MBM (kg)			*	NS	NS	**	***	NS
DOM			***	NS	NS	*	**	***
DP (days)			NS	*	**	NS	*	*
DL (days)			NS	NS	NS	NS	NS	NS
APL			***	***	NS	***	***	NS
Diet factors								
DM (g/kg)			NS	NS	NS	NS	*	**
CP (g/kg)			NS	NS	NS	NS	NS	NS
NDF (g/kg)			*	*	NS	*	NS	*
HEM (g/kg)			NS	NS	NS	NS	NS	NS
Ash (g/kg)			NS	*	NS	NS	NS	*
Environmental factors								
AT (ºC)			NS	NS	NS	NS	NS	NS
Grazing or Indoors			NS	NS	NS	NS	NS	NS
Test of random effects								
Study			***	***	***	***	***	***

AT, ambient temperature; APL, animal production level; DL, days in lactation; DP, days pregnant; DM, dry matter; BW, body weight; MBM, mature body mass; NDF, neutral detergent fibre; PhyA: physiological age; DOM, degree of maturity; CP, crude protein; HEM, hemicellulose; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load.

Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season; RF, rumen digesta load

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 7. 6 Effects climatic region and ambient temperature on scaled and unscaled (actual) rumen digesta load of browsing and grazing wild and domestic ruminants

Test of fixed effects		BW (kg)	$\log_{10}$ scaled rumen digesta load (LSM±SE) (kg)			$\log_{10}$ actual rumen digesta load (LSM±SE) (kg)		
Effect of climatic region	N		RDML ($BW^{0\ 95}$)	RWML ($BW^{1\ 0}$)	RLL ($BW^{0\ 99}$)	RDML	RWML	RL
Tropical climates	13	480.00	-1.15 ± 0.139	-0.66 ± 0.253	-0.82 ± 0.206	0.75 ± 0.213	1.70 ± 0.396	1.32 ± 0.290
Arid climates	26	285.07	-1.51 ± 0.107	-1.23 ± 0.125	-1.20 ± 0.095	0.24 ± 0.159	1.06 ± 0.195	1.32 ± 0.134
Temperate climates	440	334.89	-1.27 ± 0.033	-0.93 ± 0.042	-0.94 ± 0.032	0.50 ± 0.051	1.32 ± 0.065	1.40 ± 0.044
Cold climates	104	429.20	-1.19 ± 0.059	-0.80 ± 0.072	-0.86 ± 0.055	0.66 ± 0.089	1.64 ± 0.112	1.50 ± 0.078
Significance			*	*	*	*	*	NS
Covariate fixed effects								
Animal factors								
BW (kg)			**	***	NS	NS	*	***
MBM (kg)			NS	NS	NS	***	NS	*
DOM			NS	NS	NS	***	NS	NS
DP (days)			NS	***	*	NS	NS	NS
DL (days)			NS	NS	NS	NS	NS	NS
APL			*	**	NS	NS	*	NS
Diet factors								
DM (g/kg)			NS	NS	*	NS	***	***
CP (g/kg)			NS	NS	NS	NS	**	**
NDF (g/kg)			*	**	**	NS	***	***
HEM (g/kg)			NS	NS	NS	NS	NS	**
Ash (g/kg)			NS	*	NS	NS	NS	***
Environmental factors								
AT (ºC)			*	NS	NS	NS	NS	NS
Grazing or Indoors			NS	NS	NS	NS	NS	NS
Test of random effects								
Study			***	***	***	***	***	***

AT, ambient temperature; APL, animal production level; DL, days in lactation; DP, days pregnant; DM, dry matter; BW, body weight; MBM, mature body mass; NDF, neutral detergent fibre; PhyA: physiological age; DOM, degree of maturity; CP, crude protein; HEM, hemicellulose; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load.

Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season; RF, rumen digesta load

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 7. 7 Effects of ruminant species and feeding type on scaled and unscaled (actual) rumen digesta load of browsing and grazing wild and domestic ruminants

Test of fixed effects		BW (kg)	$\log_{10}$ scaled rumen digesta load (LSM±SE) (kg)			$\log_{10}$ actual rumen digesta load (LSM±SE) (kg)		
Effect of ruminant type	N		RDML/kgBW$^{0.95}$	RWML/kgBW$^{1.0}$	RLL/kgBW$^{0.99}$	RDML	RWML	RLL
Grazers								
Addax	2	89.8	-1.76 ± 0.213	-1.44 ± 0.372	-1.26 ± 0.358	-0.03 ± 0.203	0.82 ± 0.370	0.92 ± 0.360
African buffalo	4	750	-0.76 ± 0.136	-0.92 ± 0.139	-0.87 ± 0.155	1.20 ± 0.126	1.62 ± 0.137	1.67 ± 0.156
Black wildebeest	12	187	-1.29 ± 0.235	-1.08 ± 0.202	-1.31 ± 0.204	0.50 ± 0.228	1.29 ± 0.200	1.00 ± 0.206
Blue wildebeest	2	218	-0.96 ± 0.805	-0.44 ± 0.154	-0.70 ± 0.163	0.90 ± 0.806	1.97 ± 0.152	1.69 ± 0.164
Bushbuck	1	27.0	-1.68 ± 8.773	-	-	-0.28 ± 8.794	-	-
Cattle	343	523	-1.17 ± 0.049	-0.81 ± 0.076	-0.83 ± 0.066	0.74 ± 0.046	1.68 ± 0.075	1.70 ± 0.067
Hartebeest	3	133	-1.30 ± 1.822	-1.13 ± 0.667	-1.22 ± 1.762	0.49 ± 1.826	1.17 ± 0.665	1.08 ± 1.769
Mountain Reedbuck	1	28.0	-1.72 ± 26.587	-1.37 ± 16.252	-1.46 ± 10.02	-0.41 ± 26.651	0.35 ± 16.232	0.19 ± 10.060
Muskoxen	5	221	-1.27 ± 0.238	-	-	0.61 ± 0.234	-	-
Gemsbok	3	201	-0.94 ± 0.142	-0.66 ± 0.136	-0.76 ± 0.159	0.91 ± 0.131	1.75 ± 0.134	1.62 ± 0.161
Sheep	94	56.4	-1.50 ± 0.099	-1.11 ± 0.110	-1.16 ± 0.109	0.03 ± 0.094	0.88 ± 0.109	0.81 ± 0.110
Swamp buffalo	9	390	-1.16 ± 0.157	-0.96 ± 0.192	-0.98 ± 0.192	0.79 ± 0.147	1.60 ± 0.189	1.58 ± 0.193
Topi	2	131	-1.29 ± 5.067	-1.09 ± 0.570	-1.26 ± 1.917	0.48 ± 5.079	1.18 ± 0.569	1.01 ± 1.925
Tsessebe	1	114	-1.24 ± 2.084	-	-	0.48 ± 2.088	-	-
Waterbuck	2	258	-1.05 ± 0.142	-0.69 ± 0.142	-0.64 ± 0.204	0.83 ± 0.132	1.75 ± 0.140	1.76 ± 0.205
Browsers								
Bush duiker	1	13.0	-1.52 ± 18.219	-	-	-0.43 ± 18.263	-	-
Gerenuk	2	42.8	-1.42 ± 0.160	-0.01 ± 0.270	-0.0004 ± 0 9	-0.01 ± 0.149	1.86 ± 0.268	1.81 ± 0.873
Giraffe	2	727	-0.83 ± 0.179	-0.97 ± 0.208	-0.80 ± 0.209	1.13 ± 0.167	1.53 ± 0.205	1.74 ± 0.210
Kirk’s dik-dik	2	5.10	-1.86 ± 48.636	-1.37 ± 58.744	-1.59 ± 36 21	-1.06 ± 48.753	-0.29 ± 58.672	-0.55 ± 36.358
Kudu	1	145	-1.13 ± 0.761	-0.62 ± 0.143	-0.79 ± 0.161	0.68 ± 0.761	1.75 ± 0.141	1.57 ± 0.162
Moose	3	284	-	-0.98 ± 0.207	-	-	1.50 ± 0.204	-
Mule deer	1	57.0	-1.49 ± 1.869	-1.10 ± 2.068	-1.36 ± 1.386	0.05 ± 1.872	0.91 ± 2.065	0.65 ± 1.391
Roe deer	1	14.0	-1.62 ± 7.583	-1.32 ± 8.386	-1.56 ± 5.585	-0.51 ± 7.600	0.18 ± 8.375	-0.08 ± 5.607
Springbok	1	42.0	-1.25 ± 5.564	-0.59 ± 0.177	-0.79 ± 0.189	0.18 ± 5.577	1.23 ± 0.175	0.99 ± 0.191
Suni	2	5.30	-1.75 ± 58.723	-1.36 ± 79.613	-1.57 ± 49.08	-1.00 ± 58.864	-0.26 ± 79.515	-0.52 ± 49.275
Intermediate feeders								
Grant’s Gazelle	2	56.5	-1.41 ± 4.360	-1.21 ± 6.161	-1.38 ± 3.801	0.14 ± 4.370	0.81 ± 6.153	0.59 ± 3.816
Eland	2	554	-0.86 ± 0.144	-0.89 ± 0.155	-0.75 ± 0.169	1.13 ± 0.134	1.66 ± 0.153	1.82 ± 0.170
Fallow deer	1	40.0	-1.43 ± 2.658	-0.98 ± 2.941	-1.19 ± 1.964	0.01 ± 2.664	0.93 ± 2.937	0.70 ± 1.972
Goats	16	25.0	-1.35 ± 0.200	-1.02 ± 0.139	-1.10 ± 0.127	-0.001 ± 0.195	0.81 ± 0.138	0.71 ± 0.128
Impala	4	52.3	-1.28 ± 1.593	-0.73 ± 0.164	-0.90 ± 0.181	0.22 ± 1.596	1.23 ± 0.162	1.02 ± 0.182
Red deer	6	110	-1.48 ± 0.167	-1.18 ± 0.128	-1.27 ± 0.113	0.19 ± 0.162	0.99 ± 0.127	0.86 ± 0.113
Reindeer	9	61.8	-	-1.04 ± 0.350	-	-	1.04 ± 0.348	-
Sika deer	4	135	-	-1.15 ± 0.195	-	-	1.04 ± 0.192	-
Spotted deer	28	66.1	-	-1.30 ± 0.215	-	-	0.76 ± 0.213	-
Steenbok	2	10.8	-1.64 ± 21.765	-1.16 ± 50.663	-1.37 ± 31 23	-0.58 ± 21.817	0.14 ± 50.601	-0.12 ± 31.357
Thomson’s Gazelle	2	21.5	-1.45 ± 11.721	-1.11 ± 15.764	-1.31 ± 9.719	-0.23 ± 11.749	0.54 ± 15.745	0.28 ± 9.758
White-tailed deer	7	21.8	-1.37 ± 2.726	-1.06 ± 0.210	-1.33 ± 2.014	0.03 ± 2.732	0.64 ± 0.206	0.45 ± 2.022
Significance			***	*	NS	***	***	***
Covariate fixed effects								
Animal factors								
BW (kg)			NS	NS	NS	***	NS	NS
MBM (kg)			*	NS	NS	*	NS	NS
DOM			*	NS	NS	NS	NS	NS
DP (days)			NS	NS	*	NS	NS	*
DL (days)			NS	NS	NS	NS	NS	NS
APL			***	NS	NS	***	NS	NS
Diet factors								
DM (g/kg)			NS	NS	NS	NS	NS	NS
CP (g/kg)			NS	NS	NS	NS	NS	NS
NDF (g/kg)			***	***	*	***	***	*
HEM (g/kg)			NS	NS	NS	NS	NS	NS
Ash (g/kg)			NS	***	NS	NS	***	NS
Environmental factors								
AT (C)			NS	NS	NS	NS	NS	NS
Grazing or Indoors			NS	NS	NS	NS	NS	NS
Test of random effects								
Study			***	***	***	***	***	***

AT, ambient temperature; APL: animal production level; DL: days in lactation; DP: days pregnant; DM, dry matter; BW, body weight; MBM: mature body mass; NDF: neutral detergent fibre; DOM, degree of maturity; CP, crude protein; HEM, hemicellulose; RDML, rumen dry matter load; RWML, rumen wet matter load; RLL, rumen liquid load

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 7. 8 Chemical composition of feeds and diets fed to or eaten by ruminants based on ruminant feeding type and ruminant type

Test of fixed effects		Proximate chemical composition (g/kg DM)					
Effect of feeding type	N	DM	CP	NDF	ADF	HEM	Ash
Grazers	475	639 ± 58.83	144 ± 11.26	519 ± 30.58	308 ± 18.87	209 ± 17.39	84 ± 7.32
Browsers	28	345 ± 67.13	206 ± 14.10	384 ± 35.04	273 ± 21.79	91 ± 21.55	105 ± 8.05
Intermediate feeders	80	672 ± 63.91	133 ± 12.99	487 ± 33.31	323 ± 20.66	174 ± 19.94	91 ± 7.77
Significance		***	***	***	***	***	***
Effect of ruminant type							
Grazers							
Addax	2	874 ± 256.4	136 ± 55.28	554 ± 141.51	256 ± 94.91	298 ± 73.16	90 ± 33.20
African buffalo	4	763 ± 123.4	137 ± 29.99	559 ± 69.49	377 ± 46.06	181 ± 41.19	71 ± 15.38
Black wildebeest	12	602 ± 119.5	90 ± 28.08	651 ± 66.96	301 ± 44.52	355 ± 38.08	104 ± 15.02
Blue wildebeest	2	397 ± 137.8	92 ± 35.30	663 ± 78.37	342 ± 51.65	317 ± 49.14	146 ± 16.82
Bushbuck	1	541 ± 191.1	106 ± 53.82	457 ± 110.85	322 ± 72.23	131 ± 76.55	101 ± 22.30
Cattle	343	580 ± 39.51	135 ± 8.49	502 ± 21.82	307 ± 14.63	196 ± 11.19	84 ± 5.10
Hartebeest	3	567 ± 124.8	99 ± 30.69	698 ± 70.42	357 ± 46.63	340 ± 42.33	99 ± 15.51
Mountain Reedbuck	1	997 ± 164.1	86 ± 44.83	655 ± 94.51	386 ± 61.82	267 ± 63.41	80 ± 19.47
Muskoxen	5	803 ± 79.96	76 ± 21.01	520 ± 45.83	308 ± 30.06	210 ± 29.25	60 ± 9.53
Gemsbok	3	882 ± 119.8	130 ± 28.59	631 ± 67.24	395 ± 44.65	233 ± 39.07	76 ± 15.02
Sheep	94	792 ± 54.66	138 ± 12.11	568 ± 30.38	352 ± 20.29	213 ± 16.08	79 ± 6.94
Swamp buffalo	9	900 ± 252.2	181 ± 53.44	592 ± 138.85	371 ± 93.27	211 ± 70.33	96 ± 32.81
Topi	2	797 ± 127.0	100 ± 31.37	727 ± 71.73	371 ± 47.47	356 ± 43.28	105 ± 15.73
Tsessebe	1	945 ± 191.2	65 ± 53.82	675 ± 110.85	355 ± 72.23	317 ± 76.55	139 ± 22.30
Waterbuck	2	689 ± 130.0	130 ± 32.48	610 ± 73.58	363 ± 48.63	247 ± 44.94	79 ± 16.03
Browsers							
Bush duiker	1	607 ± 191.1	153 ± 53.82	545 ± 110.85	387 ± 72.23	155 ± 76.55	142 ± 22.30
Gerenuk	2	746 ± 125.5	140 ± 30.75	599 ± 70.76	387 ± 46.86	211 ± 42.33	78 ± 15.58
Giraffe	2	748 ± 130.4	135 ± 32.68	561 ± 73.86	360 ± 48.80	200 ± 45.27	95 ± 16.07
Kirk’s dik-dik	2	652 ± 133.5	144 ± 33.93	494 ± 75.78	320 ± 50.00	171 ± 47.20	136 ± 16.37
Kudu	1	495 ± 152.1	167 ± 40.33	490 ± 87.12	281 ± 57.18	206 ± 56.58	120 ± 18.27
Moose	3	228 ± 86.63	188 ± 23.26	367 ± 49.87	234 ± 32.63	76 ± 32.56	80 ± 10.23
Mule deer	1	294 ± 262.1	141 ± 75.68	515 ± 153.18	260 ± 99.36	278 ± 107.80	143 ± 29.80
Roe deer	1	819 ± 262.1	136 ± 75.68	704 ± 153.18	388 ± 99.36	339 ± 107.80	108 ± 29.80
Springbok	1	382 ± 171.1	149 ± 46.95	408 ± 98.68	261 ± 64.50	144 ± 66.40	110 ± 20.22
Suni	2	565 ± 151.5	165 ± 40.41	423 ± 86.85	251 ± 56.98	170 ± 56.84	140 ± 18.19
Intermediate feeders							
Grant’s Gazelle	2	584 ± 137.6	137 ± 35.43	436 ± 78.30	254 ± 51.58	179 ± 49.44	114 ± 16.78
Eland	2	644 ± 127.5	137 ± 31.55	549 ± 72.03	347 ± 47.65	202 ± 43.54	78 ± 15.78
Fallow deer	1	346 ± 262.0	124 ± 75.68	551 ± 153.18	356 ± 99.36	218 ± 107.80	133 ± 29.80
Goats	16	811 ± 64.43	131 ± 15.83	490 ± 36.43	383 ± 24.09	111 ± 21.71	95 ± 7.92
Impala	4	397 ± 121.3	118 ± 29.12	642 ± 68.16	348 ± 45.24	291 ± 39.85	98 ± 15.17
Red deer	6	800 ± 82.62	126 ± 22.17	545 ± 47.53	366 ± 31.11	186 ± 31.04	85 ± 9.77
Reindeer	9	304 ± 251.5	162 ± 53.13	442 ± 138.40	305 ± 92.99	82 ± 69.74	80 ± 32.74
Sika deer	4	282 ± 252.6	161 ± 53.63	589 ± 139.12	360 ± 93.43	229 ± 70.53	41 ± 32.85
Spotted deer	28	280 ± 252.1	211 ± 53.38	552 ± 138.77	340 ± 93.22	213 ± 70.15	80 ± 32.79
Steenbok	2	517 ± 151.6	133 ± 40.41	419 ± 86.85	277 ± 56.98	139 ± 56.84	131 ± 18.19
Thomson’s Gazelle	2	613 ± 137.6	132 ± 35.43	614 ± 78.30	323 ± 51.58	289 ± 49.44	133 ± 16.78
White-tailed deer	7	296 ± 184.4	203 ± 43.53	431 ± 104.12	320 ± 68.95	104 ± 58.35	84 ± 22.52
Significance		*	***	***	***	***	***

ADF, acid detergent fibre; DM, dry matter; CP, crude protein; HEM, hemicellulose; NDF, neutral detergent fibre
* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS, not significant ($p>0.05$)

Table 7. 9 Chemical composition of feeds and diets fed to or eaten by ruminants based on climatic region

Effect of climatic region		Proximate chemical composition (g/kg DM)					
Tropical climates	N	DM	CP	NDF	ADF	HEM	Ash
Am	5	192 ± 266.39	148 ± 50.992	263 ± 138.46	205 ± 85.45	56 ± 78.75	119 ± 33.15
Aw	8	112 ± 265.38	217 ± 50.608	401 ± 137.92	232 ± 85.89	167 ± 78.19	137 ± 33.07
Arid climates							
BSh	20	628 ± 135.63	122 ± 26.366	388 ± 70.541	249 ± 43.58	134 ± 40.65	74 ± 16.79
BSk	4	278 ± 265.38	252 ± 50.608	258 ± 137.92	165 ± 85.09	90 ± 78.19	109 ± 33.07
BWh	2	787 ± 271.32	153 ± 52.853	498 ± 141.12	249 ± 87.20	247 ± 81.45	99 ± 33.57
Temperate climates							
Cfa	55	632 ± 77.942	143 ± 15.080	519 ± 40.531	351 ± 25.03	168 ± 23.26	87 ± 9.66
Cfb	359	526 ± 45.339	165 ± 9.205	488 ± 23.637	315 ± 14.66	169 ± 14.13	100 ± 5.49
Csa	23	683 ± 155.15	167 ± 29.920	483 ± 80.666	310 ± 49.81	166 ± 46.17	89 ± 19.26
Cwa	12	799 ± 262.93	81 ± 49.688	748 ± 136.59	497 ± 84.21	243 ± 76.86	74 ± 32.86
Cold climates							
Dfa	32	623 ± 133.94	115 ± 25.745	564 ± 69.633	391 ± 42.99	171 ± 39.74	84 ± 16.64
Dfb	53	512 ± 62.218	120 ± 13.490	451 ± 32.583	300 ± 20.36	140 ± 20.61	80 ± 7.19
Dsb	10	853 ± 264.08	248 ± 50.110	498 ± 137.21	352 ± 84.62	144 ± 77.47	69 ± 32.96
Significance		NS	**	NS	*	NS	NS
Tropical climates	13	239 ± 41.416	165 ± 37.67	388 ± 93.89	225 ± 60.03	163 ± 53.33	119 ± 22.15
Arid climates	26	645 ± 23.911	140 ± 22.48	416 ± 55.35	238 ± 35.34	176 ± 31.36	79 ± 12.97
Temperate climates	440	643 ± 73.21	145 ± 7.50	543 ± 18.30	335 ± 11.67	208 ± 10.47	89 ± 4.24
Cold climates	104	646 ± 73.21	109 ± 11.28	534 ± 26.38	333 ± 16.70	196 ± 15.92	72 ± 5.82
Significance		***	*	NS	*	NS	*

ADF, acid detergent fibre; DM, dry matter; CP, crude protein; HEM, hemicellulose; NDF, neutral detergent fibre Af, tropical rain forest; Aw, tropical savannah climate; BWh, hot arid desert climate; BSh, hot arid steppe climate; BSk, cold arid steppe climate; Csa, dry temperate climate with hot summers; Csb, dry temperate climate with warm summers; Cwa, dry winter temperate climate with hot summer; Cwb, dry winter temperate climate with warm summers; Cfa, hot summer temperate climate without dry season; Cfb, warm summer temperate climate without dry season; Dsb, cold dry climate with warm summers; Dfa, cold climate with hot summers and no dry season; Dfb, cold climate with warm summers and no dry season; Dfc, cold climate with warm summers and no dry season;

* p<0.05; ** p<0.01; *** p<0.001; NS, not significant (p>0.05)

Average mature body weight of ruminants in this data set varied based on climatic region (p < 0.05) and ruminant feeding type (p<0.0001; RMSE = 237.02 kg). Ruminants inhabiting tropical (632.88 kg) and cold climates (592.00 kg) had high mature body weights compared to ruminants in temperate (425.60 kg) and arid climates (313.54 kg). Average mature body weight of grazers (526.93 kg) was higher (p<0.05) than for browsers (197.70 kg) and intermediate feeders (117.28 kg).

There were extreme observations recorded for dry and liquid digesta load (Fig. 7.2 and 7.3). Extreme observations were seen on plots of wet rumen digesta load against body weight for steenbok, roe deer, gerenuk, suni, blue wildebeest, Kirk’s dik-dik, white-tailed deer and a couple of sheep (Fig. 7.4). Extreme observations were mainly for ruminants with very low-mature weight, mainly browsers.

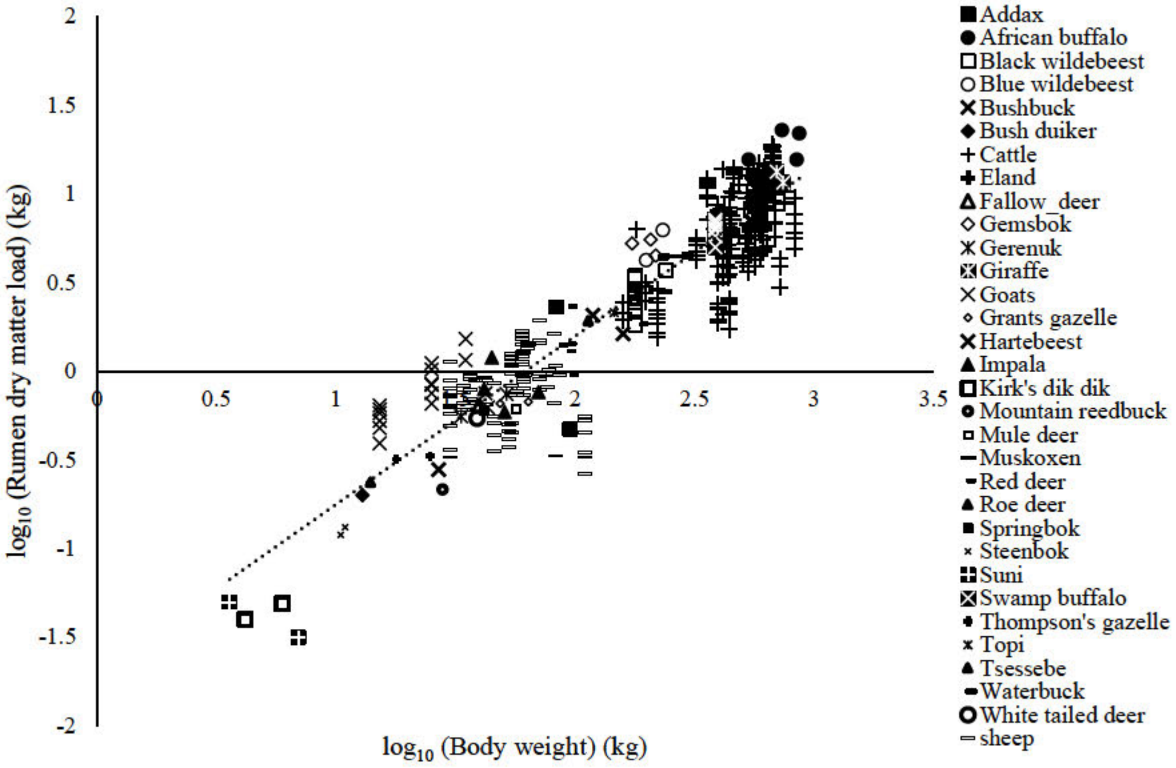


Fig. 7. 2 Log$_{10}$ transformed dry rumen digesta load against log$_{10}$ transformed body weight

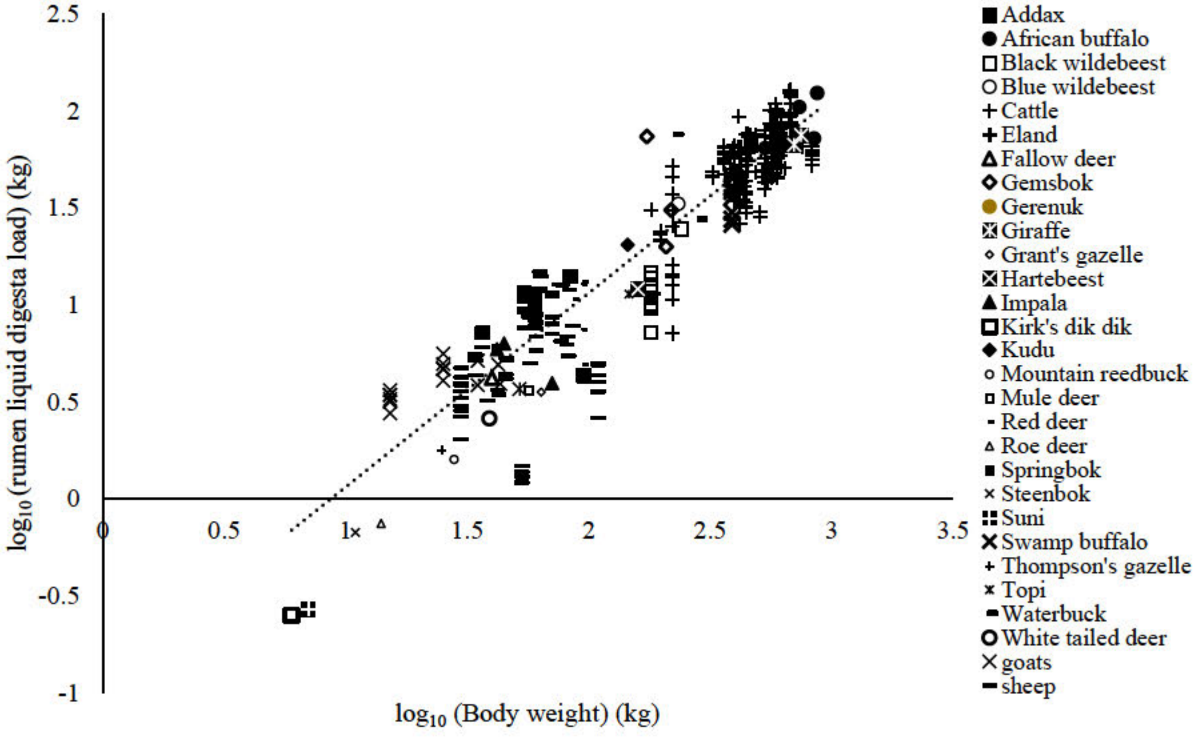


Fig. 7. 3 Log$_{10}$ transformed liquid rumen digesta load against log$_{10}$ transformed body weight

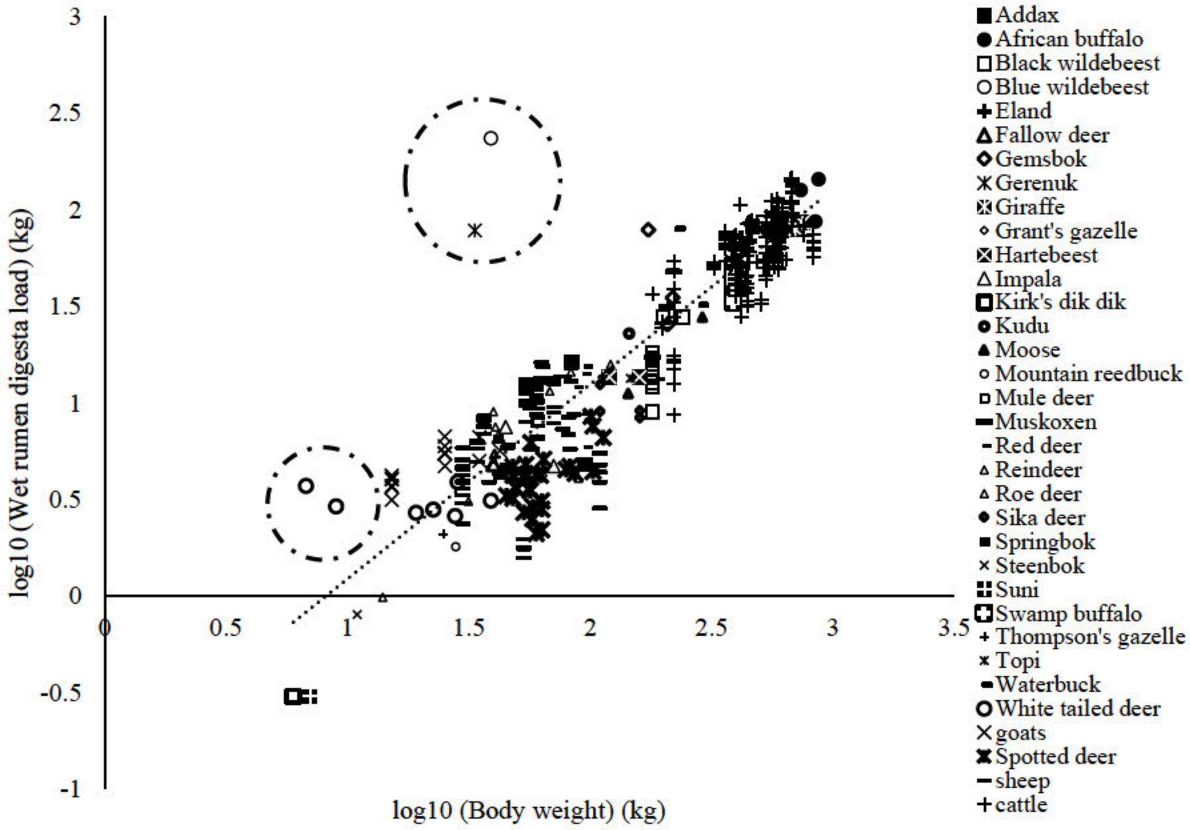


Fig. 7. 4 Log_{10} transformed wet rumen digesta load against $\log_{10}$ transformed body weight

7.3.2 Modelling of rumen digesta load

The summary statistics for the entire datasets used in Table 7.1. The training dataset for scaled RDML comprised 368 observations from 29 species of ruminants of variable physiological attributes (scaled RDML: 0.065 ± 0.0305 kg/kg BW; BW: 380.7 ± 239.80 kg; DOM: 0.79 ± 0.246), consuming diets of a wide range of qualities (DM: 587.9 ± 317.17 g/kg; NDF: 514.0 ± 154.29 g/kg; CP: 148.3 ± 64.08 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 13.4 ± 6.90°C). The testing dataset comprised 159 observations on ruminants of variable physiological attributes (scaled RDML: 0.07 ± 0.030 kg/kg BW; BW: 381.1 ± 245.96 kg; DOM: 0.77 ± 0.257), consuming diets of a wide range of qualities (DM: 584.0 ± 307.33 g/kg; NDF: 519.6 ± 142.34 g/kg; CP: 154.5 ± 62.01 g/kg), from regions of variable ambient temperatures (AT: 14.2 ± 6.84°C).

The training dataset for unscaled RDML (Table 7.10) was comprised of 368 observations from 29 species of ruminants of variable physiological attributes (unscaled RDML: 6.02 ± 4.64 kg; BW: 381.6 ± 242.62 kg; DOM: 0.77 ± 0.254), consuming diets of a wide range of qualities

(DM: 583.9 ± 313.75 g/kg; NDF: 510.6 ± 152.0 g/kg; CP: 150.2 ± 61.94 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 13.7 ± 6.91°C). The testing dataset comprised 159 observations of ruminants of variable physiological attributes (unscaled RDML: 6.1 ± 4.74 kg; BW: 378.9 ± 239.45 kg; DOM: 0.80 ± 0.236), consuming diets of a wide range of qualities (DM: 593.2 ± 315.3 g/kg; NDF: 527.7 ± 147.41 g/kg; CP: 150.0 ± 67.06 g/kg), from regions of variable ambient temperatures (AT: 13.5 ± 6.83°C).

The training dataset for RWML (Table 7.11) was comprised of 338 observations from 29 species of ruminants of variable physiological attributes (RWML: 45.4 ± 37.34 kg; BW: 331.2 ± 242.45 kg; DOM: 0.76 ± 0.251), consuming diets of a wide range of qualities (DM: 618.6 ± 310.74 g/kg; NDF: 523.4 ± 149.7 g/kg; CP: 156.6 ± 66.64 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 12.7 ± 7.42°C). The testing dataset comprised observations 146 observations of ruminants of variable physiological attributes (RWML: 41.8 ± 36.24 kg; BW: 308.2 ± 240.71 kg; DOM: 0.75 ± 0.255), consuming diets of a wide range of qualities (DM: 540.3 ± 316.25 g/kg; NDF: 533.2 ± 14670 g/kg; CP: 152.1 ± 64.19 g/kg), from regions of variable ambient temperatures (AT: 12.5 ± 7.28°C).

The training dataset for RLML (Table 7.12) comprised of 299 observations from 20 species of ruminants of variable physiological attributes (RWML: 44.1 ± 32.52 kg; BW: 360.6 ± 236.55 kg; DOM: 0.77 ± 0.252), consuming diets of a wide range of qualities (DM: 637.4 ± 313.52 g/kg; NDF: 529.5 ± 155.87 g/kg; CP: 152.2 ± 68.95 g/kg), inhabiting 4 climate types of variable ambient temperatures (AT: 13.4 ± 6.77°C). The testing dataset comprised 129 observations of ruminants of variable physiological attributes (RLML: 40.9 ± 32.85 kg; BW: 342.2 ± 247.06 kg; DOM: 0.75 ± 0.255), consuming diets of a wide range of qualities (DM: 602.5 ± 313.51 g/kg; NDF: 517.8 ± 157.95 g/kg; CP: 151.2 ± 62.27 g/kg) from regions of variable ambient temperatures (AT: 14.3 ± 6.74°C).

The models developed in this work accounted for 81% (scaled RDML) and 90% (unscaled RDML) of the variation in predicting rumen dry matter load (Table 7.13). On testing the model with an independent dataset, these models attained 59% (scaled RDML) and 84% (unscaled RDML) precision in predicting rumen dry matter load. Models attained high precision in prediction of RWML ($R^2 = 0.94$) and RLML ($R^2 = 0.85$) during training and good precision during testing of RWML ($R^2 = 0.94$) and RLML ($R^2 = 0.88$) using independent datasets. A few over- and under-predictions of the rumen dry matter load scaled to body weight were observed during model testing for cattle, eland, goats and sheep (Fig. 7.5). The unscaled RDML for the African buffalo and cattle (Fig. 7.8), and RWML of gemsbok (Fig. 7.9) were under-predicted 2-fold. The RWML for spotted deer, white-tailed deer, sheep and gerenuk were over-predicted

(Fig. 7.9).

A plot of residuals against the predicted scaled RDML gave the equation: Y = -0.01 (± 0.02) + 0.07 (± 0.028) X (R^2 = 0.02; RSE = 0.013). The plot of residuals against the predicted RWML gave the equation: Y = -1.7 (± 0.81) + 0.04 (± 0.014) X (R^2 = 0.02; RSE = 9.10). The intercepts and slopes of the residual plots for scaled RDML and RWML were different (P <0.05) from zero, showing that the models had a mean and linear bias. The plot of residuals against the unscaled RDML gave the equation: Y = -0.2 (± 0.13) + 0.03 (± 0.018) X (R^2 = 0.01; RSE = 1.45). A plot of residuals against the predicted RLML gave the equation: Y = -1.1 (± 0.77) + 0.02 (± 0.014) X (R^2 = 0.01; RSE = 7.66). The intercepts and slopes of the residual plots for unscaled RDML and RLML were not different (P >0.05) from zero, showing that the models had no mean and linear bias.

Table 7. 10 Descriptive statistics of animal and feed attributes of animals used in training of Random Forest model to predict rumen dry matter digesta load

		Feed factors			Animal factors		Environmental factor	Actual RDML (kg)
Ruminant type	N	DM (g/kg)	NDF (g/kg)	CP (g/kg)	APL	BW (kg)	AT (°C)	
Addax antelope	2	874 ± 14.7	554 ± 220.6	136 ± 8.5	1	90 ± 8.4	27.8	1.4 ± 1.30
African buffalo	3	650 ± 43.3	490 ± 21.6	158 ± 44.4	1	754 ± 188.7	22 ± 4.1	17.8 ± 3.66
Black wildebeest	8	840 ± 218.2	820 ± 107.5	74 ± 16.7	1	188 ± 21.9	17 ± 3.5	2.8 ± 0.51
Blue wildebeest	1	307	640	75	1	235	17.7	6.3
Bushbuck	1	386	444	91	1	27	25.0	0.28
Bush duiker	1	452	533	138	1	13	25.0	0.2
Cattle	241	499 ± 313.8	483 ± 144.3	158 ± 64.2	1.7 ± 0.82	524 ± 134.5	12 ± 6.4	8.1 ± 3.78
Eland	1	600	515	209	1	459	24.7	10.2
Fallow deer	1	352	590	98	1	40	9.2	0.64
Gemsbok	2	911	638	115	1	214	21 ± 5.0	5.0 ± 0.73
Gerenuk	1	600	595	153	1	52	24.7	0.7
Giraffe	2	600	490 ± 35.9	172 ± 53.0	1	726 ± 33.6	24.7	12.5 ± 1.23
Goats	13	887 ± 33.1	534 ± 191.2	134 ± 78.5	1	22 ± 7.9	22 ± 6.7	0.7 ± 0.21
Grant’s gazelle	1	428	370	143	1	64	24.7	0.7
Hartebeest	2	301 ± 72.1	636 ± 64.3	90 ± 11.8	1	140 ± 28.3	25 ± 0.2	1.9 ± 0.32
Impala	2	310	607	94	1	44 ± 2.1	17.7	1.0
Kirk’s dik-dik	2	495	447 ± 28.3	145 ± 11.0	1	5 ± 1.3	25 ± 0.2	0.04 ± 0.01
Kudu	1	431	463	150	1	145	17.7	2.7
Muskoxen	1	876	527	116	1	260	6.5	4.4
Red deer	5	845 ± 39.2	593 ± 87.8	105 ± 51.4	1	113 ± 43.2	8 ± 3.2	1.6 ± 0.52
Roe deer	1	825	743	110	1	14	9.2	0.2
Sheep	65	795 ± 236.8	548 ± 150.7	142 ± 54.7	1.1 ± 0.22	56 ± 19.6	15 ± 5.6	0.9 ± 0.37
Springbok	1	319	381	131	1	42	17.7	0.6
Steenbok	1	361	424	119	1	10.5	25.0	0.12
Suni	1	409	379	178	1	3.6	250.	0.05
Swamp buffalo	4	900	592	181	1	390	17.7	6.2 ± 0.84
Thompson’s gazelle	1	457	678	75	1	18	25.0	0.32
Waterbuck	2	457 ± 202.9	589 ± 104.5	156 ± 75.9	1	230 ± 79.0	24.7	4.9 ± 0.56
White tailed deer	1	304	442	162	1	39	9.2	0.55

DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; APL, animal production level; BW, body weight; AT, ambient temperature; RDML, rumen dry matter load

Table 7. 11 Descriptive statistics of animal and feed attributes of animals used in training of Random Forest model to predict rumen wet matter load

		Feed factors			Animal factors		Environmental factor	Actual RDML (kg)
Ruminant type	N	DM (g/kg)	NDF (g/kg)	CP (g/kg)	APL	BW (kg)	AT (°C)	
Addax antelope	2	874 ± 14.7	554 ± 220.6	136 ± 8.5	1	90 ± 8.4	27.8	11 ± 8.1
African buffalo	3	675	478	132.4	1	822 ± 71.8	20 ±4.1	119 ± 29.3
Black wildebeest	11	910 ± 23.9	835 ± 75.7	67 ± 1.4	1	182 ± 6.0	17 ± 2.9	15 ± 5.0
Blue wildebeest	1	307	640	75	1	235	17.7	39.2
Cattle	182	561 ± 328.2	490 ± 145.3	165 ± 7.0	1.6 ± 0.76	513 ± 132.5	11 ± 6.8	71 ± 26.7
Eland	2	411 ± 267.1	460 ± 78.6	174 ± 49.4	1	554 ± 135.2	24.7	81 ± 3.7
Gemsbok	1	911	638	115	1	219	17.7	35.2
Gerenuk	1	600	515.2	209.375	1	33.6	24.7	78.1
Giraffe	1	600	515.2	209.375	1	702.5	24.7	79.5
Goats	24	856 ± 100.8	572 ± 145.3	119 ± 62.3	1.0 ± 0.02	44 ± 25.8	17 ± 7.2	6 ± 2.2
Grant’s gazelle	1	428	370	142.6	1	64	24.7	4.2
Hartebeest	2	619 ± 376.9	642 ± 73.5	89 ± 13.0	1	140 ± 28.3	25 ± 0.1	14 ± 0.03
Impala	2	292 ± 24.7	619 ± 16.1	120.125	1	58 ± 18.4	21 ± 5.0	6.1 ± 2.0
Kirk’s dik-dik	1	495	467	137.5	1	6	24.7	0.3
Kudu	1	431	463	150	1	145	17.67	23
Moose	2	304	442	162	1	281 ± 193.7	2.4	25 ± 19.0
Muskoxen	3	879	596	50	1	203 ± 20.8	2.4	32 ± 15.1
Red deer	5	855 ± 46.6	549 ± 107.7	129 ± 61.5	1	113 ± 43.3	8 ± 3.3	11 ± 3.4
Reindeer	6	304	442	162	1	69 ± 34.3	0.4	9 ± 5.1
Sheep	49	827 ± 196.9	542 ± 169.1	152 ± 62.7	1.1 ± 0.25	54 ± 21.3	15 ± 5.3	10 ± 13.7
Sika deer	3	282	577 ± 49.3	160 ± 10	1	143 ± 28.9	0	9 ± 0.4
Spotted deer	17	280	547 ± 31.0	216 ± 25.3	1	66 ± 18.0	8 ± 4.3	4 ± 1.2
Steenbok	1	361	353.3	134.8	1	11	24.7	0.8
Suni	1	409	406.5	140.6	1	7	24.7	0.3
Swamp buffalo	7	900	592	181.1	1	389.6	17.7	42 ± 7.4
Thompson’s gazelle	1	457	528	155.9	1	25	24.7	2.1
Topi	1	943	662	74.3	1	114	25.98	13.3
Waterbuck	2	457 ± 202.9	589 ± 104.5	156 ± 75.9	1	258 ± 40.1	24.7	56 ± 33.6
White tailed deer	5	294 ± 5.4	460 ± 10.1	202 ± 22.5	1	23 ± 11.9	2 ± 4.2	3 ± 0.5

DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; APL, animal production level; BW, body weight; AT, ambient temperature; RDML, rumen dry matter load

Table 7. 12 Descriptive statistics of animal and feed attributes of animals used in training of Random Forest model to predict rumen liquid matter load

		Feed factors			Animal factors		Environmental factor	Actual RLML (kg)
Ruminant type	N	DM (g/kg)	NDF (g/kg)	CP (g/kg)	APL	BW (kg)	AT (°C)	
Addax antelope	1	864	710	130	1	83.8	27.8	14.0
African buffalo	2	638 ± 53.0	496 ± 26.5	171 ± 54.4	1	706 ± 239.5	21 ± 5.0	93 ± 41.4
Black wildebeest	8	840 ± 218.2	820 ± 107.5	74 ± 16.7	1	188 ± 21.9	17.7	12 ± 5.2
Blue wildebeest	1	307	640	75	1	235	17.67	33
Cattle	185	547 ± 331.3	497 ± 148.4	162 ± 72.1	1.6 ± 0.76	513 ± 129.0	11 ± 6.4	63 ± 23.6
Eland	2	411 ± 267.1	460 ± 78.6	174 ± 49.4	1	554 ± 135.2	24.7	70 ± 4.5
Gemsbok	2	756 ± 219.9	577 ± 86.8	162 ± 66.7	1	197 ± 31.6	21 ± 5.0	52 ± 30.3
Gerenuk	2	600	555 ± 56.4	181 ± 39.8	1	43 ± 13.0	24.7	41 ± 52.2
Giraffe	1	600	515.2	209 .4	1	702.5	24.7	66.2
Goats	11	823 ± 142.6	513 ± 162.8	139 ± 73.5	1.0 ± 0.03	27 ± 10.9	21 ± 7.0	4 ± 0.7
Hartebeest	1	352	590	98	1	160	24.7	12.0
Impala	3	298 ± 20.2	615 ± 13.1	111 ± 30.5	1	53 ± 15.9	20 ± 4.1	5 ± 1.3
Kirk’s dik-dik	1	495	467	137.5	1	6	24.7	0.3
Red deer	5	845 ± 39.2	589 ± 96.3	106 ± 52.8	1	113 ± 43.4	7 ± 2.2	11 ± 2.2
Sheep	64	841 ± 173.8	572 ± 159.0	138 ± 64.1	1.1 ± 0.24	58 ± 21.2	14 ± 5.3	7 ± 3.4
Springbok	1	318.7	381	131.3	1	42	17.7	6.0
Swamp buffalo	6	900	592	181.3	1	389.6	17.7	37 ± 6.6
Thompson’s gazelle	1	456.5	528	155.9	1	25	24.7	1.8
Topi	1	825	743	110	1	147	24.7	11.3
White tailed deer	1	304	442	162	1	39	9.2	2.6

DM, dry matter; NDF, neutral detergent fibre; CP, crude protein; APL, animal production level; BW, body weight; AT, ambient temperature; RLML, rumen liquid matter load

Table 7. 13 Comparison of the equations for linear regression between observed (Y) and predicted (X) rumen digesta load during training and testing of the Random Forest model

Model type	N	Regression parameters					
		Intercept	$P_{\text{intercept}}$	Slope	P_{slope}	RSE	R^2 value
		Dry rumen digesta load (kg/kg BW)					
Training	368	-0.005 ± 0.002	$P<0.01$	1.07 ± 0.028	$P<0.001$	0.013	0.8067
Testing	159	0.005 ± 0.0045	*NS*	0.95 ± 0.063	P<0.001	0.018	0.5924
		Dry rumen digesta load (kg)					
Training	368	-0.18 ± 0.130	*NS*	1.03 ± 0.018	P<0.001	1.447	0.9026
Testing	159	-0.13 ± 0.257	*NS*	1.02 ± 0.035	P<0.001	1.854	0.8470
		Wet rumen digesta load (kg)					
Training	338	-1.70 ± 0.813	$P<0.05$	1.04 ± 0.014	P<0.001	9.097	0.9407
Testing	146	-2.90 ± 1.933	*NS*	1.02 ± 0.036	P<0.001	13.97	0.8515
		Liquid rumen digesta load (kg)					
Training	299	-1.11 ± 0.775	*NS*	1.02 ± 0.014	$P<0.001$	7.664	0.9445
Testing	129	-1.25 ± 1.696	*NS*	1.04 ± 0.034	$P<0.001$	11.11	0.8784

NS: not significant; RMSE: root mean square error

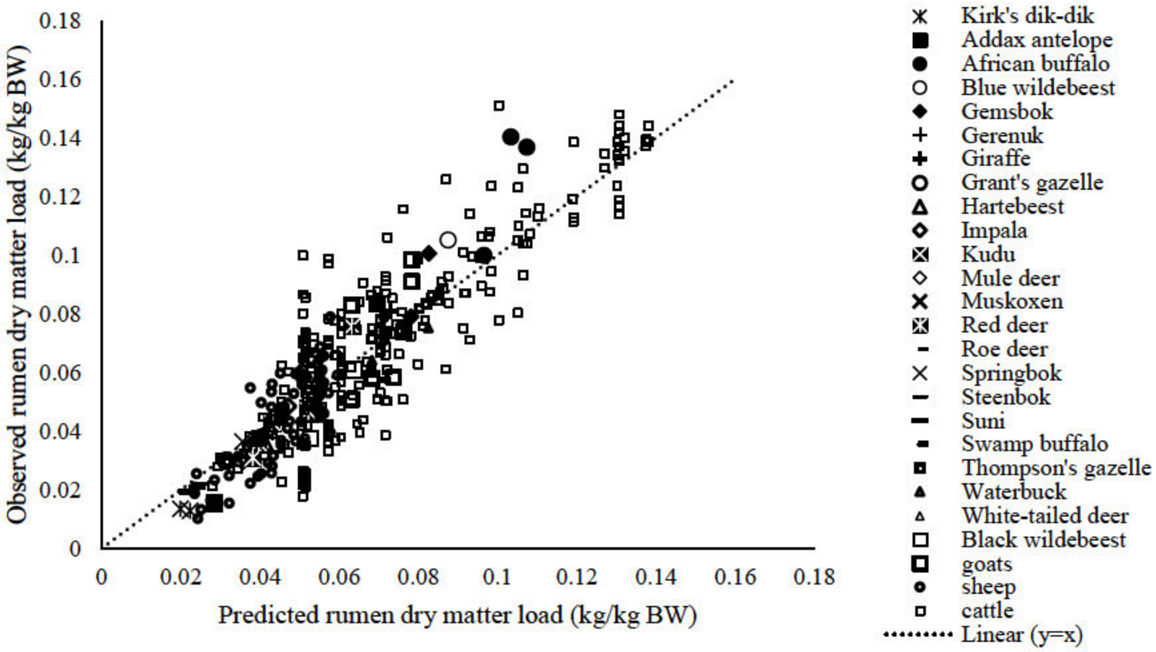


Fig. 7. 5 Relationship between the observed and predicted rumen dry matter load scaled to body weight during training of Random Forest model.

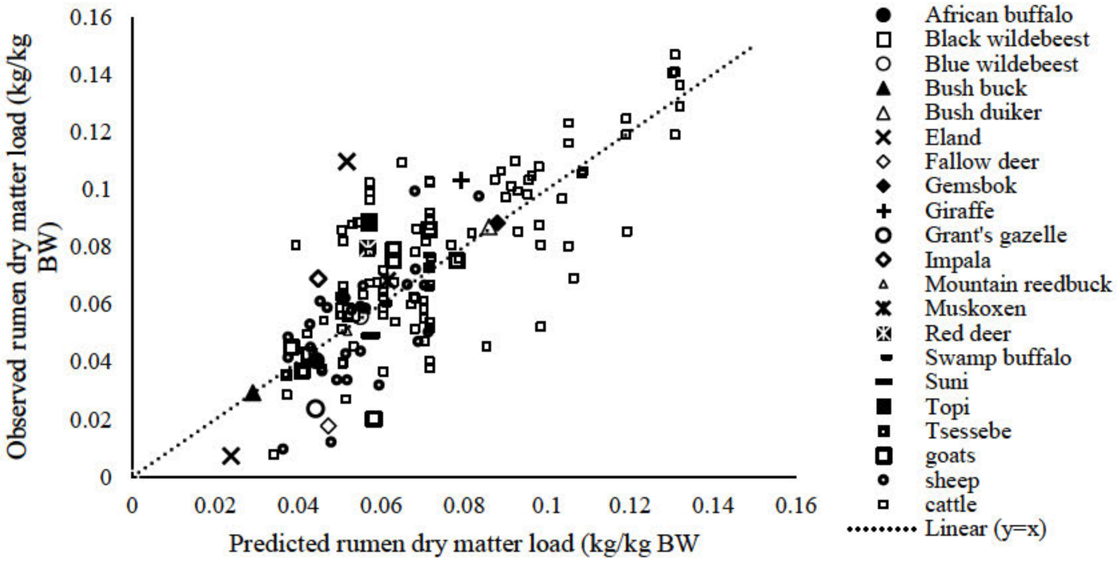


Fig. 7. 6 Relationship between the observed and predicted rumen dry matter load scaled to body weight during testing of Random Forest model.

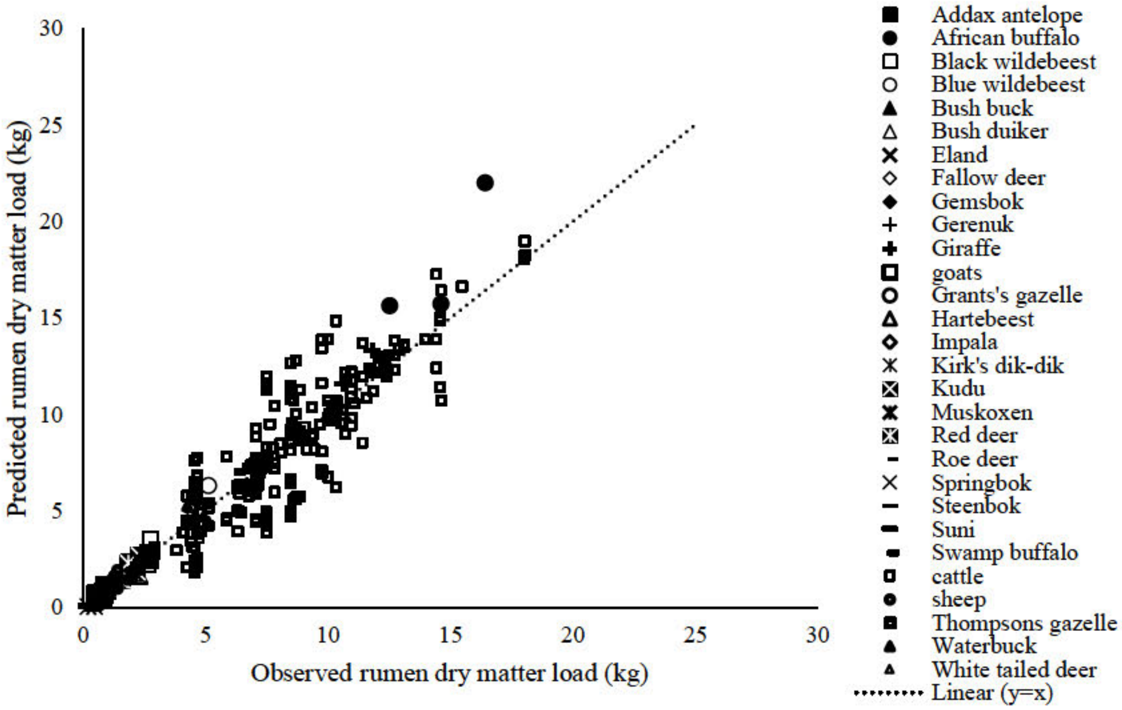


Fig. 7. 7 Relationship between the observed and predicted rumen dry matter load during training of Random Forest model.

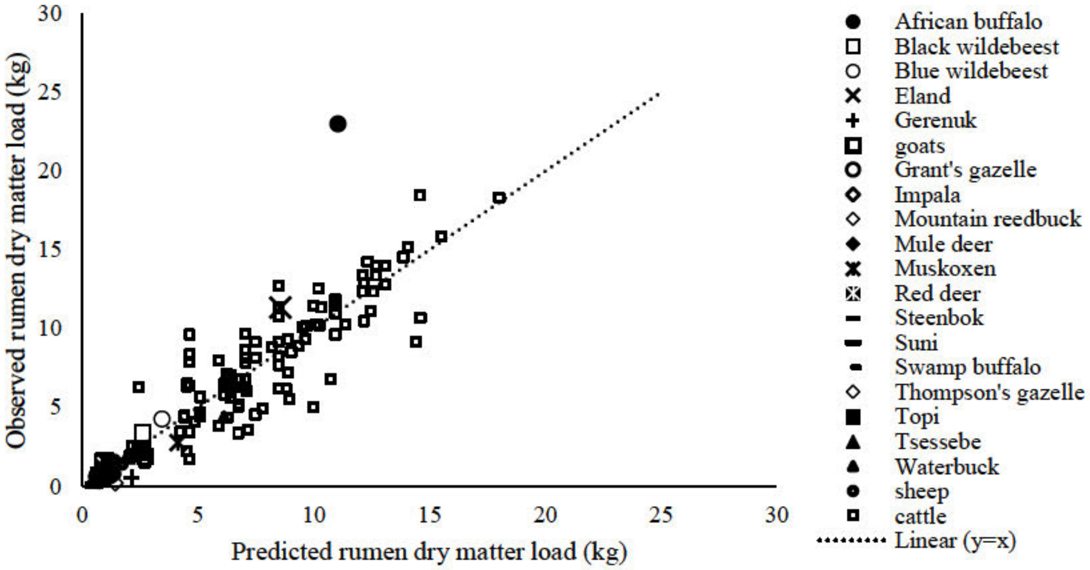


Fig. 7. 8 Relationship between the observed and predicted rumen dry matter load during testing of Random Forest model.

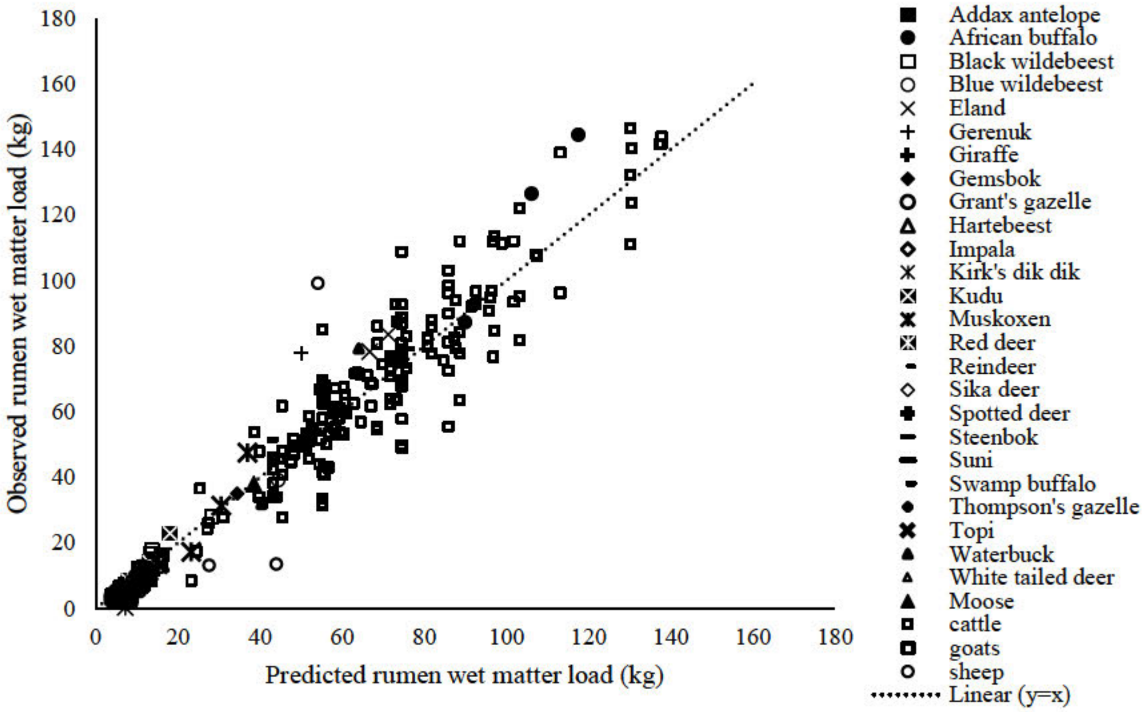


Fig. 7. 9 Relationship between the observed and predicted rumen wet matter load during training of Random Forest model.

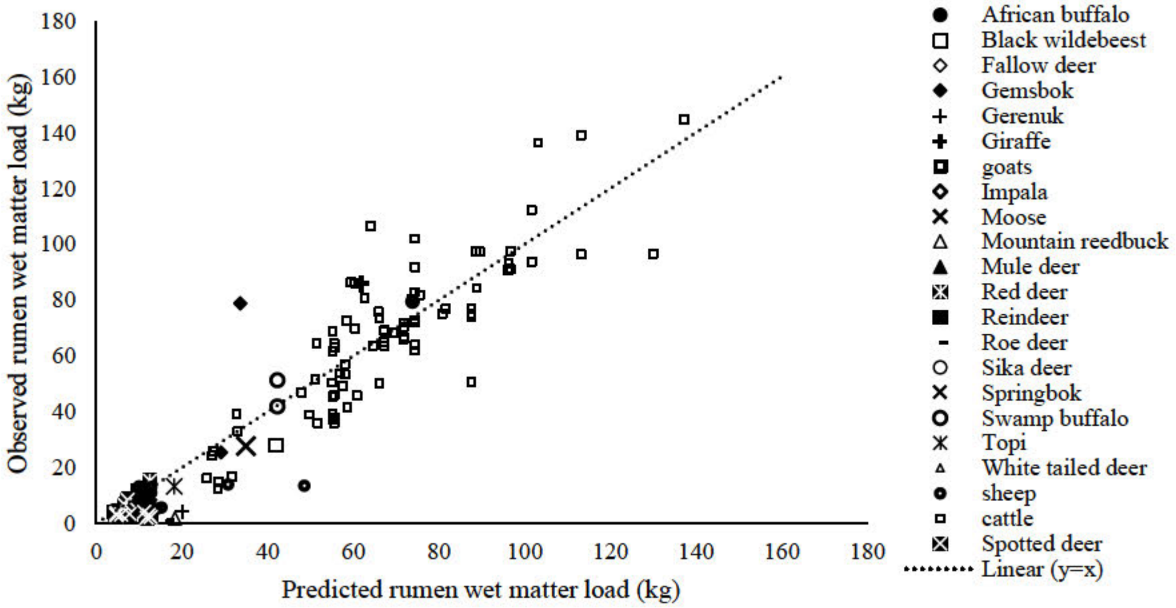


Fig. 7. 10 Relationship between the observed and predicted rumen wet matter load during testing of Random Forest model.

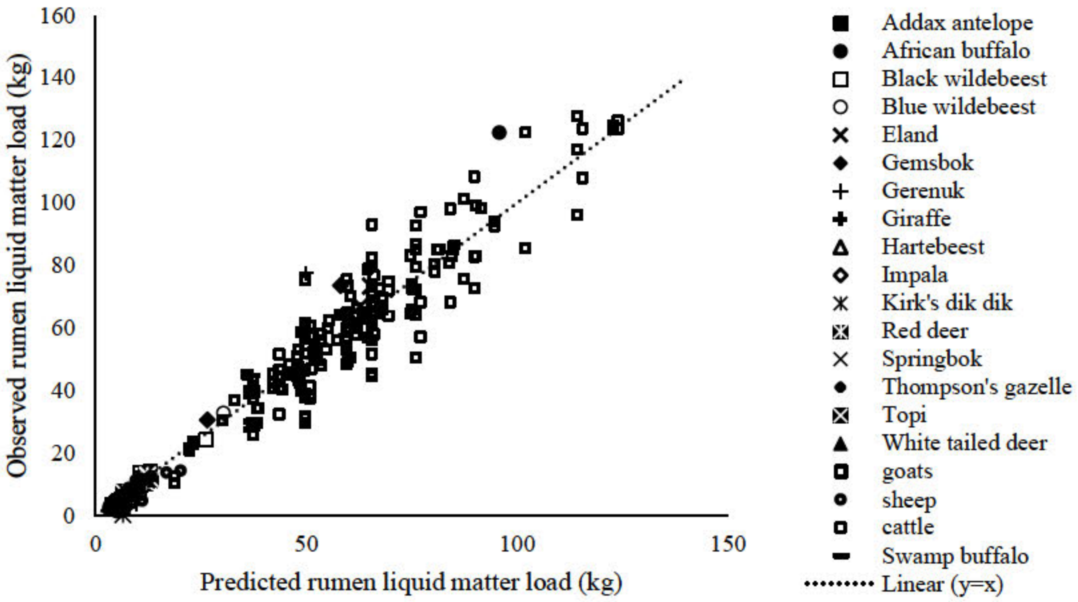


Fig. 7. 11 Relationship between the observed and predicted rumen liquid matter load during training of Random Forest model.

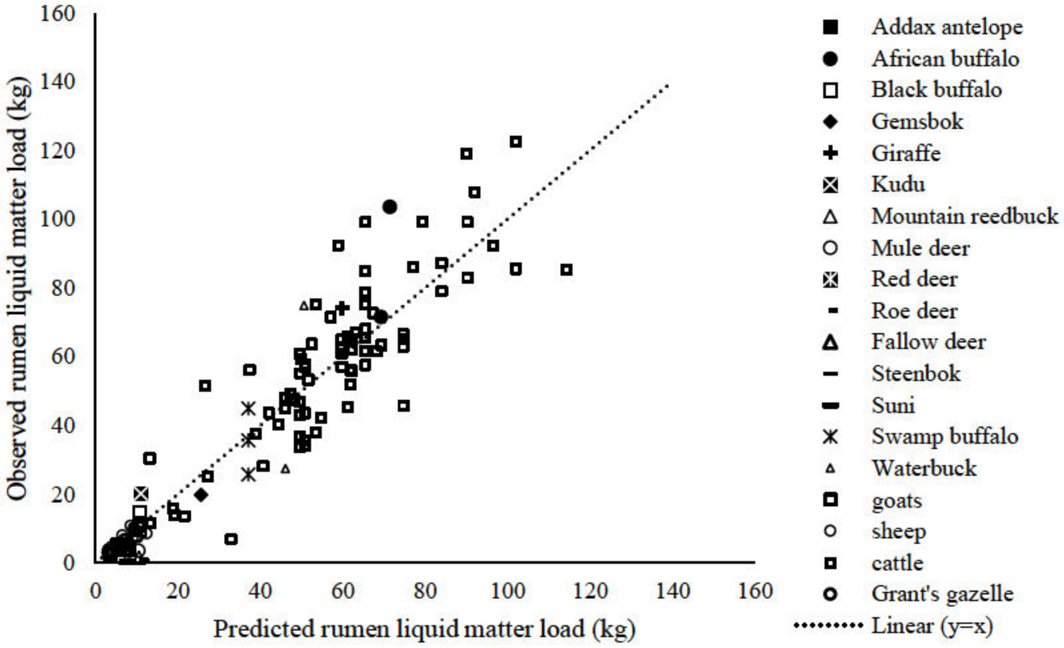


Fig. 7. 12 Relationship between the observed and predicted rumen liquid matter load during testing of Random Forest model.

7.4 Discussion

7.4.1 Meta-analysis of rumen digesta load

Measures of digestive physiology are normally scaled to metabolic body weight or body weight, although the influence of animal physiological factors such as animal production level and degree of maturity are important. Differences in allometric scaling of digestive physiological characters have the potential to explain the underlying mechanisms of ruminant diversification along a body weight gradient unravelling adaptive strategies adopted by different ruminants (Muller et al. 2013). Allometric scales of rumen digesta load and degree of maturity were obtained in this study, incomparable to the hyperallometric maturity coefficient of 2.14 (Butterfield 1988).

Differences in rumen digesta load between pregnant and non-pregnant, and between lactating and non-lactating sheep (Gunter et al. 1990; Kaske and Groth 1997; Forbes 1970) is consistent with the effects of degree of maturity and animal production level on rumen digesta load in this study. Some of these variables used in the calculation of APL i.e., days in lactation and pregnancy were positively related to rumen digesta load. In response to increases in demand for nutrients during the progression of lactation and pregnancy, ruminants would be expected to eat more, increasing rumen digesta load. The ambiguity of this trend with respect to the effect of days in pregnancy is evident. It is expected that as the foetus grows the volume of space occupied by the rumen in the abdomen decreases, decreasing rumen digesta load. While Forbes (1970) reported decreases in the volume of rumen digesta load with the progression of pregnancy in sheep, Kaske and Groth (1997) observed increased rumen digesta load from mid pregnancy to lactation. This observed trend may suggest that even though volume occupied by the rumen decreases, an increase in the elasticity of rumen wall, a reduction in sensitivity of mechanoreceptors on the rumen wall (Baile et al. 1974) and slow rates of passage of digesta (Kaske and Groth 1997) during pregnancy contribute to increased rumen digesta load. Based on the test for scaling factors namely body weight, degree of maturity and animal production level; body weight proved to be the best scaling factor accounting for a high proportion of the variation in rumen digesta load.

It has been reported that browsing ruminants tend to have lower rumen digesta load compared to grazing counterparts of similar size, and vice-versa. This concurs with differences in the rate of passage and quality of diets selected (Rutagwenda et al. 1990) exhibited by these ruminant feeding types. Differences in feeding habits of grazing and browsing ruminants were anticipated to reveal clear distinctions in scaling factors of rumen digesta load with body weight. When testing for the scaling curvature in the dataset on wet, dry and liquid rumen digesta load, the quadratic term was not significant. In wet gut digesta load of mammalian herbivores including ruminants, Muller et al. (2013) also found that the quadratic term was not significant. The linear nature of the relationship between rumen digesta load and bodyweight makes the prediction of the maximal attainable rumen digesta load as limited by body weight of ruminants difficult to estimate using regression equations. Intercepts of scaling relationships showed that browsers have proportionally lower rumen load of dry matter across all body weights compared to grazers, although there was no distinction between the 2 feeding types in either the wet or liquid rumen digesta loads. Inferences based on these findings suggest the maximal attainable body weight relative to rumen digesta load is quickly attainable by grazers than browsers (Clauss et al. 2013). These findings justify the existence of the largest extant ruminant being a browser.

Although repeatedly refuted by Weckerly (2003; 2010), wet and liquid rumen digesta load of grazers and browsers scaled isometrically with body weight (Luna et al. 2012). The net weight of the fermentation site digesta content scaled to $BW^{1.096}$ (Parra 1978) and $BW^{0.718}$ (Ramzinski and Weckerly 2007), both scalars did not differ from 1. Wet rumen digesta load scaled allometrically to $BW^{0.56}$ in moose and $BW^{0.73}$ in mule deer (Weckerly et al. 2003). Rumen digesta load in this study and others (Parra 1978, Illius and Gordon 1992, Nsahlai and Apaloo 2008, Clauss et al. 2003, 2007) increased and scaled linearly with body weight implying high rumen digesta loads for large-size ruminants. Scaling relationships obtained by Gordon and Illius (1994) were allometric and independent of ruminant feeding type. Findings of Illius and Gordon (1994) suggest that grazing and browsing ruminants adapt their digestive capacity in a similar way despite differences in feed quality consumed contrary to predictions from this study. Weight of dry rumen load scaled to $BW^{1.16}$ while wet rumen load scaled to $BW^{1.13}$ (Gordon & Illius 1994). Scaling relationships for muskoxen varied with season and sex (Forchhammer & Boomsma 1995). Rumen contents scaled to $BW^{1.63}$ in summer ($R^2 = 0.96$) and to $BW^{0.91}$ in winter ($R^2 = 0.94$; Forchhammer and Boomsma 1995).

The digestive physiology of large ruminants presents a unique problem of increased retention time for digesta in the rumen, which may limit feed intake (Clauss et al. 2013). With increasing body size and absolute energy requirements, the relative rumen digesta load would have to increase in order to compensate for the limitation in feed intake. Small-size ruminants possess low fermentation capacity compared to large ruminants and would have to develop adaptation strategies to increase digestive efficiency. Inferences based on allometry showed that the amount of dry rumen digesta load became proportionally lower in large grazers and intermediate feeders, while larger browsers have proportionally more rumen digesta load than their smaller counterparts. As an adaptive strategy, these findings suggest that small grazing ruminants have the flexibility to increase dry rumen digesta load compared to their larger counterparts, have proportionally slower digesta passage and fermentation rates to make up for their low fermentation capacity. Slow digesta passage rates would entail increased retention time for maximisation of fibre digestion. The advantage of increased retention time of digesta in the rumen is limited to a point where forages are almost completely digested, and retention beyond this point will not be beneficial.

The ability for small grazers to proportionately increase dry rumen digesta load did not hold true for small browsers. Large browsers had proportionally more rumen digesta load than small browsers. Browsers generally select or consume better quality feeds than grazers. Since browsers select high quality diets which are generally scarce in the natural environments (Van Soest 1996), it seems likely that large browsers have adapted a strategy of storing large quantities of feed in the rumen in anticipation of periods of feed shortages. Small-size browsers are not too concerned about the scarcity of high-quality feeds because their absolute feed requirements are lower than that of large browsers. Unlike small-sized grazers, small browsers did not show the adaptive capacity to increase rumen load plausibly due to the browsers ability to select and consume better quality, not needing to increase digesta load to improve digestive efficiency. The pH of rumen digesta in small browsers may become important given the quality of what they are consuming. With regards to small browsers, not increasing the rumen digesta load wouldn't pose much of a constraint to digestive efficiency unlike in much larger browsers. Low dry rumen loads for very large browsers would be a huge evolutionary disadvantage given that concentrate feeds in the wild are rare (Van Soest 1996) and that as the body size increases the total amount of energy required for maintenance and for activity increases (Demment and Van Soest 1985). Thus, large browsing ruminants need abundant storage of forage in the rumen to support these processes. Small rumen digesta loads would force large-sized browsers to expend a lot of energy with frequent meals which might prove an inefficient adaptive strategy.

The hyperallometric scalar observed for browsers partially justifies why the largest extant ruminant, a concentrate consuming giraffe (*Giraffa camelopardalis*) (Johnson and Prideaux 2004), had one of the highest dry rumen digesta loads per unit of body weight. Being large-sized browsers, giraffes had to compensate for the disadvantage linked to a decrease in gut surface to gut volume ratio that reduces digestive efficiency (Clauss and Hummel 2005). In this case, the giraffe may have developed digestive-physiological measures to adapt to reduced digestive efficiency. High levels of rumen digesta load and large capacity mean that large browsing ruminants can store a lot of feed to maximise nutrient extraction, countering the negative effects of reduced digestive efficiency; increasing liquid flow enhancing the efficiency of microbial protein synthesis. Giraffe may have developed similar adaptive strategies as the largest extant herbivore, elephants, of having unexpectedly shorter mean retention times of liquid digesta relative to their large body size.

The largest browsing ruminant had rumen digesta loads similar to large grazing ruminants (e.g. African buffalo) partially supported by the hyperallometric scaling of dry rumen load to body weight in browsers. Large-sized ruminants (African buffalo, giraffe, and eland) had the highest dry rumen digesta load. Luna et al. (2012) predicted isometric scalars for dry rumen digesta load and body weight against their expectations. Muller et al. (2013) tested the hypothesis that dry rumen digesta load scaled hypo-allometrically to body weight. Rumen dry matter load in ruminants scaled to $BW^{0.897}$ and $BW^{0.973}$ (Muller et al. 2013), which are lower than the scaling factor obtained for browsers in this study. Ruminant feeding type and diet qualities selected by ruminants seemed to have an influence on scaling factors of rumen digesta load and body weight based on differences in feeding habits. Findings of this study showed that browser diets were of a better nutritional quality compared to that of grazers and intermediate feeders. Browsers would be expected to have lower rumen digesta load because they select and consume better quality feeds (Rutagwenda et al 1990), eat frequently and retain digesta in the rumen for shorter periods compared to grazers. Low rumen digesta loads in browsers compared to grazers were not reflective of Clemens and Maloiy's (1983) findings of similar rumen digesta loads in grazers and browsers. Because grazing ruminants are less selective feeders and generally consume poor quality forages, grazers need more capacious rumens in order to maintain adequate intake and prolonged digesta retention in the rumen (Bunnell and Oillingham 1985; Van Soest 1994).

Rumen digesta load was greatly influenced by climatic region. A plausible reason for the low rumen digesta loads in ruminants inhabiting arid regions compared to those in tropical and cold climates was their low mature body weights that are accompanied by small rumen capacity. Small-sized ruminants of low mature body weights have low feed requirements which may be viewed as an evolutionary adaptation in arid regions where plant material is scant. The effect of climatic region on rumen digesta load pointed to the effects of climate as linked to ambient temperature. Inferences from this study showed an overall decrease in rumen digesta load with an increase in ambient temperature. This trend is directly linked to a decrease in feed intake and an increase in the rate of passage of digesta in the rumen with increases in ambient temperature. The lack of difference in the rate of decrease in dry rumen digesta load with increasing ambient temperature between grazers and browsers has significant implications to ruminant survival in the future. With the projected increase in ambient temperate as a result of global warming, small-sized grazers and large-sized browsers will become more important than their respective counterparts as they are able to maintain proportionally high rumen digesta load for survival. Small ruminants have low absolute nutrient requirements than large animals, meaning that small browsers would be as important under conditions of rising ambient temperature. This means that in the future, sheep and goats will be the most important ruminant livestock species (Dzama 2016) in regions were ambient temperature are expected to increase. From the modelling results observed, ambient temperature was one of the factors that had a huge influence on rumen digesta load, suggesting its inclusion in rumen digesta load prediction models would be vital.

For studies that seek to develop rumen digesta load prediction models, body weight may be used as a scaling factor. However, scaling factors used should be different for grazers and browsers. Factors that need to be included in the models for prediction of dry rumen fill are body weight, mature body weight, degree of maturity, neutral detergent fibre, crude protein and ash content of diets fed to animals, days in lactation, ambient temperature and animal production level. Most influential factors in the prediction of wet mass of digesta were body weight, mature body weight, degree of maturity, animal production level, crude protein content of diets fed to animals, days in pregnancy, ambient temperature and degree of maturity.

7.4.2 Modelling of rumen digesta load

Numerous studies have shown that feed properties including CP, ADF and NDF (Nsahlai and Apaloo 2007), animal factors such as metabolisable energy requirements (Gunter et al. 1990), lactation length (Alvarez-Rodriguez et al. 2010), stage of pregnancy and lactation (Hartnell and Satter 1979; Gunter et al. 1990; Jenks et al. 1994; Kaske and Groth 1997), body weight (Demment and Van Soest 1985; Illius and Gordon 1992), ruminant feeding type (Gordon and Illius 1996), ambient temperature, and season (Domingue et al. 1992; Sibbald and Milne 1993; Jenks et al. 1994; Barboza et al. 2006) affect rumen digesta load. Choice of the input factors to predict the weight of rumen digesta in this study were based on these literature findings. It is worth mentioning an odd observation on the behaviour of rumen digesta load measurements scaled to body weight. Predictions of Adebayo et al. [In-press] were on unscaled rumen digesta load, the authors suggested scaling of rumen contents to achieve better accuracy in predictions. The degree of maturity and animal production level only accounted between 8 – 25% of the variation in rumen digesta load. Nsahlai and Apaloo (2007) expressed rumen dry matter load scaled to DOM and obtained the relationship: scaled RDML = $e^{3.38} \times DOM^{-0.27} \times CP^{-0.17}$ that accounted for just 31% of the variation. The scaling of rumen contents to body weight accounted for > 85% of the variation (Illius and Gordon 1992; Forchhammer and Boomsma 1995). Body weight was used as a scaling factor for rumen dry matter load in this study. The model for predicting rumen dry matter load scaled to body weight accounted for 10% less variation in training and 25% less variation in testing compared to the model that predicted unscaled rumen dry matter load. The strong relationship between rumen digesta load and body weight, seems not to be evident in predicting rumen digesta load scaled to body weight.

Rumen dry matter load was under-predicted for large grazing ruminants, the African buffalo (Giesecke and Gylswyk 1975) and cattle (Elsden et al. 1946), while an over-prediction was on cattle (Carruthers et al. 1988). The model over-predicted the wet rumen digesta load of pregnant spotted deer (Ramzinski and Weckerly 2007), pregnant white-tailed deer (Jenks et al. 1994), pregnant sheep (Kaske and Groth 1997), non-productive sheep (de Vega and Poppi 1997) and gerenuk (Clemens and Maloiy 1982). Under-predictions of the wet rumen load of gemsbok (Maloiy et al. 1982) was also evident. Generally, there was an over estimation of rumen liquid load for small-sized ruminants. These included Grant’s gazelle, mountain reedbuck, steenbok and suni (Clemens and Maloiy 1983), mule and roe deer (Prins and Geelen 1971). The Artificial Neural Network model of Adebayo et al. (2020) when tested using wild ruminant species could only account for only 15% of the variation in prediction. This is lower than the variation accounted for by the Random Forest model in this study using an independent dataset containing wild ruminants. The model of Adebayo et al. (2020) and the model from this study under-predicted the dry rumen digesta load of the African buffalo. Feed intake accounted for 54% of the variation in the weight of rumen wet digesta load (Sekine et al. 1991) of sheep.

A handful of studies (Illius and Gordon 1992; Forchhammer and Boomsma 1995; Weckerly et al. 2003) used allometric regression equations to predict rumen digesta load from body weight. Allometric equations based on body weight for domestic and wild ruminants accounted for 97% of the variation in rumen digesta load (Illius and Gordon 1992). Only 29% of the variation was accounted for in morning rumen wet matter load and 32% for male and female elks (Weckerly et al. 2003). In mule deer, body weight accounted for 24% of the variation in rumen wet digesta load (Weckerly et al. 2003). Body weight of muskoxen (Forchhammer and Boomsma 1995) accounted for more variation in rumen wet matter load compared to findings from Weckerly et al. (2003). Body weight could accurately predict wet rumen digesta load for muskoxen bulls in summer ($R^2 = 0.93$) and winter ($R^2 = 0.97$), cows in summer ($R^2 = 0.96$) and winter ($R^2 = 0.92$), both male and female yearlings in summer ($R^2 = 0.96$) and winter ($R^2 = 0.94$) (Forchhammer and Boomsma 1995). Models developed in this study performed better than these allometric regressions in predicting rumen digesta load for diverse ruminants.

Gherardi and Black (1989) explored the relationship between rumen wet and organic matter load with intake and the amount of nutrients in the rumen. The total energy (MJ/d per kg $BW^{0.75}$) infused in the rumen could explain 35% of the variation in rumen organic matter load. The total energy infused in the rumen explained most of the variation in the rumen wet ($R^2 = 0.77$) and organic ($R^2 = 0.76$) matter load scaled to empty body weight (Gherardi and Black 1989). The estimated net energy intake explained 65% and 67% of the variation in the weight of rumen organic and wet rumen matter load, respectively, scaled to empty body weight (Gherardi and Black 1989). Organic matter intake per unit of body weight explained 75% of the variation in rumen organic matter load scaled to empty body weight of lambs (Gherardi and Black 1989).

An estimate of the weight of rumen liquid matter load from the water holding capacity of dry matter accounted for only 42% of the variation (Froetschel and Amos 1991). The fractional passage rate of solid in the rumen accounted for 66% of the variation in estimation of the weight of rumen liquid load scaled to the weight of dry matter in the rumen (Froetschel and Amos 1991). Models from studies discussed above gave good predictions of rumen digesta load. In comparison to Adebayo et al. (2020), models in this study were superior in prediction of rumen digesta load of wild ruminants owing to the inclusion of the effects of APL, DOM, AT and climate type on observed rumen digesta load. The use of machine learning algorithms in predicting rumen load (arising from complex processes occurring in the rumen) paves the way to the realisation of accurate prediction of feed intake for diverse ruminants.

7.5 Conclusion

Rumen digesta load scaled allometrically to body weight and the body weight was the best scaling factor compared to animal production level and physiological age. Dry rumen digesta load did not scale according to the Bell-Jarman principle unlike the wet rumen digesta load. Liquid and dry rumen digesta load were predicted to decrease in proportion by 0.02 for every 1°C increase in ambient temperature. The models gave good predictions of rumen digesta load and should be used in predicting the weight of rumen digesta. The strong relationship between RDL and body weight was not evident in modelling as prediction of RDL scaled to body weight produced lower accuracy than prediction of unscaled RDL, warranting further study.

Chapter 8

General discussion, knowledge gaps and recommendations

8.1 Background

The public domain bears important factors known to influence feed intake in ruminants. The four main factors that affect intake of ruminants were identified to be diurnal feeding behaviour (eating, rumination, and idling), the digestibility of feeds in the rumen, the rate of digesta passage in the rumen and the weight of rumen digesta load of ruminants. Theoretically, ruminants eat to meet their nutritional needs, unless constrained not to by factors such as rumen capacity (rumen digesta load). During eating the process of mastication reduces feed particle size before a bolus enters the rumen. Upon entering the rumen, feed particles undergo further particle size reduction through degradation by bacteria. Particles that have not reached a critical size to pass out of the rumen through passage are regurgitated, rechewed and reswallowed through a process called ruminantion. Rumination further breaks down digesta particles until they reach a size allowing passage out of the rumen. Thus, the disappearance of feed particles in the rumen occurs through degradation and passage. The extent of feed particle size reduction is a function of the times spent on eating and ruminating and is important in determining the rates of degradation and passage. The passage rate of feed particles in the rumen is highest during eating and rumination, and lowest during idling owing to the low frequency of rumen contractions during idling. Technically, proportions of rumen digesta load that disappears is a function of the sum of rates of passage and degradation. As feed particles disappear from the rumen, hunger pangs from the hypothalamus cause the sensation of hunger and stimulates the process of eating. How much the ruminant will eat depends on the receptive capacity of the rumen as determined by the rumen digesta load.

In order to be able to accurately predict intake, studies should predict these four factors with high precision and accuracy and develop a biological relationship between these factors towards estimating feed intake. There exists a wide variation among studies in responses of diurnal feeding behaviour, the digestibility of feeds in the rumen, the rate of digesta passage in the rumen and the weight of rumen digesta load to feed, animal, management and natural environmental factors. The four main objectives of this study were to determine the main factors affecting and developing models for estimating (1) diurnal feeding behaviour, (2) digestion of feeds in the rumen, (3) weight of rumen digesta load and (4) rate of passage of digesta in the rumen.

8.2 Discussion

Chapter 3 investigated whether the intake and feeding behaviour of small ruminants fed on a variety of diet and roughage quality would be different. This study tested the hypothesis that improvement of diet quality and period of the day has an effect on diurnal feeding behaviour patterns and intake in goats and sheep. Time spent eating and ruminating was affected by roughage quality and period of day. Period of day affected the duration of rumination sessions; improvement of roughage quality affected the duration of eating bouts and rumination sessions. In this regard, the hypothesis was accepted. It was concluded that chewing time, number of eating and ruminating bouts, and duration of eating bouts are physiologically controlled in small ruminants, though chewing time requires isometric scaling during modelling of intake.

The first meta-analysis of Chapter 4 ascertained the influence of the period of the day, ambient temperature, climatic region, and ruminant feeding type on daytime and night-time feeding behaviour of ruminants. The explicit assumption tested were that browsing and grazing ruminants adapt their feeding behaviour differently based on body size, feeding type and period of day in the diverse feed and climate environments they inhabit. Findings from the meta-analyses concur with the hypothesis as it was revealed that large ruminants prefer to spend less time eating at night probably to avoid partaking in a behaviour that compromises their levels of vigilance at a period of day when predation threat is highest. The effect of period of day on feeding behaviour corroborates with the hypothesis and confirms the findings from Chapter 3. The observed negative responses of duration of ruminating bouts during the day and at night with increasing ambient temperatures revealed that grazers and intermediate feeders are less vigilant during eating hence prefer to eat during the day when the risk of predation is low. At night when predation risk is high, grazers prefer to increase times spent ruminating and idling allowing high levels of vigilance. Information on the effect of period of day on feeding behaviour of browsers was lacking, making it impossible to understand how browsers adapt their feeding behaviour. The hypothesis was true because grazing and browsing ruminants adapted their feeding behaviours differently based on period of day and body size.

The second meta-analysis was used to investigate the influence on 24 h diurnal feeding behaviour patterns of ruminants in response to body size, ambient temperature and ruminant feeding type. An explicit assumption tested was that times spent eating and ruminating would decrease with increase in ambient temperature in grazers and browsers. Feeding behaviours scaled allometrically with body weight for all ruminant feeding types, except for time spent eating by browsers and intermediate feeders, and time spent ruminating by grazers. This led to the testing of the hypothesis that feeding behaviour of large-size ruminants make them well adapted to conditions of decreasing feed quality compared to small-size ruminants. Times spent eating and ruminating become shorter in large compared to small ruminants, with time spent ruminating became shorter in large browsers. This means that small ruminants would adapt well to decreasing feed quality where rumination become an important factor in increasing digestive efficiency, concurring with the hypothesis. Trends from this study showed that timespent eating, duration of eating sessions and idling are projected to increase with AT, while time spent ruminating is likely to decrease. In this regard, the first hypothesis tested false for time spent eating. It can be concluded that small-sized ruminants spent more time eating than their large counterparts, making small ruminants better adapted to conditions of increasing ambient temperature.

Based on the results obtained from the two meta-analysis, a total of 16 factors that affect feeding behaviour were collected and used to estimate feeding behaviour. The explicit assumption tested was that it is possible to predict the time spent on eating and ruminating for ruminants of different feeding types and from different climatic regions. The models developed in this study accounted for between 78 to 95% of the variation during development, while they attained 77 to 93% precision in prediction of feeding behaviour when testing the models using an independent dataset. The hypothesis was accepted as the study developed good simulation models for feeding behaviour of ruminants from diverse nutritional and climatic environments and are recommended for use.

Chapter 5 evaluated and predicted the nutritive and feeding value of underutilised forages as potential ruminant feeds. It was hypothesised that the starch and neutral detergent fibre contents of the diets fed to animals affect degradability and that it is possible to predict the solubility and effective degradability of forages. The main parameters that qualified for model development were starch (model for potential degradability and rate of degradation) and neutral detergent fibre contents of diet (model for degradation rate) through their effect on regulating microbial composition in the rumen, corroborating with the first hypothesis. An accuracy of 59% (model development) and 71% (model testing) was attained in prediction of the soluble fraction. The accuracy of prediction for the potential degradability was 65% (model development) and 24% (model testing). The second hypothesis was accepted because correcting for the factors that had significant effects on degradability parameters in the models, predicted solubility and effective degradability lay near the ideal prediction line; giving good predictions for these parameters.

A meta-analysis predicted the consequences of increases in ambient temperature and effect of climate type on digestibility of forages by ruminants in relation to global warming. It was hypothesised that increases in ambient temperature would decrease forage quality and that climate type would have no effect forage quality. Increases in ambient temperature increased the neutral detergent fibre content of feeds, lowering PD, “b”, and “c” of dry matter in the rumen. The hypothesis that AT would decrease forage quality was accepted because increases in AT decreased digestibility of forages. The previous meta-analysis on 24 h feeding behaviour revealed the ability of small ruminants to adapt well to decreasing feed quality where rumination would be key to increasing digestive efficiency. The adaptive strategy of small ruminants of possessing longer rumination times compared to their large-size counterparts shows their importance in the future where global warming is projected to decrease forage quality. It was concluded that the effects of AT and climate type AT should be accounted for in models that seek to predict digestibility in the rumen.

Based on the results obtained, a total of 16 factors that affect rumen degradability were used to estimate digestion in the rumen. Developed models accounted for between 76 to 93% of the variation during development, while they attained 29 to 64% precision in predictions when testing the models using an independent dataset. This study developed good simulation models for soluble and slowly degradable fractions, PD and lag; which are recommended for use. At this stage the model for the prediction of the rate of degradation of feeds is not recommended for use and requires improvement.

Chapter 6 ascertained the influence of liquid passage rates on solid digesta passage rates and the possibilities of simultaneous prediction of solid and liquid passage rates in ruminants. It was hypothesised that the rate of passage of solid is independent of the rate of passage of liquid in the rumen. Developed models accounted for 76 to 89% of the variation in prediction during training and attained 45 to 69% accuracy in prediction of passage rates using an independent dataset during model testing. Predicting solid passage rates simultaneously with liquid passage rate accounted for more variation compared to independent predictions of solid rates. The hypothesis was not accepted based on the findings that inclusion of liquid passage rate improved the prediction of solid passage rates. Given that both liquid and solid digesta phases exist intermingled together in the rumen, the findings confirm that the passage rate of solid digesta is partially dependent on the rate at which liquid flows in the rumen. Inclusion of liquid passage rate as an input variable is important as it gave better predictions of solid passage rates and should be taken as a critical factor in development of particulate passage rate models.

The meta-analysis of chapter 7 investigated the scaling relationships of rumen digesta load with body weight and evaluated the influence on ruminant digesta load in response to climatic region and ruminant feeding type. It was hypothesised that increases in ambient temperature would decrease rumen digesta load and that rumen digesta load scaled allometrically with body weight. Linear regressions revealed that grazers and intermediate feeders had hypoallometric scales of RDL with BW, while the scale was hyperallometric for browsers. Wet and liquid RDL of grazers and browsers scaled isometrically with BW. The mixed effects analysis showed that climate type and region influenced RDL and was highest for ruminants inhabiting tropical regions, followed by cold, temperate and lowest in arid climates. For all RDL, body mass and animal production were both influential covariates. It was predicted that increases in ambient temperature will decrease rumen digesta load. In this regard, both hypotheses were accepted. The effect of climatic region on rumen digesta load pointed to the effects of climate as linked to ambient temperature. A decrease in rumen digesta load with increases in ambient temperature are directly linked to a decrease in feed intake and an increase in the rate of passage of digesta in the rumen. With the projected increase in ambient temperate as a result of global warming, small-sized grazers and large-sized browsers will become more important than their respective counterparts as they are able to maintain proportionally high rumen digesta load for survival. Because small ruminants have low absolute nutrient requirements than large animals, implies that small browsers would be as important under conditions of rising ambient temperature. The findings of the meta-analysis on daytime and night-time feeding behaviour patterns also confirmed the growing importance of small-sized ruminants in areas were ambient temperatures are projected to rise decreasing forage quality.

For work that seeks to develop rumen digesta load prediction models, body weight may be used as a scaling factor. The 14 animal, feed and environmental factors accurately estimated the weight of rumen digesta load accounting for 81 to 94% of the variation in prediction during training and attained 59 to 88% precision during testing using an independent dataset. The models gave good predictions of rumen digesta load and should be used in predicting the weight of rumen digesta. The strong relationship between RDL and body weight was not evident in modelling as prediction of RDL scaled to body weight produced lower accuracy than prediction of unscaled RDL, warranting further study on this rather odd observation.

8.3 Knowledge gaps and recommendations

It is recommended that more studies in understanding daytime and night-time feeding behaviours be done. These studies should increase feeding behaviour variables to include duration and number of eating and ruminating bouts, even more of such studies should be done on browsing ruminants and in arid and cold climates for which there was a paucity of data.

More work is needs to be done in identifying the factors that are responsible for the variation that was unaccounted for in the model for the prediction of the rate of degradation. Some adjustments in the inputs for prediction of the rate of degradation are needed to improve predictions. The rate of passage of digesta needs to be corrected for the effect of temperature changes (climate change) due the El Nino effect and global warming. The strong relationship between rumen digesta load and body weight was not evident in modelling as prediction of rumen digesta load scaled to body weight produced lower accuracy than prediction of unscaled rumen digesta load, warranting further study on this rather odd observation. There is a need also to correct for the effect of time delay from the point of feeding cessation till rumen is measured on rumen digesta load; this is quite cardinal in regressing in time to the exact rumen fill when the animal stopped eating. A simultaneous evaluation of roughage intake, rumen fill levels, passage rates, digestibility and feeding behaviour are central to our understanding of the evolutionary adaptation of ruminant digestive physiology. Based on modelling results, prediction of feed intake using rumen digesta load, and the rates of passage and degradation in the rumen is now almost achievable. The rumen is a continuous system of processes that involve the rates of disappearance of feed particles through degradation and passage, replenishment of feed in the rumen through feed intake an amount regulated by rumen capacity which is itself a function of the rates of degradation and passage of feed. Future studies should focus on using rumen digesta load, passage, and degradation rates, and feeding behaviour as inputs to predict feed intake of ruminants. Before intake can be predicted, studies should seek to develop a biological relationship and link between rumen digesta load, passage, and degradation rates, and feeding behaviour the towards estimating feed intake.

8.4 Implications to practical feeding of ruminants

Understanding feeding behaviour is crucial to increase accuracy of predicting intake of roughages, aiding in grazing management, developing feed budgets and in mitigation of droughts. Previous speculation on effects of climate change on livestock can now be translated into science-based evidence. Global warming will decrease rumen digestibility of forages and these will be more pronounced in arid regions. Results from this study showed that small-sized ruminants are better adapted to their feeding behaviour and rumen digesta load than large-size ruminants. Small-sized grazing ruminants are better adapted to conditions that would require more selective feeding especially in tropical environments where scant forage that is of low nutritional quality needs to be maximised. The adoption of drought-tolerant ruminant livestock species and/or breeds that are capable of efficiently utilising poor quality roughages needs to be undertaken. Exploiting local or indigenous breeds of cattle, sheep, and goats, which are normally small in size may need to be considered as mitigation strategy for livestock farmers in arid areas.

References

Abdou N, Gouro AS, Nsahlai IV. 2017. Nutritional Characteristics of Available Feed Resources in Maradi Area of Niger. Anim Nutr Feed Technol 17(2):229-243.

Abdou N, Nsahlai IV, Chimonyo M. 2011. Effects of groundnut haulms supplementation on millet stover intake, digestibility and growth performance of lambs. Anim Feed Sci Technol 169:176-184.

Abijaoude JA, Morand-Fehr P, Tessier J, Schmidely PH, Sauvant D. 2000. Diet effect on the daily feeding behaviour, frequency and characteristics of meals in dairy goats. Livest Prod Sci 64:29-37.

Abule E, Umunna NN, Nsahlai IV, Osuji PO, Alemu Y. 1995. The effect of supplementing teff (*Eragrostis tef*) straw with graded levels of cowpea (*Vigna unguiculata*) and lablab (*Lablab purpureus*) hays on degradation, rumen particulate passage and intake by crossbred (Friesian× Boran (zebu)) calves. Livest Prod Sci 44:221-228.

Acatincăi S, Gavojdian D, Cziszter LT, Tripon I, Alungei A, Popian C. 2009. Study regarding rumination behaviour in multiparous Romanian Black and White cows during summer season. Scient Papers Anim Sci Biotech 42(2):191-194.

Adams D, Cochran R, Currie P. 1987. Forage maturity effects on rumen fermentation, fluid flow, and intake in grazing steers. J Range Manag 404-408.

Adebayo RA. 2016. Effect of roughage quality and period of meal termination on rumen fill [thesis]. Pietermaritzburg, South Africa: University of KwaZulu-Natal.

AFRC. 1993. Energy and protein requirements of ruminants. Advisory manual prepared by AFRC Technical Committee on Responses to Nutrients. CAB International, Wallingford, UK.

African Wildlife Fund (AWF). 2016. Wildlife conservation. http://www.awf.org/wildlifeconservation/all. Accessed 26 Jun. 2016.

Aharoni Y, Brosh A, Holzer Z. 1999. Comparison of models estimating digesta kinetics and faecal output in cattle from faecal concentrations of single-dosed markers of particles and solutes. J Anim Sci 77(8):2291-2304.

Alcaide EM, Martin-Garcia AI, Aguilera JF. 2000. A comparative study of nutrient digestibility, kinetics of degradation and passage and rumen fermentation pattern in goats and sheep offered good quality diets. Livest Prod Sci 64:215-223.

Allen MS, Mertens DR. 1988. Evaluating constraints on fibre digestion by ruminants. J Nutr 118:261-270.

Allen MS. 1996. Physical constraints on voluntary intake of forages by ruminants. J Anim Sci 74(12):3063-3075.

Almeida VV, Silva RR, Visintin AC, Queiroz AC, Silva FF, Sampaio CB, Lisboa MD, Mendes FB, Lins TO. 2014. Ingestive behavior of grazing heifers receiving crude glycerin supplementation during the dry-rainy season transition. Chil J Agric Res 74(3):286-292.

Álvarez-Rodríguez J, Sanz A, Ripoll-Bosch R, Joy M. 2010. Do alfalfa grazing and lactation length affect the digestive tract fill of light lambs? Small Ruminant Res 94(1-3):109-116.

Amarteifio JO, Mosase MO. 2006. The chemical composition of selected indigenous fruits of Botswana. J Appl Sci Environ Manage 10(2).

Amata IA, Lebari T. 2011. Comparative evaluation of the nutrient profile of four selected browse plants in the tropics, recommended for use as non-conventional livestock feeding materials. Afr J Biotechnol 10(64):14230-14233.

Amata IA. 2014. The use of non-conventional feed resources (NCFR) for livestock feeding in the tropics: a review. J Global Biosci 3(2):604-613.

Animal Diversity Web (ADW). 2016. University of Michigan. http://animaldiverisity.org/accounts/. Accessed 26 Jun.2016.

AOAC. 2000. Official Methods of Analysis 17th ed. Association of Official Analytical Chemists (AOAC), Arlington VA, USA.

Arkive. 2016. Explore mammal species. Arkive Organisation. http://www.arkive.org/explore/species/mammals. Accessed 27 Jun. 2016.

Arnold GW, De Boer G, Boundy CAP. 1980. The influence of odour and taste on the food preferences and food intake of sheep. Aust J Agric Res 31:571-587.

Asizua D, Mpairwe D, Kabi F, Mutetikka D, Bareeba FB, Hvelplund T, Weisbjerg MR, Madsen J. 2018. Effects of feeding systems on rumen environment, degradability and passage kinetics in Ankole × Friesian crossbred steers. Livest Sci 210:47-54.

Bach A, Calsamiglia S, Stern MD. 2005. Nitrogen metabolism in the rumen. J Dairy Sci 88:E9-E21.

Baile CA, Forbes JM. 1974. Control of feed intake and regulation of energy balance in ruminants. Physiol Rev 54(1):160-214.

Bakare AG, Chimonyo M. 2011. Seasonal variation in time spent foraging by indigenous goat genotypes in a semi-arid rangeland in South Africa. Livest Sci 135:251-256.

Balch CC, Campling RC. 1962. Regulation of voluntary intake in ruminants. Nutritional Abstracts and Reviews 32:669-686.

Barboza PS, Peltier TC, Forster RJ. 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiol Biochem Zool 79(3):497-513.

Barry TN, Manley TR, Duncan SJ. 1984. Quantitative digestion by sheep of carbohydrates, nitrogen and S-methyl-L-cysteine sulphoxide in diets of fresh kale (*Brassica oleracea*). J Agric Sci 102(2):479-486.

Barry TN, Manley TR, Millar KR. 1982. Nutritional evaluation of kale (*Brassica oleracea*) diets: 4. Responses to supplementation with synthetic S-methyl-L-cysteine sulphoxide (SMCO). J Agric Sci 99(1):1-12.

Barry TN, Manley TR. 1984. The role of condensed tannins in the nutritional value of Lotus pedunculatus for sheep: 2. Quantitative digestion of carbohydrates and proteins. Br J Nutr 51(3):493-504.

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

Baumont R, Brun JP, Dulphy JP. 1989. Influence of the nature of hay on its ingestibility and the kinetics of intake during large meals in sheep and cows. In: Jarrige, R, editors. XVI International Grassland Congress; Nice, France. France: French Grassland Society. p. 787-788.

Baumont R, Cohen-Salmon D, Prache S, Sauvant, D. 2004. A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. Anim Feed Sci Technol 112(1-4):5-28.

Baumont R, Jailler M, Dulphy JP. 1997. Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay. Ann Zootech 46:231-244.

Baumont R, Malbert CH, Ruckebush Y. 1990. Mechanical stimulation of rumen fill and alimentary behaviour in sheep. Anim Prod 50(1):123-128.

Baumont R, Prache S, Meuret M, Morand-Fehr P. 2000. How forage characteristics influence behaviour and intake in small ruminants: A review. Livest Prod Sci 64(1):15-28.

Bayat AR, Rinne M, Kuoppala K, Ahvenjärvi S, Huhtanen P. 2010. Ruminal large and small particle kinetics in dairy cows fed red clover and grass silages harvested at two stages of growth. Anim Feed Sci Technol 155(2):86-98.

Behrend A, Lechner-Doll M, Streich WJ, Clauss M. 2004. Seasonal faecal excretion, gut fill, liquid and particle marker retention in mouflon (*Ovis ammon musimon*), and a comparison with roe deer (*Capreolus capreolus*). Acta Theriol 49(4):503-515.

Bello MO, Falade OS, Adewusi SRA, Olawore NO. 2008. Studies on the chemical compositions and anti-nutrients of some lesser known Nigeria fruits. Afr J Biotechnol 7(21).

Benvenutti MA, Pavetti DR, Poppi DP, Mayer DG, Gordon IJ. 2017. Ingestive behaviour and forage intake responses of young and mature steers to the vertical differentiation of sugarcane in pen and grazing studies. J Agric Sci 155(10):1677-88.

Bernard L, Montgomery MJ. 1997. Managing intake of Lactating Dairy Cows. In: Tennessee, USA: The University of Tennessee Institute of Agriculture; 1997.

Bines JA, Davey AW. 1970. Voluntary intake, digestion, rate of passage, amount of material in the alimentary tract and behaviour in cows receiving complete diets containing straw and concentrates in different proportions. Br J Nutr 24(4):1013-1028.

Bisset NG. 1970. The African species of Strychnos, Part I. The ethnobotany. Lloydia, 33, pp.201-43.

Bognar A, Stanciu G, Cziszter LT, Acatincăi S, Tripon I, Gavojdian D, Baul S, Tetileanu R. 2010. Lactation order effects on milk production in Romanian black and white cows from Timiş county. Scient Papers Anim Sci Biotech 43(2):213-216.

Bonsi MLK, Osuji PO, Nsahlai IV, Tuah AK. 1994. Graded levels of Sesbania sesban and Leucaena leucocephala as supplements to teff straw given to Ethiopian Menz sheep. Anim Sci 59(2):235-244.

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

Brumby PJ. 1959. The grazing behaviour of dairy cattle in relation to milk production, live weight, and pasture intake. N Z J Agric Res 2(4):797-807.

Bueno L. 1975. The mechanical and digestive function of the omasum [thesis]. University of Toulouse, France: University of Toulouse; 1975.

Bunnell FL, Gillingham MP. 1985. Foraging behaviour: dynamics of dining out. Bioenergetics of wild herbivores, 53-79.

Busanello M, Velho JP, Alessio DRM, Haygert-Velho IMP, Tambara AAC, Neto AT. 2017. In situ ruminal degradability of protein feeds with distinct physical forms: a meta-analysis. S Afr J Anim Sci 47(1):91-95.

Butterfield RM. 1988. New concept of sheep growth. The Department of Veterinary Anatomy, University of Sydney and the Australian Feeding Standards for Ruminants 1990. CSIRO. 168 pp

Cannas A, Van Soest PJ. 2000. Simple allometric models to predict rumen feed passage rate in domestic ruminants. In: Modelling Nutrient Utilization in Farm Animals. Eds: McNamara JP, France J, Beever DE. CABI Publishers, Wallingford, UK. pp. 49-62.

Carro MD, Lopez S, Gonzalez JS, Ovejero FJ. 1991. The use of the rumen degradation characteristics of hay as predictors of its voluntary intake by sheep. Anim Sci 52(1):133-139.

Carruthers VR, Bryant AM, Cockrem FRM, McLeay LM. 1988. Quantity of digesta in the reticulo-rumen of cows differing in susceptibility to bloat. New Zeal J Agr Res 31(2):111-119.

Cassida KA, Barton BA, Hough RL, Wiedenhoeft MH, Guillard K. 1994. Feed intake and apparent digestibility of hay-supplemented brassica diets for lambs. J Anim Sci 72(6):1623-1629.

Castillo-Caamal JB, Jimenez-Osornio JJ, Lopez-Perez A, Aguilar-Cordero W, Castillo-Caamal AM. 2003. Feeding Mucuna beans to small ruminants of Mayan farmers in the Yucatan Peninsula, Mexico. Trop Subtrop Agroecosyst 1(2-3).

Chaiyabutr N, Buranakarl C, Muangcharoen V, Loypetjra P, Pichaicharnarong A. 1987. Effects of acute heat stress on changes in the rate of liquid flow from the rumen and turnover of body water of swamp buffalo. J Agric Sci 108(3):549-553.

Chenost M, Kayouli C. 1997. Roughage utilization in warm climates. FAO Animal Production Health Paper. Article 135.

Chermiti A, Teller E, Vanbelle M, Collignon G, Matatu B. 1994. Effect of ammonia or urea treatment of straw on chewing behaviour and ruminal digestion processes in non-lactating dairy cows. Anim Feed Sci Technol 47:41-51.

Chikagwa-Malunga SK, Adesogan AT, Szabo NJ, Littell RC, Phatak SC, Kim SC, Arriola KG, Huisden CM, Dean DB, Krueger NA. 2009. Nutritional characterization of Mucuna pruriens: 3. Effect of replacing soybean meal with Mucuna on intake, digestibility, N balance and microbial protein synthesis in sheep. Anim Feed Sci Technol 148(2-4):107-123.

Chilibroste P, Tamminga S, Van Bruchem J, Van der Togt PL. 1998. Effect of allowed grazing time, inert rumen bulk and length of starvation before grazing on the weight, composition and fermentative end-products of the rumen contents of lactating dairy cows. Grass Forage Sci 53:146-156.

Christopherson RJ, Kennedy PM. 1983. Effect of the thermal environment on digestion in ruminants. Can J Anim Sci 63(3):477-496.

Christopherson RJ. 1976. Effects of prolonged cold and the outdoor winter environment on apparent digestibility in sheep and cattle. Can J Anim Sci 56(2):201-212.

Chumpawadee S, Sommart K, Vongpralub T, Pattarajinda V. 2005. In sacco degradation characteristics of energy feed sources in Brahman-Thai native crossbred steers. J Agric Technol 1(2):192-206.

Clauss M, Deutsch A, Lechner-Doll M, Flach EJ, Tach C. 1998. Passage rate of fluid and particle phase in captive giraffe (*Giraffa camelopardalis*). Adv Ethol 33:98.

Clauss M, Frey R, Kiefer B, Lechner-Doll M, Loehlein W, Polster C, Rössner GE, Streich WJ. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia 136(1):14-27.

Clauss M, Fritz J, Bayer D, Nygren K, Hammer S, Hatt JM, Südekum KH, Hummel J. 2009. Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax, bison, red deer and moose. Comp Biochem Physiol Part A Mol Integr Physiol 152(3):398-406.

Clauss M, Hofmann RR, Hummel J, Adamczewski J, Nygren K, Pitra C, Streich WJ, Reese S. 2006. The microscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal animal surface area in 34 ruminant species. J Zool 270:346-358.

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

Clauss M, Hummel J, Streich WJ. 2006. The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: An evaluation of available, comparable ruminant passage data. Eur J Wildl Res 52(2):88-98.

Clauss M, Hummel J, Vollm. The attribution of a feeding type to a ruminant species based on morphological parameters: The example of okapi (*Okapi johnstoni*). In: Symposia of the Comparative Nutrition Society, editor. Comparative Nutrition Society; 21-25 August; Antwerp, Belgium. Silver Spring, USA: Comparative Nutrition Society; 2002. p. 123.

Clauss M, Hummel J. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. Mammal Rev 35(2):174-187.

Clauss M, Hummel J. 2017. Physiological adaptations of ruminants and their potential relevance for production systems. R Bras Zootec 46(7):606-613.

Clauss M, Lang-Deuerling S, Muller DW, Kienzle E, Steuer P, Hummel J. 2010. Retention of fluid and particles in captive tapirs. Comp Biochem Physiol Part A Mol Integr Physiol 157(1):95-101.

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

Clauss M, Schwarm A, Ortmann S, Streich WJ, Hummel J. 2007. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. Comp Biochem Physiol Part A Mol Integr Physiol 148(2):249-265.

Clauss M, Steuer P, Müller DW, Codron D, Hummel J. 2013. Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. PLoS One 8(10): e68714.

Clemens ET, Maloiy GM. 1983. Digestive physiology of East African wild ruminants. Comp Biochem Physiol A Comp Physiol 76(2):319-333.

Codron D, Hofmann RR, Clauss M. 2019. Morphological and Physiological Adaptations for Browsing and Grazing. In: Gordon I, Prins H. (ed) The Ecology of Browsing and Grazing II. Ecological Studies (Analysis and Synthesis), vol 239. Springer, Cham. pp. 81-125.

Codron D, Hofmann RR, Clauss M. 2019. Morphological and Physiological Adaptations for Browsing and Grazing. In: Gordon I, Prins H. (ed) The Ecology of Browsing and Grazing II. Ecological Studies (Analysis and Synthesis), vol 239. Springer, Cham.

Codron D, Lee-Thorp JA, Sponheimer M, Codron J, De Ruiter D, Brink JS. 2007. Significance of diet type and diet quality for ecological diversity of African ungulates. J Anim Ecol 76(3):526-537.

Coffey K, Paterson J, Saul C, Coffey L, Turner K, Bowman J. 1989. The influence of pregnancy and source of supplemental protein on intake, digestive kinetics and amino acid absorption by ewes. J Anim Sci 67(7):1805-1814.

Coffey KP, Moyer JL, Brazle FK, Lomas LW. 1992. Amount and diurnal distribution of grazing time by stocker cattle under different tall fescue management strategies. Appl Anim Behav Sci 33(2-3):121-135.

Conceição MG, Ferreira MD, Campos JM, Silva JD, Detmann E, Siqueira MC, Barros LJ, Costa CT. 2016. Replacement of wheat bran with spineless cactus in sugarcane-based diets for steers. Rev Bras Zootecn 45(4):158-164.

Cone JW, Van Gelder AH, Valk H. 1998. Prediction of nylon bag degradation characteristics of grass samples with the gas production technique. J Sci Food Agric 77:421-426.

Cushnahan A, Mayne CS, Unsworth EF. 1995. Effects of ensilage of grass on performance and nutrient utilization by dairy cattle 2. Nutrient metabolism and rumen fermentation. Anim Sci 60(3):347-359.

Dado RG, Allen MS. 1996. Enhanced intake and production of cows offered ensiled alfalfa with higher neutral detergent fibre digestibility. J Dairy Sci 79(3):418-428.

Dambe LM, Mogotsi K, Odubeng M, Kgosikoma OE. 2015. Nutritive value of some important indigenous livestock browse species in semi-arid mixed Mopane bushveld, Botswana. Livest Res Rural Dev 27:10.

De K, Kumar D, Sharma S, Kumawat P, Mohapatra A, Sahoo A. 2020. Effect of drinking earthen pot water on physiological response and behavior of sheep under heat stress. J Therm Biol 87:102476.

De Vega A, Poppi DP. 1997. Extent of digestion and rumen condition as factors affecting passage of liquid and digesta particles in sheep. J Agri Sci 128(2):207-215.

Degen AA. 2007. Sheep and goat milk in pastoral societies. Small Rumin Res 68:7-19.

Delve RJ, Cadisch G, Tanner JC, Thorpe W, Thorne PJ, Giller KE. 2001. Implications of livestock feeding management on soil fertility in the smallholder farming systems of sub-Saharan Africa. Agric Ecosyst Environ 84:227–243.

Demment MW, Van Soest PJ. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am Nat 125(5):641-672.

Demment MW. 1982. The scaling of ruminoreticulum size with body weight in East African ungulates. Afr J Ecol 20(1):43-47.

Deroche B, Pradel P, Baumont R. 2020. Long-term evolution and prediction of feed value for permanent mountain grassland hay: Analysis of a 32-year data set in relation to climate change. Grass Forage Sci 75(1):18-27.

Deswysen AG, Ehrlein HJ. 1981. Silage intake, rumination and pseudorumination activity in sheep studied by radiography and jaw movement recordings. Br J Nutr 46:327-335.

Dijkstra J, Kebreab E, Mills JAN, Pellikaan WF, Lopez S, Bannink A, France J. 2007. Predicting the profile of nutrients available for absorption: From nutrient requirement to animal response and environmental impact. Animal 1:99-111.

Dixon RM, Milligan LP. 1985. Removal of digesta components from the rumen of steers determined by sieving techniques, and fluid, particulate and microbial markers. Br J Nutr 53(2):347-362.

Domingue BF, Dellow DW, Barry TN. 1991. The chewing efficiency during eating and ruminating in goats and sheep. Br J Nutr 65(3):355-363.

Domingue BF, Dellow DW, Barry TN. 1991. Voluntary intake and rumen digestion of a low quality roughage by goats and sheep. J Agric Sci 117(1):111-120.

Domingue BF, Wilson PR, Dellow DW, Barry TN. 1992. Effects of subcutaneous melatonin implants during long daylength on voluntary feed intake, rumen capacity and heart rate of red deer (*Cervus elaphus*) fed on a forage diet. Br J Nutr 68(1):77-88.

Dominigue BMF, Dellow DW, Barry TN. 1991. The efficiency of chewing during eating and ruminating in goats and sheep. Br J Nutr 65:355-363.

Dove H. 1996. Constraints to modelling of diet selection and intake in the grazing ruminant. In: Hodgson J, Illius AW, editors. The ecology and management of grazing systems. Slough, UK: CAB International; 1996. p. 257-275.

Du Toit PCV. 1998. A comparison of the diets selected by merino and dorper sheep on three range types of the Karoo, South Africa. Arch de Zootec 47:21-32.

Egan JK, Doyle PT. 1985. Effect of intraruminal infusion of urea on the response in voluntary food intake by sheep. Aust J Agric Res 36(3):483-495.

Ellis WC, Lascano M, Teeter R, Owens FN. 1982. Solutes and particulate flow markers. In: Protein requirements for cattle. Ed: Owens FN, Oklahoma State University, Stillwater, USA. pp. 37-56.

Elsden SR, Hitchcock MWS, Marshall RA, Phillipson AT. 1946. Volatile acids in the digesta of ruminants and other animals. J Exp Biol 22:191-202.

Emebu PK, Anyika JU. 2011. Proximate and mineral composition of kale (Brassica oleracea) grown in Delta State, Nigeria. Pakistan J Nutr 10(2):190-194.

Emmans G, Kyriazakis I. 2001. Consequences of genetic change in farm animals on food intake and feeding behaviour: Nutrition and Behaviour Group Symposium on Future Perspectives in Nutrition and Behaviour Research. Proc Nutr Soc 60:115-125.

Estell RE, Galyean M. 1985. Relationship of rumen fluid dilution rate to rumen fermentation and dietary characteristics of beef steers. J Anim Sci 60(4):1061-1071.

Estes RD. 1993. The safari companion: A guide to watching African mammals. Russel Friedman Books, Halfway House, Johannesburg, South Africa.

Evans EW, Pearce GR, Burnett J, Pillinger SL. 1973. Changes in some physical characteristics of the digesta in the reticulo-rumen of cows fed once daily. Br J Nutr 29(3):357-376.

Evans EW. 1981. An evaluation of the relationships between dietary parameters and rumen liquid turnover rate. Can J Anim Sci 61:91-96.

Faichney GJ, Brown GH. 2004. Effect of physical form of lucerne hay on rumination and the passage of particles from the rumen of sheep. Aust J Agric Res 55(12):1263-1270.

Faichney GJ, Poncet C, Boston RC, Bernard L, Pochet S, Beaufort MT, Delval E, Fabre M, Pichon P, Flechet J. 1989. Passage of internal and external markers of particulate matter through the rumen of sheep. Reprod Nutr Dev 29(3):325-337.

Faichney GJ, White GA. 1988. Rates of passage of solutes, microbes and particulate matter through the gastrointestinal tract of ewes fed at a constant rate throughout gestation. Aust J Agric Res 39:481-492.

Faichney GJ. 1980. Measurement in sheep of the quantity and composition of rumen digesta and of the fractional outflow rates of digesta constituents. Aust J Agric Res 31:1129-1137.

Faichney GJ. The kinetics of particulate matter in the rumen. In: Milligan LP, Grovum WL, Dobson A, editors. 6th International Symposium on Ruminant Physiology; 10-14 September 1984; Banff, Canada. New Jersey, USA: Prentice-Hall; 1986. p. 173.

Faverdin P, Baumont R, Ingvartsen KL. 1995. Control and prediction of intake in ruminants. In: Journet M, Grenet E, Farce MH, Thériez M, Demarquilly C, editors. Recent developments in the nutrition of herbivores. IVth International Symposium on the Nutrition of Herbivores; 11-15 September 1995; Paris, France. France: INRA Editions; 1995. p. 95-120.

Feedipedia. 2019. Animal Feed Resources Information System. A programme by INRA, CIRAD, AFZ and FAO. http://www.feedipedia.org. Accessed 9 Aug. 2019.

Ferreira LM, Celaya R, Benavides R, Jáuregui BM, García U, Santos AS, García RR, Rodrigues MA, Osoro K. 2013. Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas. Livest Sci 155(2-3):373-83.

Ferwerda JG. 2005. Charting the quality of forage: measuring and mapping the variation of chemical components in foliage with hyperspectral remote sensing. Wageningen, Wageningen University. ITC Dissertation 126, 166 p. ISBN 90-8504-209-7.

Fomum SW, Scogings PF, Dziba L, Nsahlai IV. 2015. Seasonal variations in diet selection of Nguni goats: effects of physical and chemical traits of browse. Afr J Range Forage Sci 32(3):193-201.

Fonseca AJM, Dias-da-Silva AA, Ørskov ER. 1998. In sacco degradation characteristics as predictors of digestibility and voluntary intake of roughages by mature ewes. Anim Feed Sci Technol 72:205-219.

Forbes JM. 1970. The voluntary food intake of pregnant and lactating ruminants: a review. Br Vet J 126:1-11.

Forbes JM. 1970. Voluntary food intake in pregnant ewes. J Anim Sci 31(3):1222-1227.

Forbes JM. 1995. Physical limitation of intake in ruminants and its interaction with other factors affecting feed intake. In: Engelhardt WV, Leonhard-Marek S, Breves G, editors. Ruminant physiology: Digesta, metabolism, growth and reproduction. Stuttgart, Germany: Ferdinand Enke Verlag. p. 217-232.

Forchhammer MC, Boomsma JJ. 1995. Foraging strategies and seasonal diet optimization of muskoxen in West Greenland. Oecologia 104(2):169-180.

Fox DG, Tedeschi LO, Tylutki TP, Russell JB, Van Amburgh ME, Chase LE, Pell AN, Overton TR. 2004. The Cornell net carbohydrate and protein system model for evaluating herd nutrition and nutrient excretion. Anim Feed Sci Technol 112(1):29-78.

Frandsen R. 1992. Southern Africa’s mammals: a field guide. Frandsen, Sandton, Johannesburg, South Africa.

Frandson RD. 1981. Anatomy and Physiology of Farm Animals. 1st ed. Philadelphia, USA: Lea and Febiger; 1981.

Fritz J, Hummel J, Kienzle E, Arnold C, Nunn C, Clauss M. 2009. Comparative chewing efficiency in mammalian herbivores. Oikos 118:1623-1632.

Froetschel MA, Amos HE. 1991. Effects of dietary fiber and feeding frequency on ruminal fermentation, digesta water-holding capacity, and fractional turnover of contents. J Anim Sci 69(3):1312-1321.

Froetschel MA. 1995. Effect of abomasal infusion of saliva on reticular motility and ruminal liquid contents of steers. J Dairy Sci 78(11):2396-2401.

Fuller MF, Benavenga NJ, Lall SP, McCracken KJ, Omed HM, Axford RFE, Phillips CJC. 2004. The encyclopaedia of farm animal nutrition. Wallingford, United Kingdom: CAB International.

Garcia MA, Aguilera JF, Alcaide EM. 1995. Voluntary intake and kinetics of degradation and of passage of unsupplemented and supplemented pastures from semi-arid lands in grazing goats and sheep. Livest Prod Sci 44(3):245-255.

Geist V. 1974. On the relationship of social evolution and ecology in ungulates. Am Zool 14(1):205-220.

Gherardi SG, Black JL. 1989. Influence of post-rumen supply of nutrients on rumen digesta load and voluntary intake of a roughage by sheep. Br J Nutr 62(3):589-599.

Gibb MJ, Huckle CA, Nuthall R, Rook AJ. 1999. The effect of physiological state (lactating or dry) and sward surface height on grazing behaviour and intake by dairy cows. Appl Anim Behav Sci 63(4):269-287.

Giesecke D, Van Gylswyk NO. 1975. A study of feeding types and certain rumen functions in six species of South African wild ruminants. J Agri Sci 85(1):75-83.

Gonyou HW, Christopherson RJ, Young BA. 1979. Effects of cold temperature and winter conditions on some aspects of behaviour of feedlot cattle. Appl Anim Ethol 5(2):113-124.

Gordon IJ, Illius AW. 1994. The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98(2):167-175.

Gordon IJ, Illius AW. 1996. The nutritional ecology of African ruminants: a reinterpretation. J Anim Ecol 18-28.

Gordon IJ. 2003. Browsing and grazing ruminants: are they different beasts? Forest Ecol Manag 181(1-2):13-21.

Greenhalgh JFD, Reid GW. 1971. Relative palatability to sheep of straw, hay and dry grass. Br J Nutr 26:107-116.

Gregorini P, Gunter SA, Masino CA, Beck PA. 2007. Effects of ruminal fill on short-term herbage intake rate and grazing dynamics of beef heifers. Grass Forage Sci 62(3):346-54.

Gregorini P. 2012. Diurnal grazing pattern: its physiological basis and strategic management. Anim Prod Sci 52:416-430.

Gregorini P. 2015. Modelling preference and diet selection patterns by grazing ruminants: a development in a mechanistic model of a grazing dairy cow, MINDY. Anim Prod Sci 55:360-375.

Gross JE, Alkon PU, Demment MW. 1996. Nutritional ecology of dimorphic herbivores: Digestion and passage rates in Nubian Ibex. Oecologia 107(2):170-178.

Gunter SA, Judkins MB, Krysl LJ, Broesder JT, Barton RK, Rueda BR, Hallford DM, Holcombe DW. 1990. Digesta kinetics, ruminal fermentation characteristics and serum metabolites of pregnant and lactating ewes fed chopped alfalfa hay. J Anim Sci 68(11):3821-3831.

Haaland G, Tyrrell H. 1982. Effects of limestone and sodium bicarbonate buffers on rumen measurements and rate of passage in cattle. J Anim Sci 55(4):935-942.

Habib G, Hassan MF, Siddiqui MM. 1998. Degradation characteristics of straw from different wheat genotypes and their response to urea-ammoniation treatment. Anim Feed Sci Technol 72, 373-386.

Hadjigeorgiou IE, Gordon IJ, Milne JA. 2003. Comparative preference by sheep and goats for Graminaeae forages varying in chemical composition. Small Ruminant Res 49(2):147-156.

Hadjigeorgiou IE, Gordon IJ, Milne JA. 2003. Intake, digestion and selection of roughage with different staple lengths by sheep and goats. Small Ruminant Res 47(2):117-132.

Halachmi I, Meir YB, Miron J, Maltz E. 2016. Feeding behavior improves prediction of dairy cow voluntary feed intake but cannot serve as the sole indicator. Animal: An International Journal of Animal Bioscience. 10(9):1501.

Halimani TE, Ndlovu LR, Dzama K, Chimonyo M, Miller BG. 2005. Metabolic response of pigs supplemented with incremental levels of leguminous *Acacia karroo, Acacia nilotica* and *Colophospermum mopane* leaf meals. Anim Sci 81(1):39-45.

Halimani TE, Ndlovu LR, Dzama K, Chimonyo M, Miller BG. 2007. Growth performance of pigs fed on diets containing *Acacia karroo*, *Acacia nilotica* and *Colophospermum mopane* leaf meals. Livest Res Rural Dev 19:187.

Hall-Martin AJ. 1974. Food selection by Transvaal lowveld giraffe as determined by analysis of stomach contents. S Afr J Wildl Res 4(3):191-202.

Harris I, Jones PD, Osborn TJ, Lister DH. 2014. Updated high-resolution grids of monthly climatic observations – CRU TS3.10: The Climatic Research Unit (CRU) Time Series (TS) Version 3.10 Dataset. Int J Climatol 34(3):623-642.

Hartnell GF, Satter LD. 1979. Determination of rumen fill, retention time and ruminal turnover rates of digesta at different stages of lactation in dairy cows. J Anim Sci 48(2):381-392.

Helander C, Nørgaard P, Arnesson A, Nadeau E. 2014. Effects of chopping grass silage and of mixing silage with concentrate on feed intake and performance in pregnant and lactating ewes and in growing lambs. Small Ruminant Res 116(2-3):78-87.

Helander C, Nørgaard P, Jalali AR, Nadeau E. 2014. Effects of chopping grass silage and mixing silage with concentrate on feed intake, diet selection, chewing activity and faecal particle size of ewes in late pregnancy and early lactation. Livest Sci 163:69-79.

Hofmann RR, Streich WJ, Fickel J, Hummel J, Clauss M. 2008. Convergent evolution in feeding types: Salivary gland mass differences in wild ruminant species. J Morphol 269(2):240-257.

Hofmann RR. 1973. The ruminant stomach. East African Monographs in Biology 2:1–354

Hofmann RR. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. Oecologia 78(4):443-457.

Hume ID. 2005. Concepts of digestive efficiency. p.43-58. In: Physiological and ecological adaptations to feeding in vertebrates. Starck JM, Wang T. eds. Science Publishers, Enfield NH.

Hummel J, Steuer P, Sudekum KH, Hammer S, Hammer C, Streich WJ, Clauss M. 2008. Fluid and particle retention in the digestive tract of the addax antelope-adaptations of a grazing desert ruminant. Comp Biochem Physiol Part A Mol Integr Physiol 149:142-149.

Hummel J, Sudekum KH, Streich WJ, Clauss M. 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. Funct Ecol 20(6):989-1002.

Hutjens MF. Dairy efficiency and dry matter intake. In: 7th Western Dairy Management Conference; 9-11 March 2005; Reno, Nevada, USA. USA: University of Illinois; 2005. p. 71-76.

Illius AW, Gordon IJ. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. J Agric Sci 116(1):145-157.

Illius AW, Gordon IJ. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89(3):428-434.

Isaacson HR, Hinds FC, Bryant MP, Owens FN. 1975. Efficiency of energy utilization by mixed rumen bacteria in continuous culture. J Dairy Sci 58(11):1645-1659.

Jalali AR, Nørgaard P, Weisbjerg MR, Nielsen MO. 2012. Effect of forage quality on intake, chewing activity, faecal particle size distribution, and digestibility of neutral detergent fibre in sheep, goats, and llamas. Small Rumin Res 103:143-151.

Jenks JA, Leslie Jr DM, Lochmiller RL, Melchiors MA. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. J Mammal 75(4):1045-1053.

Jiang Z, Hudson RJ. 1996. Digestive responses of wapiti Cervus elaphus canadensis to seasonal forages. Acta Theriol 41(4):415-423.

Johnson CN, Prideaux GJ. 2004. Extinctions of herbivorous mammals in the late Pleistocene of Australia in relation to their feeding ecology: no evidence for environmental change as cause of extinction. Austral Ecol 29(5):553-557.

Johnson TR, Combs DK. 1991. Effects of prepartum diet, inert rumen bulk, and dietary polyethylene glycol on dry matter intake of lactating dairy cows. J Dairy Sci 74(3):933-944.

Juma HK, Abdulrazak SA, Muinga RW, Ambula MK. 2006. Evaluation of Clitoria, Gliricidia and Mucuna as nitrogen supplements to Napier grass basal diet in relation to the performance of lactating Jersey cows. Livest Sci 103(1-2):23-29.

Jung HG, Allen MS. 1995. Characteristics of plant cell walls affecting intake and digestibility of forages by ruminants. J Anim Sci 73(9):2774-2790.

Kamal TH, Shabaita MK. 1968. Climate effect on Friesians and buffaloes. 1. Blood volume using sodium dichromate. J Dairy Sci 51(6):970.

Kamalak ADEM, Canbolat O, Gurbuz Y, Ozay O. 2005. Comparison of in vitro gas production technique with in-situ nylon bag technique to estimate dry matter degradation. Czech J Anim Sci 50:60-67.

Kammes KL, Allen MS. 2012. Nutrient demand interacts with forage family to affect digestion responses in dairy cows. J Dairy Sci 95(6):3269-3287.

Kaps M, Lamberson WR. 2017. Biostatistics for animal science. CABI Publishing, Wallingford, UK.

Karsli MA, Russell JR. 2002. Prediction of the voluntary intake and digestibility of forage-based diets from chemical composition and ruminal degradation characteristics. Turk J Vet Anim Sci 26:249-255.

Kaske M, Beyebach M, Hailu Y, Goebel W, Wagner S. 2002. The assessment of the frequency of chews during rumination enables an estimation of rumination activity in hay-fed sheep. J Anim Physiol Anim Nutr 86:83-89.

Kaske M, Groth A. 1997. Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay. Reprod Nutr Dev 37(5):573-588.

Kaske M, Hatiboglu S, Engelhardt W. 1992. The influence of density and size of particles on rumination and passage from the reticulo-rumen of sheep. Br J Nutr 67(2):235-244.

Kaske M, Midasch A. 1997. Effects of experimentally impaired reticular contractions on digesta passage in sheep. Br J Nutr 78(1):97-110.

Katamzi M. 2015. Degradation parameters and modelling of degradation rate in the rumen of cattle fed non-supplemented roughages (Doctoral dissertation). University of KwaZulu-Natal, Pietermaritzurg, South Africa.

Katoh K, Sato F, Yamazaki A, Sasaki Y, Tsuda T. 1988. Passage of indigestible particles of various specific gravities in sheep and goats. Br J Nutr 60(3):683-687.

Kennedy PM, Christopherson RJ, Milligan LP. 1976. The effect of cold exposure of sheep on digestion, rumen turnover time and efficiency of microbial synthesis. Br J Nutr 36(2):231-242.

Kennedy PM, Christopherson RJ, Milligan LP. 1982. Effects of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. Br J Nutr 47(3):521-535.

Kennedy PM, Milligan LP. 1978. Effects of cold exposure on digestion, microbial synthesis and nitrogen transformations in sheep. Br J Nutr 39(1):105-117.

Kennedy PM, Murphy MR. 1988. The nutritional implications of differential passage of particles through the ruminant alimentary tract. Nutr Res Rev 1(1):189-208.

Kennedy PM. 1985. Influences of cold exposure on digestion of organic matter, rates of passage of digesta in the gastrointestinal tract, and feeding and rumination behaviour in sheep given four forage diets in the chopped, or ground and pelleted form. Br J Nutr 53(1):159-173.

Kennedy PM. 2005. Particle dynamics. In: Dijkstra J, Forbes JM, France J, editors. Quantitative Aspects of Ruminant Digestion and Metabolism. Wallingford, UK: CAB International; 2005. p. 49-86.

Ketshabile WG, Moyo M, Ahmed MA, Nsahlai IV. 2019. Daily variation in feeding and ingestive behaviour of sheep and goats grazing and browsing on grass-legume pastures. Anim Nutr Feed Techn 19(2):217-227.

Khazaal K, Dentinho MT, Ribeiro JM, Ørskov ER. 1993. A comparison of gas production during incubation with rumen contents in vitro and nylon bag degradability as predictors of the apparent digestibility in vivo and the voluntary intake of hays. Anim Sci 57(1):105-112.

Khazaal K, Dentinho MT, Ribeiro JM, Ørskov ER. 1995. Prediction of apparent digestibility and voluntary intake of hays fed to sheep: comparison between using fibre components, in vitro digestibility or characteristics of gas production or nylon bag degradation. Anim Sci 61(3):527-538.

Kibont A, Ørskov ER. 1993. The use of degradation characteristics of browse plants to predict intake and digestibility by goats. Anim Sci 57(2):247-251.

Kovacs P, Sudekum KH, Stangassinger M. 1998. Effects of intake of a mixed diet and time post-feeding on amount and fibre composition of ruminal and faecal particles and on digesta passage from the reticulorumen of steers. Anim Feed Sci Technol 71(3):325-340.

Krizsan SJ, Huhtanen P. 2013. Effect of diet composition and incubation time on feed indigestible neutral detergent fiber concentration in dairy cows. J Dairy Sci 96(3):1715-1726.

Krizsan SJ, Mateos-Rivera A, Bertilsson S, Felton A, Anttila A, Ramin M, Vaga M, Gidlund H, Huhtanen P. 2018. An in vitro evaluation of browser and grazer fermentation efficiency and microbiota using European moose spring and summer foods. Ecol Evol 8(8):4183-4196.

Lanyasunya TP, Rong HW, Abdulrazak SA, Mukisira EA. 2006. The potential of the weed, *Commelina diffusa L.*, as a fodder crop for ruminants. S Afr J Anim Sci 36:28-32.

Larsen M, Lund P, Weisbjerg MR, Hvelplund T. 2009. Digestion site of starch from cereals and legumes in lactating dairy cows. Anim Feed Sci Technol 153(3):236-248.

Lechner I, Barboza P, Collins W, Fritz J, Gunther D, Hattendorf B, Clauss M. 2010. Differential passage of fluids and different-sized particles in fistulated oxen, muskoxen, reindeer and moose: Rumen particle size discrimination is independent from contents stratification. Comp Biochem Physiol Part A Mol Integr Physiol 155(2):211-222.

Lechner I, Barboza P, Collins W, Gunther D, Hattendorf B, Hummel J, Clauss M. 2009. No 'bypass' in adult ruminants: Passage of fluid ingesta vs. fluid inserted into the rumen in fistulated muskoxen, reindeer and moose. Comp Biochem Physiol Part A Mol Integr Physiol 154(1):151-156.

Lechner-Doll M, Kaske M, Engelhardt WV. 1991. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. In: Tsuda T, Sasaki Y, Kwashima R, editors. Physiological aspects of digestion and metabolism in ruminants. San Diego, USA: Academic. p. 455-488.

Lindberg JE. 1988. Retention times of small feed particles and of water in the gut of dairy goats fed at different levels of intake. J Anim Physiol Anim Nutr 59(1-5):173-181.

Lindström T, Redbo I. 2000. Effect of feeding duration and rumen fill on behaviour in dairy cows. Appl Anim Behav Sci 70(2):83-97.

Lirette A, Milligan LP. 1989. A quantitative model of reticulo-rumen particle degradation and passage. Br J Nutr 62(2):465-479.

Lock AL, Garnsworthy PC. 2003. Seasonal variation in milk conjugated linoleic acid and Δ 9 desaturase activity in dairy cows. Livest Prod Sci 79(1):47-59.

Lopez S, Hovell FDD, Dijkstra J, France J. 2003. Effects of volatile fatty acid supply on their absorption and on water kinetics in the rumen of sheep sustained by intragastric infusion. J Anim Sci 81(10):2609-2616.

Lui JX, Orskov ER, Chen XB. 1999. Optimisation of steam treatment as a method for upgrading rice straw as feeds. Anim Feed Sci Technol 76(3):345-357.

Lukhele MS, Van Ryssen JBJ. 2003. The chemical composition and potential nutritive value of the foliage of four subtropical tree species in southern Africa for ruminants. S Afr J Anim Sci 33(2):132-141.

Luna RS, Duarte A, Weckerly FW. 2012. Rumen–reticulum characteristics, scaling relationships, and ontogeny in white-tailed deer (*Odocoileus virginianus*). Can J Zool 90(11):1351-1358.

Lunn D. 2004. Nutrient Requirements of the beef cow. Nutrifax nutrition news and information update. Canada: Shur Grain, Nutreco.

Macmillan K, Espinoza OS, Oba M. 2018. Case Study: The effects of photoperiod on feeding behavior of lactating dairy cows in tie-stalls. Prof Anim Sci 34(1):103-107.

Malaisse F, Parent G. 1985. Edible wild vegetable products in the Zambezian woodland area: a nutritional and ecological approach. Ecol Food Nutr 18(1):43-82.

Malebana IM, Nkosi BD, Erlwanger KH, Chivandi E. 2018. A comparison of the proximate, fibre, mineral content, amino acid and the fatty acid profile of Marula (*Sclerocarya birrea caffra*) nut and soyabean (*Glycine max*) meals. J Sci Food Agric 98(4):1381-1387.

Maloiy GMO, Clemens ET, Kamau JMZ. 1982. Aspects of digestion and in vivo rumen fermentation rate in six species of East African wild ruminants. J Zool (Lond) 197:345-353.

Marinas A, García-González R, Fondevila M. 2003. The nutritive value of five pasture species occurring in the summer grazing ranges of the Pyrenees. Anim Sci 76(3):461-469.

Marston TT, Blasi DA, Brazle FK, Kuhl GL. Beef cow nutrition guide. USA: Kansas State University. Cooperative Extension Service; 1998.

Mawuenyegah PO, Shem MN, Warly L, Fujihara T. 1997. Effect of supplementary feeding with protein and energy on digestion and rumination behaviour of sheep consuming straw diets. J Agric Sci 129(4):479-484.

McBride BW, Milligan LP, Turner BV. 1983. Short note: Endoscopic observation of reticulo-omasal orifice of cattle. J Agric Sci 101(3):749-751.

McCollum F, Galyean M. 1985. Influence of cottonseed meal supplementation on voluntary intake, rumen fermentation and rate of passage of prairie hay in beef steers. J Agric Sci 60(2):570-577.

McDonald I. 1981. A revised model for the estimation of protein degradability in the rumen. J Agri Sci 96(1): 251-252.

McDonald P, Edwards RA, Greenhalgh JFD, Morgan CA, Sinclair LA, Wilkinson RG. 2011. Animal nutrition. Seventh Edition, Pearson Education Limited, Edinburgh Gate, Harlow, Essex CM20 2JE, England, 692 p.

McDonald RC, Manley TR, Barry TN, Forss DA, Sinclair AG. 1981. Nutritional evaluation of kale (*Brassica oleracea*) diets: 3. Changes in plant composition induced by soil fertility practices, with special reference to SMCO and glucosinolate concentrations. J Agric Sci 97(1):13-23.

Mdziniso PM, Dlamini AM, Khumalo GZ, Mupangwa JF. 2016. Nutritional evaluation of marula (*Sclerocarya birrea*) seed cake as a protein supplement in dairy meal. J Appl Life Sci 4(3):1-11.

Merchen N, Firkins J, Berger L. 1986. Effect of intake and forage level on ruminal turnover rates, bacterial protein synthesis and duodenal amino acid flows in sheep. J Anim Sci 62(1):216-225.

Mertens D. Rate and extent of digestion. In: Dijkstra L, Forbes JM, France J, editors. Quantitative aspects of ruminant digestion and metabolism. Wallingford, UK: CAB International; 2005. p. 13-47.

Mertens DR. 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants [PhD thesis]. New York, USA: Cornell University.

Mesfin R, Ledin I. 2004. Comparison of feeding urea-treated teff and barley straw-based diets with hay-based diet to crossbred dairy cows on feed intake, milk yield, milk composition and economic benefits. Livest Res Rural Dev 16:Article #104.

Meyer HHD, Rowell A, Streich WJ, Stoffel B, Hofmann RR. 1998. Accumulation of polyunsaturated fatty acids by concentrate selecting ruminants. Comp Biochem Physiol Part A Mol Integr Physiol 120(2):263-268.

Miaron JO, Christopherson RJ. 1992. Effect of prolonged thermal exposure on heat production, reticular motility, rumen-fluid and-particulate passage-rate constants, and apparent digestibility in steers. Can J Anim Sci 72(4):809-819.

Midasch A, Kaske M, Rehage J. Sonographic investigation of reticular contractions in sheep, cows and goats. In: Giesecke D, editor. Society of Nutrition Physiology; Frankfurt, Germany. Germany: DLG-Verlag; 1994.

Minervino AH, Kaminishikawahara CM, Soares FB, Araujo CA, Reis LF, Rodrigues FA, Vechiato TD, Ferreira RN, Barrêto-Júnior RA, Mori CS, Ortolani EL. 2014. Behaviour of confined sheep fed with different concentrate sources. Arq Bras Med Vet Zootec 66:1163-1170.

Mlambo V, Dlamini BJ, Nkambule MT, Mhazo N, Sikosana JLN. 2011a. Nutritional evaluation of Marula (*Sclerocarya birrea*) seed cake as a protein supplement for goats fed grass hay. Trop Agric 41(3216):010035-09.

Mlambo VDB, Ngwenya MD, Mhazo N, Beyene ST, Sikosana JL. 2011b. In sacco and in vivo evaluation of Marula (*Sclerocarya birrea*) seed cake as a protein source in commercial cattle fattening diets. Livest Res Rural Dev 23(5).

Moleele NM. 1998. Encroacher woody plant browse as feed for cattle. Cattle diet composition for three seasons at Olifants Drift, South-Eastern Botswana. J Arid Environ 40(3):255-268.

Moore J, Poore M, Swingle R. 1990. Influence of roughage source on kinetics of digestion and passage and on calculated extents of ruminal digestion in beef steers fed 65% concentrate diets. J Anim Sci 68(10):3412-3420.

Morand-Fehr P, Owen G, Giger-Reverdin S. Feeding behaviour of goats at the trough. In: Morand-Fehr P, editors. Goat Nutrition. Wageningen, Netherlands: Centre for Agricultural Publishing and Documentation, Pudoc Press; 1991. p. 3-12.

Moyo M, Adebayo RA, Nsahlai IV. 2018. Effect of roughage quality, period of day and time lapse after meal termination on rumen digesta load in goats and sheep. Asian-Australas J Anim Sci 31:1183-1196.

Moyo M, Gueguim Kana EB, Nsahlai IV. 2017. Modelling of digesta passage rates in grazing and browsing domestic and wild ruminant herbivores. S Afr J Anim Sci 47(3):362-377.

Muchadeyi R. 1998. Herbage yields, chemical composition and in-vitro digestibility of dual-purpose legumes intercropped with maize for dry season fodder supplementation. M.Sc. Thesis. University of Zimbabwe, Harare.

Muhammad N, Omogbai IJ, Maigandi SA, Abubakar IA, Shamaki SB. 2016. Quantification of *Sclerocarya birrea* (Marula) fruits as feed supplement for ruminants in dry sub-humid zone of Nigeria. World Sci News 46:88-99.

Müller DW, Codron D, Meloro C, Munn A, Schwarm A, Hummel J, Clauss M. 2013. Assessing the Jarman–Bell principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. Comp Biochem Physiol Part A Mol Integr Physiol 164(1):129-140.

Mutimura M, Ebong C, Rao IM, Nsahlai IV. 2015. Nutritional values of available ruminant feed resources in smallholder dairy farms in Rwanda. Trop Anim Health Prod 47:1131-1137.

Mutimura M, Everson TM. 2011. Assessment of livestock feed resource-use patterns in low rainfall and aluminium toxicity prone areas of Rwanda. Afr J Agric Res 6(15):3461-3469.

Mwamba CK. 2006. Monkey orange: strychnos cocculoides (No. 8). Crops for the Future.

Navaratne HVRG, Ibrahim MNM. 1988. Degradation characteristics of some tropical feeds in the rumen. Asian-Australas J Anim Sci 1(1):21-25.

Nefzaoui A, Salem HB. 2002. Forage fodder and animal nutrition. In: Cacti: Biology and Uses, Nobel, P.S. (ed). University of California Press, Berkeley, CA, USA, pp. 190-210.

Newman JA, Parsons AJ, Thornley JHM, Penning PD, Krebs JR. 1995. Optimal diet selection by a general herbivore. Funct Ecol 9:255-268.

Nicol AM, Barry TN. 1980. The feeding of forage crops. In Supplementary Feeding (ed. K. R. Drew and P. F. Fennessy), New Zealand Society of Animal Production Occasional Publication No. 7, pp. 69-102. C/- Invermay Research Centre, Mosgiel New Zealand.

Nicory IM, de Carvalho GG, Ribeiro OL, Silva RR, Tosto MS, Costa-Lopes LS, Souza FN, de Oliveira Nascimento C. 2015. Ingestive behavior of lambs fed diets containing castor seed meal. Trop Anim Health Prod 47(5):939-944.

Njarui DMG, Gatheru M, Wambua JM, Nguluu SN, Mwangi DM, Keya GA. 2011. Feeding management for dairy cattle in smallholder farming systems of semi-arid tropical Kenya. Livest Res Rural Dev 23:111.

Nsahlai IV, Apaloo J. 2007. On the suitability of the Illius and Gordon's model for simulating the intake and digestibility of roughage diets by ruminants. S Afr J Anim Sci 37(4):275-289.

Nsahlai IV, Bryant MJ, Umunna NN. 1999. Utilisation of barley straw by steers: Effects of replacing urea with protein, source of protein and quantity of rumen degradable nitrogen on straw degradation, liquid and particulate passage rates and intake. J Appl Anim Res 16(2):129-146.

Nsahlai IV, Umunna NN, Osuji PO. 1996. An empirical model for predicting voluntary intake of forage-legume-supplemented roughages by cattle. In: All Africa conference on animal agriculture 1996. 1996 April 1-4; Pretoria, South Africa: South African Society of Animal Science; 1996. p 10.4.

Nsahlai IV, Umunna NN. 1996. Comparison between reconstituted sheep faeces and rumen fluid inocula and between in vitro and in sacco digestibility methods as predictors of intake and in vivo digestibility. J Agri Sci 126(2):235-248.

Nygren KFA, Lechner-Doll M, Hofmann RR. 2001. Influence of papillae on postruminal regulation of ingesta passage in moose (*Alces alces*). J Zool 254(3):375-380.

Okafor JC. 2004. Myrianthus arboreus. P. Beauv. In: PROTA 2: Vegetables/Legumes, Grubben GJH, Denton OA (eds). PROTA Foundation, Wageningen, Netherlands.

Okeke G, Buchanan-Smith J, Grovum W. 1983. Effect of buffers on ruminal rate of passage and degradation of soybean meal in steers. J Anim Sci 56(6):1393-1399.

Okine EK, Mathison GW. 1991. Reticular contraction attributes and passage of digesta from the ruminoreticulum in cattle fed roughage diets. J Anim Sci 69(5):2177-2186.

Orskov ER, DeB Hovell FD, Mould F. 1980. The use of the nylon bag technique for the evaluation of feedstuffs. Trop Anim Prod 5:195-213.

Ørskov ER, McDonald I. 1979. The estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. J Agri Sci 92(2):499-503.

Ørskov ER., Reid GW, Kay M. 1988. Prediction of intake by cattle from degradation characteristics of roughages. Anim Sci 46(1):29-34.

Orwa C, Mutua A, Kindt R, Jamnadass R, Simons A. 2009. Agroforestree database: a tree species reference and selection guide version 4.0. World Agroforestry Centre ICRAF, Nairobi, KE.

Oshita T, Sudo K, Nonaka K, Kume S, Ochiai K. 2008. The effect of feed regimen on chewing time, digesta passage rate and particle size distribution in Holstein non-lactating cows fed pasture ad libitum. Livest Sci 113:243-250.

Osuji PO, Fernández-Rivera S, Odenyo A. 1995. Improving fibre utilisation and protein supply in animals fed poor quality roughages. In: Wallace RJ, Lahlou-Kassi A, editors. Rumen ecology research planning. Proceedings of a Workshop Held at International Livestock Research Institute. 1995 March 13-18; Addis Ababa, Ethiopia: International Livestock Research Institute. p. 9-30.

Owens FN, Goetsch AL. 1986. Digesta passage and microbial protein synthesis. In: Milligan LP, Grovum WL, Dobson A, editors. 6th International Symposium on Ruminant Physiology; 10-14 September 1984; Banff, Canada. New Jersey, USA: Prentice-Hall; 1986. p. 196-223.

Owens FN, Goetsch AL. Ruminal fermentation. In: Church DC, editor. The Ruminant animal: Digestive Physiology and Nutrition. New Jersey, USA: Prentice-Hall; 1988. p. 145.

Panjaitan T, Quigley SP, McLennan SR, Swain T, Poppi DP. 2010. Intake, retention time in the rumen and microbial protein production of Bos indicus steers consuming grasses of varying crude protein content. Anim Prod Sci 50(6):444-448.

Parra R. 1978. Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG, editor. The ecology of arboreal folivores. Washington DC, USA: Smithsonian Institute Press. p. 209-229.

Parthasarathy D, Phillipson AT. 1953. The movement of potassium, sodium, chloride and water across the rumen epithelium of sheep. J Physiol 121(3):452-469.

Pearson RA, Archibald RF, Muirhead RH. 2006. A comparison of the effect of forage type and level of feeding on the digestibility and gastrointestinal mean retention time of dry forages given to cattle, sheep, ponies and donkeys. Br J Nutr 95(1):88-98.

Pearson RA, Smith DG. 1994. The effects of work on food intake and ingestive behaviour of draught cattle and buffalo given barley straw. Anim Sci 58(3):339-346.

Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions, European Geosciences Union 4, 439-473.

Penning PD, Newman JA, Parsons AJ, Harvey A, Orr RJ. 1997. Diet preferences of adult sheep and goats grazing ryegrass and white clover. Small Ruminant Res 24(3):175-84.

Penning PD, Parsons AJ, Orr RJ, Harvey A, Champion RA. 1995. Intake and behaviour responses by sheep, in different physiological states, when grazing monocultures of grass or white clover. Appl Anim Behav Sci 45(1-2):63-78.

Penning PD, Parsons AJ, Orr RJ, Hooper E. 1994. Intake and behaviour responses by sheep to changes in sward characteristics under rotational grazing. Grass Forage Sci 49:476–486.

Penning PD, Parsons AJ, Newman JA, Orr RJ, Harvey A. 1993. The effects of group size on grazing time in sheep. Appl Anim Behav Sci 37:101-109.

Pent GJ, Greiner SP, Munsell JF, Tracy BF, Fike JH. 2020. Lamb performance in hardwood silvopastures, II: animal behavior in summer1. Transl Anim Sci 4(1):txz177.

Pepeta BN. 2019. Use of inert markers to predict diet composition, forage intake, digestibility and passage rate in sheep (MSc dissertation). University of KwaZulu-Natal.

Pereira TC, Pereira ML, Almeida PJ, Pereira CA, Santos AB, Santos ED. 2013. Mesquite pod meal in diets for Santa Inês sheep: ingestive behavior. Acta Sci Anim Sci 35(2):201-206.

Pérez-Barbería FJ, Gordon IJ. 2001. Relationships between oral morphology and feeding style in the Ungulata: a phylogenetically controlled evaluation. Proc R Soc Lond B Biol Sci 268(1471):1023-1032.

Pfister JA, Malechek JC. 1986. Dietary selection by goats and sheep in a deciduous woodland of North-Eastern Brazil. J Range Manag 39:24-28.

Pfister JA, Malechek JC. 1986. The voluntary forage intake and nutrition of goats and sheep in the semi-arid tropics of North-Eastern Brazil. J Anim Sci 63(4):1078-1086.

Phillips CJ, Rind MI. 2001. The effects of frequency of feeding a total mixed ration on the production and behavior of dairy cows. J Dairy Sci 84(9):1979-1987.

Pinho BD, Ramos AF, Lourenço Júnior JD, Faturi C, Silva A, Nahúm BD, Manno MC, Lima KD, Sousa LF, da Silva JA, Araújo GS. 2016. Feeding behavior of sheep fed diets with Elaeis guineensis palm kernel meal. Embrapa Amazônia Oriental-Article in an indexed journal ALICE; Semina: Ciências Agrárias, Londrina, v. 37, n. 4, suplemento 1, p. 2513-2520

Polley HW, Briske DD, Morgan JA, Wolter K, Bailey DW, Brown JR. 2013. Climate change and North American rangelands: trends, projections, and implications. Rangel Ecol Manag 66(5):493-511.

Poore M, Moore J, Swingle R. 1990. Differential passage rates and digestion of neutral detergent fibre from grain and forages in 30, 60 and 90% concentrate diets fed to steers. J Anim Sci 68(9):2965-2973.

Poppi DP, Hendricksen RE, Minson DJ. 1985. The relative resistance to escape of leaf and stem particles from the rumen of cattle and sheep. J Agric Sci 105(1):9-14.

Poppi DP, Minson DJ, Ternouth JH. 1981. Studies of cattle and sheep eating leaf and stem fractions of grass. II. Factors controlling retention of feed in the reticulo-rumen. Aust J Agric Res 32:109-121.

Poppi DP, Norton BW, Minson DJ, Hendricksen RE. 1980. The validity of the critical size theory for particles leaving the rumen. J Agric Sci 94(2):275-280.

Prache S. 1997. Intake rate, intake per bite and time per bite of lactating ewes on vegetative and reproductive swards. Appl Anim Behav Sci 52:53-64.

Prins RA, Geelen MJH. 1971. Rumen characteristics of red deer, fallow deer, and roe deer. J Wildl Manag 673-680.

Purser DB, Moir RJ. 1966. Rumen volume as a factor involved in individual sheep differences. J Anim Sci 25(2):509-515.

Rahal, A., Singh, A. and Singh, M., 1997. Effect of urea treatment and diet composition on, and prediction of nutritive value of rice straw of different cultivars. Animal Feed Science and Technology 68, 165-182.

Ramírez RG, Neira-Morales RR, Ledezma-Torres RA, Garibaldi-González CA. 2000. Ruminal digestion characteristics and effective degradability of cell wall of browse species from northeastern Mexico. Small Ruminant Res 36:49-55.

Ramzinski DM, Weckerly FW. 2007. Scaling relationship between body weight and fermentation gut capacity in axis deer. J Mammal 88(2):415-420.

Raynal-Ljutovac K, Lagriffoul G, Paccard P, Guillet I, Chilliard Y. 2008. Composition of goat and sheep milk products: An update. Small Ruminant Res 79(1):57-72.

Reid A, Titchen D. 1984. Effects of vasoactive intestinal polypeptide on the reticulo-omasal orifice in lambs. Can J Anim Sci 64(5):91-92.

Rencoret J, Gutiérrez A, Nieto L, Jimenez-Barbero J, Faulds CB, Kim H, Ralph J, Martínez ÁT, José C. 2011. Lignin composition and structure in young versus adult Eucalyptus globulus plants. Plant Physiol 155(2):667-682.

Renecker LA, Hudson RJ. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. J Wildl Manage 53(2):296-302.

Riaz M Q, Südekum KH, Clauss M, Jayanegara A. 2014. Voluntary feed intake and digestibility of four domestic ruminant species as influenced by dietary constituents: A meta-analysis. Livest Sci 162:76-85.

Rinne M, Huhtanen P, Jaakkola S. 2002. Digestive processes of dairy cows fed silage harvested at four stages of grass maturity. J Anim Sci 80(7):1986-1998.

Rodgers GM, Downing B, Lesley J, Morrell LJ. 2015. Prey body size mediates the predation risk associated with being “odd”. Behav Ecol 26(1):242–246.

Rojas-Downing MM, Nejadhashemi AP, Harrigan T, Woznicki SA. 2017. Climate change and livestock: Impacts, adaptation, and mitigation. Clim Risk Manag 16:145-163.

Rook AJ, Huckle CA. 1997. Activity bout criteria for grazing dairy cows. Appl Anim Behav Sci 54: 89–96.

Rowell A, Dyer J, Hofmann RR, Lechner-Doll M, Meyer HHD, Shirazi-Beechey SP, Wood IS. 1996. The expression of intestinal sodium-glucose cotransporter in cervids. Z. Saeugetierkd 62(2):204-208.

Rowell A, Dyer J, Hofmann RR, Lechner-Doll M, Meyer HHD, Shirazi-Beechey SP, Streich WJ. 1999. Abundance of intestinal sodium-glucose cotransporter (SGLT1) in roe deer (*Capreolus capreolus*). J Anim Physiol Anim Nutr 82:25-32.

Rust JM, Rust T. 2013. Climate change and livestock production: A review with emphasis on Africa. S Afr J Anim Sci 43(3):255-267.

Rutagwenda T, Lechner-Doll M, Schwart HJ, Schultka W, Von Engelhardt. 1990. Dietary preference and degradability of forage on a semi-arid thornbush savanna by indigenous ruminants, camels, and donkeys. Anim Feed Sci Technol 31(3-4):179-192.

Rutter SM, Orr RJ, Penning PD, Yarrow NH, Champion RA. 2002. Ingestive behaviour of heifers grazing monocultures of ryegrass or white clover. Appl Anim Behav Sci 76:1-9.

Safari J, Mushi DE, Kifaro GC, Mtenga LA, Eik LO. 2011. Seasonal variation in chemical composition of native forages, grazing behaviour, and some blood metabolites of Small East African goats in a semi-arid area of Tanzania. Anim Feed Sci Technol 164(1-2):62-70.

Saka JK, Msonthi JD. 1994. Nutritional value of edible fruits of indigenous wild trees in Malawi. For Ecol Manag 64(2-3):245-248.

Salem HB, Smith T. 2008. Feeding strategies to increase small ruminant production in dry environments. Small Ruminant Res 77(2):174-194.

Sanz-Sáez Á, Erice G, Aguirreolea J, Muñoz F, Sánchez-Díaz M, Irigoyen JJ. 2012. Alfalfa forage digestibility, quality and yield under future climate change scenarios vary with Sinorhizobium meliloti strain. J Plant Physiol 169(8):782-788.

Sath K, Borin K, Preston TR. 2008. Effect of levels of sun-dried cassava foliage on growth performance of cattle fed rice straw. Livest Res Rural Dev 20.

Sauvant D, Baumont R, Faverdin P. 1996. Development of a mechanistic model of intake and chewing activities of sheep. J Anim Sci 74:2785-2802.

Sauvant D, Schmidely P, Daudin JJ, St-Pierre NR. 2008. Meta-analyses of experimental data in animal nutrition. Animal 2(8):1203-1214.

Scheel D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. Anim Behav 46:695-704

Schlecht E, Richter H, Fernandez-Rivera S, Becker K. 2007. Gastrointestinal passage of Sahelian roughages in cattle, sheep and goats, and implications for livestock-mediated nutrient transfers. Anim Feed Sci Technol 137(1):93-114.

Sebata A, Ndlovu LR. 2010. Effect of leaf size, thorn density and leaf accessibility on instantaneous intake rates of five woody species browsed by Matebele goats (*Capra hircus L*) in a semi-arid savanna, Zimbabwe. J Arid Environ 74(10):1281-1286.

Sebata A, Ndlovu LR. 2012. Effect of shoot morphology on browse selection by free ranging goats in a semi-arid savanna. Livest Sci 144:96-102.

Sekine J, Oura R, Miyazaki H, Okamoto M, Asahida Y. 1991. Effect of time after feeding on distribution of digesta in the gastro-intestinal tracts of sheep. Asian-Australas J Anim Sci 4:99-102.

Seman DH, Stuedemann, JA, Anderson JE. 1997. Spectral analysis of bovine grazing behaviour on Neotyphodium coenophialum infested tall fescue. Appl Anim Behav Sci 54:73–87.

Seo S, Lanzas C, Tedeschi LO, Fox DG. 2007. Development of a mechanistic model to represent the dynamics of liquid flow out of the rumen and to predict the rate of passage of liquid in dairy cattle. J Dairy Sci 90:840-855.

Seo S, Lanzas C, Tedeschi LO, Pell AN, Fox DG. 2009. Development of a mechanistic model to represent the dynamics of particle flow out of the rumen and to predict rate of passage of forage particles in dairy cattle. J Dairy Sci 92:3981-4000.

Seo S, Tedeschi LO, Lanzas C, Schwab C, Fox DG. 2006. Development and evaluation of empirical equations to predict feed passage rate in cattle. Anim Feed Sci Technol 128:67-83.

Seo S, Tedeschi LO, Schwab CG, Garthwaite BD, Fox DG. 2006. Evaluation of the passage rate equations in the dairy NRC (2001) model. J Dairy Sci 89(6):2327-2342.

Shem MN, Ørskov ER, Kimambo AE. 1995. Prediction of voluntary dry-matter intake, digestible dry-matter intake and growth rate of cattle from the degradation characteristics of tropical foods. Anim Sci 60(1):65-74.

Shen HS, Sundstøl F, Ni DB. 1998. Studies on untreated and urea-treated rice straw from three cultivation seasons: 2. Evaluation of straw quality through in vitro gas production and in sacco degradation measurements. Anim Feed Sci Technol 74:193-212.

Shipley LA, Gross JE, Spalinger DE, Thompson Hobbs N, Wunder BA. 1994. The scaling of intake rate in mammalian herbivores. Am Nat 143:1055-1082.

Siaw DEKA, Osuji PO, Nsahlai IV. 1993. Evaluation of multipurpose tree germplasm: the use of gas production and rumen degradation characteristics. J Agric Sci 120:319-330.

Sibbald AM, Milne JA. 1993. Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (Cervus elaphus). J Agri Sci 120(1):99-102.

Silanikove N, Gilboa N, Nitsan Z. 2001. Effect of polyethylene glycol on rumen volume and retention time of liquid and particulate matter along the digestive tract in goats fed tannin-rich carob leaves. Small Ruminant Res 40(1):95-99.

Silanikove N, Tagari H, Shkolnik A. 1993. Comparison of rate of passage, fermentation rate and efficiency of digestion of high fibre diet in desert Bedouin goats compared to Swiss Saanen goats. Small Ruminant Res 12(1):45-60.

Skogland T. 1984. Wild reindeer foraging-niche organisation. Ecography 7(4):345-379.

Smith LW, Goering HK, Gordon CH. 1972. Relationships of forage composition with rates of cell wall digestion and indigestibility of cell walls. J Dairy Sci 55(8):1140-1147.

Sowing New Seeds Project. 2018. Growing African Kale (leaflet). Garden Organic (Henry Doubleday Research Association), Coventry, Warwickshire, United Kingdom. https://www.gardenorganic.org.uk/sites/www.gardenorganic.org.uk/files/sns/factsheets/FactsheetAfricanKale.pdf [Accessed 2018/06/02]

St-Pierre NR. 2001. Invited review: Integrating quantitative findings from multiple studies using mixed model methodology. J Dairy Sci 84(4):741-755.

St-Pierre NR. 2003. Reassessment of biases in predicted nitrogen flows to the duodenum by NRC 2001. J Dairy Sci 86(1):344-350.

Suksombat W, Junpanichcharoen P. 2005. Feeding of sugar cane silage to dairy cattle during the dry season. Asian-Australas J Anim Sci 18(8):1125-1129.

Sutherland TM. Particle separation in the forestomach of sheep. In: Dobson A, Dobson MJ, editors. Aspects of digestive physiology in ruminants. Ithaca, New Jersey, USA: Cornell University Press; 1988. p. 43-73.

Tang SX, Li FW, Gan J, Wang M, Zhou CS, Sun ZH, Han XF, Tan ZL. 2011. Effects of sown season and maturity stage on in vitro fermentation and in sacco degradation characteristics of new variety maize stover. Asian-Australas J Anim Sci 24:781-790.

Taweel HZ, Tas BM, Dijkstra J, Tamminga S. 2004. Intake regulation and grazing behaviour of dairy cows under continuous stocking. J Dairy Sci 87:3417-3427.

Yansari AT. 2017. Ruminal Kinetics of Nutrients Degradation, Hydration, and Functional Specific Gravity of Three Types of Beet Pulp. Iran J Appl Anim Sci 7:17-26.

Thomson BC, Cruickschank GJ, Poppi DP, Sykes AR. 1985. Diurnal patterns of rumen fill in grazing sheep. In: New Zealand Society of Animal Production; New Zealand. New Zealand: New Zealand Society of Animal Production. p. 117-120.

Tolera A, Sundstøl F. 2001. Prediction of feed intake, digestibility and growth rate of sheep fed basal diets of maize stover supplemented with Desmodium intortum hay from dry matter degradability of the diets. Livest Prod Sci 68(1):13-23.

Toole G, Toole S. 2006. New Understanding Biology for Advanced Level. 4th ed. UK: Nelson Thornes; 698 p.

Tovar-Gomez MR, Emile JC, Michalet-Doreau B, Barriere Y. 1997. In situ degradation kinetics of maize hybrid stalks. Anim Feed Sci Technol 2:77-88.

Trach NX, Mo M, Dan CX. 2001. Effects of treatment of rice straw with lime and/or urea on responses of growing cattle. Livest Res Rural Dev 13:Article #47.

Tschuor A, Clauss M. 2008. Investigations on the stratification of forestomach contents in ruminants: An ultrasonographic approach. Eur J Wildl Res 54(4):627-633.

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

Tulloh NH, Hughes JW. 1965. Physical studies of the alimentary tract of grazing cattle. II. Techniques of estimating the capacity of the reticulo-rumen. New Zeal J Agric Res 8(4):1070-1078.

Ulyatt MJ, Dellow DW, John A, Reid CSW, Waghorn GC. 1986. Contribution of chewing during eating and rumination to the clearance of digesta from the reticulo-rumen. In: Control of digestion and metabolism in the ruminant. Englewood Cliffs, New Jersey, USA: Prentice-Hall. p. 498-515.

Umunna NN, Nsahlai IV, Osuji PO. 1995. Degradability of forage protein supplements and their effects on the kinetics of digestion and passage. Small Ruminant Res 17(2):145-152.

Urton GM, Von Keyserlingk MA, Weary DM. 2005. Feeding behavior identifies dairy cows at risk for metritis. J Dairy Sci 88(8):2843-2849.

Van Soest PJ, Wine RH. 1968. Determination of lignin and cellulose in acid-detergent fiber with permanganate. J Assoc Off Anal Chem 51:780-785.

Van Soest PJ. 1994. Nutritional ecology of the ruminant., 2nd edn (Comstock Publishing Associates/Cornell University Press: Ithaca, NY, USA).

Van Soest PJ. 1996. Allometry and ecology of feeding behaviour and digestive capacity in herbivores: a review. Zoo Biol 15(5):455-479.

Van Soest PJ. 2018. Nutritional ecology of the ruminant. Cornell university press.

Van Vuuren AM, Tamminga S, Ketelaar RS. 1991. In sacco degradation of organic matter and crude protein of fresh grass (*Lolium perenne*) in the rumen of grazing dairy cows. J Agric Sci 116:429-436.

Van Weyenburg S, Sales J, Janssens G. 2006. Passage rate of digesta through the equine gastrointestinal tract: A review. Livest Sci 99(1):3-12.

Van Wieren SE. 1996. Do large herbivores select a diet that maximises short-term energy intake rate? For Ecol Manag 88(1-2):149-156.

Varga GA, Harpster HW. Gut size and rate of passage. In: Intake by feedlot cattle; Oklahoma, USA. Stillwater, USA: Oklahoma State University; 1995. p. 85-96.

Varga GA, Prigge E. 1982. Influence of forage species and level of intake on ruminal turnover rates. J Anim Sci 55(6):1498-1504.

Vásquez CG, Olvera L, Siqueiros Y, Kuri ML, Navarro VA, Rovelo AE, Shimada A. 2004. Nursing and feeding behaviour of confined red deer (Cervus elaphus scoticus) in the Mexican highlands. N Z J Agric Res 47(1):1-9.

Veldhuis MP, Hofmeester TR, Balme G, Druce DJ, Pitman RT, Cromsigt JP. 2020. Predation risk constrains herbivores' adaptive capacity to warming. Nat Ecol Evol 1:1-6.

Von Engelhardt W, Haarmeyer P, Kaske M, Lechner-Doll M. 2006. Chewing activities and oesophageal motility during feed intake, rumination and eructation in camels. J Comp Physiol B 176:117-124.

Wanapat M, Khampa S. 2007. Effect of levels of supplementation of concentrate containing high levels of cassava chip on rumen ecology, microbial-N supply and digestibility of nutrients in beef cattle. Asian-Aust J Anim Sci 20(1):75-81.

Warly L, Fariani A, Mawuenyegah OP, Matsui T, Fujihara T, Harumoto T. 1994. Studies on the utilisation of rice straw by sheep. IV. Effect of soybean meal and barley supplementation on eating and rumination behaviour. Asian-Australas J Anim Sci 7:273-277.

Warren W, Martz F, Asay K, Hilderbrand E, Payne C, Vogt J. 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchardgrass hay in 18°C and 32°C ambient temperatures. J Anim Sci 39(1):93-96.

Waybright TR, Varga GA. 1991. Effects of water filled bags in the rumen of wethers on ruminal digesta kinetics and total tract nutrient digestibility. J Anim Sci 69(5):2157-2167.

Weckerly FW, Bleich VC, Barbara Chetkiewicz CL, Ricca MA. 2003. Body weight and rumen-reticulum capacity in tule elk and mule deer. J Mammal 84(2):659-664.

Weckerly FW. 2010. Allometric scaling of rumen–reticulum capacity in white-tailed deer. J Zool (Lond) 280(1):41-48.

Welch JG. 1982. Rumination, particle size and passage from the rumen. J Anim Sci 54:885-894.

Welch JG. 1986. Physical parameters of fibre affecting passage from the rumen. J Dairy Sci 69(10):2750-2754.

Wenninger PS, Shipley LA. 2000. Harvesting, rumination, digestion, and passage of fruit and leaf diets by a small ruminant, the blue duiker. Oecologia 123(4):466-474.

Weyreter H, Engelhardt WV. 1984. Adaptation of Heidschnucken, Merino and Blackhead sheep to a fibrous roughage of poor quality. Can J Anim Sci 64(5):152-153.

Williams YJ, Doyle PT, Egan AR. 2014. Diurnal variation in rumen fill of dairy cows grazing Persian clover at different pasture allowances. Anim Prod Sci 59(9):1388-1393.

Williams YJ, Walker GP, Wales WJ, Doyle PT. 2000. The grazing behaviour of cows grazing Persian clover or perennial ryegrass pastures in spring. Asian–Australas J Anim Sci 13:509-512.

Wolfger B, Schwartzkopf-Genswein KS, Barkema HW, Pajor EA, Levy M, Orsel K. 2015. Feeding behavior as an early predictor of bovine respiratory disease in North American feedlot systems. J Anim Sci 93(1):377-385.

Woolnough AP, du Toit JT. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. Oecologia 129:585–590.

Wyburn RS. The mixing and propulsion of the stomach contents of ruminants. In: Ruckebusch Y, Thivend P, editors. Digestive Physiology and Metabolism in Ruminants. Westport, Connecticut, USA: AVI Publishing Company; 1980. p. 35-51.

Xiao X, Zhang T, Peter Angerer J, Hou F. 2020. Grazing seasons and stocking rates affects the relationship between herbage traits of alpine meadow and grazing behaviors of Tibetan sheep in the Qinghai–Tibetan plateau. Animals 10(3):488.

Yayota M, Karashima J, Kouketsu T, Nakano M, Ohtani S. 2009. Seasonal changes in the digestion and passage rates of fresh dwarf bamboo (*Pleioblastus argenteostriatus f. glaber*) in sheep. Anim Feed Sci Technol 149:89-101.

Zali SM, Teimouri Yansari A, Jafari Sayyadi A. 2015. Effect of particle size and fragility of corn silage and alfalfa hay on intake, digestibility, performance, and chewing activity of fattening male lambs. J Vet Scie Res Review 1:47-57.

Zhao YL, Yan SM, He ZX, Anele UY, Swift ML, McAllister TA, Yang WZ. 2015. Effects of volume weight, processing method and processing index of barley grain on in situ digestibility of dry matter and starch in beef heifers. Anim Feed Sci Technol 199:93-103.

Appendices

Appendix 1: Studies used in meta-analysis and modelling of feeding behaviour

Abijaoudé JA, Morand-Fehr P, Tessier J, Schmidely P, Sauvant D. 2000. Diet effect on the daily feeding behaviour, frequency and characteristics of meals in dairy goats. Livest Prod Sci 64(1):29-37.

Acatincăi S, Gavojdian D, Cziszter LT, Tripon I, Alungei A, Popian C. 2009. Study regarding rumination behaviour in multiparous Romanian Black and White cows during summer season. Scient Papers Anim Sci Biotech 42(2):191-194.

Acatincăi S, Gavojdian D, Stanciu G, Cziszter LT, Tripon I, Baul S. 2010. Study regarding rumination behavior in cattle–position adopted by cows during rumination process. Scient Papers Anim Sci Biotech 43(2):199-202.

Aitchison EM, Gill M, Dhanoa MS, Osbourn DF. 1986. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. Br J Nutr 56(2):463-476.

Almeida VV, Silva RR, Visintin AC, Queiroz AC, Silva FF, Sampaio CB, Lisboa MD, Mendes FB, Lins TO. 2014. Ingestive behavior of grazing heifers receiving crude glycerin supplementation during the dry-rainy season transition. Chil J Agric Res 74(3):286-292.

Animut G, Goetsch AL, Aiken GE, Puchala R, Detweiler G, Krehbiel CR, Merkel RC, Sahlu T, Dawson LJ, Johnson ZB, Gipson TA. 2005. Performance and forage selectivity of sheep and goats co-grazing grass/forb pastures at three stocking rates. Small Ruminant Res 59(2-3):203-215.

Animut G, Goetsch AL, Aiken GE, Puchala R, Detweiler G, Krehbiel CR, Merkel RC, Sahlu T, Dawson LJ. 2007. Effects of pasture inclusion of mimosa on growth by sheep and goats co-grazing grass/forb pastures. J Appl Anim Res 31(1):1-10.

Baumont R, Jailler M, Dulphy JP. 1997. Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay. Ann Zootech 46 (3):231-244.

Bines JA, Davey AW. 1970. Voluntary intake, digestion, rate of passage, amount of material in the alimentary tract and behaviour in cows receiving complete diets containing straw and concentrates in different proportions. Br J Nutr 24(4):1013-1028.

Bøe KE, Andersen IL. 2010. Competition, activity budget and feed intake of ewes when reducing the feeding space. Appl Anim Behav Sci 125(3-4):109-114.

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

Bovolenta S, Saccà E, Corti M, Villa D. 2005. Effect of supplement level on herbage intake and feeding behaviour of Italian Brown cows grazing on Alpine pasture. Ital J Anim Sci 4(sup2):169-171.

Brandão RK, de Carvalho GG, Silva RR, Dias DL, Mendes FB, Lins TO, Abreu Filho G, de Souza SO, Barroso DS, de Almeida Rufino LM, Tosto MS. 2016. Comparison of protein and energy supplementation to mineral supplementation on feeding behavior of grazing cattle during the rainy to the dry season transition. SpringerPlus 5(1):933.

Brumby PJ. 1959. The grazing behaviour of dairy cattle in relation to milk production, live weight, and pasture intake. New Zeal J Agri Res 2(4):797-807.

Cândido EP, Gonzaga Neto S, Bezerra LR, Saraiva EP, Pimenta Filho EC, Araujo GG. 2012. Ingestive behavior of Guzerat and Sindhi heifers under the effects of feed restriction. Acta Sci Anim Sci 34(3):297-303.

Celaya R, Oliván M, Ferreira LM, Martínez A, García U, Osoro K. 2007. Comparison of grazing behaviour, dietary overlap and performance in non-lactating domestic ruminants grazing on marginal heathland areas. Livest Sci 106(2-3):271-281.

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

Chiofalo V, Dulphy JP, Baumont R, Jailler M, Ballet JM. 1992. Influence of the method of forage conservation on feeding behaviour, intake and characteristics of reticulo-rumen content, in sheep fed ad libitum. Reprod Nutr Dev 32(4):377-392.

Cirne LG, Baroni MR, De Oliveira GJ, Jaeger SM, Bagaldo AR, De Oliveira PA, Oliveira RL, da Silva Lêdo CA, Barbosa JC, De Carvalho GG. 2016. Feed value of Gliricidia fodder salt for sheep. Semin Cienc Agrar 37(2):921-932.

Coleman SW, Hart SP, Sahlu T. 2003. Relationships among forage chemistry, rumination and retention time with intake and digestibility of hay by goats. Small Ruminant Res 50(1-2):129-140.

Conceição MGD, Ferreira MDA, Campos JMDS, Silva JDL, Detmann E, Siqueira MCBD, Barros LJAD, Costa CTF. 2016. Replacement of wheat bran with spineless cactus in sugarcane-based diets for steers. R Bras Zootec 45(4):158-164.

Cozzi G, Gottardo F. 2005. Feeding behaviour and diet selection of finishing Limousin bulls under intensive rearing system. Appl Anim Behav Sci 91(3-4):181-192.

da Paz CC, do Rêgo AC, Faturi C, de Souza Rodrigues LF, Rodrigues Filho JA, de Souza PH, Conceição DM. 2016. Tropical kudzu as a protein source in sheep diets. Semin Cienc Agrar 37(2):933-945.

da Silva PC, Ítavo CC, Ítavo LC, da Graça Morais M, da Silva JA, da Silva Heimbach N, de Melo GK, da Costa MC. 2017. Protein-energy supplementation for lambs: feed intake, ingestive behavior, rumen parameters and nutrient digestibility. Semin Cienc Agrar 38:2631-2640.

Daniel JLP, Nussio LG, Zopollatto M, Goulart RS, Santos VP, Toledo Filho SG. 2010. Volatile fraction from sugarcane silage and forage proportion on the ingestive behaviour of beef steers. In Schnyder H, Isselstein J, Taube F, Auerswald K, Schellberg J, Wachendorf M, Herrmann A, Gierus M, Wrage N, Hopkins A (Eds). Grassland in a changing world. Duderstadt: Mecke Druck und Verlag Grassland 527.

Das A, Singh GP. 1999. Eating behaviour, VFA production, passage rate and nutrient digestibilities in cattle fed on wheat straw supplemented with different levels of berseem. Asian-Australas J Anim Sci 12(7):1040-1048.

de Araújo Camilo D, Sales Pereira E, Guimarães Pimentel P, Lopes Oliveira R, Duarte Cândido MJ, Goes Ferreira Costa MR, da Silva Aquino RM. 2012. Intake and feeding behaviour of Morada Nova lambs fed different energy levels. Ital J Anim Sci 11(1):e3.

de Carvalho GG, Rebouças RA, Campos FS, Santos EM, Araújo GG, Gois GC, de Oliveira JS, Oliveira RL, Rufino LD, Azevedo JA, Cirne LG. 2017. Intake, digestibility, performance, and feeding behavior of lambs fed diets containing silages of different tropical forage species. Anim Feed Sci Technol 228:140-8.

de Moura JH, de Araújo GG, Saraiva EP, de Albuquerque ÍR, Turco SH, Costa SA, Santos NM. 2016. Ingestive behavior of crossbred Santa Inês sheep fed water with different salinity levels. Semin Cienc Agrar 37(2):1057-1068.

de Oliveira Sichonany MJ, da Rocha MG, Pötter L, da Rosa AT, de Oliveria AP, Ribeiro LA, Stivanin SC, Alves MB. 2017. Effect of supplementation frequency in feeding behavior, displacement patterns and forage intake of beef heifers. Semin Cienc Agrar 38(5):3215-29.

Deswysen AG, Ehrlein HJ. 1981. Silage intake, rumination and pseudorumination activity in sheep studied by radiography and jaw movement recordings. Br J Nutr 46:327-335.

Dias DL, Silva RR, Silva FF, Carvalho GG, Barroso DS, Carvalho VM. 2014. Correlation between performance and ingestive behavior of steers post-weaned on pastures. Acta Sci Anim Sci 36(1):93-99.

Domingue BF, Dellow DW, Wilson PR, Barry TN. 1991. Comparative digestion in deer, goats, and sheep. New Zeal J Agric Res 34(1):45-53.

dos Santos AB, Pereira ML, de Oliveira Silva HG, de Jesus Pereira TC, Ribeiro LS, Azevêdo JA, Sousa LB, Sousa LB, da Silva SN, Ferreira FA, Barreto FO. 2016. Feeding behavior of lambs fed diets containing peach palm meal. Semin Cienc Agrar 37(3):1629-1641.

Durunna ON, Mujibi FD, Nkrumah DJ, Basarab JA, Okine EK, Moore SS, Wang Z. 2013. Genetic parameters for production and feeding behaviour traits in crossbred steers fed a finishing diet at different ages. Can J Anim Sci 93(1):79-87.

El-Kaschab O, Saddick IS, El-Aref M. 2009. Influence of housing floor bedding on welfare of lactating buffalo cows. In Proceedings of the 2nd Scientific Conference of animal wealth research in the Middle East and North Africa, Cairo International Convention Center, 24-26 October 2009. Massive Conferences and Trade Fairs. pp. 37-54

Enriquez-Hidalgo D, Hennessy D, Gilliland T, Egan M, Mee JF, Lewis E. 2014. Effect of rotationally grazing perennial ryegrass white clover or perennial ryegrass only swards on dairy cow feeding behaviour, rumen characteristics and sward depletion patterns. Livest Sci 169:48-62.

Estrada JC, Delagarde R, Faverdin P, Peyraud JL. 2004. Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. Anim Feed Sci Technol 114(1-4):59-74.

Fotius AC, Ferreira MD, Bispo SV, Véras AS, Salla LE, Chagas JC. 2014. Behavior of sheep fed different sequences of ingredients in a spineless cactus (Nopalea cochenillifera Salm-Dyck) based-diet. Rev Bras Health Prod Anim 15(1):74-82.

Fregonesi JA, Leaver JD. 2001. Behaviour, performance and health indicators of welfare for dairy cows housed in strawyard or cubicle systems. Livest Prod Sci 68(2-3):205-216.

García MA, Aguilera JF, Alcaide EM. 1995. Voluntary intake and kinetics of degradation and passage of unsupplemented and supplemented pastures from semiarid lands in grazing goats and sheep. Livest Prod Sci 44(3):245-255.

Gherardi SG, Black JL. Influence of post-rumen supply of nutrients on rumen digesta load and voluntary intake of a roughage by sheep. Br J Nutr 62(3):589-599.

Ghorbani B, Yansari AT, Sayyadi AJ. 2018. Effects of sesame meal on intake, digestibility, rumen characteristics, chewing activity and growth of lambs. S Afr J Anim Sci 48(1):151-161.

Gibb MJ, Huckle CA, Nuthall R, Rook AJ. 1999. The effect of physiological state (lactating or dry) and sward surface height on grazing behaviour and intake by dairy cows. Appl Anim Behav Sci 63(4):269-287.

Gilbert TC, Turner M. 2003. The long and the short of it! The effect of Lucerne fragment size on rumination and oral stereotypies in okapis (*Okapia johnstoni*). In Proceedings of the 5th Annual Symposium on Zoo Research, Marwell Zoological Park, Winchester, UK, 7-8th July 2003. Federation of Zoological Gardens of Great Britain and Ireland. pp. 275-280.

Gorgulu M, Akyol MA, Boga M, Goncu S. 2012. The effects of choice feeding and season on the feeding behaviour and growth performance of calves. J Anim Feed Sci 21:263-275.

Gregorini P, Eirin M, Refi R, Ursino M, Ansin OE, Gunter SA. 2006. Timing of herbage allocation in strip grazing: Effects on grazing pattern and performance of beef heifers. J Anim Sci 84(7):1943-1950.

Greter AM, AlZahal O, Duffield TF, McBride BW, Widowski TM, DeVries TJ. 2014. Effect of frequency of feed delivery on the feeding behaviour, growth, and rumen temperature of limit-fed dairy heifers. Can J Anim Sci 94(1):11-20.

Hadjigeorgiou IE, Gordon IJ, Milne JA. 2003. Comparative preference by sheep and goats for Graminaeae forages varying in chemical composition. Small Ruminant Res 49(2):147-156.

Helander C, Nørgaard P, Jalali AR, Nadeau E. 2014. Effects of chopping grass silage and mixing silage with concentrate on feed intake, dietary selection, chewing activity and faecal particle size of ewes in late pregnancy and early lactation. Livest Sci 163:69-79.

Heublein C, Dohme-Meier F, Südekum KH, Bruckmaier RM, Thanner S, Schori F. 2017. Impact of cow strain and concentrate supplementation on grazing behaviour, milk yield and metabolic state of dairy cows in an organic pasture-based feeding system. Animal 11(7):1163-73.

Holtshausen L, Schwartzkopf-Genswein KS, Beauchemin KA. 2013. Ruminal pH profile and feeding behaviour of feedlot cattle transitioning from a high-forage to a high-concentrate diet. Can J Anim Sci 93(4):529-533.

Iason GR, Sim DA, Gordon IJ. 2000. Do endogenous seasonal cycles of food intake influence foraging behaviour and intake by grazing sheep?. Funct Ecol 14(5):614-622.

Ingrand S, Agabriel J, Dedieu B, Lassalas J. 2000. Effects of within-group homogeneity of physiological state on individual feeding behaviour of loose-housed Charolais cows. Ann Zootech 49(1):15-27

Jalali AR, Nørgaard P, Weisbjerg MR, Nadeau E. 2012. Effect of stage of maturity of grass at harvest on intake, chewing activity and distribution of particle size in faeces from pregnant ewes. Animal 6(11):1774.

Jalali AR, Nørgaard P, Weisbjerg MR, Nielsen MO. 2012. Effect of forage quality on intake, chewing activity, faecal particle size distribution, and digestibility of neutral detergent fibre in sheep, goats, and llamas. Small Ruminant Res 103(2-3):143-151.

Jørgensen GH, Andersen IL, Bøe KE. 2007. Feed intake and social interactions in dairy goats-The effects of feeding space and type of roughage. Appl Anim Behav Sci 107(3-4):239-251.

Kammes KL, Allen MS. 2012. Nutrient demand interacts with forage family to affect digestion responses in dairy cows. J Dairy Sci 95(6):3269-3287.

Kaske M, Beyebach M, Hailu Y, Goebel W, Wagner S. 2002. The assessment of the frequency of chews during rumination enables an estimation of rumination activity in hay-fed sheep. J Anim Physiol Anim Nutr 86:83-89.

Kaske M, Groth A. 1997. Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay. Reprod Nutr Dev 37(5):573-588.

Kaske M, Midasch A. 1997. Effects of experimentally-impaired reticular contractions on digesta passage in sheep. Br J Nutr 78(1):97-110.

Kennedy PM. 1985. Influences of cold exposure on digestion of organic matter, rates of passage of digesta in the gastrointestinal tract, and feeding and rumination behaviour in sheep given four forage diets in the chopped, or ground and pelleted form. Br J Nutr 53(1):159-173.

Leite RF, Krizsan SJ, Figueiredo FOM, Carvalho VB, Teixeira IAMA, Huhtanen P. 2015. Contribution of different segments of the gastrointestinal tract to digestion in growing Saanen goats. J Anim Sci 93(4):1802-1814.

Li S, Khafipour E, Krause DO, Gonzalez LA, Plaizier JC. 2011. Effects of grain-pellet and alfalfa-pellet subacute ruminal acidosis (SARA) challenges on feeding behaviour of lactating dairy cows. Can J Anim Sci 91(2):323-330.

Lima LA, Silva AM, Bezerra LR, Morais JS, Araújo MJ, Oliveira RL, Pereira ES. 2018. Effects of the buriti (Mauritia flexuosa L.) oil supplementation on crossbred lactating goats: behavioral, physiological, and hematological responses. R Bras Zootec 47.

Lindström T, Redbo I. 2000. Effect of feeding duration and rumen fill on behaviour in dairy cows. Appl Anim Behav Sci 70(2):83-97.

Linnane MI, Brereton AJ, Giller PS. 2001. Seasonal changes in circadian grazing patterns of Kerry cows (Bos taurus) in semi-feral conditions in Killarney National Park, Co. Kerry, Ireland. Appl Anim Behav Sci 71(4):277-292.

Liu FY, Hodgson J, Barry TN. 1998. Effects of grazing sequence and condensed tannins on ingestive behaviour, herbage intake, and performance of lambs grazing Yorkshire fog pasture. New Zeal J Agric Res 41(3):359-366.

Maldini G, Allen MS. 2018. Temporal effects of ruminal propionic acid infusion on feeding behavior of Holstein cows in the postpartum period. J Dairy Sci 101(4):3077-3084.

Marchesini G, Segato S, Berzaghi P, Andrighetto I. 2011. Effect of non-forage roughage replacement on feeding behaviour and milk production in dairy cows. Ital J Anim Sci 10(4):e44.

Mattiauda DA, Tamminga S, Gibb MJ, Soca P, Bentancur O, Chilibroste P. 2013. Restricting access time at pasture and time of grazing allocation for Holstein dairy cows: ingestive behaviour, dry matter intake and milk production. Livest Sci 152(1):53-62.

Mawuenyegah PO, Shem MN, Warly L, Fujihara T. 1997. Effect of supplementary feeding with protein and energy on digestion and rumination behaviour of sheep consuming straw diets. J Agric Sci 129(4):479-484.

Mazzenga A, Gianesella M, Brscic M, Cozzi G. 2009. Feeding behaviour, diet digestibility, rumen fluid and metabolic parameters of beef cattle fed total mixed rations with a stepped substitution of wheat straw with maize silage. Livest Sci 122(1):16-23.

McLeod MN, Kennedy PM, Minson DJ. 1990. Resistance of leaf and stem fractions of tropical forage to chewing and passage in cattle. Br J Nutr 63(1):105-119.

McQueen RE, Robinson PH. 1996. Intake behaviour, rumen fermentation and milk production of dairy cows as influenced by dietary levels of fermentable neutral detergent fiber. Can J Anim Sci 76(3):357-365.

Minervino AH, Kaminishikawahara CM, Soares FB, Araujo CA, Reis LF, Rodrigues FA, Vechiato TD, Ferreira RN, Barrêto-Júnior RA, Mori CS, Ortolani EL. 2014. Behaviour of confined sheep fed with different concentrate sources. Arq Bras Med Vet Zootec 66:1163-1170.

Mizubuti IY, Sestari BB, de Azambuja Ribeiro EL, Pereira ES, de Freitas Barbosa MA, do Prado OP, Cunha GE, da Costa Gomes R, Costa CB. 2013. Ingestive behavior of Nellore steers in feedlot fed with diets containing different corn hybrids. Semin Cienc Agrar 34(2):4203-4211.

Moon SH, Jeon BT, Lee SM, Kim KH, Hudson RJ. 2000. Seasonal comparison of voluntary intake and feeding behaviour in Korean spotted deer (*Cervus nippon*). Asian-Australas J Anim Sci 13(10):1394-1398.

Morris ST, Parker WJ, Grant DA. 1993. Herbage intake, liveweight gain, and grazing behaviour of Friesian, Piedmontese× Friesian, and Belgian Blue× Friesian bulls. New Zeal J Agric Res 36(2):231-236.

Moyo M, Adekunle RA, Nsahlai IV. 2019. Effects of diet and roughage quality, and period of the day on diurnal feeding behaviour patterns of sheep and goats under subtropical conditions. Asian-Australas J Anim Sci 32(5):675-690.

Mullins CR, Mamedova LK, Brouk MJ, Moore CE, Green HB, Perfield KL, Smith JF, Harner JP, Bradford BJ. 2012. Effects of monensin on metabolic parameters, feeding behavior, and productivity of transition dairy cows. J Dairy Sci 95(3):1323-1336.

Neta ER, Alves KS, Mezzomo R, Gomes DÍ, Oliveira LR, Carvalho FF, Luz JB, Lacerda NG, Bourdon VD. 2017. Behavior of sheep fed babassu cake (*Orbygnia speciosa*) as a substitution for elephant grass silage. Anim Sci 88(8):1171-1177.

Nicory IM, de Carvalho GG, Ribeiro OL, Silva RR, Tosto MS, Costa-Lopes LS, Souza FN, de Oliveira Nascimento C. 2015. Ingestive behavior of lambs fed diets containing castor seed meal. Trop Anim Health Prod 47(5):939-944.

Nikkhah A. 2013. Chronophysiology of ruminant feeding behavior and metabolism: an evolutionary review. Biol Rhythm Res 44(2):197-218.

Nugroho TA, Dilaga WS, Purnomoadi A. 2015. Eating Behaviour of Sheep Fed at Day and/or Night Period. J Indones Trop Anim Agric 40(3):176-182.

Oliveira HC, Garcia R, de Almeida VV, Oliveira AC, Pires AJ, Nascimento Filho CS, Veloso CM, Silva RR, Oliveira UL. 2016. Feeding behavior of lambs fed castor meal. Semin Cienc Agrar 37(3):1451-1460.

Oshita T, Sudo K, Nonaka K, Kume S, Ochiai K. 2008. The effect of feed regimen on chewing time, digesta passage rate and particle size distribution in Holstein non-lactating cows fed pasture ad libitum. Livest Sci 113(2-3):243-250.

Palmieri AD, de Carvalho GG, Tosto MS, Leite VM, Santos SA, Borja MS, Azevêdo JA, Júnior JE, Leite LC, de Almeida Rufino LM. 2017. Feeding behavior of finishing goats fed diets containing detoxified castor meal, co-product of the biodiesel industry. Trop Anim Health Prod 49(2):389-395.

Pearson RA, Smith DG. 1994. The effects of work on food intake and ingestive behaviour of draught cattle and buffalo given barley straw. Anim Sci 58(3):339-346.

Penning PD, Parsons AJ, Orr RJ, Harvey A, Champion RA. 1995. Intake and behaviour responses by sheep, in different physiological states, when grazing monocultures of grass or white clover. Appl Anim Behav Sci 45(1-2):63-78.

Pereira TC, Pereira ML, Almeida PJ, Pereira CA, Santos AB, Santos ED. 2013. Mesquite pod meal in diets for Santa Inês sheep: ingestive behavior. Acta Sci Anim Sci 35(2):201-206.

Phillips CJ, Rind MI. 2001. The effects of frequency of feeding a total mixed ration on the production and behavior of dairy cows. J Dairy Sci 84(9):1979-1987.

Pimentel LR, Silva FF, Silva RR, Schio AR, Rodrigues ES, Oliveira PA. 2015. Feeding behavior of lactating cows fed palm kernel cake in the diet. Acta Sci Anim Sci 37(1):83-89.

Pinho BD, Ramos AF, LOURENÇO JÚNIOR JD, Faturi C, SILVA A, Nahúm BD, Manno MC, Lima KD, Sousa LF, da Silva JA, Araújo GS. 2016. Feeding behavior of sheep fed diets with Elaeis guineensis palm kernel meal. Semin Cienc Agrar 37(4):2513-2530.

Poorkasegaran S, Yansari AT. 2014. Effects of different sources of carbohydrates on intake, digestibility, chewing, and performance of Holstein dairy cows. J Anim Sci Biotechnol 5(1):6.

Renecker LA, Hudson RJ. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. J Wildl Manage 53(2):296-302.

Roca-Fernández AI, Ferris CP, Gonzalez-Rodriguez A. 2013. Behavioural activities of two dairy cow genotypes (Holstein-Friesian vs. Jersey x Holstein-Friesian) in two milk production systems (grazing vs. confinement). Span J Agric Res 11(1):120-126.

Rook AJ, Huckle CA. 1995. Synchronization of ingestive behaviour by grazing dairy cows. Anim Sci 60(1):25-30.

Rook AJ, Huckle CA. 1997. Activity bout criteria for grazing dairy cows. Appl Anim Behav Sci 54:89-96.

Rutter SM, Orr RJ, Penning PD, Yarrow NH, Champion RA. 2002. Ingestive behaviour of heifers grazing monocultures of ryegrass or white clover. Appl Anim Behav Sci 76:1-9.

Saraiva CA, Gonzaga Neto S, Henriques LT, Queiroz MF, Saraiva EP, Albuquerque RP, Fonseca VD, Nascimento GV. 2015. Forage cactus associated with different fiber sources for lactating Sindhi cows: production and composition of milk and ingestive behavior. R Bras Zootec 44(2):60-66.

Schlecht E, Hiernaux P, Kadaouré I, Hülsebusch C, Mahler F. 2006. A spatio-temporal analysis of forage availability and grazing and excretion behaviour of herded and free grazing cattle, sheep and goats in Western Niger. Agric Ecosyst Environ 113(1-4):226-242.

Schori F, Münger A. 2008. Grazing behaviour and intake of two Holstein cow types in a pasture-based production system. Grassland in a changing world 895-897.

Segabinazzi LR, Menezes LF, Silva CE, Clederson Martinello BB, Molinete ML. 2014. Diurnal ingestive behavior of Holstein calves reared in different systems: feedlot or pasture. Acta Sci Anim Sci 36(2):225-231.

Semiadi G, Muir PD, Barry TN, Veltman CJ, Hodgson J. 1993. Grazing patterns of sambar deer (*Cervus unicolor*) and red deer (*Cervus elaphus*) in captivity. New Zeal J Agric Res 36(2):253-260.

Silva JC, Véras AC, Carvalho FR, Ferreira MA, Souza EO, Barreto LG, Lopes LA, Silva JV. 2017. Nutritional value, performance, feeding behavior and serum biochemical profile of sheep fed with alfalfa hay replacing Bermuda grass (Cynodon dactylon (L.) Pers.) hay. Chil J Agric Res 77(4):340-345.

Somparn P, Juengprasobchok P. 2015. Provision of designated defecation areas to reduce the spatial distribution of faeces by grazing swamp buffalo heifers. Buffalo Bull34(3).

Souza-Rodrigues RT, Chizzotti ML, Rodrigues-Martins S, Ávila-Queiroz MA, Costa-Busato K. 2014. Digestibility, ingestive behaviour and performance of non-descript breed hair lambs of different sexual classes subjected to feed restriction. J Anim Feed Sci 23(2):117-23.

Spolders M, Meyer U, Flachowsky G, Coenen M. 2004. Comparison of resting and feeding behaviour for cows milked by an automatic milking system versus by a milking parlour. J Appl Anim Res 25(2):69-80.

Tafaj M, Kolaneci V, Junck B, Maulbetsch A, Steingass H, Drochner W. 2005. Influence of fiber content and concentrate level on chewing activity, ruminal digestion, digesta passage rate and nutrient digestibility in dairy cows in late lactation. Asian-Australas J Anim Sci 18(8):1116-1124.

Teimouri Yansari A. 2014. Physically effectiveness of beet pulp-based diets in dairy cows as assessed by responses of feed intake, digestibility, chewing activity and milk production. J Anim Physiol Anim Nutr 98(1):158-168.

Trach NX, Mo M, Dan CX. 2001. Effects of treatment of rice straw with lime and/or urea on responses of growing cattle. Livest Res Rural Dev 13(5):47.

Tripon I, Acatincăi S, Bura M, Cziszter LT, Gavojdian D, Erina S, Bognar IA, Răducan GG. 2011. Researches on Rumination Behavior in Six Months of Age Calves from Romanian Black and White Breed Fed Using Different Feed Space Allowance. Sci Papers Anim Sci Biotechnol 44(2):325-329.

Varlyakov I, Radev V, Slavov T, Mihaylov R. 2015. Ethological and haematological indices in yearling sheep fed various dietary nitrogen sources. Agric Sci Technol 7(4):423-430.

Vásquez CG, Olvera L, Siqueiros Y, Kuri ML, Navarro VA, Rovelo AE, Shimada A. 2004. Nursing and feeding behaviour of confined red deer (*Cervus elaphus scoticus*) in the Mexican highlands. New Zeal J Agric Res 47(1):1-9.

Warly L, Fariani A, Mawuenyegah OP, Matsui T, Fujihara T, Harumoto T. 1994. Studies on the utilization of rice straw by sheep IV. Effect of soybean meal and barley supplementation on eating and rumination behavior. Asian-Australas J Anim Sci 7(2):273-277.

Wenninger PS, Shipley LA. 2000. Harvesting, rumination, digestion, and passage of fruit and leaf diets by a small ruminant, the blue duiker. Oecologia 123(4):466-474.

Williams YJ, Doyle PT, Egan AR. 2014. Diurnal variation in rumen fill of dairy cows grazing Persian clover at different pasture allowances. Anim Prod Sci 54(9):1388-1393.

Williams YJ, Walker GP, Wales WJ, Doyle PT. 2000. The grazing behaviour of cows grazing Persian clover or perennial ryegrass pastures in spring. Asian–Australas J Anim Sci 13:509-512.

Wolfger B, Quinn C, Torres GW, Taylor M, Orsel K. 2016. Comparison of feeding behavior between black and red Angus feeder heifers. Can J Anim Sci 96(3):404-409.

Yansari AT, Valizadeh R, Naserian A, Christensen DA, Yu P, Shahroodi FE. 2004. Effects of alfalfa particle size and specific gravity on chewing activity, digestibility, and performance of Holstein dairy cows. J Dairy Sci 87(11):3912-3924.

Yıldırım A, Ulutaş Z, Ocak N, Kaptan M. 2013. Effects of birth weight and feeding system on fattening performance and feeding behaviour of Karayaka male lambs. Ital J Anim Sci 12(4):e89.

Zali SM, Teimouri Yansari A, Jafari Sayyadi A. 2015. Effect of particle size and fragility of corn silage and alfalfa hay on intake, digestibility, performance, and chewing activity of fattening male lambs. J Vet Sci Res Rev 1:47-57.

Appendix 2: Studies used in meta-analysis and modelling of rumen degradation

Abate A, Kiflewahid, B. 1992. Use of the nylon-bag technique in determining the complementarity of feedstuffs for dairy cattle rations. In The complementarity of feed resources for animal production in Africa, Proceedings of the joint feed resources networks workshop, Gaborone, Botswana 4-6 March 1991; Stares JES, Said AN, Kategile JA. Eds; African Feeds Research Network, Addis Ababa Ethiopia (1992); pp. 223-231.

Abdulrazak SA, Fujihara T, Ondiek JK, Ørskov ER. 2000. Nutritive evaluation of some Acacia tree leaves from Kenya. Anim Feed Sci Technol 85(1-2):89-98.

Abule E, Umunna NN, Nsahlai IV, Osuji PO, Alemu Y. 1995. The effect of supplementing teff (*Eragrostis tef*) straw with graded levels of cowpea (*Vigna unguiculata*) and lablab (*Lablab purpureus*) hays on degradation, rumen particulate passage and intake by crossbred (Friesian× Boran (zebu)) calves. Livest Prod Sci 44:221-228.

Ahmed MH, Babiker SA, Fadel Elseed AEMA, Mohammed AM. 2013. Effect of urea-treatment on nutritive value of sugarcane bagasse. ARPN J Sci Technol 3(8):834-838.

Alcaide EM, García AM, Aguilera JF. 2000. A comparative study of nutrient digestibility, kinetics of degradation and passage and rumen fermentation pattern in goats and sheep offered good quality diets. Livest Prod Sci 64(2-3):215-223.

Alcaide EM, García MA, Aguilera JF. 1997. The voluntary intake and rumen digestion by grazing goats and sheep of a low-quality pasture from a semi-arid land. Livest Prod Sci 52(1):39-47.

Anele UY, Arigbede OM, Südekum KH, Oni AO, Jolaosho AO, Olanite JA, Adeosun AI, Dele PA, Ike KA, Akinola OB. 2009. Seasonal chemical composition, in vitro fermentation and in sacco dry matter degradation of four indigenous multipurpose tree species in Nigeria. Anim Feed Sci Technol 154(1-2):47-57.

Apori SO, Castro FB, Shand WJ, Ørskov ER. 1998. Chemical composition, in sacco degradation and in vitro gas production of some Ghanaian browse plants. Anim Feed Sci Technol 76(1-2):129-137.

Asizua D, Mpairwe D, Kabi F, Mutetikka D, Bareeba FB, Hvelplund T, Weisbjerg MR, Madsen J. 2018. Effects of feeding systems on rumen environment, degradability and passage kinetics in Ankole× Friesian crossbred steers. Livest Sci 210:47-54.

Asizua D, Mpairwe D, Kabi F, Mutetikka D, Bareeba FB, Hvelplund T, Weisbjerg MR, Madsen J. 2018. Effects of feeding systems on rumen environment, degradability and passage kinetics in Ankole × Friesian crossbred steers. Livest Sci 210:47-54.

Balgees A, Elmnan A, Elseed AF, Mahala A, Amasiab E. 2013. In situ degradability and in vitro gas production of selected multipurpose tree leaves and alfalfa as ruminant feeds. World's Vet J 3:46-50.

Bamikole MA, Babayemi OJ. 2008. Chemical composition and in sacco dry matter degradability of residue and by-products of palm fruit processing in the rumen of steers. Anim Sci J 79(3):314-321.

Bárcena-Gama R, Swingle RS, Moore JA, Poore MH. 2002. Effect of roughage source on ruminal kinetics and passage of individual feed components in finishing diets for steers. J Appl Anim Res 21(1):109-121.

Basha NA, Scogings PF, Fon FN, Ahmed MA, Nsahlai IV. 2015. Effects of season and species on in sacco degradability of forages in the sub-humid subtropical savannah. Afr J Agric Res 10(11):1312-1319.

Baumont R, Jailler M, Dulphy JP. 1997. Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay. Ann Zootech 46 (3):231-244.

Belachew Z, Yisehak K, Taye T, Janssens GPJ. 2013. Chemical composition and in sacco ruminal degradation of tropical trees rich in condensed tannins. Czech J Anim Sci 58(4):176-192.

Bogoro S, Kalla DJU, Gaiya O. 2006. Effect of positioning of feed samples in two segments of the rumen on in-situ degradability of feed stuffs. Pakistan J Nutr 5(2):152-155.

Bonsi MLK, Osuji PO, Nsahlai IV, Tuah AK. 1994. Graded levels of *Sesbania sesban* and *Leucaena leucocephala* as supplements to teff straw given to Ethiopian Menz sheep. Anim Sci 59:235–244.

Bonsi MLK, Osuji PO. 1997. The effect of feeding cottonseed cake, sesbania or leucaena with crushed maize as supplement to teff straw. Livest Prod Sci 51(1-3):173-181.

Bonsi MLK, Tuah AK, Osuji PO, Nsahlai IV, Umunna NN. 1996. The effect of protein supplement source or supply pattern on the intake, digestibility, rumen kinetics, nitrogen utilisation and growth of Ethiopian Menz sheep fed teff straw. Anim Feed Sci Technol 64(1):11-25.

Bruining M, Bakker R, van Bruchem J, Tamminga S. 1998. Rumen digesta kinetics in dairy cows fed grass, maize and alfalfa silage. 1. Comparison of conventional, steady-state and dynamic methods to estimate microbial degradation, comminution and passage of particles. Anim Feed Sci Technol 73(1-2):37-58.

Buthelezi LS, Mupangwa JF, Muchenje V, Nherera-Chokuda FV. 2019. Influence of drying technique on chemical composition and ruminal degradability of subtropical *Cajanus cajan L*. Anim Nutr 5(1):95-100.

Carro MD, Lopez S, Gonzalez JS, Ovejero FJ. 1991. The use of the rumen degradation characteristics of hay as predictors of its voluntary intake by sheep. Anim Sci 52(1):133-139.

Chakeredza S, Ter Meulen U, Ndlovu LR. 2002. Ruminal fermentation kinetics in ewes offered a maize stover basal diet supplemented with cowpea hay, groundnut hay, cotton seed meal or maize meal. Trop Anim Health Prod 34(3):215-230.

Chiofalo V, Dulphy JP, Baumont R, Jailler M, Ballet JM. 1992. Influence of the method of forage conservation on feeding behaviour, intake and characteristics of reticulo-rumen content, in sheep fed ad libitum. Reprod Nutr Dev 32(4):377-392.

Chumpawadee S, Sommart K, Vongpralub T, Pattarajinda V. 2005. In sacco degradation characteristics of energy feed sources in Brahman-Thai native crossbred steers. J Agric Technol 1(2):192-206.

Cushnahan A, Gordon FJ. 1995. The effects of grass preservation on intake, apparent digestibility and rumen degradation characteristics. Anim Sci 60(3):429-438.

Cushnahan A, Mayne CS, Unsworth EF. 1995. Effects of ensilage of grass on performance and nutrient utilization by dairy cattle 2. Nutrient metabolism and rumen fermentation. Anim Sci 60:347–359.

De Vega A, Poppi DP. 1997. Extent of digestion and rumen condition as factors affecting passage of liquid and digesta particles in sheep. J Agric Sci 128(2):207-215.

Ding G, Chang Y, Zhao L, Zhou Z, Ren L, Meng Q. 2014. Effect of Saccharomyces cerevisiae on alfalfa nutrient degradation characteristics and rumen microbial populations of steers fed diets with different concentrate-to-forage ratios. J Anim Sci Biotechnol 5(1):24.

Fonseca AJM, Dias-Da-Silva AA, Ørskov ER. 1998. In sacco degradation characteristics as predictors of digestibility and voluntary intake of roughages by mature ewes. Anim Feed Sci Technol 72:205–219.

García MA, Aguilera JF, Alcaide EM. 1995. Voluntary intake and kinetics of degradation and passage of unsupplemented and supplemented pastures from semiarid lands in grazing goats and sheep. Livest Prod Sci 44(3):245-255.

Gasa J, Holtenius K, Sutton JD, Dhanoa MS, Napper DJ. 1991. Rumen fill and digesta kinetics in lactating Friesian cows given two levels of concentrates with two types of grass silage ad lib. Br J Nutr 66(3):381-398.

Ghorbani B, Yansari AT, Sayyadi AJ. 2018. Effects of sesame meal on intake, digestibility, rumen characteristics, chewing activity and growth of lambs. S Afr J Anim Sci 48(1):151-161.

Goto M, Morio T, Kojima E, Nagano Y, Yamada Y, Horigane A, Yamada H. 2000. Characteristics of digestion dynamics of rice and oat straw relating to microbial digestion in the rumen of sheep given high-concentrate diets. Asian-Australas J Anim Sci 13(9):1219-1227.

Gralak MA, Kamalu T, Von Keyserlingk MAG, Kulasek GW. 1997. Rumen dry matter and crude protein degradability of extracted or untreated oilseeds and *Leucaena leucocephala* leaves. Arch Anim Nutr 50(2):173-185.

Gusha J, Ngongoni NT, Halimani TE. 2013. Nutritional composition and effective degradability of four forage trees grown for protein supplementation. J Anim Feed Res 3(4):170-175.

Habib G, Hassan MF, Siddiqui MM. 1998. Degradation characteristics of straw from different wheat genotypes and their response to urea-ammoniation treatment. Anim Feed Sci Technol 72:373-386.

Hackmann T. 2008. Studies of ruminant digestion, ecology, and evolution (Doctoral dissertation, University of Missouri-Columbia).

Hameed AA, Salih MA, El-Seed F. 2012. Effect of urea treatment on the chemical composition and rumen degradability of Groundnut Hull. Pakistan J Nutr 11(12):1146-1151.

Hamidi BA, Mansouri H, Yansari AT, Mnafiazar GH. 2007. Determination of ruminal nutrient degradability of some feeds and total mixed ration in buffalo using in situ methods. Ital J Anim Sci 6(sup2):433-436.

Herbert F, Thomson EF, Capper BS. 1994. Effect of genotype on the morphological characteristics, chemical composition and feeding value of nine barley straws, and responses to soya-bean meal supplementation. Anim Sci 58(1):117-126.

Hindrichsen IK, Osuji PO, Odenyo AA, Madsen J, Hvelplund T. 2004. Effect of supplementation of maize stover with foliage of various tropical multipurpose trees and Lablab purpureus on intake, rumen fermentation, digesta kinetics and microbial protein supply of sheep. Anim Feed Sci Technol 113(1-4):83-96.

Hüther L, Drebes S, Lebzien P. 2005. Effect of glyphosate contaminated feed on rumen fermentation parameters and in sacco degradation of grass hay and corn grain. Arch Anim Nutr 59(1):73-79.

Ikhimioya I, Isah OA, Ikhatua UJ, Bamikole MA. 2005. Rumen degradability of dry matter and crude protein in tree leaves and crop residues of humid Nigeria. Pakistan J Nutr 4(5):313-320.

Kabatange MA, Shayo CM. 1991. Rumen degradation of maize stover as influenced by Leucaena hay supplementation. Livest Res Rural Dev 3(2):19-22.

Kamalak ADEM, Canbolat O, Gurbuz Y, Ozay O. 2005. Comparison of in vitro gas production technique with in-situ nylon bag technique to estimate dry matter degradation. Czech J Anim Sci 50:60-67.

Kariuki JN, Tamminga S, Gachuiri CK, Gitau GK, Muia JMK. 2001. Intake and rumen degradation in cattle fed napier grass (*Pennisetum purpureum*) supplemented with various levels of *Desmodium intortum* and *Ipomoea batatus* vines. S Afr J Anim Sci 31(3):149-157.

Karsli MA, Russell JR. 2002. Prediction of the voluntary intake and digestibility of forage-based diets from chemical composition and ruminal degradation characteristics. Turk J Vet Anim Sci 26:249-255.

Kayongo SB, Wanyoike MM, Nyagah PN, Mailho TE, Mbugua PN. 1992. Caged-layer waste as a nitrogen source in crop-residue utilisation. In The complementarity of feed resources for animal production in Africa, Proceedings of the joint feed resources networks workshop, Gaborone, Botswana, 4-6 March 1991; Stares JES, Said AN, Kategile JA, Eds; African Feeds Research Network, Addis Ababa Ethiopia (1992); pp. 265-277.

Khalili H, Osuji PO, Umunna N, Crosse S. 1994. The effects of forage type (maize-lablab or oat-vetch) and level of supplementation (wheat-middlings) on food intake, diet apparent digestibility, purine excretion and milk production of crossbred (Bos taurus× Bos indicus) cows. Anim Sci 58(3):321-328.

Khan MA, Sarwar M, Khan MS, Rehman MS, Nisa M, Lee WS, Kim HS. 2008. Use of additives to capture nitrogen in ammoniated wheat straw: Intake, ruminal parameters, digestibility and nitrogen utilization in buffaloes. Livest Sci 114(2-3):347-353.

Khazaal K, Dentinho MT, Ribeiro JM, Ørskov ER. 1993. A comparison of gas production during incubation with rumen contents in vitro and nylon bag degradability as predictors of the apparent digestibility in vivo and the voluntary intake of hays. Anim Sci 57:105-112.

Khazaal K, Dentinho MT, Ribeiro JM, Ørskov ER. 1995. Prediction of apparent digestibility and voluntary intake of hays fed to sheep: comparison between using fibre components, in vitro digestibility or characteristics of gas production or nylon bag degradation. Anim Sci 61:527–538.

Khazaal K, Markantonatos X, Nastis A, Ørskov ER. 1993. Changes with maturity in fibre composition and levels of extractable polyphenols in Greek browse: effects on in vitro gas production and in sacco dry matter degradation. J Sci Food Agric 63(2):237-244.

Kibont A, Ørskov ER. 1993. The use of degradation characteristics of browse plants to predict intake and digestibility by goats. Anim Sci 57(2):247-251.

Lanyasunya TP, Rong HW, Abdulrazak SA, Mukisira EA. 2006. The potential of the weed, *Commelina diffusa L*., as a fodder crop for ruminants. S Afr J Anim Sci 36:28-32.

Larbi A, Dung DD, Olorunju PE, Smith JW, Tanko RJ, Muhammad IR, Adekunle IO. 1999. Groundnut (*Arachis hypogaea*) for food and fodder in crop-livestock systems: forage and seed yields, chemical composition and rumen degradation of leaf and stem fractions of 38 cultivars. Anim Feed Sci Technol 77(1-2):33-47.

Ledoux DR, Williams JE, Stroud TE, Garner GB, Paterson JA. 1985. Influence of forage level on passage rate, digestibility and performance of cattle. J Anim Sci 61(6):1559-1566.

Lopez S, Hovell FD, Manyuchi B, Smart RI. 1995. Comparison of sample preparation methods for the determination of the rumen degradation characteristics of fresh and ensiled forages by the nylon bag technique. Anim Sci 60(3):439-450.

Mediksa T. 2017. Comparison of In Sacco Rumen Dry Matter Degradability and Feeds intake and Digestion of Crossbred Dairy Cows (Holestian Friesian X Horro) Supplemented with Concentrate Diet. Am J Biosci Bioeng 5(6):121-130.

Mero RN, Udén P. 1997. Promising tropical grasses and legumes as feed resources in Central Tanzania II. In sacco rumen degradation characteristics of four grasses and legumes. Anim Feed Sci Technol 69(4):341-352.

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

Moyo M, Adebayo RA, Nsahlai IV. 2018. Effects of roughage quality, period of day and time lapse after meal termination on rumen digesta load in goats and sheep. Asian-Australas J Anim Sci 31(8):1183-1196.

Muinga RW, Topps JH, Rooke JA, Thorpe W. 1995. The effect of supplementation with *Leucaena leucocephala* and maize bran on voluntary food intake, digestibility, live weight and milk yield of Bos indicus× Bos taurus dairy cows and rumen fermentation in steers offered *Pennisetum purpureum* ad libitum in the semi-humid tropics. Anim Sci 60(1):13-23.

Mulligan FJ, Quirke J, Rath M, Caffrey PJ, O'Mara FP. 2002. Intake, digestibility, milk production and kinetics of digestion and passage for diets based on maize or grass silage fed to late lactation dairy cows. Livest Prod Sci 74(2):113-124.

Nandra KS, Hendry A, Dobos RC. 1993. A study of voluntary intake and digestibility of roughages in relation to their degradation characteristics and retention time in the rumen. Anim Feed Sci Technol 43(3-4):227-237.

Navaratne HVRG, Ibrahim MNM. 1988. Degradation characteristics of some tropical feeds in the rumen. Asian Australas J Anim Sci 1:21–25.

Ndlovu LR, Buchanan-Smith JG. 1985. Utilization of poor-quality roughages by sheep: effects of alfalfa supplementation on ruminal parameters, fiber digestion and rate of passage from the rumen. Can J Anim Sci 65(3):693-703.

Nedelkov K, Todorov N, Girginov D, Simeonov M, Ribarski S. 2017. Comparison of the rumen degradability and intestinal digestibility of dm and cp of dried distillers's by-products from Bulgarian distillery companies. Bulg J Agric Sci 23(2):280-288.

Nedelkov K, Todorov N, Simeonov M, Girginov D, Ganchev G. 2017. In situ rumen degradability and intestinal digestibility of two different types of rapeseed meal. Bulg J Agric Sci 23(3):462-466.

Ngwa AT, Nsahlai IV, Bonsi MLK. 2001. The effect of feeding pods of multipurpose trees (MPTs) on the degradability of dry matter and cell wall constituents of maize stover and alfalfa incubated in the rumen of sheep. J Sci Food Agric 81(13):1235-1243.

Nouala FS, Akinbamijo OO, Smith OB, Pandey VS. 2004. Horticultural residues as ruminant feed in peri-urban area of The Gambia. Livest Res Rural Dev 16(6):1-6.

Nsahlai IV, Bryant MJ, Umunna NN. 1998. Utilisation of barley straw by steers: the effect of quantity and source of nitrogen on the degradation of straw fractions, particle outflow rate and intake. J Appl Anim Res 14(1):33-50.

Nsahlai IV, Bryant MJ, Umunna NN. 1999. Utilization of barley straw by steers: effects of replacing urea with protein, source of protein and quantity of rumen degradable nitrogen on straw degradation, liquid and particle passage rates and intake. J Appl Anim Res 16:129-146.

Nsahlai IV, Umunna NN. 1996. Comparison between reconstituted sheep faeces and rumen fluid inocula and between in vitro and in sacco digestibility methods as predictors of intake and in vivo digestibility. J Agric Sci 126:235-248.

Orden EA, Yamaki K, Ichinohe T, Fujihara T. 2000. Feeding value of ammoniated rice straw supplemented with rice bran in sheep: II. In situ rumen degradation of untreated and ammonia treated rice straw. Asian Australas J Anim Sci 13(7):906-912.

Panjaitan T, Quigley SP, McLennan SR, Swain AJ, Poppi DP. 2014. Digestion of forages in the rumen is increased by the amount but not the type of protein supplement. Anim Prod Sci 54(9):1363-1367.

Peyrat J, Nozière P, Le Morvan A, Férard A, Protin PV, Baumont R. 2014. Effects of ensiling maize and sample conditioning on in situ rumen degradation of dry matter, starch and fibre. Anim Feed Sci Technol 196:12-21.

Philippeau C, Michalet-Doreau B. 1998. Influence of genotype and ensiling of corn grain on in situ degradation of starch in the rumen. J Dairy Sci 81(8):2178-2184.

Rahal A, Singh A, Singh M. 1997. Effect of urea treatment and diet composition on, and prediction of nutritive value of rice straw of different cultivars. Anim Feed Sci Technol 68:165-182.

Salcedo-Meza JR, Castellanos-Molina R, Garza-Flores JD, Tejada-Castaneda ZI, Segura-Correa JC, Rodriguez-Vazquez R, Ku-Vera JC. 2004. Effect of dehydrated pig faeces in the ration on rumen degradability, kinetics of passage and in vivo digestibility in Holstein steers. J Appl Anim Res 25(2):109-116.

Shem MN, Ørskov ER, Kimambo AE. 1995. Prediction of voluntary dry-matter intake, digestible dry-matter intake and growth rate of cattle from the degradation characteristics of tropical foods. Anim Sci 60:65-74.

Shen HS, Sundstøl F, Ni DB. 1998. Studies on untreated and urea-treated rice straw from three cultivation seasons: 2. Evaluation of straw quality through in vitro gas production and in sacco degradation measurements. Anim Feed Sci Technol 74:193-212.

Siaw DEKA, Osuji PO, Nsahlai IV. 1993. Evaluation of multipurpose tree germplasm: the use of gas production and rumen degradation characteristics. J Agric Sci 120(3):319-330.

Sibanda S, Ndlovu LR, Bryant T. 1992. Veld hay as feed for Matebele goats during the last trimester of pregnancy. In The complementarity of feed resources for animal production in Africa, Proceedings of the joint feed resources networks workshop, Gaborone, Botswana 4-6 March 1991; Stares, J.E.S.; Said, A.N.; Kategile, J.A., Eds; African Feeds Research Network, Addis Ababa Ethiopia pp. 205-213.

Sibanda S, Ndlovu LR, Smith T. 1992. Effects of undegradable protein supplements on the performance of weaner steers fed veld hay sprayed with urea. In The complementarity of feed resources for animal production in Africa, Proceedings of the joint feed resources networks workshop, Gaborone, Botswana 4-6 March 1991; Stares, J.E.S.; Said, A.N.; Kategile, J.A., Eds; African Feeds Research Network, Addis Ababa Ethiopia pp. 287-297.

Silva LFP, Cassoli LD, Roma Júnior LC, Rodrigues ACDO, Machado PF. 2008. In situ degradability of corn stover and elephant-grass harvested at four stages of maturity. Sci Agric 65(6):595-603.

Tahseen O, Abdallah J, Omar JA. 2014. In situ degradability of dry matter, crude protein, acid and neutral detergent fiber of olive cake and greenhouse wastes of tomato and cucumber. Rev Med Vet 165(3-4):93-98.

Tas BM, Taweel HZ, Smit HJ, Elgersma A, Dijkstra J, Tamminga S. 2006. Rumen degradation characteristics of perennial ryegrass cultivars during the growing season. Anim Feed Sci Technol 131(1-2):103-120.

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

Tolera A, Sundstøl F. 2001. Prediction of feed intake, digestibility and growth rate of sheep fed basal diets of maize stover supplemented with Desmodium intortum hay from dry matter degradability of the diets. Livest Prod Sci 68:13–23.

Tovar-Gomez MR, Emile JC, Michalet-Doreau B, Barriere Y. 1997. In situ degradation kinetics of maize hybrid stalks. Anim Feed Sci Tech 2:77-88.

Umunna NN, Nsahlai IV, Osuji PO. 1995. Degradability of forage protein supplements and their effects on the kinetics of digestion and passage. Small Rumin Res 17:145-152.

Umunna NN, Osuji PO, Nsahlai IV, Khalili H, Mohamed-Saleem MA. 1995. Effect of supplementing oat hay with lablab, sesbania, tagasaste or wheat middlings on voluntary intake, N utilization and weight gain of Ethiopian Menz sheep. Small Ruminant Res 18(2):113-120.

Valente TNP, Detmann E, Queiroz ACD, Valadares Filho SDC, Gomes DI, Figueiras JF. 2011. Evaluation of ruminal degradation profiles of forages using bags made from different textiles. Rev Bras Zootec 40(11):2565-2573.

Valk H, Kappers IE, Tamminga S. 1996. In sacco degradation characteristics of organic matter, neutral detergent fibre and crude protein of fresh grass fertilized with different amounts of nitrogen. Anim Feed Sci Technol 63(1-4):63-87.

Verbič J, Stekar JM, Resnik-Čepon M. 1995. Rumen degradation characteristics and fibre composition of various morphological parts of different maize hybrids and possible consequences for breeding. Anim Feed Sci Tech 54(1-4):133-148.

Warambwa AR, Ndlovu LR. 1992. Use of whole sunflower seeds and urea as supplements to crop-residue based diets for goats. In The complementarity of feed resources for animal production in Africa, Proceedings of the joint feed resources networks workshop, Gaborone, Botswana 4-6 March 1991; Stares JES, Said AN, Kategile JA. Eds. African Feeds Research Network, Addis Ababa Ethiopia pp. 197-203.

Yanez Ruiz DR, Moumen A, Martin Garcia AI, Molina Alcaide E. 2004. Ruminal fermentation and degradation patterns, protozoa population, and urinary purine derivatives excretion in goats and wethers fed diets based on two-stage olive cake: Effect of PEG supply. J Anim Sci 82(7):2023-2032.

Yansari AT, Sadeghi H, Ansari-Pirsarai Z, Mohammad-Zadeh H. 2007. Ruminal dry matter and nutrient degradability of different olive cake by-products after incubation in the rumen using nylon bag technique. Int J Agric Biol 9:439-442.

Yansari TA. 2017. Ruminal Kinetics of Nutrients Degradation, Hydration, and Functional Specific Gravity of Three Types of Beet Pulp. Iran J Appl Anim Sci 7:17-26.

Yayota M, Karashima J, Kouketsu T, Nakano M, Ohtani S. 2009. Seasonal changes in the digestion and passage rates of fresh dwarf bamboo (*Pleioblastus argenteostriatus f. glaber*) in sheep. Anim Feed Sci Tech 149:89-101.

Zali SM, Teimouri Yansari A, Jafari Sayyadi A. 2015. Effect of particle size and fragility of corn silage and alfalfa hay on intake, digestibility, performance, and chewing activity of fattening male lambs. J Vet Sci Res Rev 1:47-57.

Zewdu T, Baars R, Yami A, Negassa D. 2002. In sacco dry matter and nitrogen degradation and their relationship with in vitro dry matter digestibility of Napier grass (*Pennisetum purpureum Schumach.*) as influenced by height of plant at cutting. Aust J Agric Res 53(1):7-12.

Zhao YL, Yan SM, He ZX, Anele UY, Swift ML, McAllister TA, Yang WZ. 2015. Effects of volume weight, processing method and processing index of barley grain on in situ digestibility of dry matter and starch in beef heifers. Anim Feed Sci Tech 199:93-103.

Appendix 3: Studies used in modelling of rate of passage of solid and liquid in the rumen

Abdullah N, Ho YW, Mahyuddin M, Jalaludin S. 1991. Studies in fibre digestion and passage rate of liquid and solid in cattle and buffaloes. J Anim Sci 4(2):137-141.

Abdullah N, Liang JB, Ho YW. 2012. Effects of diets of differing fiber contents on digestibility, passage rate of digesta and heat production in lesser mouse deer (*Tragulus javanicus*). Mamm Biol 77(6):385-390.

Abule E, Umunna NN, Nsahlai IV, Osuji PO, Alemu Y. 1995. The effect of supplementing teff (*Eragrostis tef*) straw with graded levels of cowpea (*Vigna unguiculata*) and lablab (*Lablab purpureus*) hays on degradation, rumen particulate passage and intake by crossbred (Friesian×Boran (zebu)) calves. Livest Prod Sci 44(3):221-228.

Adams DC, Cochran R, Currie P. 1987. Forage maturity effects on rumen fermentation, fluid flow, and intake in grazing steers. J Range Manag 404-408.

Adams DC, Galyean ML, Kiesling HE. 1981. Influence of viable yeast culture, sodium bicarbonate and monensin on liquid dilution rate, rumen fermentation and feedlot performance of growing steers and digestibility in lambs. J Anim Sci 53(3):780-789.

Alcaide EM, Garcia AM, Aguilera JF. 2000. A comparative study of nutrient digestibility, kinetics of degradation and passage and rumen fermentation pattern in goats and sheep offered good quality diets. Livest Prod Sci 64:215-223.

Arthun D, Holechek JL, Wallace JD, Gaylean ML, Cardenas M. 1992. Forb and shrub effects on ruminal fermentation in cattle. J Range Manag 1:519-522.

Barboza PS, Peltier TC, Forster RJ. 2006. Ruminal fermentation and fill change with season in an arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). Physiol Biochem Zool 79(3):497-513.

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

Bayat AR, Rinne M, Kuoppala K, Ahvenjärvi S, Huhtanen P. 2010. Ruminal large and small particle kinetics in dairy cows fed red clover and grass silages harvested at two stages of growth. Anim Feed Sci Tech 155:86-98.

Bayat AR, Rinne M, Kuoppala K, Ahvenjärvi S, Huhtanen P. 2011. Ruminal large and small particle kinetics in dairy cows fed primary growth and regrowth grass silages harvested at two stages of growth. Anim Feed Sci Tech 165:51-60.

Behrend A, Lechner-Doll M, Streich WJ, Clauss M. 2004. Seasonal faecal excretion, gut fill, liquid and particle marker retention in mouflon (*Ovis ammon musimon*), and a comparison with roe deer (*Capreolus capreolus*). Acta Theriol 49(4):503-515.

Bonsi MLK, Tuah AX, Osuji PO, Nsahlai IV, Umunna NN. 1996. The effect of protein supplement source or supply pattern on the intake, digestibility, rumen kinetics, nitrogen utilisation and growth of Ethiopian Menz sheep fed teff straw. Anim Feed Sci Tech 64:11-25.

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

Branine ME, Galyean ML. 1990. Influence of grain and monensin supplementation on ruminal fermentation, intake, digesta kinetics and incidence and severity of frothy bloat in steers grazing winter wheat pasture. J Anim Sci 68:1139-1150.

Bruining M, Bakker R, Van Bruchem J, Tamminga S. 1998. Rumen digesta kinetics in dairy cows fed grass, maize and alfalfa silage. 1. Comparison of conversional, steady state and dynamic methods of estimate microbial degradation, comminution and passage of particles. Anim Feed Sci Tech 73:37-58.

Burns JC, Pond KR, Fisher DS, Luginbuhl JM. 1997. Changes in forage quality, ingestive mastication, and digesta kinetics resulting from switchgrass maturity. J Anim Sci 75:1368-1379.

Cappellozza BI, Bohnert D, Schauer C, Falck S, Vanzant E, Harmon D, Cooke R. 2013. Daily and alternate day supplementation of urea or soybean meal to ruminants consuming low quality cool-season forage: II. Effects on ruminal fermentation. Livest Sci 155(2):214-222.

Castle EJ. 1956. The rate of passage of foodstuffs through the alimentary tract of the goat. Br J Nutr 10(2):115-125.

Cherney DJ, Mertens DR, Moore JE. 1991. Fluid and particulate retention times in sheep as influenced by intake level and forage morphological composition. J Anim Sci 69(1):413-422.

Clauss M, Lunt N, Ortmann S, Plowman A, Codron D, Hummel J. 2011. Fluid and particle passage in three duiker species. Eur J Wildl Res 57(1):143-148.

Coleman SW, Hart SP, Sahlu T. 2003. Relationships among forage chemistry, rumination and retention time with intake and digestibility of hay by goats. Small Ruminant Res 50(1):129-140.

De Vega A, Poppi DP. 1997. Extent of digestion and rumen condition as factors affecting passage of liquid and digesta particles in sheep. J Agric Sci 128(2):207-215.

Dhanoa MS, Siddons RC, France J, Gale DL. 1985. A multicompartmental model to describe marker excretion patterns in ruminant faeces. Br J Nutr 53:663-671.

Dittmann MT, Hummel J, Hammer S, Arif A, Hebel C, Mueller DW, Fritz J, Steuer P, Schwarm A, Kreuzer M, Clauss M. 2015. Digesta kinetics in gazelles in comparison to other ruminants: evidence for taxon specific rumen fluid throughput to adjust digesta washing to the natural diet. Comp Biochem Physiol Part A Mol Integr Physiol 185:58-68.

Erdman RA, Vandersall JH, Russek-Cohen E, Switalski G. 1987. Simultaneous measures of rates of ruminal digestion and passage of feeds for prediction of ruminal nitrogen and dry matter digestion in lactating dairy cows. J Anim Sci 64:565-577.

Flores-Miyamoto K, Clauss M, Ortmann S, Sainsbury AW. 2005. Nutrition of captive lowland anoa (*Bubalus depressicornis*): A study on ingesta passage, intake, digestibility, and a diet survey. Zoo Biol 24(2):125-134.

Froetschel ME, Amos HE. 1991. Effects of dietary fiber and feeding frequency on ruminal fermentation, digesta water-holding capacity, and fractional turnover of contents. J Anim Sci 69:1312-1321.

Froetschel ME, Croom Jr W, Hagler Jr W, Argenzio R, Liacos J, Broquist H. 1987. Effects of slaframine on ruminant digestive function: liquid turnover rate and fermentation patterns in sheep and cattle. J Anim Sci 64(4):1241-1248.

Grant RJ, Cotanch KW. 2012. Higher forage diets: dynamics of passage, digestion, and cow productive responses. Chazy, NY: William H. Miner Agricultural Research Institute.

Gross JE, Alkon PU, Demment MW. 1996. Nutritional ecology of dimorphic herbivores: Digestion and passage rates in Nubian Ibex. Oecologia 107(2):170-178.

Gunter S, Judkins M, Krysl L, Broesder J, Barton R, Rueda B, Holcombe D. 1990. Digesta kinetics, ruminal fermentation characteristics and serum metabolites of pregnant and lactating ewes fed chopped alfalfa hay. J Anim Sci 68(11):3821-3831.

Haaland G, Tyrrell H. 1982. Effects of limestone and sodium bicarbonate buffers on rumen measurements and rate of passage in cattle. J Anim Sci 55(4):935-942.

Hebel C, Ortmann S, Hammer S, Hammer C, Fritz J, Hummel J, Clauss M. 2011. Solute and particle retention in the digestive tract of the Phillip's dikdik (*Madoqua saltiana phillipsi*), a very small browsing ruminant: Biological and methodological implications. Comp Biochem Physiol Part A Mol Integr Physiol 159:284-290.

Hjeljord O, Sundstøl F, Haagenrud H. 1982. The nutritional value of browse to moose. J Wildl Manag 1:333-343.

Huhtanen P, Asikainen U, Arkkila M, Jaakkola S. 2007. Cell wall digestion and passage kinetics estimated by marker and in situ methods or by rumen evacuations in cattle fed hay 2 or 18 times daily. Anim Feed Sci Tech 133(3):206-227.

Hummel J, Clauss M, Zimmermann W, Johanson K, Nørgaard C, Pfeffer E. 2005. Fluid and particle retention in captive okapi (*Okapia johnstoni*). Comp Biochem Physiol Part A Mol Integr Physiol 140(4):436-444.

Hummel J, Hammer S, Hammer C, Ruf J, Lechenne M, Clauss M. 2015. Solute and particle retention in a small grazing antelope, the blackbuck (*Antilope cervicapra*). Comp Biochem Physiol Part A Mol Integr Physiol 182:22-26.

Hummel J, Steuer P, Südekum KH, Hammer S, Hammer C, Streich WJ, Clauss M. 2008. Fluid and particle retention in the digestive tract of the addax antelope – adaptations of a grazing desert ruminant. Comp Biochem Physiol Part A Mol Integr Physiol 149:142-149.

Judkins MB, Stobart RH. 1988. Influence of two levels of enzyme preparation on ruminal fermentation, particulate and fluid passage and cell wall digestion in wether lambs consuming either a 10% or 25% grain diet. J Anim Sci 66:1010-1015.

Judkins MB, Wallace JD, Galyean ML, Krysl LJ, Parker EE. 1987. Passage rates, rumen fermentation, and weight change in protein supplemented grazing cattle. J Range Manag 100-105.

Kammes KL, Allen MS. 2012. Rates of particle size reduction and passage are faster for legume compared with cool-season grass, resulting in lower rumen fill and less effective fiber. J Dairy Sci 95:3288-3297.

Kaske M, Groth MKA. 1997. Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay. Reprod Nutr Dev 37:573-588.

Kaske M, Midasch A. 1997. Effects of experimentally impaired reticular contractions on digesta passage in sheep. Br J Nutr 78:97-110.

Kattnig RM, Pordomingo AJ, Schneberger AG, Duff GC, Wallace JD. 1992. Influence of saline water on intake, digesta kinetics, and serum profiles of steers. J Range Manag 45(6):514-518.

Köster HH, Cochran RC, Titgemeyer EC, Vanzant ES, Abdelgadir I, St-Jean G. 1996. Effect of increasing degradable intake protein on intake and digestion of low-quality, tallgrass-prairie forage by beef cows. J Anim Sci 74:2473-2481.

Kovacs P, Südekum KH, Stangassinger M. 1998. Effects of intake of a mixed diet and time post-feeding on amount and fibre composition of ruminal and faecal particles and on digesta passage from the reticulorumen of steers. Anim Feed Sci Tech 71(3):325-340.

Lechner I, Barboza P, Collins W, Fritz J, Günther D, Hattendorf B, Clauss M. 2010. Differential passage of fluids and different-sized particles in fistulated oxen, muskoxen, reindeer and moose: Rumen particle size discrimination is independent from contents stratification. Comp Biochem Physiol Part A Mol Integr Physiol 155(2):211-222.

Lechner I, Barboza P, Collins W, Günther D, Hattendorf B, Hummel J, Clauss M. 2009. No ‘bypass’ in adult ruminants: Passage of fluid ingested vs. fluid inserted into the rumen in fistulated muskoxen, reindeer and moose. Comp Biochem Physiol Part A Mol Integr Physiol 154(1):151-156.

Ledoux DR, Williams JE, Stroud TE, Garner GB, Paterson JA. 1985. Influence of forage level on passage rate, digestibility and performance of cattle. J Anim Sci 61(6):1559-1566.

Leite RF, Krizsan SJ, Figueiredo FO, Carvalho VB, Teixeira IA, Huhtanen P. 2015. Contribution of different segments of the gastrointestinal tract to digestion in growing Saanen goats. J Anim Sci 93(4):1802-1814.

McCollum F, Galyean M. 1985. Influence of cottonseed meal supplementation on voluntary intake, rumen fermentation and rate of passage of prairie hay in beef steers. J Agric Sci 60(2):570-577.

Merchen N, Firkins J, Berger L. 1986. Effect of intake and forage level on ruminal turnover rates, bacterial protein synthesis and duodenal amino acid flows in sheep. J Anim Sci 62(1):216-225.

Moolchand M, Wang J, Gui H, Shen Z. 2013. Ruminal butyrate infusion increased papillae size and digesta weight but did not change liquid flow rate in the rumen of goats. J Anim Plant Sci 23:1516-1521.

Moore J, Poore M, Swingle R. 1990. Influence of roughage source on kinetics of digestion and passage and on calculated extents of ruminal digestion in beef steers fed 65% concentrate diets. J Anim Sci 68(10):3412-3420.

Mulligan FJ, Quirke J, Rath M, Caffrey PJ, O’Mara FP. 2002. Intake, digestibility, milk production and kinetics of digestion and passage for diets based on maize or grass silage fed to late lactation dairy cows. Livest Prod Sci 74(2):113-124.

Ndlovu LR, Buchanan-Smith JG. 1985. Utilization of poor-quality roughages by sheep: effects of alfalfa supplementation on ruminal parameters, fiber digestion and rate of passage from the rumen. Can J Anim Sci 65:693-703.

Okeke G, Buchanan-Smith J, Grovum W. 1983. Effects of buffers on ruminal rate of passage and degradation of soybean meal in steers. J Anim Sci 56(6):1393-1399.

Oshita T, Sudo K, Nonaka K, Kume S, Ochiai K. 2008. The effect of feed regimen on chewing time, digesta passage rate and particle size distribution in Holstein non-lactating cows fed pasture ad libitum. Livest Sci 113:243-250.

Panjaitan T, Quigley SP, McLennan SR, Swain T, Poppi DP. 2010. Intake, retention time in the rumen and microbial protein production of Bos indicus steers consuming grasses varying in crude protein content. Anim Prod Sci 50(6):444-448.

Pond KR, Ellis WC, Matis JH, Deswysen AG. 1989. Passage of chromium-mordanted and rare earth-labelled fiber: time of dosing kinetics. J Anim Sci 67(4):1020-1028.

Rankins Jr DL, Bransby DI. 1995. Performance, dry matter intake, digesta kinetics, and ruminal fermentation of steers grazing Sorghum halepense at three stocking rates. Trop Grassl 29:102-110.

Robles AY, Belyea RL, Martz FA. 1981. Intake, digestibility, ruminal characteristics and rate of passage of alfalfa diets fed to sheep. J Anim Sci 53(3):774-779.

Schlecht E, Richter H, Fernández-Rivera S, Becker K. 2007. Gastrointestinal passage of Sahelian roughages in cattle, sheep and goats, and implications for livestock-mediated nutrient transfers. Anim Feed Sci Tech 137(1):93-114.

Shem MN, Ørskov ER, Kimambo AE. 1995. Prediction of voluntary dry-matter intake, digestible dry-matter intake and growth rate of cattle from the degradation characteristics of tropical foods. Anim Sci 60(1):65-74.

Silanikove N, Gilboa N, Nitsan Z. 2001. Effect of polyethylene glycol on rumen volume and retention time of liquid and particulate matter along the digestive tract in goats fed tannin-rich carob leaves. Small Ruminant Res 40(1):95-99.

Silanikove N, Tagari H, Shkolnik A. 1993. Comparison of rate of passage, fermentation rate and efficiency of digestion of high fiber diet in desert Bedouin goats compared to Swiss Saanen goats. Small Ruminant Res 12(1):45-60.

Tafaj M, Steingass H, Drochner W. 2001. Influence of hay particle size at different concentrate and feeding levels on digestive processes and feed intake in ruminants. 2. Passage, digestibility and feed intake. Arch Anim Nutr 54(3):243-259.

Varga GA, Prigge E. 1982. Influence of forage species and level of intake on ruminal turnover rates. J Anim Sci 55(6):1498-1504.

Yayota M, Karashima J, Kouketsu T, Nakano M, Ohtani S. 2009. Seasonal changes in the digestion and passage rates of fresh dwarf bamboo (*Pleioblastus argenteostriatus f. glaber*) in sheep. Anim Feed Sci Tech 149:89-101.

Appendix 4: Studies used in meta-analysis and modelling of rumen digesta load

Aitchison EM, Gill M, Dhanoa MS, Osbourn DF. 1986. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. Br J Nutr 56(2):463-476.

Akingbade AA, Hovell FDD. 1998. Effect of rumen fill on voluntary food intake and pattern of eating in Holstein steers. J Appl Anim Res 13(1-2):145-152.

Álvarez-Rodríguez J, Sanz A, Ripoll-Bosch R, Joy M. 2010. Do alfalfa grazing and lactation length affect the digestive tract fill of light lambs? Small Ruminant Res 94(1-3):109-116.

Bárcena-Gama R, Swingle RS, Moore JA, Poore MH. 2002. Effect of roughage source on ruminal kinetics and passage of individual feed components in finishing diets for steers. J Appl Anim Res 21(1):109-121.

Baumont R, Jailler M, Dulphy JP. 1997. Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay. Ann Zootech 46 (3):231-244.

Bayat AR, Rinne M, Kuoppala K, Ahvenjärvi S, Huhtanen P. 2011. Ruminal large and small particle kinetics in dairy cows fed primary growth and regrowth grass silages harvested at two stages of growth. Anim Feed Sci Tech 165(1-2):51-60.

Bayat AR, Rinne M, Kuoppala K, Ahvenjärvi S, Vanhatalo A, Huhtanen P. 2010. Ruminal large and small particle kinetics in dairy cows fed red clover and grass silages harvested at two stages of growth. Anim Feed Sci Tech 155(2-4):86-98.

Bines JA, Davey AWF. 1970. Voluntary intake, digestion, rate of passage, amount of material in the alimentary tract and behaviour in cows receiving complete diets containing straw and concentrates in different proportions. Br J Nutr 24(4):1013-1028.

Bines JA, Suzuki S, Balch CC. 1969. The quantitative significance of long-term regulation of food intake in the cow. Br J Nutr 23(3):695-704.

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

Bruining M, Bakker R, van Bruchem J, Tamminga S. 1998. Rumen digesta kinetics in dairy cows fed grass, maize and alfalfa silage. 1. Comparison of conventional, steady-state and dynamic methods to estimate microbial degradation, comminution and passage of particles. Anim Feed Sci Tech 73(1-2):37-58.

Cappellozza BI, Bohnert DW, Schauer CS, Falck SJ, Vanzant ES, Harmon DL, Cooke RF. 2013. Daily and alternate day supplementation of urea or soybean meal to ruminants consuming low-quality cool-season forage: II. Effects on ruminal fermentation. Livest Sci 155(2-3):214-222.

Carruthers VR, Bryant AM, Cockrem FRM, McLeay LM. 1988. Quantity of digesta in the reticulo-rumen of cows differing in susceptibility to bloat. New Zeal J Agr Res 31(2): 111-119.

Chilibroste P, Tamminga S, Van Bruchem J, Van der Togt PL. 1998. Effect of allowed grazing time, inert rumen bulk and length of starvation before grazing on the weight, composition and fermentative end-products of the rumen contents of lactating dairy cows. Grass Forage Sci 53(2):146-156.

Chiofalo V, Dulphy JP, Baumont R, Jailler M, Ballet JM. 1992. Influence of the method of forage conservation on feeding behaviour, intake and characteristics of reticulo-rumen content, in sheep fed ad libitum. Reprod Nutr Dev 32(4), 377-392.

Clemens ET, Maloiy GM. 1983. Digestive physiology of East African wild ruminants. Comp Biochem Physiol Part A Comp Physiol 76(2):319-333.

Conceição MGD, Ferreira MDA, Campos JMDS, Silva JDL, Detmann E, Siqueira MCBD, Barros LJAD, Costa CTF. 2016. Replacement of wheat bran with spineless cactus in sugarcane-based diets for steers. R Bras Zootec 45(4):158-164.

Daniel JLP, Nussio LG, Zopollatto M, Goulart RS, Santos VP, Toledo Filho SG. 2010. Volatile fraction from sugarcane silage and forage proportion on the ingestive behaviour of beef steers. In Schnyder H, Isselstein J, Taube F, Auerswald K, Schellberg J, Wachendorf M, Herrmann A, Gierus M, Wrage N, Hopkins A (Eds). Grassland in a changing world. Duderstadt: Mecke Druck und Verlag Grassland 527.

De Vega A, Poppi DP. 1997. Extent of digestion and rumen condition as factors affecting passage of liquid and digesta particles in sheep. J Agric Sci 128(2):207-215.

Demment MW, Van Soest PJ. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am Nat 125(5):641-672.

Dixon RM, Milligan LP. 1985. Removal of digesta components from the rumen of steers determined by sieving techniques and fluid, particulate and microbial markers. Br J Nutr 53(2):347-362.

Domingue BF, Dellow DW, Wilson PR, Barry TN. 1991. Comparative digestion in deer, goats, and sheep. New Zeal J Agric Res 34(1):45-53.

Domingue BF, Wilson PR, Dellow DW, Barry TN. 1992. Effects of subcutaneous melatonin implants during long daylength on voluntary feed intake, rumen capacity and heart rate of red deer (Cervus elaphus) fed on a forage diet. Br J Nutr 68(1):77-88.

Dulphy JP, Dardillat C, Jailler M, Jouany JP. 1994. Comparison of the intake and digestibility of different diets in Ilamas and sheep: a preliminary study. Ann Zootec 43(4):379-387.

Elsden SR, Hitchcock MWS, Marshall RA, Phillipson AT. 1946. Volatile acids in the digesta of ruminants and other animals. J Exp Biol 22:191-202.

Estrada JC, Delagarde R, Faverdin P, Peyraud JL. 2004. Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. Anim Feed Sci Tech 114(1-4):59-74.

Faichney OJ, Barry TN. 1986. Effects of mild heat exposure and suppression of prolactin secretion on gastro-intestinal tract function and temperature regulation in sheep. Aust J Biol Sci 39(1):85-98.

Froetschel MA, Amos HE. 1991. Effects of dietary fiber and feeding frequency on ruminal fermentation, digesta water-holding capacity, and fractional turnover of contents. J Anim Sci 69(3):1312-1321.

Froetschel MA, Croom Jr WJ, Hagler Jr WM, Argenzio RA, Liacos JA, Broquist HP. 1987. Effects of slaframine on ruminant digestive function: liquid turnover rate and fermentation patterns in sheep and cattle. J Anim Sci 64(4):1241-1248.

Gasa J, Holtenius K, Sutton JD, Dhanoa MS, Napper DJ. 1991. Rumen fill and digesta kinetics in lactating Friesian cows given two levels of concentrates with two types of grass silage ad lib. Br J Nutr 66(3):381-398.

Giesecke D, Van Gylswyk NO. 1975. A study of feeding types and certain rumen functions in six species of South African wild ruminants. J Agric Sci 85(1):75-83.

Golchin-Gelehdooni S, Teimouri-Yansari, A, Farhadi A. 2011. The effects of alfalfa particle size and acid treated protein on ruminal chemical composition, liquid, particulate, escapable and non-escapable phases in Zel sheep. Afr J Biotechnol 10(63): 13956-13967.

Gunter S, Judkins M, Krysl L, Broesder J, Barton R, Rueda B, Holcombe D. 1990. Digesta kinetics, ruminal fermentation characteristics and serum metabolites of pregnant and lactating ewes fed chopped alfalfa hay. J Anim Sci 68(11):3821-3831.

Hoppe PP, Qvortrup SA, Woodford MH. 1977. Rumen fermentation and food selection in East African Zebu cattle, wildebeest, Coke's hartebeest and Topi. J Zool 181(1):1-9.

Huhtanen P, Asikainen U, Arkkila M, Jaakkola S. 2007. Cell wall digestion and passage kinetics estimated by marker and in situ methods or by rumen evacuations in cattle fed hay 2 or 18 times daily. Anim Feed Sci Tech 133(3-4):206-227.

Huhtanen P, Dakowski P, Vanhatalo A. 1992. Composition, digestibility and particle-associated enzyme activities in rumen digesta as influenced by particle size and time after feeding. Anim Feed Sci Tech 1(3-4):223-235.

Jenks JA, Leslie Jr DM, Lochmiller RL, Melchiors MA. 1994. Variation in gastrointestinal characteristics of male and female white-tailed deer: implications for resource partitioning. J Mammal 75(4):1045-1053.

Jiang Z, Hamasaki S, Takatsuki S, Kishimoto M, Kitahara M. 2009. Seasonal and sexual variation in the diet and gastrointestinal features of the sika deer in western Japan: implications for the feeding strategy. Zool Sci 26(10):691-697.

Kammes KL, Allen MS. 2012. Nutrient demand interacts with forage family to affect digestion responses in dairy cows. J Dairy Sci 95(6):3269-3287.

Kaske M, Groth A. 1997. Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay. Reprod Nutr Dev 37(5):573-588.

Kaske M, Midasch A. 1997. Effects of experimentally-impaired reticular contractions on digesta passage in sheep. Br J Nutr 78(1):97-110.

Köster HH, Cochran RC, Titgemeyer EC, Vanzant ES, Abdelgadir I, St-Jean G. 1996. Effect of increasing degradable intake protein on intake and digestion of low-quality, tallgrass-prairie forage by beef cows. J Anim Sci 74(10):2473-2481.

Kovacs PL, Südekum KH, Stangassinger M. 1998. Effects of intake of a mixed diet and time post-feeding on amount and fibre composition of ruminal and faecal particles and on digesta passage from the reticulo-rumen of steers. Anim Feed Sci Tech 71(3-4):325-340.

Krämer M, Lund P, Weisbjerg MR. 2013. Rumen passage kinetics of forage-and concentrate-derived fiber in dairy cows. J Dairy Sci 96(5):3163-3176.

Leite RF, Krizsan SJ, Figueiredo FOM, Carvalho VB, Teixeira IAMA, Huhtanen P. 2015. Contribution of different segments of the gastrointestinal tract to digestion in growing Saanen goats. J Anim Sci 93(4):1802-1814.

Maloiy GMO, Clemens ET, Kamau JMZ. 1982. Aspects of digestion and in vitro rumen fermentation rate in six species of East African wild ruminants. J Zool 197(3):345-353.

McLeod MN, Kennedy PM, Minson DJ. 1990. Resistance of leaf and stem fractions of tropical forage to chewing and passage in cattle. Br J Nutr 63(1):105-119.

McQueen RE, Robinson PH. 1996. Intake behaviour, rumen fermentation and milk production of dairy cows as influenced by dietary levels of fermentable neutral detergent fiber. Can J Anim Sci 76(3):357-365.

Moyo M, Adebayo RA, Nsahlai IV. 2018. Effects of roughage quality, period of day and time lapse after meal termination on rumen digesta load in goats and sheep. Asian-Austral J Anim Sci 31(8):1183-1196.

Nandra KS, Hendry A, Dobos RC. 1993. A study of voluntary intake and digestibility of roughages in relation to their degradation characteristics and retention time in the rumen. Anim Feed Sci Technol. 43(3-4):227-237.

Oshita T, Sudo K, Nonaka K, Kume S, Ochiai K. 2008. The effect of feed regimen on chewing time, digesta passage rate and particle size distribution in Holstein non-lactating cows fed pasture ad libitum. Livest Sci 113(2-3):243-250.

Panjaitan T, Quigley SP, McLennan SR, Swain T, Poppi DP. 2010. Intake, retention time in the rumen and microbial protein production of *Bos indicus* steers consuming grasses varying in crude protein content. Anim Prod Sci 50(6):444-448.

Pinares-Patiño CS, Waghorn GC, Machmüller A, Vlaming B, Molano G, Cavanagh A, Clark, H. 2007. Methane emissions and digestive physiology of non-lactating dairy cows fed pasture forage. Can J Anim Sci 87(4):601-613.

Poore MH, Moore JA, Swingle RS. 1990. Differential passage rates and digestion of neutral detergent fiber from grain and forages in 30, 60 and 90% concentrate diets fed to steers. J Anim Sci 68(9):2965-2973.

Prins RA, Geelen MJH. 1971. Rumen characteristics of red deer, fallow deer, and roe deer. J Wildl Manag 673-680.

Ramzinski DM, Weckerly FW. 2007. Scaling relationship between body weight and fermentation gut capacity in axis deer. J Mammal 88(2):415-420.

Rankins Jr DL, Bransby DI. 1995. fermentation of steers grazing Sorghum halepense at three stocking rates. Trop Grassl 29:102-110.

Sibbald AM, Milne JA. 1993. Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (*Cervus elaphus*). J Agric Sci 120(1), 99-102.

Silanikove N, Gilboa N, Nitsan Z. 2001. Effect of polyethylene glycol on rumen volume and retention time of liquid and particulate matter along the digestive tract in goats fed tannin-rich carob leaves (*Ceratonia siliqua*). Small Ruminant Res 40(1):95-99.

Staaland H, Jacobsen E, White RG. 1979. Comparison of the digestive tract in Svalbard and Norwegian reindeer. Arct Alp Res 11(4):457-466.

Stanley TA, Cochran RC, Vanzant ES, Harmon DL, Corah LR. 1993. Periparturient changes in intake, ruminal capacity, and digestive characteristics in beef cows consuming alfalfa hay. J Anim Sci 71(3):788-795.

Stensig T, Weisbjerg MR, Hvelplund T. 1998. Evaluation of different methods for the determination of digestion and passage rates of fibre in the rumen of dairy cows. Acta Agric Scand A-Anim Sci 48(3):141-154.

Tahas SA, Martin Jurado O, Hammer S, Arif A, Reese S, Hatt JM, Clauss M. 2017. Gross measurements of the digestive tract and visceral organs of addax antelope (*Addax nasomaculatus*) following a concentrate or forage feeding regime. Anat Histol Embryol 46(3):282-293.

Tjardes KE, Buskirk DD, Allen MS, Ames NK, Bourquin LD, Rust SR. 2002. Neutral detergent fiber concentration of corn silage and rumen inert bulk influences dry matter intake and ruminal digesta kinetics of growing steers. J Anim Sci 80(3):833-840.

Van Hoven W, Boomker EA. 1981. Feed utilization and digestion in the black wildebeest (Connochaetes gnou, Zimmerman, 1780) in the Golden Gate Highlands National Park. S Afr J Wildl Res 11(2):35-40.

Waghorn GC, Shelton ID, Sinclair BR. 1990. Distribution of elements between solid and supernatant fractions of digesta in sheep given six diets. New Zeal J Agr Res 33(2):259-269.

Waghorn GC. 1986. Changes in rumen digesta of cows during a restricted feeding period when offered fresh red clover, lucerne, or lucerne hay. New Zeal J Agric Res 29(2):233-241.

Wickersham TA, Cochran RC, Titgemeyer EC, Farmer CG, Klevesahl EA, Arroquy JI, Johnson DE, Gnad DP. 2004. Effect of postruminal protein supply on the response to ruminal protein supplementation in beef steers fed a low-quality grass hay. Anim Feed Sci Technol 115(1-2):19-36.

Williams YJ, Doyle PT, Egan AR. 2014. Diurnal variation in rumen fill of dairy cows grazing Persian clover at different pasture allowances. Anim Prod Sci 54(9):1388-1393.

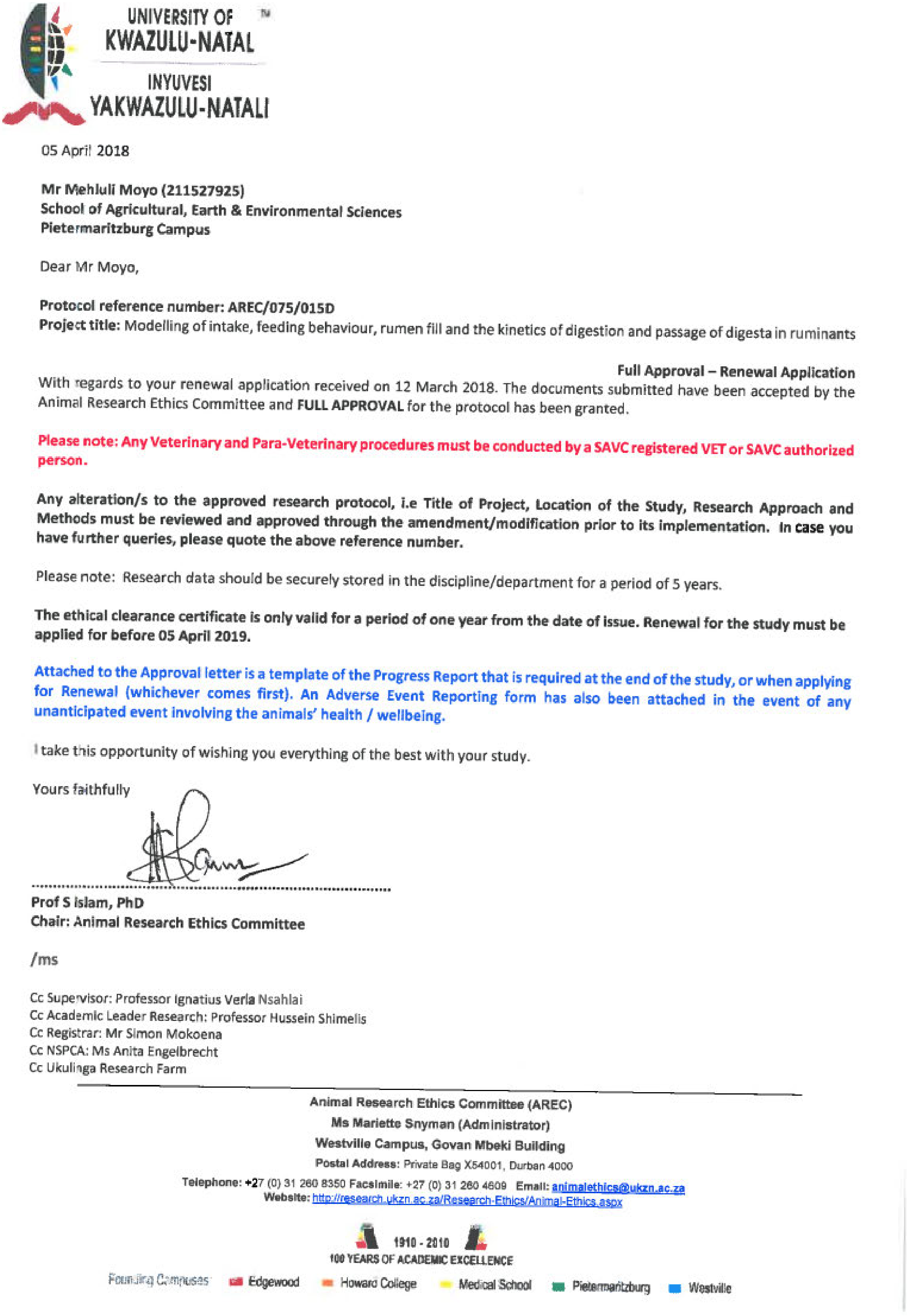
Yansari T, Hamidi A, PirMohamadi R, Azary M. 2007. Rumen contents and ruminal digesta particle size distribution in buffalo steers fed three different size of alfalfa. Ital J Anim Sci 6(sup2):429-443.

Appendix 5: Sample of R-code program used for development of Random Forest models

```
# loading packages
> library(caret)
> library(randomForest)
> require(caTools)
> require(dplyr)
> library(pastecs)
> library(writexl)

# loading of data
> data <- read.csv(file.path(“C:\\Users\\Documents”, “ANN TSE.csv”),
stringsAsFactors=FALSE, header=TRUE)

# summarising and checking whole data
> summary(data)
> sapply(data, class)
> dim(data)
> correlations <- cor(data[,1:18])
> print(correlations)

# splitting data into training and validation datasets, 70% for training and 30% for
validation.
> set.seed(2019)
> sample = sample.split(data$output, SplitRatio = 0.7)
> train = subset(data, sample == TRUE)
> test = subset(data, sample == FALSE)

# summarising training and validation datasets
> dim(train)
> dim(test)

# model development to determine the optimal mtry value to avoid over- or underfitting
the model
```

```
> trainControl <- trainControl (method=”repeatedcv”, number=10, repeats=3,
search=”random”)
> set.seed(12345)
> rfTSE <- train (TSE~., data=train, method=”rf”, metric=”RMSE”, tuneLength=15,
trControl=trainControl)
> print(rfTSE)
> FinalrfTSE <- randomForest (TSE~., train, mtry=8, ntree=2000)
> print (FinalrfTSE)

 # making predictions on test and train dataset using the final model
> PredictionsTSEtest <- predict (FinalrfTSE, test)
> PredictionsTSEtrain <- predict (FinalrfTSE, train)
> PredictionsTest <- data.frame (actualTest=test$TSE, predictionTest=PredictionsTSEtest)
> PredictionsTrain <- data.frame (actualTrain=train$TSE,
predictionTrain=PredictionsTSEtrain)

# saving model
> saveRDS (FinalrfTSE, “./FinalrfTSE.rds”)

# using the saved model to make predictions
> data <- read.csv(file.path(“C:\\Users\\Documents”, “ANN TSE.csv”),
stringsAsFactors=FALSE, header=TRUE)
> RFTSE <- readRDS(“./FinalrfTSE.rds”)
> Predictions <- predict(RFTSE, data)
> PredictionsAll <- data.frame(actualAll=data$TSE, predictionAll=Predictions)

# export predictions to excel
> write_xlsx(as.data.frame(PredictionsTest), path=”PredictionsTest.xlsx”)
> write_xlsx(as.data.frame(PredictionsTrain), path=”PredictionsTrain.xlsx”)
> write_xlsx(as.data.frame(test), path=”test.xlsx”)
> write_xlsx(as.data.frame(train), path=”train.xlsx”)
> write_xlsx(as.data.frame(PredictionsAll), path=”PredictionsAll.xlsx”)
```

Appendix 6: Animal ethics certificate



UNIVERSITY OF KWAZULU-NATAL™
INYUVESI YAKWAZULU-NATALI

05 April 2018

Mr Mehluli Moyo (211527925)
School of Agricultural, Earth & Environmental Sciences
Pietermaritzburg Campus

Dear Mr Moyo,

Protocol reference number: AREC/075/015D
Project title: Modelling of intake, feeding behaviour, rumen fill and the kinetics of digestion and passage of digesta in ruminants

Full Approval – Renewal Application

With regards to your renewal application received on 12 March 2018. The documents submitted have been accepted by the Animal Research Ethics Committee and **FULL APPROVAL** for the protocol has been granted.

Please note: Any Veterinary and Para-Veterinary procedures must be conducted by a SAVC registered VET or SAVC authorized person.

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 05 April 2019.

Attached to the Approval letter is a template of the Progress Report that is required at the end of the study, or when applying for Renewal (whichever comes first). An Adverse Event Reporting form has also been attached in the event of any unanticipated event involving the animals' health / wellbeing.

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

Yours faithfully

....

Prof S Islam, PhD
Chair: Animal Research Ethics Committee

/ms

Cc Supervisor: Professor Ignatius Verla Nsahlai
Cc Academic Leader Research: Professor Hussein Shimelis
Cc Registrar: Mr Simon Mokoena
Cc NSPCA: Ms Anita Engelbrecht
Cc Ukulinga Research Farm

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