

Comparative body composition and feed efficiency between Merino and maternal sheep breeds

By

Chad Averill

Bachelor of Science in Animal Science and Animal Health



Supervisors: Sarah Blumer and Andrew Thompson

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Declaration


I declare that this thesis is my own account of my research and contains, as its main content, work which has not previously been submitted for a degree at any tertiary education institution.

Student: Chad Averill

Signed: 

Date: 23/10/2017

Supervisor: Sarah Blumer

Signed: 

Date: 23/10/2017

Abstract

The Australian flock structure has been changing through the last few decades, and lambs from maternal type ewes make up roughly 45% of the Australian lamb supply. However, management guidelines to maximise the profitability of sheep enterprises based on maternal sheep have not been properly developed. Recent work quantified the ewe and lamb production responses to changes in ewe liveweight during pregnancy and lactation, however using formulae from the Australian Feeding Standards which were largely developed using Merino sheep. These were unable to predict changes in liveweight at both above and below maintenance requirements, and hence unable to develop optimum management guidelines for maternal ewes. In the current study, whole body fatness measures, in combination with feed intake and liveweight data, were used to examine the efficiency of energy use comparing Merino ewes and maternal ewes. Feed intake was measured over 42 days, with 20 of each breed split in to two diet groups (*ad libitum* and maintenance). Computerized axial tomography (CAT) scan data was analysed to show fat depositions for each breed, as well as relative intake associated with liveweight change. Breed did not affect potential intake, while fat depositions were different between the breeds. Intake was affected by body composition, with ME intake reduced by 0.26 MJ/day for every 10 cm² increase in fat tissue, but increased by 0.06 MJ/day for every 10 cm² increase in soft tissue. Therefore, naturally fatter ewes require less ME to maintain liveweight. However, there was no breed effect on RFI. This means that differences in potential intake or maintenance requirement are unlikely to explain why maternal ewes appear to perform better than Merino ewes and what is predicted by Australian Feeding Standards.

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1. Literature Review

1.0 Introduction

The proportion of Merino ewes in the Australian sheep flock has decreased from 90% to 70% during the last decade, with non-Merinos now producing 45% of the current Australian lamb supply (B. Thomas, Meat and Livestock Australia, personal communication). Many factors are likely to have contributed to this recent change in flock demographic. This includes higher sheep meat prices (Meat and Livestock Australia 2017), increased reproductive performance of non-Merinos compared to Merinos under identical conditions (Babiszewski and Hocking Edwards 2013; Hocking-Edwards in press) and increased economic pay-off for improving reproduction in non-Merinos compared to Merinos (Young *et al.* 2014). Blumer *et al.* (2016) also reported non-Merinos to lose less and gain more liveweight, than Merinos, in restrictive and excessive environments respectively, which may imply they can run at increased stocking rates with less requirements for supplementary feeding.

A clear understanding of the nutritive requirements of breeding ewes and appropriate management skills are required to attain maximum reproductive performance for minimal cost. The Lifetime Ewe Management program, which is a small-group extension model developed by LifetimeWool (Curnow *et al.* 2011), aims to help producers to manage their Merino ewes to achieve condition score targets during pregnancy and lactation to improve reproductive performance. These robust management guidelines, based on economic modelling of ewe and lamb production responses (Young *et al.* 2011), have been widely adopted and aim to be clear and influential so that when adopted by industry innovators, others would be encouraged to follow suit (Jones *et al.* 2011). Farmers that have participated in the program have achieved a 14% increase in stocking rates, a decrease in ewe mortality by 43% and an 11-13% increase in lamb marking percentage (Trompf *et al.* 2011). While Trompf *et al.* (2011) observed improvements in lamb marking percentages in farms with non-Merino flocks participating in the Lifetime Ewe Management program, there is uncertainty whether

the guidelines promoted are optimum for these enterprises. Babiszewski and Hocking Edwards (2013) suggested that if inputs were to be matched accurately to non-Merino requirements, reproductive efficiency and stocking rates could be increased, while supplementation feeding costs would be reduced. This is due to the conclusion that non-Merinos had a lower feeding requirement than Merinos per kg liveweight. Therefore, the optimum management guidelines set by the Lifetime Ewe Management program may need to be recalibrated for other breed types within the Australian production systems.

This review will address potential factors that could contribute to differences in performance between Merino and non-Merino ewes. This includes the required energy use for maintenance, efficiency of energy use for maintenance, energy content for liveweight gain, and fat partitioning. In addition, influences such as: genotypes, hormones, digestibility, adaptation, temperament, hybrid vigour and overall breed will also be considered.

1.1 The effects of breed on liveweight and reproduction traits

Recent work has established relationships between ewe liveweight change during pregnancy, and feed on offer during late pregnancy and lactation, on birth weights, survival, weaning rates (Thompson 2017). Breed can become a factor in reproductive potential as their utilization of feed and mothering ability ultimately affect production.

Langlands (1972) analysed the average daily gain of lambs raised by different breeds. Border Leicester and Merinos were used in this experiment, which saw four groups with a different combination of dam and offspring. Border Leicester lambs, as well as ewes, outperformed the Merinos for average daily gain. This in part may be since Border Leicesters are known for their maternal qualities, such as mothering and reproductive ability (Daetwyler *et al.* 2010). Lambs raised by Border Leicester ewes were ingesting more milk but less pasture than lambs raised by Merinos. Comparing voluntary intake between lamb breeds, Merino lambs consumed less

milk and pasture than the Border Leicester lambs. This resulted in slower growth of the Merinos (Langlands 1972). Babiszewski and Hocking Edwards (2013) stated that under identical conditions and management, non-Merino ewes outperformed Merino ewes significantly. A lesser feed intake requirement per kg bodyweight would further lead to a decreased supplementary feed for non-Merino ewes. Therefore, an increase in reproductive efficiency and a reduced cost of production will be seen if ideal inputs are supplied to non-Merino ewes. Blumer *et al.* (2016) noted that Border Leicester x Merino ewes gained more weight than the Merino ewes on average, however site impacted the consistency of this average. This was also seen with weight lost under nutritional strain. It was further concluded that heavier ewes, phenotypically, have a decreased sensitivity to nutritional planes than lighter ewes.

Maternal ewes, such as Border Leicesters, have greater reproductive traits than Merinos, including fecundity, fertility and lamb survival. Fertility has been shown to effect reproductive rate and lambing percentages, noted by Fogarty *et al.* (2007), and this has been shown to be affected by breed. Fogarty *et al.* (2007) demonstrated through lambing performance that high significance was seen when different sire breeds were used. Corriedale-sired ewes had a fertility of 0.24 ± 0.07 , whereas East Friesians performed at 0.71 ± 0.06 . Holst *et al.* (2002) found that ewe breed had a significant impact on lamb birth weight and gestation length, with Merino lambs being 0.3kg lighter and spending 2 days longer in gestation. Furthermore, birth weight and lamb survival has been shown to have a large positive correlation (Thompson 2017). When comparing the same breeds, Thompson (2017) stated that, naturally, survival rates are greater for non-Merinos when pressured under similar conditions. A fair conclusion to this could be that crossbreeds having bigger lambs and greater lamb survival may be due to higher condition scores of the ewes at lambing.

In theory, when breeding yearling ewes, younger ages of maturity, with the right management, can lead to greater levels of efficiency. Breed has also been seen to affect live weight at puberty, with significant variations between breeds (Fogarty et al. 2007). This included East Friesian cross sired ewes at 43.1kg, while Corriedales sired ewes were 37.1kg on average. It was also further noted by Fogarty et al. (2007) that reproductive rate and lambing percentages were also affected. Quirke (1981) also summarized that lambing rates had a significant range for different ewe lamb breeds. Kenyon et al. (2014) further concluded that the variation was also significant when different genetic potential for wool, carcass and growth traits were present. Not only do weaning and conception rates become of greater importance, but the requirement to know the optimum feeding level becomes inherently more significant. This is due to the speculation that lambs grow quicker when ewes are fatter at lambing. This was seen with the crossbreeds (Thompson 2017), which had greater intakes and a higher milk production, further leading to a potential of greater intake from the lambs.

The impact of these breed differences heightens the necessity to understand breed as a factor in a production system that could potentially alter its success and efficiency. It would also enable greater levels of selection to occur, through understanding the drivers of breed differences, the variation of these traits can be selected for when developing an existing breed or introducing new breeds.

1.2 Hybrid Vigour

Hybrid vigour, also known as heterosis, is the enhancement of genetic traits in the hybrid offspring and is frequently used to increase productivity in a farming system. This can be something simple, such as temperament of livestock to make handling easier which is moderately heritable (Burrow 1997), or more complex such as impacting body composition.

Heterosis is testable when comparing purebreds to their reciprocating crosses (Trail *et al.* 1982), and by looking at both combination possibilities of parents (Rastogi *et al.* 1982). Trail *et al.* (1982) showed hybrid vigour when looking at Boran and Red Poll cattle breeds. The cross was significantly heavier at weaning, and this effect increased with age. Crossbred calves were also more likely to survive, with additive maternal effects being present. This was found with birth weight as crossbred calves with Boran dams were 6kg lighter than crossbred calves with Red Poll dams. This was reversed at weaning as crossbred calves with Red Poll dams were 7.1 kg heavier than the crossbreds with Boran dams.

This indicates that further selection and management care is also important when attempting heterosis as there are many factors contributing to differing outcomes. This is most certainly an issue when considering milk due to whether a system is focussed on rewarding for milk solids or on milk volume (Lopez-Villalobos and Garrick 2002). Heterosis within milk production is certainly present (Pedersen and Christensen 1989) between Finnish Ayrshire, Red Danish and Holstein-Friesian cattle, with F1 heterosis for 305-day milk production traits being approximately 7% when crossing these three breeds. McAllister *et al.* (1994) found an increase in lifetime milk yield, as well as annual net return for crossbreeds of Holstein and Ayrshire cattle breeds over the base breeds, while Touchberry (1992) concluded crossbreeds of Holstein and Guernsey cattle yield higher levels of milk, fat and protein. Therefore, it can lead to increasing farm profit through economic heterosis, although this increased profit has also been found to be negatively correlated with reproduction, health and survival (Lopez-Villalobos and Garrick 2002).

In sheep, Hohenboken and Cockran (1976) stated that crossbreeds had greater lamb production, with increased fertility, prolificacy and lamb birth and weaning weights than the base breeds of Hampshire, Suffolk and the Williamette. Rastogi *et al.* (1982) took this further using Columbia, Suffolk and Targhee breeds, but also added three way breed combinations

(second cross). The three way crosses outperformed first cross lambs, which in turn performed better than the purebreds when tested for multiple traits including birth weight and age at market weight. However, like Trail *et al.* (1982) noticed, the specific parents each had made a significant effect, such as Suffolk dams having lambs with superior preweaning average daily gains, weaning weight and age at market than Targhee and Columbia dams. Furthermore, Targhee-Suffolk sires and Columbia dams produced lambs with greater post weaning average daily gains than any other combination (Rastogi *et al.* 1982).

Significant but small differences in crossbreed performance has been observed to be dependent on which breeds the dam or sire were, when analysing the Merino and Corriedale. It was noted that there was some heterotic effect with lamb survival, the number born per ewe, weight of lambs weaned per ewe and lamb weaning weight Iwan *et al.* (1971). Pitchford (1993) found that heterosis was significant for mature weight in sheep, but had no significance when looking at maturation weight. Ch'ang and Evans (1985) compared Merino, Corriedale and Dorset Horn rams with their six F1 crossbreeds and observed multiple heterotic effects in cold carcass weight, edible meat and fat trim. However, it was unspecified in the direction of heterosis as fat trim may have been reduced to promote a greater meat yield. This could be unwise in a production system where reproduction is key and fat has a large impact on the survival of the ewes. It is also noted that combining a Merino with a Border Leicester may also potentially lead to less wool produced, when compared to a Merino (Kleemann *et al.* 1984), increasing a further importance in trait selection and heterotic outcomes.

Some traits appear to be more affected by heterosis than other traits, but breeds (Oxford *et al.* 2009) and diet do have an impact on this process.

1.3 *The effects of breed on intake*

Work by Thompson (2017) showed that modern maternal sheep gain significantly more liveweight than expected, when compared on a prediction model. This meant that based on the Australian Feeding Standard for Merinos, non-Merinos were gaining more liveweight than expected, leading to the assumption that they were being fed above requirement. Thompson (2017) observed that during supplementary feeding at pasture, there was a wider gap between observed and predicted liveweight gain as feed on offer increased. This gap was smaller when supplementary feeding was reduced and pasture was a high percentage of the diet. Border Leicester x Merinos also generally had a higher condition score and liveweight than the Merinos. This led to the understandable speculation of either greater feed efficiency or greater overall appetite. Other studies have also shown that both dry matter intake and water intake are different between breeds (Quick and Dehority 1986), and forage selection has also been demonstrated (Animut *et al.* 2005). Roeder and Chow (1972), stated that undernutrition can diminish functional capabilities and lead to numerous abnormalities if occurring during early development, as well as affecting reproductive potential in the following year (Thompson 2017).

Diet selection can easily be affected by many factors, which may result in different intakes by different sheep over a certain period of time. Eating rate has been known to affect forage selection, with reduction in intake material resulting in higher amounts ingested (Kenney and Black 1984). Intake per prehending bite was decreased when pasture height and density was reduced, but the bite rate doubled as intake per bite was increased, leading to preferences in paddock that allowed faster eating (Black and Kenney 1984). Decreases in rate of intake can be compensated by longer grazing times, however this may be difficult to fully compensate if pasture is of poor quality. This would also further be difficult as digestibility decreases after a certain age (Langlands 1968). It was also seen by Langlands (1968) that intake of Merinos on a poor diet previously, had a greater intake when put in a paddock with Merinos from a high

quality diet. Furthermore, breed became an effector for a significance in faecal output and digestibility, leading to the potential assumption of intake differences between breeds.

Potential intake (PI) is important as it represents the amount an animal will eat when there is an abundance of feed at high quality. Relative intake quality (RIqI) and relative intake quantity (RIqN) are also important as they also affect how the animal eats. RIqI is when an animal consumes less when feed on offer is lacking digestibility, while RIqN relates to consuming less when there is a decrease in feed on offer. All three have related genotypes expressed in animals, with PI increase resulting in higher drive to eat throughout the year. RIqI sensitivity decrease resulting in an elevated drive to eat when quality is low, and RIqN sensitivity decrease results in an elevated drive when feed on offer is low (Thompson 2017). Each one of these, as observed by Thompson (2017), results in an increased grazing time, which may further explain maternals outperforming Merinos when run together.

1.4 *Required energy use for maintenance*

There is a required level of energy intake associated with maintaining a specific body weight and regular bodily functions. This is influenced by state of health, physiological state, sex, body weight, as well as variations between individuals (Pellet 1990). This can also be affected by foetus and lamb size due to the requirement of more energy and potential nutrient intake of the offspring (Freer *et al.* 1997).

Many experiments have compared maintenance levels of different breeds of cattle and goats that have shown different energy requirements, especially in different stages of life and in different environments. Work by Fernandez *et al.* (2007) demonstrated that the net energy and protein requirements in bred-for meat crossbred Boer goats exceeded previously published requirements and guidelines for dairy goats. The Texel breed of sheep was analysed by Galvani *et al.* (2008) to understand the energy requirements of crossbred Texel sheep and

discovered the growing lambs they used had a lower energy requirement than what was previously suggested for similar animals. The Net Energy requirement for maintenance was 58.6 kcal/kg^{0.75} which was significantly different to the value suggested by the CSIRO (2007) of 66 kcal/kg^{0.75}. However experimental conditions, genotype and environmental circumstances may be responsible for this discrepancy.

Maintenance energy requirements can also be assessed using heat production and is measurable using the equation where energy metabolized is equal to heat produced by the animal plus the quantity of work performed (King and Farner 1961). This has been proven by Derno *et al.* (2005) and is used to measure maintenance levels in livestock with a relative degree of accuracy. Freetly *et al.* (1995) aimed to understand various levels of heat production between Suffolk and Texel ewes, observing that Texels had a lower level of heat production, however concluded that this was due differences in maturity. Freetly *et al.* (2002) also compared Finnsheep and Rambouillet ewes. Differences in both growth rate and heat production were evident, with the Rambouillet reaching a mature body weight with a lower level of heat production. This suggests the necessity to not only consider age, but breed as well to achieve an accurate metabolic rate measurement. In addition to these differences in heat production when directly comparing sheep breeds, studies of separate breeds have arrived at different energy level requirements for maintenance. Twelve-month-old Baluchi male wethers required 0.342 MJ of ME per kg metabolic liveweight (Kamalzadeh and Shabani 2007) while Omami ram lambs required 0.526 MJ of ME per kg liveweight (Early *et al.* 2001). This research was included in a report by Babiszewski and Hocking Edwards (2013). The summarized Table 1, shows German Merino Landsheep, Awassi, second cross Suffolk, Dorper, as well as at least twelve other breeds from numerous studies, all with different requirements. The LifetimeWool feed budgeting for Merinos demonstrates a 50kg medium framed dry ewe would require approximately 0.425 MJ of ME per kg LW (Curnow *et al.* 2011). While these are different

values, there are different ages, diets and environments involved, with few controlled experiments directly comparing breeds.

Table 1: The energy requirements at maintenance (ME; kJ/kgBW^{0.75}/day) of different breeds at different stages of development (Babiszewski and Hocking Edwards 2013).

Reference	Breed	Age	Status	ME
Early <i>et al.</i> (2001)	Omani	Lambs	Growing	526
Bellof and Pallauf (2004)	German Merino Landsheep	Lambs	Growing	520
Rattray <i>et al.</i> (1973b)	Mixed; Targhee and Finn and their crosses	Lambs	Growing	502
Jassim <i>et al.</i> (1996)	Awassi	Lambs	Growing	466
Ferrell <i>et al.</i> (1979)	2X Suffolk	Lambs	Growing	463
Elliott & O'Donovan (1969)	Dorper	Lambs	Growing	444
Galvani <i>et al.</i> (2008)	Texel x Ile de France	Lambs	Growing	381
Thomson <i>et al.</i> (1979)	2X Suffolk	Lambs	Growing	339
Santos <i>et al.</i> (2002)	Bergamacia	Lambs	Growing	229
Kamalzadeh and Shabani (2007)	Baluchi	Hoggets	Wethers	294
Duarte-Vera <i>et al.</i> (2012)	Pelibuey	Hoggets	Wethers	444
Young and Corbett (1968)	Merino	Mature	Wethers	552*
Dawson and Steen (1998)	Blackface, Suffolk and Texel x Blackface	Mature	Wethers	460
Liu <i>et al.</i> (1991)	Hu	Mature	Wethers	310 - 402
Olthoff <i>et al.</i> (1989)	Columbia x Hampshire x Suffolk	Mature	Dry ewe	708
Olthoff <i>et al.</i> (1989)	Finn x Suffolk x Targhee	Mature	Dry ewe	581
Elliott & O'Donovan (1969)	Dorper	Mature	Dry ewe	373*
Ball <i>et al.</i> (1998)	Coopworth	Mature	Dry ewe	290
Average (\pm SD) across all ME values		425.6*kJ/kgBW ^{0.75} /day \pm 97*		

While required energy for maintenance is a crucial factor in nutritional management, there are many different processes the energy can be used for such as growth, reproduction and lactation. This inevitably leads to variation in the efficiency of animals to maintain a constant level of survival and reproductive fitness.

1.5 Efficiency of energy use

The efficiency in which an animal utilises food to maintain liveweight is a key aspect in profitability of a production system. This can be affected by the quality of feed offered as well as what an animal may selectively seek (Osoro *et al.* 1999) but also the physiological state that an animal is in, such as maturity and reproductive status.

Predictably there are differences between species and breeds in terms of efficiency. Sanz Sampelayo *et al.* (1995) showed that goats have greater efficiency in terms of energy for protein storage but lower levels of fat deposition. Work by Taylor *et al.* (1986) made comparisons between multiple breeds of cattle such as Hereford, Dexter, Aberdeen Angus, British Friesian and Jersey, and found that as the genetic potential for milk increased, feed efficiency for maintenance was reduced. Beef cattle such as Herefords and the Aberdeen Angus had an equilibrium efficiency (E_m) of 0.150 and 0.142 respectively. These were the most efficient when managed at maintenance, followed by the dual purpose breeds such as Dexters showed an E_m of 0.031. The British Friesian and Jersey displayed an E_m of -0.176 and -0.146 respectively. This is assumed to be caused by genetic differences in milk production, arising from selection pressures. Molina *et al.* (2001) also hypothesized that a difference in genetics would lead to differences in energy utilization between the Lacaune and Manchega sheep breeds in during late pregnancy and lactation. While both being milk breeds, the Lacaune has a higher milk yield and was found to have higher energy requirements, however the higher yield was not completely explained by the increased intake and suggested these ewes were more efficient. A study by Kleeman and Dolling (1978) compared Merinos with first cross lambs (Border Leicester x Merino) and found that Merino lambs took longer to reach the same slaughter weight and consumed more feed overall. It was concluded that each breed could be more efficient depending on the stages of life, however a direct comparison between Merino and maternal ewes for metabolic rate and energy requirements for maintenance has yet to be seen.

While breed may be considered important, physiological state is an added factor to consider. This is due to energy partitioning with maintenance requirements changing particularly during growth and reproduction. During lactation, energy is partitioned towards milk production with the energy demand peaking at the beginning and declining as lactation progresses (Prendiville

et al. 2011). As Prendiville *et al.* (2011) state, there is increase in an energy requirement specifically for this milk production and this causes an increase in intake. Molina *et al.* (2001) found that during late pregnancy, while the intake levels were similar for Lacaune and Manchega breeds, the Lacaune produced a lighter lamb suggesting that Manchega ewes had partitioned more energy towards lamb growth during this period.

The interplay between selection for desired traits must be balanced with the increased or decreased cost of supporting that production and the economic value of the production unit whether this is wool, or milk, or lamb. In addition, the economic value of liveweight gain will differ at each physiological state and be influenced by the partitioning of energy into fat and muscle tissues as well as the response of production traits to that gain.

1.6 *Energy content for liveweight gain*

When an animal eats above maintenance requirements, the excess energy is usually expressed as liveweight gain. The conversion of metabolizable energy into fat or muscle tissue is a key profit driver in the livestock industry and the efficiency of this conversion varies between species, breeds and individuals. This is likely to be related to changes in body composition. Babiszewski and Hocking Edwards (2013) stated that lean sheep have a higher ME requirement, than fatter sheep at the same liveweight, due to lean tissue demanding a higher metabolic level to maintain. As maternal breeds often have higher genetic fat levels, an assumption of a lower metabolizable energy requirement can be made as a body composition at similar liveweights would show a higher representation of fat. It then becomes essential to know how much metabolizable energy is in feed as different feeding levels can result in different liveweight gains (Jassim *et al.* 1996). Actual requirements for protein are variable between breeds, sex, and physiological state. Steers have lower requirements than bulls, while breeds that mature earlier also have a lower requirement (Geay 1984). Early maturing breeds have nearly twice the lipid content at similar empty body weights than late maturing breeds,

while steers and heifers have 1.5 times the lipid levels of bulls (Robelin and Daenicke 1980). Freetly *et al.* (2002) also implied a higher metabolic rate is seen in slower maturing breeds, when compared to faster maturing breeds at the same age. This relates to the higher cost of protein turnover in slow maturing animals, which have comparatively higher fat and protein levels at the same age.

Babiszewski and Hocking Edwards (2013) noted that lean tissue has a higher metabolic activity, therefore fatter sheep at the same liveweight have a lower metabolizable energy requirement. This means fat tissue is cheaper to maintain than protein tissue in ewes. It is also known that fat weighs less than protein (Downs *et al.* 2005), therefore body composition can vary for sheep at the same liveweight. Protein tissue is also more expensive to accumulate than fat tissue. Rattray *et al.* (1974) analysed growing and mature sheep, noting that fat synthesis required 10.2 ± 3.58 kcal ME per gram of fat deposited, whereas protein synthesis needed 45.6 ± 8.69 kcal ME per gram of protein deposited.

Lu and Potchoiba (1990) concluded that energy concentration affected efficiency of deposition in goats. Average daily gain decreased as dietary energy content increased, however average daily gain increased when crude protein content increased. This change in liveweight corresponded with decreased intake on the high energy diets and increased intake on the high protein diets. There was also a difference in efficiency between breeds, with intake for British Alpine goats being greater than Anglo Nubian goats, at similar average daily gains. This suggested that British Alpines required more energy to reach similar liveweight gains, so were less efficient.

Breed differences have also been demonstrated by Wilkes *et al.* (2012) when comparing Damara and Merino sheep. When fed a poor quality diet Damara sheep had a greater average daily gain, with an ability to obtain a greater level of nutrients from the feed than Merino

sheep. This also may be due to a lower requirement for maintenance, which has also been observed in Brahman cattle by Frisch and Vercoe (1969). Intake requirements may also be associated with adaptation to the environment (Cannas and Atzori 2005). For example, Omani sheep required more energy for growth compared to sheep that were more adapted to those temperatures (Early *et al.* 2001).

While it is important for farmers to know what the nutrient requirements are to reach specific targets, many factors contribute to the estimation of energy requirements for maintenance and growth. With variation existing between animals for the energy converted into liveweight gain, selection for efficiency of energy use becomes a useful tool for livestock production.

1.7 Digestibility

Digestibility is affected by several factors, primarily the availability of nutrients in the feed offered, and the individual's ability to extract the maximum value out of the feed offered, but also including feed type, feeding level, physiological status, environment (which may include weather), the feed on offer due to region, as well as stress levels. Palatability, selective grazing and feeding time may also indirectly affect digestibility as they can affect the overall intake of the animals. In addition, crude protein has been shown to be more digestible when higher levels of digestible food are being fed (Margan *et al.* 1982). This is important as both energy and protein are known as limiters for growth (Poppi and McLennan 1995).

Mature Latxa and Gallega ewes were studied, where selective grazing was a key part in digestibility based on the diet. When a preferred pasture species was prolific, the Latxa had a greater liveweight gain. However, when that species became scarce, the Gallega showed a greater liveweight gain, even though the Latxa maintained a greater overall intake (Osoro *et al.* 1999).

It has been stated by the National Research Council (1985) that higher levels of feed intake may prove detrimental to the absorption of nutrients due to the depression of digestibility. This is likely due to reduced retention time and decreasing organic matter digestion in the rumen (Margan *et al.* 1982), as well as affecting starch, fibre and nitrogen digestibility (Rust and Owens 1981). Some breeds have a greater appetite and this leads to the greater overall intake, as well as responsiveness to different diets (Almeida *et al.* 2013).

Digestibility has also been demonstrated to be different between breeds. Damara sheep are a meat breed well suited to extremely marginal farming areas (Almeida *et al.* 2013). Wilkes *et al.* (2012) demonstrated that when fed either a low or high-quality diet the Damara had an overall digestible energy intake greater than the Merino via two pathways. When on a high-quality diet, it was achieved by a greater overall intake with no digestibility differences between breeds. However, when on a low-quality diet, the intake was similar between breeds, but the Damara had a significantly higher digestibility than the Merino.

Lopez *et al.* (2001) found a small difference between Merino and Churra sheep breeds when testing the difference herbage maturity had on digestibility. In contrast, Ranilla *et al.* (1998) compared the Merino and Churra sheep breeds and showed that when comparing digestibility, digesta passage, and the mean total rumen retention times, there were no significant differences between the breeds. Work by Molina *et al.* (2001) compared Lacaune and Manchega breeds during pregnancy and lactation. While there was a noticeable difference between the two in intake, it was determined that digestibility was very similar, and that this difference was due to the excessive energy demands for the Lacaune breed in terms of milk yield and mammary development. This demonstrates that energy demands must also be considered when examining digestibility.

It is evident from the literature that digestibility may potentially be different for different breeds and therefore further contribute to efficiency and fat storage of the breeds involved.

1.8 Hormonal levels impacting fat storage

Of the many hormones, there are some in particular that have a direct and indirect correlation with production and efficiency, especially concerning fat tissue storage. Fat mobilization in ewes is influenced by energy balance and whole-body fatness and of the hormones potentially implicated in efficiency, one of the most important is insulin.

Insulin affects fat metabolism through slowing down lipolysis, increasing triglyceride uptake and transportation to adipose tissue, as well as increasing fatty acid synthesis (Dimitriadis *et al.* 2011). Work by Ponnampalam *et al.* (2012) found a greater sensitivity to insulin in Merino lambs, as opposed to second cross lambs (Merino x Border Leicester dam x Poll Dorset sire), in terms of a hypoglycaemic response as well as a cortisol response. Insulin levels are lower in lactating ewes (Hatfield *et al.* 1999) and Chilliard *et al.* (2000) has demonstrated that adipose tissue metabolism is enhanced during lactation, due to an insulin resistance. While increasing insulin results in stimulated lipogenesis, growth hormone and leptin have both been known to inhibit it (Kersten 2001).

Growth hormone reduces lipogenesis, and both feeding levels and physiological state impact its concentration. Lactating ewes have a higher peak, as well as higher average concentrations of growth hormone, than non-lactating ewes. Growth hormone is higher when feeding a maintenance diet, than *ad libitum* (Hatfield *et al.* 1999). Leptin has been noted as being positively correlated with fat levels, as well as being negatively impacted by underfeeding, with the adipose tissue acting as an endocrine gland (Chilliard *et al.* 2000). Low levels of leptin in women are associated with decreased fertility, and improved ovarian function is associated with increased birth weight and fatness at birth (Power and Schulkin 2008). Blood plasma

concentrations of leptin are associated with the liveweight and feed efficiency of sheep. Ewes with higher levels of leptin displayed a reduction in liveweight lost as well as a lower daily intake in comparison to ewes with low leptin concentrations (Blumer *et al.* 2016).

Glucocorticoids such as cortisol are also implicated in feed and production efficiency (Chilliard *et al.* 2000). Petherick *et al.* (2009) identified that cortisol levels in a well-treated cattle group were significantly lower than poorly treated cattle. Pajor *et al.* (2010) showed that cortisol levels in more reactive sheep were highly correlated and that the lower level cortisol sheep showed greater production outputs in terms of weight gain and milking. Elevated levels of cortisol can negatively impact liveweight as well as fat depots in terms of unnecessary energy usage being wasted, caused by stress (Maglione-Garves *et al.* 2005).

These hormones, as well as many others, exist to help the body maintain homeostasis and promote productive functionality. In combination with physiological status and management, hormones contribute to the control of intake and efficiency and also to the direction of energy intake into energy expenditure and/or energy stores.

1.9 *Energy partitioning and body reserves*

Energy storage occurs when an excess of feed is consumed, when compared to the daily metabolic rate of the living specimen (Norgan and Durnin 1980). This can be affected by the quality of the diet (Leng. 1990), the environment surrounding the animal (Gillooly *et al.* 1980), and the depot location can be affected by the species and breed involved (Butler-Hogg 1984). Fat is maintained in several depots with the main sites being the omental, mesenteric, subcutaneous, perirenal, pelvic and inter-muscular (Vezinhet and Prud'Hon 1975). It acts as a form of energy storage, but also supports cell membrane construction, insulation, thermoregulation, as well as endocrine function (Paus *et al.* 2007).

An on-farm measure of body fatness is condition scoring (Russel 1984), which has become a widespread practice to determine the nutritional or energy status of sheep. While this is common practice, reports by researchers such as Treacher and Filo (1995) have shown that it may not be entirely accurate to indicate whole body fatness as it is a measure of the subcutaneous fat depot. This was further proven by Ferguson (unpublished) showing that condition scoring only explains 50-60% of variance in whole body fat. In cattle, Wright and Russel (1984) discovered that British Friesian cattle appeared fatter at any given condition scoring, than other breeds they used, due to them having the lowest level of subcutaneous fat storage and the highest intra-abdominal depots. Castrillo *et al.* (1988) suggested that condition scoring is not recommended to predict fat reserves through the reproductive cycle as empty body fat level measurements produce variability under similar condition scores. Castrillo *et al.* (1988) used Romanov x Rasa ewes, while utilising the technique of Russel *et al.* (1969) which was developed using Scottish Blackface ewes. McClelland and Russel (1972) then concluded that the rate of deposition was different for separate depots when comparing breeds such as the Scottish Blackface and Finnish Landrace.

Another study analysing the body condition score relationship with fatness showed that using liveweight as a fat predictor in Churra ewes was in fact superior to the body condition scoring as it was unable to assess internal fat depots such as omental depots (Frutos *et al.* 1997). This included an R² of 0.59 when predicting using equations involving liveweight, while being 0.33 using equations involving body condition score. However, conflicting studies, using Rasa Aragonesa ewes, showed that the body condition score was indeed accurate in terms of predicting the internal fat depots (Teixeira *et al.* 1989). It was indicated that from a body condition score of 1-5, all fat depots remained highly correlated with the condition score given and that overall fat was accurately predicted. This breed, however, is predominantly a wool and meat breed (Altarriba *et al.* 1998) whereas the Churra is a dairy breed (Anel *et al.* 2005), and was seen to have similar intra-abdominal composition as other dairy breeds (Frutos *et al.*

1997). This means that condition scoring can work for some breeds, where the main fat depot is subcutaneous, but may not be accurate for others. Butler-Hogg (1984) observed the differences between body composition and total fat partitioning between breeds. This study compared two breeds of sheep, the Southdown and Clun, which were both bred for meat. Findings showed that breed had no influence on fat proportion and body composition but there was a substantial difference in actual fat partitioning. Clun was seen to deposit more intra-abdominally compared to Southdowns.

For production animals, these body reserves become increasingly important for reproductive purposes as it also has the potential to affect the progeny of these animals. Mainly, this is due to the mother relying on these reserves to provide for offspring as the peak energy demands may not be met by diet. This happens particularly during later stages of gestation and during lactation, so the negative net energy is made up by the breakdown of fat reserves in the body (Weber *et al.* 2013).

A more efficient sheep with greater fat partitioning ability will have a greater reproductive success, although this may be expressed more in some environments and under some conditions. Partitioning of energy is dependent on food intake and the availability and quality of the nutrition on offer, but will also be affected by the animal's genetic potential to maintain and gain lean and fat tissue.

1.10 Genotypes affecting fat levels and efficiency

Feed efficiency can be influenced by genetic control, with a number of traits that can directly impact efficiency. Production traits and characteristics can also have an indirect effect on composition and hence efficiency. Interrelationships between the major production traits can then further affect efficiency at various stages of life and impact management decisions (Archer *et al.* 2002).

Genetic selection can then be used to alter animal efficiency from selection for broad commonly measured traits. Mrode and Kennedy (1993) concluded that a genetic selection for increased lean growth rate would also lead to a correlated increase in feed efficiency. Hegarty (2004) demonstrated the significant impact that rumen function could have on feed efficiency in sheep, and dairy and beef cattle. Hegarty (2004) also concluded that productivity could be affected by the efficiency of microbial activity as well as changes in the production of volatile fatty acids. Mann *et al.* (1987) observed that the Barbados Blackbelly and its cross with the Dorset breed could prove to be beneficial in environments limiting quality of feed and this was due to the digestive tract kinetics involved such as forage and crude protein digestibility. This is important as the Barbados Blackbelly is known as a hardy breed that has evolved to survive on low quality diets.

Breed can play a significant role due to notable genetic and phenotypic differences. Osoro *et al.* (1999) concluded that a significant breed and environment interaction altered diet selection and overall performance and concluded that, between the Latxa and Gallega breeds, smaller body sizes are more suitable when presented with limited resources. These showed noticeable levels of liveweight gain under different circumstances, with Fitzhugh (1978) concluding that production environment and genotype interactions exist for production efficiency. This further argues for differences between breeds with gene expression noted to be reliant on the interaction between genetic makeup and the environment involved (Cassar-Malek *et al.* 2008). Greeff *et al.* (2003) determined that increased selection for clean fleece weight resulted in decreased muscle traits, decreasing fibre diameter was correlated with higher levels of muscling, and that improving staple strength led to greater fat depots. In contrast Li *et al.* (2008) stated that a trade-off between nutrient deposition and enhanced genetic selection for wool growth was non-existent and that selection for greater wool growth led to greater levels of efficiency for protein and energy use for both tissue and wool growth. Blumer *et al.* (2016)

illustrated that increasing a sire's breeding value for fat reduced the liveweight loss in adult ewes in poor environments.

Some work has also demonstrated genetic variation in efficiency traits such as feed conversion ratio and residual feed intake. Arthur *et al.* (2001) demonstrated that the feed conversion ratio was genetically negatively correlated with average daily gain, while rib fat depth and residual feed intake had a small genotype and phenotype correlation in cattle. These authors concluded that genetic selection can lead to improved intake efficiency. Herd and Bishop (2000) analysed residual feed intake, being the difference between predicted and actual feed intake. They showed that residual feed intake was heritable although low, and demonstrated the lack of correlation between residual feed intake and size and growth rate. This means selection for residual feed intake can lead to reductions in feed intake without altering growth rate or mature size and indicates the potential to use genetic selection to increase production efficiency.

1.11 Adaptation associated with survivability and metabolism

Constant exposure to a set of climatic conditions has been seen leading to adaptation (Hansen 2004), however it takes time for this occur. This can include a change in region, ambient temperature, a change in the type of feed on offer amongst other variables, which can lead to poor performance in animals not accustomed.

The importance of a greater ability to adapt to environmental conditions is that it can potentially affect the productivity and survival of an animal. Due to the effects the environment can have on feed quality and availability, it also has the potential to affect energy storage and reproductive capabilities. Periods of under nutrition that an animal may not be adapted for can place increasing importance on body reserves.

The amount of fat an animal is able to mobilize is important as it may give the animal time to adapt to nutrient deficiency and increase the chance of survival. This is due to the use of lipid stores when energy balance is negative, but may see an increase in net negative energy balance when exposed to an unadapted environment. Metabolic and behavioural regulations affecting both fitness and reproduction are evident, such as reducing unnecessary movement, as trade-offs against milk production, gestational support and homeostasis (Bocquier *et al.* 2000). Reduction of tissue mass leads to lower levels of energy expenditure in the animal (Chilliard *et al.* 1998) and goats are a good example of adaptation to environmental stressors as they can minimise their nutrient requirements, whether food or water. Work by Silanikove (2000) demonstrated that in goats the grazing behaviour, digestive efficiency and ability to suppress their metabolism allows for productivity even in areas of limited nutrient availability. In contrast, a standard diet, such as the suggested feeding standards for Merino sheep, can be detrimental in other breeds. Kilminster and Greeff (2011) showed a decreasing reproductive efficiency in Dorper and Damara ewes when fed to LifetimeWool recommendations. An increased level of fatness was seen with no increase in reproductive rate. Therefore, it is important to determine the correct feeding level for all animals in a farming system in order to maximise productivity.

When a comparison of 6 breeds of English sheep was tested to see any difference between metabolism, feed intake, feed utilization and climate resistance, significant differences were found. The study, by Blaxter *et al.* (1966), compared the Scottish blackface, Hampshire Down, Cheviot, Suffolk Down, Kent and Welsh Mountain breeds. There were some significant differences in liveweight between the breeds, but were mostly similar at a metabolic level. Differences became noticeable when exposed to environmental stressors such as wind or rain, with the Hampshire and Scottish Blackface most resistant (respectively), while the Welsh Mountain had the least resistance to the effects of wind. This indicated different levels of adaptation to environmental stressors, which in turn would lead to different levels of

efficiency in different environments. Scottish and Suffolk breeds have also been shown to express greater maternal care given an ideal environment, which would also impact lamb survival and therefore reproductive efficiency (Dwyer 2008).

Heat stress in hot hotter environments can also severely affect productivity of animals that are not acclimatized, with some breeds being less susceptible to the effects of heat. Paula-Lopez *et al.* (2003) concluded that Holstein and Angus embryos were less resistant to heat shock than Brahman. Paula-Lopez *et al.* (2003) theorized that adaptation to a hotter climate has resulted in genetic selection for cellular heat resistance in the Brahman and Senepol breed. This is supported by the work of Hansen (2004) who concluded that the Zebu breed is superior to *Bos taurus* breeds for thermoregulation during periods of heat stress. This was due to decreased metabolic rates in addition to a greater capacity for heat loss. This also means that diet intake may be impacted as well as the ability to reserve fat, with less energy being focussed on thermoregulation. This means that appropriate breed selection is important for greater productive potential, as well as survival in harsh conditions.

Behaviour was then analysed in conjunction with milk characteristics by Dwyer and Lawrence (2005). When comparing Hill and Lowland breeds at pregnancy and lactation, they discovered that lipid content in Hill ewe's colostrum was higher, as well as having higher thyroid hormone concentrations. These both contribute to thermoregulation and have been hypothesized to be due to an adaptation of more efficient physiological and behavioural practices to promote survival. Temperament may also aid in adaptation and survivability due to adaptation to avoid unnecessary energy output Hammond *et al.* (1996).

1.12 Temperament affecting stress levels

When being handled and moved around, a poor temperament can lead to unnecessary stress, as well as energy exertion due to the chemical and physical stress responses. If this becomes a

constant occurrence, production can be affected. This has led to selection for temperament, as well as developing better techniques to handle animals. There have are studies that have shown that temperament is moderately heritable and breed related, which has been a key reason why some farmers prefer to use certain breeds.

Zambra *et al.* (2015) looked at the direct temperament heritability for each breed, and observed a moderate heritability which was higher for Merino ewes compared to Corriedales. Corriedales were less temperamental than Merinos when being assessed using an isolated box test measuring agitation. Romanov sheep have also been shown to be noticeably more reactive when compared to breeds such as the Ile de France breed (Romeyer and Bouissou 1992), the Arles Merino, as well as a cross with the Arles Merino (Le Neindre *et al.* 1993). When compared to the Ile de France, they were shown not only to be more fearful of human interaction, but to also be more so if they were dam reared, as opposed to being artificially reared (Romeyer and Bouissou 1992). When being compared to the Arles Merino in multiple tests in different surroundings, they were far more reactive with the cross breeds displaying temperaments closer to the Romanov's behaviour indicating a genetic contribution (Le Neindre *et al.* 1993).

Differences in reactivity can also be seen when comparing breeds of other species. Boer goats, when compared with Boer crossbreeds, Xhosa lob-eared and Nguni goats, were the calmest and the others less so respectively (Ndou *et al.* 2010). Breed effects on temperament have also been observed in multiple cattle studies. One study compared Pirenacia and Parda de Montana calves, showing that Pirenaica were far more reactive and experienced higher levels of stress from weaning and handling (Blanco *et al.* 2009). Burrow (2001) showed that flight speed and temperament scores were also moderately heritable in tropical breed composites and suggested a requirement for an adoptable standardized scoring system to better describe variation in this trait. Brahman cross cattle are also said to show higher temperamental scores

than breeds such as the Africander cross, while the Africander in turn exhibits a greater reaction than British breeds (Fordyce *et al.* 1982). Studies of Angus, Hereford and Shorthorn breeds have also been done by Tulloh (1961), showing that Shorthorns were the most difficult to handle. Temperamental behaviour in response to handling was also analysed by Gauly *et al.* (2001). A comparison was made between German Angus and Simmental cattle, using a multitude of measurable parameters that showed Simmentals were significantly more difficult to handle.

It is important to consider that genetic differences as well as previous experiences (Ndou *et al.* 2010) have the potential to influence temperament and affect handling by humans. This can alter whether, for example, going through a squeeze chute leaves an animal having baseline cortisol and relatively calm, or elevated cortisol and an agitated temperament for another (Grandin 1997). This becomes an economical issue as the stressors involved have a negative impact due to harmful effects on reproduction and immune function, as well as the potential to affect growth performance and the carcass traits (Burdick *et al.* 2011).

Experiments by Tulloh (1961) and Gauly *et al.* (2001) have both demonstrated that higher temperament scores and reactivity leads to lower body weights and decreased average daily gains. A further study was performed using Braford, Simmental x Red Angus, Tarentaise x Angus, Red Brangus, Simbrah and Angus breeds to show the effect of temperament on the growth of animals. Across each breed group, higher temperament scores resulted in decreased average daily gains, while quieter and calmer animals (low temperament scores) had higher average daily gains (Voisinet *et al.* 1997). Petherick *et al.* (2009) observed similar results, with calm handling reducing stress levels and poor handling leading to a decrease in average daily gain.

Blache and Bickell (2010) worked with dairy sheep and stressed ewes were more difficult on entry into the milking area and took longer for the milking apparatus to be attached. As well as the reduced labour, calm ewes produced significantly more milk than stressed ewes (462 ± 36 g/day vs 394 ± 33 g/day). Work by Pajor *et al.* (2010) looking at the Tsigai breed, found that lambs of stressed ewes had a decreased preweaning weight and weaning weight, while the lambs of calm ewes were also calmer and had greater levels of fat. Furthermore, cortisol and lactic acid levels showed moderate to high correlation to the temperament scores, which is important as it indicates stress (Stark *et al.* 2006).

Temperament has a substantial influence on productivity and there are demonstrated associations between breed and temperament, and also between temperament and growth and composition.

1.13 Conclusion

Liveweight change and nutritional efficiency are driven by a number of physiological differences including: energetic efficiency of maintenance and liveweight gain, nutrient utilisation and differences in energy deposition, hormone levels, temperament, adaptability and genetics. These pathways have been extensively explored and appear to differ between breeds, but direct breed comparisons for conversion and deposition are uncommon. By understanding differences in whole body composition and efficiency between breeds, we can further develop an understanding of optimum feeding levels to ensure the best level of productivity for farmers.

We therefore hypothesise that at maintenance, maternal type ewes will have a higher proportion of fat tissue than Merino ewes, and during liveweight gain, maternal type ewes will deposit proportionally more energy into fat depots than Merino ewes. The results will guide conclusions regarding the accuracy of the Lifetime Ewe Management program for sheep

enterprises utilising sheep other than Merinos with the option of implementing adjustments for the use of different breeds in the Australian production system. This likely will contribute to the formulation of an optimum condition score profile for maternal ewes, which will differ to those for Merinos which are promoted to the sheep industry via the Lifetime Ewe Management program.

1.14 References

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2. Introduction

Optimising the stocking rate, nutrition and management of breeding ewes is an essential part of productive and economically efficient sheep enterprises (Young *et al.* 2011, 2014, 2016). Economic modelling of responses for ewe and lamb production, to varying levels of nutrition during pregnancy and lactation underpinned the development of ewe management guidelines for Merino ewes and subsequently the Lifetime Ewe Management extension program (Curnow *et al.* 2011; Trompf *et al.* 2011; Young *et al.* 2011). Over the last decade, this small-group extension program has been delivered to more than 3,000 sheep producers with Merino and maternal (non-Merino) ewes. On average, participants have increased stocking rate by 15%, and increased lamb survival and marking rates by an approximate of 11-13%, while decreasing ewe mortality by 30% (Curnow 2016; Thompson, unpublished data). Maternal ewes currently produce roughly 45% of the current Australian lamb supply (MLA 2017), but management guidelines to maximise the profitability of sheep enterprises based on maternal ewes have not yet been developed.

The reproductive performance of maternal ewes has been shown to be greater than Merino ewes when grazed together (Babiszewski and Hocking Edwards 2013; Paganoni *et al.* 2014; Hocking Edwards *in press*). The economic pay-off from improving reproductive performance is also greater in maternal ewes compared to Merino ewes (Young *et al.* 2014). Recent work was attempted to develop management guidelines for non-Merino ewes that would maximise profitability, using formulas based on the Australian Ruminant Feeding Standards. These were unable to predict the observed changes in liveweight, of maternal ewes, both above and below maintenance requirements (Thompson 2017). These formulae, largely developed using Merino sheep, underpin the bio-economic models such as MIDAS which were successfully used to develop the management guidelines for Merino ewes (Young *et al.* 2011). Babiszewski and Hocking Edward (2013) concluded that maternal ewes had a lower feeding requirement than Merino ewes per kg of liveweight. This could contribute to maternal ewes performing better

than Merinos under similar grazing conditions, hence the discrepancies with Australian Ruminant Feeding Standards. Factors leading to these discrepancies might include differences in potential intake, relative intake associated with pasture quality and quantity, efficiency of energy usage for maintenance and liveweight gain, and energy content of liveweight gain.

Breed effects on body composition have been documented (Butler-Hogg 1984; Frutos *et al.* 1997), with studies across species demonstrating links between body composition and the energetic efficiencies of protein versus fat synthesis (Nielson *et al.* 1997; Roux 2013). Ball and Thompson (1995) showed that sheep selected for genetically higher carcass fat had a lower feed intake requirement to maintain liveweight, compared to sheep with less fat. Leptin is an indicator of whole body fatness (Blache *et al.* 2000) and higher leptin levels were associated with decreased daily feed intake and reduced weight loss (Blumer *et al.* 2016). Blumer *et al.* (2016) reported a positive correlation between concentrations of leptin and feed efficiency in adult Merino ewes. Breed differences in body composition may also explain the differences in liveweight gain under *ad libitum* feeding conditions. Blumer *et al.* (2016) introduced the term Residual Liveweight Change which described the variability in liveweight change at similar feed intakes. They found that when adult Merino ewes were fed a low quality diet *ad libitum*, to achieve close to maintenance, there was a difference of 94 g/day between the least and most efficient ewes. The concentrations of leptin showed a positive correlation with Residual Liveweight Change, so fatter sheep gained more weight than predicted from their level of intake. As maternals are speculated likely to be fatter than Merinos, difference in liveweight gain between maternal and Merino ewes at the same level of intake may be reflected by differences in tissue deposition.

We therefore reasoned that sheep with proportionately more fat will require less feed to maintain liveweight regardless of breed. Furthermore, maternal ewes will be proportionately fatter than Merino ewes and will therefore require less feed to maintain liveweight. We also

tested a third hypothesis that maternals will have a greater appetite when on an *ad libitum* diet, resulting in a higher energy intake and leading to higher fat deposition. These differences will explain why maternal ewes in the study reported by Thompson (2017) performed better than predicted by the Australian Ruminant Feeding Standards under grazing.

3. Materials and Methods

The experiment was conducted on the Murdoch University campus (latitude -32.07, longitude 115.84). All animal procedures conducted adhered to the Australian Code for the Care and Use of Animals Used for Scientific Purposes, and under approval from the Animal Ethics Committee of Murdoch University. The permit number was R2691/16.

3.1 *Sheep, experimental design and nutritional treatments*

Thirty dry adult ewes were randomly selected from a traditional Merino line (breach strike resistant flock, Katanning WA) and thirty from a maternal composite line (Greeline breed (NZ), Glenridge Park, Mount Barker WA), The ewes were transported from their farms of origin and maintained in the university feedlot for 10 days prior to commencement of the experiment. They were fed *ad libitum* hay and slowly introduced to a pelleted diet (Morgan's, 10.5 MJ ME/kg, 14.5% crude protein per kg dry matter). All ewes were drenched with Cydectin on entry to the shed.

Ewes were weighed and condition scored at the end of the 10-day acclimatisation period and 20 ewes with similar liveweights were selected within each breed. These were housed in separate raised pens (0.87m X 1.45m) in an animal house for 49 days. Ewes were randomly assigned a pen number and diet (maintenance or *ad libitum*), so that each treatment block (breed X diet) contained 10 ewes. The ewes spent 7 days acclimatising on a maintenance diet, estimated for individual ewes by liveweight based on the Australian Ruminant Feeding Standards (6.7 MJ ME for a 50 kg dry ewe in confinement), before nutritional treatments were

imposed for a 42-day period. The maintenance group were initially fed at the recommended levels for maintenance, which was adjusted three times weekly following weighing, to achieve individual liveweight maintenance. The *ad libitum* group was fed based on a rolling five-day maximum intake, so that 120% of the highest intake over the previous five days was supplied to ensure the ewes were provided with feed in excess of their consumption. Animals were fed and the pens were cleaned each day at the same time.

3.2 *Animal measurements and body composition*

Ewes were weighed three times per week and condition scored once weekly. The efficiency of energy deposition, through changing fat tissue change, was tested by the quantification of feed intake, liveweight and the measurement of whole body fatness using a computerised axial tomography (CAT) scan. These scans are also used to identify correlations between subcutaneous (carcass) and internal fat depots, as well as deposition differences between two breeds. CAT scans took place in the Murdoch Animal Hospital, with preparation and recovery from anaesthesia taking place within the barn. Anaesthetic drugs used included Diazepam and Propofol, with appropriate dosages given by anaesthetists. This occurred following the first week of acclimatisation in the animal house, with the ewes scanned in a randomized order across a week. Ewes were fasted overnight and then moved to the barn (approx. 500m) by trailer first thing in the morning. Ewes were returned to their pens approximately one hour after the final ewe of the group had recovered (standing, moving and responsive). At the end of the trial, the ewes were again CT scanned in the same order.

Ewes were scanned using a Siemens 16 slice SOMATOM Emotion Scanner, with exposure factors at 130kV 180mAs. A 16x1.2mm detector array and a 1.5mm reconstructed slice thickness was used to perform helical scans at a slice thickness of 0.75mm through the ewes. Scanning was rostral-caudal at a pitch of 0.8 and the scan field was set to include all relevant anatomy (Figure 1). Siemens 'syngo' CT Workplace software was used to construct images in

the transverse plane, using a soft tissue algorithm and B50s standard reconstruction kernel.

These transverse images were then used for analysis.

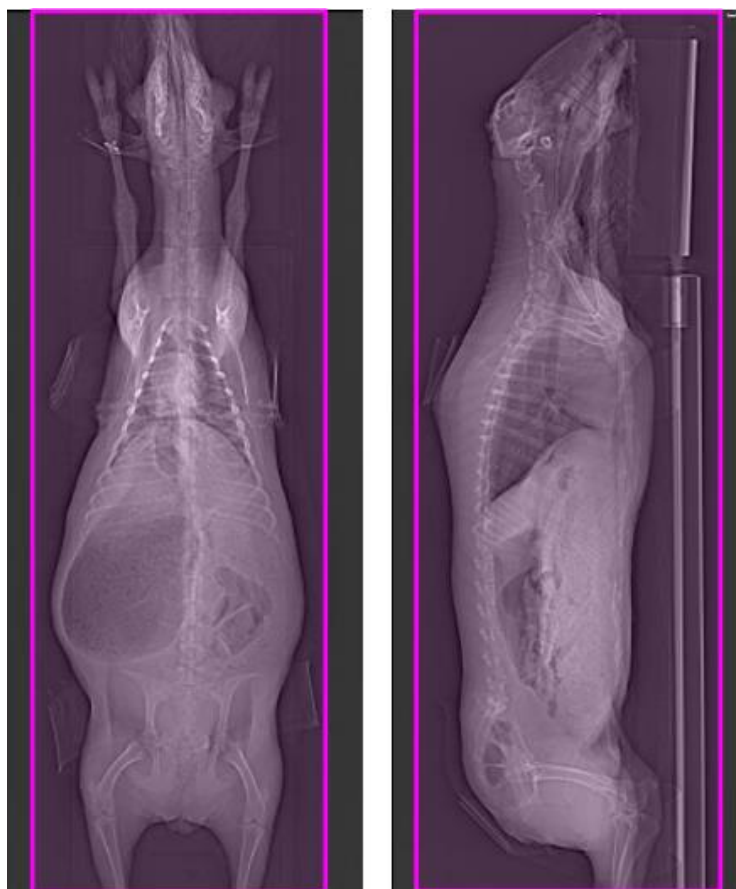


Figure 1: Topograms displaying the acquired scan field to include all relevant anatomy

Analysis of the CAT scan data was based on 7 scans per ewe (Figure 2) which has been proven to be an acceptable representation of the entire set of scans (Chowdhury *et al.* 1994).

Anatomical waypoints were used when selecting specific sites as representations of whole body fat depots, to ensure slices were accurate and comparable between individual sheep.

Skeletal points such as joints (slide 1,7), and rib or spine numbers were used (slide 1,3,4,6), as well as organ structures (slide 2,5). The slides represent specifically the sternal, epicardial, mesenteric, omental, pelvic and mammary fat depots as well as demonstrating the divide between carcass and internal fat depots.

For each of these CT slices, ImageJ was used to remove artefacts (CT cradle, supporting equipment) and demarcate the carcass and internal tissues by the same operator. For slides 1-3 the ribs were used to segment the cross section into internal and carcass partitions. For slides 4-6 the psoas major and the psoas minor muscles were included as carcass tissues, then the perineal line was followed to segment the internal tissues from the carcass. This ensured that the obliquus abdominus internus, the obliquus externus and the rectus abdominus were also included in the carcass tissue. For the 7th slide a line was drawn from the spinous process to the visible dorsal point of the ilium and then from the ventral process of the acetabulum down between the quadriceps femoris and adductor muscles.

Each slide was saved as two text files (whole body [1] and carcass only [2]), which saved each pixel as a Hounsfield unit value. Files were then exported to excel (Microsoft Office) for categorisation of pixels based on Hounsfield units. Pixels were classified as air, gas and lungs (-1001 to -191 HU), fat tissue (-190 to -30 HU), soft tissue (including muscle and organs; -29 to +151 HU), or hard tissue (skeletal; +152 to +2500 HU). Each image is 512 x 512 pixels and each pixel is 0.94mm². Pixels classified as fat or soft tissue were then converted to cm² for each slide.

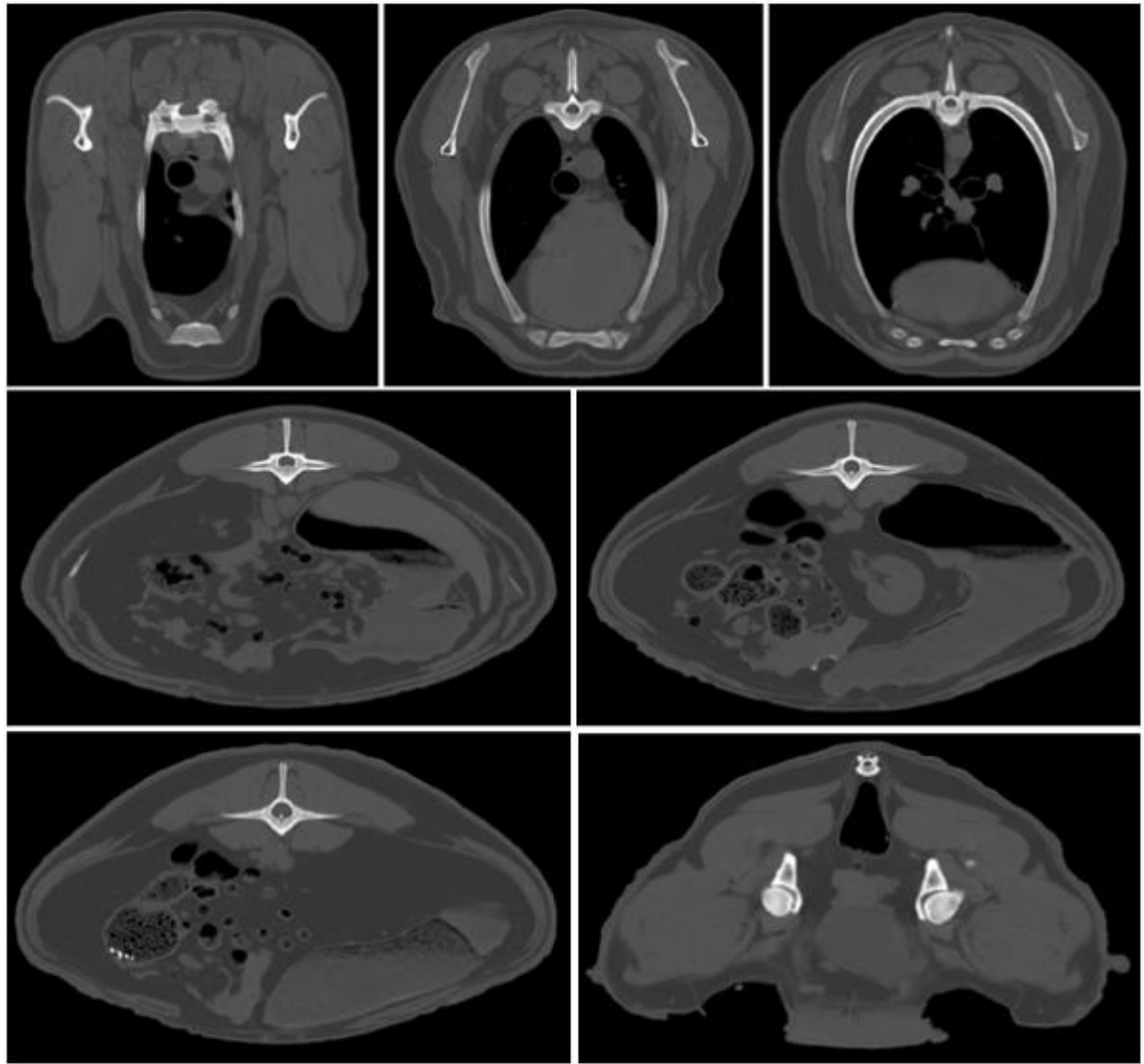


Figure 2: The 7 scans used to represent the entirety of the ewe. Specifically, these represent (left to right, top to bottom) sternal fat pad, epicardial, epicardial and omental, lesser omental, greater omental and perirenal, greater omental, perirenal and urogenital, and urogenital, as well as each displaying intermuscular fat.

3.3 Statistical analysis

The proc mixed procedure in SAS (SAS Institute 2002) was used to estimate ANOVA differences between the treatment groups for tissue area within the CT slides at the start. Groups included breed (Merino, Greeline), slide (1-7) and partition (carcass, internal), while all first level interactions were considered. Groups and interactions showing non-significance ($P>0.05$) were removed in a step-wise fashion. Changes in CT tissue area, between first and second scans, was analysed as the dependent variable, while independent variables were treatment effects

(breed, slide, partition, diet). First level interactions were included and removed if non-significant ($P>0.05$). One ewe had data removed from CT analysis due to complications during anaesthesia at the first scan.

Residual feed intake (RFI) values were generated within diet, to examine the relationship between efficiency and composition. These values represent the variance (error) not explained by liveweight and liveweight change. RFI also describes how an individual differs from the cohort mean, with a negative value indicating a less than expected consumption by said individual. This means it's more efficient. The residual was then analysed as the dependent variable in a general linear model that included breed as a fixed effect, and included (in separate models) starting fat tissue area and starting soft tissue area as covariates. EWE ID was included as a random term to account for repeated measures. First level interactions with breed were included and terms were removed in a stepwise fashion if non-significant ($P>0.05$).

Correlations between covariates tested, liveweight, condition score, as well as the partitions for fat tissue were tested using the MANOVA procedure in SAS (SAS Institute 2002) to generate Pearson correlation coefficients. Fixed effects included in this MANOVA model were the treatment effects; breed and diet.

4. Results

4.1 Initial body composition

Initial modelling included the treatments (breed and diet), as well as slide (1-7) and tissue partition (internal and carcass) as fixed effects. There was no interaction between slide and treatments or slide and partition area, so slide 1-7 were condensed into a single average slide for all comparative models.

At the beginning of the trial, Greeline ewes had significantly ($P < 0.05$) more fat tissue than Merinos and significantly ($P < 0.05$) more fat, on average, was carried internally than in the carcass (Table 2). Breed had no significant ($P > 0.05$) effect on the area of soft tissue (including muscle and organ structures), but there was significantly ($P < 0.05$) more tissue carried in the carcass than internally (Table 2).

Table 2: The average fat and soft tissue deposition for Greeline and Merino ewes, and distribution between carcass and internal depots, at the beginning of the 42-day feeding period.

	Breed			Partition		
	Greeline	Merino	P-value	Carcass	Internal	P-value
Fat tissue (cm ²)	116.3	100.3	0.0305	104.9	111.7	0.0255
Std error	5.0	5.1		3.8	3.8	
Soft tissue (cm ²)	154.8	146.7	0.2205	178.8	122.7	<0.0001
Std error	4.5	4.7		3.8	3.8	

The partitioning by breed interaction was significant ($P < 0.05$) for starting fat tissue area (Figure 3). Greeline ewes carried their fat evenly between internal and carcass stores, whereas Merino ewes partitioned fat preferentially to the internal deposits, compared to carcass deposits. The breed and partition interaction was also significant ($P < 0.05$) for soft tissue area (Figure 4). Merino ewes partitioned soft tissue preferentially towards the carcass, compared to internal areas. This partition difference was greater in Greeline ewes, also storing more in the carcass than internally.

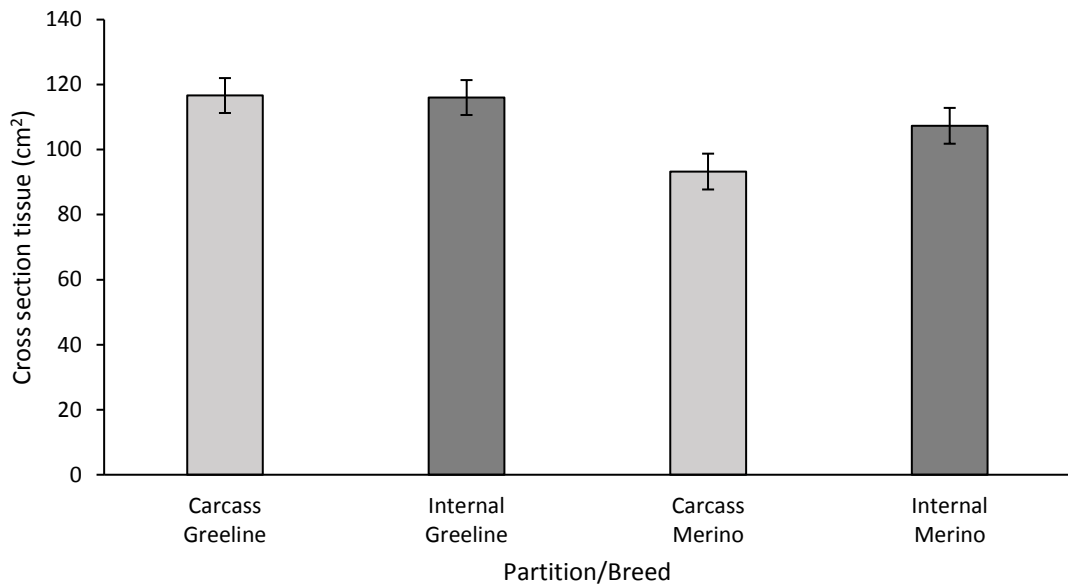


Figure 3: Breed and partition interaction for fat tissue deposition for Merino and maternal ewes, and the distribution between carcass and internal depots, at the beginning of the 42-day feeding period.

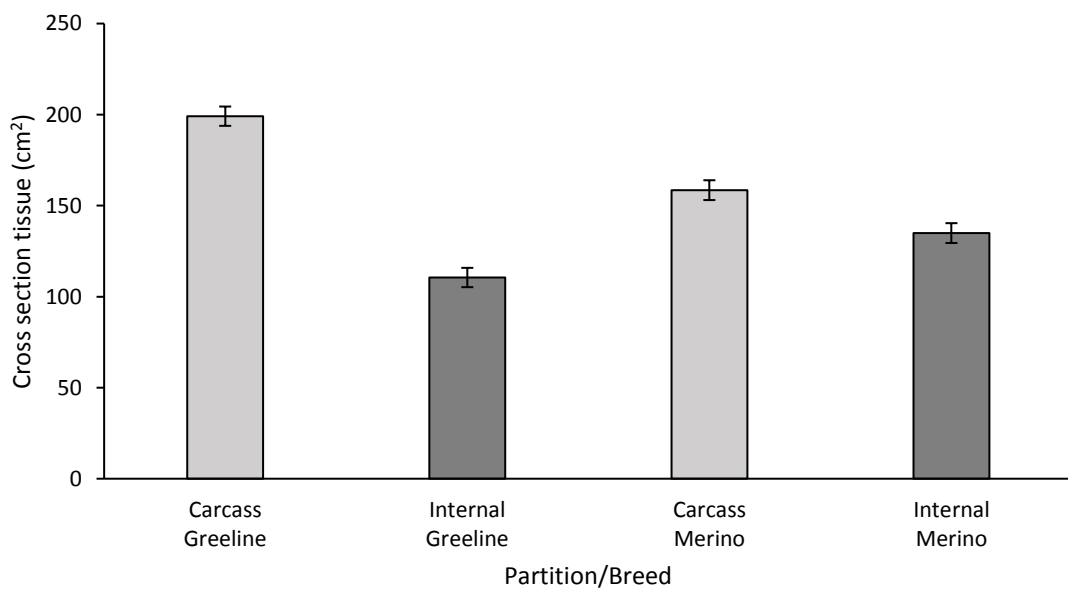


Figure 4: Breed and partition interaction for soft tissue deposition for Merino and maternal ewes, and the distribution between carcass and internal depots, at the beginning of the 42-day feeding period.

4.2 Changes in deposition of tissue

Change in fat tissue area over the 42-day treatment period was significantly associated with breed ($P<0.05$) and diet ($P<0.05$). The area of fat tissue increased by 23.1 cm^2 for Merino ewes compared to 8.8 cm^2 for Greeline ewes. Ewes consuming the *ad libitum* diet gained more fat in comparison to ewes consuming the maintenance diet (29.8 cm^2 v 2.1 cm^2 ; $P<0.05$).

On average, the area of soft tissue carried internally was reduced by 8.2 cm^2 over the 42-day period while carcass soft tissue area increased by 1.8 cm^2 . However, there was also a significant breed by partition interaction ($P<0.05$). Greeline ewes had a reduced soft tissue area in both carcass and internal partitions, while Merinos gained soft tissue area in the carcass partition and had a reduction of soft tissue in the internal partition (Figure 5).

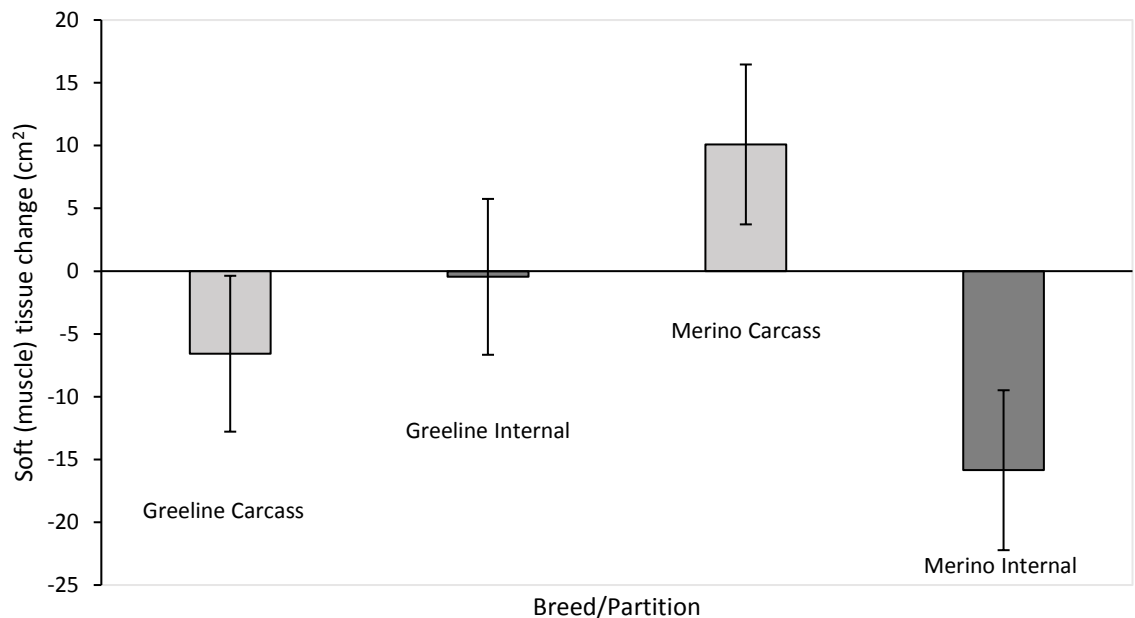


Figure 5: Breed and partition interaction for soft tissue deposition change for Merino and maternal ewes, and the distribution between carcass and internal depots, at the end of the 42-day feeding period.

4.3 The effect of tissue on residual feed intake

When residual feed intake was analysed as a dependent variable, there was a significant positive association with soft tissue area so that ewes with a larger area of soft tissue had a

higher RFI and were less efficient than the cohort ($P < 0.05$; Figure 6). Metabolizable energy intake was increased above the average by 0.06 MJ/day for every 10 cm² increase in soft tissue area. There was also a trend towards association with fat tissue area ($P = 0.08$) so that ewes with a larger area of fat tissue has lower RFI (more efficient) than ewes with a smaller area of fat tissue (Figure 7). ME intake was reduced by 0.26 MJ/day for every 10 cm² increase in fat tissue area.

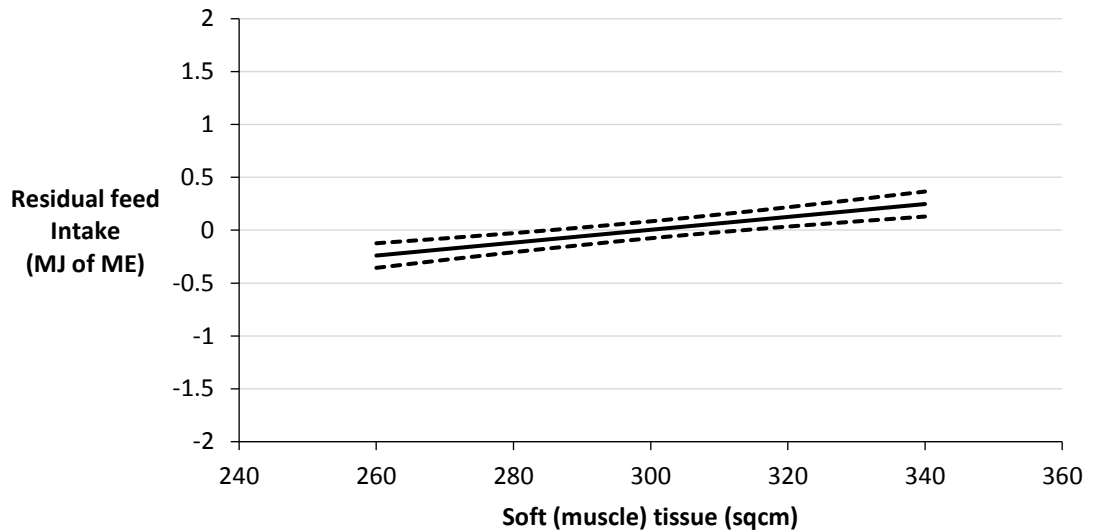


Figure 6: The interaction of soft tissue area with residual feed intake, based on a maintenance diet throughout the course of the 42-day trial with 10 maternal and 10 Merino ewes.

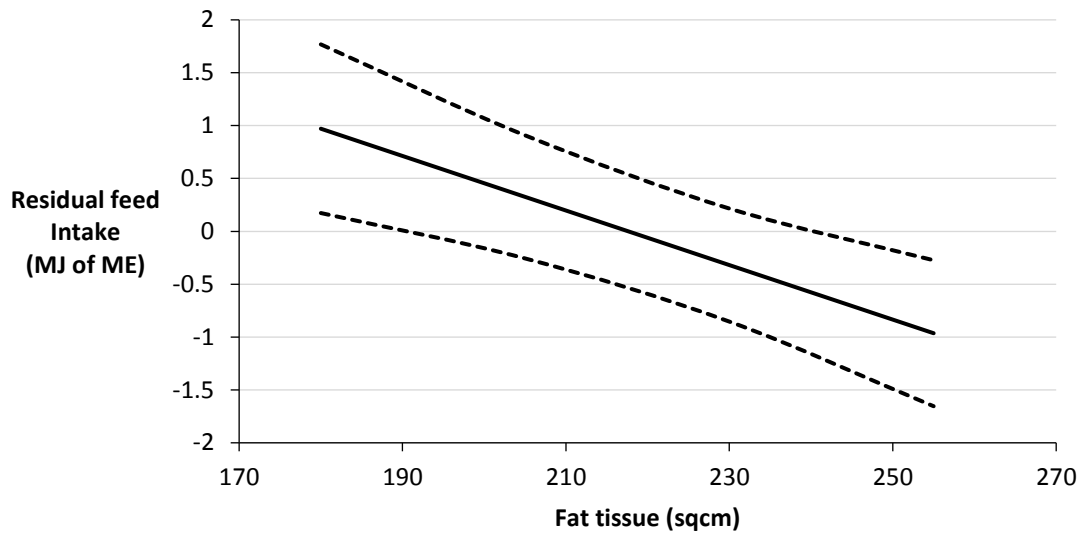


Figure 7: The interaction of fat tissue area with residual feed intake, for ewes on an *ad libitum* diet throughout the course of the 42-day trial with 10 maternal and 10 Merino ewes.

4.4 Pearson correlation of covariates

The Pearson correlation coefficients from the MANOVA procedure are shown in Table 3. Fat tissue area at the start was moderately correlated ($P < 0.01$) with condition score and strongly correlated ($P < 0.001$) with the individual fat partitions (carcass and internal), but was not significantly ($P > 0.05$) associated with liveweight. Internal fat area was significantly ($P < 0.001$) and highly correlated with carcass fat area. Condition score had a significant ($P < 0.05$) moderate correlation with the internal fat partition and a significant ($P < 0.001$) high correlation with the carcass fat partition, but was not significantly ($P > 0.05$) associated with liveweight. Liveweight and soft tissue area were not significantly ($P > 0.05$) correlated with any of the other included variables (Table 3).

Table 3: A Pearson Correlation coefficient table showing the correlation between covariates and significance of these factors involved.

DF = 36	Fat (cmsq)	Condition score	Fasting liveweight	Soft tissue (cmsq)	Internal fat	Carcass fat
Fat (cmsq)		0.495842 **	0.121677	0.012525	0.915112 ***	0.941593 ***
Condition score			0.22354	-0.232525	0.350819 *	0.55285 ***
Fasting liveweight				0.086973	0.102575	0.121897
Soft tissue (cmsq)					0.001442	0.020162
Internal fat						0.725884 ***
Carcass fat						

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

5. Discussion

The initial hypothesis that proportionately fatter ewes will require less energy intake to maintain liveweight was partially supported, as ME intake for maintenance tended to decline by 0.26 MJ/da for every 10 cm² increase in fat tissue. By contrast, ME intake for maintenance increased by 0.06 MJ/day for every 10 cm² increase in soft tissue. Leaner sheep had a higher ME requirement than fatter sheep at the same liveweight, which is consistent with lean tissue having a higher metabolic requirement to maintain and synthesize than fat tissue (Ratnayake *et al.* 1974). These responses of RFI to tissue area are consistent with numerous studies on composition causing variation with residual feed intake, that saw fatter ewes having a reduced intake but losing less weight (Blumer *et al.* 2016; Knott *et al.* 2006; Ball and Thompson 1995). This means that genetically fatter ewes were more efficient, for ME intake to maintain liveweight. This would lead to cheaper management through periods of energy deficits, as they would require less supplementary feed. A Pearson correlation test (table 6) further showed that soft tissue and fat tissue had no significant correlation with each other. This meant that fat ewes could also have a high level of soft tissue or not.

Maternal ewes had significantly higher proportions of fat than Merinos. Many studies have also shown differences in fat between breeds (Donald *et al.* 1970; McClelland and Russel 1972; Wood *et al.* 1980). While there was a significant breed difference for fat composition, the relationship between RFI and fat was insignificant. There were also no significant differences in RFI between maternal and Merino ewes. Furthermore, while soft tissue interaction was significant with RFI, breed and soft tissue was not significantly different. However, while the fat tissue relationship was not significant, it has been proven to cause variance with RFI (Blumer *et al.* 2016; Knott *et al.* 2006). When looking at the data from the significant ($P < 0.05$) interaction between breed and partition for fat (figure 3), we can see a difference of 32.18 for total fat tissue area. According to the relationship between RFI and fat tissue area (figure 7), this equates to a reduced ME intake of 0.837 MJ/day for Greelines based on fat area. This would indicate that the Greelines were more efficient, in terms of maintaining weight, and that breed may have an indirect effect on RFI. While this would answer that the proportionately fatter Greelines would require a lower intake of MJ/day to maintain liveweight, it cannot be concluded. The insignificance of some relationships involved suggests that there may be other factors involved to explain the differences in performance between maternal and Merino ewes.

Partitioning was significant for fat tissue deposition as well as for soft tissue deposition. It was noted that there was slightly more fat tissue internally than in the carcass, but the difference between soft tissue was much higher, with 178.82 cm² in the carcass and 122.72 cm² internally. This is expected, with ewes often having more muscle than fat in the body.

Interaction of both partition and breed was not performed on the same model for soft tissue (Figure 4) and fat tissue (Figure 3), but partition areas and the compositions can be made note of. The Greeline internal section was 41.8% of body tissue with 48.8% soft tissue and 51.2% fat tissue. The carcass area was 58.2% of body tissue, with 63.1% soft tissue and 36.9% fat tissue. The Merino internal section was 49% of body tissue, with 55.7% soft tissue and 44.3% fat

tissue. The Merinos carcass area was 51% body tissue, with 63% soft tissue and 37% fat tissue. Greelines had a higher difference in overall tissue deposition between internal and carcass regions, compared to Merinos being relatively even. Merinos and Greelines had the same proportions of fat and muscle tissue in their carcass area. Merinos had a higher difference in tissue proportions in the internal regions, compared to the relatively even split for Greelines. Furthermore, overall composition and partitioning of tissues can be mentioned. Greelines consisted of 42.9% fat tissue, with 50.1% partitioned in the carcass area and 49.9% being internal. Soft tissue was 57.1% of overall tissue, with 64.3% partitioned in the carcass and 35.7% internally. Merinos consisted of 40.6% fat tissue, with 46.5% partitioned in the carcass and 53.5% being internal. Soft tissue was 59.4% of overall tissue, with 54% partitioned in the carcass and 46% in internal areas. Merinos, while having less composition percentage of fat than Greelines, partitioned tissue relatively evenly throughout their bodies. While Greelines had an equal representation of fat between the internal and carcass areas, more soft tissue was deposited in the carcass.

This raises issues for condition scoring, based on a Merino standard, centred on guidelines involved with the Lifetime Ewe Management program. Correlations shown by the Pearson coefficients indicated fat area significantly impacted condition score but an insignificance between soft tissue area and condition score, regardless of breed (Table 3). However, it has been well documented that condition score is best predicted from both fat and muscle (van Burgel *et al.* 2011). This means that the higher proportion of tissue in the carcass area for Greelines will impact the condition score accuracy when compared to Merino scores. Greeline condition scores would not be able to reflect internal partitioning as well, due to the disproportionate partitioning of soft tissue in the carcass. However, sub-cutaneous fat measurement would have a greater representative accuracy for internal fat in Greelines compared to Merinos. This aligns with studies indicating that condition scoring is a poor representation of whole body fatness and overall composition due to its focus on the

subcutaneous fat depot (Treacher and Filo 1995; Wright and Russel 1984). Furthermore, rate of deposition (McClelland and Russel 1972) and reproductive state (Castrillo *et al.* 1988) further suggest condition score inaccuracies, between breeds, due to internal composition changes.

The third hypothesis, was disproven as there was no breed impact on diet whatsoever, whether *ad libitum* or even maintenance was fed. This also ruled out potential intake (PI), relative intake quality (RIqI) or relative intake quantity (RIqN) as factors affecting intake. This means that maternals and Merinos do not have differing genotypes for PI, RIqI or RIqN, so abundance of feed as well as digestibility did not impact the experiment. Diet did effect fat tissue deposition, due to a higher energy intake by the *ad lib* group. This saw a difference of 27.73 cm² between the ad lib and maintenance groups, which is expected due to the intake of more energy than exerted resulting in weight gain (Swinburn *et al.* 2004). There was no significance seen for soft tissue change.

Fat deposition change was affected by breed as Merinos gained more than Greelines. However, there was no significant affect with partition or a breed and partition relationship. This meant that any fat gained was spread consistently between partitions, regardless of breed and tissue change. Soft tissue change had no breed significance but a significant difference between partitioning, and breed by partition. The Merino carcass' soft tissue change had a difference between partitions of 25.945 cm² and a net loss of 5.76 cm². This was less than the total loss of Greeline ewes, which had difference of 6.122 cm² between partitions and a net loss of 7.03 cm². A further potential to affect condition score was seen due to the uneven distribution of soft tissue. This is also unexpected as there was initially more soft tissue distributed in the internal regions for Merinos (figure 4), however it raises speculation of the body attempting to adjust to the environment. This is more peculiar as the net soft tissue loss

would be likely due to inactivity in pens, therefore partitioning more soft tissue to carcass regions of the body is surprising.

6. Conclusion

Feed intake was affected by body composition, with fatter ewes being more efficient than leaner ewes. Furthermore, breed wasn't a significant effector on RFI, the maternal breed was naturally fatter and showed signs of greater levels of efficiency because of this fatness, but more factors have to be considered to conclude its performances. Appetite was completely unaffected by breed, so when presented with an *ad libitum* intake there was no difference between maternals and Merinos.

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8. Appendices

8.1 Appendix 1

Example of a feed sheet used, showing pen allocations and distribution of diet (shaded-*ad lib*)

31/03/2017

PEN	BIN WT	PELLETS IN
1		0.85
2		0.85
3		0.90
4		0.90
5		2.00
6		3.45
7		0.55
8		1.80
9		0.85
10		3.05
11		0.70
12		1.90
13		0.80
14		0.65
15		0.70
16		2.70
17		0.85
18		2.35
19		2.50
20		0.60

PEN	BIN WT	PELLETS IN
21		2.60
22		1.95
23		1.20
24		1.90
25		0.55
26		2.55
27		2.30
28		0.75
29		1.00
30		1.40
31		0.90
32		0.65
33		2.50
34		1.95
35		0.75
36		2.80
37		3.00
38		0.55
39		0.60
40		1.60

Feed as per sheet - *ad lib*
ewes are automatically
adjusted from a 3 day max.