

# final report

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## **Red Meat Energetics Phase 1 Understanding whole animal and tissue based energetics using prime lambs with divergent genetic merit for muscle development, fat and efficiency as an experimental model for the red meat industry**

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## Abstract

A literature review “Improving the on-farm energetic efficiency of the Australian lamb industry: a review” has been completed. The review has wide application across the lamb supply chain and focuses on the efficient conversion of feed resources to product (lamb). The review incorporates sections on; the derivation of energy, causes of variation in efficiency of energy use, evidence of variation in efficiency and definitions of and methods of assessment of energetic efficiency (systems efficiency, whole animal efficiency and tissue based measures of efficiency). Final consideration is given to future directions and priorities which include: setting future targets for industry efficiency gains, lifetime efficiency (with particular regard to the ewe flock), systems efficiency - not just component efficiency, the impact of new selection areas on efficiency, and how improvements in animal efficiency can be extended to a wide network of producers?

## Project objectives

To define energetic differences between high and low muscle and fat genotype lambs, and to devise appropriate management interventions that optimise performance on-farm and for subsequent supply chain members.

Primary outcome; Management interventions that are matched to genotypic and phenotypic requirements of lambs. Such interventions would contribute to improved productivity and compliance to market specifications, giving increased lamb industry performance.

Target audiences for the project outcomes can be divided into three groups, those with the likelihood of receiving a benefit in the short term, the medium term or the longer term. The initial target audience, that is those who are likely to receive a benefit in the short term will largely consist of lamb finishers. Mid term benefits will be received by lamb breeders and boning room operators (anticipated as within 1 to 2 years of project outcomes being generated). Longer-term improvements will continue to flow to buyers and processors. The time lines associated with these longer-term improvements would be dependent on the structure of the supply chain and the ability of the supply chain to recognise and respond to a change in supply.

## Success in achieving milestone

Literature review has been completed after consultation with Alex Ball (structure and content) and Graham Gardner (overall review). While the review has not been published in a scientific journal, and the current format is more ‘expansive’ than what would be suitable to publish (given the inclusion of sections on derivation of energy and methodologies for assessment of energy use). The author plans to seek further review on the “Causes of variation in efficiency of energy use” section- with a view to publishing this component of the review.

The review has been instrumental in establishing experimental direction, and along with experimental outputs, has formed the basis of a number of industry based presentations (to be outlined in B.BFG.0043 Milestone report 2).

## **Overall progress of the project**

Data from the second group of lambs has been collated, with summary results forwarded to Rob Banks and Alex Ball. The final group of lambs to be fed have been weaned and are currently being subjected to a nutritional treatment (either restricted or unrestricted growth between weaning and finishing) prior to assessing feed intake during finishing.

Statistical analysis is being conducted for the first scientific publication from the prior experiment “An early restriction in growth and development has no detrimental impact on body composition or energetic efficiency, but lamb age does impact on growth rates and efficiency during finishing” (Proposed title).

A field day and numerous industry based presentations have been conducted in the past six months (to be outlined in B.SGN.0117 Milestone report 3).

## **Recommendations**

Emerging opportunities to address ewe efficiency (as identified in the literature review) may form the basis of a future research project proposal and may warrant future discussion.

## **Appendices**

Please find attached the literature review – Improving the on-farm energetic efficiency of the Australian lamb industry: a review.

## List of abbreviations

Adenosine triphosphate	ATP
Arterio-venous	AV
Australian sheep breeding values	ASBV
Average daily feed intake	ADFI
Average daily gain	ADG
Co-operative research centre	CRC
Dry matter	DM
Estimated breeding value	EBV
Feed conversion efficiency	FCE
Feed conversion ratio	FCR
Gross energy	GE
Insulin growth factor	IGF
Live weight	LW
Megajoule	MJ
Metabolisable energy	ME
Net feed intake	NFI
Residual feed intake	RFI
Thermal heat index	THI
Volatile fatty acid	VFA

## Executive summary

Reviewed literature shows considerable variation in the efficiency of growth and development of ruminants, as well as for the heritability of various measures of efficiency. Causes of variation in animal efficiency can be separated along the lines of genetic and environmental factors, with both groups having potential to be manipulated for improvements in overall efficiency.

Much of the recent lamb (and more widely ruminant) research that has investigated genotype and environmental considerations has not measured animal efficiency. In part this has been due to differing research priorities, but is also due to the difficulties associated with measuring feed intake, and ultimately animal efficiency. Accordingly, measures of animal efficiency for modern lamb genotypes are scarce. Where measures of efficiency are provided, there is a tendency to report the limited measure of feed conversion ratio, as opposed to residual feed intake (that considers expected feed intake, is independent of growth and does not result in increased mature weight).

This review identifies a number of opportunities for improving the energetic efficiency of the Australian lamb industry. Key to this is 1) the development of an appropriate target for improvement in feed efficiency, 2) the need to assess the impacts of new selection pressures (such as increasing lean meat yield) on lamb efficiency and 3) the need to assess efficiency for a range of supply chain components, across a range of timeframes (whereas efficiency during finishing may be appropriate for some industry segments, others may require assessment over a whole lifetime).

Recommendations are not just confined to research, with extension and ultimately uptake of research outcomes also required. While new research tools, such as emerging DNA based technologies (particularly for identification of specific gene markers) hold great promise for improvements in feed efficiency there remains a need for an understanding of how fundamental elements of on-farm management (eg. weaning weight, growth path and maturity pattern) impact on the efficiency of lambs during finishing. An understanding of how these basic principles effect efficiency during finishing would ideally become key messages for appropriate extension activities.

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# 1. Introduction

Modern meat industries are faced with the dual challenge of addressing market specifications whilst maintaining a viable, sustainable supply chain. Industry sustainability is largely dependant upon the efficiency with which these twin needs can be fulfilled and is in turn influenced by 1) how efficiently the various components of the supply chain interact, and 2) the efficiency of the various supply chain components.

Market specifications continue to evolve, and vary from traditional concerns such as food safety, and weight and fat thresholds, to emerging credence values that include animal welfare and environmental standards. At the same time as meeting consumer expectations for a range of considerations, production systems need to be highly efficient. Efficiency of resource use is being driven not only by economic imperatives, but also by environmental and social considerations.

Whilst industry segments are constantly evaluating their own performance (as well as the performance of those around them), it appears that the efficiency of various supply chain structures has been little studied, with no published literature available that models the efficiency of different lamb supply chain structures. The role of various supply chain structures to aid in the adoption of specific technologies, such as environmental management systems (Linden, 2005) has been discussed, but has not included an analysis of the efficiency of differing supply chain structures.

Improvements in processing efficiencies have been driven by technological gains within the abattoir and boning room, and by changes in input specifications. Genetic improvement in the lamb industry has been significant (4% per year genetic gain since the 1990's)(Pethick *et al.* 2006) with a trend towards increased lean meat yield with a higher percentage of the carcass in the high value cuts.

Amongst other factors, on-farm efficiency gains have been driven by improvements in reproductive performance as well as by improvements in the growth rates of terminal genetics (Banks 1994). Growth is such a fundamental component of systems efficiency that modelling by Snowden and Van Vleck (1988) has shown a twofold improvement in economic returns from selection based on daily gain versus direct selection for feed conversion ratio. Poor animal growth in young stock (that results in; increased mortality, reduced reproductive performance in ewe lambs/hoggets, delayed attainment of market specifications and a reduction in fleece quality) has significant negative implications on animal efficiency in later life (Graham and Searle, 1975).

Clearly there are significant benefits from improving lamb growth and many studies have targeted this goal. Improvements in growth have been achieved through a variety of means including increased nutrition (Hegarty *et al.* 2006a, Hall *et al.* 2002), hormonal manipulation (Lindsay *et al.* 1993) and genetic improvement (Banks, 1994).

The emergence and establishment of an intensive finishing industry provided the impetus for the beef industry to assess feed efficiency, with a significant body of work being conducted within the framework of the Beef CRC during the late 1990's

and early 2000's. Comparatively, the sheep meat industry has been slow to build on earlier work (such as that conducted by Oddy in the early 80's). With the recent emergence of a grain finishing sector within the lamb supply chain, such earlier work has been shown to be almost ahead of its time with many current applications.

Like any business, the lamb production system is based on inputs and outputs, with research on growth focusing attention on the production of outputs. Whilst there are obvious benefits associated with improvements in growth, a sole focus on growth is a dangerous prospect for the lamb industry. The risks associated with single trait selection for high production efficiency in the poultry meat, pig and dairy industries are well documented by Rauw *et al.* (1998) while Cameron and Curran (1995) discuss the implications of selection for a range of feed efficiency traits in pigs on distribution of fat tissue, with concerns that the selection for high lean food conversion can lead to not only a reduction in subcutaneous fat but also in intramuscular fat which can have negative implications on eating quality.

Selection for growth rate can increase the mature weight of ewes, which may in turn lead to an increase in production costs based on higher maintenance requirements (Snowder and Van Vleck 2003). To limit the impact of negative correlations with growth, the development of any strategy to improve system efficiency needs careful consideration of both the system inputs as well as outputs.

Should system outputs be varied (through a range of measures such as selection for increased growth rates) it is logical that there will be a change in utilisation of system inputs. To understand what impacts a change in animal growth has on inputs it is essential that there is a thorough understanding of the impacts on muscle metabolism (Hocquette *et al.* 1998).

There are many different definitions for animal efficiency, they range from simple ratios to more complex regression based calculations with little direct biological bearing. Industry needs to find a measure that delivers repeatable results and can drive forward necessary improvements. To a large extent the definition that is selected will define the methodology that is used to assess animal efficiency.

Accordingly, the methodologies by which efficiency is measured vary greatly. There remain significant issues with simplified methods that rely on an input:output ratio, however, there can be a difficulty in gaining accurate data beyond this at a commercial level. The need for simple assessments at a commercial level must be balanced with the presentation of credible and valuable data.

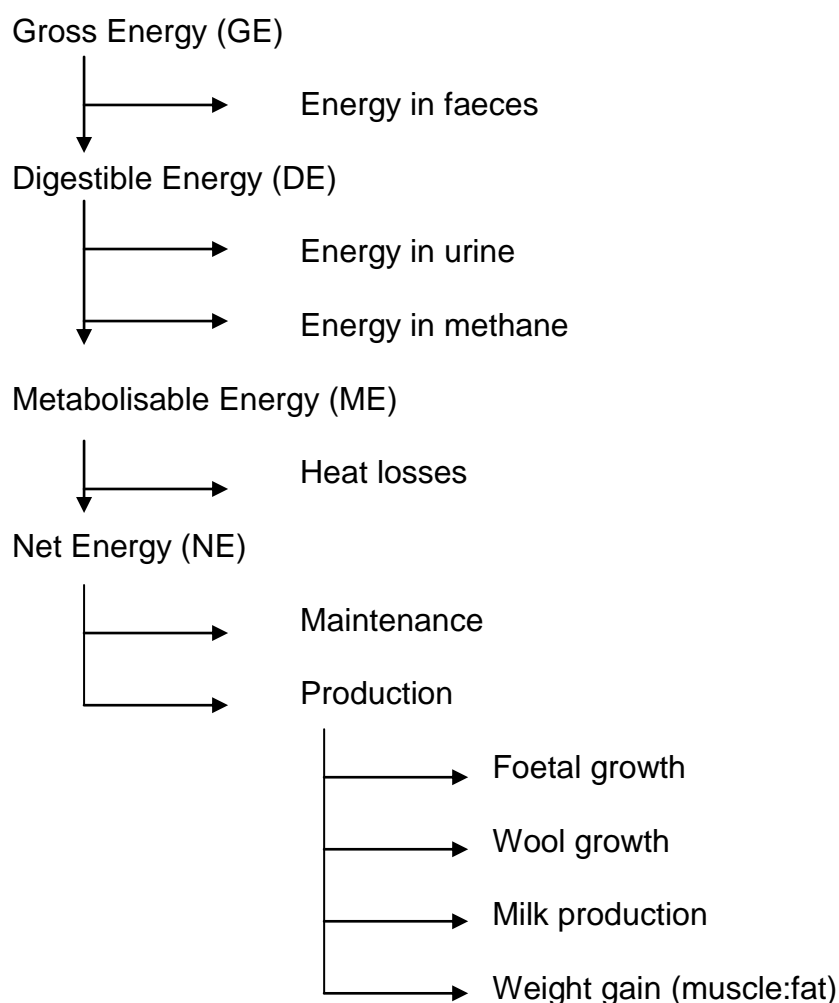
It is the purpose of this review to assess work that has been conducted at a whole animal level, with a view to improving the feed energy efficiency of the Australian lamb industry. Whilst not the primary focus, where possible there has also been recognition of research that has addressed appropriate areas of tissue and organ based efficiency.



## 2. Derivation of energy, its partitioning and use

The amount of ingested energy that remains in the animals system for productive purposes is the result of the gross intake and the losses that occur between ingestion and final use (Figure 2.1).

Scientifically and anecdotally we know that individual animals differ in the efficiency in which they convert food energy to live weight gain, as well as the ability for the composition of the live weight gain to also differ. However at this stage the biological mechanisms for variation in efficiency of energy use in animals with similar body weight and growth rates are not well understood (Nkrumah *et al.* 2006).



**Figure 2.1** Partition of feed energy (Coleman and Henry 2002)

Similar to most mammals, ruminants have an absolute requirement for glucose due to the metabolic specificity of the brain and central nervous system for that substrate. Comparatively small amounts of glucose are directly absorbed from the gastrointestinal tract because of fermentation within the rumen (Bergman, 1973). For this reason ruminants depend largely on gluconeogenesis (synthesis of glucose from non-hexose sources) to meet their basal glucose requirements with approximately

90% synthesised endogenously (Leng 1970). Carbohydrates are fermented within the rumen into Volatile Fatty Acids (VFA's), the three major VFA's being acetic, propionic and butyric (in approximate ratios of 70:20:10) acid which provide approximately 70% of an animals total caloric requirements. However, only propionate is gluconeogenic and thus represents about 50% of all gluconeogenic precursors. For this reason the supply of glucose precursors can be a limiting factor for animal productivity, and possibly survival – with ewes at most risk during late pregnancy.

While fully fed, skeletal muscle in ruminants utilises significant quantities of glucose (as well as short-chain fatty acids) as an energy source (Pethick, 1984). The susceptibility of ruminants to ketosis may be tied to their dependence on gluconeogenesis for their glucose supply (Butler *et al.* 1988).

Regardless of the means by which increases in animal growth rates are achieved (nutritional, hormonal or genetic) there remains a need to understand the impacts of such changes on the energy metabolism of muscle. The efficiency of adenosine triphosphate (ATP) production and utilisation, and the balance between ATP supply and ATP requirements for muscle (and other physiological functions) is an important component of animal efficiency (for review, see Hocquette *et al.* 1998). Hocquette *et al.* (1998) recommends that changes to the energy metabolism of muscle needs to be assessed by (i) the partition of nutrients between oxidative and non-oxidative pathways, including nutrient storage, (ii) the efficiency of ATP production and utilization, and (iii) the balance between ATP supply and ATP requirements for muscle functions. When considering energy metabolism of muscle tissue potentially conflicting needs such as efficiency of muscle development and meat eating quality must be considered - in the past meat quality in pigs has often been disregarded at the expense of productivity, but improved product quality has become one of the pork industries major recent challenges (Hocquette *et al.* 1998))

## 2.1 Gross energy, losses of faecal energy

Faecal losses are the major and most variable form of energy loss, and are considerably greater than those from either methane or urine. For a highly digestible feed such as cereal grain (where a high percentage of dry matter is retained by the animal), twice as much energy is lost in faeces as in urine and methane (McDonald *et al.* 1995).

Faecal losses on a dry matter basis can vary from less than 200g per kg DM when fed green leafy pasture to more than 600g per kg DM for dry, mature, stemmy pasture (Coleman and Henry, 2002). The proportion of dry matter not excreted by the animal is termed digestibility. For example, a feed of 80% digestibility, results in 800g per kg fed being retained in the animal.

## 2.2 Digestible energy, losses in urine and methane

### *Urinary*

As feed intake increases, there is no significant change in the percentage of digestible energy as either methane or urine, with methane and urine production both accounting for 6-8% of digestible energy (Table 2.1)(Graham and Searle, 1975). The percentage of digestible energy as ME varied from 84% to 87% as feed intake increased from 400 to 1300 g DM/day respectively.

**Table 2.1** Partition of digestible energy at several intake levels (Graham and Searle, 1975)

Nominal intake (g DM/day)	Percentage of digestible energy			Net Energy
	Methane	Urine	Metabolisable	
400	8	8	84	63
800	8	6	86	61
1100	8	6	86	55
1300	7	6	87	55
Standard error	0.3	0.2	0.5	1.4

Additional work by Graham and Searle (1979) found energy losses in urine to be 8% during “normal growth” (when fed at 90% of ad libitum levels). This elevated to 11-14% during a period of restricted feeding (lambs fed at 50% maintenance levels). Upon reorientation to ad libitum levels of nutrition energy losses in urine decreased to 6% during periods of compensatory weight gain (Graham and Searle 1979).

### *Methane production*

Methane production is closely related to feed intake, and at maintenance levels is about 8% of gross energy, or 12% of digestible energy. At higher levels of feeding the proportion of energy lost as methane drops to 6-7% of gross energy, the fall being greatest for highly digestible feeds (McDonald *et al.* 1995).

The proportion of energy losses as urine increase as lambs enter a phase of restricted feeding, as do energy losses as methane. During normal growth (90% of ad libitum feeding) methane levels generally tend to decline over time, averaging 4% of digestible energy. This was half of the levels observed by Graham and Searle (1975) but no explanation for the difference is offered. Upon nutritional restriction, energy losses in methane increased to 10% of digestible energy (Graham and Searle 1979). The cause of large differences in methane production between sheep was not determined, however similar results have been observed in experiments with young sheep on ground and pelleted (roughage and cereal grain) diets (Graham and Searle 1980).

There appears to be some correlation between reduced methane emissions and increased animal efficiency. Nkrumah *et al.* (2006) found that while Feed Conversion Ratio (FCR) was not correlated to methane production, Residual Feed Intake (RFI) was correlated with both daily methane production and energy lost as

methane. Methane production from low RFI steers (more efficient) was 28% and 24% lower than high and medium RFI steers respectively.

Similar results were reported by Hegarty *et al.* (2007) from a study of 76 angus steers. A subset of steers with low and high RFI were assessed for methane production, with the low RFI steers having reduced daily methane production (25% less methane per day), and their growth also had a lower methane cost (24% less methane per unit of Average Daily Gain (ADG)). While there was no difference in the ADG of the high and low RFI steers, the low RFI steers ate 41% less feed per day.

### 2.3 Metabolisable energy, losses in heat production

Energy losses as heat can be affected by both animal condition and level of nutrition. At either ad libitum or restricted feeding levels, fat sheep had greater levels of heat production than thin sheep (Graham 1969)

During periods of under nutrition, fasting heat production is depressed by 10%, while during the first month of weight regain fasting heat production was elevated by 10%. For periods of both feed restriction and ad libitum feeding, one quarter of fasting heat production was generated from protein oxidation (Graham and Searle 1975).

Basarab *et al.* (2003) adjusted RFI for live animal measures of body composition (backfat thickness and marble score) and assessed the correlation between animal efficiency and heat production. The trend was both positive and linear, with young growing steers with low RFI (more efficient) having 4.5% less heat production than medium RFI steers, and 9.3% less heat production than high RFI steers. Adjusted RFI values ranged from -2.1 to 1.9, for each unit increase in RFI heat production increased by  $59.9 \text{ kJ (kg}^{0.75}\text{d)}^{-1}$ . Therefore a high RFI steer of 1.5 produces 22.1% more heat than a low -1.5 RFI steer (Basarab *et al.* 2003).

The efficient -1.5 RFI (adjusted for body composition) steer used 67.3% of ME intake for heat production (with 32.7% being retained as energy) while the 1.5 RFI (adjusted for body composition) steer has expended 75.1% as heat production (with 24.9% retained as energy) (Basarab *et al.* 2003). As adjusted RFI increases (animals became less efficient) more of the ME intake was partitioned towards heat production, as opposed to retained energy.

### 2.4 Net energy, maintenance and production

Efficiency with which ME is used for productive purposes is largely the result of the energetic efficiency of the metabolic processes by which absorbed nutrients are synthesised into fat and protein (McDonald *et al.* 1995).

Prior to considering the energy available for animal growth, basic maintenance requirements must be met. Primary maintenance functions such as the need to gather feed, seek shelter and digest food are essential metabolic processes, they

must be undertaken to maintain the animal, prior to excess energy being directed towards live weight gain.

Total energy requirements are defined as;

$$E_r = E_m + E_g \quad (1)$$

Where  $E_r$  = total energy requirements,  $E_m$  = energy requirement for maintenance and  $E_g$  = energy requirement for growth (Hill *et al.* 2003).

The energy that is retained in the tissue of growing lambs, ie retained energy (RE) is defined as the difference between ME intake (MEI) and total heat production,  $H$  (equation 2)(this excludes the small energy cost associated with wool growth).  $H$  being equal to the heat generated from both maintenance and growth.

$$RE = MEI - (H_e + H_d + H_r) \quad (2)$$

Where;

$H_e$  = endogenous heat energy (ie fasting heat production)

$H_d$  = heat of digestion, absorption and assimilation

$H_r$  = heat produced during growth (cost of product synthesis)

(Oddy and Sainz, 2002)

RE is defined by the National Research Council (NRC, 1985) as being equal to Net energy for growth ( $NE_g$ ).

$$ME_g = MEI - ME_m = MEI - (H_e + H_d) \quad (3)$$

A different approach to calculating  $NE_g$  is to multiply the ME for gain ( $ME_g$ ), (equation 3) by the net efficiency of energy use for growth,  $k_g$  (equation 4).

$$NE_g = ME_g - H_r = k_g ME_g \quad (4)$$

Where;

$K_g$  = efficiency of energy retention =  $1 - H_r/ME_g$  ( $K_g$  is often given an empirical value of 0.0435 the ME density of ingested dry matter M/D)(Oddy and Sainz, 2002).

Differing maintenance requirements have been identified as one of the critical differences between energetic efficiency of diverse genotypes (Ferrell and Jenkins, 2007). Causes of variation in maintenance requirements include: body size, temperament, voluntary activity, body composition, proportion of visceral organs, substrate cycling, uncoupling proteins and proton leak (Ferrell, 1988; Ferrell and Jenkins, 2007).

## 2.5 Relationship between fat and protein deposition

The growth and development of sheep is well addressed in the seminal piece of work on the subject by Butterfield (1988).

Butterfield (1988) encapsulated 25 years of the authors own research, as well as that of others from relevant fields. Much work was done in assessing changes in body composition of merino sheep as they progressed to maturity. From Table 2.2 it can be seen the percentage that various body components contributed towards overall body maturity at different stages of development. For example, at 10% of mature weight, bone is already 17.7%, muscle 12.3% and fat 1.8% of mature weight (Butterfield, 1988). Hence at a lower percentage of mature weight, bone is relatively more mature and will therefore represent proportionately more of total carcass weight than it does at maturity relative to muscle and fat.

**Table 2.2** The progress of carcass tissues of a merino ram to maturity at 100kg live weight relative to the progress to maturity of shorn full live weight (Butterfield, 1988)

	Percentage maturity											kg
Live weight	4	10	20	30	40	50	60	70	80	90	100=100	
Carcass muscle	5.0	12.3	24	35	46	56	66	75	84	92	100=22.5	
Carcass bone	8.1	17.7	27	39	50	60	70	79	87	94	100= 5.5	
Carcass fat	0.6	1.8	5	10	18	27	38	50	65	82	100=21.8	

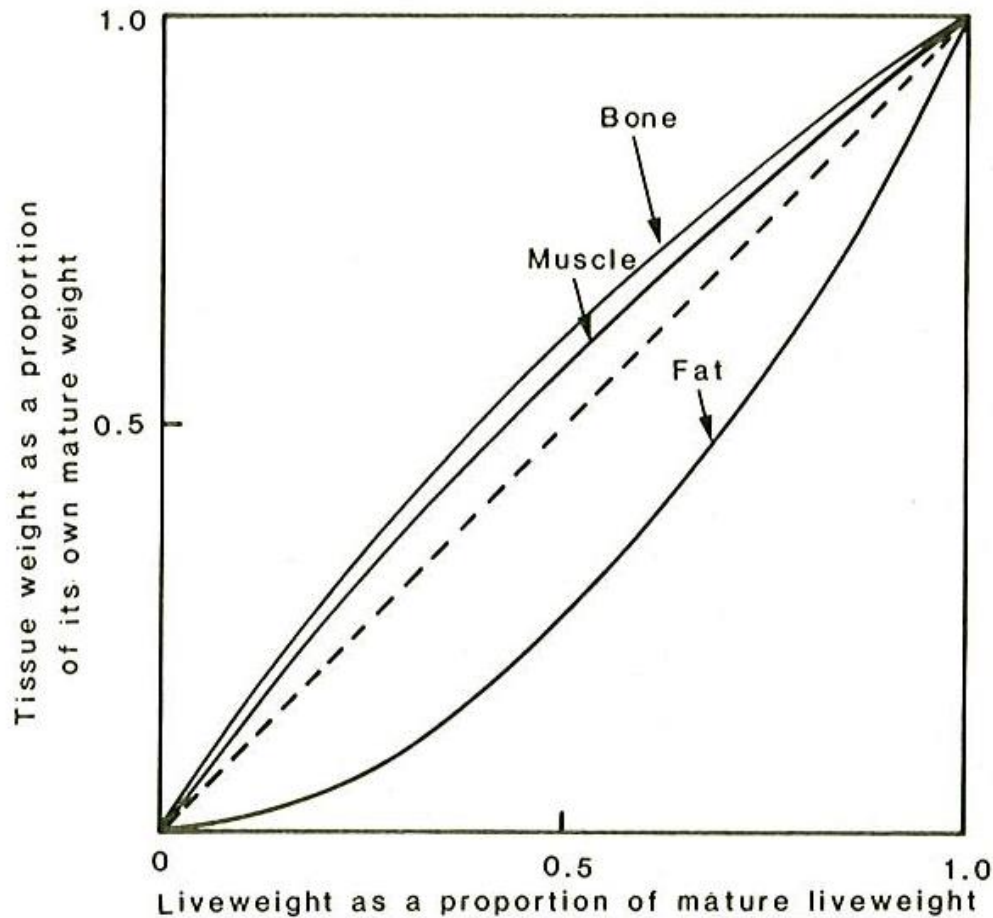
The pathway by which the different body tissues progress towards maturity have been represented by Butterfield (1988) as a single maturity coefficient ( $q$ )(Table 2.3). The maturity coefficients are calculated based on the weight of the carcass tissue as a proportion of their own mature weight.

**Table 2.3** Maturity coefficients of carcass muscle, bone and fat relative to live weight from birth to 20% mature ( $q^*$ ) and from 20% mature up to maturity ( $q$ ) of a merino ram proceeding to a mature weight of 100kg (Butterfield, 1988)

Tissue	Maturity coefficients	
	$q^*$	$q$
Muscle	1.05	1.25
Bone	1.66	1.41
Fat	0.44	0.07

The higher the  $q$  value the lower the growth impetus. Hence fat, which has the lowest  $q$  value has the greatest growth impetus and thus represents an increasing proportion of the animal live weight as the animal matures – whereas bone with a low growth impetus (high  $q$  value) declines as a proportion of live weight as the animal matures (Butterfield, 1988).

The maturity pattern for the different carcass tissues is presented in Figure 2.2.



**Figure 2.2** Maturing patterns of muscle, bone and fat in a Merino ram (Butterfield, 1988)

Recent work is indicating that lamb maturity pattern may be being altering due to changes in genetics. As selection for muscle has increased due to new selection tools (LAMBPLAN and ViaScan) and industry specifications (Lean Meat Yield) we may be seeing a change in biological development.

Hegarty *et al.* (2006b) found that when well fed, lambs selected for high levels of muscling were leaner than those not selected for muscling. While control and high growth lambs both deposited significantly greater levels of carcass fat under high levels of nutrition, high muscled lambs had no increase in carcass fat in response to high levels of nutrition. The fact that high muscle genotypes did not deposit any more carcass fat when subjected to higher levels of nutrition was unexpected, and the mechanisms responsible are unknown (Hegarty *et al.* 2006b). A possible explanation may be that high muscle genotypes are not only depositing higher levels of muscle, but are partitioning energy at the expense of fat deposition. Such a change in developmental priorities has significant implications for animal maturity and compliance to market specifications.

### 3. Causes of variation in efficiency of energy use

#### 3.1 Environmental factors

The external environment, the way in which the diet is presented and the nutritive characteristics of the feed all have the potential to influence the performance, and hence efficiency, of lambs on feed.

##### 3.1.1 Physical characteristics of feed

Kirby (2004) assessed lamb performance when finished on pellets, total mixed ration or a free choice of fibre or grain system. Regrettably while growth rates were monitored (with a trend towards higher gains for lambs on pelleted rations) there was no assessment of feed intake, hence no extrapolation of the relative efficiency of the different systems could be made.

For ruminants, fine grinding and pelleting of roughages results in them being digested differently to unground/chopped roughages. The finely ground roughage will have a faster rate of passage through the rumen (Beever *et al.* 1972), and the fibrous component may be less completely fermented (McDonald *et al.* 1995). Additionally the fine grinding of roughages will lead to an increased faecal loss of energy, but this can be partly off set by a reduction in methane production (McDonald *et al.* 1995).

The proportions of digested energy and structural carbohydrates disappearing prior to the small intestine are significantly reduced when chopped grass is replaced with ground and pelleted grass, while the amounts disappearing within the caecum and colon are significantly increased (Beever *et al.* 1972).

In cases where pellets are fed to lambs, the role of the small and large intestines in nutrient absorption is increased, with a need for clarification of their contribution to supply of nutrients to the whole body. It is worth noting that the work of Beever *et al.* (1972) and McDonald (1995) both cite reduced digestibility of diets fed in a pelleted as opposed to chopped form (Table 3.1).

Beever *et al.* (1972) found differences in cellulose and hemicellulose digestion for pelleted versus chopped feeds to be greatest in early cut pastures (as opposed to medium cut) and was also apparent at both low and high levels of feeding.

**Table 3.1** Digestion of chopped or ground and pelleted dried grass in successive portions of the alimentary tract of sheep (McDonald *et al.* 1995)

Food Constituent	Organic matter		Cellulose	
	Chopped	Pelleted	Chopped	Pelleted
Form of grass				
Portion digested in:				
Stomach	0.52	0.45	0.80	0.56
Small intestine	0.27	0.20	0.02	-0.02
Large intestine	0.04	0.13	0.05	0.23
Overall	0.83	0.78	0.87	0.77



Fine grinding of fibrous roughage resulted in a reduced fibre digestibility by as much as 20 percentage units, and of the dry matter as a whole by 5-15 percentage units (McDonald *et al.* 1995).

Malik *et al.* (1996) investigated the impact of feed quality on feed intake and animal performance (Table 3.2). Under the studied conditions (which included relatively high ME levels for all diets that would be representative of 'typical' finishing diets; 11 - low, 11.9 – medium and 12.7 MJ/kg DM – high) feed intake was found to decrease as the feed digestibility increased, although animal performance was more favourable for the high digestibility ration.

**Table 3.2** The effect of diet quality on average daily feed intake (ADFI), average daily gain (ADG) and feed conversion ratio (FCR)(Malik *et al.* 1996)

Diet	ADFI (g DM/day)	ADG (g/day)	FCR
Low metabolisable energy	1093	200	6.43
Medium metabolisable energy	1093	202	6.28
High metabolisable energy	1028	205	5.59
	(P<0.02)	n.s	(P<0.05)

Ahmad and Lloyd Davies (1986) do not provide the ME levels for the high and low energy rations they fed to Merino x Border Leicester lambs (equal mix of rams, wethers and ewes). However, they found that feed conversion efficiency (FCE) was significantly better (5.3:1) for a high energy than for a low energy diet (7.8:1). It is highly likely that such a difference in FCE was correlated with the improved growth rates between lambs on the high (200 g/day) versus low energy diet (151 g/day).

In the beef industry sire breeding values for net feed intake (NFI) have been calculated for a feedlot environment where bulls (and progeny groups) are fed on energy dense diets that enable individuals to express variation in appetite and growth potential. It is valid to question whether the progeny from bulls ranked under such conditions will perform in a similar way to their sires when placed in a different production system, such as pasture based conditions.

When grazed on pasture, steers that have been sired by low NFI bulls are more efficient than steers sired by high NFI bulls. A 1kg/day reduction in estimated breeding value (EBV) for NFI produces steer progeny that grow 19% faster, with no increase in the feed consumed, a 26% lower NFI and a 41% better FCR (Herd *et al.* 2004).

### 3.1.2 Photoperiod, temperature and humidity

An increase in photoperiod has been found to not only increase feed intake, but also to improve feed efficiency. Both wether and ram lambs exposed to longer

photoperiods (16 hr daylight per 24 hr versus 8 hr daylight per 24 hr) had improved growth rates and feed efficiency (345 g/day, FCR 4.6:1) when compared to lambs exposed to shorter photoperiods (300 g/day, FCR 4.8:1) (Schanbacher and Crouse, 1980).

Exposure of livestock to periods of thermal stress (both reduced and increased temperatures) has been shown to impact on efficiency of protein deposition (Ames and Brink, 1977, Payne and Jacob, 1965).

Work by Ames and Brink (1977) with 25 kg cross bred wether lambs found both weight gain and feed efficiency were optimised between 10 and 20 °C (Table 3.3). An increase in maintenance requirements during periods of thermal stress (Graham *et al.* 1959) along with reduced feed intake (Fuller, 1965) reduces the energy available for gain, resulting in lower weight gains and reduced feed efficiency at temperatures outside of the ideal range.

**Table 3.3** Effect of temperature on lamb performance (Ames and Brink, 1977)

Temperature (°C)	ADG (g/day)	Feed Efficiency (gain/feed)	Feed Conversion Ratio (feed/gain)*
-5	72.6	.038	26.3
0	129.9	.080	12.5
5	169.8	.108	9.3
10	192.1	.145	6.9
15	197.0	.138	7.2
20	184.3	.134	7.6
30	106.5	.081	12.3
35	41.4	.044	22.7

\* Results for FCR are not presented in work by Ames and Brink (1977). They have been calculated from cited values of “feed efficiency”, and are presented here as a useful comparison to more frequently used figures.

#### *Inadequacies in current knowledge*

While it is understood that the physical characteristics of the diet will influence animal performance via impacts on 1) site of digestion, 2) rate of passage and 3) the extent of digestion, there are knowledge gaps around the performance of feeder lambs on certain rations. Additionally the climatic environment during the time of finishing may also impact on lamb efficiency during finishing.

- Efficiency of development for lambs consuming processed versus non processed rations, including pellets, cubes and total mixed rations.
- An appropriate Thermal Heat Index (THI) for lambs in finishing environments which incorporates the impact of interactions between wind speed, temperature and humidity on animal performance. These environmental factors become important considerations for feedlot design.

### 3.2 Animal factors – sex, birth type and temperament

Not only do ram lambs have greater weight gains than ewe lambs, but they are also more energetically efficient. Frederiksen *et al.* (1967) found that while ram lambs consumed more feed than ewe lambs (+0.74 kg/day), they required 0.81 kg less feed per kg of weight gain compared to ewe lambs. Ram lambs were also leaner than ewe lambs (based on a 1 – 15 ranking of body condition) at the conclusion of the feeding period.

Similar trends are repeated for cattle, with bull calves having not only greater feed intakes than steer calves, but also having more favourable feed conversion ratios (Miller *et al.* 1987). Carcasses from bull calves were significantly leaner, and had greater lean tissue than those of steer calves.

Ball and Thompson (1995) found no difference between the amount of feed required for rams and ewes to maintain body weight between 21-34 weeks of age. Hence, there was no gender effect on the maintenance requirements of immature sheep. For mature sheep (>2.5 yrs) from the same selection lines, rams required 19% extra feed (1.11 kg/wk) to maintain live weight. When adjusted to the same proportion of carcass fat or lean, rams required 0.44 and 0.55 kg/wk more feed than ewes to maintain body weight.

Birth and rear type had no significant effect on feed conversion ratio, despite single lambs having higher daily feed intakes than either twins or twins raised as single lambs. Birth and rear type will cause significant variation in birth weights, but did not cause significant changes for weight gain from 1) birth to weaning, 2) weaning to finishing and 3) during finishing. Single lambs had greater weight gain during phase 1, twin lambs greatest gains during phase 2 and twins raised as single lambs having the highest weight gains during finishing (Frederiksen *et al.* 1967).

Although there has been little research undertaken, evidence is emerging that temperament plays a role in the performance of animals within an intensive finishing environment. Unpublished work by Café has identified ‘quiet’ cattle (as defined by flight speed) as having higher weight gains than ‘flighty’ cattle (pers comm., Linda Café). Flighty cattle produced smaller and leaner carcasses, and accordingly ate less during a feedlot period than quiet cattle, however there was no significant difference in either FCR or NFI between the flighty and quiet cattle.

#### *Inadequacies in current knowledge*

Previous research has shown that for sheep and cattle male progeny not only grow faster, but are energetically more efficient than female progeny. This is despite work that shows there being no gender effect on the maintenance requirements of lambs. While birth type is often one of the larger experimental effects, Frederiksen *et al.* (1967) found that birth and rear type had no effect on feed efficiency, with differences in feed intake corresponding to differences in growth rates. At this stage there is little published literature on the impact of ruminant temperament on feed efficiency.

- Lack of published data that expresses phenotypic and genotypic correlations between temperament (such as flight time) and feed efficiency.
- The effect of birth and rear type on energetic efficiency during finishing.

### 3.3 Genotype

A number of studies have assessed the energetic efficiency of various sheep (Sakul *et al.* 1993; Malik *et al.* 1996; Fogarty *et al.* 2006; Notter *et al.* 1984), beef (Solis *et al.* 1988) and dairy (Grainger and Goddard, 2004) breeds. These studies are typically broad, and while they do provide divergence for relevant production traits (such as growth, muscle and fat deposition) the analysis of results is often not presented from this perspective, with measurements of differing biological types not always presented, eg. no muscle yield data for work by either Sakul *et al.* (1993) or Malik *et al.* (1996).

Different breeds of cattle have been shown to differ in their ability to digest high fibre diets, and the efficiency with which they utilise dietary energy, indicating that some breeds of cattle are better suited than others to survive on high fibre, low ME diets (Solis *et al.* 1988).

When assessing the maintenance requirements of different breeds of cattle, Solis *et al.* (1988) considered genetic, environmental, physiological, body composition and nutritional aspects of the production system. The selection of individual animals that are to perform most efficiently in a range of different environments (be they 1100 mm or 350 mm rainfall, or feedlot versus pasture based finishing) needs to also consider the same (and possibly more) factors.

Ferrel and Jenkins (2007) highlight that cows with lower maintenance requirements (and low production potential) are favoured in nutritionally restrictive environments while those with greater production potential are favoured in the less restrictive environments. Indeed genetic suitability for different environments is evident in the changes in efficiency of Hereford and Simmental cattle subjected to varying nutritional inputs. Under a period of restricted feeding Herefords are more efficient, while under periods of ad libitum feeding, Simmentals are more efficient.

Archer *et al.* (1999) found no published estimates of genetic variation for genotypic residual feed intake for growing cattle. In part the lack of data relating to the genetic variation in efficiency (particularly maintenance efficiency in adults) is due to the difficulty in obtaining feed intake data on the large number of animals that are required to display genetic variation.

Herd and Arthur (2009) identify that 73% of variation in RFI could be attributed to 1) heat produced from metabolic processes, 2) body composition and 3) physical activity. The genetic basis to the physiological mechanisms responsible for the variation in these mechanisms is still unknown.

### 3.3.1 Impact of high growth potential

Protein deposition rates are higher in lambs selected for, as opposed to against, weaning weight. Oddy *et al.* (1995) utilised merino lambs selected for divergent weaning weight over 10 generations at Trangie, NSW Australia, to assess the impacts of divergent weaning weight on protein metabolism. Body composition was similar at comparable ages and stage of maturity between the divergent lines, with the proportion of fat, protein and ash being largely unchanged by selection for weaning weight. However, long term selection for weaning weight does result in changes to the dynamics of muscle metabolism via differences in protein breakdown in muscle (Oddy *et al.* 1995).

Selection for live weight at weaning increased lamb efficiency at 14 months of age. Lambs selected for higher weaning weight had lower feed intakes per unit of live weight gain at 14 months of age, although this difference was not apparent during earlier ages or prior to weaning. High weaning weight lambs had lower oxygen consumption by hind limb muscle than low weaning weight lambs. Should this observation be extended to the rest of the body it is probable that there would be a reduction in energy required for maintenance and growth of high weaning weight lambs (Oddy *et al.* 1995).

An earlier investigation with lambs from these divergent lines has shown that N retention per unit of N intake to be not different between high and low weaning weight lambs. However, the high weaning weight lambs deposit greater amounts of N in body tissues, and relatively less N in wool than the low weaning weight lambs (Oddy, 1993). Thus selection for growth has led to a gain in body weight, with a related decrease in wool weight per unit of feed eaten.

Notter *et al.* (1984) present data on the impact of breed (Rambouillet, Dorset and Finn) on growth and feed efficiency of ram lambs. When assessed between 22 to 38 kg live weight, body weight gain/kg feed and body protein weight gain/kg feed did differ significantly between the breeds (greatest for Rambouillet and lowest for Finn for both traits). However there were no significant differences in relative feed intake (Feed intake divided by cumulative metabolic body weight) between breeds. While there was no significant difference in relative feed intake, there were differences in the factors that contributed to overall animal efficiency, it appears that strengths in differing traits had masked potential differences in efficiency between the breeds – for example Finn rams were earlier maturing and had a greater energy density of gain, while Dorset rams had lower relative feed intakes.

A further breed based assessment was made by Sakul *et al.* (1993) who evaluated the FCE of lambs sired by three sire breeds (Targhee, Merino and Rambouillet) out of purebred Targhee ewes. There were two strains of both the Merino (fine and strong wool) and Rambouillet genotypes. The Targhee and strongwool Merino sired lambs were most efficient (FCE 6.2:1), followed by the Rambouillet (Dubouis and Texas) (FCE 6.5:1 and 6.6:1 respectively). Lambs sired by fine wool merino rams were least efficient (FCE of 6.8:1). Only the differences between the most efficient (Targhee and strongwool merino) and the least efficient lambs differed significantly. In agreement with the work by Arthur *et al.* (2001) FCR and growth rates were

correlated, with the breeds with the greatest (Targhee) and lowest weight gains (fine wool Merino) having the highest and lowest FCR respectively.

Selection for growth rate in laboratory mice was found to have no impact on body fatness, up until the age of selection. However fat levels in larger adult mice were found to be increased (Roberts, 1979). Such a finding, whereby selection for growth rate has increased fat levels in adults may have significant implications for efficiency of the breeding flock.

### 3.3.2 Impact of high muscling potential

The work of Sakul *et al.* (1993) with Targhee, Merino and Rambouillet sired lambs showed that Targhee sired lambs (which had the lowest FCR and highest growth rate) had the highest back fat thickness, but were leanest when expressed as a percentage of carcass fat – an indication of superior muscling. Thus from their work, higher muscled genotypes had the most favourable FCR. Conversely, the fine wool merino sired lambs (highest FCR and lowest growth rate) had the greatest percentage of carcass fat, indicating lesser muscle development.

Highly muscled Piedmontese sired calves had greater energetic efficiency (92.4 g/kg<sup>0.75</sup>) than lesser muscled Hereford, Angus cattle (87.0 g/kg<sup>0.75</sup>). Against the trend of highly muscled calves being more efficient, and making it hard to describe a clear correlation between muscling and efficiency Belgium Blue sired calves were least energetically efficient (84.2 g/kg<sup>0.75</sup>) (Ferrell and Jenkins, 1998).

Sire breed (and by extrapolation, muscling) also affected maintenance requirements with Piedmontese sired calves having a lower maintenance requirement than Belgium Blue sired calves (0.34 MJ/kg<sup>0.75</sup>) versus 0.55 MJ/(kg<sup>0.75</sup>). Efficiency of ME use for empty body gain also differed between genotypes, ranging from 0.27 for Piedmontese to 0.44 for Belgium Blue sired calves (Ferrell and Jenkins, 1998).

Variation between the maintenance requirements for beef versus dairy cattle may indicate that different levels of muscling play a role in variation in energetic efficiency.

Beef breeds of cattle (Angus, Hereford and Brahman) have been shown to have a lower maintenance requirement than dairy breeds (Holstein and Jersey). ME for maintenance varied from a low of 0.38 MJ/kg<sup>0.75</sup> for Angus cows to a high of 0.59 MJ/kg<sup>0.75</sup> for Jersey cows (Solis *et al.* 1988).

In addition to having a lower maintenance requirement, the beef breeds were also found to be energetically more efficient in tissue energy exchange (storage and retrieval). The differences between breeds were the result of both body composition and physiological differences. The beef breeds of cattle (Angus, Brahman and Hereford) were energetically more efficient at using ME for tissue energy gain or loss than dairy breeds (Holstein and Jersey) 80.6, 66.8 and 66.0 versus 36.5 and 36.2% respectively, with an average energetic efficiency across all breeds of 60.1%.

Genotype and nutrition interactions were not found to be significant for high muscle versus low muscle genotypes (Greenwood and Café 2007). Whilst this particular study did not assess the efficiency of development, concentrating on the impacts of a

genotype x nutrition interaction in body composition (as assessed at slaughter), it still has meaningful implications from a growth and development perspective. As discussed within section 3.5, muscle is energetically less expensive to deposit than fat (Lindsay *et al.* 1993). Thus, high muscle genotypes should be energetically more efficient than low muscle animals.

The impact of muscling on lamb carcass quality, as well as the interaction between lamb muscling and level of nutrition has been well studied (Hegarty *et al.* 2006a; Hegarty *et al.* 2006b). Regrettably, neither study monitored feed intake of the lambs – hence interpretation of animal efficiency is limited. Indeed, many experiments that have selected animals of divergent merit for muscling have not provided data on animal efficiency.

### 3.3.3 Impact of low back fat potential

The various impacts of 14 years of selection for back fat depth on Coopworth ewes is discussed by McEwan *et al.* (2001). While this reference provides no data on the metabolic efficiency of lines for and against back fat depth, the researchers do present data based on productivity and ‘systems efficiency’ of the two lines. The approach of McEwan *et al.* (2001) assesses the level of lamb and wool production (outputs) on a per ewe (input) basis. While this approach neglects to assess the varying inputs that the ewes may have, and hence does not address complete systems efficiency, it does serve as a useful indication of the impacts of selection for fat depth on production – and recognises the need to assess the impacts of single trait selection from an efficiency (inputs and outputs) basis.

Such a measure of efficiency combines not only the growth potential of the lamb, but also considers the reproductive performance of the ewe (incorporating both the number of lambs weaned and the lactation of the ewe). Further assessments of overall productivity were made by the incorporation of fleece weights into the measure. Ewes selected for back fat depth tended to wean more lambs per ewe joined (0.788 v’s 0.755) than lean ewes, although the weight of weaned lambs was less from fat than from lean ewes (26.2 v’s 27.8kg). When the ewe traits were combined into an overall productivity index, ewes selected for reduced back fat measurements had apparently higher values than ewes selected for increased back fat, although the difference was not significant (McEwan *et al.* 2001).

Ball and Thompson (1995) using the same Coopworth back fat selection lines concluded that selection for increased back fat decreased maintenance requirements. Ewes from the fat line had lower maintenance requirements than the control line during both growth (20% lower at 21-34 weeks of age) and adult phases (5% lower in ewes >2.5 yrs). A reduction in maintenance associated with selection for increased back fat was found to have only a small impact on the ewes biological efficiency. In the case where the change in ewes body composition is assumed to influence the fatness of progeny (with impacts on market specification) the small gains from reduced maintenance efficiency of fat ewes is offset by negative product attributes of the progeny. To this end, despite leaner ewes having greater maintenance requirements, if their progeny have increased levels of carcass protein, the ewes become more profitable from a systems perspective.

### 3.3.4 Maternal genetics

The effect of lamb maternal genetics on the feed efficiency of cross bred lambs has been little studied. Research by Fogarty *et al.* (2006) concluded that sire breed did not affect crossbred ewe feed intake. However, improvement in feed efficiency are still be possible given the considerable variation (>30%) between sire progeny groups within most sire breeds, and the high levels of heritability for feed intake (0.41). When adjusted for differences in live weight, previous reproduction and fat depth, Finn cross ewes had 7% lower feed intakes than the average of the whole group (which included East Friesian, Coopworth and Border Leicester) with most of the Finn cross wether lambs also having below average feed intakes. Correlations of feed intake to growth, carcass, wool and reproductive performance were low, and not significantly different from zero.

In a further study on maternal genetics Malik *et al.* (1996) evaluated lambs sired by Naeemi rams (a fat tailed breed local to the Arabian Gulf) out of cross bred merino ewes (Border Leicester, Dorset or Suffolk). Each breed group consisted of 36 lambs, and no significant differences were detected for either ADG or FCR.

In a review of the effect of dairy breed on FCE, Grainger and Goddard (2004) estimated that to identify a 6% variation in FCE would require a minimum of 80 cows per breed type. Their review found that there were no differences in energy loss as faeces, urine and methane per  $LW^{0.75}$  between differing dairy breeds. Research in USA, Europe and New Zealand shows Jersey cows consistently having higher feed intakes as a percentage of body weight, related to a larger gastrointestinal tract per kg LW when compared to Holstein or Friesian cows (Grainger and Goddard, 2004).

When efficiency is assessed as milk solids per unit of DM intake (as opposed to total milk volume per unit DM), Jerseys are more efficient than Holstein or Friesian cows. Jerseys have a higher percentage of milk solids as fat (protein being the more valuable component of milk solids) so the benefit of increased efficiency is somewhat eroded.

#### *Inadequacies in current knowledge*

In many cases differences in efficiency are not being caused by 'breed' per se, but by differences in biological type. Whilst breed based assessments may provide for diversity in genotypes, further investigation of impacts on efficiency should be based on biological type, such as growth, fat and muscle potential.

- Feed efficiency (either FCR or RFI) of modern Australian lamb genetics is not well known. There remains little published data that outlines differences in maintenance and production energy requirements between high and low genetic merit lambs (divergent for growth, muscle and fat).
- The lack of knowledge in this area is also matched by a lack of facilities where large scale assessments of feed intake (and animal efficiency) can be made. It is hoped that the establishment of a 34 unit feed intake facility at DPI Rutherglen will help address this weakness.
- Genotype x Environment interactions on animal efficiency are not well understood. With emerging issue of climate change it is critical to address animal



efficiency under different stocking rates and pasture growth, availability and pattern of supply scenarios.

- Lack of data on animal efficiency measured during either ad lib or periods of restricted feed intake – this becomes a critical knowledge gap when efficiency based research moves from the finishing phase work with terminal lambs to lifetime ewe efficiency.
- Pig and poultry industries have been acutely aware of the importance of feed efficiency to overall systems profitability/supply chain performance. They also have a far greater understanding of genetic variation in energy metabolism and nutritional strategies appropriate to various genotypes. We do not know genetic variation in energy metabolism for lamb, and we do not know the appropriate management strategies for the different genotypes (if they are actually needed).
- While there is an association between lamb growth rate and eating quality, and lamb growth rate is correlated to FCR, there is no data on the relationship between energetic efficiency independent of growth rate (RFI) and various meat quality traits in lamb.

### 3.4 Growth path

The growth path of an individual refers to the animals rate of live weight gain between birth and slaughter. Prior to entry to a finishing phase, store lambs may have been subjected to a number of nutritional restrictions, resulting in many different growth paths.

Compensatory growth refers to a period of greater than normal growth associated with a reintroduction to adequate nutritional levels, following a period of weight loss (or reduced weight gain) due to nutritional restriction (Thornton *et al.* 1979). It is viewed as the most widely acknowledged form of growth path manipulation (Ball *et al.* 1997).

Many feedlot operators preferentially source light weight weaner calves within breed type on the basis that the lighter calves 1) provide a reduction in fixed costs per head (such as transport) and 2) there are anticipated improvements in animal efficiency once in the feedlot (Hennesy and Arthur, 2004). This improvement in efficiency being driven by faster weight gains as the calves compensate for their lighter weights when compared to normally grown cattle.

In addition to potential impacts on weight gain, the impact of an animal's growth path prior to entry to a finishing system has been shown to affect carcass composition and retail yield at slaughter (Greenwood and Café 2007). When compared at the same age, pre-natal and pre-weaning growth and nutrition has been shown to have a significant impact on carcass composition at slaughter. Calves that were subjected to a nutritional restriction have a reduced carcass yield (when compared to calves that have been well grown early in life) driven by a reduction in weight of retail beef (from lighter carcass weight) and an increase in fat trim (Greenwood and Café 2007). Thatcher and Gaunt (1992) found that lambs subjected to an early nutritional restriction had significantly less fat in the omental and kidney deposits than lambs that were not subjected to a period of nutritional restriction, GR measurements also

tended to be reduced in the nutritionally restricted lambs. Work by Thatcher and Gaunt (1992) did not include any measures of lamb efficiency during finishing.

Such differences in carcass composition may impact on the metabolic efficiency of restricted versus unrestricted animals. Interestingly, when compared at the same carcass weight (as opposed to at the same age) the retail yield and carcass composition of calves that suffered an early restriction and unrestricted well grown calves was similar.

Earlier research has demonstrated an increase in efficiency of energy use during a period of compensatory growth. Meyer and Clawson (1964) (cited by Graham and Searle, 1975) reported an incidence of enhanced efficiency during the phase of compensation post growth retardation. This finding was based on the assumption that maintenance was the same during the period of restriction as it was during compensation. Further work in this area by Graham and Searle (1975) was unable to accept or support this finding “*given that this assumption was not based on particular evidence*”.

Contrary to the assumptions of Meyer and Clawson (1964) where maintenance levels remained constant between a period of restriction and compensation Graham and Searle (1975) found basal metabolism was suppressed during prolonged periods of severe malnutrition. Metabolisable energy for maintenance was 75% at the end of the period of weight stasis, and after one month of underfeeding was reduced to 66%. Post the nutritional restriction period animals were subjected to one month of ad libitum feeding, during this time net availability of ME for growth did not change and remained constant at 62%.

The mechanisms responsible for compensatory growth have been identified as 1) reduced maintenance and/or 2) a change in the ratio of fat:protein in the tissues deposited (Ryan *et al.* 1993).

Ryan *et al.* (1993) found no difference in feed intake between restricted and control sheep in the 12 weeks of feeding post a period of restriction, with restricted sheep unable to compensate to a point of attaining the same body weight as unrestricted sheep (Table 3.4). Given the similar growth rates of both groups of sheep by the end of the experiment, it was concluded that restricted sheep would have been unlikely to have reached similar weights as the unrestricted sheep had the experiment been continued.

**Table 3.4** Mean body weights (kg) of control and restricted sheep at the start of the experiment, at the end of restriction and at the end of the experiment. (Ryan *et al.* 1993)

	Start of experiment	End of restriction	End of experiment
Control	30.9	38.6	58.5
Restricted	32.1	22.2	52.8
Difference	1.2	16.4	5.7

Higher weight gains during the first 12 weeks post restriction (Table 3.5) were associated with increased animal efficiency (given no increase in feed intake). After this the higher weight gains were accounted for by a trend to increased voluntary feed intake.

It took 80 to 100 days before feed intake of restricted sheep exceeded the feed intake of the controls. However, the differences in feed intake between restricted and unrestricted sheep during the period of ad libitum feeding were not statistically significant at any stage (despite there being a trend for previously restricted sheep to consume more than unrestricted sheep).

**Table 3.5** Growth rates (g/day) of control and restricted sheep for each 5kg interval from 25 to 55 kg (Ryan *et al.* 1993)

Weight range	Control	Restricted
25-29		161
30-34	110	139
35-39	105	116
40-44	98	108
45-49	88	87
50-54	69	

Whilst not convinced that there was an increase in efficiency of energy use Graham and Searle (1975) found that animals from a restricted growth path had significantly higher voluntary feed intake in periods of weight recovery, when compared to animals at the same weight from a consistent, unrestricted growth path.

Graham and Searle (1979) were unable to determine the cause or mechanism for increased voluntary intakes post a period of feed restriction but did conclude that recovery from a period of weight loss is characterised by a period of increased feed intake, rather than by enhanced efficiency of energy metabolism. While an improvement in gross efficiency (beyond that warranted by plane of nutrition) was observed in the first week of weight recovery post a period of restriction, after this period higher rates of gross efficiency were driven by increases in voluntary feed intake (which had been observed to last for at least 30 weeks). Thus higher voluntary feed intake was established to be the catalyst for greater weight gains (Graham and Searle 1975).

Berge (1991) is in agreement with this viewpoint, and determined that the increase in voluntary feed intake, post a period of nutritional restriction was one of the main factors responsible for compensatory growth in cattle.

Hence, voluntary feed intake has been shown to increase after a period of restriction but neither Graham and Searle (1975) nor Berge (1991) knew why this was the case. By definition, an increase in feed intake does not necessarily relate to an increase in efficiency.

The timing of the nutritional restriction prior to unrestricted feeding may have an impact on subsequent animal performance. Voluntary feed intake increases

immediately post a period of nutritional restriction (Graham and Searle, 1975; Berge, 1991; Tudor and O'Rourke, 1980 and Ryan *et al.* 1993). More recent work by Hennessy and Arthur (2004) found that an earlier period of nutritional restriction (prior to weaning) lead to a reduction (8%) in feed intake during feedlot finishing. This reduction in feed intake was responsible for a subsequent improvement in FCR.

Similarly Greenwood and Café (2007) reported a reduction in daily feed intake during a period of feedlot finishing for steers that had a pre-weaning nutritional restriction. Restricted steers also tended to have more favourable FCR during finishing, however the trend was not found to be significant.

In further contrast to work by Graham and Seale (1975) (who identified an increase in voluntary feed intake post a period of nutritional restriction) the effect of a nutritional restriction pre-weaning on feed intake during a finishing phase was not apparent when assessed at the same feedlot entry weight (Greenwood and Café, 2007).

Hennessy and Arthur (2004) and Greenwood and Café (2007) have both shown reduced feed intake during a period of compensatory growth. Whereas Greenwood and Café (2007) found a trend towards improved FCR Hennessy and Arthur (2004) found the improvement in FCR during a period of compensation to be significant.

Ryan *et al.* (1993) found no difference in feed conversion ratio between restricted and control sheep at any time during their experiment. While Tudor and O'Rourke (1980) did find that restricted calves had significantly better FCE than unrestricted calves from 200 days until slaughter. While the improvement may have been the result of increased energetic efficiency, it was hypothesised that the lower maintenance requirements of the restricted calves (due to lower live weights) was responsible. Regrettably no comparison of efficiency for the two groups could be made at the same live weight, given the calves were on different diets at this stage.

There have been documented improvements in some measures of efficiency, such as FCR, during a period of compensatory growth. However we know that there are a number of limitations with FCR, the most significant being that it does not allow for expected energy use based on either live weight or body composition.

The respective contributions of changes in voluntary feed intake, and the actual efficiency with which available energy is utilised during a period of compensatory growth remains unknown (Berge, 1991).

When feed efficiency was calculated as RFI as opposed to FCR, differences in efficiency were no longer significant for animals during a period of compensatory growth (Hennessy and Arthur 2004). This suggests that there is actually no net improvement in metabolic efficiency during a period of compensation.

To assess the efficiency of feed utilisation following a period of nutritional restriction various studies have fed steers a constant level of energy per unit of live weight. Under these conditions Thomson *et al.* (1982) did observe higher weight gains in previously restricted steers, indicating that they have indeed utilised the available energy more efficiently than the unrestricted steers. Contrary to this finding is the

work of Robelin and Chillard (1989) who under the same methodology did not observe any differences in growth between restricted and unrestricted calves.

Despite additional work being undertaken in the area of growth path and compensatory growth, earlier comments of Berge (1991) “The effect of an early growth restriction on subsequent efficiency is still not clear cut” still appear to be valid.

#### *Inadequacies in current knowledge*

Previous research shows a pattern of increased awareness and conflicting data. While initial claims of increased efficiency were based on increased growth rates, further work identified that the increased growth rates were accompanied by increased voluntary feed intakes – resulting in no net increase in animal efficiency during a period of compensatory growth. More recent work has further added to the debate surrounding increased efficiency during periods of compensation by finding reduced voluntary feed intakes during a period of feedlot finishing, post a period of nutritional restriction.

- Majority of studies have based gains in efficiency during compensatory growth on the limited measure of FCR.
- No studies that report RFI of lambs during a period of compensatory growth.
- No studies that have assessed the impact of a pre-weaning versus post-weaning nutritional restriction in lambs.
- Previous growth path work in lambs has not assessed animal efficiency (Thatcher and Gaunt, 1992)

### **3.5 Fat score and body composition**

One of the most significant changes to the lamb industry in recent years has been the success with which seed stock operators have been able to increase muscle and reduce the fat of terminal genetics.

The impact of sire breeding values on cross bred lamb performance has been well researched. Recent studies have shown that sires with divergent Australian sheep breeding values (ASBV's) for fat and muscle depth will impart a level of divergence amongst their progeny from cross bred ewes (Fogarty *et al.* 1997; Hall *et al.* 2002; Hegarty *et al.* 2006b). Subsequently, the whole lamb supply chain has benefited from the improvements in terminal sire genetics, with industry monitoring showing an increase in carcass weights along with a reduction in fat levels of slaughter lambs through the mid 1990's to the early 2000's (Linden, 2002).

Differences in body composition have been found to be one of the causes of differences in maintenance and energetic efficiency between breeds of beef and dairy cattle (Solis *et al.* 1988). These differences are in part due to the different biological tissue priorities of the different breeds, with dairy breeds having a greater propensity for deposition of internal fat while beef breeds have higher rates of subcutaneous fat deposition.

However recent work such as that of the Australian Sheep Industry CRC (Sheep CRC1) has investigated the effects of genetic selection for a suite of live animal traits (muscle, fat and growth), but has not investigated the metabolic efficiency with which these divergent animals deposit tissue (lean and fat).

Earlier research by Graham (1969) and Graham and Searle (1972;1975) did investigate the impact of body weight and condition on metabolic efficiency. There is considerable evidence that overall efficiency declines as animals become fatter. Graham (1969) found a strong negative relationship between adult sheep condition and gross efficiency (energy storage divided by gross energy intake), with declining levels of efficiency as body weight (fatness) increased (body weight of the mature wethers was used as the primary measure of body fatness, although weight of fat was also estimated from tritiated water space). In adult wethers fed an ad libitum diet, thin sheep achieved an efficiency of 26%, fat sheep 21% with very fat sheep never exceeding 10% efficiency, correspondingly the maintenance requirements of the three groups were different with thin, fat and very fat sheep requiring 400, 500 and 650g DM/day for maintenance (zero gross efficiency).

The ME required for maintenance was also less for thin than very fat adult wethers (3.89 versus 8 MJ/day respectively). Although there are limitations on the accuracy of this weight gain information (due to the short feeding periods, 2-3 wks) it was found that at any given energy balance, fat sheep gained less weight than thin sheep (Graham, 1969). In their work with dairy and beef cattle, Solis *et al.* (1988) reported a negative relationship between fatness and maintenance energy requirements.

Contrary to the work of Graham (1969) with sheep, Klosterman *et al.* (1968) concluded that maintenance requirements of beef cattle decreased with increasing fatness (this was based on a weight:height ratio which had a highly significant correlation with body condition). Environmental considerations can also become important, with fatter cows having lower maintenance requirements during periods of winter conditions (Thompson *et al.* 1982).

The relative efficiency with which fat and protein are deposited remains difficult to quantify due to three factors; 1) efficiency can be defined in a number of ways (either tissue or calorie based), 2) protein and fat accretion rates are correlated, but difficult to quantify separately, and 3) maintenance requirements can not be easily distinguished from accretion requirements (Owens *et al.* 1995).

Given the inherent difficulties in quantifying energy that is being used for fat versus protein deposition, it is not surprising that there is conflicting data on the relative efficiency of both.

There is a general acceptance that the net efficiency of ME use for protein gain (kp) is lower than for fat deposition (kf) (CSIRO, 2007). After reviewing 21 journal articles Owens *et al.* (1995) concluded that the amount of energy required to accrete 1g of dry fat was surprisingly similar to the amount of energy required to accrete 1g of dry protein. However, on a caloric basis, fat accretion had an average efficiency of 76% (heat loss of 24%), while efficiency of protein accretion was only 47% (heat loss >53%). Therefore, fat accretion was 1.6 times more efficient as protein accretion.

Protein accretion was thought to be less efficient than fat accretion due to the faster and less efficient turnover of depots of protein than fat.

Owens *et al.* (1995) presumed that the large range in efficiency of protein gain is dependant on the turnover of protein (ratio of synthesis to accretion). With ratios of synthesis of 1, 5 and 10, the efficiency of protein accretion theoretically declines from 80%, 55% to 38% respectively. Higher protein turnover rates will also increase energy losses to heat, thus further reducing the gross energetic efficiency.

Contrary to the position of ME use for protein gain being less efficient than for fat deposition, Lindsay *et al.* (1993) concluded that the energetic efficiency with which protein is deposited differs from the efficiency with which fat is deposited, and that muscle is energetically less expensive to deposit than fat. Oddy and Sainz (2002) cite Owens *et al.* (1995) as reporting energetic efficiency of protein deposition as 0.2, while the efficiency of deposition of energy in fat is 0.75.

Should the energetic efficiency of fat and protein deposition vary (with protein being more efficient to deposit than fat (Lindsay *et al.* 1993; Oddy and Sainz, 2003; Hill *et al.* 2003), it follows that if there are differences in body composition of gain, then the overall energetic efficiency of animals should also differ. With highly muscled lean lambs being more efficient than lowly muscled fatter lambs.

Present feeding systems do not assess efficiency on the basis that it is affected by either rate or composition of gain, nor stage of maturity (Oddy and Sainz, 2002).

Overall efficiency is not only determined by the cost to deposit, but also by the cost to maintain body tissues, hence the differing maintenance requirements of the two tissues needs to be considered. Indeed, animals do not store fat and protein without retaining tissue fluids (Owens *et al.* 1995). The metabolic rate of muscle tends to be greater than that of fat, as does the stored water. Each unit of muscle protein deposited requires 3.5 units of water, while a comparable unit of deposited fat only requires 0.1 units of water. So while Hill *et al.* (2003) concluded that muscle require less energy to deposit, it was more expensive to maintain due to the higher metabolic demands associated with storing, 'carrying' and maintaining the extra water which is associated with higher muscled genotypes.

Contra to this indication of higher metabolic maintenance requirements for higher muscled, leaner genotypes is the work of Owens *et al.* (1995). Despite their research showing greater efficiencies for fat than protein deposition when calculated on a caloric basis they concluded that when efficiency was calculated on a wet-tissue basis (given fat deposits contain approximately 10% water and lean tissue contains 78% water) the kilocalories required per unit of protein is reduced to less than one-fourth that of fat (0.005 v's 0.034 MJ/g)(Owens *et al.* 1995).

In their work with beef and dairy cattle Solis *et al.* (1988) found that beef breeds had lower maintenance requirements than dairy breeds, and that the location of fat deposits has a substantial impact on their maintenance requirements. Dairy breeds deposited a higher percentage of their total fat as internal fat and a lower percentage as subcutaneous fat when compared to beef breeds. Specifically, Jersey cows were

found to have the highest percentage of internal fat and Hereford and Angus cows the lowest.

There is some evidence that fat score alone is not the only factor related to body fatness that is contributing to energetic efficiency. Within dairy cattle, additional internal fat did not decrease the maintenance requirements of cows. This raises the possibility that internal fat has a higher maintenance requirement than subcutaneous fat, possibly due to the insulation that is provided by fat stored in subcutaneous locations (Thompson *et al.* 1982).

#### *Inadequacies in current knowledge*

There remains a strong industry awareness that overall animal efficiency declines as animals become fatter. However, such a statement needs to also consider the facts associated with both deposition and maintenance of body weight (fat and protein). The general consensus is that the net efficiency of ME use for protein gain is lower than for fat deposition (fat accretion is 1.6 times more efficient than protein accretion). However, there are conflicting reports that cite protein as being energetically less expensive to deposit than fat. The metabolic rate of muscle is greater than that of fat, giving different maintenance requirements. Fat deposits contain only 10% water versus muscle that is 78% water, hence higher muscle genotypes can have higher maintenance requirements due to the added cost of storing and maintaining the extra water that is associated with high muscle genotypes. Accordingly we have seen selection for increased back fat in ewes reducing maintenance requirements in both immature and mature ages. Such facts need to be considered from a wider context, hence the recommendations of Ball and Thompson (1995) who temper the benefits of reduced ewe maintenance (due to increasing back fat depths) against the negative product attributes of over fat progeny.

- Current methods for assessing feed efficiency make no allowance for body composition or differential rates of gain in different tissues.
- The relative efficiency with which various genotypes deposit protein versus fat.
- Role of new technologies (such as VIAScan) for predicting body composition at slaughter.
- Need for maintenance efficiency to be discussed on a per unit of body weight basis.
- Understanding of the effects of genetic selection for a suite of live animal traits (muscle, fat and growth) on the metabolic efficiency with which these divergent animals deposit tissue (fat and protein).

### **3.6 Maturity and age**

Maturity pattern of an individual has direct links to body composition. Given that a later maturing animal, at the same age will be leaner than the earlier maturing animal

Malik *et al.* (1996) found a significant relationship between lamb age and FCR, whereby the efficiency of feed conversion declined with increasing age (Table 3.6).



**Table 3.6** Relationship between lamb age and FCR Malik *et al.* (1996)

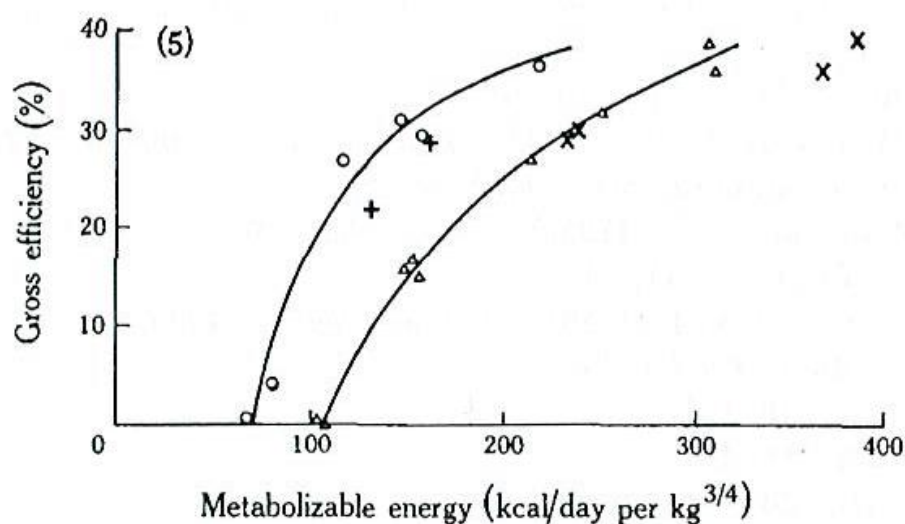
Age (wks)	9-13	13-17	17-21	21-25	25-29
FCR	4.41	5.74	6.37	7.26	6.73

The age at which the efficiency of gain starts to decline, will be determined by the maturity pattern of the lambs in question. Earlier maturing lambs will be at optimum efficiency at a younger age than later maturing genotypes.

Whilst research by Malik (1996) showed that as lambs aged their growth rates declined, no assessment was made of body composition. As such, whilst it might be hypothesised, it cannot be deduced that the older lambs were also getting fatter as their efficiency declined.

Sakul *et al.* (1993) had four predetermined slaughter weight groups (43, 48, 52 and 57 kg) and the efficiency of gain decreased as slaughter weight increased (FCR of 6.3, 6.4, 6.5 and 6.6 respectively). Body composition was assessed for all four slaughter groups, with back fat thickness and percentage carcass fat both increasing as slaughter weight increased.

While they cite research that shows protein accounting for over 30% of energy gain in young stock, and only 10% in aged animals Graham and Searle (1972) discuss body weight as being the major determinant of growth composition, with age being largely unimportant, referring to the most extensive phase of fattening in sheep beginning at a body weight of 30 kg.



**Figure 3.1** Gross energetic efficiency (gain/ME) in relation to energy intake per  $\text{kg}^{3/4}$  for sheep aged 10 months ( $\Delta$ ) (Graham and Searle, 1972) and for adult sheep given a similar diet (O) (Graham, 1969)

The net energy requirement for maintenance was found to vary substantially with both age and plane of nutrition, and the energetic efficiency in growing stock was not the same as in adult stock (Figure 3.1).

Net efficiency of energy use was fairly constant over the ranges of 5-14 months, 18-72 kg (10-40% fat and 47-70cm body length), although was somewhat less efficient than that of 10 month old lambs of 28 and 44 kg live weight (Table 3.7).

**Table 3.7** Utilisation of metabolisable energy by growing sheep of various ages and weights (Graham and Searle, 1972)

Age (months)	Body Weight (kg)	R <sup>2</sup>	Net availability Of metabolisable Energy %	Maintenance Requirement (kcal/day per kg <sup>3/4</sup> )
10	28	0.997	62+-2	115+-8
	44	0.982	52+-2	109+-4
	28 and 44	0.988	58+-2	111+-6
5-14	18-72	0.960	57+-2	104+-10
	28-72	0.988	58+-2	107+-6

Immature animals had higher maintenance requirements per kg<sup>3/4</sup> body weight and voluntary feed intake per kg<sup>3/4</sup> was greatest for younger animals, (declining as young sheep grew, or as adults gained weight). Coupled with the higher maintenance requirements of young stock, it can be seen that overall productivity is driven by both age and body weight (Graham and Searle, 1972).

#### *Inadequacies in current knowledge*

Lamb growth efficiency has been shown to decrease as lambs age. However, previous work has not always considered the linkage that exists between body composition and stage of maturity, hence variation in efficiency has not always been explained as being related to changes in body composition versus changes in age and maturity. Predictive tools for estimating animal maturity (such as frame score in beef cattle) may be of more use in the lamb industry as market segmentation continues to develop.

- Measures of feed efficiency at different stages of animal maturity (that incorporate appropriate measures of body composition).
- Appropriate measures of whole animal and tissue/metabolic maturity in live lambs beyond simple assessments of lamb age. With a need to assess the impact of various growth paths on metabolic efficiency.

### **3.7 Prenatal influences on energetic efficiency**

Prenatal growth has a carry over effect on energy metabolism and body composition in the neonatal lamb (Greenwood *et al.* 1998).

Lambs subjected to an in-utero growth restriction had higher neonatal feed intake per unit of body weight (g feed/kg LW per day) than high birth weight lambs (when compared on an age basis across both slow and rapid neonatal growth paths).

Low birth weight lambs have lower maintenance requirements during the early postpartum period than high birth weight lambs, with differences in maintenance

present until lambs were 10 kg LW. The combination of lower maintenance requirements and greater weight specific feed intake results in faster fractional growth rates for lighter lambs during the early postnatal period (Greenwood *et al.* 1998). The greater weight specific feed intake in smaller lambs is similar to compensatory growth in older animals where voluntary feed intakes have been shown to be higher for steers subjected to an earlier nutritional restriction.

The work of Greenwood *et al.* (1998), which found that low birth weight lambs exhibited growth rates in excess of previously unrestricted lambs (when subjected to a period of ad libitum feeding) is supported by Tulloh *et al.* (1986).

After a period of nutritional restriction (in which body weight had been maintained at birth weight until day 43) restricted lambs had larger brain, carcass and femur weight, while liver and channel fat weight were smaller than unrestricted lambs (Tulloh *et al.* 1986) – hence liver and channel fat reserves had been metabolised during the nutritional restriction. Once the lambs had been fed to 35kg live weight there were no significant differences for these measurements between restricted and control lambs.

Neonatal nutrition has a greater impact than lamb birth weight on neonatal efficiency (feed to gain ratio). Irrespective of birth weight, lambs grown quickly to 20 kg live weight had significantly lower (more favourable) feed to gain ratios, and were 17% more efficient at converting feed to live weight than slowly grown lambs (Greenwood *et al.* 1998).

Hodge (1974) found that although voluntary feed intake of milk was greater for neonatal pigs than lambs, the utilisation of the milk was similar between both species – with the digestible energy content of the milk being high for both species. The digestibility and the ME value of the milk was unaffected by either level of feeding or by the age of the neonate.

Birth weight had no effect on proportion of fat or energy density in the whole empty body at birth. However, an assessment of the composition of low birth weight lambs, once they have reached a live weight equivalent to the birth weight of high birth weight lambs, shows them to have greater levels of fat (and GE) than high birth weight lambs (Greenwood *et al.* 1998).

Low birth weight lambs had increased mass of fat deposits at any given empty body weight when compared to high birth weight lambs. The increased fat levels were accounted for largely by a reduction in ash than in protein content (Greenwood *et al.* 1998).

The work of Hodge (1974) that looked at neonatal development of lambs and pigs found interesting differences between the two species when subjected to a food intake that was 80% of ad libitum levels. Under these restricted nutritional conditions neonatal pigs had significantly improved food conversion efficiency, while there was no significant effect on lamb efficiency. Additionally, and very interestingly, under these restricted nutritional conditions, lambs had reduced rates of protein and fat deposition while only the pigs suffered a reduction in fat deposition. Thus during a period of nutritional restriction neonatal pigs were able to prioritise available energy,

and continue to deposit protein. Such a finding is supported by Hegarty *et al.* (2006a) which showed high muscle lamb genotypes having slightly lower fat levels than low muscle genotypes when subjected to either a low or high plane of nutrition.

There was no impact of birth weight on daily accretion rates of DM, fat, ash and GE for lambs grown slowly between birth and 20 kg LW. For lambs subjected to a fast neonatal growth path daily gains of DM, fat, ash and GE were all greater for high birth weight lambs than for low birth weight lambs.

Neither Tulloh *et al.* (1986) nor Greenwood *et al.* (1998) assessed the impact of prenatal or neonatal nutrition on efficiency of lambs post weaning, with current research in this field limited to a maximum of 35 kg LW. Despite a period of severe nutritional restriction during neonatal development interrupting the division of cell nuclei, there is no evidence that this has a longer term permanent effect (Tulloh *et al.* 1986). Indeed, the number of cells per unit of tissue weight in previously restricted lambs falls within the same range as for previously unrestricted lambs, however only a long term experiment would determine if impacts of an early nutritional restriction would persist into adult life.

Progeny from ewes that were poorly feed during pregnancy have been found to be much fatter at mature sizes than progeny from ewes that were well fed during pregnancy (Thompson, 2006). Thompson (2006) fed 3.5 year old merino wethers from ewes subjected to restricted or good nutrition nutrition during pregnancy. Wethers were offered a roughage based pellet (10.9 MJ/kg; 16.5% CP) for eight weeks with body composition assessed by dual energy x-ray absorptiometry (DEXA) at the end of the feeding period. When corrected for live weight, wethers from 'low' nutrition ewes were fatter (33.8 v's 24.0%) and had less lean tissue (63.1 v's 72.0%) than wethers from high nutrition ewes. The majority of differences in body composition were driven by the variation in the live weight of wethers, however more than 80% of the variation in lean and fat was explained by differences in live weight of the progeny, ewe live weight at joining and changes in ewe live weight between joining and day 90 of pregnancy and day 90 and lambing.

#### *Inadequacies in current knowledge*

Prenatal growth will have a carry over effect on energy metabolism of the neonatal lamb, with light birth weight lambs having greater feed intakes (relative to body weight) than heavier birth weight lambs. Neonatal nutrition is more important than lamb birth weight on neonatal efficiency, with quickly grown lambs having the more favourable feed to gain ratios. While this work has studied lambs grown to 20 kg LW, further studies on these lambs at older ages/heavier weights have not been conducted.

- Nutrient requirements and metabolic development of very low birth weight lambs.
- Understanding of the level of nutrition required to optimise efficiency of development (based on feed efficiency and body composition) across a range of genotypes.
- Longer term effects of prenatal and neonatal nutrition on energetic efficiency of feeder lambs in a finishing environment.

## 4. Evidence of variation in efficiency

Published literature that cites values for RFI of lambs is exceedingly scarce. In many cases where efficiency has been estimated it is only values for FCR that are provided. While of limited value, such data does show the variation that exists for FCR across a range of ages, weight gains, weights, fatness and genotypes (Table 4.1).

**Table 4.1** Feed conversion ratio values across a range of lamb based research projects

Reference	Age (wks)	FCR	ADG (g/hd/day)	Final Wt (kg)	Backfat thickness (mm)
Schanbacher and Crouse (1980)	10- 24	4.4 <sup>a</sup>	375	56	5.2
Sakul <i>et al.</i> (1993)	12 <sup>c</sup>	4.7 <sup>b</sup>	323	52	6.5
		6.3	280	43	3.3
		6.4	280	48	4.5
		6.5	280	52	5.0
Malik <i>et al.</i> (1996)	9-21 21-25 25-29	6.6	280	57	6.7
		5.5	218		
		7.3	182		
Ahmad and Lloyd Davies (1986)		6.7	176		
		5.8 <sup>a</sup>	197	35	3.7
		6.6 <sup>b</sup>	186	35	5.2
Ryan <i>et al.</i> (1993)	28-56	7.2 <sup>d</sup>	144	35	5.0
		8.8-12.1 <sup>b</sup>		52.8-58.8	

<sup>a</sup> Ram lambs <sup>b</sup> Wether lambs <sup>c</sup> 12 wks at start of test, duration varied with lambs slaughtered at predetermined live weight not time points <sup>d</sup> Ewe lambs.

Other efficiency based research has presented data as a function of calorimetric efficiency (Notter *et al.* 1984), but often such results provide a statistical approach with little biological meaning, making direct comparison of one set of data with another difficult.

Due to the low cost of maintenance, and their rapid generational turnover, mice have been commonly used as a model to study changes from selection for efficiency. Sutherland *et al.* (1971) bred four lines of mice, the first three being selected for growth rate in the first 9 generations, with line 1 selected for efficiency (FCE), line 2 for feed consumption and line 3 for weight gain in generations 10-21. The fourth line was maintained as a control group and subjected to random selection across all generations.

**Table 4.2** Summary of the changes in rate of gain, feed consumption and feed efficiency for mice selected for these traits from generation 10 onwards

	Generation 9 mean change			Generation 21 mean change		
	Rate of gain (g)	Feed consumption (g)	Efficiency gain/feed (g)	Rate of gain (g)	Feed consumption (g)	Efficiency gain/feed (g)
Line 1	14.7	147	0.0993	25.8	175	0.1457 <sup>P</sup>
Line 2	12.6	138	0.0918	20.4	183 <sup>P</sup>	0.1106
Line 3	13.7	160	0.0839	19.7 <sup>P</sup>	191	0.1020
Line 4	8.3	124	0.0673	10.2	138	0.0002

<sup>P</sup> Primary trait under selection

Changes in Line 1 between generation 10 and 21 were “noteworthy” with gains in efficiency achieved through reduced feed intake (compared to Lines 2 and 3) with a larger than anticipated rate of gain. Interestingly, the rate of gain of Line 1 between generations 10-21 was even larger than that obtained in Line 3 that had been primarily selected for rate of gain (Table 4.2). Whilst the authors hypothesised that this large increase in growth rate of Line 1 mice may have been due to a favourable mutant, it was more likely to be due to the selection pressure for feed efficiency (Sutherland *et al.* 1971).

Cameron (1994) selected Large White pigs over four generations for divergent lean growth rate under ad-libitum feeding (LGA), lean feed conversion (LFC) and for daily food intake (DFI). Cumulative response in the low LGA and LFC lines and the high DFI line changed by 0.23 s.d. per generation, on average, and the average rate of change in the high LGA and LFC lines was 0.15 s.d. They concluded that while greater gains were made in LGA and LFC than for DFI, considerable genetic variation exists for these traits and that a substantial response to selection for them can be achieved.

After testing 966 bulls and heifers (Arthur *et al.* 1997) concluded that genetic variation in net FCE exists in the Australian beef herd and is moderately heritable. There would be little reason to expect that the same findings would not hold for the lamb industry, however at least one reference (Lee *et al.* 2001) cites the heritability of feed intake in sheep of 0.12.

Arthur *et al.* (2001) concluded that genetic improvement in efficiency of beef cattle could be made. This observation was based on data from 1180 young Angus bulls and heifers that supported the existence of both genetic and phenotypic variation in feed efficiency in beef cattle and the moderate heritability of the major feed efficiency traits of FCR and RFI.

The greatest variation in energetic efficiency of cows is in maintenance requirements. Not only is it the largest single use of energy (73%) but also displays the greatest variation, up to 25% between animals of diverse genotypes (Ferrell and Jenkins, 2007). In contrast, the variation in net efficiency of milk production and gestation both appear to be small. Variation in energy costs of lactation are driven by impacts of total milk production and milk production potential on maintenance requirements.

*Inadequacies in current knowledge*

There are a number of studies that provide measures for FCR of lambs at various age and weights. It is apparent that there is considerable variation, and that such variability may be exploited. At this stage there are very few published records of RFI for growing lambs, with most work in this area coming from pigs, poultry, beef cattle and mice. Increasing interest in RFI for the beef industry has been based on 1) considerable variability, 2) moderate heritability, and 3) it is largely independent of other traits (Hill and Azain, 2009).

- Little published data for lambs that provides data for RFI, and accordingly very little data that correlates measures of efficiency to other phenotypic traits.
- Validation of the hypothesis that the heritability of net feed conversion in lambs is similar to that of cattle.

## **5. Definition of and methods for assessing efficiency of energy use**

Efficiency both of, and within the lamb supply chain, can be assessed at a variety of levels, ranging from whole of chain interactions down to cellular and tissue based efficiency of individual animals. Accordingly the definitions and methods of assessment are dependant upon the level of assessment.

### **5.1 Systems and supply chain efficiency**

The attainment of systems efficiency for the lamb industry involves challenges that are different to those faced by intensive industries such as the pig and poultry industries, eg importance of maintenance efficiency of breeding stock.

There remain very few references that provide methodologies for assessing whole of supply chain efficiency, or the efficiency of different supply chain structures. In his report on Systems efficiency in the Australian lamb industry, Pitchford uses a model to assess the impact of a number of variables on the efficiency of three lamb production systems (merino, first and second cross). The model was designed on the theory of Parks (1982) which describes two asymptotic curves, one for feed intake as a function of time and a second that describes growth as a function of cumulative feed intake (Pitchford, undated).

Changes to the three production systems were assessed at three turnoff weights (lamb live weights of 40, 55 and 70kg). Reducing feed costs by 20% increased profits by \$5.11, \$5.84 and \$7.39 for the three turnoff weights (which was a smaller effect than increases of 20% for lamb and wool values).

The heavy carcass weight production system proved to be the highest cost, highest return system, and as such most affected by changes in price and feed costs.

Not surprisingly, given the dominance of Merino genetics in the Australian lamb industry, the greatest return on investment and profit to industry was achieved through manipulation of the merino ewe. Perhaps what was surprising, given the

current climate, was that the greatest returns were generated from improvements in merino wool quality and quantity. Merino growth rates were of most importance for heavy lamb production systems (Pitchford, undated).

The greatest return from an investment in reducing feed intake was clearly aligned to merino genetics, followed by maternal genetics with an almost negligible return from a reduction in feed intake of terminal genetics. In this study heritability of feed intake was assumed to be 12% (based on previous alkane studies). Should the heritability of feed intake for sheep be assumed to be similar to that of cattle (calculated from measured intake as opposed to alkane based studies) of 30-40% then the importance of feed intake of merinos could be as much as three times the estimate provided in this reference, and provide the greatest return on investment and profit to industry. Benefits associated with a reduction in maintenance efficiency were greatest for merinos (but was applicable to all industry sectors) and was consistent between poor and improved soil fertility conditions (Pitchford, undated).

Pitchford concluded that while both efficiency of lean meat production and overall profitability were positively influenced by genetic improvement in maternal (e.g. Border Leicester) and terminal (e.g. Poll Dorset) breeds they would have little impact on overall system efficiency. “In contrast, genetic improvement in the Merino is the key to improving system efficiency. It is important to continue with existing emphasis of increasing wool value by increasing clean wool production and decreasing fibre diameter. There will be some, albeit small, return on selecting for increased reproductive performance and meat yield. It appears there are large gains to be made by decreasing maintenance feed requirements by selection of ewes that are smaller and eat less per unit body weight.” Pitchford (undated).

For livestock industries where greater than 50% of food energy is consumed by breeding stock, any improvements in efficiency with which the breeding animals maintain body weight will lead to an increase in total meat production per unit of feed consumed (Pitchford, undated).

The majority of food consumed by the pig and poultry industries is by slaughter animals, not by breeding animals (Table 5.1). Under such a scenario it is most efficient to select for higher growth rates with resultant larger mature size, and slaughter animals when they are relatively small when compared to the dam (Webster, 1988).

However, the lamb industry is faced with a different scenario whereby the majority of feed is consumed by the breeding stock, not by the slaughter animals. Under these conditions selection for greater size at maturity can reduce overall efficiency.



**Table 5.1** Maintenance and growth of parents and progeny (Webster, 1988)

	Broiler fowl	Pig (Pork)	Sheep	Cattle (Beef)
Weight of Dam (kgs)	3.0	180	75	450
Weight of carcass (kgs)	1.5	45	18	250
Progeny/year	240	22	1.5	1.0
Weight of carcass per yr/dam weight	120	5.5	0.36	0.55
Proportion of food energy per year				
To Dam	4	16	70	50
To progeny	96	84	30	50

Recent research projects such as the Maternal Central Progeny Test (Fogarty *et al.* 2005) and the Australian Sheep Industry CRC (Sheep CRC1) that adopted an integrated approach to understanding the effects of genetic selection for growth, muscle and fatness (Pethick *et al.* 2006) have contributed to the improvement of lamb industry efficiency via improvements in weaning percentages, growth rates and improvements in body composition. All factors that increase the relative proportion of food energy consumed by progeny, as opposed to breeding stock.

Ferrell and Jenkins (2007) take the concept of energy use further and break down the energy use of the breeding beef cow, indicating that 73% of total feed costs were attributable to maintenance, 20% for milk production with 7% required for pregnancy. Feed energy for maintenance was found to vary by as much as 25% or more among diverse genotypes – such differences have a large impact on the total feed requirements of a cow during a production cycle (or calendar year) , with resultant large differences in overall systems efficiency.

#### *Inadequacies in current knowledge*

What modelling that has been done to assess ‘whole of chain’ efficiency has highlighted the importance of the efficiency of the breeding flock, with terminal genetics having a relatively small contribution to systems efficiency. This is at odds with intensive agricultural industries such as pigs and broiler poultry.

- Inadequate measures of whole of supply chain efficiency, as well as of the efficiency of various supply chain structures.
- The development of a breeding objective for the maternal flock that incorporates relevant components of animal efficiency that enables a true assessment of maternal efficiency (maintenance levels as well as reproductive efficiency).
- Understanding of correlations between efficiency at pasture and in an intensively fed environment.
- Understanding of correlations between efficiency in a nutritionally restricted versus ad libitum environment.

## 5.2 Whole animal measures

### Feed intake

Predictions of feed intake have traditionally been based on phenotypic regression of feed intake on measures of production and body weight (Kennedy *et al.* 1993).

Thus, central to the various definitions of efficiency is the ability to monitor the level of feed consumed by individual animals. Monitoring feed intake is generally regarded as difficult due to high labour requirements and the long test periods that are required to assess changes in animal live weight (Archer *et al.* 1999, Snowder and Van Vleck, 2003).

In estimating the economic returns from an investment in monitoring feed intake, Snowder and Van Vleck (2003) cite the high costs associated with measuring feed intake as a factor that needs to be considered. A potentially expensive measurement (with a need for costly facilities, equipment and labour) must be balanced against the potential return to industry.

In addition to the high costs associated with individual pen feeding of lambs is the impacts of such an environment on lamb performance. Kroman *et al.* (1971) found a 10% reduction in daily live weight gain for individually penned lambs when compared to group fed lambs, and while Graham and Searle (1975) do not provide data, they do state that in their experience confinement of sheep in cages has an adverse impact on lamb appetite. To reduce costs, without compromising lamb performance not all work on feed efficiency has monitored individual feed intake, Malik *et al.* (1996) grouped lambs of the same genotype in pens of four and calculated intakes on a pen average basis. While this approach doesn't compromise lamb performance, it does compromise the data on feed intake and for some investigations would be of limited value due to its inability to account for variation between individual animals.

Due to the difficulties associated with measuring feed intake, much of the published literature that addresses feed intake and efficiency comes from projects that utilise animals in feedlots or animal houses. However there remains a need to be able to assess animal intake at pasture, or under a grazing based management program.

Monitoring feed intake of animals in a grazing environment is largely dependant on the use of a faecal marker dilution. Such a technique utilises rumen controlled-release devices that administer a tracer element, such as chromium sesquioxide (Fogarty *et al.* 2006) or a synthetic alkane such as C<sub>32</sub> and C<sub>36</sub> (Herd *et al.* 2004). For both methodologies faecal samples are collected, and in the case of chromium sesquioxide, samples are assessed for chromium (Cr) concentration, via atomic absorption technology.

Daily faecal DM Output =  $\frac{\text{Daily release rate of Cr}}{\text{Concentration of Cr in faecal DM}}$  (Fogarty *et al.* 2006).

In combination with feed quality parameters such as crude fibre percentage, neutral detergent fibre (NDF), Acid Detergent Fibre (ADF) and lignin the daily faecal DM output is used to calculate the pasture intake of individual animals.

Arthur and Herd (2005) surmised that current information supported the existence of genetic variation in feed efficiency and that most traits associated with feed efficiency were moderately heritable across all livestock species.

#### Feed Conversion Ratio (FCR)

FCR is a simple input: output ratio based on kg of feed consumed per kg live weight gained (or unit of agricultural production). Due to the ease with which a pen average value for FCR can be generated, it remains the most widely used indicator of animal efficiency in commercial finishing systems (for both cattle and lambs).

Hennessy and Arthur (2004) outlined the major limitations of such a simplistic approach to measuring the efficiency of a biological system. Whilst FCR does provide a measure of efficiency based on inputs: outputs, it does so with no consideration of the size of the animal, and the energetic cost of maintenance.

Feed conversion ratio is correlated with ADG, while residual feed intake is not (Arthur *et al.* 2001). Genetically, FCR was negatively correlated with direct effects of 200 and 400 day weights in Angus cattle.

Heritability of feed conversion for Angus cattle has been estimated as 0.31 (Arthur *et al.* 1997) and as 0.29 (Arthur *et al.* 2001).

FCR is most commonly assessed on a fixed time point basis, whereby feed intake and change in live weight are both assessed over a fixed period of time. There have been reported variations to this technique where feed intake is monitored not over a time basis, but relative to 1) a change in live weight (from x kg's live weight to y kg's live weight), 2) maturity pattern or 3) subcutaneous fat depth (Sutherland *et al.* 1971). Such modifications have been designed to remove the effect of maturity or scale on results, however the increase in the data required means that the practical application of a weight, maturity or fat based measure is considerably more difficult to achieve than the traditional time based assessment of FCR (Archer *et al.* 1999).

#### Feed Conversion Efficiency (FCE) and Gross Efficiency

Various studies in the dairy industry have used FCE as a measure of animal efficiency. FCE is the inverse of FCR, and is defined as the units of the outputs (milk) divided by the energy intake. Units of input and output are varied depending on the use FCR is being calculated for. Outputs tend to be milk (Australia) and milk solids (New Zealand) or are stated as units of energy. Beever and Doyle (2007) defined FCE as "kg milk of standardised composition with respect to protein and fat concentrations produced per kg feed dry matter consumed". Inputs may be assessed on either a per hectare (to allow for the generally grass fed nature of the dairy industry – although there are obvious weaknesses with this approach as supplements are included in the diet) or on an energy, including kg DM basis (Kolver, 2007).

Gross efficiency (kg live weight gained:kg feed consumed) is the same as FCE and provides an alternate ratio to FCR for the assessment of animal efficiency. As with FCR, it has been associated with a positive correlation with growth rate resulting in larger mature weights (Hughes and Pitchford, 2004).

Gross efficiency has been used to reduce the standard error in reporting efficiency. Where a trait with greater variance is used as a denominator of a ratio (such as the case with FCR), the end result is a higher standard error, thus needing a larger relative difference between selection lines to produce a significant difference (Hughes and Pitchford, 2004). The use of gross energy as opposed to FCR removes the need for such large variation in selection lines to achieve statistically significant results.

Hughes and Pitchford (2004) saw significant divergence in gross efficiency, but not in FCR. Their justification for this was based on the relative accuracy of measurements for feed intake and weight gain. Feed intake was assessed on a daily basis and was the cumulative total of a number of feeding events, insulating the measure from daily variability. Weight gain was in this case determined from three measurements and thus reflects to some degree the daily variability associated with monitoring live weight.

When gain and weight components were incorporated within a phenotypic index of intake, the relationship between intake, growth rate and mature size was effectively uncoupled. This would indicate that there may be a more suitable measure of animal efficiency than the simple input:output ratio provided by FCR and the output:input ratio of FCE and gross efficiency.

#### Residual Feed Intake (RFI)

Archer *et al.* (1999) suggest that RFI was first developed by Koch *et al.* (1963). This first application was for work with beef cattle, and addressed the major limitations of FCR. RFI is the difference between an animals actual feed intake and its expected feed intake based on 'standard requirements' for the animals size and production over a specified test period (Kennedy *et al.* 1993; Richardson *et al.* 2002; Fogarty *et al.* 2006).

Residual feed intake  $y_r$ , is calculated as follows (Kennedy *et al.* 1993; van der Werf, 2004), where subscripts  $f$  and  $p$  indicate traits of feed intake and production respectively.

$$y_r = y_f - b(y_p - \mu_p) \quad \mu = \text{population mean}$$

where  $b$  is the phenotypic regression

$$b = \text{cov}(y_f y_p) / \text{var}(y_p).$$

Formula that further outlines the phenotypic and genetic parameters of RFI as a function of the constituent traits are presented by Kennedy *et al.* (1993) and van der Werf (2004).

Residual feed intake can be used to assess efficiency of production of a range of agricultural products such as eggs, milk and live weight gain. The efficient animal will eat less than expected over the given period of time, and have a negative RFI, while the inefficient animal will eat more than expected, thus having a positive RFI.

Residual feed intake is not correlated to live weight gain or mature animal weight. As such it can be used as a selection tool at any live weight or level of production. RFI reflects differences in the utilisation of dietary energy of an individual compared to the mean, and accordingly offers insight into differences in the partial efficiencies of maintenance, gain or lactation (Kolver, 2007).

Cammack *et al.* (2005) used data from 1239 ram lambs fed at the US Meat Animal Research Centre between 1986 and 1997 to estimate heritability of RFI and found it to be 0.11. This is similar to the estimate of pasture based feed intake work by Lee *et al.* (2001) that calculated the heritability of feed intake to be 0.12.

These figures are low compared to estimates for the heritability of RFI from beef research. The heritability of RFI was calculated from a dataset of 966 bulls and heifers by Arthur *et al.* (1997) as 0.47, further work by Arthur *et al.* (2001) that utilised a dataset of 1180 angus bulls and heifers estimated the heritability of RFI as 0.39. Such estimates are in agreement with work conducted by Basarab *et al.* (2003) who deemed RFI to be moderately heritable ( $h^2=0.29-0.46$ ).

Arthur *et al.* (2001) concluded that due to the inherent problems associated with selection based on a ratio trait such as FCR, and given that their work showed a strong correlation between FCR and RFI, that future genetic improvements in post weaning feed efficiency should be made based on RFI.

Whilst RFI offers benefits over the simple ratios such as FCE, there is scope for RFI to be improved. How well RFI accounts for biological efficiency depends upon 1) the way production is measured and defined, and 2) the magnitude of measurement errors. Given that a large percentage of variation in RFI is attributable to changes in body composition, the definition of RFI would more accurately reflect biological efficiency if it allowed for the composition of both live weight and weight gain (van der Werf, 2004).

Other terms

Net Feed Intake (NFI)

Arthur *et al.* (1997) highlights that NFI and RFI are interchangeable terms with the same definition and method of assessment. Accordingly, the benefits of using NFI are the same as with RFI, and avoid the complications associated with using a ratio as a selection criterion (Hughes and Pitchford, 2004).

Richardson *et al.* (1998) used the term Net Feed Efficiency (NFE) when assessing the feed efficiency of growing steers. NFE was measured as Net Feed Intake, and accordingly was the difference between feed consumed and the feed intake predicted based on live weight and growth rate data.

### Net Feed Conversion Efficiency (Net FCE)

Richardson *et al.* (1996) use the term net FCE as a measure of animal efficiency. The definition of net FCE (the difference between what animals were expected to eat (based on live weight and growth rate) and what they actually consumed is as per RFI and NFI.

### Energetic Efficiency

To assess animal efficiency Solis *et al.* (1988) calculated 'energetic efficiency' from a regression of daily RE (kcal/kg.<sup>0.75</sup>) on ME intake (kcal/kg.<sup>0.75</sup>).

$$\text{Thus, energetic efficiency} = \frac{\text{regression of daily RE (kcal/kg}^{0.75}\text{)}}{\text{ME intake (kcal/kg}^{0.75}\text{)}}$$

Where RE is a linear regression of the change in retained energy. Retained energy being determined from changes in empty body protein and fat (given calorific densities of 0.023 and 0.039 MJ/g for protein and fat)(Solis *et al.* 1988).

Maintenance was then defined at the ME at which RE equalled 0 (Solis *et al.* 1988).

### Relative Feed Intake

Distinct to RFI, Notter *et al.* (1984) used Relative Feed Intake as a measure of animal efficiency. Relative feed intake was defined as being equal to feed intake (kg) divided by cumulative metabolic body weight (kg<sup>0.75</sup>). A variation on the definition of metabolic weight was offered by Hill *et al.* (2003) who define it as live weight raised to the power of 0.73.

Applications of RFI utilise data from national feed standards to generate the values for 'standard requirements' (Kennedy *et al.* 1993; Richardson *et al.* 2002; Fogarty *et al.* 2006).

### *Inadequacies in current knowledge*

There remain many different definitions of animal efficiency, ranging from simple ratios to more complex regression based calculations with little direct biological bearing. Industry needs to find a measure that delivers repeatable results and can drive forward necessary improvements. Accordingly, the methodologies by which efficiency is measured vary greatly. There remain significant issues with simplified methods that rely on an input:output ratio, however, there can be difficulty in gaining accurate data beyond this at a commercial level. It is likely that 'one size' of energetic assessment will not fit all available applications. While scientifically RFI is the preferred measure, the need for simple assessments at a commercial level must be balanced with the presentation of credible and valuable data.

- Assessment of the heritability of feed efficiency traits for lambs – current figures for other ruminants appear to be greater than those that have been suggested for lamb.
- The implications for an altered form of RFI that incorporate measures of lamb body composition.

## Phenotypic indicators

The uncovering of an easily measured production trait that is highly correlated with important measures of feed efficiency, would provide a boon for animal improvement. Such a trait would enable all the benefits associated with improving feed efficiency without the costs associated with measuring feed intake.

In search of a simple indicator of animal efficiency Arthur *et al.* (1997) looked at various phenotypic correlations to NFI. A number of the traits investigated (average daily gain, 365 day weight and eye muscle area (EMA)) had no significant relationship to NFI, while feed intake, FCR and rib fat depth had correlations of 0.52, 0.51 and 0.19 respectively. Further work by Arthur *et al.* (2001) showed FCR to be genetically and phenotypically correlated with RFI.

Aside from some significant relationships to carcass weight, correlations of feed efficiency traits with carcass traits is generally low (Hennessy and Arthur, 2004). Correlations between feed efficiency traits (FCR and RFI) and scrotal circumference, ultrasonic rib and rump fat depths and EMA have been found to be near zero (Arthur *et al.* 2001).

Snowder and Van Vleck (2003) found that live weight (mid test period) and average daily gain have a positive linear relationship with total feed intake ( $r^2 = 0.76$  and  $0.54$  respectively). However, there was no relationship between either mid-weight or ADG and residual feed intake.

While growth rate is correlated to FCR, there remains a distinct lack of phenotypic indicators that are closely correlated to the most desirable measure of animal efficiency, RFI (Arthur *et al.* 2001). Regrettably, both of the studied traits with a moderate correlation to NFI (Feed intake and FCR) are still reliant on the expense and time associated with measuring feed consumption over a fixed period of time.

There have been no estimates of genetic variation for genotypic residual feed intake published for growing cattle (Archer *et al.* 1999). Where there are estimates for genetic variation in RFI in growing cattle they have been calculated from a regression of a correlation with phenotypic traits, yet Arthur and Herd (2005) identified an almost complete lack of information on genetic relationships among feed efficiency traits and other traits at different phases of the production cycle.

It is worth noting that there would be inherent weaknesses associated with estimations of genetic variation for genotypic RFI based on phenotypic correlations, in which case the variation in RFI may be due to the genetic correlation of RFI with the production traits. The calculation of genotypic RFI, from a genotypic regression (as opposed to a phenotypic one) would be independent of production, and therefore be a better indicator of the true genetic variation in efficiency (Archer *et al.* 1999).

## Blood parameters and metabolites

Richardson *et al.* (2002) aimed to identify haematological parameters (white and red blood cell profiles) that differed both significantly and consistently between high and low efficiency feedlot steers. They concluded that it was unlikely that a blood sample taken prior to feedlot entry (while animals were still at pasture as well as immediately

prior to feedlot induction) could be used to predict the RFI of steers within the feedlot environment.

However, they did find a number of blood parameters (haemoglobin level and haematocrit) that were correlated with sire EBV for RFI, providing some evidence of a genetic association between blood parameters and RFI. The increase in haemoglobin level and haematocrit in high RFI steers was consistent with an increase in the oxygen carrying capacity of the blood of high RFI steers. High RFI steers (ie less efficient) have been found to eat more feed, have higher heat production (Richardson *et al.* 2001a), higher levels of activity (Richardson *et al.* 2001 b) and higher rectal temperatures (Richardson *et al.* 2002). These differences result in increased oxygen requirements compared to low RFI animals.

Further work by Richardson *et al.* (2004) looking at blood metabolites found significant positive correlations between both beta-hydroxy butyrate and aspartate aminotransferase (AST) concentration taken at weaning and RFI in angus steers selected for divergent RFI. Concentration of beta-hydroxy butyrate was also positively correlated with average daily feed intake and FCR.

Despite this difference in blood metabolites at weaning, there were no significant differences in metabolite levels at the conclusion of the feedlot feeding period between high and low RFI lines of cattle (Richardson *et al.* 2004).

Clark *et al.* (1996) investigated the correlations between various blood plasma metabolites and body composition, as well as the repeatability of the metabolite measurements. Lambs selected for low back fat thickness, or high lean growth tended to show lower blood urea and creatinine concentrations. Correlations between protein:fat deposition and metabolites tended to be higher when metabolite levels were assessed in 4-6 month old lambs, compared with 12-14 month lambs. The association was found to be negative for urea (-0.5), positive for creatine (0.35) and low and variable for beta-hydroxy butyrate.

The repeatability of beta-hydroxy butyrate measurements between samples at 5 and 14 months was low (0.09), however were moderate for both plasma urea and creatinine concentrations (0.24 and 0.38 respectively).

#### Hormonal differences

Hormones are responsible for regulation of cellular activity, and as such play a key role in controlling growth in livestock (Scanes, 2003). As such, hormonal differences have the potential to offer significant insights into the variability in growth and efficiency between certain lines or even breeds of sheep. Of most interest are insulin and the insulin-like growth factors -1 and 2 (IGF-1 and IGF-2), growth hormone, as well as other hormones such as leptin that have linkages to body composition.

Maintenance of stable blood glucose concentrations is one of the most finely regulated of all homeostatic mechanisms, with the hormone insulin playing a major role (Bender and Mayes, 2006). Insulin is secreted in direct response to hyperglycemia, stimulating the liver to store glucose as glycogen (Bender and Mayes, 2006) as well as increasing blood flow (Hocquette *et al.* 1998). In addition to



the stimulation of uptake of glucose, insulin will also stimulate the uptake of other nutrients such as acetate. Opposing the action of insulin, is glucagon which is secreted in response to hypoglycaemia and stimulates the release of glucose into the blood stream. Glucose is thus synthesised from noncarbohydrate precursors via the process of gluconeogenesis and glycogenolysis (Bender and Mayes, 2006).

The addition of insulin to a perfused rat hindquarter (where 95% of oxidative metabolism was due to muscle tissue) resulted in a six fold increase in glucose uptake and stimulated oxygen consumption by 40% (Ruderman *et al.* 1971).

High growth animals that are selected for increases in lean body composition have been found to have an enhanced sensitivity to plasma insulin levels (Oddy, 1993; Hocquette *et al.* 1998).

Concentration of IGF-1 has been shown to vary between sheep bred for high or low weaning weight, with high weaning weight sheep having higher plasma concentrations of IGF-1 than low weaning weight sheep (Oddy, 1993). Despite plasma IGF-1 concentrations not being well correlated to muscle protein gain in sheep of either selection line, concentrations did increase with increasing whole body protein mass.

The consistent differences in plasma IGF-1 levels between the high and low weaning lines of sheep may account for the lower rates of protein degradation that was observed in high weaning weight sheep. Adding to this is the additional work of Oddy *et al.* (1991) that found infusing IGF-1 into the bloodstream of 5 month old Hyfer lambs decreased hind limb protein degradation rates by 35%.

Afolayan and Fogarty (2008) assessed IGF-1 levels of 1,246 young crossbred ewes and investigated correlations with maintenance grazing feed intake at maturity. IGF-1 levels were found to be moderately heritable (0.28) and moderately positively correlated with feed intake (0.32). They postulated that some of the variation in IGF-1 concentrations between cohorts (given similar ages) may have been due to between year variations.

The prospect of such a source of variation could be a possible restriction to the application of IGF-1 as a physiological indicator of animal efficiency. Other sources of variation in IGF-1 levels have included; sex (males greater IGF-1 concentrations than females) and dam age (older dams have progeny with greater IGF-1 concentrations at weaning).

Despite large standard errors associated with their dataset (due to limited size) Afolayan and Fogarty (2008) concluded that selection for low levels of IGF-1 may offer some reduction in feed intake and an improvement in maintenance efficiency. Prior to inclusion of IGF-1 as a physiological indicator of animal performance and efficiency into a breeding program, more validation is needed.

Despite there being no significant difference in circulating concentration of IGF-1 and IGF-2 between Angus cattle from divergent lines for net FCE, the role of hormones of the growth axis to influence net FCE should not be discounted (Richardson *et al.*

1996). IGF-1 is also closely linked to growth hormone and in turn postnatal growth (Afolayan and Fogarty, 2008).

Administration of growth hormone has been shown to have a greater impact in pigs than ruminants, however the impacts on daily gain (increase 10-18%), carcass lean content (increase 5-10%) fat content (decrease 10-20%) and feed efficiency (improve 9-20%) in sheep and cattle are still considerable. Responses in the various traits are also highly variable dependant on hormonal and nutritional status (Hocquette *et al.* 1998). Growth hormone appears to have a greater impact on red than white muscles, and may have an impact on meat quality. In growth hormone treated pigs the semispinalis muscle is changed to a less oxidative more glycolytic type, while no comparable changes are noted on the longissimus thoracis, a white muscle. In both cases the intramuscular fat concentration is decreased, which may be responsible for a slight decline in tenderness for growth hormone treated pigs. Despite these impacts on meat quality, carcasses from growth hormone treated animals (pigs and ruminants) have been shown to show no difference in ultimate pH (Hocquette *et al.* 1998).

Serum leptin levels have been found to differ between lines of Large White pigs selected for high or low daily feed intake. Pigs selected for high daily feed intake had higher food intakes, higher serum leptin concentrations and higher rates of fat deposition (Cameron *et al.* 2000). However, results indicated that the higher levels of serum leptin were largely correlated to high levels of fat deposition, rather than an increase in energy intake. As such, while serum leptin levels may be a useful selection tool for manipulating body composition, the poor correlation between serum leptin at lower body weights (prior to finishing) and feed intake during finishing mean it is of limited value as an indicator of an animals feed intake and potential efficiency (Cameron *et al.* 2000). Such a finding is however worthy of future consideration, given the potential for feed efficiency to be influenced by body composition. While serum leptin levels on their own may not give an indication of potential animal efficiency, they may provide insight into differences in body composition with an associated effect on animal efficiency. Such a hypothesis would be supported by the work of Graham (1969); Solis *et al.* (1988) and Lindsay *et al.* (1993) who support the general premise that the overall energetic efficiency of animals should vary along with a changed body composition, with highly muscled lean lambs being more efficient than lowly muscled fatter lambs.

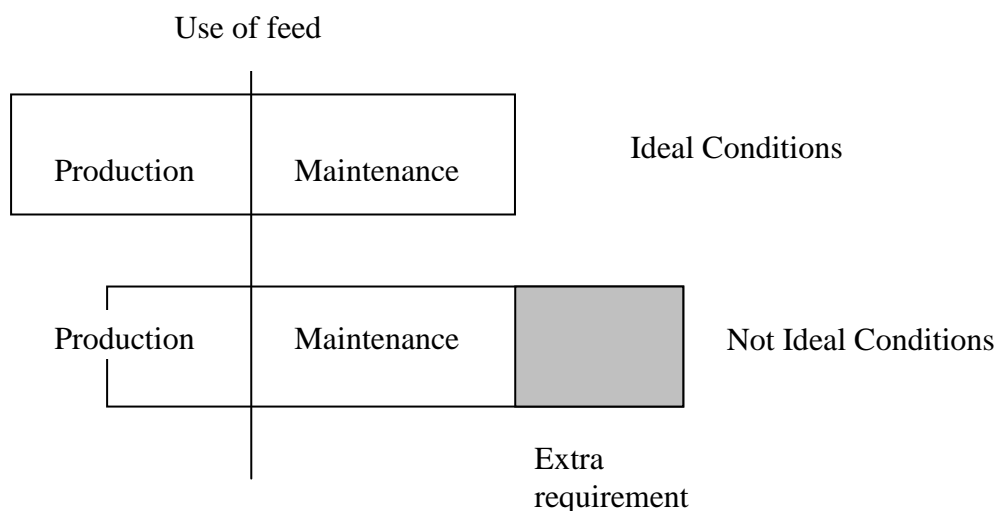
#### Energy Balance (Calorimetry)

While the assessment of an energy balance of an animal can be used to determine the nutritive value of a feedsource, it can also be used to determine how the energy requirements of an animal differ under a variety of conditions.

Indirect calorimetry provides a controlled environment where temperature and humidity are maintained at predetermined levels. Whole animal energy balances are determined from the measurement of the calorific energy value of the nutrients ingested. Metabolisable energy is calculated from energy intake minus the energy in faeces, urine and combustible gas energy. The energy balance is calculated as ME minus heat production (Verstegen *et al.* 1987).

In addition to using indirect calorimeters to monitor whole animal energy balances, nitrogen balances (N inputs in feed and emissions in faeces, urine and NH<sub>3</sub>) can also be assessed.

Calorimetry provides a useful tool by which the impact of environmental conditions (such as temperature and health status) impact on the energy metabolism of individual animals (Figure 5.1). Most experimental work is conducted over an extended period of time from 1 week up to several months to enable detectable changes in animal live weight to have occurred.



**Figure 5.1** Effect of conditions which increase maintenance and partitioning of ingested metabolisable energy into maintenance and production (Verstegen *et al.* 1987)

### 5.3 Tissue based efficiency

A change in energy metabolism (and hence energetic efficiency) would be reflected by changes in the aerobic/anaerobic capacity of the muscle. Such changes in metabolic efficiency dictate the need to assess energy metabolism on the basis of the partitioning of nutrients between oxidative and non-oxidative pathways, including nutrient storage (Hocquette *et al.* 1998).

The implications of a change in the ratio of anaerobic to aerobic activity are two fold and are important from an animal efficiency and eating quality perspective. 1) Animals with decreased glycolytic capacity have a theoretical greater metabolic efficiency (Gardner *et al.* 2006). A period of nutritional restriction has been shown to not only affect muscle fibre type and size, but will generally lead to more oxidative muscle types (a decrease in glycolytic capacity), leading to a theoretical improvement in metabolic efficiency (Gardner *et al.* 2006; Brandstetter *et al.* 1998), 2) Animals with an increased ratio of anaerobic to aerobic activity will more rapidly deplete and more slowly replete glycogen levels. Despite the propensity for such a pattern of glycogen use to result in darker muscle colour post slaughter Hopkins *et al.* (2005) did not report any genotypic effect on loin colour between medium wool and superfine bloodlines. This was in contrast to isocitrate dehydrogenase (ICDH)

activity which did differ significantly between the two bloodlines, which was consistent with a change in the anaerobic to aerobic capacity of the two genotypes (with the medium wool bloodline having a greater aerobic capacity than the superfine bloodline).

Although not tested within this work it was hypothesised that such changes in metabolism, as indicated by changes in the anaerobic and aerobic ratios may have been driven by a change in fibre type frequency between the two genotypes. Further work by Gardner *et al.* (2006) reported a generally poor association between fibre type and glycolytic activity, so it is not apparent that changes in anaerobic to aerobic ratio would have been driven by muscle fibre differences between the two studied bloodlines.

The anaerobic and aerobic metabolism of tissue has been assessed by monitoring the level of activity of specific enzymes. Gardner *et al.* (2006) and Briand *et al.* (1981) assessed the level of activity of lactate dehydrogenase (LDH) and ICDH to monitor anaerobic and aerobic metabolism of hind limb muscles in lamb. Hopkins *et al.* (2005) also assessed the potential of fructose 1,6-bis-phosphatase as a new enzyme based indicator of anaerobic activity.

Animals with a high level of glycogen phosphorylase activity, combined with low levels of glycogen synthase and hexokinase activity have muscle groups with an increased ratio of anaerobic to aerobic activity Hopkins *et al.* (2005).

Work reported by Hopkins *et al.* (2005) showed a change in enzyme activity between wethers from medium and fine wool bloodlines consistent with a change in the ratio of anaerobic to aerobic capacity (an increase in the ratio of anaerobic to aerobic capacity will more rapidly deplete and more slowly replete glycogen levels). While the relationship between fructose 1,6-bis-phosphatase and anaerobic capacity was not significant for the two genotypes, the trend did support the above observation related to anaerobic to aerobic capacity of medium and fine wool bloodlines.

#### Arterio-venous (AV) difference

Annison (1991) outlines various techniques for the continuous assessment of blood flow and blood oxygen content to assess metabolism in defined tissues. Such techniques include the use of AV difference (including the combined approach of AV difference and isotope dilution), mammary gland metabolism, hind limb metabolism and peripheral tissue metabolism.

Arterio-venous difference primarily involves sampling venous blood that has drained from the muscles of the hind limb. The nutrient concentration of venous blood can then be compared to that of arterial blood (Pethick, 1993; Annison, 1991) enabling an assessment of nutrient usage.

Teleni and Annison (1986) validated the use of AV difference as a technique for assessing muscle metabolism in the hind limb of sheep. They cite two prerequisite data requirements for the accurate assessment of AV difference of circulating substrates (muscle mass and blood flow).

*Muscle mass:* Estimations of muscle mass via the tested methodologies (titrated water and dye-dilution for measuring blood flow to estimate muscle mass) were comparable with true muscle mass. True muscle mass was established via dissection. Teleni and Annison (1986) concluded that the tested methodologies offered sufficient accuracy to determine metabolite exchange across the hind limb. The author is unaware of any work that was utilised VIAscan estimates of hind limb muscle mass as a comparable source of muscle mass data.

*Blood flow:* Sampled venous blood must be representative of total venous drainage, and the contribution of blood from other tissues should be insignificant. However, blood flow through different muscles in the hind limb is not identical (Oddy *et al.* 1981) and metabolic activity between different muscle groups within the hind limb may vary (Teleni and Annison 1986). To ensure the most appropriate sampling site for hind limb AV collections Teleni and Annison (1986) assessed which muscles were draining to the lateral saphenous vein. Resultantly they determined that the placement of the catheter tip for sample collection was critical and that to minimise drainage from non-muscle tissues, should be 25-26 cm from the junction of the cranial and caudal branches of the lateral saphenous vein.

#### *Inadequacies in current knowledge*

Changes to the ratio of anaerobic:aerobic metabolism within tissue has the propensity to impact on animal efficiency, with more oxidative muscle types having a theoretical improvement in metabolic efficiency. Such changes may result from either genetic variation or nutritional manipulation. While various enzyme based assays are being used to determine levels of anaerobic and aerobic metabolism, the remains a need to test the correlations between tissue based measures of efficiency and whole animals measures.

- If changes in metabolism, as indicated by changes in the anaerobic and aerobic ratios are driven by a change in fibre type frequency.
- If changes in metabolism, as indicated by changes in the anaerobic and aerobic ratios result in changes to various eating quality and shelf life parameters.
- If changes in tissue based metabolism, as indicated by changes in the anaerobic and aerobic ratios result in changes to whole animal efficiency (indicated by improvements in FCR and RFI).

## **6. Future directions and priorities**

### **6.1 Setting future targets for industry efficiency gains**

The New Zealand dairy industry has set itself a target of improving FCE of the national dairy herd from 77 kg Milk Solids/t DM consumed in 2005/06 to 100 kg milk solids/t DM consumed in 2015/16 (Kolver, 2007). This is an ambitious target, if the current rate of gain in FCE was maintained through to 2015/16, FCE would rest at 83 kg milk solids/t DM consumed.

Meat and Livestock Australia (MLA) have established a target of decreasing cost of production by 5% by 2011 (MLA 2006). Both continuing (gene markers for improved growth and efficiency in sheep) and new opportunities for R&D (reduced maintenance requirements) are identified as required to achieve the target. However, at this stage industry wide targets for improvements in feed efficiency have not been established for the Australian lamb industry.

## **6.2 Lifetime Efficiency (with particular regard to the ewe flock)**

Lifetime efficiency may be defined as the rate by which an animal converts their lifetime feed intake into product (Kolver, 2007). It will be affected by the efficiency of maintenance, growth and lactation of the individual, as well as by the lifetime production of the individual, such as the number and weight of lambs weaned for a ewe or slaughter weight and lean meat yield for terminal lambs.

Lifetime efficiency is contributed to by a number of research areas that address reproductive performance and length of productive life of breeding animals (ewes and rams). However, we know that the most significant consumer of food energy is maintenance of the breeding flock and there remains a need for further work to assess maintenance energy use of breeding animals.

Research findings from such an area of investigation would contribute important data to a maternal selection index.

## **6.3 Systems Efficiency, not just component efficiency**

There are almost an unlimited number of different supply chain structures, and the efficiency of one structure compared to another remains largely unknown.

For sustainable, long lasting benefits, not only must individual segments of the supply chain have improvements in efficiency, but there also needs to be a whole of chain improvement. It is important that there is an understanding of the impact that a change by one individual component of the supply chain will have on not only other immediate supply chain members, but on the whole supply chain.

There are a variety of ways in which supply chain efficiency may be improved.

1) An improvement by one supply chain component that benefits other supply chain members. An example would be the reduced production of over fat lambs, not only is the efficiency during finishing improved (impacting on finisher efficiency), but processing efficiency also benefits. 2) Improved supply chain processes that improve overall systems efficiency. Such whole of chain benefits may be the result of improved supply management or improvements within the supply chain structure.

It is likely that there is a role for computer modelling in determining the efficiency of different supply chain structures. However, as with all modelling there remains a need for an appropriate level of benchmarking and testing of modelled outputs.

## 6.4 What impact new selection areas will have on efficiency?

As a generalisation we are seeing changes in ewe selection. More commonly the merino ewe is being seen as a truly dual purpose animal with increasing emphasis on muscle, growth and fertility. It can reasonably be hypothesised that such changes will impact on animal, and systems efficiency.

Selection pressure in terminal genetics has responded to an increased awareness of lean meat yield. While Arthur *et al.* (1997) hypothesised that as with the relationships between growth, eye muscle size and efficiency, there would also be little relationship between meat yield and efficiency. Meat yield is of growing economic importance, yet this hypothesis remains to be tested.

## 6.5 How are improvements in animal efficiency extended to a wide network of producers?

Despite numerous studies to identify phenotypic traits that are correlated to feed efficiency, there remains no stand out indicators of animal efficiency. Indeed the traits with the greatest correlation to RFI still require the assessment of feed intake – a position of no net gain in terms of assessing animal efficiency in a large population of animals. As such, the ability to share the benefits from potential gains associated with improved animal efficiency has been limited.

To deliver industry wide benefits from improvements in efficiency the beef industry worked with key seed stock producers across a range of breeds. However it is the authors opinion that many of these breeders are no longer assessing feed intake in the herds – again limiting potential industry benefits.

There is little doubt the new technologies such as gene markers have the potential to play a key role in identifying energy efficient animals. However Hill and Azain (2009) still identify 2 barriers to the progress of gene markers for increased understanding of RFI, 1) understanding of genetic interactions of genes that are seemingly unrelated to feed efficiency, 2) the limitations imposed by having small populations of animals that are well characterised for RFI. Once these limitations can be overcome the possibility to incorporate animal efficiency within breeding values becomes a very real possibility – at this point feed efficiency science becomes a powerful tool that can be accessed by the wider industry. Indeed, at this point industry has the option to utilise the information or not. Currently this decision is not there to be made, given the appropriate information on feed efficiency is not available.

There remains a need for efficiency based research projects to assess not only genetic causes of variation in efficiency, but also related elements of on farm management. By understanding the implications of 1) different weaning weights, 2) growth paths and 3) lamb ages at finishing on efficiency during finishing, it becomes possible for a wide range of producers to benefit at an on farm level from research into energetic efficiency. Central to this benefit is the need for research outcomes to be effectively delivered to appropriate extension agencies and services.

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