



Department of
Primary Industries



Final report

Revise Australian feeding standards to better achieve product specifications and improve ruminant efficiency

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Abstract

The Australian feeding standards were developed throughout the 1980s culminating in the publication “Feeding Standards for Australian Livestock – Ruminants” in 1990 (SCA, 1990). The standards were based largely upon the UK system (ARC, 1980) but adapted and expanded upon to better reflect the livestock and conditions prevalent in Australia. The standards were significantly updated in 2007 with the publication “Nutrient Requirements of Domesticated Ruminants” (CSIRO, 2007). In the intervening years the genetics of ruminant livestock have changed in response to selecting for higher production rates and the feedbase has also changed. In particular the prediction of empty body weight and protein and fat composition was considered to no longer reflect commercial conditions. There was also poor understanding of the relationship between live body weight and empty body weight. Thus, the conversion of energy in the diet to production of muscle, fat, empty body and, ultimately, live body weight was no longer fit for purpose in defining the energy requirements on modern ruminants.

A novel model that divides the body into two pools for energy metabolism has been developed and evaluated. Energy expenditure in the viscera is handled separately to energy expenditure in the remainder of the empty body, as viscera is a more dynamic and energy hungry component of the empty body.

The current project has developed an improved model for estimation of body composition and hence energy requirements for maintenance, growth and reproduction, an improved model for estimation of voluntary feed intake and a technique for measuring the energy cost of activity under extensive grazing conditions. The current approach has greatly improved upon the understanding of energy requirements and advances our understanding beyond a notion of static efficiencies for maintenance and growth. Ongoing model development has expanded the concept to include reproductive ruminants and to account for the energy requirements of activity. This new model can be used with current measures of feed energy values and is capable of being expanded into a full replacement for Australian feeding standards for ruminants at all stages of production.

New models will be incorporated into existing programs, for example; GrazFeed, BeefSpecs, Drought and Supplementary Feed Calculator (DASFC) and CSIROs CLEM. Further work is required to link models with other decision support tools (DSTs) and explore adoption/user pathways.

Executive summary

Background

The Australian feeding standards were developed throughout the 1980s culminating in the publication “Feeding Standards for Australian Livestock – Ruminants” in 1990 (SCA, 1990). The standards were based largely upon the UK system (ARC, 1980) but adapted and expanded upon to better reflect the livestock and conditions prevalent in Australia. The standards were significantly updated in 2007 with the publication “Nutrient Requirements of Domesticated Ruminants” (CSIRO, 2007). In the intervening years the genetics of ruminant livestock have changed in response to selecting for higher production rates and the feedbase has also changed. In particular the prediction of empty body weight and protein and fat composition was considered to no longer reflect commercial conditions. There was also poor understanding of the relationship between live body weight and empty body weight. Thus, the conversion of energy in the diet to production of muscle, fat, empty body and, ultimately, live body weight was no longer fit for purpose in defining the energy requirements on modern ruminants.

Objectives

This project will revise the Australian Feeding Standards to:

- include prediction of body composition to inform efficiency metrics and predict market- related attributes of fatness, yield, and MSA score
- better predict nutrient requirements and responses to supplementation of cattle on seasonally and spatially heterogeneous low-quality diets
- account for genetic variation in traits including efficiency of feed utilisation
- further develop and refine a dynamic rumen model utilizing new data on rumen function and rumen microbiology in particular on prediction of microbial protein supply and energy digestion.

Methodology

A novel model that divides the body into two pools for energy metabolism has been developed and evaluated. Energy expenditure in the viscera is handled separately to energy expenditure in the remainder of the empty body, as viscera is a more dynamic and energy hungry component of the empty body.

Results/key findings

The current project has developed an improved model for estimation of body composition and hence energy requirements for maintenance, growth and reproduction, an improved model for estimation of voluntary feed intake and a technique for measuring the energy cost of activity under extensive grazing conditions. The current approach has greatly improved upon the understanding of energy requirements and advances our understanding beyond a notion of static efficiencies for maintenance and growth. Ongoing model development has expanded the concept to include reproductive ruminants and to account for the energy requirements of activity. This new model can be used with current measures of feed energy values and is capable of being expanded into a full replacement for Australian feeding standards for ruminants at all stages of production.

Benefits to industry

New models will be incorporated into existing programs, for example; GrazFeed, BeefSpecs, Drought and Supplementary Feed Calculator (DASFC) and CSIROs CLEM. Further work is required to link models with other decision support tools (DSTs) and explore adoption/user pathways.

Future research and recommendations

More data is required in a number of areas to improve the models, including:

- Variation in mature size and composition by breed/sex.
- Examine variation in feed intake by genotype.
- Data from animals at/near maintenance to finalise values for k_p and k_f more.
- Better representation of effect of feed characteristics on k_m and on viscera (not just M/D, but fibre, type of feed or other feed components).
- Develop similar models for cattle.

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1. Background and need for model development

1.1 Importance of Livestock Models

Science-based systems for allocating feed to productive purposes in ruminant livestock have been under systematic development for more than 120 years. Ferrell and Oltjen (2008) provide an historical perspective of the development of ruminant feeding systems and net energy systems in particular. The development of feeding systems has been strongly influenced by their intended purpose: initially feeding systems were primarily designed to assign different feeding values to feeds to allow cost effective allocation of scarce resources, such as the starch equivalent system developed in Europe (Kellner, 1909) or the physiological fuel values developed by Atwater (see Armsby, 1903). To achieve this meant that animal responses to the different feed sources needed to be quantified, which has been accomplished via a variety of methods (Ferrell and Oltjen, 2008). Most animal responses were, and still are, quantified in practical terms as changes in liveweight; although energy is the currency from which weight, and weight change, is calculated.

In Australia, the purpose to which feeding systems have been put has shifted from allocation of feed to livestock during drought, to intensive feeding operations (sheep and cattle feedlots) and more recently to assisting with feed allocation, including supplementation, in pasture-based systems. These underpin products such as GrazFeed (Freer et al., 1997) and GrassGro (Moore et al., 1997) and simpler applications such as the Drought (<https://www.dpi.nsw.gov.au/animals-and-livestock/nutrition/feeding-practices/drought-feed-calculator-app>) and Drought and Supplementary Feeding Calculators (<https://www.dpi.nsw.gov.au/animals-and-livestock/nutrition/feeding-practices/drought-and-supplementary-feed-calculator>), which are available as apps for livestock producers. These applications help end users select the lowest cost feed to achieve growth performance. However, growth and hence liveweight gain are associated with variation in potential product yield and quality, mainly through association of growth with fatness as animals progress towards physiological maturity and therefore increasing fatness, as fat depots develop later than protein or bone. Tools to assist end users increase compliance with carcass specifications have been developed and used to assist end users better comply with meat quality standards at least in cattle (BeefSpecs, BeefSpecs drafting tool, <https://www.mla.com.au/extension-training-and-tools/tools-calculators/beefspecs-calculator/>) and tools that explicitly relate growth with carcass yield and estimated eating quality in live cattle are under development (McPhee et al., 2020).

A common feature of these new tools is the need to integrate nutrient inputs with estimation of body composition and liveweight. This requires a shift in the order in which feeding standards calculate liveweight gain from nutrient intake. Present feeding systems (including SCA, 1990: CSIRO, 2007) derive liveweight gain from energy transactions in the animal by estimating the energy content of the body from historical relationships between weight and liveweight gain. They then assign different efficiency of feed energy use to different functions (maintenance, growth, pregnancy, lactation) on the basis of estimated energy content and from this calculate liveweight gain (or gain of conceptus or milk production). There is no consistent method for estimating change in body composition across different feeding systems. The PISC derives change in liveweight gain and gain in the empty body, and then partitions it into energy and fat within each unit of empty body gain according to feeding level and relative maturity but does not provide a method to estimate extant levels of fat and protein within animals. Conversely, the current US sheep NRC feeding standards address changes of body composition primarily with regard to mature females, and changes in composition are calculated based on perceived changes in body condition score, rather than from any inherent accretion or depletion of fat and protein due to direct changes in liveweight.

Since the 1980's alternate methods of integrating nutrient supply and estimation of body composition have been developed. These range from an understanding of and computer modelling of biochemical pathways in the

animal and the rumen as envisaged by Baldwin and Black (1979), to simplifications that utilize basic assumptions about how animals grow and Hess's law of constant heat summation. This law, briefly described, is that regardless of how many intermediate steps occur in a reaction, the total change in energy is the sum of all changes. This approach was subsequently embodied in the extreme case by the simplifications used in energy systems developed by Blaxter ARC, Lofgreen and Garrett NRC and in a dynamic form in a model of beef cattle growth devised by Oltjen et al. (1986). The advantage of the dynamic form is it produces a more realistic representation of the continuous response of an animal as protein and fat deposition vary in response to variation in nutrient input. The simpler additive systems, although easier to use without computer assistance, show discrete changes in animal energy content and liveweight response to changes in nutrient supply but do not readily convert the energy content of the animal into protein and fat, nor can they adequately represent cases where one pool may be increasing at the expense of the other, such as situations where animals may be losing fat but gaining protein. This is especially key for representing responses to situations like drought or illness and predicting an animal's ability to regain their growth potential.

2. Why is it necessary to better estimate body composition within feeding standards?

Sale of livestock is increasingly moving to payment for fit with market specifications. For sheep meat that process is not yet as advanced as for beef cattle where producers sell into various grids defined by estimated carcass weight, fatness, MSA grade, and in some markets, total denuded meat yield. There is ongoing research into better ways to describe animals pre-slaughter and as carcasses which is anticipated will increase alignment of price with compliance to specifications (e.g. ALMTech project – <https://www.almtechau.com/>). Cost to industry of not meeting specifications for beef cattle has variously been estimated as from \$55m pa to \$280m pa (MLA reports). The BeefSpecs suite of tools (Walmsley et al., 2014, McPhee et al., 2014) was originally designed as a tool to assist producers increase compliance with specifications of live cattle within the Marketing module of More Beef From Pastures (<https://mbfp.mla.com.au/meeting-market-specifications/>). The science used in the BeefSpecs tools uses data originally obtained from research conducted within the Beef Co-operative Research Centres (1993-2015), and a model of body composition derived from work at the USDA Meat Animal Research Centre (Keele et al., 1992). Recent developments include establishment of methods within the BeefSpecs framework to estimate total denuded lean, intramuscular fat and potential MSA grade in beef cattle (McPhee et al. 2020).

For practical purposes, the BeefSpecs tools use producer inputs such as animal growth rate instead of nutrient input. This constrains capability to provide advice on alternate methods to alter nutrient supply (supplementation, change in feed supply) to achieve targets when pasture conditions deteriorate. To achieve that requires a better method to integrate changes in nutrient supply with changes in body composition so that prediction of animal performance is improved, and the costs of changing management can be easily calculated. This is also key for enabling producers to better target feeding management to help animals bounce back from drought or other times of growth restriction, so that animals can be grown to achieve market specifications in a cost and feed efficient manner. However, current systems have difficulty predicting compensatory growth and its subsequent effects on carcass fat and lean yields, and do not integrate the nutritional needs of animals to allow remedial management actions to be taken.

In addition to the above, improved farm or animal breeding model performance requires better methods to estimate body composition in response to variation in nutrient supply in sheep and cattle than currently available. For example, following suggestions that stocking rates for maternal ewes were inadequately represented in the MIDAS model using the equations in the Australian feeding standards (Young et al., 2014) a

number of targeted studies were conducted to ascertain the basis for uncertainty (MLA Project L.LSM.0008 – Blumer et al. 2019).

These concluded “During the recalibration process for whole farm modelling, 1) the energy value of gain and 2) the impact of relative condition on potential intake were two components highlighted as being the least robust. However, both of these components have the potential to significantly impact the guidelines and profitability. Differences in both the relative condition on intake, and energy value of gain were considerable between the animal house experiments and there are a number of plausible reasons (experimental design, genotype, starting maturity/leanness/fatness/body composition). Therefore it is recommended that these are areas requiring further data collection to support accurate estimation of these parameters in economic analysis.”

Australian feeding standards (CSIRO, 2007) underpin the phenotype models used in BreedObject (<http://www.breedobject.com/>) to estimate economic value of traits for genetic selection in beef cattle. To improve BreedObject, Brad Walmsley has expressed the need for improved estimation of composition of gain to achieve 2 objectives. One is to improve modelling of energy cost of change in condition score of cows, the other is to better estimate the cost of finishing cattle to different market specifications.

3. Objectives

This project will revise the Australian Feeding Standards to:

- include prediction of body composition to inform efficiency metrics and predict market- related attributes of fatness, yield, and MSA score
- better predict nutrient requirements and responses to supplementation of cattle on seasonally and spatially heterogeneous low-quality diets
- account for genetic variation in traits including efficiency of feed utilisation
- further develop and refine a dynamic rumen model utilizing new data on rumen function and rumen microbiology in particular on prediction of microbial protein supply and energy digestion

Specifically, this milestone will revise the feeding standards through:

- Revision of the method used in feeding standards to estimate feed intake by livestock in extensive pasture systems where a spatially and temporally heterogeneous forage base elicits a strong behaviour driver for nutrient intake.
- Identify where critical data is not available and design or reanalyse independent studies to obtain such data to fill the gaps. This approach will enable a strong case to be made for new targeted R & D to obtain missing data that can immediately be used in a comprehensive framework to build industry-applicable decision support tools.

In this report (Milestone 8 a,b,c), we describe the compilation of information from previous reports and highlight where data is required and future developments.

3.1 Success in meeting objectives

The report describes several components, including the following:

- Model for heat production and body composition in sheep.
- Activity, gestation and lactation.
- Rumen model and nutrient supply.
- Framework for pasture intake that accounts for variable pasture morphology in tropical feeds.
- Review of tropical pasture intake.
- Further models required and future developments

4. Methodology

4.1 Methods and data used

The project team (Drs. Oddy, Dougherty, Evered, Clayton, Black and Oltjen) contributed to this work through face-to-face meetings (when Prof. Oltjen visited Armidale from UC Davis for several weeks in November 2019) and by sharing work through email and Zoom meetings. The work process was iterative and involved shared discussions around model structure, process to simplify parameter and search for independent data to justify parameter values, and in the case of the Sainz et al. (1995) data, provide direct access to the original data courtesy of Prof. Oltjen. Dr. Clayton obtained an extensive collection of energy balance data on different feeds in sheep and cattle from the literature and directly from original sources at the Rowett Research Institute and the ADAS Feed Evaluation unit in the UK.

Data sources for development and evaluation were derived from comparative slaughter studies in which animals had different prior growth rates generated by different dietary regimens, followed by growth determined by constrained energy intake due to either controlled intake on the same diet, or ad-libitum intake of diets of different composition (energy density). Composition of the empty body was obtained by chemical analysis of carcass, soft tissues (viscera) skin and head and hooves (sheep and Trangie cattle study) or by estimation of carcass composition by specific gravity and remaining tissues by chemical analysis (1 cattle study). The reason to choose such studies was to maximise the impact of prior plane of nutrition on body composition to provide a range of responses to subsequent nutrition. This reflects real world exposure of the animal to variable nutrition to a greater extent than data used to generate the original PISC equations.

An example of the different growth trajectories in the data used is shown in Figure 1 (from Hegarty et al., 1999). In Hegarty et al., (1999), ME content of feed (M/D) was derived from measurements of digestibility and nitrogen (N) balance made during the study, using a constant correction for energy lost as methane.

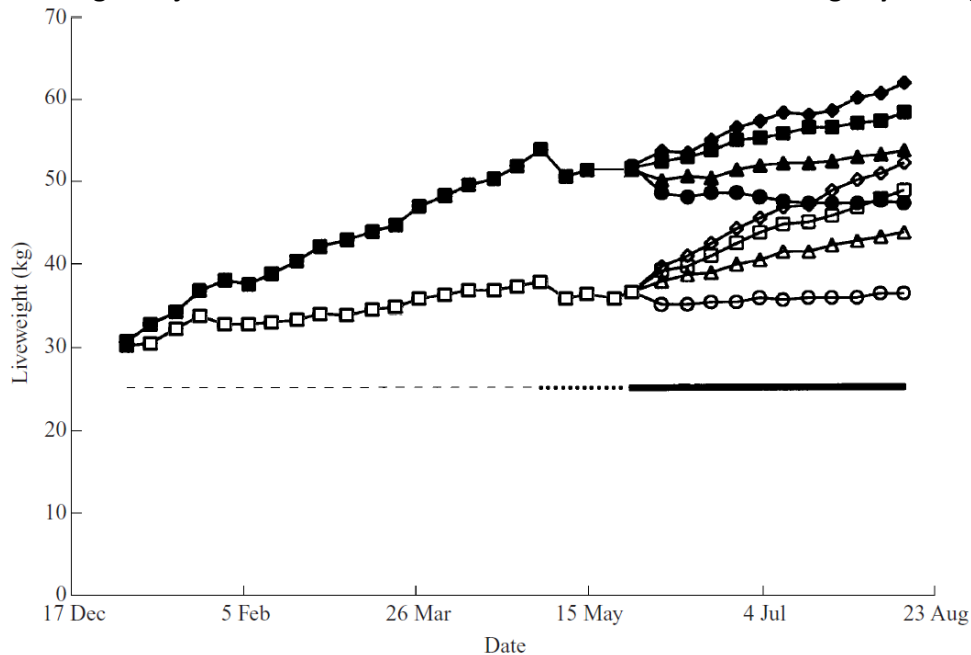
Figure 4.1. Weight trajectories of restricted and unrestricted lambs from Hegarty et al. (1999).

Fig. 1. Lamb liveweights throughout experiment. Lambs were initially allocated to either HIGH (solid symbols) or LOW planes of nutrition (hollow symbols), and six lambs were slaughtered. After this 18-week introductory period (-----) a further cohort group of eight lambs (4 HIGH, 4 LOW) were slaughtered and lambs adjusted to a fixed intake (LOW 500 g, HIGH 850 g/day) for 4 weeks. At the end of this adjustment period (-----) another cohort group of 4 HIGH and 4 LOW lambs was killed and the 16 experimental diets were fed to the remaining 96 lambs for 12–15 weeks (——). For clarity, liveweights are averaged for protein inclusions at each feed intake (○: 500, △: 850, □: 1200, ◇: 1500 g as fed/day).

Figure 4.1 above shows the weight trajectory of animals from the DAN 56-1 experiment reported on in Hegarty et al. (1999), indicating that compensatory gain was induced in animals that had been previously restricted.

The method for estimating model parameters is shown in Appendix 1. Model estimates of protein and fat in empty body were compared with observed values and those obtained using PISC equations. The root mean square prediction errors (RMSPE) obtained by the difference between observed and predicted estimates were calculated using R (R Core Team, 2020; RStudio, 2020) and expressed as a % of observed mean. The primary data sources used for simulation are shown in Appendix 2.

Wherever possible during model development, values for model parameters were derived from first principles and compared to published data. An example of this process is outlined in Appendix 3.

5. Model for heat production and body composition in sheep

A series of publications are being prepared outlining the development of the model describing heat production and body composition in sheep. Full papers will be available for the Final Report. A summary of the research that will be incorporated into these publications that were presented at the EAAP International Symposium on Energy and Protein Metabolism and Nutrition (ISEP) are presented below.

5.1 Paper 1 – Model Structure

Estimation of energy transactions and body composition in sheep

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Introduction

Traditional feeding systems calculate energy transactions from fasting heat production and energy density of the feed. Body composition is calculated from fixed relationships between fat and protein content of weight and weight gain (Freer et al., 2007). This empirical approach attributes variation in energy retained and heat produced (HP) to variation in energy intake (MEI) and dietary energy density (M/D) and fails to adequately capture the relationship between feed eaten and prior growth pattern on the gain of protein and fat in the period in which animals transition to the new equilibrium state.

However, in growing animals, HP also arises from changes in body composition (fat and protein) and composition of gain. A simple way has been devised to combine these two approaches to calculate total HP in growing sheep. Here we describe simple dynamic model that mechanistically represents heat production and protein and fat gain to estimate composition of gain in both the short and longer term. It uses the observation that heat production is proportional to feed intake, protein content and gain of protein and fat of the body, and that the protein in visceral organs accounts for at least 50% of energy expended in the body (Oddy et al., 2019). Energy not deposited as protein or lost as heat is deposited in fat.

Current ruminant feeding systems (Freer et al. 2007, NASEM 2007, NASEM 2016) calculate energy transactions as the sum of energy used for maintenance and growth/production, with associated efficiencies (k_m and k_g) for the conversion of feed energy toward these purposes. These efficiencies reflect the amount of heat (HP) produced from using metabolizable energy from feed (MEI) for maintenance and gain. Growth is predicted from Net Energy available for gain (NE_g), where NE_g is calculated as the difference between energy intake and energy expended for maintenance. In these systems, body composition is calculated from an empirical relationship between Retained Energy (RE, which is partitioned into energy retained in protein and fat), body weight (BW) and body weight gain (BWG). The quantitative relationships between energy transactions for growth use estimates of partial efficiency of energy use for maintenance and gain where partial efficiency is a measure of the heat produced (lost) to deposit protein, fat or that associated with feed intake.

The underlying basis for variation in heat loss from ingested feed in growing ruminants is complex and has been attributed to a range of mechanisms including – conversion of energy yielding substrates, principally VFA, to ATP (Blaxter 1962), protein turnover and Na-K ATPase activity (Baldwin 1999, McBride et al. 1985) relative differences in size of organs with different energy expenditure (Ferrell 1988). Baldwin and Black (1979) outlined a framework to incorporate these sources of variation in responses of animal growth to feed into a computer program. Subsequent workers (Baldwin et al, 1987; Black et al 1987; Gill et al, 1989) have incorporated aspects

of metabolic control of nutrient utilisation into research scale models, without explicit consideration of effects of relative contributions of different organs. Di Marco and Baldwin (1989) and Di Marco et al. (1989) developed a model that simplified organ size and turnover into 2 pools (viscera and non-viscera) and metabolism. These research models have demonstrated feasibility but suffer from data requirements far beyond current feeding systems.

Oltjen et al. (1986) introduced a simplified model of growth using a single protein pool and energy transactions derived from the California Net Energy system. At the time it predicted growth at least as well as the NRC (1976), but it underpredicted fatness on high energy diets. An alternate approach using 2 protein pools and the SCA (Corbett et al. 1990) system for energy transactions was developed by Soboleva et al. (1999) using data from the complex growth path studies of sheep Ferrell et al. (1986). This model was further developed by Oltjen et al. (2006) who suggested an alternate form of HP may be used. Oddy et al. (2019) suggested that HP could be calculated internally from the amount and gain of protein in fast (visceral organs) and slow (non-visceral, predominantly carcass) turnover protein pools. Partition into fast and slow pools was on that basis that energy expenditure (oxygen consumption) was strongly related to rate of turnover of protein in these different organ classes.

The work described here extends the model of Oltjen et al. (2006) by calculating HP internally within the model. It features revised protein pool equations and the addition of a wool protein pool. This paper describes the development of the revised model and the use of new data to evaluate its performance versus that of current Australian sheep feeding systems (CSIRO, Freer et al. 2007).

Materials & Methods

Underlying Assumptions

The work presented here is based on axioms of animal growth articulated in Soboleva et al. (1999) and elsewhere in the history of this model (Oltjen et al. 1986, Oltjen et al. 2000, Oltjen et al. 2006, Oddy et al. 2019, 2021, 2022; Dougherty et al. 2020, 2022a,b,c,d). Specifically:

1. Growth is driven by energy intake, and for purposes of this model, other nutrients (amino acids, vitamins, minerals) are assumed nonlimiting.
2. Protein in the fleece-free empty body can be classified into two pools based on relative turnover rates and their respective rates of energy use/heat production per gram of tissue protein:
 - a. A smaller protein pool consisting of tissues with high rates of protein turnover and high specific heat production. This pool, called viscera (v), consists of the empty gut, liver, kidneys, heart, and lungs.
 - b. A larger pool with a slower turnover rate and lower heat production per unit of tissue protein. This pool, called "muscle" (m), contains not just muscle protein but protein in all non-visceral tissues in the fleece-free empty body (skin, head, hocks, blood, brain, etc).
 - c. Wool (w) is a separate protein pool and is a protein sink
3. Protein in visceral and non-visceral pools have their own respective upper bounds.
 - a. In non-visceral tissue, this upper bound, m^* , is defined as mature protein mass and is calculated from mature size and composition, factoring in the effects of breed and sex.
 - b. In visceral protein, this upper bound, v^* , is a function of feed intake, feed characteristics, and the relative maturity of the animal. This is not a fixed target like m^* . Because visceral tissues are more sensitive to energy supply than non-visceral tissues, v^* represents "equilibrium" visceral mass for a given feed and feeding level, and stage of maturity of the animal.

4. When energy intake is close to the point where retained energy (RE) equals 0, animals can gain protein while mobilizing fat. This potential diminishes in non-visceral tissue as animals reach maturity, but not in viscera or in wool.
5. Gain of protein in the non-visceral (“muscle”) pool is proportional to net energy available for gain (NEG) and relative protein deposition potential, as defined by the animal’s relative maturity.
6. Energy not lost as heat production, or used for protein gain in wool, viscera, or non-visceral tissue, is deposited as fat.

Description of Previous Version of Model

Oltjen et al. (2006) used lamb growth and body composition data from Ferrell et al. (1986) to evaluate and investigate a prior version of the model (Soboleva et al. 1999, Oltjen et al. 2000).

The model of Oltjen et al. (2006) is:

$$dm/dt = k_m \times (NEG + c_m \times f_a) \times (1-m/m^*) \quad [1]$$

$$f_a = (1-m/m^*)^{e_2} \quad [2]$$

$$dv/dt = k_v \times (v^*-v) \quad [3]$$

$$v^* = (cs_1 \times MEI) + (cs_2 \times m) \quad [4]$$

$$df/dt = NEG - dm/dt - dv/dt \quad [5]$$

$$NEG = MEI - HP \quad [6]$$

$$HP = b_1 \times m + b_2 \times v + b_3 \times dm/dt + b_4 \times dv/dt \quad [7]$$

$$dEBW/dt = ((dm/dt + dv/dt) / (23800 \times 0.2201)) + (df/dt \times 39600) \quad [8]$$

Where v and m are the visceral and non-visceral pools as described above, f is the fat pool, NEG is net energy available for gain, all in KJ. In equations 1-8, k_m and k_v are rate constants for the partition of retained energy (RE) into muscle and viscera, respectively; $c_m f_a$ is an adjustment to account for continued deposition of protein in muscle when retained energy is negative, and the terms c_m , e_2 , cs_1 , cs_2 , b_1 , b_2 , b_3 , and b_4 are constants. As described above, m^* is the upper bound on the m pool, representing non-visceral protein at maturity, and v^* is the upper bound on visceral crude protein for a given level of intake (MEI) and animal size (m). Change in empty body weight (EBW) is calculated from the change in the energetic content of the protein and fat pools (KJ/d), where 0.2201 is the crude protein content of 1kg of fat-free tissue, and 23800 and 39600 are the energy density (KJ/kg) of protein and fat, respectively. This was the starting point for the revised model presented here.

Statistical Analysis

The model was developed in R (R Core Team, 2022) as a dynamic, mechanistic model with a daily timestep. The coefficients in the revised v^* equation were estimated from experimental data (Oddy et al. 1997, Hegarty et al. 1999, Dougherty et al. 2022a) via multiple regression in Minitab (Minitab LLC, 2022) as described below. However, the parameters of the heat production equations presented required a simultaneous nonlinear approach, as the set of differential equations for muscle, viscera, and fat is solved numerically but the parameter values to be estimated affect all three tissue pools. Parameter estimation and optimization must therefore consider the different scales and variances of these pools, as well as the covariances of the residuals.

Parameters were estimated in simultaneous equations by minimising the determinant of the residual matrix. This corresponds to the maximum likelihood estimate for multivariate normal residuals, as described in Bates and Watts (1988).

Initial parameter estimates were derived from literature values and then parameter estimation for the simultaneous nonlinear set of equations was performed using the L-BFGS-B (Byrd, 1995) and Nelder and Mead (1965) methods of the R 'optim' function (R Core Team, 2023) to minimise the determinant of the residual matrix of muscle, viscera and fat using growing lamb data from Hegarty et al. (1999) and Dougherty et al. (2022a). Standard errors of parameters fitted with optim() were obtained as in Steenbergen, (2006). This was cross-checked using the Metro_Hastings function from the MHadaptive package (Chivers, 2012) to estimate parameter values and correlations using Markov Chain Monte Carlo methods and a Metropolis-Hastings algorithm with 100,000 runs (Tanner, 1996).

Prediction error was calculated as the determinant of the residuals matrix for the response variables (muscle protein, visceral protein, and fat). Parameter values were varied within a specified range and relative error for a specific parameter was calculated iteratively by running the model with the specific parameter value, taking the determinant of the residuals matrix, and dividing that value by the lowest value of the determinant from prior runs in that range of parameter value runs.

Results & Discussion

Model Revision & Parameter Estimation – Retained Energy

The major changes from Oltjen et al. 2006 are a) inclusion of wool in the protein pools and b) reworking of the manner in which heat production is represented. The representation of the muscle and viscera pools were refined using more comprehensive data than available in Ferrell et al. 1986. The representation of a fat pool (*f*) as shown above in equation 5, remains unchanged from Oltjen et al. 2006.

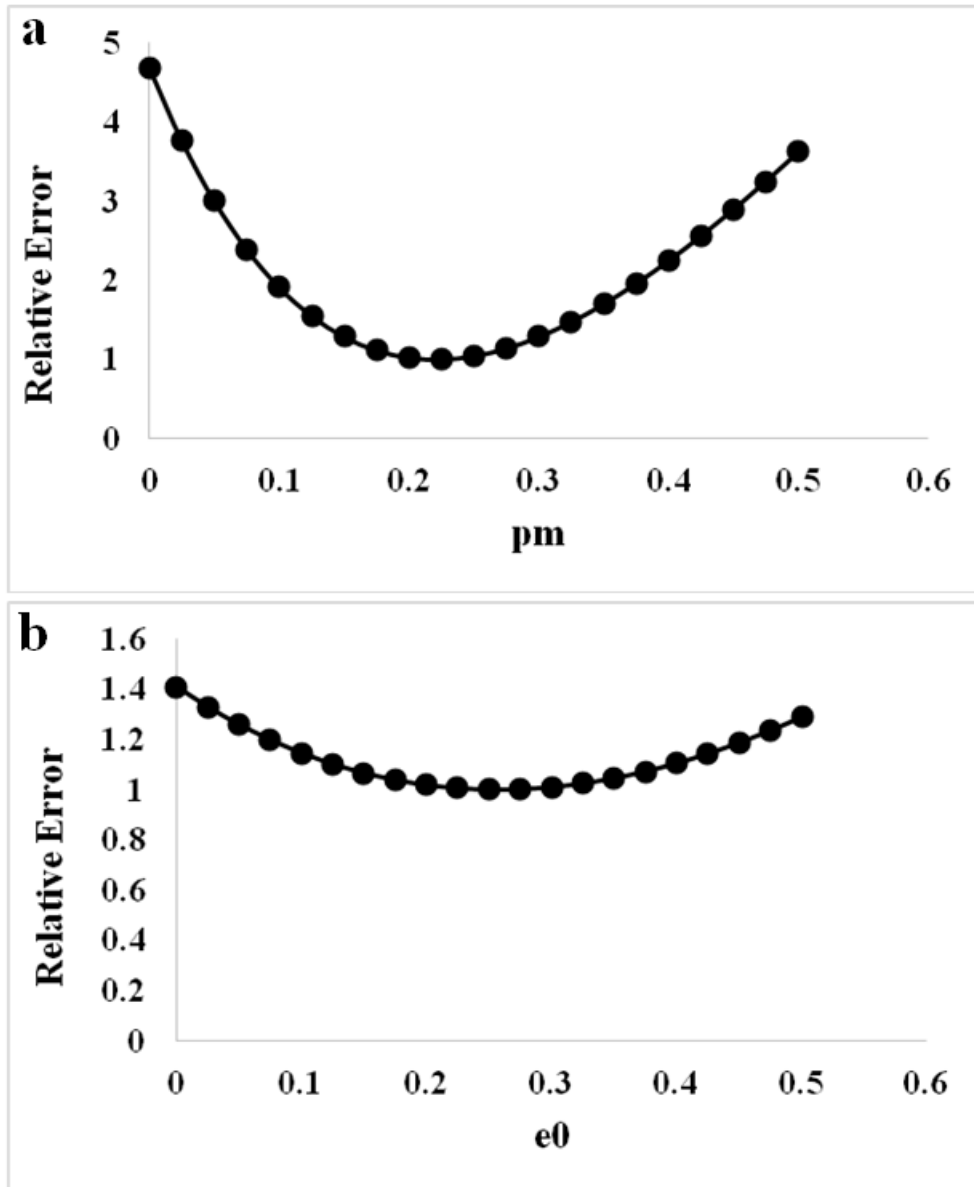
Non-Visceral Empty Body Protein

The non-visceral pool, “muscle” (*m*) contains protein in the non-visceral empty body (NVEB) as defined above. Oltjen et al. (2006) examined the data from Ferrell et al. (1986) and obtained values of $e_2 = 3.4$ and $c_m = 1340$ kJ/d for the continued protein gain in the NVEB pool equations when $NEG < 0$ (equations 1 and 2, as described above). However, when these equations were fit to the data of Hegarty et al. (1999) and Dougherty et al. (2022a), the value for e_2 was determined to be 0.25 (SE 0.99); i.e. not different from zero. Accordingly, the value of equation 2 approaches 1 and can be subsumed into equation 1 with a single term e_0 to account for protein gain when $NEG < 0$, as shown in equation 9.

$$dm/dt = (p_m \times NEG + e_0) \times (1 - m/m^*) \quad [9]$$

An initial independent estimate for p_m was obtained from data on protein gain measured by A-V difference in the hindlimb of growing lambs (Early et al. 1988; Harris et al. 1992; Oddy and Owens 1996) and an estimate of NEG from the same data. This suggested that p_m may lie in the range of 0.18-0.24. On the basis of a summary of the literature reporting the relationship between nitrogen and energy balance (Black and Griffiths 1975, Graham 1964 a,b,c; 1969, Wainman et al. 1970) and from the hindlimb AV difference studies summarised in Oddy (1993), a value for e_0 between 0.16-0.3 MJ/d was expected. When p_m and e_0 were fitted simultaneously to data from Hegarty et al. (1999) and Dougherty et al. (2022a), the values obtained were $p_m = 0.226 (\pm 0.016)$ (Fig. 5.1a) and $e_0 = 0.2486 (\pm 0.034)$ (Fig. 5.1b).

Figure 5.1. Relative error vs values for (a) pm and (b) $e0$ fitted one at a time against data from Hegarty et al. (1999) and Dougherty et al. (2022a). Relative error was calculated iteratively by running the model with the specific parameter value, taking the determinant of the residuals matrix, and dividing that value by the lowest value of the determinant from prior runs in the range of parameter values used.



Mature NVEB protein mass (m^*) is calculated from standard reference weight (SRW; Freer et al. 2007) and mature body composition as described by Dougherty et al. (2020, 2022b). As sheep mature and m approaches m^* , the rate of protein in the non-visceral body deposition declines (e.g. Thompson et al. 1985, Butterfield 1988).

Dougherty et al. (2020, 2022b) provided a method to calculate m^* from SRW but noted the importance of accounting for variation in mature body composition by breed and sex. The CSIRO (Freer et al. 2007) model defines SRW as the average fleece-free weight of mature ewe in average condition, while NASEM (2007) states that a mature sheep at SRW is assumed to contain approximately 25% fat. However, data from continuous

growth of animals suggest that fatness at maturity (SRW) can be over 40% (Searle and Griffiths, 1976; Butterfield, 1988). Additional data on variation in mature size and composition is needed to more accurately underpin estimates of SRW and/or m^* to improve the ability of the model to capture variation in mature size and its effects on animal growth rates.

Visceral Protein

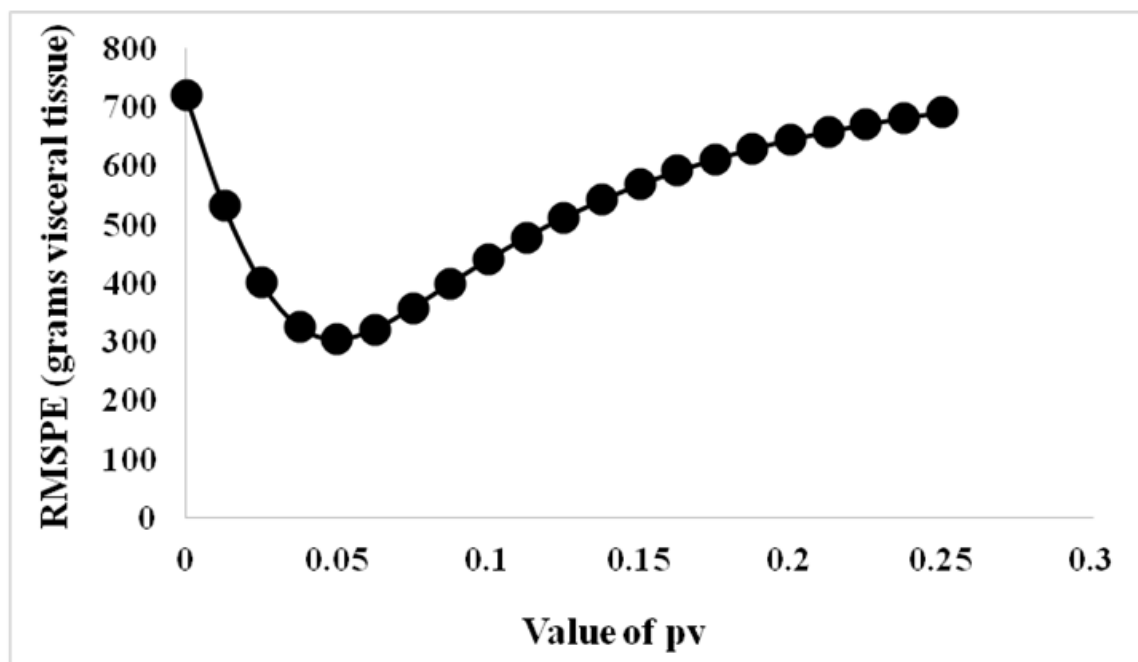
Visceral protein (v) refers to protein in visceral tissue i.e. empty reticulo-rumen and gastrointestinal tract, liver, kidneys, heart, and lungs. Visceral protein in the revised model is calculated as described by Oltjen et al. 2006:

$$dv/dt = p_v \times (v^* - v) \quad [3]$$

Where p_v (k_v in Oltjen et al. 2006) is the rate of change in visceral organ protein energy content following a change in energy intake, and v^* is the upper bound of protein in viscera.

Estimation of p_v requires data on visceral protein mass measured during the period in which viscera is responding to change of feeding level. Studies in which data on oxygen uptake by the splanchnic bed (Burrin et al. 1989) and in which visceral organ weights were recorded at 14 d intervals (Burrin et al. 1990) were used to derive an estimate of p_v of 0.05 (Figure 5.2). This value of p_v is similar to 0.093, the value obtained by Freetly et al. (1995) for the rate constant for change in O_2 consumption by the splanchnic bed; it is also similar to the value for the lag in energy expenditure (0.05, corresponding to a lag of 20 days) derived by Soboleva et al. (1999) using the data of Ferrell et al. (1986).

Figure 5.2. RMSPE (grams of visceral tissue) versus value of p_v for data from Burrin et al. (1990).



The target to which visceral protein mass is attracted is v^* . In practice, it is the mass of visceral protein achieved after 8 weeks of eating the same feed (estimated from data of Burrin et al, 1990 and Freetly et al, 1995).

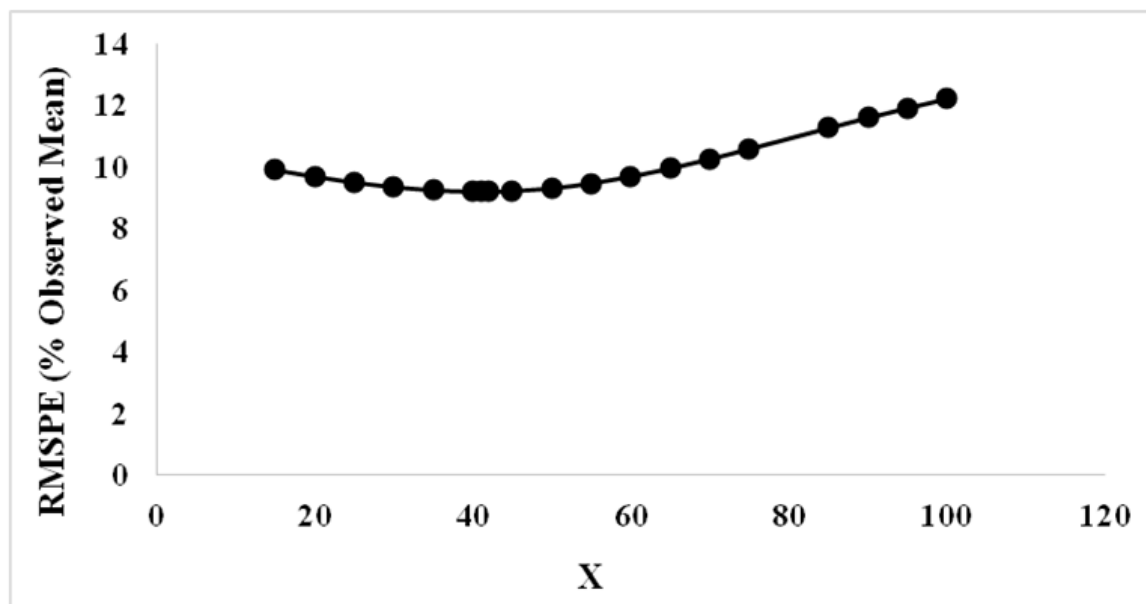
Analysis of data from Hegarty et al. (1999) and Dougherty et al. (2022a) using pelleted diets, and Oddy et al. (1997) who used mixtures of hays and protein supplements, indicated that MEI, energy density of the feed (M/D) and mass of NVEB protein affected visceral protein mass as shown in equation 10.

$$v^* = C_{MEI} \times MEI + C_m \times (m^{0.41}) - C_{MD} \times M/D \quad [10]$$

Where C_{MEI} , C_m , and C_{MD} are coefficients describing the effects of energy intake, non-visceral protein, and dietary energy density (M/D, MJ/kg DM) on v^* , respectively, as described in Oddy et al. (2021).

The v^* term was derived from data in growing sheep eating different amounts of a range of diets (Oddy et al. (1997), Hegarty et al. (1999), and Dougherty et al. (2022a)). Records were selected from lambs that had been fed the same diet for at least 42d prior to slaughter and v^* was estimated by regressing observed visceral protein against MEI (MJ/d), dietary energy density (M/D, MJ ME/kg DM) and non-visceral protein (m) in the fleece-free empty body (FFEB). The curvilinear relationship between v^* and m (Figure 5.3) is consistent with observations by Butterfield (1988) that visceral tissues are “early maturing”, i.e. that they achieve maximum mass prior to other body tissues.

Figure 5.3. RMSPE (%Observed Mean) for visceral protein (MJ) versus exponent on muscle crude protein (M^x) in v^* equation.



The equation for v^* is:

$$v^* = 0.679 (\pm 0.024) \times MEI + 1.895 (\pm 0.100) \times m^{0.41} - 0.4344 (\pm 0.075) \times M/D \quad [11]$$

Using the data used to develop equation 11 the RMSPE for visceral protein was 1.49 MJ (9.21% of the observed mean) with a mean bias of -0.0017 MJ (-0.07g). When applied only to the data of Hegarty et al. (1999) and Dougherty et al. (2022a), the RMSPE for visceral protein was 9.24% of the observed mean, with mean bias of 0.27 MJ (11.3g), indicating that there are still some unresolved differences in estimating either v^* or dv/dt for pelleted compared to chopped hay diets. This is not dissimilar to the observations of Blaxter and Boyne (1978) that k_m of pelleted and chopped diets was best estimated separately for the different types of feeds. Future

research should examine this relationship across a wider range of diets and stages of animal maturity; however, due to data limitations it was not feasible for the present study.

Wool Growth

Daily clean wool growth is calculated based on the methods of CSIRO (Freer et al. 2007, Freer et al. 2012) and is calculated as a lagged function of the weighted sum of today's daily (instantaneous) wool growth (W_t) and the prior day's wool growth (dw/d_{t-1}), where:

$$dw/dt = (0.96 \times dw/d_{t-1}) + (0.04 \times W_t) \quad [12]$$

$$W_t = W_{Br} \times W_Z \times MEI \times (23.8/1000) \quad [13]$$

The W_t term is a function of breed (W_{Br}), energy intake (MEI), and relative maturity (W_Z), where Z = current liveweight/standard reference weight (SRW). The CSIRO model (Freer et al., 2007) calculates W_Z as a function of age; however, the revised model calculates W_Z as a function of empty body weight (EBW) and current fleece weight relative to SRW. The CSIRO model also includes a basal level of wool growth in maintenance, which is then subtracted from predicted wool growth to calculate NE available for gain that is retained in the wool pool. The model presented here does not include this offset; it calculates total clean wool growth and energy retained in wool protein.

Wool growth is an important part of sheep production and metabolism but is often omitted from studies on growth and body composition. Wool is a protein sink and cannot be mobilized to support bodily protein or energy requirements, unlike muscle and viscera. However, at low levels of growth and/or intake, such as in mature animals or animals close to maintenance, a large proportion of nitrogen and therefore energy balance is retained in wool (Hegarty et al. 1999, Dougherty et al. 2022a). Accordingly, if total RE is close to or at zero, wool growth and its concomitant RE gain requires the mobilization of resources from the rest of the body (Hegarty et al. 1999, Dougherty et al. 2022a), which then has implications for the sheep's ability to mobilize body stores to support the m pool (e_0 in the model presented here). It is essential to include wool to obtain a realistic estimate of the efficiency of energy use for protein gain in the whole-body, as discussed below.

Heat Production

Oltjen et al. (2006) suggested an alternate for calculation of heat production could be:

$$HP = b_1 \times m + b_2 \times v + b_3 \times dm/dt + b_4 \times dv/dt \quad [7]$$

Where b_1 ... b_4 represent heat produced per unit of protein mass or their respective rates of change. Estimates of b_1 ... b_4 were obtained from fitting to the data of Ferrell et al. (1986). Oddy et al. (2019) attempted to derive estimates of b_1 through b_4 independently from blood flow and A-V data of oxygen and amino acid fluxes. They found that estimates of b_1 and b_2 were identifiable, b_3 was somewhat identifiable, but it was not possible to independently estimate b_4 , the oxygen consumption (heat production) associated with visceral protein gain because of inability to quantify protein gain due to the simultaneous deposition and secretion of protein from the liver and gastrointestinal tract. Attempts to fit equation 7 to data from Ferrell et al. 1986, Hegarty et al. (1999) and Dougherty et al. (2022a) by combining dm/dt and dv/dt to dP/dt (where $dP/dt = dm/dt + dv/dt$) to estimate HP from protein gain did not improve the fit to the data. Moreover, the fitting process consistently found a portion of HP was associated with MEI.

The form of the equation that best fit the data of Ferrell et al. 1986, Hegarty et al. (1999) and Dougherty et al. (2022a) was:

$$HP = b_1 \times m + b_2 \times v + b_0 \times MEI \quad [14]$$

$b_m \times m + b_v \times v$ and Fasting Heat Production

Graham et al. (1974) summarised a range of studies of fasting heat production in sheep (FHP, called BMR in Graham et al. 1974), some of which had different growth rates prior to measurement. In these studies, Graham observed a near linear relationship between fat-free tissue mass of weaned sheep and FHP and noted that there was systematic variation in FHP due to prior growth rate and feed intake. Ferrell (1988) presented data to show that much of the variation in FHP was due to variation in visceral organ size. Subsequent studies (Eisemann & Neinaber 1990; Reynolds et al. 1991; Ortigues & Durand 1995) have demonstrated that the splanchnic bed (liver, reticulorumen and gastrointestinal tract) has a rate of oxygen consumption as much as 10 times higher than peripheral tissues (predominantly muscle). It is now well established that rate of oxygen consumption and rate of protein turnover varies across organs and tissues (Reynolds 2002). Ortigues & Durand (1995) observed that in sheep fed at maintenance and half maintenance, the splanchnic bed accounts for approximately half the energy expenditure in the body.

The findings discussed above show that variation in the proportion of visceral and non-visceral tissues contributes to the variation in FHP due to prior feed intake and stage of maturity. This is represented in the model as shown in Equation 11, which explicitly represents the effect of prior feed intake on v^* and subsequently on dv/dt and when integrated across time, v . Accordingly $b_m \times m + b_v \times v$ varies with prior level of feeding and stage of maturity. Moreover, Dougherty et al. (2021) used this approach to demonstrate that our model can recapitulate the relationship between FHP and EBW, and FHP and fat free mass reported in sheep by Graham et al. (1974).

Fasting heat production has been shown to be relatively constant per kg liveweight and $LWT^{0.75}$ in the same animal over extended periods of time (Blaxter, 1962). FHP is used as the baseline for energy expenditure in most feeding systems (ARC 1980; Freer et al. 2007; NASEM2007). FHP is considered by convention to be linearly related to $EBW^{0.75}$, and the basis for the exponent of 0.75 has been subject to intense speculation. By using the construct above, which assigns HP to the protein in low (NVEB) and high (viscera) energy expenditure tissues, Dougherty et al. (2021) showed that we can reconstruct the relationship between HP and EBW and FFEBW reported by Graham et al. (1974). This strongly suggests that the relationship between FHP and LWT is a function of the proportion of protein in the NVEB and viscera as well as the fat content of the body.

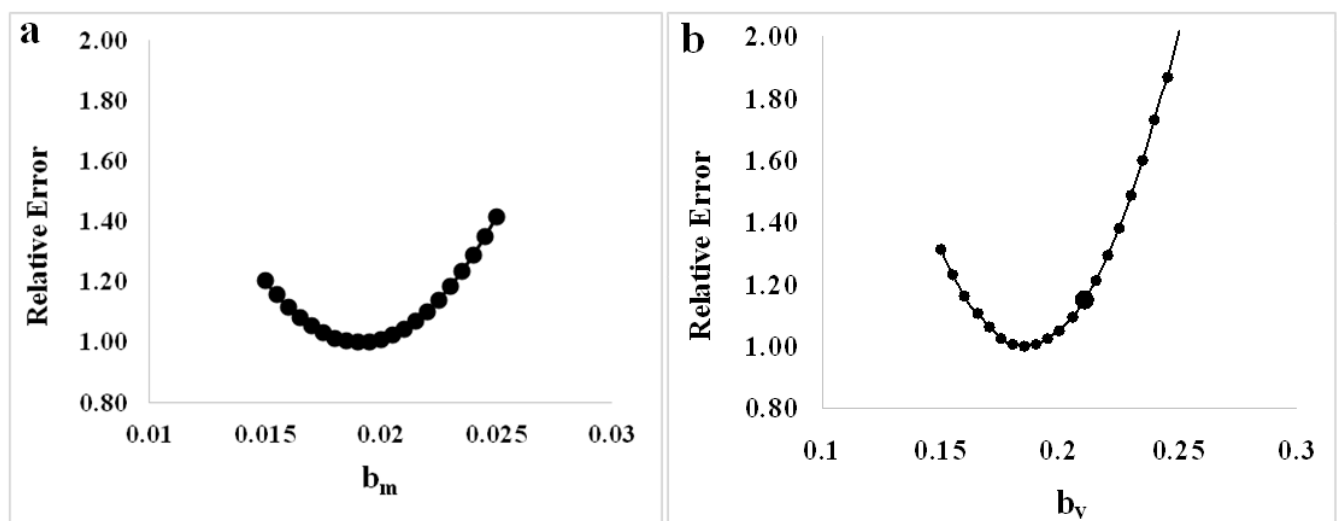
As MEI approached 0, $b_m \times m + b_v \times v$ approached FHP, so that in principle:

$$FHP = b_m \times m + b_v \times v \quad [15]$$

Initial estimates of b_m and b_v were obtained by setting MEI to 0, using the FHP observed by Graham et al. (1974) and the observation of Ortigues & Durand (1995) that in sheep fed between half maintenance and maintenance, half of the whole-body oxygen consumption (HP) was generated by the splanchnic bed. Initial values of non-visceral empty body protein and visceral protein were derived from the proportion of tissue masses in the fat-free mass summarised in Butterfield (1988), and the proportion of protein in NVEB (0.21) and viscera (0.16) reported by Dougherty et al. (2020).

The initial estimates of b_m (0.017) and b_v (0.17) were similar those subsequently obtained from fitting b_m and b_v to data from lambs fed a range of diets predominantly above maintenance (Hegarty et al. 1999, Dougherty et al. 2022a) vis b_m (0.019 ± 0.0057) and b_v (0.185 ± 0.048). Equation 15 represents variation in FHP due to variation in body composition and the proportion of viscera. This allows for representation of the effects of prior level of feeding on FHP, as seen elsewhere (Marston 1948, Graham et al. 1974, Ferrell et al. 1986).

Figure 5.4. Relative error vs parameter values for b_m and b_v obtained from the combined dataset of Hegarty et al. (1999) and Dougherty et al. (2022a). Relative error was calculated as described in Figure 5.1.



What is $b_0 * MEI$?

Approximately 30% of MEI is converted to heat at or below maintenance (i.e. $RE = 0$). There is systematic variation due to the type of feed eaten (pellets, forages, mixed diets) and the ME density (metabolisability) of the feed, as summarised by Blaxter and Boyne (1978). This is represented in ME-based systems as k_m , the efficiency of ME use for maintenance, where $k_m = FHP/ME_m$. On average, for sheep on forage-based diets k_m as calculated from M/D has a mean value of 0.7, such that $1 - 0.7 = \sim 0.3$ of ME eaten is lost as heat (Blaxter & Boyne 1978, Clayton et al. 2022). Heat loss associated with feed intake at or below maintenance is attributed to cost of eating, rumen fermentation, digestion and excretion. It has been assumed that when $RE > 0$, the efficiency of gain (k_g) is due to variation in composition of feed (Lofgreen & Garrett 1968, Blaxter & Boyne 1978, ARC 1980, NASEM 2007, NASEM 2016, Oltjen 2019), composition of gain (Rattray et al. 1973; Ferrell et al. 1979) or a combination of both (Williams and Jenkins, 2003, Tedeschi, 2019). Williams and Jenkins (2003) developed a construct to describe HP above maintenance as:

$$MEI - ME_m = RE + H_iE_r + H_iE_v \quad [16]$$

Where H_iE_r is heat produced from fat and protein gain and H_iE_v is heat produced from support functions and is proportional to MEI.

Williams and Jenkins (2003) then presented evidence that heat produced above maintenance due to everything other than gain of protein and fat (kH_iE_v/kME_m from Table 5.4 and Table 5.5 of Williams and Jenkins 2003a) was 30-33% of MEI, and was a relatively constant proportion of the feed eaten across a range of breeds of cattle. This proportion of heat produced by support functions is similar to the accepted mean for heat associated with MEI at and below maintenance ($1-k_m$, where $k_m \sim 0.7$, ~ 0.3 of MEI), and suggests that the arguments used to justify HP as a function of MEI below maintenance (cost of eating, rumen fermentation, digestion and excretion) could also apply above maintenance and contribute to the variation in HP associated with gain.

Not accounting for HP due to MEI above RE=0 overestimates HP due to protein and fat gain. For example, estimates of the partial efficiency of protein and fat gain using multiple regression, which assumes no loss of energy due to eating the additional feed above maintenance other than that due to energy cost of protein and fat deposition, are 12-13% for protein and 67% for fat (Rattray et al. ,1973; Ferrell et al., 1979). The efficiency of protein gain estimated as above (12-13%) is substantially less than the mean of that reported in other species ($\sim 47\%$; Owens et al. 1995). The corresponding estimate of efficiency of fat gain (67%) is also less than the mean of that reported in other species (76%, Owens et al. 1995) and theoretical costs of fat synthesis (70-72%, Baldwin 1968).

We incorporated the ideas of Williams and Jenkins (2003) into our understanding of the $b_0 \cdot MEI$ term by extending the concept of heat produced by support functions above maintenance but explicitly describing it as the heat associated with feeding (termed HAF hereafter) generally (above and below maintenance). The heat produced by gain of protein and fat is as H_pE , the heat of product formation (NRC, 1981).

This allows a description of total HP as:

$$HP = FHP + H_pE + HAF \quad [17]$$

Where FHP = $b_m \times m + b_v \times v$ as described above

Heat associated with gain of protein can be calculated as $(1/k_p) - 1$ and with heat associated gain of fat as $(1/k_f) - 1$. Therefore :

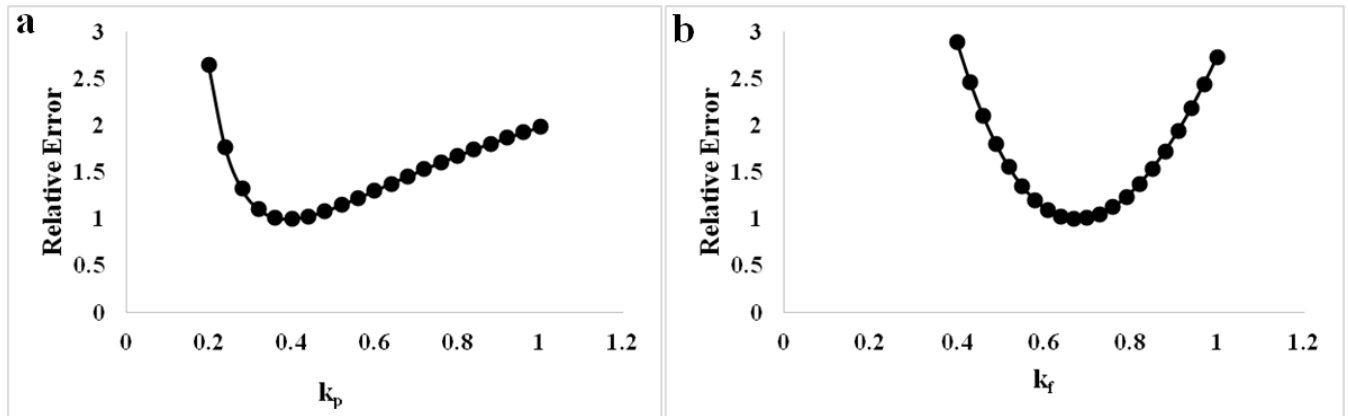
$$H_pE = ((1/k_p) - 1) \times dP/dt + ((1/k_f) - 1) \times df/dt \quad [18]$$

and HAF = heat associated with MEI (at any level of feeding) can be calculated by iteratively fitting values for k_p , k_f and HAF to data. The estimate of HAF derived in this way for the data of Hegarty et al. 1999 and Dougherty et al. 2022 is $b_{MEI} \times MEI$, where $b_{MEI} = (1-k_m)$ or 0.3 for an average k_m value of 0.7.

It is not possible to obtain useful estimates of the heat produced from gain of protein, gain of fat and heat associated with feeding using multiple regression because of the high correlations between $(MEI - ME_m)$, dP/dt and df/dt (see Bernier et al, 1987). Accordingly, an iterative process was used in which estimates of heat produced by fat and protein gain, and that associated with MEI were informed by consensus estimates obtained from various sources in the literature including independent and theoretical estimates and iteratively tested in the entire model to determine goodness of fit for the final traits. Since the model simultaneously predicts multiple traits (i.e. final m , v , and f), goodness of fit was calculated as the determinant of the residuals matrix for these traits (Bates and Watts, 1988). Using this approach, the estimates of k_p , k_f and b_{MEI} which provided the best fit of the model were values of 0.4, 0.7 and 0.3 for k_p , k_f and b_{MEI} respectively. Using this approach, the estimate of HP from MEI available for gain of 30%, and partial efficiency of 0.7 for fat gain, estimates of partial efficiency of protein gain are 0.4, much closer to values observed in monogastric species (Owens et al, 1995) and

more in line with the energetic efficiency of protein gain calculated from the rate of whole-body protein synthesis relative to protein gain observed in growing lambs (Oddy et al, 1997).

Figure 5.5. Relative error vs values for (a) k_p and (b) k_f fitted one at a time against data from Hegarty et al. (1999) and Dougherty et al. (2022a). Relative error was calculated as described in Figure 5.1.

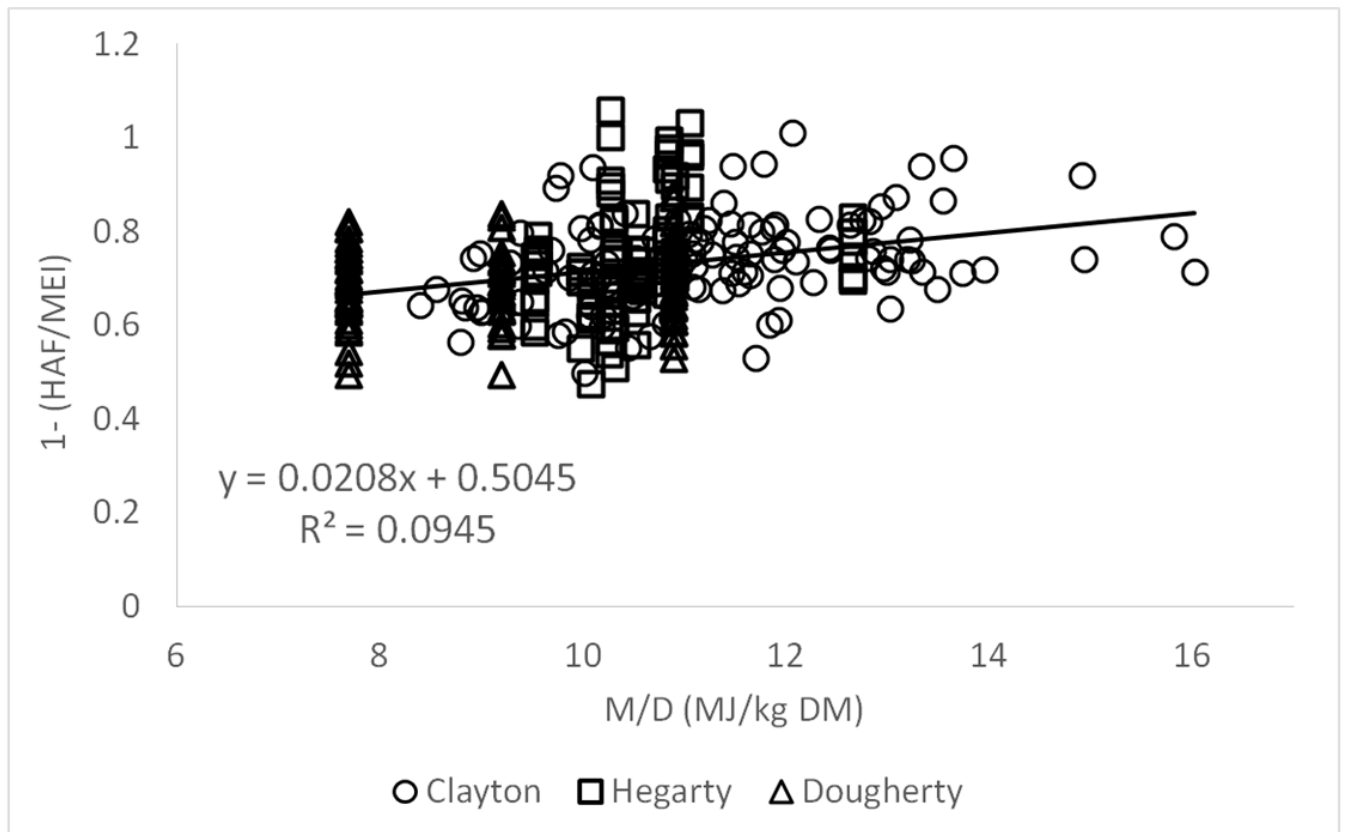


It is possible that HAF, like k_m (which is equivalent to $1-(\text{HAF}/\text{MEI})$ at all levels of feeding), is systematically related to M/D as in traditional feeding systems (Freer et al. 2007, NASEM 2007, 2016). In Figure 5.6, we overlaid the relationship between $1-(\text{HAF}/\text{MEI})$ and M/D obtained with data from Hegarty et al. (1999) and Dougherty et al. (2022a) for animals with intakes predominantly greater than maintenance upon that of k_m vs M/D from the 91 ruminant calorimetry studies examined by Clayton et al. (2022). For the sake of this exercise, we have decided that k_m as determined from independent data (Clayton et al. 2022) and $1-(\text{HAF}/\text{MEI})$ as determined from Hegarty et al. (1999) and Dougherty et al. (2022a) are equivalent, and are related to heat associated with feeding (HAF), where HAF is $(b_{\text{MEI}} \times \text{MEI})$ or $(1-k_m) \times \text{MEI}$. The data points from the animals fed above maintenance fit within the data cloud used to estimate the relationship between relationship between M/D and k_m at or below maintenance. Although, when fitted to the data from Hegarty et al. (1999) and Dougherty et al. (2022a) the relationship between M/D and $1-\text{HAF}/\text{MEI}$ was not significantly different to using a mean value of $k_m = 0.7$. This may be due to the iterative process of fitting; during initial model evaluation, there was no difference between using a fixed value of $k_m=0.7$ and k_m as calculated from M/D in model fit for the data of Hegarty et al. (1999) and Dougherty et al. (2022a). Therefore, a fixed value of $k_m = 0.7$ was used for the subsequent fitting of other parameters against the same data

For the combined data (Figure 5.6), the relationship between k_m and $1-\text{HAF}/\text{MEI}$ was $0.02 * \text{M/D} + 0.5$, similar to the accepted relationship between k_m and M/D (Freer et al. 2007). However, there was considerable variation in the data and the relationship was not strong ($R^2 = 0.1$) suggesting other factors may also contribute to variation in k_m and/or $1-(\text{HAF}/\text{MEI})$. This observation is not new, as Blaxter and Boyne (1978) suggested that separate relationships between types of feed (forages, hays, pelleted and mixed diets) better described the relationship with k_m than all diets combined. . A few additional factors may help explain this relationship as it applies to the model: it is possible that k_m is relatively fixed, and acts as a counter to variation in viscera. The model represents visceral protein as a function of v^* , which itself is a function of M/D, and it is possible that the relationship between M/D and v^* may be stronger than that of k_m and M/D. For the data of Hegarty et al. (1999) and Dougherty et al. (2022a) there was no advantage in a variable k_m , and the slope of the relationship between k_m and M/D was not very strong, as seen elsewhere (Clayton et al. 2022).

Accordingly, we suggest that for the time being unless M/D differs widely from a mean of 10 MJ ME/kg DM then a fixed value of 0.7 for k_m should be used in calculation of b_{MEI} , i.e. $b_{MEI} = 0.3$, and 30% of MEI above maintenance is lost as heat associated with feeding, in addition to that associated with gain of fat and protein. Otherwise the standard relationship between k_m and M/D can be used, where $k_m = 0.02 \times M/D + 0.5$ (Freer et al. 2007, Figure 5.6).

Figure 5.6. Efficiency of energy use for maintenance (k_m) vs dietary energy density (M/D, MJ/kg DM) for sheep data as summarized in the review by Clayton et al. (2022), where k_m is estimated as FHP/ME_m at RE=0. Above maintenance, the equivalent term (1-HAF/MEI) is reported here with the data Hegarty et al. (1999) and Dougherty et al. (2022a), where HAF = Heat Associated with Feeding.



The revised model calculates HP as:

$$HP = (b_m \times m + b_v \times v) + (b_p \times dP/dt + b_f \times df/dt) + (b_{MEI} \times MEI) \quad [19]$$

Which is equivalent to

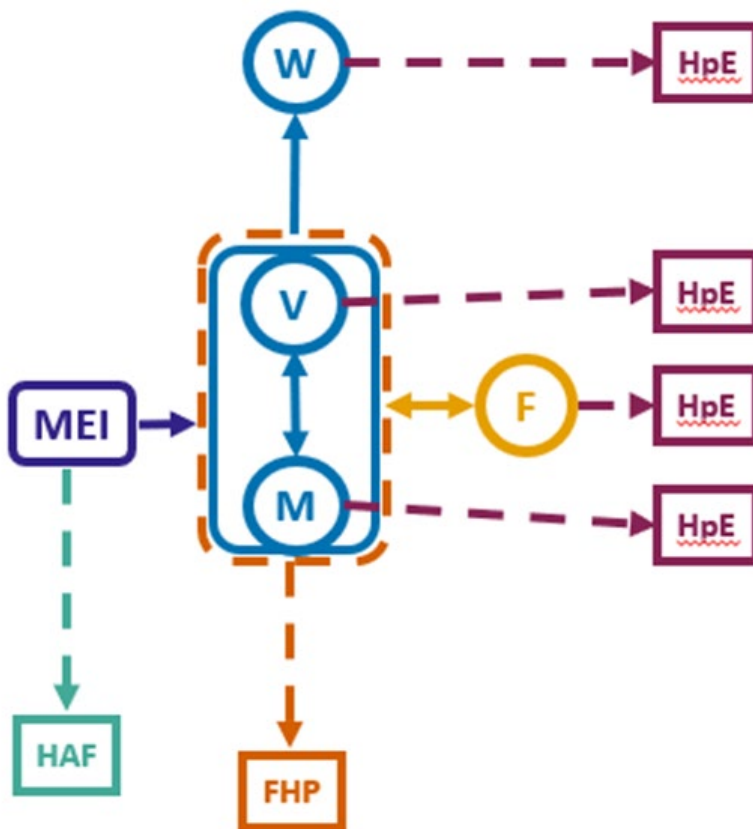
$$HP = FHP + HpE + HAF \quad [20]$$

Final Model Structure & Parameter Values

The final model structure and its equations are as shown in Figure 5.7, with terms as defined above in the text and in Table 5.1. Model coefficient values and their standard errors are shown in Table 5.1; parameter estimation and model evaluation are discussed in below in the results section. Units of prior versions of the

model (Oltjen et al. 2006, Oltjen et al. 2000, Soboleva et al. 1999) were in KJ. The revised model uses MJ for all pool sizes and MJ/d for rates of change. As in Oltjen et al. (2006), the revised model defines the energetic value of protein as 23.8 MJ/kg, and fat as 39.6 MJ/kg. These values differ slightly from the values used by the current Australian feeding standards (Freer et al. 2007) which are 23.6 MJ/kg and 39.3 MJ/kg for fat and protein, respectively.

Figure 5.7. The complete model described above. MEI = metabolizable energy intake; M, V, W are protein pools representing non-visceral tissues (M), viscera (V) and wool (W) respectively, and F is the fat pool. The solid arrows represent mass and energy flows and the dotted arrows loss of energy as heat. All fluxes are MJ/d.



The equations which describe this model are :-

$$NEG = MEI - HP$$

$$HP = FHP + HPe + HAF$$

$$dm/dt = (p_m \times NEG + e_0) \times (1 - m/m^*)$$

$$dv/dt = p_v \times (v^* - v)$$

$$v^* = CMEI \times MEI + Cm \times (m^{0.41}) - CMD \times M/D$$

$$dw/dt = fn(dw/dt_{(t-1)}^t, W_{Br}^t, W_z, MEI)$$

$$dP/dt = \sum(dm/dt + dv/dt + dw/dt)$$

$$dF/dt = NEG - dm/dt - dv/dt - dw/dt$$

$$FHP = b_m \times m + b_v \times v$$

$$HPE = b_p \times dP/dt + b_f \times dF/dt$$

$$HAF = b_{MEI} * MEI$$

The values of each parameter are shown in Table 5.1.

Table 5.1. Model parameter values for revised sheep model \pm standard error.

Term	Definition	Value	Units
b_m	Heat production from muscle protein	0.019 \pm 0.0057	d ⁻¹
b_v	Heat production from visceral protein	0.185 \pm 0.048	d ⁻¹
b_p	Heat production from change in body protein	If dP/dt < 0, $b_p = 0$; else, $b_p = 1.5$	Unitless
b_f	Heat production from change in body fat	If dF/dt < 0, $b_f = 0$; else, $b_f = 0.43$	Unitless
b_{MEI}	Heat production per MJ of MEI	0.7 or (1- k_m) where $k_m = 0.5 + 0.02 \times M/D$	Unitless
p_m	Rate constant for partition of energy into non-viscera protein	0.226 \pm 0.016	% per day
e_0	Energy lost as fat to sustain energy gain in protein when energy balance = 0	0.2486 \pm 0.034	MJ/d
p_v	Rate constant for partition of energy into visceral protein	0.05 \pm 0.0345	% per day
C_{MEI}	Regression coefficient for the relationship between MEI and v^*	0.676 \pm 0.2824	MJ d ⁻¹
C_m	Regression for the relationship between $m^{0.41}$ and v^*	2.061 \pm 1.555	MJ ^{0.41}
C_{MD}	Regression for the relationship between M/D and v^*	-0.53 \pm 0.997	MJ/kg DM

Model Evaluation

The revised model was evaluated, and its performance compared to that of CSIRO (Freer et al. 2007) using individual data from 3 experiments where body composition was measured in Merino cross lambs of similar ages but with different weights, growth rates, and nutritional histories (Hegarty et al. 1999, Dougherty et al. 2022a, Keogh et al. 2023), and 9 treatment means from a similar study with Suffolk x Rambouillet lambs by Turgeon et al. (1986) (Table 5.2). All lambs in Hegarty et al. (1999) and Dougherty et al. (2022a) were castrated males, while Turgeon et al. (1986) and Keogh et al. (2023) used a mix of females and castrated males. Energy intake varied from below maintenance to ad libitum and feed intake was recorded daily. For the serial slaughter studies of Turgeon et al. (1986), Hegarty et al. (1999), and Dougherty et al. (2022a), tissue and organ weights were recorded at harvest and body composition was measured by post-mortem chemical analysis. For Keogh et al. (2023), composition of the fleece-free empty body was estimated via CT scan. For all studies, heat production was calculated as the difference between MEI and RE. All diets were a mix of forage and concentrate, and all diets were pelleted except those of Turgeon et al. (1986). Data from the final (experimental) phases of Hegarty et al. (1999) and Dougherty et al. (2022a) were used for model development and fitting (Development Data,

n=187), while data from Turgeon et al. (1986), Keogh et al. (2023), and the preliminary phase of Dougherty et al. (2022a) were not used in model development, but were used for evaluation of model performance on novel data (Evaluation Data, n=121). A fixed value of $k_m = 0.7$ was used for the evaluation presented here, as discussed above; this was deemed appropriate as the values of k_m estimated from reported M/D were close to 0.7 for both datasets (0.7 ± 0.03 for development data, 0.72 ± 0.01 for evaluation data). Standard Reference Weight (SRW) was derived using available information about the breeds of lambs used in each study and all lambs within a study were assumed to have the same SRW. The lambs from Hegarty et al. (1999) and Dougherty et al. (2022a) were sourced from the same research flock; therefore, SRW was assumed the same for lambs in both studies. SRW was used to calculate mature non-visceral protein mass, as described in Dougherty et al. (2020, 2022b).

Table 5.2. Summary of Studies used in model development and evaluation

Measure	Development Data (n=187) ¹			Evaluation Data (n=121) ²		
	Mean	SD	Range	Mean	SD	Range
Initial Age (m)	7.63	0.91	6.7-8.5	5.43	2.09	2.9-11.0
SRW (kg)	70	0	70-70	76.2	6.98	70-100
MEI (MJ/d)	11.8	4.03	4.9-22.8	12.3	3.04	5.0-15.3
M/D (MJ/kg DM)	9.87	1.25	7.7-12.7	10.9	0.53	8.5-11.3
DOF (d)	89	5.1	75-99	63	15.4	36-207
Initial LWT (kg)	38.7	8.97	24.3-58.0	34.7	6.27	20.0-51.0
Initial %EBF	24.4%	3.51%	19.5%-33.2%	16.1%	3.43%	8.2%-25.4%
Final LWT (kg)	49.7	7.49	31.1-69.8	42.3	7.49	25.0-60.5
Final %EBF	26.7%	4.57%	15.4%-36.7%	22.9%	4.66%	11.4%-31.7%
CWG (g/d clean)	7.4	1.98	3.6-13.1	9.3	1.24	5.3-9.9
ADG in FFEB (kg/d)	0.11	0.07	-0.05-0.29	0.11	0.07	-0.07-0.24
RE in FFEB (MJ/d)	1.80	1.51	-1.95-5.49	6.50	2.88	-0.31-11.4

¹Individual lamb data from the final (experimental) phases of Hegarty et al. (1999) and Dougherty et al. (2022a);

²Individual lamb data from Keogh et al. (2023), the preliminary phase of Dougherty et al. (2022a), and treatment means from Turgeon et al. (1986).

Models were evaluated for their ability to predict final fleece-free empty body composition (MJ protein and fat), fleece-free empty body weight (FFEBW, kg), and clean wool growth (g/d) (Tables 5.3 and 5.4, Figures 5.7 and 5.8). A fixed k_m of 0.7 was used for all evaluation runs.

For the development dataset (Table 5.3), the Oddy et al. model predicted protein better than CSIRO (Fig. 7a), with lower RMSPE (% observed mean) and mean bias. The CSIRO model underpredicted protein by an average of 474g (11.3 MJ), while the Oddy et al. model overpredicted protein by 3.41g (0.08 MJ). Within the protein pools of the Oddy et al. model, the RMSPE for muscle and visceral protein were 6.95% and 9.08% respectively, and the model overpredicted muscle protein by an average of 9.22g, but underpredicted viscera by 5.81g. Mean bias and slope bias were higher for viscera than for muscle, but both terms were <1% of the total error

decomposition for both protein pools, and mean bias was <1% of the observed mean for muscle and viscera (data not shown).

Both models had similar RMSPEs for predicting final empty body fat (EBF) in the development dataset, but the Oddy et al. model had lower mean bias than the CSIRO model, underpredicting fat by 94.2g (3.73 MJ), while the CSIRO model overpredicted EBF by 176g (6.95 MJ). Variation in EBF was higher than in other measures, and error for both models increased as observed fat increased, trending toward overpredicting fat in lambs that were fatter at slaughter (Fig. 7b). However, both models had RSR values <0.5, indicating satisfactory ability to capture the observed variation in the data (Moriasi et al. 2007).

The Oddy et al. model had lower mean bias and RMSPE than the CSIRO model for prediction of fleece-free EBW (FFEBW) in the development dataset. On average, both models underpredicted FFEBW, though CSIRO model underpredicted EBW for a larger proportion of data than the Oddy et al. model (Fig. 7c). Both models substantially underpredicted wool growth in the development dataset (Fig. 7d), with high mean bias (>20% of observed mean). Neither the CSIRO model nor the model described here adequately predicted wool growth. Further work is required to develop a better model of wool growth for inclusion in simple models of animal growth.

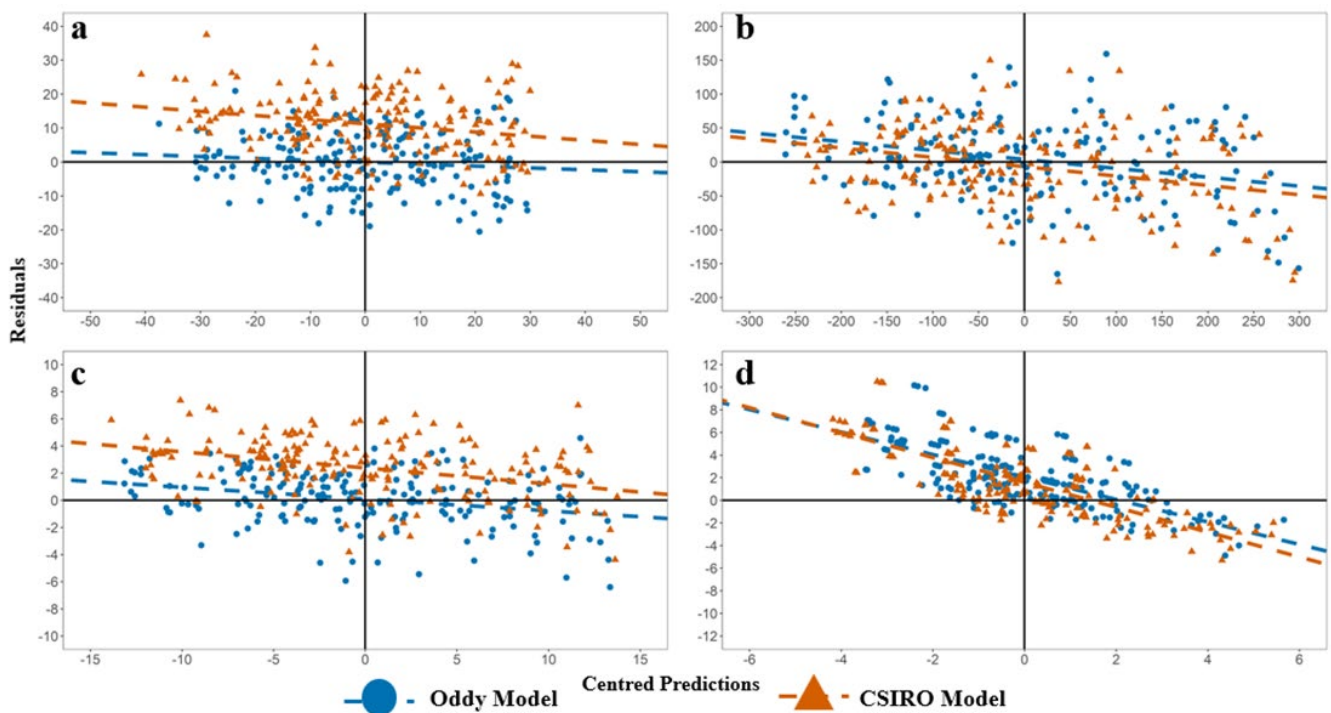
Table 5.3 Evaluation of the Oddy 2023 model versus the CSIRO model (Freer et al., 2007) for prediction of development data on final body composition, fleece-free EBW, and wool growth (n=187).

Measure	Protein in Fleece-Free Empty Body (MJ)		Empty Body Fat (MJ)		Fleece-Free Empty Body Weight (kg)		Clean Wool Growth (grams/day)	
	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.
Mean of Observed Values	138.25		426.62		39.60		7.40	
CV of Observations	12.56		30.43		16.19		26.70	
Model	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.
Mean of Predicted Values	138.33	126.98	422.89	433.57	39.52	37.22	5.35	5.82
Mean Bias	-0.08	11.27	3.73	-6.95	0.09	2.39	2.06	1.58
Mean Bias %Obs Mean	-0.06%	8.15%	0.87%	-1.63%	0.22%	6.02%	27.77%	21.37%
MSEP	74.50	207.98	3449.71	3551.12	4.13	10.50	11.94	11.69
RMSEP	8.63	14.42	58.73	59.59	2.03	3.24	3.46	3.42
RMSPE (%Obs Mean)	6.24	10.43	13.77	13.97	5.13	8.18	46.69	46.20
RSR	0.50	0.83	0.45	0.46	0.32	0.51	1.75	1.73
r	0.87	0.86	0.90	0.90	0.95	0.95	0.01	-0.11
r ²	0.75	0.74	0.81	0.81	0.91	0.90	0.00	0.01

Mean Bias (%MSPE)	0.01	61.05	0.40	1.36	0.18	54.21	35.37	21.40
Slope Bias (%MSPE)	1.06	2.08	9.01	9.81	8.07	6.33	32.09	45.74
Random Error (%MSPE)	98.93	36.87	90.58	88.83	91.74	39.46	32.54	32.85

CV, coefficient of variation (%); RMSPE, square root of mean square pre-diction error (% of observed mean); RSR, ratio of the root square mean prediction error to the standard deviation of the observations as per Moriasi et al. (2007)

Figure 5.8. Residuals vs Centred Predictions for (a) MJ Protein in Fleece-Free EBW, (b) MJ Fat, (c) kg Fleece-Free EBW, (d) g/d Clean Wool Growth. Development dataset: data from Hegarty et al. (1999) and Dougherty et al. (2022a).



In general, the CSIRO model performed better than the Oddy et al. model presented here when tested against the evaluation data (Table 5.4, Figure 5.9). Both models overpredicted protein for the evaluation dataset (Fig. 8a), but the CSIRO model had a lower RMSPE (% observed mean), while the Oddy et al. model had lower. The Oddy et al. model predicted muscle protein better than visceral protein (8.03% vs 16.2%), overpredicting muscle protein by 162g but underpredicting visceral protein by 75.6g; visceral protein had higher mean and slope bias than muscle protein (data not shown).

The CSIRO model predicted EBF better than the Oddy et al. model for the evaluation dataset, with lower RMSPE and lower mean bias (610g vs 1196g). However, both models underpredicted EBF, and the degree of underprediction tended to be higher in lambs that were fatter at slaughter (Fig. 8b). On average, the CSIRO model tended to overpredict FFEBW in the evaluation dataset, while the Oddy et al. model tended to underpredict (Fig. 8c); however, the CSIRO model had lower mean bias and RMSPE than the Oddy et al. model. As in the development dataset, neither model predicted wool growth adequately (Fig. 8d), and performance

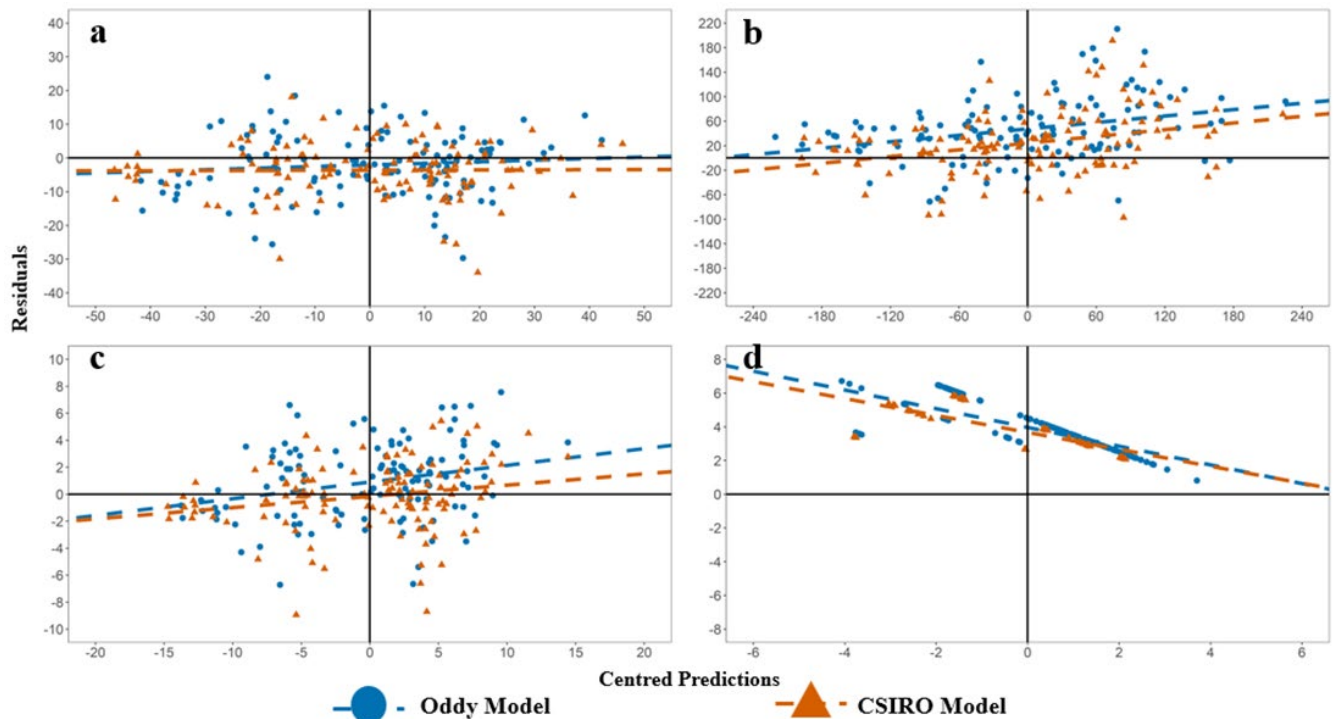
was similar between the models, though the CSIRO model had lower mean bias and RMSPE than the Oddy et al. model. The RSR for the CSIRO model was consistently lower than that of the Oddy model, and for all non-wool measures in the evaluation dataset, both models were either in the “good” ($0.5 \leq \text{RSR} \leq 0.6$) or “very good” ($\text{RSR} < 0.5$) categories for their ability to model observed variation in data (Moriassi et al. 2007).

Table 5.4. Evaluation of the Oddy et al. 2023 model versus the CSIRO model (Freer et al., 2007) for prediction of evaluation data on final body composition, fleece-free EBW, and wool growth (n=121). (i.e. Keogh et al. 2023, Dougherty et al. 2022a, Turgeon et al. 1986).

Measure	Protein in Fleece-Free Empty Body (MJ)		Empty Body Fat (MJ)		Fleece-Free Empty Body Weight (kg)		Clean Wool Growth (grams/day)	
	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.
Mean of Observed Values	127.73		327.10		35.06		9.31	
CV of Observations	17.30		35.66		20.54		13.35	
Model	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.	Oddy et al.	Freer et al.
Mean of Predicted Values	129.78	131.35	279.73	302.94	34.15	35.22	5.35	5.64
Mean Bias	-2.06	-3.62	47.37	24.15	0.91	-0.16	3.96	3.67
Mean Bias %Obs Mean	-1.61%	-2.84%	14.48%	7.38%	2.58%	-0.45%	42.57%	39.39%
MSEP	93.83	78.04	4840.70	3159.41	8.65	6.43	17.64	15.01
RMSEP	9.69	8.83	69.58	56.21	2.94	2.54	4.20	3.87
RMSPE (%Obs Mean)	7.58	6.92	21.27	17.18	8.39	7.23	45.09	41.59
RSR	0.44	0.40	0.60	0.48	0.41	0.35	3.38	3.12
r	0.90	0.93	0.91	0.91	0.93	0.94	0.67	0.70
r ²	0.82	0.87	0.83	0.83	0.86	0.88	0.45	0.49
Mean Bias (%MSPE)	4.51	16.83	46.35	18.46	9.48	0.39	89.12	89.71
Slope Bias (%MSPE)	0.87	0.01	5.10	8.41	6.18	4.17	6.09	5.12
Random Error (%MSPE)	94.62	83.17	48.55	73.13	84.33	95.43	4.79	5.17

CV, coefficient of variation (%); RMSPE, square root of mean square prediction error (% of observed mean); RSR, ratio of the root square mean prediction error to the standard deviation of the observations as per Moriassi et al. (2007)

Figure 5.9. Residuals vs Centred Predictions for (a) MJ Protein in Fleece-Free EBW, (b) MJ Fat, (c) kg Fleece-Free EBW, (d) g/d Clean Wool Growth. Independent dataset: data from Turgeon et al. (1986), Dougherty et al. (2022a), and Keogh et al. (2023).



Average lean protein mass was similar between the development and evaluation datasets, differing by only 0.44kg, or ~8%. However, the average final empty body fat was 2.5 kg lower in the independent dataset than in development dataset, a difference of 23%, and between-individual variation was higher in the evaluation data. This difference in fatness between datasets may have contributed to the higher error seen by both models when predicting fat for the evaluation data. Differences in experimental methods between the two datasets may have also contributed to differences in model performance: the majority of the data in the evaluation dataset was individual lamb data from Keogh et al. (2023), who estimated body composition and tissue weights from CT scan data; the other studies used in model development and evaluation were serial slaughter trials where tissue weights were weighed post-mortem and body composition was measured chemically.

Both models substantially underpredicted wool growth. This may be due to the nature of the wool data available, which was less detailed than data on body composition – the only study where individual wool growth data was available was the experimental period of Dougherty et al. (2022), and treatment means, or other estimates of wool production were used for the other datasets. These limitations meant that there was a poorer linkage between variation in body composition and variation in wool growth, reducing predictive power for both models and to a lesser extent, overall model predictive capacity for other measures. Wool growth is a key component of whole-body energy transactions, and a significant component of RE when RE is close to 0. It is an important addition to this model to fully account for energy transactions. It is clear that neither model predicts wool well, but additional data on wool growth and a revision of the wool growth equations are needed to improve wool prediction and overall model performance.

General Discussion

The model presented here continues the work of Oltjen et al. (2006) on modelling of energetics and body composition in sheep. A novel aspect of the revised model is the calculation of heat production (HP) internally within the model. Unlike current feeding systems it combines information on both heat associated with feeding and heat generated by protein and fat transactions in the body with an internal representation of FHP as a function of the mass of protein in visceral and non-visceral tissues. Body composition and composition of gain are derived dynamically, with a flexible relationship between fat and protein that allows for situations where fat is mobilized to support body protein reserves, or other situations where fat and protein are moving in opposite directions. Recognition of the substantial role of wool as an energy sink has allowed estimates of HP from protein gain congruent with estimates of efficiency of protein gain reported in other species (Owens et al 1995). Our method of estimating deposition of energy in protein and allowing the balance of energy not lost as heat to accrue as fat provides estimates of body composition not dissimilar to those obtained by regression analysis of past studies that have underpinned current feeding systems (ARC 1980, Freer et al. 2007; NASEM 2007, 2016).

This construct is more flexible in that short term variation in body composition arising from changes in feed supply and composition relative to maturity is accommodated without recourse to fixed proportions of protein and fat deposition used in existing feeding systems. The addition of a wool protein pool is necessary allows for more accurate representation of energy utilisation. Estimation of HP can be obtained internally within the model, although that calculation relies on estimates of HP using various methods not traditionally associated with feeding systems. It is well known that accurate estimation of parameters for highly correlated components of a system is difficult to achieve. We used as much independent evidence as it was possible to assemble to support initial parameter values, followed by iteration to minimise errors for the entire suite of output parameters, rather than rely on interpretation of regression coefficients. This has resulted in exposure of underlying processes (such as the relationships between energy costs associated with visceral and non-visceral protein informing the basis of FHP; the contribution of heat associated with eating and heat of product formation for protein and fat gain). Although this approach yields similar estimates of body composition as traditional methods it has the advantage of exposing the factors contributing to variation in HP which in turn allows a somewhat more rational understanding of the causes of variation in protein and fat deposition and HP in sheep.

Conclusions & Implications

The revised model presented here is simpler than current Australian feeding standards (Freer et al. 2007) and better represents the underlying biology of the system. When evaluated against novel data, the revised model performed closely to that of the current CSIRO model (Freer et al. 2007), though it underpredicted fat and therefore empty body weight. Neither model performed well at predicting wool growth, highlighting the need for additional data on the relationship between nutrition, body composition, and wool growth. In general, lack of data on body composition and tissue weights in animals at lower planes of nutrition will be needed to improve estimates, as will additional data on mature body size and composition. Future developments to the revised model include the representation of pregnancy and lactation, the energetic cost of activity, and internal calculation of gut fill. Work is underway on a beef cattle version of this model, based on the same underlying structures and principles presented here in sheep.

Though additional data is needed for further development, the model presented here provides a mechanistic, flexible, and transparent approach to calculating heat production and body composition in sheep. This approach is algebraically equivalent to other feeding systems, but gives better biological meaning to model terms and parameters, and is able to be extrapolated to a wide variety of production scenarios.

Appendix: Model Initialization

The model requires initial values for masses of protein in the m and v pools (m_{init} and v_{init} respectively), as well as initial wool, fat (f_{init}), and fleece-free empty body weight (FFEBW). Initial wool cover is provided by the user, but where initial FFEBW, protein and fat are not available, they can be calculated from Fleece-Free Liveweight (FFLWT), Z , and SRW as follows, using equations derived from Butterfield et al. (1988) and Searle & Griffiths (1976):

$$\text{GutFillInit (kg)} = (2.487 \times Z - 1.482 \times Z^2 + 0.001) \times 9.1 \times (\text{SRW}/100) \quad [\text{A1}]$$

$$\text{ShrinkInit (\%)} = ((\text{FFLWT} - \text{GutFillInit})/\text{FFLWT}) \times (0.35 + 0.106 \times \text{M/D} - 0.004 \times \text{M/D}^2) \quad [\text{A2}]$$

$$\text{FFEBWInit (kg)} = \text{FFLWT} \times \text{ShrinkInit} \quad [\text{A3}]$$

$$v_{\text{init}} \text{ (MJ)} = \text{SRW} \times (2.732 \times Z - 1.731 \times Z^2 - 0.0014) \times \text{SexFac} \times 23.8 \times 0.157 \quad [\text{A4}]$$

$$f_{\text{init}} \text{ (MJ)} = ((98.797 \times Z - 38.035 \times Z^2 - 14.499)/100) \times \text{Fleece-Free Liveweight} \times 39.6 \quad [\text{A5}]$$

$$m_{\text{init}} \text{ (MJ)} = (\text{FFEBWInit} - (v_{\text{init}} / 23.8/0.157) - (f_{\text{init}}/39.6)) \times 23.8 \times 0.21 \quad [\text{A6}]$$

Where GutFillInit is initial gut fill, ShrinkInit is the conversion factor for converting FFLWT to FFEBW, M/D is energy density of the previous diet (MJ/kg DM), SexFac is 0.047 for intact males, 0.051 otherwise, 0.157 and 0.21 are the crude protein content of fat-free viscera and muscle, respectively (Dougherty et al. 2021, 2022a); and 23.8 and 39.6 are the energetic content (MJ/kg) of protein and fat, respectively (Oltjen et al. 2006, Oddy et al. 2019).

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5.2 Paper 2 – Mature size

Dougherty HC, Oddy VH, Evered M, Clayton EH and Oltjen JW (2022). Variation in mature body composition affects energy requirements and fat and lean deposition in sheep of different breeds and sex. *In* "7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition (ISEP)" (I Fernández-Fígares, M Lachica, R Nieto, M García Gallego and JM Porres, eds.), European Association of Animal Production, Granada, Spain, pp. 196

Variation in mature body composition affects energy requirements and fat and lean deposition in sheep of different breeds and sex

Key words: Sheep, Ruminant Nutrition, Energetics, Modelling, Metabolism

Introduction

Feeding systems account for variation in energy requirements of sheep of different breeds and sex by scaling requirements and composition relative to mature size, sometimes called Standard Reference Weight (SRW). This term is poorly defined within and between systems and in the literature: there is no consistent estimate of SRW for different sexes and breeds of sheep.

The Australian feeding system (Freer et al., 2007) uses SRW to derive body composition and feed intake, and from this calculates energy and protein requirements. There is no clear definition of fat or protein content at SRW for a breed, or for different sexes of the same breed. A large part of uncertainty in composition at maturity is due to the experimental procedures used. Some (Blaxter et al., 1982; Thompson et al., 1985) define maturity as when weight and feed intake of sheep eating a medium quality diet ad-libitum are stable for a period of months. Others (Freer et al., 2007; NRC 2007) define it as the weight of a mature animal at midrange body condition score. This lack of clarity affects estimates of energy requirements and body composition. Heat production is strongly linked with the amount and metabolic activity of protein (Oddy et al., 2019; Dougherty et al., 2021). Dougherty et al. (2021) derived maximum protein in the body at maturity from weight and fat content at maturity (assumed to be SRW). Heat production per unit empty body weight (EBW) declines with maturity due to a decrease in the proportion of protein relative to fat, a rate which is affected by sex, breed, and nutritional history (Butterfield et al., 1984; Thompson et al., 1985; Dougherty et al., 2021). If SRW is to be used as a proxy for mature size and a scalar for energy requirements and composition, there must be a clearer description of the protein and fat content of the body at maturity, one which includes effects of breed and sex.

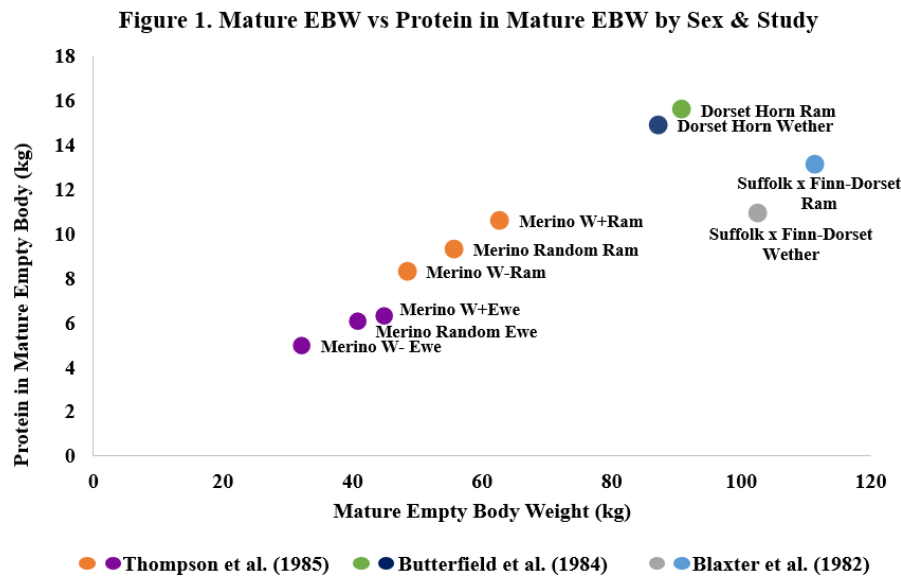
Materials and Methods

Data from three studies of sheep growth to maturity (Blaxter et al., 1982; Butterfield et al., 1984; Thompson et al., 1985) were compared. Within each study, sheep of different sexes were reared under similar conditions and nutritional histories.

Results & Discussion

Data comparing mature size and composition of different breeds and/or sexes reared under similar conditions is sparse; where such data is present, rams are heavier and leaner at maturity than ewes or wethers of the same breed (Figure 1). However, current sheep feeding standards (Freer et al., 2007; NRC 2007) focus primarily on ewes. The only adjustment for sex is to increase maintenance energy requirements for rams; the effect of on mature size and protein and fat content of the body is not considered.

Mature weight and composition at maturity vary depending on rearing environment, reproductive status, breed and nutritional history (Thompson et al., 1985). The weight at maturity and fat content of an animal that is grown until intake and weight stabilize appears to be larger than in animals that have passed through multiple reproductive cycles before reaching "maturity". Furthermore, it is unclear if animals have reached their maximum protein accretion in the non-visceral body at this definition of "maturity".



Conclusion & Implications

Energy expenditure is highly correlated with the amount of protein in the body, and a target for protein mass is required for dynamic calculation of energy expenditure and changes in body composition. Therefore, describing maturity in terms of a target protein mass is more useful than simply using weight and an estimate of fatness at maturity. Additional data should be collected to quantify the extent to which mature protein mass is influenced by breed, sex, and environment. This will contribute to development of tools with improved prediction of performance of sheep.

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5.3 Paper 3 – Predicting k_m and k_g

Clayton EH, Oltjen JW, Evered M, Dougherty HC and Oddy VH (2022). Predicting the efficiency of utilisation of energy for maintenance (k_m) or gain (k_g) for sheep and cattle from feed quality components. *In* "7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition (ISEP)" (I Fernández-Fígares, M Lachica, R Nieto, M García Gallego and JM Porres, eds.), European Association of Animal Production, Granada, Spain, pp. 05.

Predicting the efficiency of utilisation of energy for maintenance (k_m) or gain (k_g) for sheep and cattle from feed quality components

EH Clayton, JW Oltjen, M Evered, HC Dougherty and VH Oddy

Key words Efficiency; maintenance; growth

Introduction In the current Australian feeding standards for ruminants (CSIRO, 2007) the metabolisable energy intake (MEI) required for maintenance (ME_m), where retained energy (RE) is zero, is estimated from fasting heat production (FHP) and the efficiency of utilisation of energy for maintenance (k_m). The efficiency of utilisation of energy for gain (k_g) is estimated from the regression of RE:MEI at all levels of feeding (LoF). As FHP is affected by prior LoF, the accuracy of prediction of k_m and k_g relies on feeding at maintenance prior to measurement. The UK feeding system (ARC, 1980) uses fixed values of k_m and k_g for different feedstuffs. The Australian system predicts efficiencies from the energy density (M/D, MJ/kg DM) of the diet ($k_m = 0.02 \times M/D + 0.5$, $k_g = 0.043 \times M/D$), however, it is unclear where the data used to derive these relationships was obtained. Therefore, the aim of the current study was to determine the relationship between k_m or k_g and M/D or other proximate analysis components using data obtained from *in vivo* calorimetry studies.

Materials and methods A database of 91 calorimetry studies in sheep (n = 47) and cattle (n = 44) from 1925-2019 was developed. ME_m was determined from the regression of MEI:RE at different LoF. Efficiencies were calculated as: $k_m = \text{FHP}/\text{ME}_m$ and $k_g = \text{slope of RE:MEI}$ (Blaxter, 1968). Additional analysis was conducted for Merino ewes fed a crushed wheat, lucerne, molasses (5:4:1) diet where FHP was measured after several different prior LoF (Marston, 1948). Relationships between feed components and efficiencies were analysed by regression using SAS. Sub-group analyses were conducted for feeds described as 'whole' or 'chopped and pelleted' as described previously (Blaxter and Boyne, 1978).

Results and Discussion Estimated k_m was positively correlated with M/D for all data ($r^2 = 0.082$, RMSEP = 0.094, $p < 0.001$) and for sheep but not cattle when analysed separately (Figure 1A). The prediction of k_m for sheep was higher for ground/pelleted compared with whole feeds (Table 1). Estimated k_m was also significantly predicted by crude fibre (CF) for cattle and acid detergent fibre (ADF) for sheep (Table 1). FHP was significantly positively correlated with prior LoF ($\text{FHP} = 0.936 \times \text{Prior LoF} + 2.716$, $r^2 = 0.996$, $p < 0.001$), therefore, k_m was also positively related to prior LoF (Figure 1B).

Estimated k_g was significantly predicted by M/D for whole ($k_g = 0.032 \times M/D + 0.109$), but not processed feeds (Table 1). Estimated k_g was also predicted for whole feeds by ADF + Wt for sheep ($k_g = -0.004 \times ADF + 0.005 \times Wt + 0.309$) and CF for cattle ($k_g = -0.007 \times CF + 0.62$).

Table 1. Prediction of k_m or k_g for sheep and cattle for all feeds or whole and processed feeds analysed separately.

Prediction	Species	Predictor ¹	Feed Type	n	r^2	RMSEP ²	p -value
k_m	Sheep	M/D	All	118	0.122	0.091	< 0.001
	Sheep	M/D	Whole	103	0.102	0.095	0.001
	Sheep	M/D	Processed	14	0.503	0.043	0.005
	Sheep	ADF	All	79	0.078	0.095	0.014
	Cattle	CF	All	35	0.131	0.100	0.033
k_g	All	M/D	Whole	100	0.308	0.085	< 0.001
	All	M/D	Processed	85	0.017	0.103	0.234
	Sheep	ADF+Wt	Whole	57	0.649	0.059	< 0.001
	Sheep	ADF+Wt	Processed	17	0.463	0.066	0.013
	Cattle	CF	Whole	19	0.466	0.084	0.001

¹M/D = MJ/kg DM, ADF = acid detergent fibre, CF = crude fibre. ²RMSEP = Route mean square error of prediction.

Conclusions and implications The estimation of k_m from M/D was better for sheep compared with cattle and the relationship for sheep was similar to current guidelines (CSIRO, 2007). However, k_m was not predicted with a high precision by M/D for either sheep or cattle (RMSEP = 0.091 and 0.095, respectively) and was predicted equally as well by dietary CF for cattle. As the determination of k_m relies on FHP, its prediction will not be accurate if prior FHP was determined at a LoF other than at MEm. A dynamic system that accounts for HP from body composition (viscera, non-visceral protein and fat) may improve the prediction of energy requirements.

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6. Activity, gestation and lactation

6.1 Revised HP equation

Initial tests of data from pregnant and lactating animals using the HP equation developed with a dataset from growing animals indicated that it did not properly account for variation in HP due to level of feeding and energy density of the feed. We reconstructed the HP equation to better reflect the data as below (HP equation reported in Dougherty et al 2022) :-

The HP equation that accounts for pregnancy. Lactation and activity is:

$$HP = b_m * m + b_v * v + (1 - k_m) * MEI + (1/k_p - 1) * dp/dt + (1/k_f - 1) * df/dt + (1/k_c - 1) * dc/dt + (1/k_l - 1) * dl/dt + A \quad (1)$$

Where MEI = ME intake, $b_m * m + b_v * v = FHP$, k_m is the efficiency of feed utilisation for maintenance, and $k_p =$ partial efficiency of protein deposition (dp/dt , where $dp/dt = dm/dt + dv/dt + dw/dt$) and $k_f =$ partial efficiency of fat deposition (df/dt). k_c is partial efficiency of conceptus growth (dc/dt) and k_l partial efficiency of milk production (dl/dt). k_m can be derived from the energy density of feed (M/D) using standard equations specifically $k_m = 0.5 + 0.02M/D$ or approximated as 0.7. However, as pointed out by Blaxter and Boyne (1978), any appropriate method of description of the relationship between a feed (type; forage, pellets, chopped, mixed) and its energy density and k_m can be used. A is heat produced by activity (primarily walking).

6.1.1 Gestation

Energy gain in the gravid uterus was described in PISC (CSIRO, 2007) using a Gompertz function. We have improved on the functions used to describe growth of the conceptus in sheep and cattle as follows.

Sheep

The data used to generate the parameters for sheep in CSIRO (2007) appear to have been derived from the data of Langlands and Sutherland (1968). They fitted energy gain in Merino ewes with single lambs well, but did not fit data for larger breeds of sheep with multiple lambs (e.g. Rattray et al. 1974; Robinson et al. 1977) as well. Given that the Australian industry has shifted to a much greater dependence on lamb production from crossbred ewes joined to terminal meat sires we therefore determined a set of parameters to better describe retention of energy in the gravid uterus for a wider range of sheep breeds.

We settled on the same equation form as CSIRO, 2007 to describe the energy content of the gravid uterus of sheep carrying single and twin lambs, specifically:

$$\text{init_c} = \text{stdBirthWt}/4 \exp(A - B \exp(-Ct))$$

$$dc/dt = \text{init_c} B C \exp(-Ct)$$

Where init_c is the energy content of the gravid uterus at time t , StdBirthWt is average birthweight of lamb for the breed type and parity of the ewe, $A = 5.963$, $B = 11.20$, $C = 0.00945$ (RMSPE 8.2%) and $t =$ days post coitus.

These parameters compare with CSIRO (2007) $A = 7.64$, $B = 11.46$, $C = 0.00643$ (RMSPE 9.2% when applied to the expanded data set).

We have retained (for now) the standard birth weight of a single lamb of 4kg to scale for the average birthweight of a lamb. This can be changed once more data is available.

To account for the effect of maternal nutrition on conceptus growth we introduced a term, $(1 + q (dm/dt)/m)$, which reflects the change in protein in the non-viscera component of the maternal body. This allows for normal rates of fat loss during pregnancy to be unrelated to changes in fetal growth, and allows for a constraint on fetal growth as the rate of loss of maternal body protein increases. The value for q ($= 23$) was derived from fitting data from Rattray et al. (1974) as described in the appendix.

The final form for dc/dt that accounts for uterine growth and an effect of change in maternal body protein becomes:

$$dc/dt = \text{current_c} B C \exp(-Ct) (1 + q (dm/dt)/m)$$

and the model is initialised with $\text{init_c} = \text{stdBirthWt}/4 * \exp(A - B \exp(-Ct))$ where init_c is current_c for the first date simulated after joining.

For sheep the parameters are:

$$A = 5.963, B = 11.20, C = 0.00945, q = 23$$

The measured increment in heat production as a consequence of conceptus growth (heat production of pregnancy) is 340-355 kJ/kg of fetus (Graham 1964; Rattray et al. 1974). On an energy:energy basis the efficiency of energy retention in the gravid uterus is reported to be in a range of 10-16% with a mean of 13.3%. We used an efficiency of conversion of feed energy into conceptus (k_{cc}) of 13.3% for both sheep and cattle. HP due to conceptus growth was calculated as energy gain in conceptus $(dc/dt) / 0.133 - dc/dt$. This is equivalent to HP of conceptus growth of $(1/k_c - 1) = 6.52 * dc/dt$.

Comparison with published data

We intended to use the mature pregnant sheep data in Rattray et al (1974) to compare observed versus predicted retained energy (RE) using both our model and SCA. However, close inspection of the reported RE values suggests that there is an error in reporting in the original paper. However, Rattray et al. (1973) reported on energy requirements for maintenance, gain and pregnancy in ewe lambs. The data in that publication was used for the comparisons between observed and predicted RE shown below. For beef cattle we used data reported by Ferrell et al. (1976).

Sheep

A comparative slaughter experiment which involved ewe lambs fed 2 diets of different energy density fed at maintenance and ad-lib to non-pregnant ewes and ad-lib to pregnant ewes was used. The data is reported in Rattray et al. (1973).

The figures below show fit of observed v predicted values for RE in pregnant and non-pregnant sheep from Rattray et al (1973) using the earlier version of our HP calculations and SCA. The version of the HP equation described above is expected to be more precise. The key point is that even with a less than optimal HP equation, our model is performing better than SCA for the data of Rattray et al (1973).

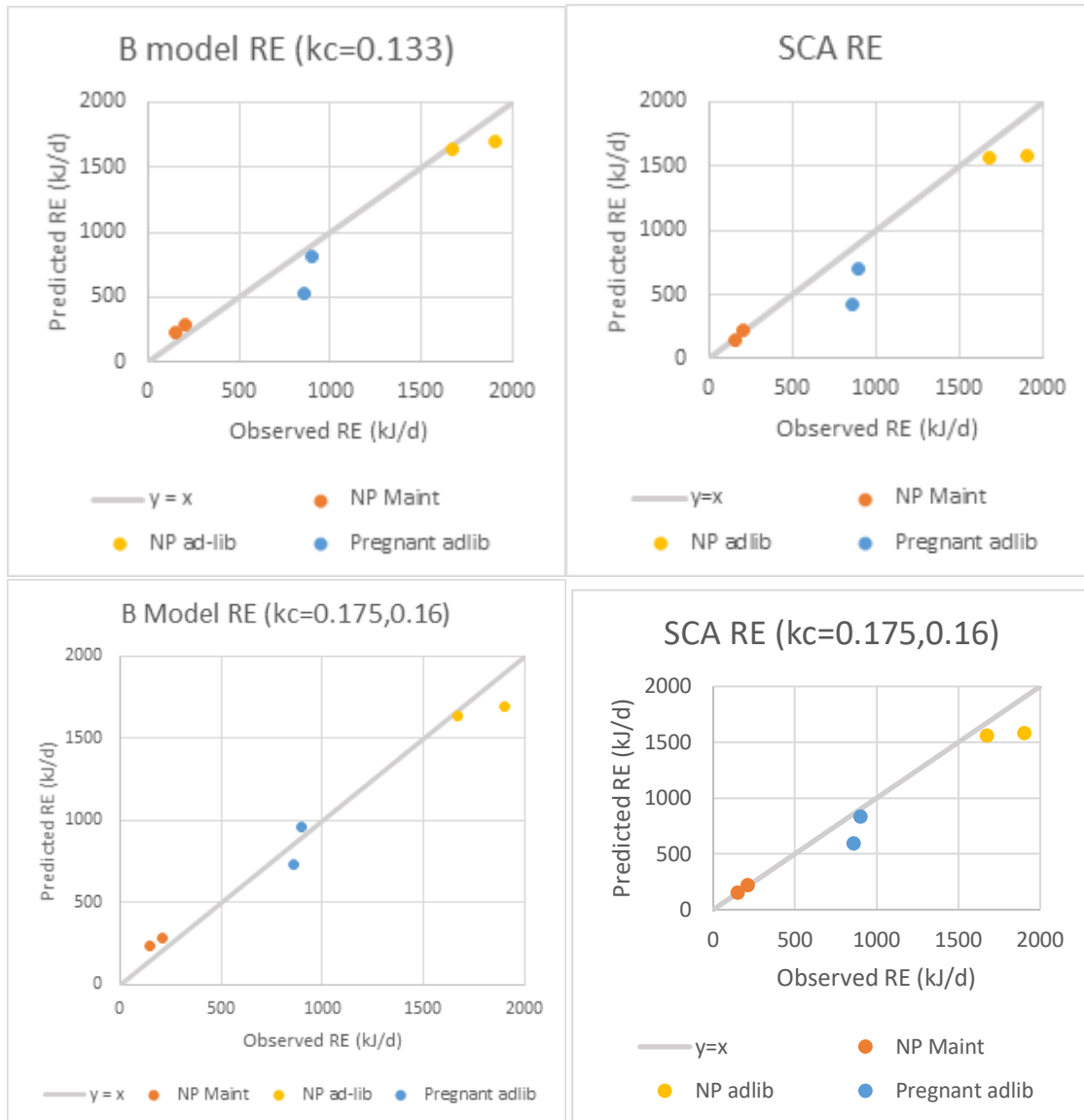


Figure 6.1. Comparison of observed Retained Energy (kJ/d) with that predicted by our model (B Model) and PISC for non-pregnant ewe lambs fed maintenance (NP Maint), non-pregnant ewes lambs fed ad-lib (NP adlib) and pregnant ewe lambs adlib (Pregnant adlib). Two diets with different net energy content were used for each class of animals, and points are means of each reported treatment. The grey line is $y=x$. The upper panel uses efficiency of energy for conceptus growth of 13.3% the lower panel uses the reported values for k_c .

We used an efficiency of energy use in conceptus (k_c) of 13.3% which is the mean value used by CSIRO, (2007) and others. With this value for k_c the RMSPE (expressed as % of observed mean) for all the treatments is 17.9% for the B model and 25.4% for SCA. Rattray et al. (1973) reported k_c as 17.5% for the higher energy diet and 16% for the lower energy diet. When these values for k_c are used the fits for the B model are shown below. The RMSPE for all the treatments was reduced to 11.9% using the B model and 18.9% for SCA.

Cattle

We used the data published by Ferrell et al. (1976) on pregnant and non-pregnant beef heifers fed 2 levels of the same feed and measured at 134, 189, 237 and 264 days post conception to conduct the comparisons reported below. These comparisons are also with the previous, less precise, method for estimating HP.

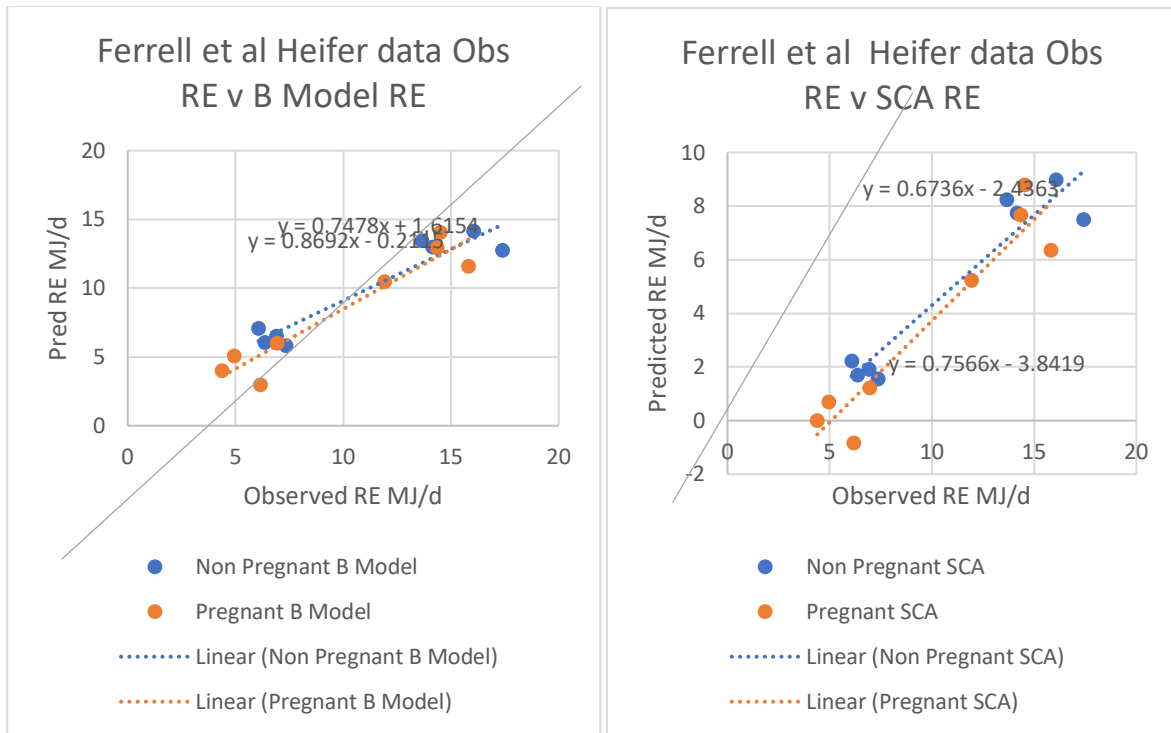


Figure 6.2. Comparison of observed vs predicted retained energy (RE, MJ/d) in pregnant and non-pregnant heifers (data from Ferrell et al., 1976). The left hand panel is a comparison of predictions from our model and the right hand panel is the comparison of predictions from SCA.

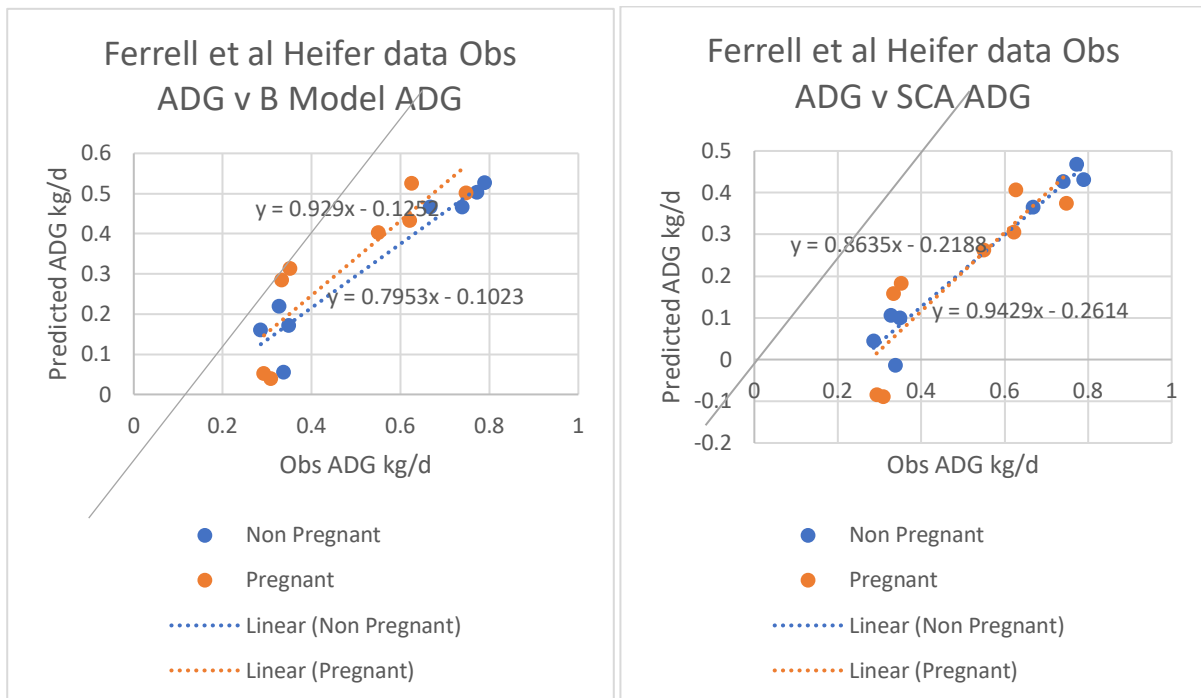


Figure 6.3 Comparison of observed vs predicted average daily gain (ADG, kg/d) in pregnant and non-pregnant heifers (data from Ferrell et al., 1976). The left hand panel is a comparison of predictions from our model and the right hand panel is the comparison of predictions from SCA.

Estimation of RE is significantly better using the proposed model than SCA. Although the proposed model provides estimates of ADG closer to observed than does SCA, it underestimates ADG. We suspect that the conversion of RE in protein and fat in these animals is somewhat different to the values used in our method. This is under further investigation.

6.1.2 Lactation

Three issues were addressed in including lactation into the growth model.

Milk production: PISC describes potential milk production as a general function of days since birth for both sheep and cattle. We compared the values estimated by PISC with those observed over a wide range of studies and concluded there was substantial difference between the milk production expected from the curves used in PISC and that observed. To avoid confusion we used measured milk production to compare energy balance and body composition changes. When the model is finalised we will adjust the milk production of sheep and cows on the basis of growth rate of offspring, as data (e.g. Herd, 1990) suggests that offspring demand drives quantity of milk produced.

Higher visceral mass is associated with higher intake during both pregnancy and lactation; however, it was initially unclear if there was a specific effect of pregnancy and lactation on viscera size other than that due to increased intake. Reynolds et al. (2004) suggested that there were no specific effects of lactation on visceral mass over and above those related to changes in feed intake. We specifically addressed this as shown below.

During early lactation, a substantial proportion of milk energy is derived from energy lost from the tissues of the cow. It is important that any calculation of tissue energy exchanges with milk, and the subsequent effect on body reserves, accurately represents this. How our proposed calculation procedure represents this in lactation heifers is shown below. We anticipate this will also accurately represent energy transactions in lactating cows.

Visceral mass

It was initially unclear if there was a specific effect of pregnancy and lactation on viscera size other than that due to increased intake. Reynolds et al. (2004) published data on visceral mass in late pregnant and early lactation dairy cows. In that paper they suggested that there is no evidence of a specific effect of lactation on mass of viscera other than that due only to the increase in feed intake. If this were true, we could have confidence that our method for estimating viscera protein mass from MEI, M/D and stage of maturity of the animal (m/m^*) would apply to both pregnancy and lactation.

The figure in the top panel is an amalgamation of multiple data sources from the literature (references are in Appendix 3) showing mass of viscera protein (sum of heart, lungs, liver, kidneys, and empty weight of reticulorumen, omasum, abomasum, and small and large intestine including caecum, all multiplied times protein content), relative to the weight of the Fat-free empty body. The data for pregnant and lactating cows (orange points) fit within the data for steers and dry cows. The bottom panel shows data from pregnant and lactating cows within the observed versus predicted viscera protein predicted from MEI, M/D and non-viscera protein mass^{0.75} as used to estimate v^* . These results support the contention of Reynolds et al. (2004) that the mass of viscera during early lactation is a function only of amount of feed eaten and not specifically affected by lactation per-se.

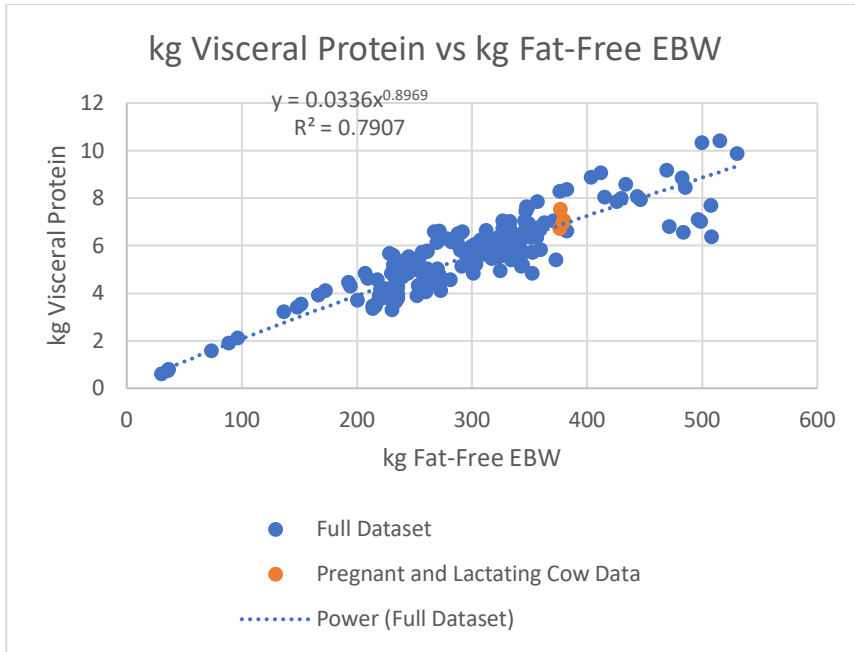


Figure 6.4. Relationship between visceral protein (kg) and fat-free empty body weight in cattle illustrating that data from pregnant and lactating cows (orange dots) falls within the same range of data as for growing cattle and dry cows.

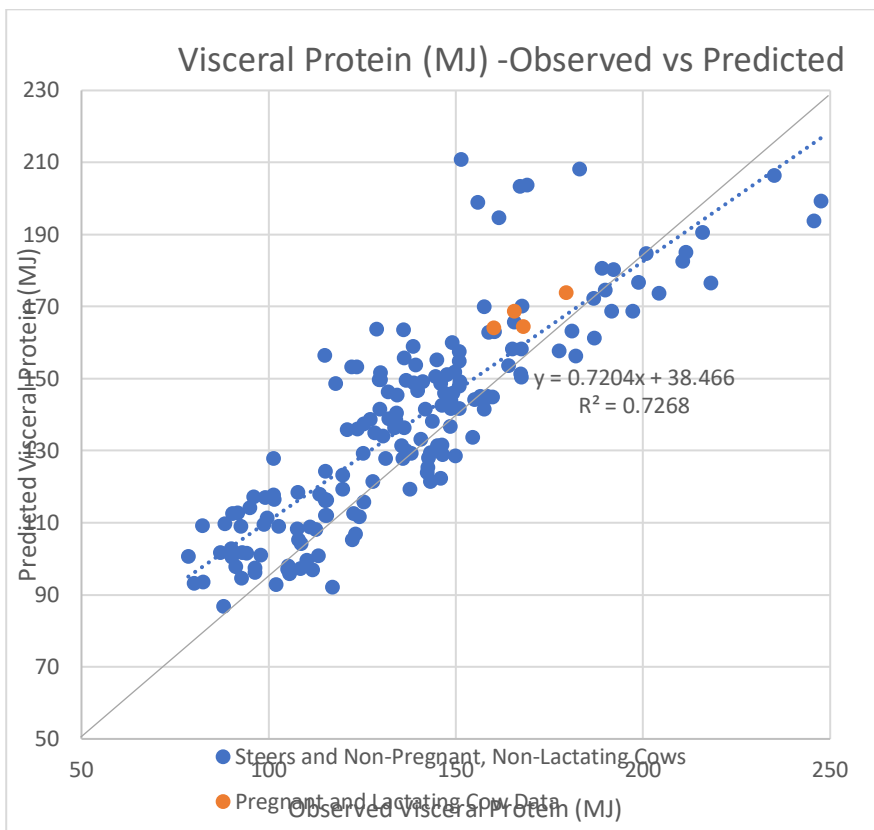


Figure 6.5. Observed visceral protein energy (MJ) vs predicted visceral protein energy (MJ) v^* where $v^* = 0.1399*MEI + 0.6791*m^{0.75} - 3.048*M/D$. Data for pregnant and lactating cows (orange dots) are within the data prediction developed from growing and dry cattle.

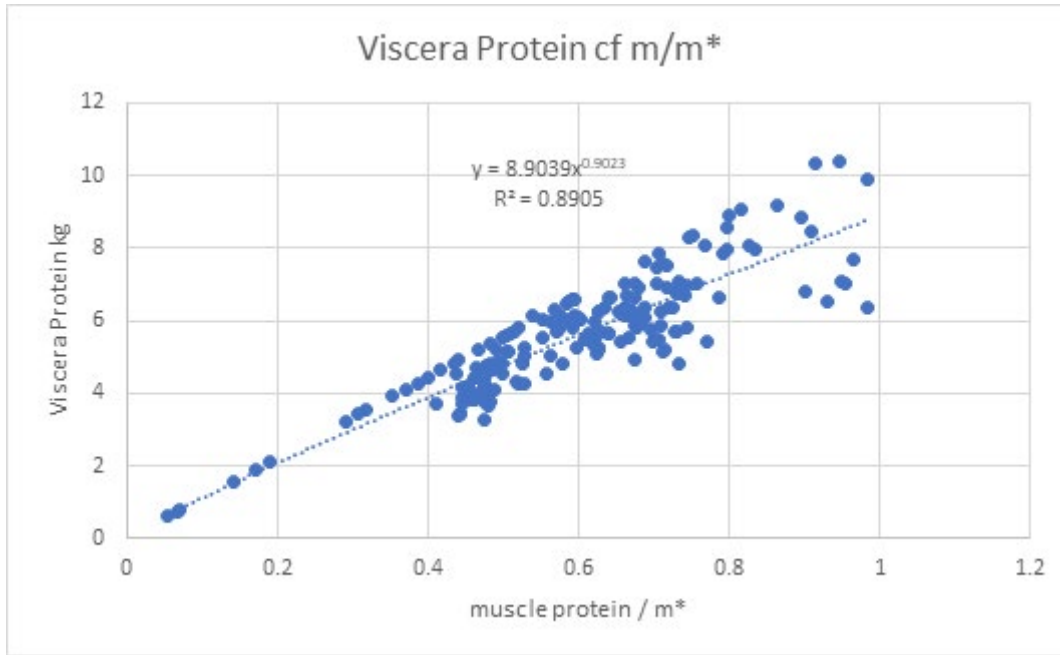


Figure 6.6. Relationship between protein in viscera (kg) and maturity expressed as muscle protein mass / m* (target muscle protein mass) for cattle.

6.1.3 Partitioning of Energy between tissue and milk

Using the observations above, that the method for estimating v* in steers and dry cows is the same as for lactating animals, we used data on milk energy and tissue energy retention in lactating beef heifers from Freetly et al. (2006) - kindly provided by Harvey Freetly (USDA, Meat Animal Research Centre) to compare our new model with SCA.

The graphs below are of heat production (MJ/d), tissue energy balance (after accounting for secretion in milk, MJ/d) and tissue protein balance (expressed as MJ/d). They show observed values (x axis) vs predicted values (y axis) for both the model and SCA. The grey line is y=x.

The proposed model fits the data for tissue energy transactions and for HP better than PISC (lower RMSPE's) and not as good as PISC for body weight change and tissue protein energy (for which neither the proposed model or PISC provide satisfactory predictions).

Table 6.1 Root mean square prediction error (RMSPE) for Heat Production (HP), Tissue energy gain or loss (TE), Tissue energy stored as protein (TPE) and body weight gain (BWG) for data from Freetly et al. (2006) predicted with the proposed model B and SCA. Values shown are % of observed mean.

RMSPEs

	HP (MJ/d)	TE (MJ/d)	TPE (MJ/d)	BWG (kg)
B model	6.44	8.31	3.02	18.44
SCA	7.05	9.23	2.37	14.3

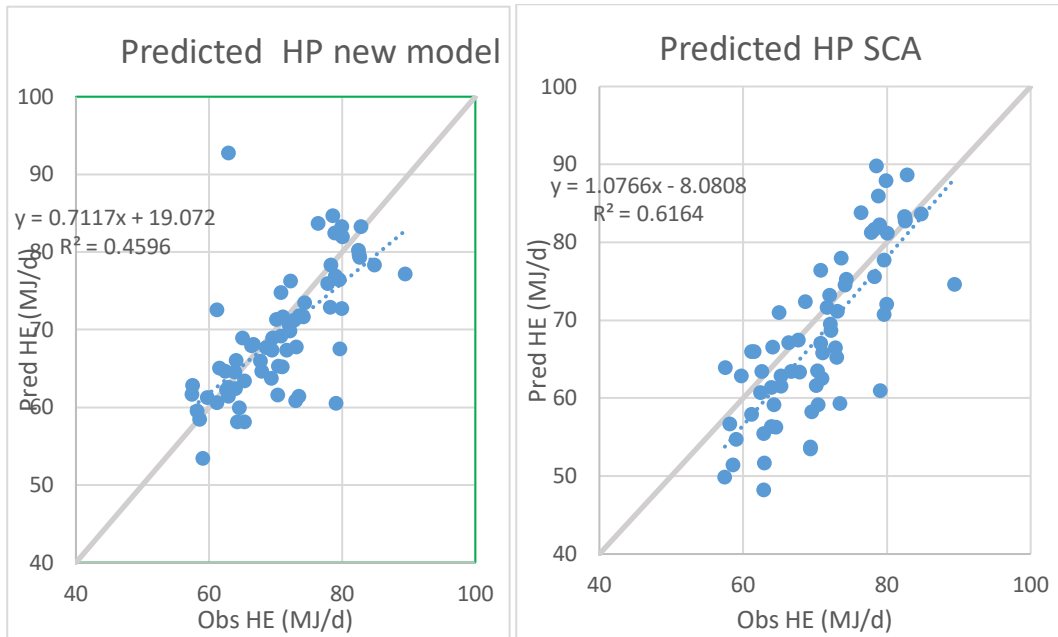


Figure 6.7. Observed (x axis) compared to predicted (y axis) heat production (MJ/d) in lactating heifers (Freetly et al. 2006). The left hand panel is HP predicting using the model described in this report, the right hand panel is the prediction of the same data obtained using PISC (CSIRO 2007). The grey line is $y = x$.

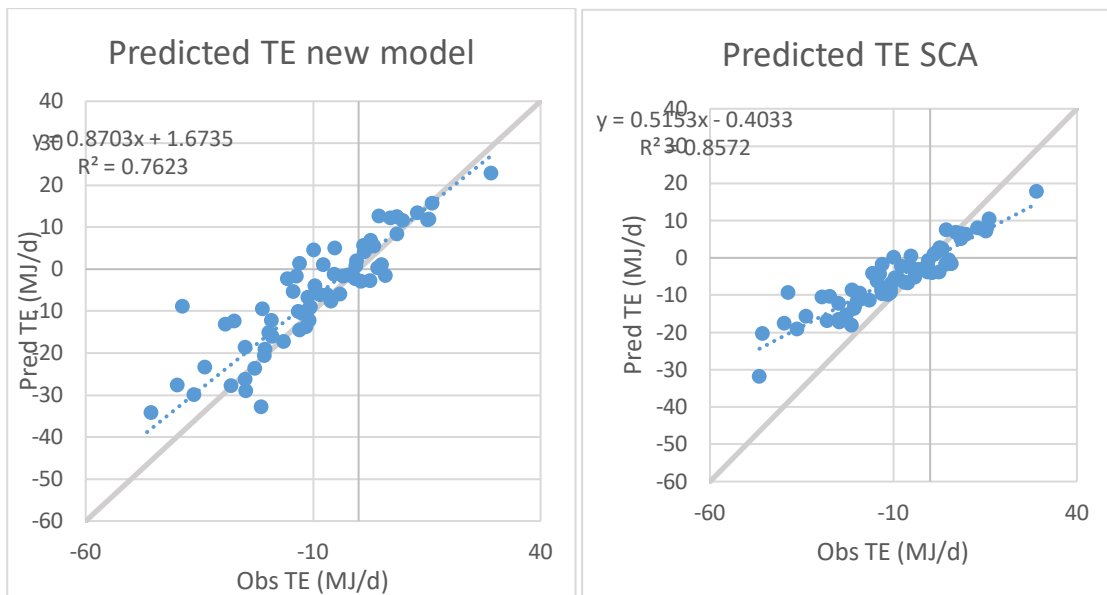


Figure 6.8. Tissue energy. Observed (x axis) compared to predicted (y axis) energy retained (Tissue energy TE) in the tissues (MJ/d) of lactating heifers (Freetly et al. 2006). The left hand panel is TE predicting using the model described in this report, the right hand panel is the prediction of the same data obtained using PISC (CSIRO 2007). The grey line is $y = x$.

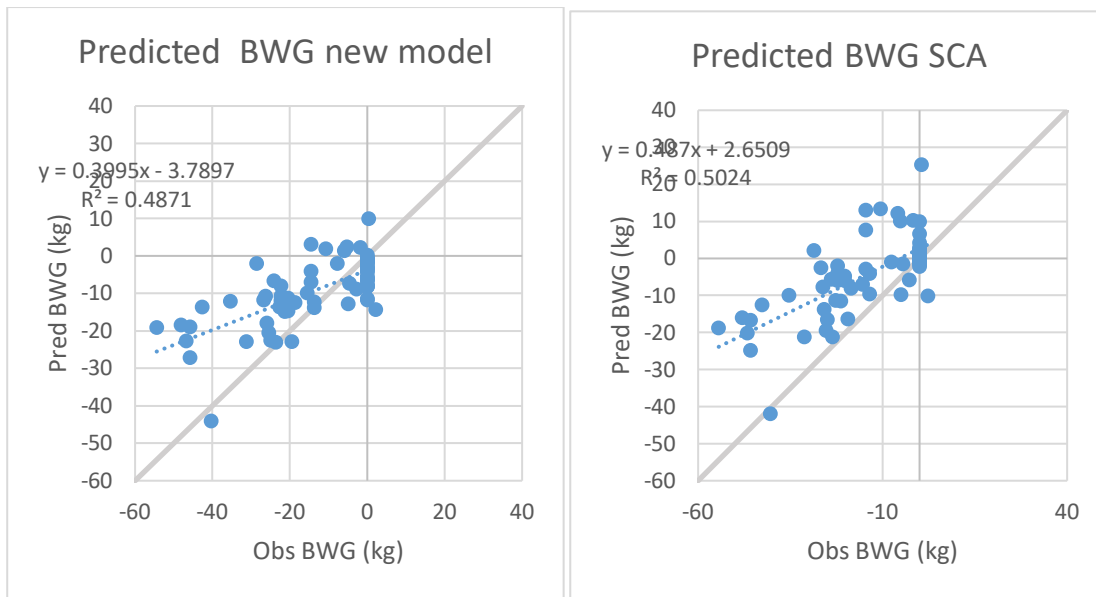


Figure 6.9. Body weight change. Observed (x axis) compared to predicted (y axis) body weight change (BWG, kg) in lactating heifers (Freetly et al. 2006). The left hand panel is TE predicting using the model described in this report, the right hand panel is the prediction of the same data obtained using PISC (CSIRO 2007). The grey line is $y = x$.

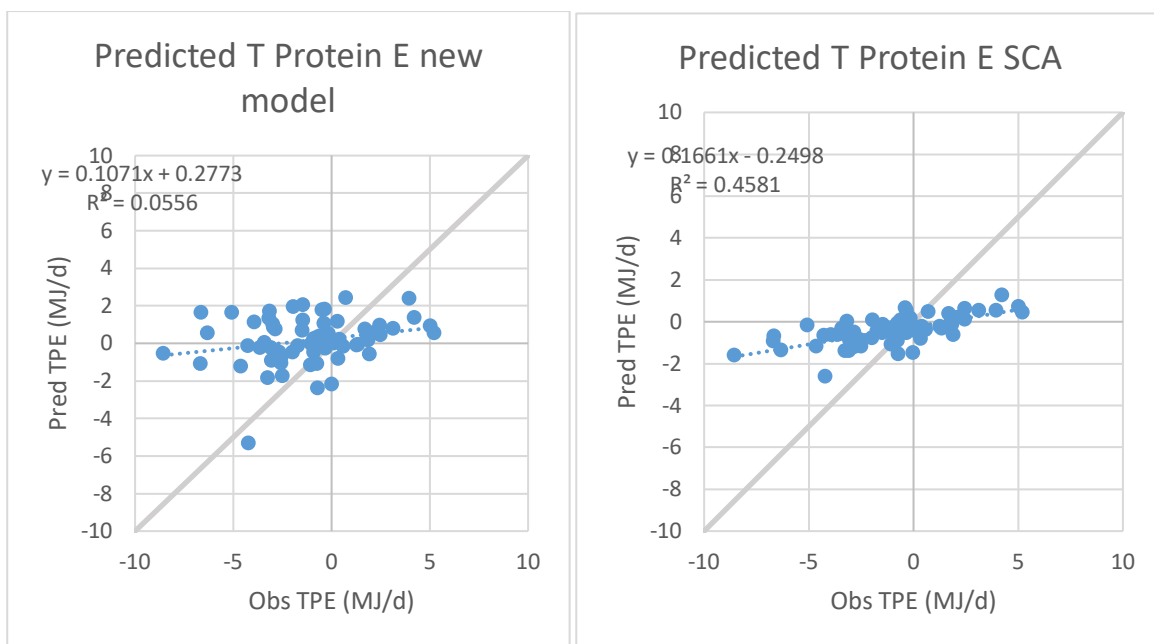


Figure 6.10. Tissue energy retained as protein. Observed (x axis) compared to predicted (y axis) energy retained as protein (Tissue protein energy TPE) (MJ/d) in lactating heifers (Freetly et al. 2006). The left hand panel is TPE predicting using the model described in this report, the right hand panel is the prediction of the same data obtained using PISC (CSIRO 2007). The grey line is $y = x$.

The proposed model fits the lactating beef heifer data of Freetly et al. (2006) as well, if not better, for tissue energy retention, than SCA. Compared to SCA, the proposed model has slightly improved fit of HP but there is substantial bias in estimation of tissue protein energy, and in body weight change, in both the proposed model and SCA. We are currently working to resolve this.

6.2 Activity

For activity we use the same construct as SCA/ CSIRO (2007). We add the energy cost of activity to the HP equation, this is equivalent to adding activity to the maintenance calculation in SCA/CSIRO (2007). However, we do not include the energy cost of chewing and ruminating into activity, because these activities contribute to the HP related to the feed.

7. Rumen model and nutrient supply

Modelling the physical and biological processes within the rumen has the potential to improve a ruminant growth model in a number of ways. Representation of rumen fill, digestion, and passage rates can be used to improve predictions of intake, as well as the effects of feed and feeding level on response to supplementation, digestibility of nutrients, and methane yield. After comparing the features and performance of extant rumen models, the model of Hyer et al (1991) was used as a base for a simple mechanistic rumen model that can be used to predict digestion and fermentation of feed, as well as microbial activity. This model was then further modified by the team with revised stoichiometry for prediction of methane and VFA production, as well as revisions to outflow rates and microbial growth rates. Data from sheep was used to create a new function relating rumen volume to the animal's current physical maturity. The model uses feed inputs that can be readily obtained from commercial feed analyses, making it relatively straightforward to use. When tested against experimental data from sheep, the expanded rumen model provides good predictions of microbial crude protein production, methane yield, and the response of microbes to changes in rumen dry matter content and crude protein content in the feed. The following sections describe the basis for developing the rumen model with an emphasis on dietary nitrogen content and intake.

7.1 Relationship between N content of the diet and intake

7.1.1 Rumen model

A rumen model has been built based on the Hyer model, which was a much simpler model than AusBeef and required less inputs. The development of this model demonstrates that intake is affected by the level of N in the diet. The following section details the review of the effect of N (Crude Protein) that intake is limited when rumen degradable CP is below approximately 5%.

Intake model: Effect of feed CP%

Modelling the voluntary intake of feed is a complex problem influenced by many factors including stage of maturity, prior intake and quality of feed. One factor important for predicting intake across a large range of pasture varieties is the nitrogen(N) content of the feed, usually expressed as crude protein (CP%).

Hunter and Siebert (1987) conducted a series of experiments on cattle to quantify this effect, using low-nitrogen roughages along with supplements of rumen-degradable protein and formaldehyde-treated casein. The effect can be seen in the graph below, derived from their results.

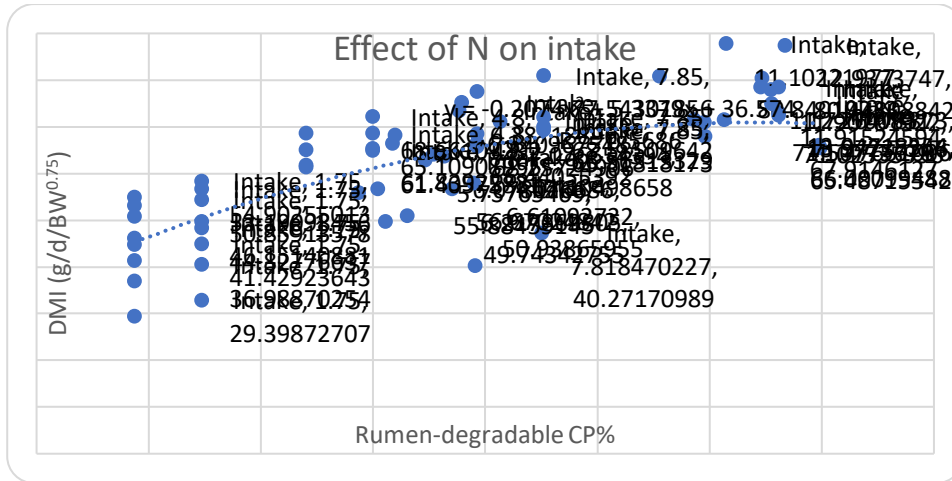


Figure 7.1. Relationship between rumen degradable crude protein (CP) and daily dry matter intake (DMI, g kg⁻¹LW^{0.75}, ◇). Data from Hunter and Siebert (1987).

The data show that DMI begins to drop off below about 9% rumen-degradable CP. This effect can be explained in terms of processes occurring within the rumen. The lack of sufficient N limits the growth of rumen microbes which in turn reduces the amount of feed hexose that can be degraded and fermented. This leads to an increase in rumen fill which then suppresses intake.

In order to capture this effect, we experimented with using a simple rumen model as a component of our intake model. We based our rumen model on the Hyer model (1991) since it is relatively simple while still modelling the relevant factors such as the microbial pool size.

The Hyer rumen model maintains pools for alpha-hexose, degradable and non-degradable beta-hexose, degradable and non-degradable protein, water-soluble CHO, non-protein nitrogen and microbial population. Flow rates between these pools are determined by pool concentrations, feed intake, saliva inflow and particle and fluid outflow rates. In the original model, pools are represented as concentrations. We modified this to represent pools as mass amounts, in line with other rumen models. This allows for a dynamic rumen volume independent of pool sizes. We also tuned the model parameters using outflow rates, microbial CP and methane measurements from Barbieri (2014) and Goopy (2013).

Microbial growth rate is calculated using Michaelis-Menten kinetics as:

$$U = U_{max} / (1 + k_c/C_{WSC} + k_n/C_{NPN})$$

Where C_{WSC} is the concentration of water-soluble CHO in the rumen and C_{NPN} is the concentration of non-protein nitrogen.

The rate of change of the NPN pool is calculated as:

$$dQ_{NPN}/dt = D_{NPN} + Sa_{NPN} - Q_{NPN} I_{pr} + k_{prot} Q_{PROT} Q_{BUG} - mn Q_{BUG} U + mn Q_{BUG} L$$

based on diet and saliva inflow, rumen outflow, microbial degradation of protein, uptake of NPN for microbial growth and release of NPN from microbial catabolism. Rates of change of the alpha-hexose and degradable beta-hexose pools are calculated as:

$$dQ_{AH}/dt = D_{AH} - Q_{AH} p_{pr} - k_{ah} Q_{AH} Q_{BUG}$$

$$dQ_{BH}/dt = D_{BH} - Q_{BH} p_{pr} - k_{bh} Q_{BH} Q_{BUG}$$

Where Q_{BUG} is the size of the microbe pool.

Together these equations will result in a build-up of hexose in the rumen for low values of degradable protein and non-protein nitrogen intake. This effect can be seen in the graph below which shows the results of running the rumen model with varying N intake for a reference animal and feed.

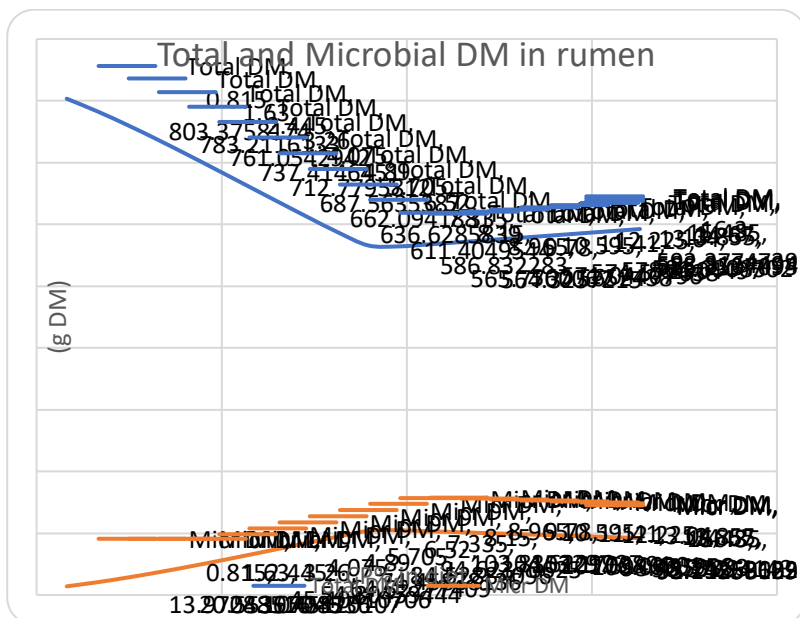


Figure 7.2. Relationship between dietary crude protein (CP) and Total and Microbial DM in the rumen.

Hyer (1991) proposes an intake model based on the rumen model by postulating that an animal will eat the amount of feed which leads to a certain total rumen dry matter concentration, taken to be 56.97 g/L for the reference animal. DMI is then predicted by using numerical optimisation to determine the intake which results in this steady-state rumen DM concentration for a certain feed composition. Using this method for their reference data, they report a sum of squares error of 227, which corresponds to an RMSPE of 2.3kg for the predicted DMI. Using the same approach, our modified and tuned version of the model gives a slight improvement with an RMSPE of 2.0kg. Observed versus predicted DMI are shown in the graph below. In simple terms this suggests that one of the consequences of low N in feed is reduced digestion of DM in the rumen, and consequent increase in rumen feed DM. This in turn leads to reduced DM intake.

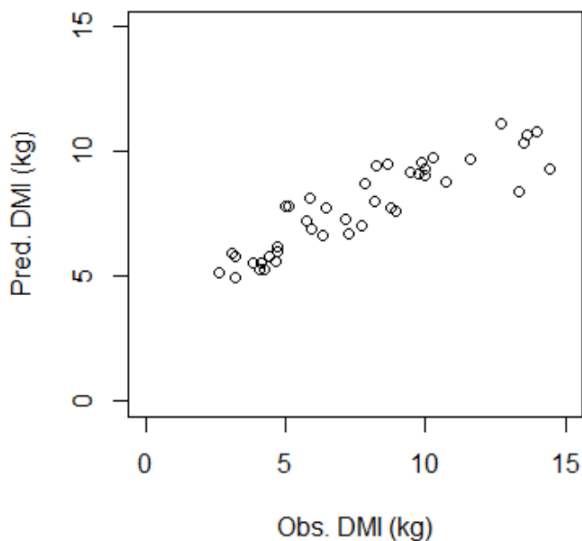


Figure 7.3. Observed vs predicted DMI using the simple rumen model based on rumen dry matter.

The approach clearly under-predicts intake for higher observed intakes. This poor result is not really surprising since running the model with the observed DMI values leads to rumen DM concentrations ranging from 58 g/L to 145 g/L, not a constant value as assumed. By analysing the Hyer reference data, we found that a better target rumen fill can be calculated as a linear function of body weight. This then gives a much better RMSPE of 1.4 kg and observed versus predicted DMI as shown below.

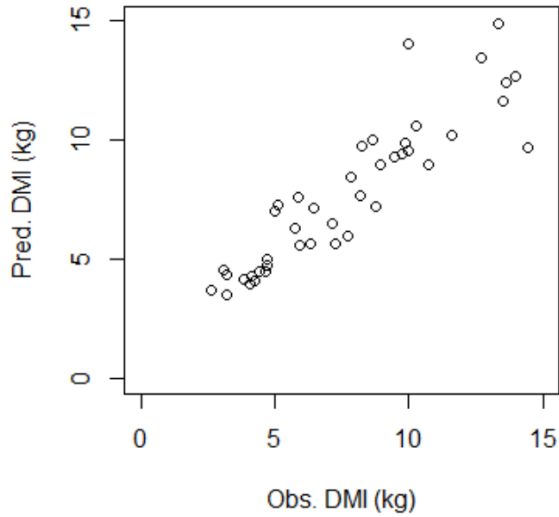


Figure 7.4 Observed vs predicted DMI using the simple rumen model based on body weight.

We then applied this model to the Hunter (1987) data to test whether it would work for a greater range of N values in the feed. The target rumen DM for the intake model was calculated as:

$$\text{RDM (kg)} = 0.01 \text{ BW} + 1.3$$

and, as before, the predicted DMI for each data point is that which results in the target steady-state RDM value. This approach gives an RMSPE of 0.91kg with observed versus predicted DMI as shown below, where the black data points are those where no N supplement was given, and the blue data points are with supplementation.

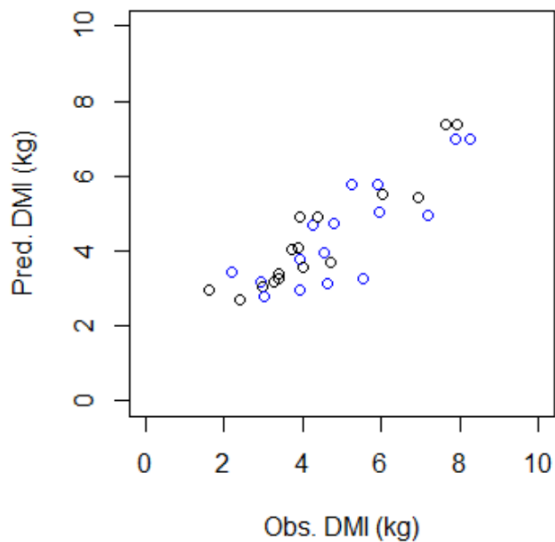


Figure 7.5. Observed vs predicted DMI using the revised simple model.

The use of a rumen model to predict DMI comes at the cost of significant computational overhead. The Hyer model requires a time-step of about 500 steps per day and, even with an efficient algorithm, the optimisation to determine the DMI requires several runs of the rumen model. This overhead is only justified if the approach produces much better results or covers a wider variety of feed compositions than a simpler approach.

As a comparison, we tried a linear regression approach to predicting the DMI for the Hunter data. Using body weight alone, this gives:

$$\text{DMI} = 0.0107 \text{ BW} + 1.05$$

with an RMSPE of 1.0kg.

Using body weight and degradable CP% of feed gives:

$$\text{DMI} = 0.00996 \text{ BW} + 0.188 \text{ CP} + 0.0262$$

with an RMSPE of 0.71kg which is better than the rumen model result.

The only other feed component which is significant in a multiple linear regression is the non-degradable beta-hexose component (NBH%). Taking this into account gives:

$$\text{DMI} = 0.00742 \text{ BW} + 0.116 \text{ CP} - 0.276 \text{ NBH} + 12.2$$

with an RMSPE of 0.58kg.

Finally, given the shape of the response to N in the Hunter data, it is worth considering a non-linear effect for the feed CP% with either a broken-stick or a curvilinear factor. For example:

$$\text{DMI} = 0.00747 \text{ BW} + 0.725 \ln(\text{CP}) - 0.265 \text{ NBH} + 11.3$$

gives an RMSPE of 0.54kg.

Although the rumen model approach does capture the biological effect of low-nitrogen feeds, the computational overhead does not appear to be justified compared with a simpler model, at least for the data considered so far. A further exercise should be to use the data from pen fed cattle used by Charmley et al (the current report) to determine the utility of the above approach.

7.1.2 Low N diets

Of specific concern for tropical pastures is the low N content of pastures throughout the dry season (Poppi et al. 1981, Panjaitan et al 2010). At N levels below approximately 1% N, the supply of rumen degradable protein (RDP) is insufficient to sustain adequate rates of microbial protein synthesis of 130 g/kg DOM (SCA, 2007). Panjaitan et al (2010) elegantly demonstrated this effect when feeding tropical grasses at CP content of 2.5, 3.0 and, 7.5%. Dry matter intakes increased linearly with CP content from 5 to 15 g/kg LW. However, total rumen digesta weights also increased with increasing CP content showing that the restriction in DM intake was not primarily physical for these low CP diets. In a series of papers by Hunter and Siebert (1985a, 1985b, 1987), this aspect was evaluated and demonstrated a clear response in intake to supplementation with RDP. This response was accompanied by an increase in rumen ammonia concentration or plasma urea N in excess of 100 mg/L as compared with values below 40 mg/L in unsupplemented diets. In the pen and grazing trials datasets in this project rumen ammonia N values ranged between 4 and 6 mg/L in the grazing studies and between 4 and 12 mg/L in the indoor trials where Rhodes grass was supplemented with up to 48% legume. From these data, it is clear that all diets were considered low in N, relative to those supplemented diets used by Hunter and Siebert (1985a, 1985b). However it could be argued that such high rumen ammonia concentrations are indicative of N wastage (Poppi and McLennan, 1995).

Examination of the results from the two pen studies with grass/legume diets was not ideal as these trials were designed for other purposes. However, in the Leucaena trial there was a clear two-phase response in intake to N with a linear increase up to 1.2 % OM, but no further increase in OMI as N content increased to 1.6% OM. These results confirm the point that for diets below about 1 % N or 6% CP factors not related to physical restriction may be influencing intake.

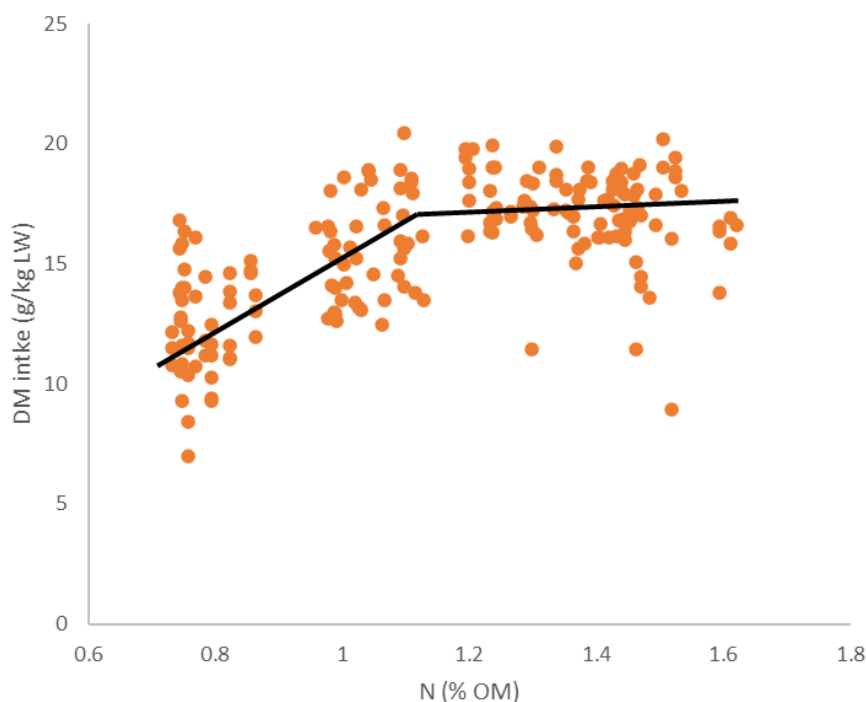


Figure 7.6. Relationship between DM intake and N content of the diet in cattle fed Rhodes grass hay supplemented with leucaena.

8. Framework for pasture intake that accounts for variable pasture morphology in tropical feeds

The following section describes Results presented in Report 6a,b,c. The following sections are included:

- Literature review
- Review of data for tropicals
- Assessment of GPS data

8.1 Literature review. Measuring and modelling forage intake of cattle grazing tropical pastures

8.1.1 Objective

Revise the methodology used in the Feeding Standards to estimate feed intake by livestock in extensive pasture systems where a spatially and temporally heterogeneous forage base elicits a strong behavioural driver for nutrient intake.

8.1.2 Introduction

“Despite many decades of research, there is still no unified theory of how animals control their intake of, and selection between, foods with different nutritional characteristics in relation to their physiological state” (Forbes 2007). And, despite the large number of associated publications there is no synthetic view on of the main determinants of bite mass, which is often considered the smallest scale process in foraging (Boval and Sauvant 2019). Two general approaches have been used to model diet selection and intake. The first is related to optimal foraging, where an animal behaves in such a way as to increase its rate of nutrient intake or increase its time associated with eating. For the second, different sets of factors control the processes of diet selection and intake, based around the animal’s perception of the physical and chemical characteristics of the forage components available (Dove 2006). In situations where pastures have less complexity (generally with few species), several factors such as grazing time, sward biomass, leaf:stem ratio and canopy height may be used to accurately predict intake (Neto et al. 2006).

In the existing Australian ruminant intake model (PISC 1990), feed intake is predicted as the product of two factors; i) the potential intake of feed by the animal (based on energy demand), and ii) the relative intake offered by the feed or pasture (based on the quality and quantity of herbage available). To deal with complexity due to the heterogeneity of forage in the pasture, the PISC model distributes the forage biomass into quality pools (based on digestibility), and animals consume progressively down the quality pools to meet their requirements, where this can be achieved.

Further to this, non-mechanistic methods of estimating the intake of grazing animals have been developed, such as from animal liveweight and growth on pasture (Minson and MacDonald, 1985), and advanced analysis of data from livestock wearable sensors (Greenwood et al. 2017). The modelling and prediction of ruminant intake from extensive pastures has been the subject of regular review, discussing aspects of research to progress methods for the generic and reliable assessment of voluntary feed intake (Cottle 2013; Gonzalez 2018; Smith 2021). In this review, we have aggregated the various methodologies into categories relating to i) Animal Production, ii) Animal Physiology, iii) Animal Indicators, iv) Animal Behaviour and v) Sward Characteristics.

8.1.3 Animal Production

(Weighing, Walk Over Weighing, Body scanning, Body measurements)

Determining the energy required to meet the observed maintenance and growth requirements of livestock can be used to estimate forage intake. This concept has been shown to predict intake accurately in cattle grazing tropical pastures as a function of their liveweight and growth rate (Minson and MacDonald, 1987). The formula used by Minson and MacDonald (1987) for estimating intake per steer (I, kg DM/d) from liveweight (L, kg) and growth rate (G, kg/d) is:

$$I = (1.185 + 0.00454L - 0.0000026L^2 + 0.315G)^2$$

There are concerns about the limitations of this method, in terms of its generalisability across other types of diets, classes of livestock and potential differences in feed efficiency among individuals (Gonzalez et al. 2018). To evaluate the performance of the Minson and MacDonald model, we reviewed grazing scenarios where intake has been estimated and associated liveweight and growth rate information is available (Table 8.1). Further, we compared these results using the QuikIntake calculator developed by McLennan and Poppi (2016), which applied the current PISC equations to estimate intake. We found that the evaluation was limited by the lack of published research where intake was reliably measured for an extended period of time, such that a reasonable estimate of the rate of growth of the animals could be determined.

Table 8.1 Review of DM intake prediction in cattle.

Forage	Pasture DMD (%)	Cattle	Mean live weight (kg)	Growth (kg/d)	DM Intake (kg DM/d)			Observed intake method	References
					Observed	Predicted*	Predicted**		
<i>Dactylis, Festuca</i>	61	12-mo Angus steers and heifers	345	0.93	8.79	7.48	12.08	#CH4	Velazco et al. 2017
Formulated	62	5-mo Simmental heifers	200	1.60	6.55	6.22	10.93	Feeder	Madruga et al. 2017
<i>Bermudagrass hay (C. dactylon L.)</i>	58	12-mo Angus x Brangus steers	303	1.22	7.34	7.32	12.09	Feeder	Krueger et al. 2008
Wheat crop	82 [^]	~12-mo Angus crossbred steers	282	1.04	8.61	6.69	6.5	Yb	Lippke et al. 2000; and in Decruyenaere 2009
Kleingrass (<i>Panicum coloratum L.</i>)	65	2-yo Brahman x Angus cows	420	2.02	14.7	10.69	17.07	Yb	Sprinkle et al. 2000; and in Decruyenaere 2009
			437	1.61	12.0	10.11	14.96	Yb	
<i>Dichanthium spp.</i>	67 [^]	Creole heifers	208	n.a.	3.74	n.a.	n.a.	Total faecal collection	Boval et al. 2007 and in Decruyenaere 2009
			208	n.a.	6.38	n.a.	n.a.	Cr2O6 est.	
Range grasses	72 [^]	Steers	199	0.44	5.7	4.51	4.45	Cr2O6 est. faecal output	Kloppenburg et al. 1995 and in Decruyenaere 2009
			252	0.73	5.3	5.74	6.49		
			299	0.31	6.6	5.80	5.53		
Fescue/Bermudagrass	74 [^]	Steers	282	0.46	7.1	5.78	5.66	Cr2O6 est. faecal output	Kloppenburg et al. 1995 and in Decruyenaere 2009
			336	0.73	7.8	7.01	7.65		
			395	0.64	8.4	7.69	8.08		
Wheatgrass/Bluestem	72 [^]	Steers	283	0.49	6.5	5.83	6.06	Cr2O6 est. faecal output	Kloppenburg et al. 1995 and in Decruyenaere 2009
			332	0.60	5.3	6.73	7.34		
			378	0.47	7.2	7.17	7.38		
<i>Paspalum notatum</i>	61 [^]	16-mo Brahman x British steers			4.5			Total faecal collection and IADF marker	Arthington et al. 2005 and in Decruyenaere 2009
<i>Cynodon dactylon</i>	56 [^]				4.2	n.a.	n.a.		
<i>Hemarthria altissima</i>	58 [^]		256	n.a.	3.4				
<i>Cynodon spp.</i>	53 [^]				4.4				

* Predicted with the equation $I = (1.185 + 0.00454L - 0.0000026L^2 + 0.315G)^2$, where I is intake (kg DM/d), L is liveweight (kg) and G is growth rate (kg/d).

** Predicted with the QuikIntake calculator, based on liveweight and growth rates of cattle (McLennan SR, Poppi DP (2016) 'QuikIntake version 5 spreadsheet calculator.'

[^]OM digestibility (%)

#A value of 19.9 g CH4/kg DMI is used in these calculations, which is an unweighted mean of the values 19.6, 20.8, 17.1, 22.1 g CH4/kg DMI obtained from Kennedy and Charmley (2012), McGinn et al. (2006), Grainger et al. (2007) and Ramin and Huhtanen (2013).

Despite the limited data, our initial evaluation revealed that the formula of Minson and McDonald (1987) showed a high prediction skill, with an r^2 value of 0.983 when the intercept was set at (0, 0). The associated trend line had a slope of 0.86, indicating that predicted intake was lower than observed intake overall (Figure 8.1). The datasets tended to be of younger, fast-growing cattle that were generally lighter, so the data were not well distributed with few observations above 10 kg DMI/day.

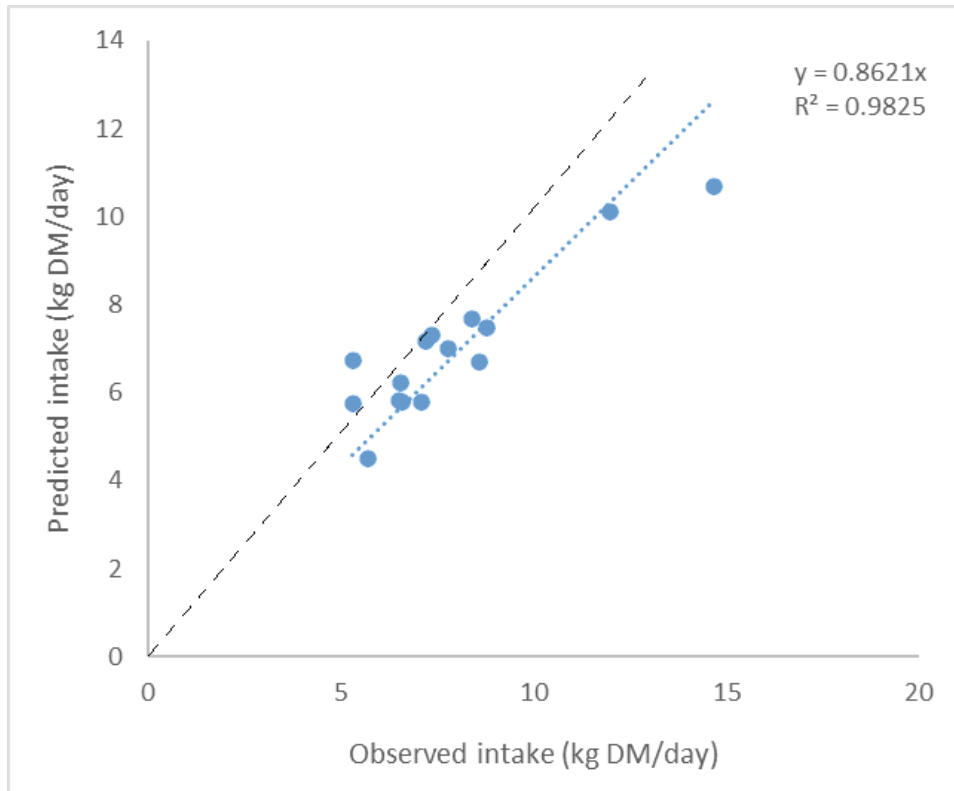


Figure 8.1. Observed and predicted (Minson and MacDonald, 1987) intakes of cattle taken from published studies of beef cattle in extensive grazing environments. Dash line (- -) represents $y = x$.

8.1.4 Animal physiology

(Bite rate, Bite mass, Grazing time)

Intake methods based on eating behaviour, the number of eating bites and bite size, have been tested (Chacon et al. 1976), but have not yet been developed into a practical system for sheep or beef cattle. Intake is equal to bite weight (area·depth·density) x bite rate x grazing time (Cottle 2013). The predominant constraint in reliability in the physiological approach is difficulty in the assessment of bite mass, associated with the broad heterogeneity of swards in space and time, resulting in high variability of bite depths and densities (Stobbs 1973a).

Feed intake is commonly predicted as a function of animal weight, physiological status and the quantity and quality of feed (PISC 1990). However, predicting the composition of intake (component and quantity of plants being eaten) is difficult (Tobias et al. 2006). The poor predictive ability of DMI is likely to be the result of insufficient characterisation of the sward and its low integration in predictive models, particularly in relation to the bulk density of forage (Boval and Sauvant 2019; Figure 8.2).

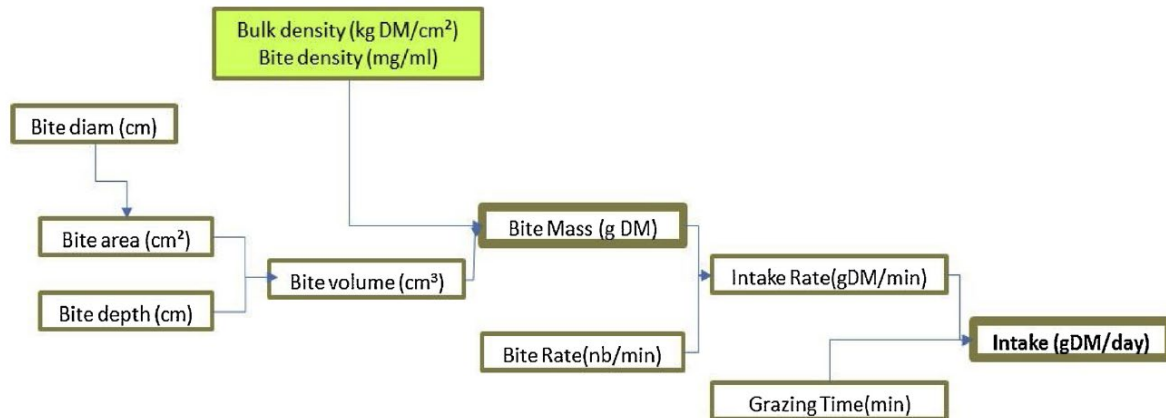


Figure 8.2. Functional relationships in the biophysical determination of intake from feeding behaviour. Taken from Boval and Sauvant 2019.

Baker et al. (1992) developed the FORAGE model of herbage intake by simulating changes in the mechanistic components of grazing behaviour, where grazing behaviour was divided into i) diet selection and ii) intake components and intake was determined as the product of grazing time and rate of intake, consistent with the mechanistic model proposed in Figure 8.2. The intention was to improve the accuracy of forage intake for a wide range of grazing situations, and because differential intake throughout the canopy was predicted, effects of herbivory on canopy structure were also possible. Baker et al. (1992) used relative crude protein content to determine relative preference values among functional plant groups. Maximum bite size determined on a metabolic weight basis, and a hyperbolic relationship between bite size and the sward biomass were then used to estimate the mass of forage consumed per bite. Bite frequency (or rate) was also determined as a function of sward biomass. The intake limit was determined based on physical limits associated with lower quality diets and physiological limits when diet digestibility was greater than 67%. Grazing time was calculated as a function of three limits, i) forage demand ii) potential grazing time (allowing for other behaviours during a 24 hr cycle) and iii) a maximum bite number limit.

In a large meta-analysis of grazing studies, bite mass was found to closely relate to sward height, and herbage bulk density explained variability among the different forage types, for a given sward height (Boval and Sauvant 2019; Figure 8.3). Bite mass reached a common plateau of 3.65 mg DM/kg BW in livestock.

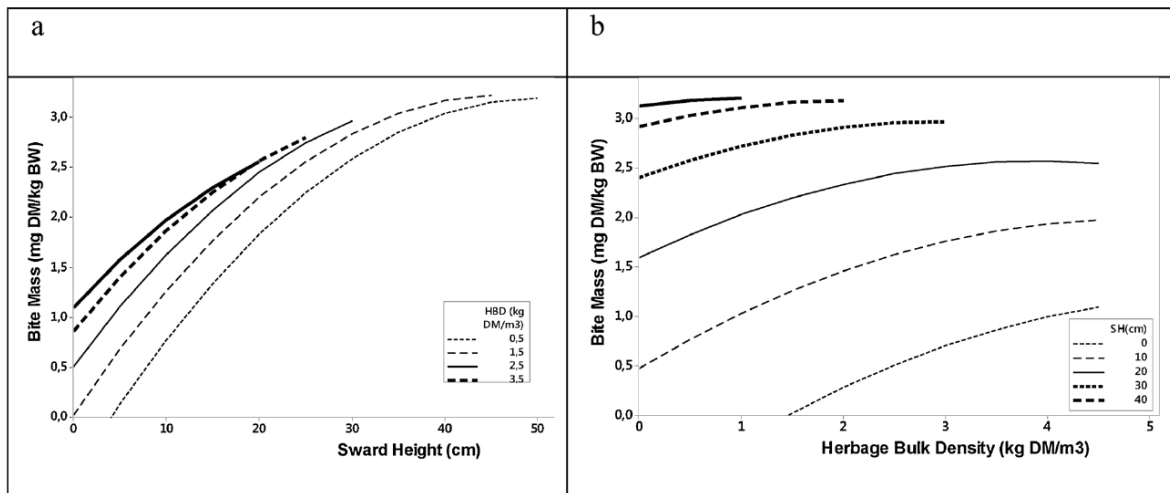


Figure 8.3. Influence of interactions between sward height and herbage bulk density on bite mass (Boval and Sauvant, 2019).

8.1.5 Animal indicators

(Artificial markers, Extrusa and Faecal N, Faecal NIRS, Carbon Isotope)

Both artificial and naturally occurring markers have been used to estimate intake in tropical grazing systems. The development and application of various methods has recently been reviewed by Smith et al. (2021). N intake has been identified as a promising marker for many decades, and a suitable calibration to pasture and animal type could be expected have high predictive skill (e.g. Siebert and Hunter, 1977; Figure 8.4). Similarly Faecal N and the application of NIRS has also been used to predict cattle intake and liveweight gain (Boval et al. 2004).

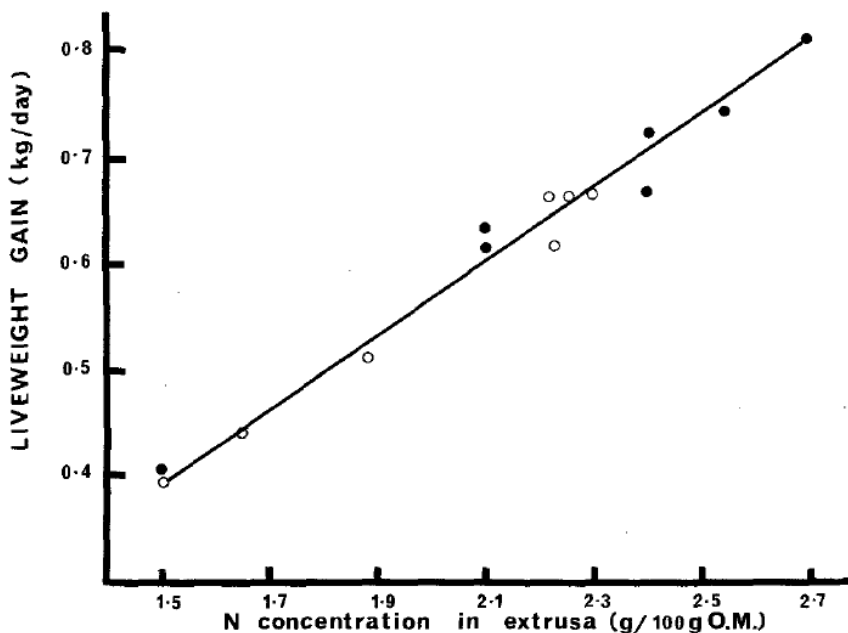


Figure 8.4. The relationship between liveweight gain and N concentration of extrusa (Siebert and Hunter, 1977).

8.1.6 Animal behaviour

(Ruminating time, resting time, grazing time)

Relating animal behaviours to intake

Implementing mechanistic models of intake (e.g. Baker 1992; Boval and Sauvant, 2019) relies on the quantification of sward characteristics such as the height, density, spatial distribution, quality and species preferences by livestock and animal grazing characteristics such as bite rate and mass (Black 1990; Cottle 2013). These characteristics are difficult to estimate or measure across large areas such as rangeland grazing systems. Here, the application of new sensor technologies may offer a solution. The use of accelerometer-based sensors has been developed to characterise and quantify cattle behaviours, such as walking, grazing and resting (e.g. Smith et al. 2016). However, the possibility of using sensors on livestock to populate mechanistic models that predict intake has received less attention. Further, the direct estimation of intake based on raw or classified sensor data, through analytical methods including machine learning has been proposed (Greenwood et al. 2017, Suparwito et al. 2021).

Behavioural activities of cattle are influenced by their grazing environment, and the availability and access to feed. As a result, some key behaviours have been considered as having potential to predict the feed supply and associated pasture intake in extensive grazing systems (Carvalho 2013). However, developing equations to predict feed supply and pasture intake have proven difficult, at least in part due to the high variability in grazing systems and experimental conditions. Further, as pointed out by Searle et al. (2007), plasticity in foraging behaviour enables animals to protect their rate of energy intake, to some degree, under changing forage conditions. One point of contention has been understanding time spent by the animal ruminating, in relation the quantity and quality of feed ingested. Reports on time cattle spend ruminating have shown increased, decreased or no effect in situations where intake has reduced. Some of this may be related to variability in the grazing environment and management. For example, in studies where feed availability was reduced by less time of access to pastures the rumination time of cattle was increased (Kennedy et al. 2011). However, in studies where cows were offered a lower pasture allowance, daily rumination times in these cattle decreased (Werner et al. 2019). A diagram by Searle et al. (2007) describing the intersection of 'landscape' and 'foodscape' by herbivores provides insights into how cattle might act when foraging in relation to changes in their foraging environment (Figure 8.5).

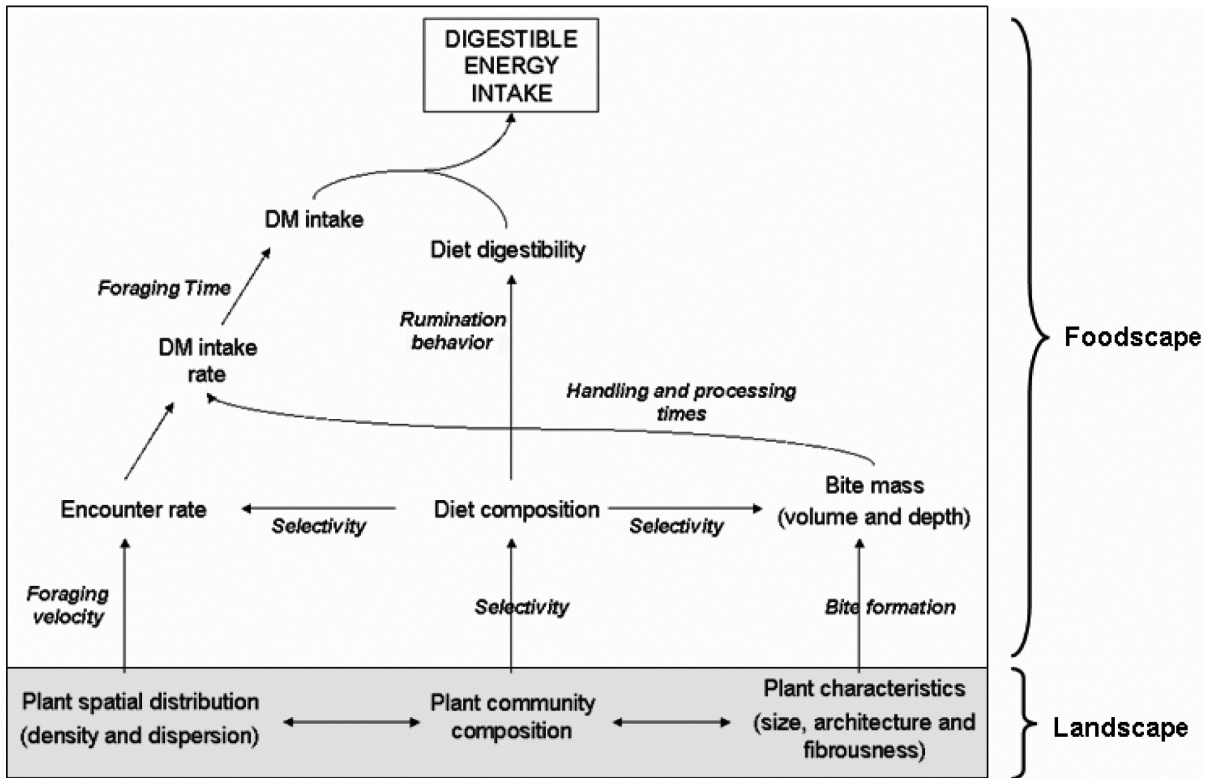


Figure 8.5. Components of landscapes and foraging behaviour that together determine the intake of digestible energy for ruminant herbivores. Unrestricted access to feed is assumed. Diagram taken from Searle et al. (2007).

The diagram in Figure 8.5 illustrates the breadth of area where cattle behaviours might be influenced by sward characteristics, and may then be related to voluntary feed intake. This agrees with the concept of using behavioural metrics as the basis for estimating liveweight gain and feed intake that is becoming more common. Based on this, we have reviewed published behavioural metrics that were recorded using on-animal sensors for the purpose of estimating weight gain or feed intake in livestock (Table 8.2). These were classified by the areas of behaviour outlined in Figure 8.6.

Table 8.2 Summary of behavioural metrics applied in the estimation of weight gain or feed intake in ruminant livestock.

Behaviour class	Metrics (sensor)	Publications
Foraging characteristics (velocity, tortuosity, geographic extent, duration, prehension)	Speed (GPS)	Suparwito et al. (2021),
	Distance (GPS)	Suparwito et al. (2021),
	Home range area (GPS)	Suparwito et al. (submitted),
	MSSI (GPS)	Suparwito et al. (submitted),
	Turning frequency (GPS, accelerometer)	Underwood (1983),
	Daily grazing time (accelerometer, acoustic)	Oudshoorn et al. (2013), Bishop- Hurley et al. (2020), Greenwood et al. (2014), Greenwood et al. (2017), Neto et al. (2006)
Rumination characteristics (duration, activity)	Bite rate (accelerometer, acoustic)	Galli et al. (2018),
	Daily rumination time (3-axis accelerometer, acoustic)	Kennedy et al. (2009), Clement et al. (2014), Krause et al. (2002), Shirmann et al. (2012), Bishop- Hurley et al. (2020), Benvenuti et al. (2015), Greenwood et al. (2014), Greenwood et al. (2017)
	Intensity (3-axis accelerometer)	
	Biochemical conditions (temperature, pH)	

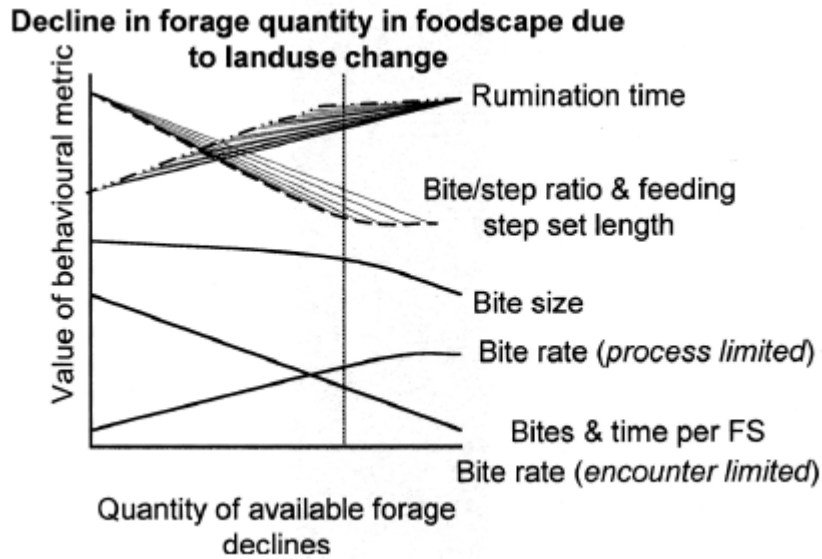


Figure 8.6. Summary of behavioural changes in key indicators in response to decline in the quality and quantity of the foodscape for a grazing ruminant. Diagram taken from Searle et al. (2007).

A Web of Science search was conducted using key words “cattle”, “intake” and “rumination”. The search contained 330 results, and from these papers were selected that revealed results of grazing studies where rumination behaviour was measured and related to the pasture conditions and intake of cattle. In one study where cattle were grazed in small plots on temperate pastures, there was a significant relationship between both grazing time and resting time and dry matter intake, however not for ruminating time, which ranged between 5.8 and 8.4 hours per day across three treatment levels of pasture availability (Greenwood et al. 2017). In another study with cattle grazing tropical pastures, the range of time spent ruminating was similar, however ruminating times lower than 7 hours per day were only reported under conditions of high pasture depletion and low intake (Benvenuti et al. 2015). Other studies of dairy cattle fed concentrate diets found no clear effects of daily intake on rumination time (Schirmann et al. 2012; Clement et al. 2014).

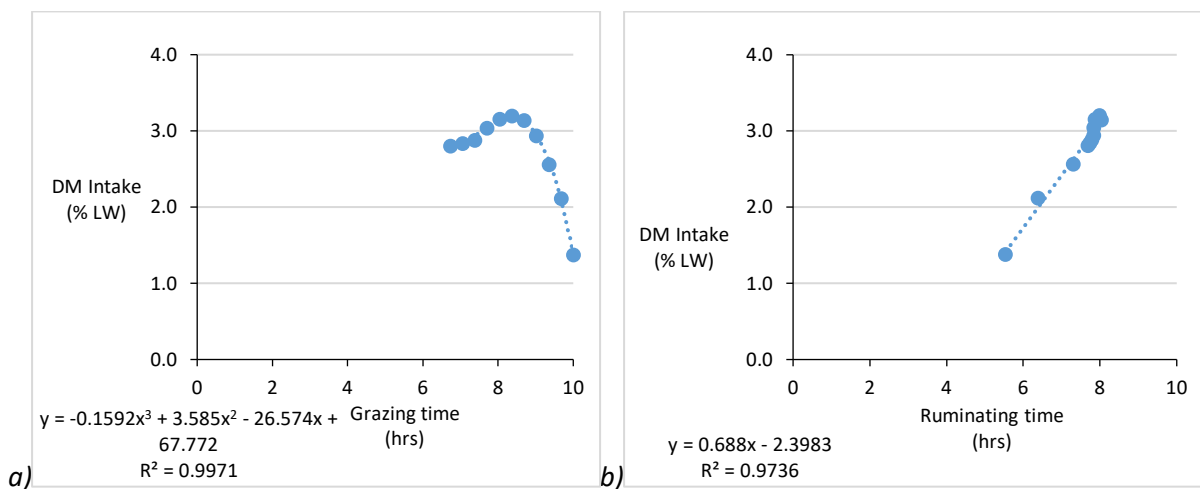


Figure 8.7. Relationship between a) grazing time, b) ruminating time and dry matter intake in cattle grazing tropical grass. Data taken from Benvenuti et al. (2015).

High variability across grazing systems can be a limitation to developing predictions of intake based on livestock behaviours (Rombach et al. 2019). In these cases larger datasets for model training data, and improved characterisation of the grazing system will be key components in improving the skill of these models.

The question as to whether machine learning would be best applied in quantifying components of a mechanistic model, or to predict intake directly from sensor data will also need to be considered. The advantage of populating a mechanistic model is that this may allow the method to be transferred more easily to a new grazing scenario where some pasture characteristics are known, but animal sensor data is not available. However, as commercial wearable sensors become available (Werner et al. 2019; Lee and Seo 2021), direct prediction of intake via internal processing of data from the wearable device may be a better option.

8.1.7 Sward characteristics

The current PISC model bases relative intake, which is the constraint to potential intake, primarily on the dry matter digestibility of the sward. Adjustment based on sward type (e.g. legume-based and C4 species) are additionally considered. These adjustments consider interactions that exist between characteristics of the sward that may affect intake for the same level of digestibility. Examples of these differences are shown in Figure 8.8 (Allden and Whittaker 1970; Neto et al 2006; Tobias et al 2006; Boval et al 2014; Benvenuti et al. 2016; Dixon and Mayer 2020; Black 1990; Da Trindade et al 2019; Dove 1996; Herrero 2000). Figure 8.8 highlights some effects of underlying differences in the physical structure of feeds with the same measured digestibility, including the higher intake of leaf material compared with stem for the same digestibility, and much higher intake of ground and pelleted forage. These differences could be attributed to the higher rate of passage of finer materials as they are less likely to be held up in the rumen and may also compact more efficiently in the rumen. A confounding effect could also occur, whereby digestibility could be reduced when material passes through the digestive tract more rapidly. Tropical grasses in northern pasture may pack down more densely in the rumen compared with material from southern pastures of the same digestibility (John Milton pers. comm). This view was supported by Minson (1981), who stated that “the higher intake of tropical grasses is apparently due to a difference in structure; tropical grasses with a digestibility of 60% are young and relatively leafy, while temperate grasses of similar digestibility are very mature and stemmy”.

Differences in intake observed for the same DMD in Figure 8.8 also contain parameters including different physiological states of animals of the same species and differences between species. These factors will need to be considered with further research into the ability to predict intake from changes in DMD.

The characteristics and structure of forage swards may also limit intake through the reduced potential intake rate, as was observed among different tropical grasses (Stobbs 1973a). Stobbs (1973a) observed that stem content and leaf/height ratio appeared to be the major factor affecting the size of bites taken by cows grazing tropical grasses. A strong preference for leaf components over stem may result in a greatly slowed rate of intake in these pastures as they mature resulting in the observation that “cows can be starving in the midst of plenty” (Stobbs 1973b). Leaf components have a higher N content than stems (Stobbs 1973b), which may motivate the high level of selectivity. There is some possibility that forage N concentration, particularly in the leaf, may be predictive of intake (Boval et al 2007; Figure 8.9). However, research of Romero and Siebert (1980) suggested that

the primary limitation to the growth of cattle on tropical pastures is one of digestibility, rather than nitrogen concentration. Thus, the difficulty in determining a predictive model in tropical pastures seems the complexity of phenology, stem/leaf ratios, and defoliation patterns for cattle grazing tropical pastures compared with temperate grazing systems.

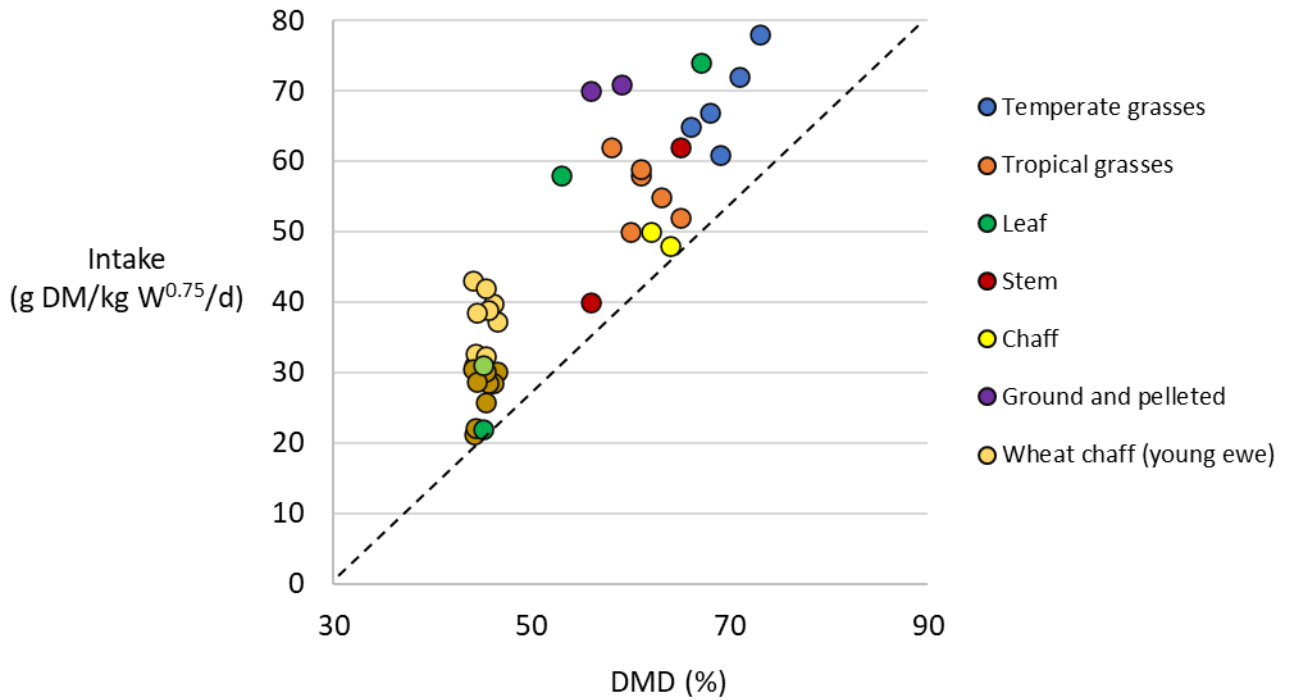


Figure 8.8. Relationship between diet Dry Matter Digestibility (%) and *ad libitum* voluntary intake (g DM/kg W^{0.75}).

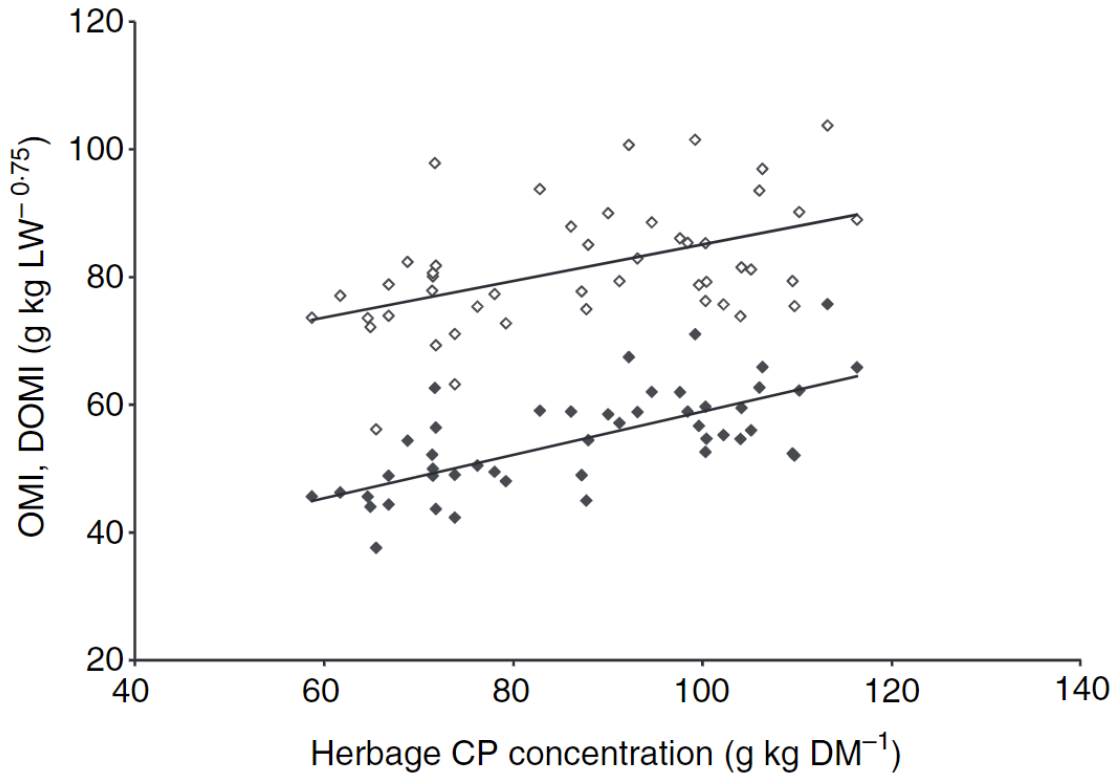


Figure 8.9. Relationship between crude protein (CP) concentration in herbage (CP, g kg⁻¹) and daily organic matter intake (OMI, g kg⁻¹LW^{0.75}, ◇) and daily digestible organic matter intake (DOMI, g kg⁻¹LW^{0.75}, ◆) for Creole heifers grazing a tropical native pasture (taken from Boval et al. 2007).

8.2 Review of Potential Intake Models in PISC

In CSIRO 2007 and GrazFeed® (Freer et al 1997), intake of pasture (and feed generally) by ruminant livestock is computed as the product of 2 components

- a) Potential intake – the intake of nutrients without any constraint due to availability and quality of feed , and
- b) Relative intake – constraints to intake imposed by availability (in the case of pasture this equates to the amount of pasture / ha and its height) and the nature of feed available (predominantly digestibility, but also if the available feed is a C3 or C4 grass or legume) and the proportion of available feed in digestibility classes.

This method of breaking intake into components set by the animal (potential intake) and feed (relative intake) and the interaction between them is a useful simplification because it readily facilitates computation and enables the complex field of measurement of feed intake to be broken into parts which can be subject to independent experimentation.

The notion of an animal's potential intake is useful because it should enable aeration in the pattern of intake due to sex, breed and genotype within breed to be explicitly shown. At present CSIRO (2007) only allows for effects of physiological state (stage of maturity and lactation) on intake. It does not provide any information about the effect of sex and genotype on intake as a function of maturity. It is now clear that phenotypic selection for weight, the largest component by far of the effect of genetic improvement programs in ruminant livestock, is predominantly driven by changes in feed intake (Oddy 1997; Walmsley and Oddy 2015).

An example of the effect of sex, breed and selection for weight in a breed of sheep is shown in the figure below. The potential intake suggested by CSIRO 2007 is shown for comparison. It is clear that in males and larger breeds that potential intake is greater than expected in less mature animals by the generalised CSIRO 2007 equation. It is also clear that selection for weight has shifted the point at which peak intake occurs towards a lower maturity.

The data for these comparisons is from a series of papers on the relationships between intake, weight and development to maturity of large and small Merino rams by Butterfield et al (1983a,b,c,) for Dorset horn rams and wethers (Butterfield et al (1984), Thompson & Parks (1983)) and for the Trangie Merino weaning weight selection lines (Thompson et al, 1985 a,b).

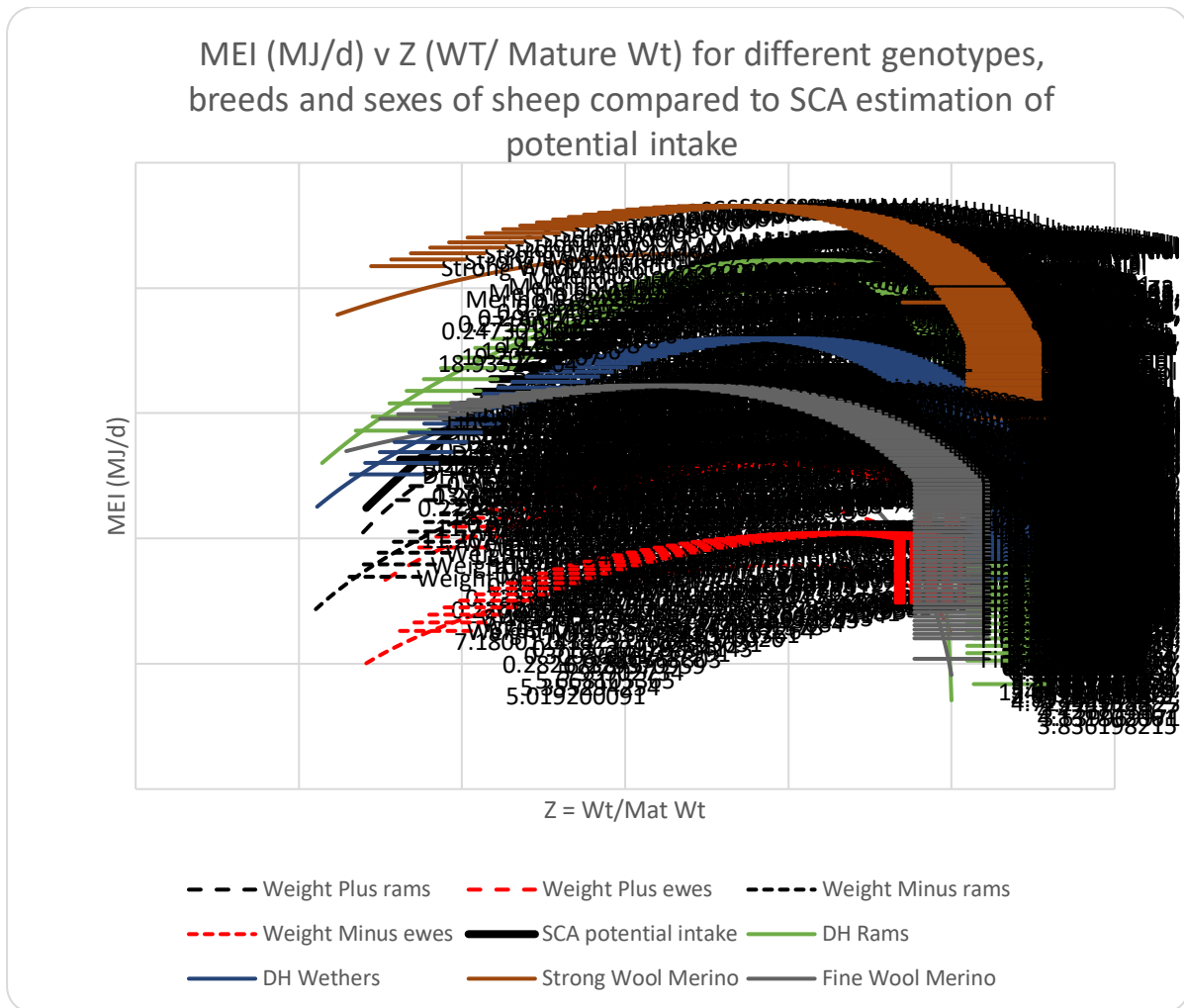


Figure 8.10. Metabolisable Energy Intake (MEI) versus weight as a proportion of mature weight for different lines of sheep.

To obtain a generalised method of including sex, breed and genotype we expressed intake as metabolizable energy intake (MEI) as proportion of estimated maintenance (MEI/M) and expressed this as a function of maturity (current weight / mature weight). A summary figure of all the data is shown in the Figure below. It clearly shows that the intercepts and slopes of MEI/maintenance as a function of maturity (z) vary between sexes, breeds and selection lines within breed. It is clear however that MEI/Maintenance generally declines with maturity. The graphs suggest that as a first approximation a linear function of MEI/Maintenance v z for each sex by breed and selection could capture more of the actual variation in intake than simply assuming that sheep of different breeds and sexes have the same pattern of intake.

As an example, the equation for Strong wool Mo ram is $MEI/maint = 4.517 - 3.343*z$

And for weight minus ewes is $MEI/main = 2.924 - 1.697*z$

This illustrates that the potential ME intake ranges from somewhere between 2 and 4 times maintenance at around 30% of maturity ($z = 0.3$) and that intake (expressed as MEI /maint) decays to 1 at or near maturity ($z = 1$).

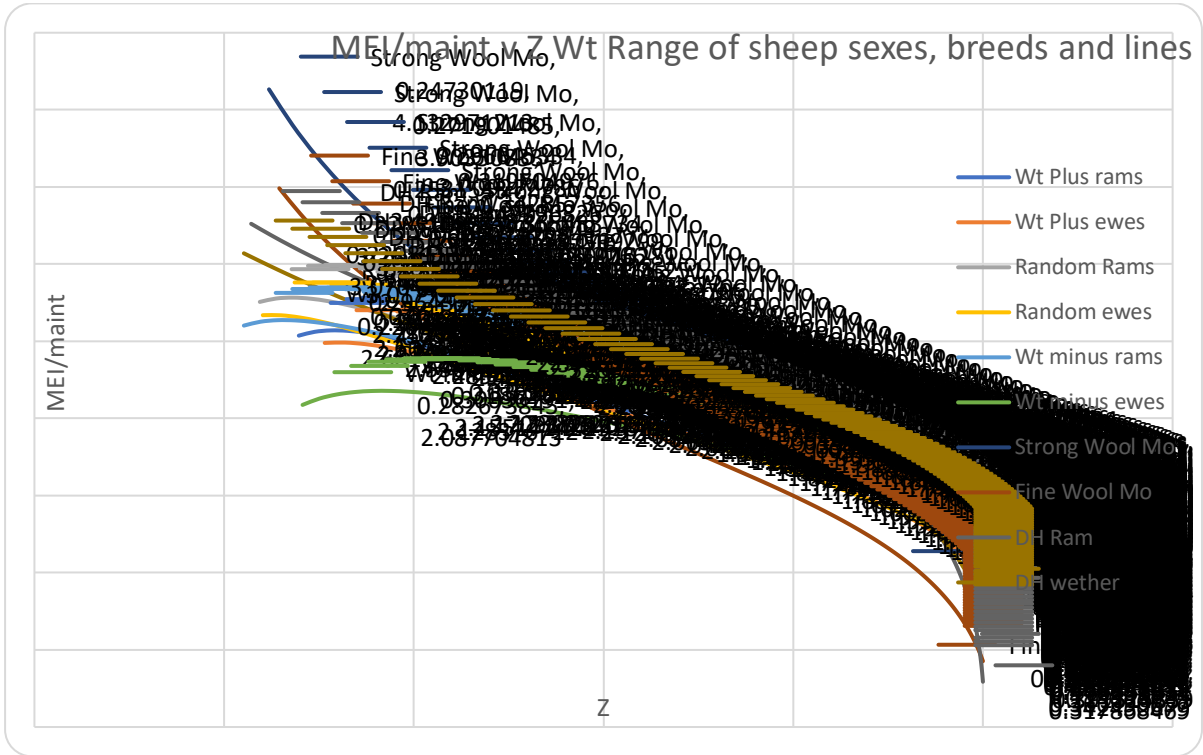


Figure 8.11. Metabolisable Energy Intake (MEI) versus weight as a proportion of mature weight for different breeds.

This approach may have utility for better estimating potential intake than the current form used in CSIRO 2007. It certainly allows for systematic variation due to sex, breed and effect of selection not possible in the current formulation.

8.3 An analysis of existing data from tropical grazing trials

Five research trials conducted since 2014 at Lansdown Research Station provided a data bank which was interrogated to develop relationships between diet characteristics, animal production and feed intake.

Three trials were pen studies where voluntary intake, animal weight change and diet nutritional characteristics were measured. The remaining two trials were grazing studies, with growing cattle set stocked on semi-improved tropical pastures.

In the pen studies, the objective was to derive intake equations based on diet nutritive value (CP or DMD). In the grazing studies the objective was to test these equations along with equations from the literature for prediction of voluntary DM intake on pasture. These equations were also used to compare predicted intake with observed intake measures taken from the literature. Equations were based on animal characteristics (e.g. LW, LWG, sex, age, etc) or pasture characteristics (e.g. digestibility, N content) or a combination of both. The intake prediction equations used in PISC (2007) were used as a baseline measurement against which other equations were evaluated.

8.3.1 Pen feeding trials with low quality hays supplemented with legumes

Three studies were conducted to determine the relationship between either DMD or CP in the diet and voluntary feed intake (Suybeng et al. 2020; Stifkens et al. 2022) In two of the studies, diet quality was changed by including differing levels of either desmanthus or leucaena to low quality Rhodes grass hays. The CP content of the diets ranged from approximately 5 to 12 % and DMD from 40 to 55%. There was a linear response in intake to DMD with an r^2 of 0.16 and 0.40 for the Desmanthus and leucaena trials, respectively. Results for CP were inconsistent with there being no intake response to increasing CP by adding Desmanthus to the diet. However, when leucaena was included in a Rhodes grass hay diet there was a curvilinear response to CP content of the diet (Table 8.3). In a third study differing quality Rhodes grass hays were offered to growing Brahman heifers ad libitum. For all studies the response in intake to increasing either DMD or CP content of the diets was lower than predicted using either PISC (2007) or Minson and McDonald (1987) being around 0.4. For this reason, none of the response equations were used further. Evaluation of DMI in the grazing studies was based on equations from the literature.

Table 8.3. Equations derived from pen-based intake measurements evaluated for prediction of intake in grazing studies.

Equation designation	units	Equation	r^2
Desmanthus DMD	DMD %, DMI (kg/d)	$DMI = 0.24DMD - 7.27$	0.16
Leucaena DMD	DMD %, DMI (kg/d)	$DMI = 0.23DMD - 4.22$	0.40
Hays DMD	DMD %, DMI (g/kg/LW)	$DMI = 0.26DMD + 2.86$	0.31
Desmanthus CP	CP %, DMI (kg/d)	$DMI = 0DMD + 4.26$	0.0
Leucaena CP	CP %, DMI (kg/d)	$0.17CP^2 + 3.13CP - 6.75$	0.54
Hays CP	CP %, DMI (g/kg LW)	$0.44CP + 0.44 + 12.51$	0.18

8.3.2 Evaluation of the PISC (2007) method for estimating pasture intake

The PISC equation to estimate relative ingestibility (RQ; below) was found to be deficient.

$$RQ = 1 - 1.7(\max((0.8 - (1 - P_{\text{legume}})g) - D), 0.0)$$

where:

P_{legume} = proportion of legume in the pasture

D = DMD of selected diet

g = 0.00 for C3 grasses or 0.16 for C4 grasses.

The factor g (0.16) to accommodate the higher intake for a tropical forage of similar digestibility compared to a temperate forage was found to inflate intake levels well above those expected or estimated, for example by LW change of ME intake. Examination of the data to support the 0.16 factor published in Hodgson et al (1977) revealed that at the common OMD of 60% there was no appreciable difference between tropical and temperate grasses. However, across their range of OMD (tropical, 40 to 62%) and temperate (60 to 80%) the slopes of the relationships between OM intake and OMD were very different. Other data reviewed previously also indicates that the intake of tropical forages is not higher at a similar DMD to temperate forages (see Section 4.1.7). At this time we have not included the 0.16 factor (g) when estimating RQ as its inclusion resulted in unrealistic intake estimates based on observation and ME requirements for observed growth.

At this stage we have also not included an intake discount for pasture availability relative to stocking rate as this was not a limitation for all data collected in the two grazing studies.

Finally, it was noted that the legume factor apparently reduced intake when the proportion of legume in the diet increased. This was replaced by a factor derived from published results by Kennedy and Charmley (2102) where poor quality Rhodes grass (OMD ~ 48%) was supplemented with either dolichos, burgundy bean or seca stylo, all of similar OMD to the grass. The combined relationship between proportion of legume and OMI was;

$$\text{OMI (kg/d)} = 2.0 \times \text{legume proportion} + 4.33$$

Thus a factor of 2 was included to adjust intake according to the proportion of legume in the diet. This factor was considerably below that derived by Freer and Jones (1984) that was used in the PISC equation.

To evaluate the utility of the revised PISC equation (PISC 2007) as a baseline estimator of pasture intake, predictions were compared with the observed pen-based measurements from the hay trial. The agreement between observed and predicted DMI was good for the PISC_r equation but less so for the Minson and McDonald equation when DMI was relative to LW. The relationships held when DMI was not scaled for LW but correlation coefficients were markedly lower. The results demonstrate that the PISC_r equation was representative of pen-based data and this method was subsequently chosen as the baseline estimation of voluntary DM intake on pasture (Figure 8.12).

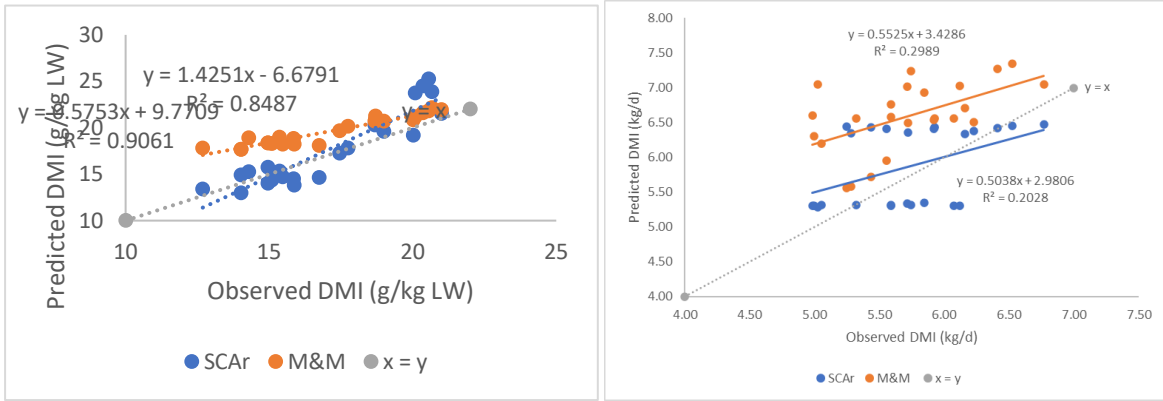


Figure 8.12. The relationship between estimated and measured DM intake in pen fed cattle for the revised PISC equation (blue) and Minson and McDonald (orange; 1993). Data shown scaled for LW and unscaled.

8.4 Pasture trials with cattle grazing heterogenous tropical swards

8.4.1 Pasture finishing trial with crossbred (taurus x indicus) steers grazing heterogenous tropical swards

Eighty-eight tropical composite steers were studied between August 2015 and July 2017. Cattle were mustered at approximately two-monthly intervals weighed and samples of faeces and rumen fluid taken. At approximately the same dates, the pasture was sampled for nutrient and species composition. Data were analysed based on variables collected in the dry and wet seasons (Table 8.5). Summary design and measurements are presented in Table 8.4. Rainfall data was used to divide the trial into four seasons (two dry and two wet).

Table 8.4. Description of seasons and measurement times.

Seasons	
Dry season 2015	Aug to Nov 2015
Wet Season 2016	Dec to May 2016
Dry season 2016	June to dec 2016
Wet season 2017	Jan to July 2017

Summary results are presented in Table 8.5. Of note are the marked seasonal differences in all parameters measured and the marked differences in nutritive value of the diet compared to the pasture sward. Cattle were able to select for a diet higher in nutritive value than the overall sward. This was particularly noticeable in the dry seasons.

Table 8.5. Summary results for pasture, diet and rumen metrics as measured over seasons.

	2015/16		2016/17	
	Dry	Wet	Dry	Wet
LW change (kg/d)	0.15	0.91	0.24	0.70
Botanal based measurements				
Biomass (T/ha)	1.39	4.40	2.14	1.51
Legume (%)	33.1	25.2	38.2	42.8
Nutritive value of pasture measured by NIR				
Crude protein (% DM)	5.55	10.38	8.07	10.29
DM digestibility coefficient	0.21	0.36	0.54	0.41
Neutral detergent fibre (% DM)	75.1	61.0	68.2	69.6
Acid detergent fibre (% DM)	56.1	38.8	44.9	41.1
Nutritive value of diet measured by faecal NIR				
Dietary crude protein (% DM)	8.81	10.69	7.57	13.0
DM digestibility coefficient	0.56	0.60	0.54	0.59
Non-grass in diet (%)	41.1	43.3	52.1	40.8

8.4.2 Pasture grower trial with heifers grazing heterogenous tropical swards

Fifty-six Brahman heifers were studied between December 2020 and November 2021. Cattle were divided into four replicated paddocks and mustered at approximately two-monthly intervals, weighed and samples of faeces and rumen fluid taken. At approximately the same dates, the pasture was sampled for nutrient and species composition. Twenty-four of the heifers were removed from pasture and placed in pens for individual measurement of feed intake and fed Rhodes grass hay of similar nutritive value to the pasture at the time of removal from paddocks (DMD = 53 and 60%; CP = 10 and 13%). The main aim of this trial was to study feed efficiency and formed part of the companion project P.PSH.1000. Figures 8.13 and 8.14 show the change in DMD and CP over the course of the trial and demonstrate the higher nutritive value of consumed feed (faecal NIR) compared to feed on offer (pasture NIR). These results confirm the findings in the first grazing trial and cast concern on the use the nutritive value of the feed on offer as an indicator of the nutritive value of feed consumed in tropical grazing situations.

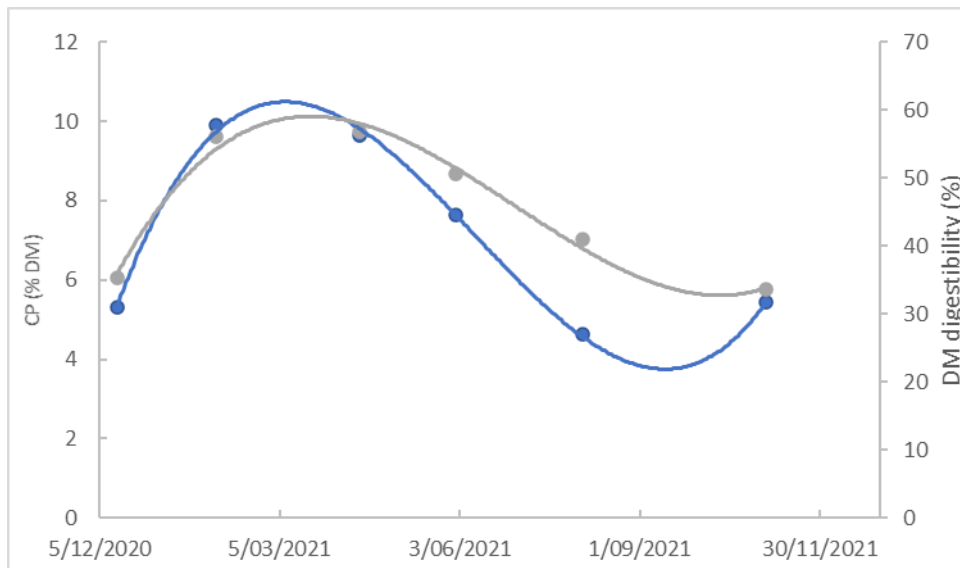


Figure 8.13. Polynomial relationships for DM digestibility (grey) and crude protein (blue) of pasture over the duration of the trial.

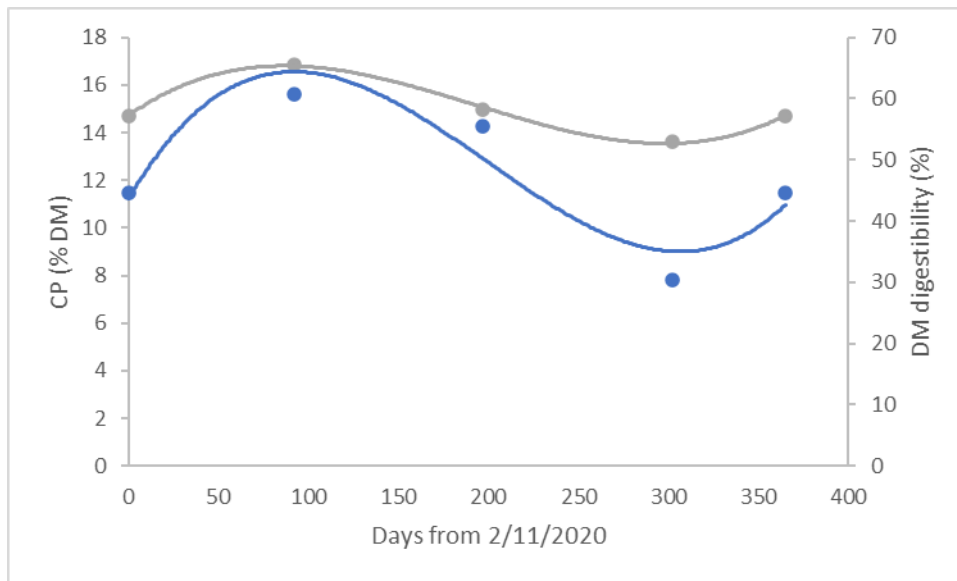


Figure 8.14. Polynomial relationships for DM digestibility (grey) and crude protein (blue) of the diet over the duration of the trial.

The DMD and CP values of consumed forages, and LW and LW change were used to estimate DM intake according to a range of published equations. The comparison of the various approaches was used to elucidate where there were issues in the techniques and explore gaps in information or consider alternative methods.

8.5 Inferences from the data sets

The grazing trials provide useful datasets for evaluation of various methods of estimating intake from either measured of animal productivity or diet quality, or in some cases a combination of both. The data included frequent measurement of LW and LW change over periods of one or two years. Faeces samples were collected from mustered cattle and analysed using faecal NIR (FNIR) for diet CP, DMD and percent non-grass (equivalent to legumes). Samples of pasture were taken at similar intervals and estimates using the Botanal technique made of biomass, and the proportions of grass, legume and weeds. Ten % of quadrats were cut and analysed for DMD and CP by NIR. Additionally, in grazing trial 2, cattle were fitted with GPS enabled activity collars that collected data on the spatial distribution of grazing patterns in relation to the spatial distribution of biomass, grass or legume (derived from Botanal sampling). Data also was collected for grazing time, ruminating time and total activity.

8.5.1 Evaluation of published equations for prediction of pasture intake

In the absence of measurement of intake using direct measurement either from markers, oesophageally cannulated animals or disappearance of sward biomass, all equations assessed were compared to the revised PISC (2007) method of intake estimation, which relies on an understanding of the utilization of ME by the animal and the quality of the diet.

The performance of an animal is related to the ME intake. Assuming N is non-limiting, then the rate of gain is related to the amount of ME intake available for growth after accounting for maintenance, pregnancy, lactation and activity. For non-reproductive, growing animals it is possible to derive an estimate of voluntary intake from the LW and LW gain of the animal. Allowance can be made for the activity of the animal as well as breed and sex. In the grazing trials FNIR methods were used to determine ME of the diet. This was used to estimate expected intakes through a knowledge of ME requirements for gain, maintenance and an assumed activity of approximately 6 km/d (McGavin et al 2018). For both trials, the expected range in intake was 4.5 to 8 kg DM/d (1.5 to 2 % LW).

Other modifying characteristics of the pasture and sward also contribute to voluntary intake of the grazing animal (SCA, 2007). These include the sward biomass and pasture species, particularly legumes versus grasses (Minson, 1990). Hodgson et al (1977) demonstrated that for the same digestibility, intake to tropical grasses is greater than that of temperate grasses, however This report cast doubt on the practical implications when developing intake prediction equations. An additional compromising factor is that the composition of the consumed biomass is very different than that of the feed on offer (Bohman and Lesperance, 1967). Data shown earlier highlights this issue clearly. In both grazing studies DMD of consumed pasture was higher than the DMD of pasture on offer. In grazing trial 1 DMD of consumed pasture averaged 57% over the two-year trial compared to 38% for the pasture on offer. These values were very similar in grazing trial 2, being 56 % and 32 %, respectively. Similarly, the CP of the selected diet was higher than the pasture on offer. In grazing trial 1 CP was 9.2 and 8.6 % DM for diet and pasture and for grazing trial 2, CP was approximately 12 and 6 % DM for diet and pasture, respectively. Under conditions of low to moderate grazing pressure and in heterogeneous swards, cattle exhibit selectivity. Thus the use of faecal NIR is essential to characterise the quality of consumed pasture.

The PISC method was developed for temperate pastures, with the predominance of data derived using sheep, and rather less data was available for cattle. It is unwise to extrapolate factors that influence voluntary intake in tropical conditions using the much larger amount of data collected under temperate conditions. Pasture species and animal genetics are both quite different. Added to this is the high degree of heterogeneity of tropical swards and seasonal variability in both quantity and quality. Following careful examination of the PISC relationship some modifications were made and the revised PISC equation (SCAr) was used as a baseline for intake, when evaluating published intake equations.

A range of models have been published in the literature and were used to estimate voluntary intake of cattle. Table 8.6 summarises the equations used to predict intake in cattle in the two grazing studies carried out at Lansdown Research Station. Detailed measurements were taken of the cattle, the pasture and the diet of 144 growing cattle. Of the eight models tested, a number were considered unsuitable due to low correlations, response slopes divergent from unity and marked under- or over prediction of intake. A selected number of models are detailed in the report that represent different approaches to intake estimation and highlight the pros and cons of these varied approaches.

Table 8.6. Description of the equations used to estimate voluntary intake from liveweight and liveweight change, nutritive value of the diet or both.

Source	Equation
PISC (2007) ¹	$RQ = 1 - 1.7(\max((0.8 - (1 - P_{\text{legume}})g) - D), 0.0)$
PISCr (this report) ²	$RQ = 1 - 1.7(\max((0.8 - g) - D), 0.0)(P_{\text{legume}})(LF)$
Equations based on LW and LW change	
Minson and McDonald (1987)	$DMI = (1.185 + 0.00454LW - 0.0000026LW^2 + 0.315LWG)^2$
Azevedo et al (2016)	
indicus x taurus	$DMI = -2.6098 + 0.8844LW^{0.75} + 4.4672LWG - 1.3579 LWG^2$
indicus	$DMI = -2.7878 + 0.8789LW^{0.75} + 5.0487LWG - 1.6835 LWG^2$
Fernandes et al (2022)	$DMI = 0.055 + (0.069 \times LW^{0.75}) + (0.304 \times LWG)$
Equations based on digestibility, crude protein or digestibility and LW	
Elliott et al. (1961)	$OMI \text{ (kg/d)} = 18.11OMD \text{ (\%)} - 0.92$
Hodgson et al. (1977)	$OMI \text{ (kg/d)} = 0.89OMD \text{ (\%)} - 30.5$
Siebert and Hunter (1977)	$OMI \text{ (g/kgLW}^{0.75}\text{/d)} = 19.3N \text{ (\% OM)} + 54.4$
Coleman et al (2014)	$OMI \text{ (kg/d)} = 4.56 + 0.0053LW \text{ (kg)} - 0.00002 \times LW^2 - (0.0553 \times DMD \text{ (\%)} + 0.0032LW)$

¹ P_{legume} = legume proportion, $g = 0.0$ for C3 and 0.16 for C4 grasses, $D = DMD$ as a proportion

² P_{legume} = legume proportion, $g = 0.0$ for C3 and C4 grasses, $D = DMD$ as a proportion, LF legume factor = 2.0

The mean DMI for equations of best fit are shown in Table 8.6. The Minson and McDonald (1993) equation, based on LW and LWG, produced estimates of DMI that agreed well with PISCr estimates, although correlations were low (Table 8.7). The slope of the line was closer to unity for grazing trial 1 (0.97) than trial 2 (0.38). The Hodgson et al (1977) equation for tropical conditions based on digestibility, also produced mean DM intake similar to SCAr. The equation performed well in grazing trial 2 compared to grazing trial 1, with a better correlation coefficient ($r^2 = 0.62$) and a slope closer to unity (1.3 versus 1.7). Siebert and Hunter (1977), used CP as the determining variate. Although the slopes were close to unity in both trials (1.1 and 1.2), the model overestimated intake in grazing trial 2 by 30%. The Coleman et al (2014) equation that use both LW and DMD as variates and performed quite differently in the two trials. In the first study the slope was much steeper than unity but mean intake was close to SCAr. In grazing study 2, there was no relationship between the PISCr and the Coleman predictions. This result was surprising given that the equation accounted for both differences in LW and diet quality. Graphical representations of these relationships are shown in Figures 8.15 to 8.18.

Table 8.7. Mean estimates of pasture intake in comparison to the PISCr estimates for grazing trials 1 and 2. Four of eight tested models are included to highlight the different approaches.

Equation	Grazing study 1		Grazing study 2	
	SCAr	Prediction	SCAr	Prediction
Minson and McDonald (1987)	7.12	6.74	6.46	6.29
Hodgson et al. (1977)	7.12	6.88	6.46	6.83
Siebert and Hunter (1977)	7.12	7.73	6.46	8.40
Coleman et al (2014)	7.12	7.31	6.46	7.51

Table 8.8. Relationships between published equations for the prediction of dry matter intake and the modified equation of PISC (2007).

Equation designation	Input data	Trial	Equation	r ²
Minson and McDonald (1987)	LW, LWΔ	1	0.97DMD + 0.46	0.13
		2 ¹	0.38DMD + 4.10	0.10
Hodgson et al (1977) tropical equation	DMD	1	1.72DMD – 4.29	0.34
		2	1.32DMD – 1.54	0.62
Siebert and Hunter (1977)	CP	1	1.10DMD + 0.62	0.10
		2	1.23CP +0.46	0.69
Coleman et al (2014)	LW, DMD	1	0.51DMD + 3.50	0.14
		2	-0.1DMD +8.50	0.03

¹ Equation does not include data from period 1

It was not surprising that models using digestibility or CP alone (Hodgson et al. 1977; Siebert and Hunter 1977) did not perform equally in both grazing trials as these equations do not consider the size of the grazing animal. Clearly at similar nutritive value, a smaller animal will have a lower intake. In fact, when these equations are used to predict relative intake (g/kg LW), they performed quite well. The Hodgson et al (1977) equation included only OMD (converted here to DMD) to predict DMI. In grazing trial 1 with cattle covering a wide weight range the equation predicted mean intake well but the variation in predictions (3 to 12 kg/d) was high resulting in a low r². In grazing trial 2 where the variation in LW as smaller, DMD was able to accurately predict intake relative to SCAR, with an r² of 0.62.

Equations that included animal LW gain and digestibility (Coleman, 2014) did not perform universally well. In particular, equations did not adequately deal with extremes in LW and/or LWG. This was true in grazing trial 1 where there were light (year 1) and heavy (year 2) cattle close to maintenance in the dry season then gaining over 0.7 kg/d in the wet season. In grazing trial 2, data collected for lighter cattle grazing “green pick” and high in nutritive value but low in biomass was problematic.

The PISC equation relies on a prediction of potential intake predicted from expected LW for age which is then modified by diet digestibility, percent legume in the diet and the proportion of C4 grasses. It provides a point in time estimate according to conditions in place at the time of estimation. When considering the use of LW and LWG as estimates there is a requirement that these are measured over a time period. In grazing trial 1 this was several months and corresponded to clear seasonal differences between dry and wet conditions. During these periods cattle exhibited relatively constant performance and diet characteristics (i.e., green versus senescent pasture). Grazing trial 2 was only one year duration and when intervals between weighing were short (4 to 5 weeks), predictions were generally disappointing. Averaging LW and LW gain over 7 to 8 weeks improved predictions and data shown are for the longer weigh period. This highlights the need to reduce difference error by increasing the days between successive weighing.

In grazing trial 2, the Minson and McDonald (1987) equation appeared to under-estimate DM intake (relative to SCAR) in period 1 of the trial (December 2020 to March 2021). Consequently, the equation in Table 8.7 does not include data from Period 1. Period 1 was characterised by low biomass “green pick” that was 100% C4 grasses and with high DMD (~ 60 – 65%) and CP (~ 15 -20% DM). These small cattle (247 kg) had high rates of LWG (0.70 kg/d). By comparison in period 2 cattle were heavier (331 kg) but exhibited similar LWG (0.67 kg/d) and diet DMD and CP had dropped by 10 and 20%, respectively. The Minson and McDonald (1993) equation is driven solely by LW and LWG, whereas PISCr (2007) does account for diet nutritive value and species composition. Thus, under certain conditions, Minson and McDonald (1987) may not accurately predict intake.

Simple regression equations cannot capture the range of animal and dietary characteristics that contribute to modifying voluntary intake. This review has focussed mainly on data from tropical grazing conditions. A feature of many of the equations was the lack of congruence with PISC across the range of pasture conditions and animal characteristics.

While these results are disappointing, they are not altogether surprising. Given the difficulty of obtaining data on diet quality, if a simple approach is to be used, the equation of Minson and McDonald (1987) may suffice for many tropical situations. The PISC approach is more sophisticated and attempts to consider a range of known factors that influence pasture intake. However, under practical grazing situations many of the required variables are not available.

The results of the selected prediction equations are shown in Figures 8.15 to 8.18.

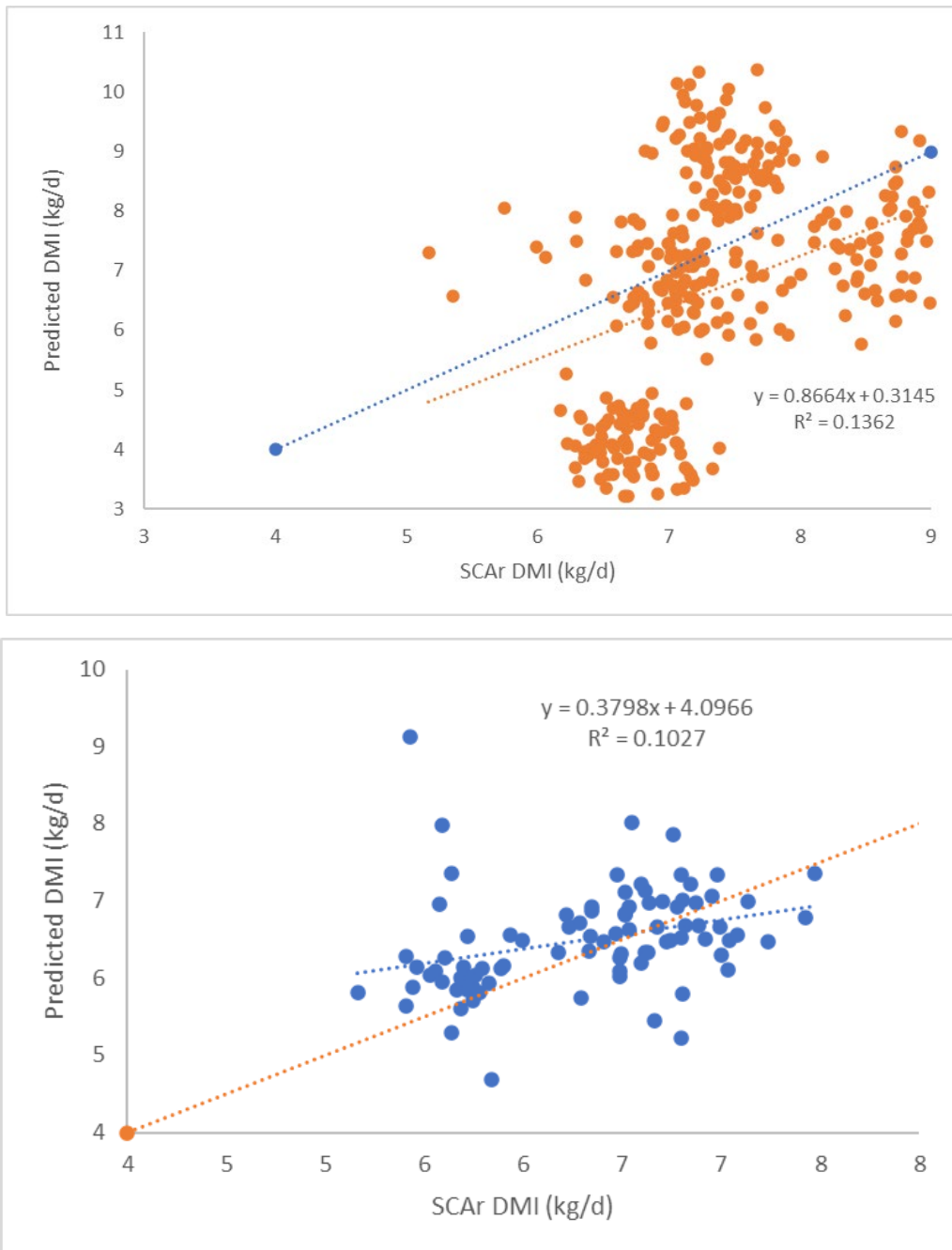


Figure 8.15. Correlation between PISC (2007) and Minson and McDonald (1993) using LW and LWG. Grazing trials 1(top) and 2 (excluding period 1; bottom).

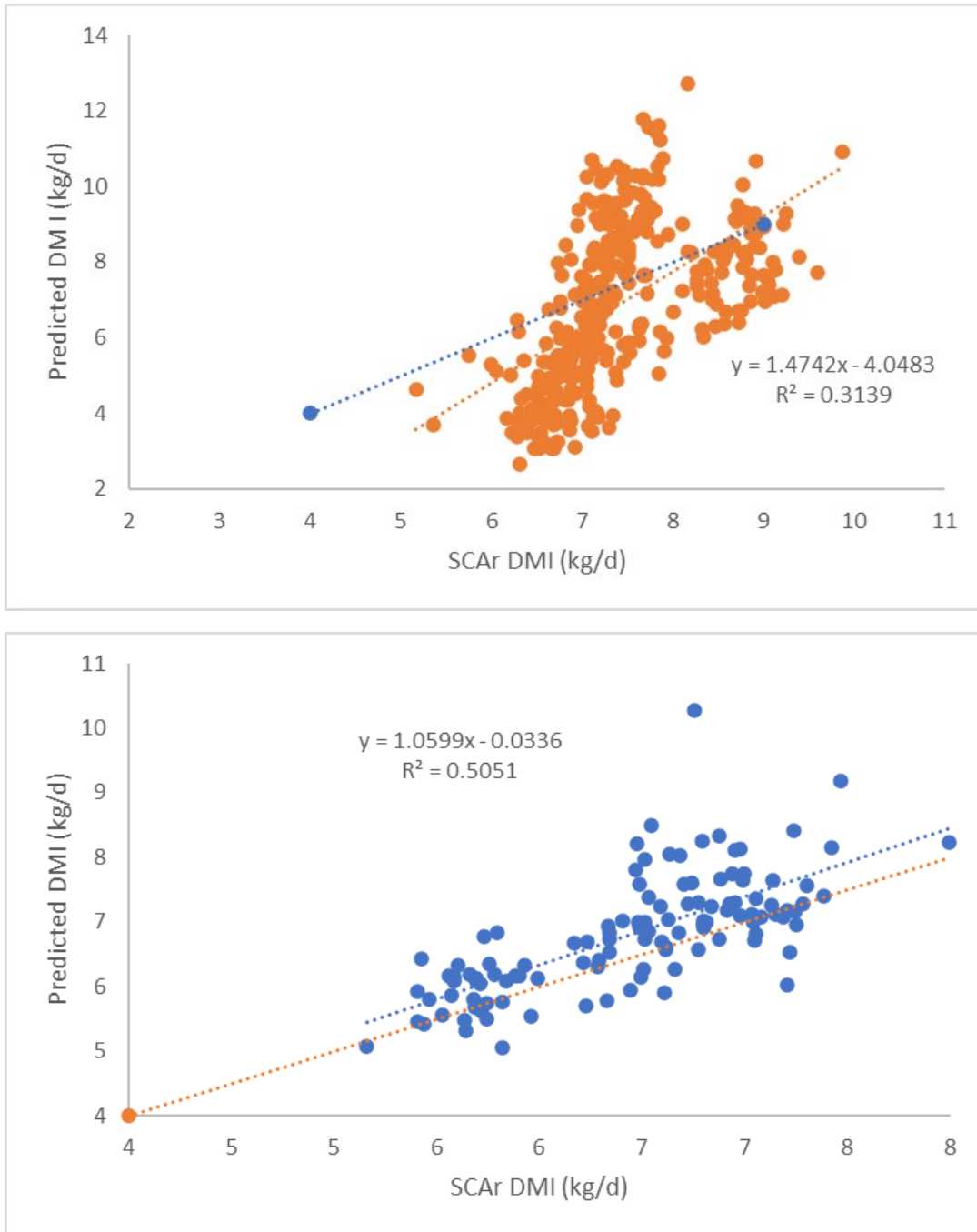


Figure 8.16. Correlation between PISC (2007) and Hodgson et al (1977) using OMD adjusted to DMD. Grazing trials 1(top) and 2 (bottom).

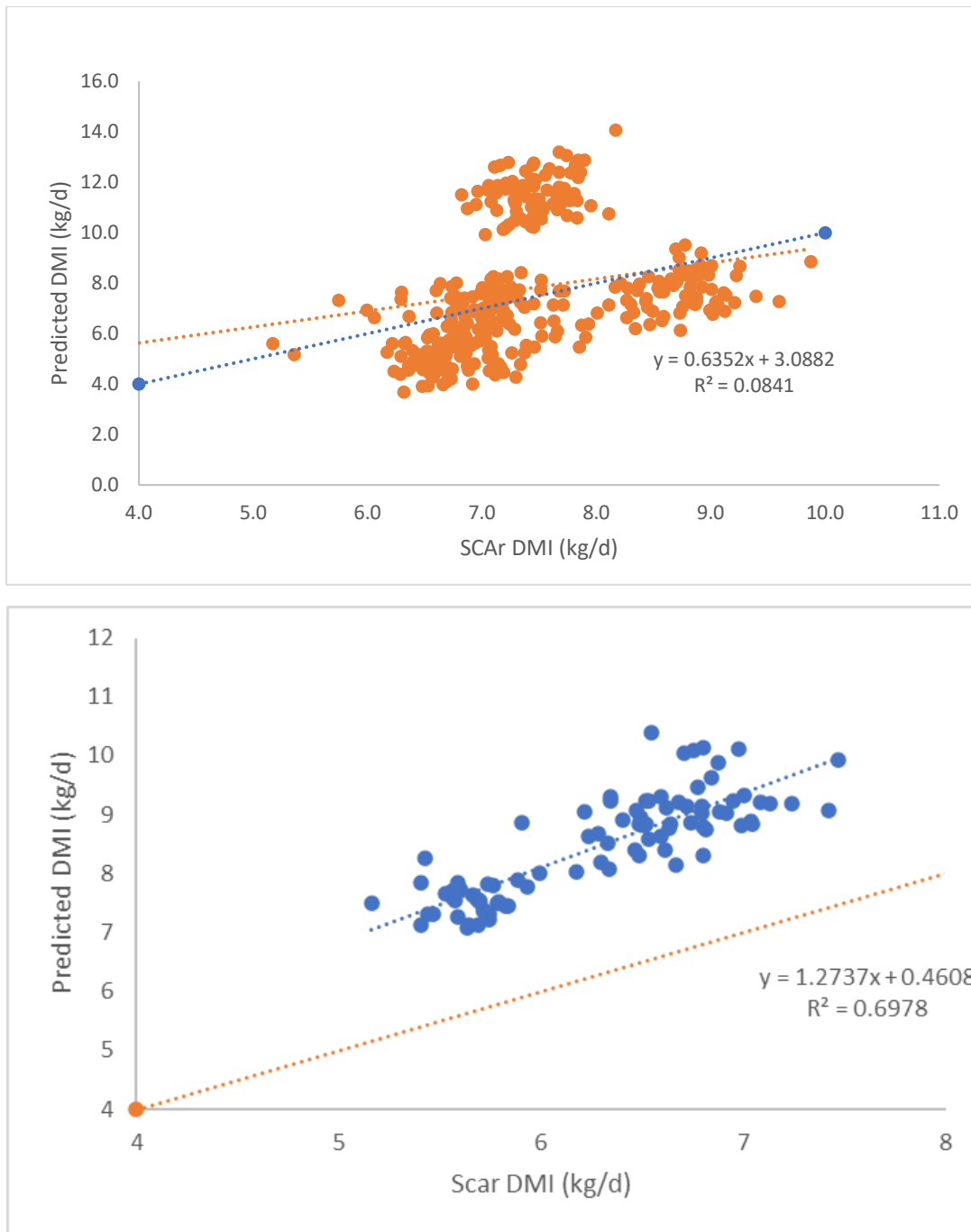


Figure 8.17. Correlation between PISC (2007) and Siebert and Hunter (1977) equation using CP. Grazing trials 1(top) and 2 (bottom).

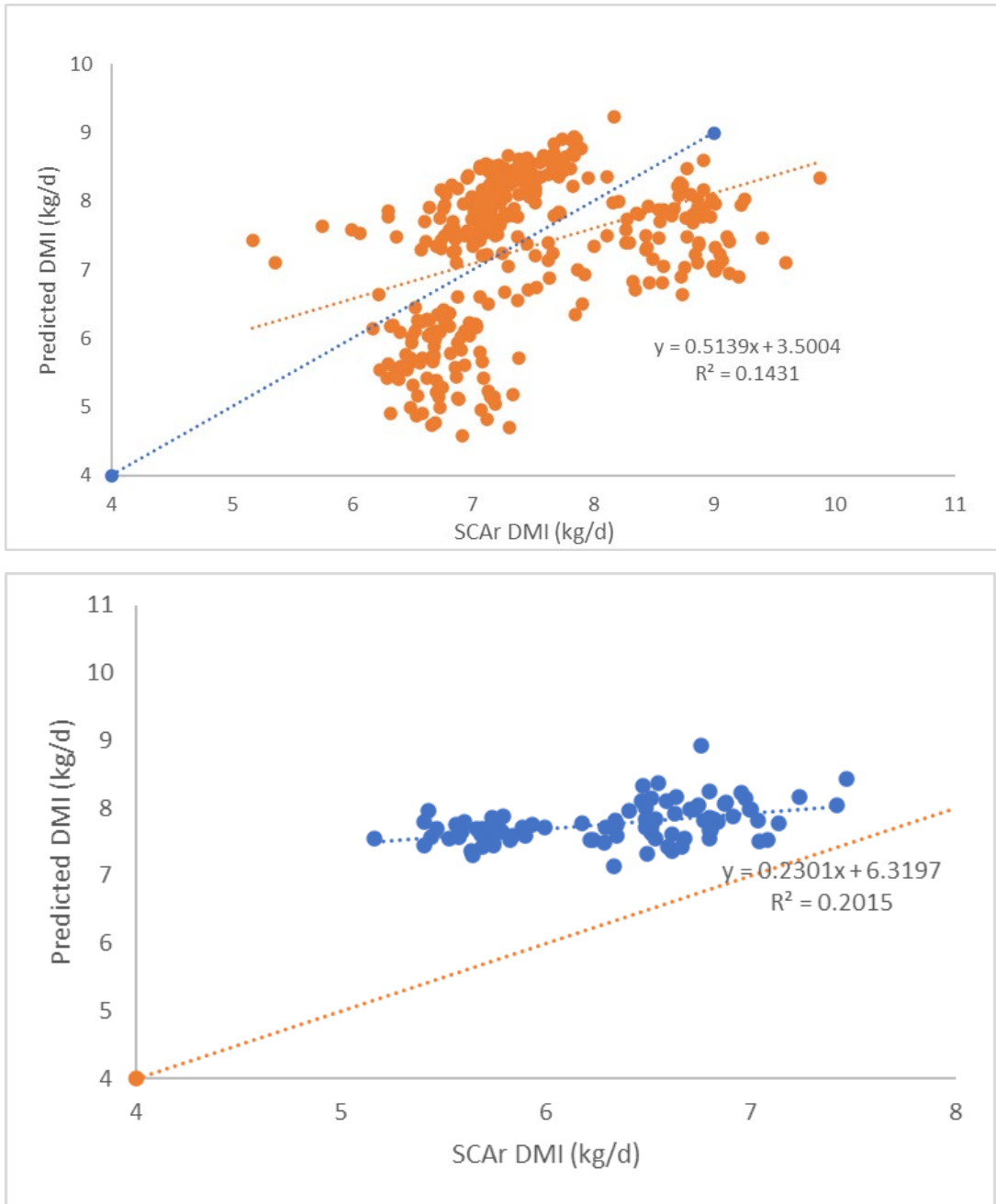


Figure 8.18. Correlation between PISC (2007) and Coleman et al (2014) equation using LW and DMD. Grazing trials 1(top) and 2 (bottom).

8.6 Analysis of published equations against direct measures of pasture intake

The opportunity to test the PISC equation against measures of intake from the pen trial in this study (Section 9.4) revealed problems. Therefore, ten trials where direct measurements of DM intake under grazing conditions with 18 datasets were used to further evaluate selected published equations for prediction of DMI reviewed. Of these, 15 datasets were considered suitable for use. One publication was removed as it was studying mature cows, and another removed as there was no data for LW gain. Predicted intake using SCAR, Minson and McDonald (1987), Hodgson et al. (1977), Siebert and Hunter (1977) and Coleman (2014) were compared with the observed intake data from published trials detailed in Table 8.1. The relationships are shown in Figure 8.19.

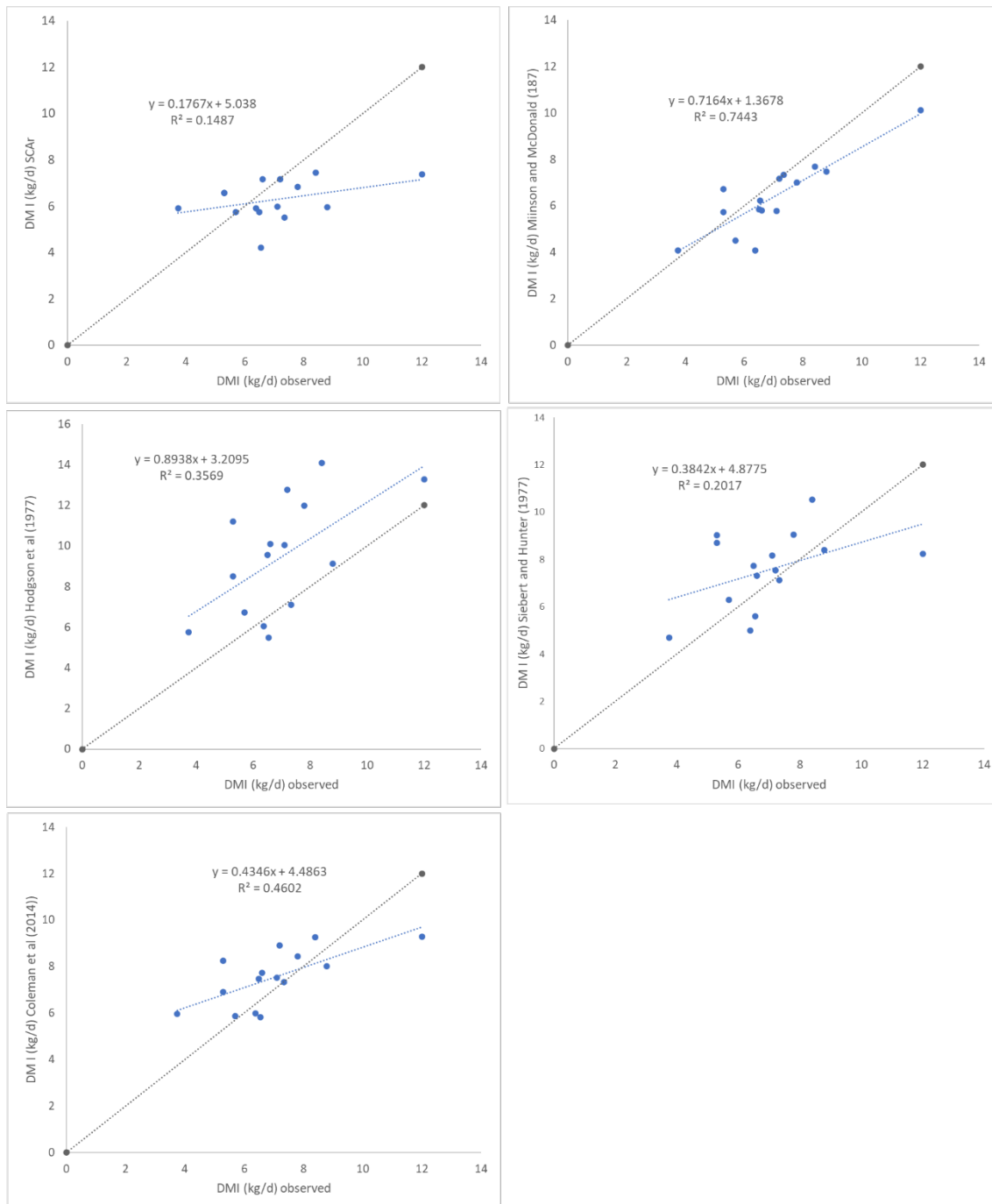


Figure 8.19. Correlation of five intake prediction equations with published measured pasture intake data.

The selected equations gave quite different results. The PISCr model failed to adequately predict observed intakes, as was observed with our pen trial data. A lack of data on the age and genetics of the animals involved in the published literature may have contributed to poor performance as these are key inputs required for the model. The Minson and McDonald (1987) equation produced the best results with a slope of 0.71 and r^2 of 0.74. The mean predicted intake across all trials was 6.6 kg/d compared to the observed mean of 7.4 kg/d. The Hodgson et al (1977) model using OMD demonstrated an adequate response in intake with a slope of 0.9, but overestimated intake by approximately 2 kg/d. In contrast the Siebert and Hunter (1977) model using CP and the Coleman et

al (2014) model using LW and OMD failed to predict observed intakes, but the mean values were close to the mean of observed data.

8.7 Analysis of QuikIntake model (McLennan et al, 2020)

The poor performance of the PISC (2007) model for predicting intake of tropical forages by tropically adapted cattle was addressed by McLennan (2014) and McLennan *et al.* (2020). They observed the model overpredicted DMI, especially at higher intakes, i.e. the slope of the relationship was significantly different to 1. These authors revised the equations defining the utilization of energy by cattle for growth and released a spreadsheet intake calculator (QuikIntake) which utilized the PISC (2007) approach to predict energy requirements to achieve a particular level of performance. From a knowledge of the ME content of DM they were then able to estimate intake. The relationship between predicted intakes using QuikIntake and those predicted from LW and LW change (Minson and McDonald, 1987) are shown in Figure 8.20 for grazing trial 1 and 2. The correlation coefficients were markedly better than for previous published equations, particularly for Grazing trial 1. However, for both trials the slopes were greater than unity showing that as DMI increased the Quikintake model progressively overpredicted the data generated by the Minson and McDonald (1987) model. Detailed analysis of the individual results indicated that wet season rates of gain were likely over-inflated due to compensatory gain.

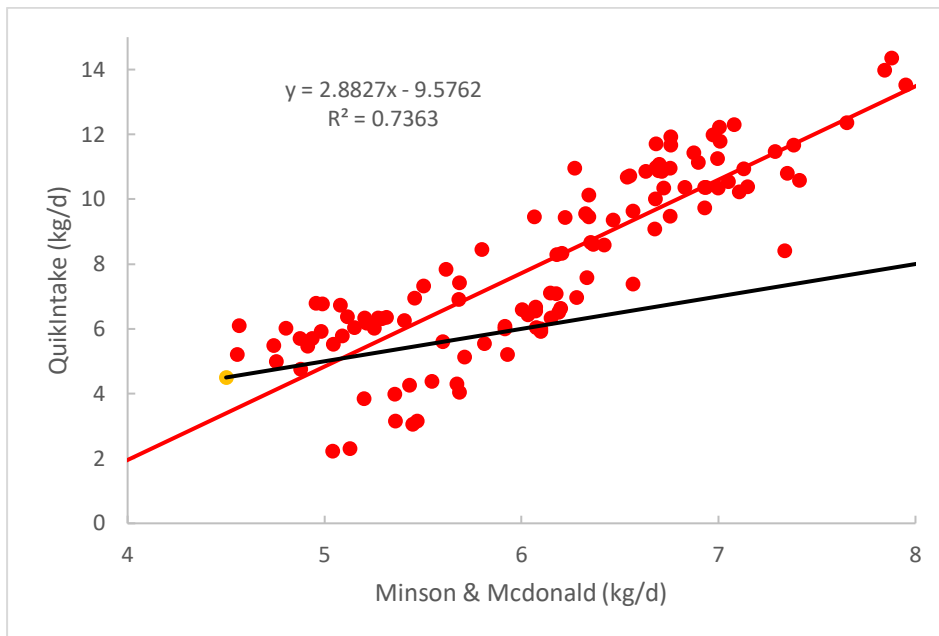
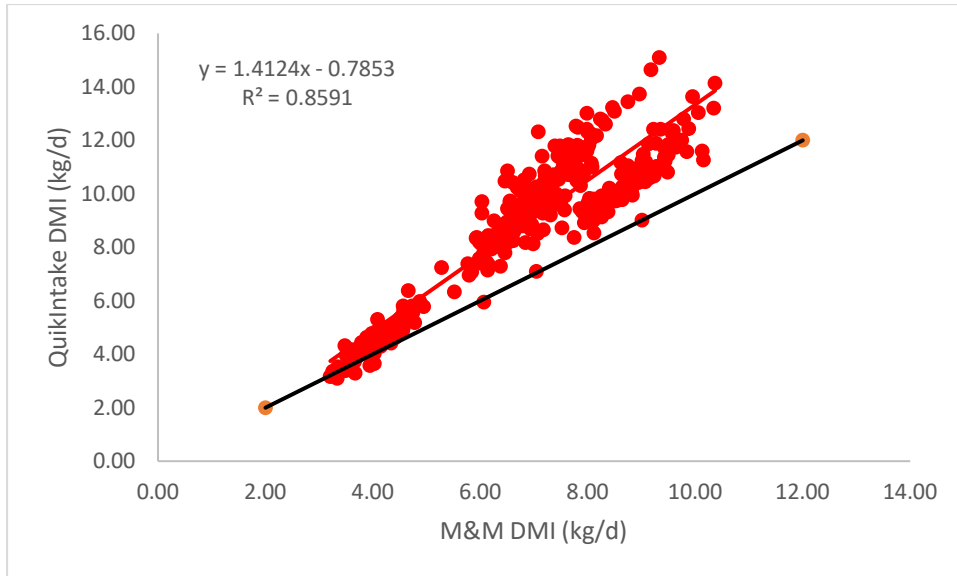


Figure 8.20. Correlation between Minson and McDonald (1987) and QuikIntake (McLennan et al, 2020) equation for prediction of liveweight gain. Grazing trials 1(top) and 2 (bottom).

Several reasons for this lack of agreement between the two models can be postulated. Firstly, the Minson and McDonald (1987) equation may not respond as expected – the response in intake to increasing LW gain being too small. The Minson and McDonald equation cannot account for the legume content of the diet or the amount of energy partitioned to activity. The legume content in the grazing studies varied between 20 and 40% increasing intakes by approximately 5 to 8%. However, this factor would increase the intercept not the slope of the line. Activity, particularly walking, can account for a large proportion of ME and is related to paddock size. The Minson and McDonald (1987) equation is insensitive to paddock size, whereas the QuikIntake model is not.

The second proposition is that the QuikIntake model may overestimate the response in intake to increasing performance. The slope of the line can be reduced to equal that of the Minson and McDonald line by increasing the efficiency of utilization of ME for gain from 0.36 to 0.68. Since this is biologically unlikely we conclude that the Minson and McDonald (1997) equation may underestimate intake for cattle when rates of gain increase.

8.8 GPS-assisted grazing behaviour analysis and estimation of intake

General methodologies for developing and refining behaviour-based algorithms, estimation of intake, and determination of cattle location and distances travelled are included in Greenwood et al. (2014, 2016, 2017), Smith et al. (2016) and McGavin et al. (2018). These include cattle selection and training, pasture intake plots and their management, pasture biomass measurements, benchmark pasture intake data using pasture biomass disappearance and marker methods, sensor devices, behavioural annotation and classification using sensor devices, and use of GPS.

CSIRO electronic cattle monitoring collars and/or other devices were deployed on cattle during pasture intake experimental periods. Cattle behaviour annotation methods and a cattle behaviour model (Smith et al. 2016) has been used to continuously classify the behaviour of each animal across consecutive, non-overlapping time intervals spanning the duration of the pasture intake period. The model used observations from the accelerometer within the collars to discriminate between five different cattle behaviours based on their respective motion patterns and head orientation. The five behaviours classified were Grazing, Ruminating, Resting, Walking and an aggregated class of all 'Other' less frequent behaviours.

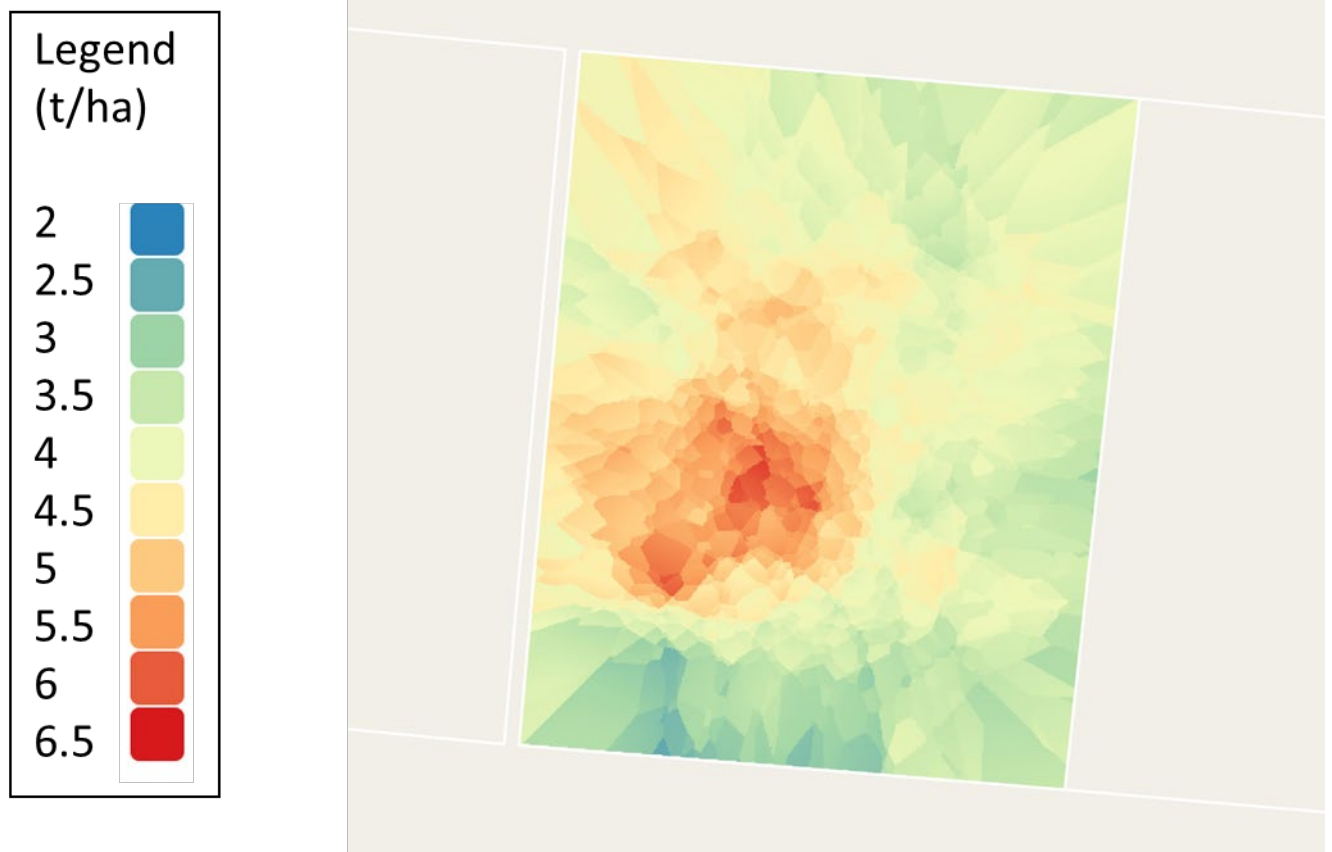
GPS collars were placed on select animals in each of the 4 groups of heifers in grazing trial 2. Two collar deployments occurred during the experimental period, the first from the 10th February 2021 to the 19th May 2021 and the second from the 28th September 2021 to the 3rd November 2021. The collars are programmed with an algorithm that identifies the following activities: grazing, walking, resting, drinking, ruminating and other. The collar recorded the distance travelled and activity the animal performed every second. During the deployments the collars were regularly checked to ensure they were correctly fitted, not causing rubbing or discomfort to the animals and functioning as normal. The animals that were moved to the pens during a deployment had their collars removed.

The movements of each animal were filtered to 10 second sampling points, mapped with QGIS and aligned with corresponding Botanal Kriging prediction maps, which included biomass, grass biomass, legume biomass, pasture CP, pasture ME, green and weed. By quantifying the grazing time of individuals and the group in relation to pasture quality measurements, diet quality and intake estimates can be made.

The Botanal data allowed for a response surface to be developed for each paddock for a range of pasture variables (total biomass, CP biomass, ME content, legume, grass and weed percentage). The response surface for biomass is shown in Figure 8.21. The relationship between frequency of grazing events as measured using GPS enabled collars in a 20 x 20 m square and biomass (T/ha), percent green material and percent legume are shown in Table 8.9. In this preliminary analysis, there appeared to be a preference for spending more time in areas of low biomass close to a waterpoint (top middle of paddock in Figure 9.22) and in resting areas (top and bottom right corners of paddock (Figure 8.2).

Table 8.9. Preliminary data relating the percentage of time spent grazing according to pasture biomass (t/ha), percent green material or percent legume.

Biomass (t/ha)	% time grazing by category	Percent green or legume	% time grazing by category	
			Green	Legume
0 - 2.5	32	5	15	46
2.5 - 5.0	20	10	29	17
5.0 - 7.5	23	15	12	
7.5 - 10	20	20	28	22
>10.0	4	30	3	3
		50	13	12

**Figure 8.21.** Spatial distribution of biomass (t DM/ha) measured on Nov 6th, 2021 in the same paddock as Figure 8.22.

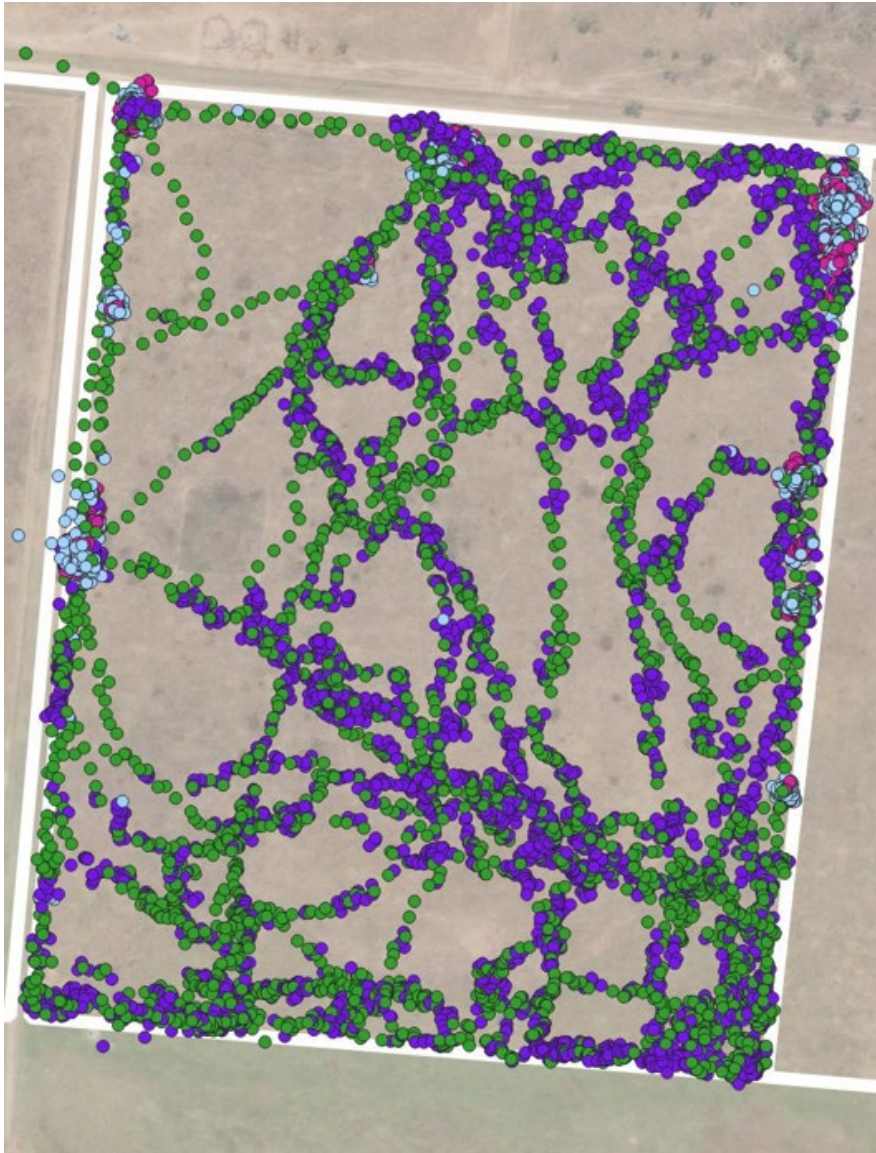


Figure 8.22 Behavioural activity of one animal over three days in the same paddock as Figure 8.21. Purple = grazing, green = walking, blue = resting, red = ruminating.

8.9 Key points

The ability to derive a strong relationship between the diet characteristics and pasture intake is essential if one wishes to predict future pasture intake, as for example in feedbase budgeting. However, when a range of approaches were considered, none proved to be ideal. This demonstrates the complexity of dietary features that influence intake. While some of these can be accounted for (e.g. legume content, $C_3:C_4$ ratios), there is often insufficient empirical data to derive widely applicable factors. Therefore, without a universally applicable equation correlating pasture characteristics to intake, any predictive model is of limited value. Including animal factors into the analysis improves predictive capacity. Indeed, the Minson and McDonald (1987) equation relies solely on the LW of the animal and the rate of LW gain and typically out-performed pasture-based equations. However, such a model cannot be used in a predictive capacity as there is no provision to

account for the dynamics of future pasture growth and quality. The method is highly sensitive to accurate prediction of LW and LW change and cannot account for compensatory gain.

Pasture intake can be predicted from a knowledge of pasture quantity and quality together with an understanding of the energy requirements of the animal according to the equation

Dry matter intake (kg/d) = ME requirement (ME/d)/ ME content of diet (ME/kg DM).

This approach lends itself to predicting future pasture intake. Seasonal models of pasture growth and quality can be developed (Charmley et al, 2008) and used to predict performance and intake of cattle using the ME system of energy partitioning. This is challenging as pasture growth and quality is affected by climatic conditions that may deviate from expected trajectories. Grazing behaviour can lead to patch grazing that compromises the biomass influence on intake. Energy requirements for activity can also be difficult to estimate (Charmley et al. 2023). As with Minson and McDonald (1987), the approach is sensitive to accurate determination of animal LW. Nevertheless, the fundamentals of this approach exist, and digital technologies may offer solutions to some of these limitations (Charmley et al. 2023). These include near real time estimation of LW from in-field autonomous animal weighting systems and GPS monitoring of animal activity (walking, grazing, ruminating, etc).

It is concluded that tropical pasture intake can be most effectively determined from detailed knowledge of the energy requirements of the animal. These include maintenance, activity, live weight, loss or gain of LW, pregnancy and lactation. The efficiencies with which ME is utilized for these activities are well understood and can be readily updated with new and more precise factors, as developed in Sections 6, 7 and 8. Digital technologies can be used under experimental conditions to measure weight change and activity in near real time to create reliable factors for use under commercial conditions. Faecal NIR is the preferred method for estimating digestibility of consumed pasture. This can be readily converted to ME. While the measurement of pasture biomass and its heterogeneity remains difficult, advances in satellite or drone measurements of biomass will eventually overcome this limitation. Linking pasture data at the sub-20 x 20 m pixel scale with grazing activity from GPS will allow pasture intake to be scaled to the grazing patch as opposed to the paddock.

For predictive purposes, climate-driven models of pasture growth and quality linked to growth curves of growing cattle and reproductive predictions of mature animals should allow for seasonal prediction of pasture intake for feedbase budgeting and management purposes.

8.10 Link to intake paper

<https://doi.org/10.1071/AN23045>

Title: Revisiting tropical pasture intake – what’s changed in 50 years?

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ABSTRACT.

The measurement and prediction of pasture intake in extensive grazing systems, typical of northern Australia remains elusive after 50 years of research. The aim of this paper is to review research conducted over the last 50 years, highlight advances in understanding, discuss remaining challenges and consider future developments with digital technologies. While the fundamental components of voluntary intake are well understood, their measurement is difficult particularly in extensive grazing systems which has limited the development of predictive models that adequately address the interplay of factors influencing intake from the bite to the landscape scale. Ongoing research by the authors is used as an example to highlight the potential application of digital technologies to overcome limitations in measurement and prediction. Digital technologies offer the opportunity for monitoring factors that control voluntary pasture intake at scale and under commercial conditions. However, our ability to ground-truth novel indices of intake remain limited without ongoing development of physical methods. This will limit the accuracy and precision of predictive models incorporating digital technologies that can be applied to the extensive grazing conditions of northern Australia. The advent of precision livestock management for extensive cattle production is essential if the industry is to remain viable in a future where production is transparent, ethically sound and environmentally defensible as well as profitable.

9. Conclusion

The Australian feeding standards were developed throughout the 1980s culminating in the publication “Feeding Standards for Australian Livestock – Ruminants” in 1990 (SCA, 1990). The standards were based largely upon the UK system (ARC, 1980) but adapted and expanded upon to better reflect the livestock and conditions prevalent in Australia. The standards were significantly updated in 2007 with the publication “Nutrient Requirements of Domesticated Ruminants” (CSIRO, 2007). In the intervening years the genetics of ruminant livestock have changed in response to selecting for higher production rates and the feedbase has also changed. In particular the prediction of empty body weight and protein and fat composition was considered to no longer reflect commercial conditions. There was also poor understanding of the relationship between live body weight and empty body weight. Thus, the conversion of energy in the diet to production of muscle, fat, empty body and, ultimately, live body weight was no longer fit for purpose in defining the energy requirements on modern ruminants. The prediction of feed intake of the grazing animal is complex and both PISC (1990) and CSIRO (2007) developed a method that considered the nature of the animal (breed, sex, maturity) and the nature of the diet (digestibility, botanical composition). Much foundational work was conducted on sheep, and to a lesser extent, cattle, under temperate climatic conditions. Where data was available, requirements were adapted to reflect tropical cattle and conditions. However the lack of good datasets was a limitation.

This project was developed to address some emerging weaknesses in the current feed requirements and was designed around three components:

- 1) Improved prediction of empty body weight and protein and fat composition
- 2) Improved rumen model to better predict feed intake derived from rumen fill, rate of passage, feed degradability, and protein content.
- 3) Better predictions of feed intake by cattle in extensive northern grazing systems

A novel model that divides the body into two pools for energy metabolism has been developed and evaluated. Energy expenditure in the viscera is handled separately to energy expenditure in the remainder of the empty body, as viscera is a more dynamic and energy hungry component of the empty body. This approach has greatly improved upon the understanding of energy requirements and advances our understanding beyond a notion of static efficiencies for maintenance and growth. Ongoing model development has expanded the concept to include reproductive ruminants and to account for the energy requirements of activity. This new model can be used with current measures of feed energy values and is capable of being expanded into a full replacement for Australian feeding standards for ruminants at all stages of production.

The PISC intake model cannot account for the central role the rumen plays in controlling intake. A rumen model has been built based on the Hyer (1991) model. This model is simpler than that incorporated into AusBeef and required fewer inputs. The new model was specifically designed to accommodate diets with less than 5 to 6% crude protein, typical of northern pasture diets in the dry season.

The PISC intake model was critically examined in relation to its suitability for tropical pasture diets. It was found to overpredict intake and failed to properly account for the inclusion of legumes and C4 grasses into the diet. Using datasets from recent grazing studies the PISC model was evaluated together with other models specifically developed under tropical conditions. Of these models, the one developed in this project had the highest precision and accuracy. Understanding the energetics of activity in extensive grazing conditions is critical. Throughout much of the year cattle may be close

to maintenance owing to the poor nutritive value of the pasture and the energy cost of activity accounts for over 30% of ME intake. The use of GPS collars equipped with accelerometers can measure the position and activity of the animal at high frequency. Initial results have demonstrated the potential of this method to calculate the energy requirements of grazing cattle attributed to walking, grazing and ruminating.

Collectively, this project has developed an improved model for estimation of body composition and hence energy requirements for maintenance, growth and reproduction, an improved model for estimation of voluntary feed intake and a technique for measuring the energy cost of activity under extensive grazing conditions. A common thread throughout all the research is the need to keep input requirements to a minimum and limited to those that can be readily obtained under commercial conditions. The research also accounts for the advances in information technology that is transforming our understanding of the animal within the production environment. Thus, the ability to measure variables at high frequency in the paddock from walk-over-weigh technology (body weight and bodyweight change) and smart ear tags (total activity) and integrate these with real time body composition estimates points to a future where precision livestock management in the paddock becomes reality.

While some of these components of the system are well advanced in their development (e.g. the body composition work) and are ready to be incorporated into a “Nutrient Requirements Application”, others require further research. The project has exposed areas where more research is required. These include;

- Further development of the rumen model for tropical grazing conditions. Existing equations were unsatisfactory due to lack of input data, poor accuracy, and low precision
- Lack of direct observation of intake under tropical grazing conditions to calibrate machine learning algorithms. Investment to define an effective and fully-recoverable internal marker and analytical method (NIR)
- Faecal NIR is critical to estimate pasture quality of input into models. Ongoing development of a cloud-based NIR model for real time diet analysis is essential
- Development of algorithms to differentiate among component behaviours that contribute to overall grazing behaviours, particularly for tropical pastures. Current methods appear to be site-specific and a suite of regionally specific algorithms needed. Requires ongoing recording and classification of behaviours under a range of tropical conditions
- Development and evaluation of an energy model that includes animal performance, animal activity and diet composition that can operate in a low- or high-resolution mode, according to requirements. Model based on improved understanding of energetic efficiency in the animal.

9.1 Key findings

The current project has developed an improved model for estimation of body composition and hence energy requirements for maintenance, growth and reproduction, an improved model for estimation of voluntary feed intake and a technique for measuring the energy cost of activity under extensive grazing conditions. The current approach has greatly improved upon the understanding of energy requirements and advances our understanding beyond a notion of static efficiencies for maintenance and growth. Ongoing model development has expanded the concept to include reproductive ruminants and to account for the energy requirements of activity. This new model can be used with current measures of feed energy values and is capable of being expanded into a full replacement for Australian feeding standards for ruminants at all stages of production.

9.2 Benefits to industry

New models will be incorporated into existing programs, for example; GrazFeed, BeefSpecs, Drought and Supplementary Feed Calculator (DASFC) and CSIROs CLEM. Further work is required to link models with other decision support tools (DSTs) and explore adoption/user pathways.

10. Future research and recommendations

A number of further models are required to be developed or finalised, including:

- High demand for model to be developed in cattle. We would like to get agreement between CSIRO and DPI and UC Davis (and MLA) to develop.
- Finalise incorporation of lactation and pregnancy into model and develop for cattle.
- Update and finalise incorporation of activity and energy required for grazing.
- Explicitly link rumen model and methane with animal model.

More data is required in a number of areas to improve the models, including:

- Variation in mature size and composition by breed/sex.
- Examine variation in feed intake by genotype.
- Data from animals at/near maintenance to finalise values for k_p and k_f more.
- Better representation of effect of feed characteristics on k_m and on viscera (not just M/D, but fibre, type of feed or other feed components).

10.1 Implementation

Incorporate new models into existing programs, for example; GrazFeed, BeefSpecs, Drought and Supplementary Feed Calculator (DASFC) and CSIROs CLEM. Further work is required to link models with other DSTs and explore adoption/user pathways.

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12. Appendix 1: Publications arising from the current project

12.1 Refereed publications

Charmley, E., Thomas, D., and Bishop-Hurley, G. 2023. Revisiting tropical pasture intake: what has changed in 50 years? *Animal Production Science*. <https://doi.org/10.1071/AN23045>.

Dougherty, H.C., M. Evered, J.W. Oltjen, R.S. Hegarty, S.A. Neutze, and V.H. Oddy. 2022. Effects of dietary energy density and supplemental rumen undegradable protein on intake, viscera, and carcass composition of lambs recovering from nutritional restriction. *Journal of Animal Science*. <https://doi.org/10.1093/jas/skac158>.

Oddy, V.H., H.C. Dougherty and J.W. Oltjen. 2019. Integration of energy and protein transactions in the body to build new tools for predicting performance and body composition of ruminants. *Animal Production Science* 59(11): 1970-1979 doi: <https://doi.org/10.1071/AN19229>.

12.2 Conference Abstracts/Presentations

Dougherty, H.C., M. Evered, E.H. Clayton, J.W. Oltjen, and V.H. Oddy. 2023. An Improved Method to Estimate Heat Production by Growing Sheep. Presentation to be given at the 14th Recent Advances in Animal Nutrition Conference, July 2023, *Surfers Paradise, Queensland, Australia*.

Dougherty, H.C., M. Evered, E.H. Clayton, J.W. Oltjen, and V.H. Oddy. 2022. A Revised Model of Heat Production by Growing Ruminants. Oral presentation given at the 10th Workshop on Modelling Nutrient Digestion and Utilization in Farm Animals (MODNUT 2022). September 2022, *Alghero, Sardinia, Italy*.

Dougherty, H.C., M. Evered, E.H. Clayton, J.W. Oltjen, and V.H. Oddy. 2022. Evaluation of a Revised Model of Heat Production by Ruminants. Poster presented at the 10th Workshop on Modelling Nutrient Digestion and Utilization in Farm Animals (MODNUT 2022). September 2022, *Alghero, Sardinia, Italy*.

Dougherty, H.C., V.H. Oddy, M. Evered, E.H. Clayton, and J.W. Oltjen. 2022. Variation in mature body composition affects energy requirements and fat and lean deposition in sheep of different breeds and sex. Oral presentation given at the 7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition. September 2022, *Granada, Spain*.

Oddy, V.H., H.C. Dougherty, M. Evered, E.H. Clayton, and J.W. Oltjen. 2022. An Alternative Approach To Estimation Of Energy Transactions And Body Composition In Sheep. Oral presentation given at the 7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition. September 2022, *Granada, Spain*.

Clayton, E.H., J.W. Oltjen, M. Evered, H.C. Dougherty and V.H. Oddy. 2022. Predicting the efficiency of utilization of energy for maintenance (km) or gain (kg) for sheep and cattle from feed quality components. Oral presentation given at the 7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition. September 2022, *Granada, Spain*.

Dougherty, H.C., M. Evered, J.W. Oltjen, and V.H. Oddy. 2021. How Does Fasting Heat Production Vary Relative to Liveweight In Sheep and Cattle? Proceedings of the 13th Recent Advances in Animal Nutrition Conference, 42-43. June 2021, *Gold Coast, Queensland, Australia*.

- V.H. Oddy, H.C. Dougherty, M. Evered, and J.W. Oltjen. 2021. Estimating visceral mass in a new method to predict body composition of sheep. Proceedings of the Australian Association of Animal Sciences 33rd Biennial Conference February 2021 in *Perth, Western Australia, Australia*.
- Dougherty, H.C., J.W. Oltjen, M. Evered, and V.H. Oddy. 2020. Dynamic Modelling for Nutritional Management of Ruminants in the Face of Climate Change. Invited keynote presentation. Proceedings of the European Association of Animal Science, Vol 26, p 144. (online conference organized by professional organization based out of *Rome, Italy*).
- Dougherty, H.C., M. Evered, J.W. Oltjen, R. Hegarty, and V.H. Oddy. 2020. A method for estimating the target for protein energy retention in sheep. Journal of Animal Science 98(S4), 143. <https://doi.org/10.1093/jas/skaa278.260>.
- Dougherty, H.C., M. Evered, J.W. Oltjen, R. Hegarty, and V.H. Oddy. 2020. Crude protein content of fat-free muscle and viscera in sheep. Journal of Animal Science 98(S4), 144. <https://doi.org/10.1093/jas/skaa278.262>.

12.3 Other presentations/Invited Talks

- Dougherty, H.C. May 3, 2022. Invited guest speaker on The Science Pawdcast – Special Twitter Spaces Event. *Online podcast based out of Alberta, Canada; Livestreamed presentation with opportunity for audience questions.* <https://bunsenbernerbmd.buzzsprout.com/413041/10980645-scichat-livestock-scientist-doctor-holland>
- Dougherty, H.C., J.W. Oltjen, M. Evered, and V.H. Oddy. March 17, 2021. “Modelos Dinámicos de la Nutrición del Ruminantes Ante el Cambio Climático” (Dynamic Modeling for Nutritional Management of Ruminants in the Face of Climate Change). Invited keynote speech at the Celebration of the Anniversary of the Institute of Agricultural Science, Universidad Autónoma del Estado de Hidalgo (Autonomous University of Hidalgo State), *Tulancingo, Hidalgo, Mexico*.
- Dougherty, H.C. July 7, 2020. Invited TED-Style Talk: Cows on Computer Chips – Math, Technology, & The Future of Food Systems. Curious Minds Winter Conference (online). *Online talk invited by Curious Minds program, sponsored by Australian Science Innovations/Australian Government Dept of Education/ Australian National University / the Australian Maths Trust*
- Dougherty, H.C. and Kenya Scarlett. June 17, 2020. Invited guest lecturer on The Alphabet Lectures. Alphabet Radio (Soho Radio). *Online appearance for radio station in Soho, London, United Kingdom* <https://www.mixcloud.com/sohoradio/alphabet-radio-alphabet-lectures-17062020/>
- Dougherty, H.C. November 2020. Guest speaker on The Science Pawdcast Episode 22: Trees vs Climate Change and Dr. Holland with a talk about Cows! *Online podcast based out of Alberta, Canada* <https://bunsenbernerbmd.buzzsprout.com/413041/2132915-episode-22-trees-vs-climate-change-and-dr-holland-with-a-talk-about-cows>
- Walmsley BW, Oddy VH (2018) Managing the livestock pasture interface. Series of presentations given to Northern NSW SAMRC February – March 2018 and throughout 2019

Oddy VH (2018) Revise Australian Feeding Standards to better achieve product specifications and improve efficiency Talk given to Southern Australia Livestock Council, Adelaide, August 2018

Oddy VH (2019) Modelling growth paths of cattle to predict carcass outcomes :- what's in it for a nutritionist? Talk given to Australian Association of Ruminant Nutritionists, Melbourne, October 2019