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Sire carcass breeding values affect body composition in lambs - 1. Effects on lean weight and its distribution within the carcass as measured by computed tomography.

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Abstract

Data are obtained from computed tomography scanning of 1665 lambs at locations around Australia. Lambs were progeny of Terminal, Maternal and Merino sires with known Australian Sheep Breeding Values for post weaning c-site eye muscle depth (mm; PEMD) and fat depth (mm; PFAT), and post weaning weight (kg; PWWT). Across the 7.8 unit range of sire PEMD, carcass lean weight increased by 7.7%. This lean was distributed to the saddle section (mid-section) where lean became 3.8% heavier, with fore section lean becoming 3.5% lighter. Reducing sire PFAT across its 5.1 unit range increased carcass lean weight by 9.5%, and distributed lean to the saddle section which was 3.7% heavier. Increasing sire PWWT increased lean at some sites in some years, and on average increased saddle lean by 4% across the 24.7 unit PWWT range. Changes in lean weight and distribution due to selection for carcass breeding values will increase carcass value, particularly through increased weight of high value loin cuts.

Keywords: lamb, lean, muscling, breeding values, computed tomography

1. Introduction

The financial value of a carcass is influenced by its lean meat yield percentage, which represents the proportion of the carcass that is lean meat (muscle). Consumer preferences in domestic and international markets drive the industry to produce meat cuts that are larger and leaner (Banks, 2002; Hall, Kelf, Fogarty, & Murray, 2000; Laville, Bouix, Sayd, & Bibé, 2004). To achieve this goal, Australian lamb producers currently select for lean meat yield percentage indirectly via three existing Australian Sheep Breeding Values (ASBVs) for post-weaning weight (PWWT), c-site fat depth (PFAT) and eye muscle depth (PEMD), which are used to select for improved growth, leanness and muscling respectively. The effects of selection using these ASBVs have previously been investigated using indicators like muscle depths (Hopkins, Stanley, Martin, Ponnampalam, & van de Ven, 2007), and weights of specific cuts (Gardner et al., 2010), however have not been quantified in terms of the change in whole carcass lean composition or distribution of lean tissues carcass regions.

Whilst there is evidence that a strong emphasis on PWWT ASBV will increase growth rate and mature size (Huisman & Brown, 2008), there is little data showing the effects of this ASBV on carcass composition. It has been shown that lambs growing at a faster rate are proportionately leaner when compared at the same weight, largely due to a correlated increase in mature weight (Bennett, Kirton, Johnson, & Carter, 1991; Butterfield, 1988). However, Hegarty et al. (2006) showed that the genetic potential for growth (or increased PWWT) did not impact significantly on the proportion of lean in the carcass. Likewise, Gardner et al. (2010) showed no effect of PWWT on carcass composition as assessed by computed tomography (CT), in spite of the increased live weight and hot carcass weight (HCWT) at slaughter.

Numerous studies have shown that selection for increased sire PEMD impacts on muscle depth at its site of measurement, the c-site (Hall, Gilmour, Fogarty, & Holst, 2002; Hegarty, Hopkins, et al., 2006). Likewise, Gardner et al (2010) also demonstrated an increased weight of the *M. longissimus lumborum* in response to increasing PEMD, although in this case there was little impact on other muscle weights or the percentage of lean in the carcass. Alternatively, Hegarty et al. (2006) showed that lambs selected for increased PEMD increased the mass and dimensions of the loin muscle and had a small increase in four different hind limb muscles, suggesting a carcass wide effect. However the latter study only utilised nine sires compared to 93 sires used in the Gardner et al. (2010) study. Hence we can expect that increasing sire PEMD will increase the proportion of carcass lean, with this effect predominantly focused in the saddle region.

Decreasing sire PFAT ASBV has been shown to increase eye muscle depth at the c-site (Nsoso, Young, & Beatson, 2004). Gardner et al. (2010) showed that progeny of sires with low PFAT had increased weight and dimensions of muscles within the saddle (loin weight and eye muscle area) and hind (round) sections of the carcass, indicating a more widespread impact of PFAT on muscle. However in this case there was no increase in the proportion of carcass lean.

Lastly, sire type has also been shown to impact on carcass lean tissue (Ponnampalam, Hopkins, Butler, Dunshea, & Warner, 2007). When compared at the same age, Merino sired lambs had lower values for loin weight, eye muscle area and depth compared to Maternal (Border Leicester) and Terminal (Poll Dorset) sired lambs. Compared at the same weight, the Terminal sired lambs had a greater proportion of carcass lean than Maternal sired and pure Merino lambs (Ponnampalam et al., 2008). Other studies highlight the Poll Dorset and Texel

cross lambs as having a higher muscle to bone ratio than Maternal (Border Leicester) or Merino sired lambs (Atkins & Thompson, 1979; Hopkins & Fogarty, 1998). On this basis it is expected that the amount of carcass lean will be higher in Terminal sired lambs when compared at the same weight.

This paper describes the association of factors such as site (research station), birth year, sex, birth type (litter size), rearing type, dam breed, and sire type on CT lean, plus the impact of genetic selection using PWWT, PFAT and PEMD ASBVs. Preliminary results of parts of this experiment have been previously published (Anderson, Williams, Pannier, Pethick, & Gardner, 2013). We hypothesised that when lambs are compared at the same carcass weight, decreasing sire PFAT will increase the weight of carcass lean, whereas increasing sire PWWT will have no effect on the weight of carcass lean. In addition we expect that increasing sire PEMD will increase the weight of lean in the saddle region but have no impact on the proportion of lean in the whole carcass. We also hypothesised that the Terminal sired lambs will have a greater proportion of carcass lean than the Maternal and Merino sired lambs.

2. Material and methods

2.1. Experimental design and slaughter details

The Australian Cooperative Research Centre (CRC) for Sheep Industry Innovation established an Information Nucleus Flock (INF) in 2007, with details of the design of the flock presented by Fogarty et al. (2007). Some of the objectives were to measure a diverse range of phenotypic traits, including CT lean and to assess the impact of genetic selection on these traits. From 2007 to 2010, approximately 6000 lambs were born and raised at one of six research sites across Australia (Katanning WA, Kirby NSW, Stuan SA, Turretfield SA, Hamilton Vic. and Rutherglen Vic), with these sites representing a broad cross-section of the

sheep producing regions of Australia. These lambs were produced from Merino or Border-Leicester x Merino dams which were artificially inseminated using semen from 100 sires per year, representing the major sheep breeds used in the Australian sheep industry. Individual sires were chosen as they were representative of a full range of ASBVs for key traits within each sire type. The sire types included Terminal sires (Hampshire Down, Ile De France, Poll Dorset, Southdown, Suffolk, Texel, White Suffolk), Maternal sires (Bond, Booroola Leicester, Border Leicester, Coopworth, Corriedale, Dohne Merino, East Friesian, Prime South African Meat Merino (Prime SAAM), White Dorper), and Merino sires (Merino, Poll Merino). Within each site, the aim of selection of lambs for CT was to include at least two progeny from each sire used at the site, selected across a live weight strata. Lambs were grazed under extensive pasture conditions and supplemented with grain, hay or pellets when pasture was limited which varied between sites (Ponnampalam et al., 2014).

2.2. *Slaughter protocol*

Within each year, at each of the six research stations, lambs were divided into groups based on live weights, with each group killed separately (kill groups) at a target carcass weight of 23 kg, with a total of 1665 lambs slaughtered. Lambs within kill groups were on average within 5 days of age of each other and within a year there was an attempt to represent all sire types in each kill group. Across the 9 site-year combinations in this experiment there was a total of 25 kill groups, with the average age within a slaughter groups ranging from 168 to 420 days of age and the number of lambs within each kill group ranging from 20 to 99 lambs (Table 1).

(insert table 1 near here)

At all INF sites, lambs were yarded within 48 hours before slaughter, maintained off-feed for at least 6 hours, and then weighed to determine pre-slaughter live weight. They were then transported for 0.5-6 hours via truck to one of 5 commercial abattoirs, held in lairage at the abattoir for between 1 and 12 hours, and then slaughtered.

All carcasses were electrically stimulated and trimmed according to AUSMEAT standards (Anonymous, 2005) and HCWT was then measured within 40 minutes of slaughter. All lambs were measured and sampled for a wide range of carcass, meat and growth traits.

2.3. *Computed tomography scanning*

Carcasses were transported for CT scanning to either Murdoch University (Picker PQ 5000 spiral CT scanner) or the University of New England (Picker, Bavaria, Germany) within 72 hours of slaughter to determine the proportions of fat, lean and bone. Prior to scanning the carcasses were split into three primal components to enable more rapid post scanning processing of the CT images for the distribution analysis: fore-section, saddle and hind section. The fore section was separated from the saddle by a cut between the fourth and fifth ribs. The hind section was separated from the saddle by a cut through the mid-length of the sixth lumbar vertebrae. In both cases the spiral abdomen protocol was selected with settings: pilot scan length of 512 mm, field of view set at 480mm, Index 20, kV 110, mA 150, revs 40, pitch 1.5 and standard algorithm. At Murdoch University, the carcasses were scanned in 10 mm slice widths, with each slice taken 10 mm apart. The University of New England used similar settings with some differences: field of view set at 450 mm, kV 130, mA 100, 5 mm slice width and distance between images of 15 mm.

The images produced from the CT scan were edited to remove non-carcass image artefacts and were partitioned into bone, muscle and fat components (Image J version 1.37v, National Institutes of Health, Bethesda, MD, USA, used in conjunction with Microsoft Excel). The discrimination point to identify the Hounsfield barriers for associating pixels with fat, muscle and bone were -235 to 2.3 for fat, 2.4 to 164.3 for lean and >164.3 for bone. An estimate of volume using Cavalieri's method (Gundersen & Jensen, 1987; Gundersen, Bendtsen, Korbo, Marcussen, & Møller, 1988) was calculated as follows:

$$\text{Volume}_{\text{Cav}} = \frac{m}{g-1} \left(d \times \sum_{g=1}^m \text{area}_g - t \times \text{area}_{\text{max}} \right)$$

in which m is the number of CT scans taken and d is the distance between cross-sectional CT scans, in this case 10 mm. The value of t is the thickness of each slice (g), in this example 10 mm, and area_{max} is the maximum area of any of the m scans.

The average of the Hounsfield units of the pixels of each component was then determined and converted into density (kg/L) using a linear transformation (Mull, 1984). This was then used along with the volume of each component to determine the weight of fat, lean and bone, which was then expressed as a percentage of total carcass weight at the time of scanning. Given the density of the marrow tissue, it is classified as either fat or lean using the boundary discrimination method described above. Additional editing within Image J enabled the isolation of the marrow component of bone within all images. Thus the above procedures could be repeated on the 'marrow only' images. This enabled back correction for these pixels, reallocating them as bone and removing their associated volumes from the lean and fat components of the first iteration of image analysis. Thus using the CT scans it is possible to determine the percentage of fat, lean and bone within each carcass.

2.4. Data used

CT scanning data from a total of 1665 animals from the 9 site-year combinations was available for analysis of lean composition within the carcass (Table 1). The 111 animals from Katanning in 2007 were not scanned in sections, therefore when analysing distribution of lean between carcass sections, 1554 lambs were included in the analysis. The mean carcass weight of the slaughtered lambs was 23.3kg. The mean, maximum and minimum weights of the fat, lean and bone for each of the sections is reported in Table 2.

(insert table 2 and 3 near here)

Of the 85 Maternal, 119 Merino and 155 Terminal sires, 70, 109 and 154 had ASBV values for PWWT, PEMD, and PFAT available (Table 3). The breeding values for PEMD and PFAT are based upon live ultrasound measurements at the c-site (12th ribs 45 mm from the midline), and PWWT is based upon live weight, all measured at the post weaning time point (about 240 days of age). The sires used were representative of a range of the ASBVs used for selection for lean meat yield. A percentage of sires selected in a year were used in the subsequent year to provide linkage between years. These ASBV values were all sourced from Sheep Genetics, which is Australia's national genetic evaluation database for sheep (Brown et al., 2007). The sire breeding values and index estimates were generated within 3 separate data-bases for Terminal, Maternal, and Merino sired progeny and were from an analysis completed in April 2013. Some of the youngest sires used in this experiment lacked industry records and therefore did not have ASBVs available. Therefore when the ASBV's were included in the model, only 1612 animals were used in the analysis.

2.5. Statistical analyses

2.5.1. Data transformation

All data was converted to natural logarithms in order to utilise Huxley's allometric equation ($y = ax^b$) (Huxley & Teissier, 1932). Where x is the independent variable, a is the proportionality coefficient and b the growth coefficient of y relative to x . The value of the b coefficient describes, the relative growth rate of the component (y) to either the whole carcass weight or the weight of lean and will be either: early maturing ($b < 1$), late maturing ($b > 1$) or maturing at the same rate as that of x ($b = 1$).

By transforming all of the values to natural logarithms, ($\log_e y = \log_e a + b \cdot \log_e x$) the data is linearised and solved by least squares regression. A significant advantage of using the log form of the equation is that it homogenises the variance over the entire range of sample data. It also allows for the direct comparison of the differences in $\log_e y$ values as percent differences (Cole, 2000) and it is on this basis that the data in this paper has been interpreted. In this paper, the b coefficient describes the rate of development of either the whole carcass lean (or the section weight of lean) as a component of either carcass weight (or total weight of lean). In both instances the b term was examined with relevant first order interaction with the core terms of sire type, sex within sire type, dam breed within sire type, birth type-rear type, site year, site year within kill group. A similar approach to the analysis of the fat and bone composition of the same lambs was taken so that the model could be constrained, meaning in the analysis of whole carcass lean, reported increases or decreases in lean are offset by similar changes in either fat or bone. Additionally, the allometric approach allows the relative rates of development of carcass tissue types to be determined.

2.5.2. Linear mixed effects models

The \log_e transformed CT data were analysed using linear mixed effects models in SAS (SAS version 9.0, SAS Institute, Cary, NC, USA). The examination of the data was divided into two parts. Firstly whole body composition was assessed using the \log_e total weight of carcass fat, lean or bone as the dependent variable, and \log_e carcass weight at the time of CT scanning as the covariate. These 3 models were constrained such that they maintained the exact same form across all three tissue types, enabling the addition of differences in fat, lean, and bone to approximately off-set each other and thus the addition of the tissues can still approximate carcass weight. Secondly, to assess the distribution of lean between the fore section, saddle, and hind section, the \log_e weight of lean within each of the 3 carcass regions was used as the dependent variable, and the \log_e total lean weight within the carcass was used as the covariate. Again, these 3 models were constrained such that they maintained the exact same form across all three carcass regions, enabling the addition of differences in fore, saddle, and hind sections of lean to approximately off-set each other and thus the addition of lean across the 3 carcass regions can still approximate total lean weight.

For all of the models described above, we tested a standard set of fixed effects, and random terms which denotes the base model. The fixed effects included site-year (combined effect of site and year of lamb birth: Katanning (2007, 2008, 2011), Kirby (2007, 2008,) Hamilton 2009, Turretfield 2009 and Struan 2010); birth type and rearing type (combined effect of animals born as single, twin or triplet and reared as single, twin or triplet); sire type (Maternal, Merino and Terminal); sex within sire type (wether Merino, wether Maternal, female Terminal, wether Terminal); dam breed within sire type (Merino x Merino, Maternal x Merino, Terminal x Merino, Terminal x Border Leicester-Merino) and kill group within site-year. The random terms included sire and dam identification by lamb birth year. All

appropriate first and second order interactions between fixed effects and covariates were tested. Non-significant ($P > 0.05$) terms were removed in a step-wise manner resulting in a base model, constrained to be the same for the 3 models within the whole body analysis (ie across fat, lean and bone), or for the 3 models within the lean distribution quarter analysis (ie across fore, saddle, and hind section). Of the total number of carcasses undergoing CT scanning, 1665 had entries for sex, sire type, birth-type rear-type, dam breed, and kill group and were included in the base model (table 4).

(insert table 4 near here)

The base models described above were also tested with sire ASBVs for PWWT, PEMD and PFAT in the model. Initially, all 3 ASBVs were included simultaneously as covariates in the model, as well as their first order interactions with other terms. Non-significant ($P > 0.05$) terms were removed in a stepwise manner. Due to the correlations that exist between these breeding values in this data set (PWWT vs PEMD = 0.3; PWWT vs PFAT = 0.3; PEMD vs PFAT = 0.1) this process was repeated with the breeding values included one at a time to test the independence of their effects.

3. Results

3.1. Production and management effects

Between site-years the proportion of lean tissue within the carcass varied ($P < 0.01$, Table 5) by as much as 8.8% (Table 6), with Rutherglen 2010 having the least and Kirby 2007 the most. The distribution of this lean was also different between site-years. At a constant lean weight the Kirby 2007 lambs had the most fore section lean, the least saddle section lean and one of the lowest weights of hind section lean. By contrast, lambs from Turretfield 2009 had the least fore section lean, one of the most saddle section lean and the greatest hind section

lean, which compared to Kirby 2007 was about 12% less in the fore, 8.7% more in the saddle and 4.2% more in the hind section.

Within each of these site-years there was also considerable variation between kill groups ($P < 0.01$, Table 5) the greatest difference occurring at Katanning in 2011 which varied in carcass lean by as much as 5.57% (data of individual kill groups not shown). At the majority of the 8 site-year combinations where kill group comparisons were possible, within a year there was a greater proportion of carcass lean in the earlier kill group, compared to the oldest kill group ($P < 0.05$). Within each site, the amount of lean in a section (fore, saddle and hind) varied significantly between each kill groups. The greatest variation was at Turretfield in 2009 where the amount of lean varied by 6.89% and 8.38% in the fore and saddle sections. Within a site-year there was a trend for the earlier kill groups to have less fore section lean and greater saddle section lean than the later kill groups, with this occurring at 6 of the 7 site-year combinations ($P < 0.05$). There was no consistent pattern in the change in proportion of hind lean.

A comparison between sexes was only able to be made within the Terminal sired lambs. There were marked differences between wethers and ewes in both in the amount of lean within the carcass ($P < 0.01$, Table 5) and in the distribution of lean between sections ($P < 0.01$, Table 5). Wether lambs from Border Leicester-Merino and Merino dams had 2.76% and 2.15% more lean than female lambs (Table 6). Wethers from Border Leicester-Merino and Merino dams had 2.13% and 1.93% more lean ($P < 0.01$) in the fore section. In the saddle section wethers had 1.06% less lean than the ewe lambs ($P < 0.05$, Table 6), however this was only for lambs born to Border Leicester-Merino dams. The Merino and Maternal sired lambs were all wethers, therefore sex comparisons were unable to be explored in these animals.

The birth-type rear-type did not impact on the proportion of lean in the carcass but did impact on the distribution of lean ($P<0.05$, Table 5). Lambs born as triplets and reared as triplets, had about 2.2% less lean tissue in the hind section when compared to lambs not born as triplets (Table 6). This was offset by non-significant increases in lean weight in the fore and saddle sections.

(Insert table 5, and. 6, near here.)

3.2. *Impact of genetics*

3.2.1. *Sire, sire type and dam breed*

When evaluating whole carcass lean in the base model there were marked differences between sires ($P<0.01$), with 95% of the sire estimates for all three sire types lying within $\pm 3.3\%$ at any given carcass weight. The distribution of lean between carcass sections also differed between sires ($P<0.01$). The sire estimates for lean within a section varied, with 95% of the sire estimates from the fore, saddle and hind lying within $\pm 1.7\%$, $\pm 3.0\%$ and $\pm 1.4\%$ at any given weight of whole carcass lean when analysed in the base model.

Sire type comparisons could be made between wether lambs born to Merino dams (Table 6). The amount of lean in the carcass differed between sire types ($P<0.01$, Table 5) with the Terminal sired lambs having 2.8% and 4.4% more lean than the Merino and Maternal sired lambs (Table 6). The distribution of lean tissue also differed between the sire types ($P<0.01$, Table 5). The Terminal sired lambs had the most lean in the saddle and hind sections but the least lean in the fore section compared to the Merino and Maternal sired lambs (Table 6).

There were also differences between dam breeds in the proportion of lean in the carcass ($P < 0.01$, Table 5), with comparisons only possible within Terminal sired lambs. In the female lambs the progeny of Merino dams had 1.5% more lean than those from Border Leicester x Merino dams, and similarly in wether lambs the progeny of Merino dams had 0.9% more lean than those from the Border Leicester x Merino dams (Table 6).

3.2.2. Australian Sheep Breeding Value Effects

Sire PWWT ASBV was associated with both the amount and distribution of carcass lean ($P < 0.05$, Table 7) but only at some sites on some years. Sire PWWT increased carcass lean at Rutherglen in 2010 by 6.2% across the increasing 24.7 unit range of sire PWWT (kg) (Table 8). Within sites the biggest variation was seen at Kirby in 2008, where increasing PWWT across the 24.7 unit range, increased the mean weight by as much as 6.9% in one kill group and reduced it by 4% in another (data of individual kill groups not shown).

Increasing sire PWWT increased saddle lean on average by 4.0% (Table 8) across the 24.7 unit range. This effect varied between sites ($P < 0.05$, Table 7) resulting in as much as 10.9% more saddle lean across the PWWT range at the Katanning site in 2008 (Table 8). On average, the increases in saddle lean were offset by reduced fore-section lean ($P < 0.05$, Table 7).

Decreasing sire PFAT resulted in an increase in carcass lean and redistribution of lean to the saddle section ($P < 0.01$, Table 7). Across the 5.1 unit range (mm) of decreasing PFAT, whole carcass lean increased by 9.5% (Table 8). Within the carcass lean tissue there was a 3.7% increase in saddle lean across the decreasing PFAT range (Table 8), which was offset by a smaller, non-significant reduction in lean of the fore and hind sections.

Increasing the sire PEMD ASBV resulted in an increase in carcass lean and redistribution of lean from the fore section to the saddle region ($P<0.01$, Table 7). Over the 7.8 unit PEMD (mm) range there was an increase in carcass lean of 7.7% (Table 8 and Figure 1). When animals were compared at the same lean weight an increasing sire PEMD ASBV (mm) resulted in a 3.8% increase in saddle lean, offset by a 3.5% reduction in fore section lean (Table 8).

(insert table 7 and table 8 near here)

(insert figure 1 near here)

3.3. Allometric (*b*) coefficients

There were no significant interactions of the fixed effects (site-year, sex, sire type, dam breed and kill group) with the *b* coefficient. Compared to the growth rate of the whole carcass, lean tissue was relatively early maturing ($P<0.01$, Table 5), with an allometric coefficient of 0.86 (Table 6). The rate of maturation of the lean tissue was similar between all sections of the carcass ($P<0.01$, Table 5) with the allometric coefficients of the fore, saddle and hind section being 1.0, 1.05 and 0.97 respectively (Table 6).

4. Discussion

4.1. Allometric (*b*) coefficient

Relative to whole carcass weight lean tissue was early maturing, with an allometric coefficient of 0.86 which is similar to that reported in previous studies (Butterfield, Griffiths, Thompson, Zamora, & James, 1983; Fourie, Kirton, & Jury, 1970). Alternatively, the growth coefficient of lean in the fore, saddle and hind sections was close to 1 indicating that musculature across these regions developed at a similar rate. This is contrary to earlier work

that showed that individual muscles within the carcass have different rates of development (Butterfield, Reddacliff, et al., 1984). In particular the ‘spinal muscles’ were reported to be early maturing, with significant growth in the early postnatal period, reaching a peak of their portion of lean weight in the carcass at about 20% maturity, then slowly declining as the lamb approaches maturity (Butterfield, 1988). However, the lean growth coefficients from this earlier work can be difficult to compare to ours as the points of dissection and types of data analysis has varied. Given that the saddle region in our study describes more than simply the loin musculature and at a time point of approximately 50% of mature size, this may explain why our results do not match the results of this earlier work. Hence while these results align with the well-known trend for lambs to reduce the proportional lean composition of their carcass as they mature, we can also conclude that this effect will occur at a relatively consistent rate within the fore, saddle and hind sections of the carcass. As such slaughter endpoints which try to optimise the weight of lean in the saddle region relative to other carcass sections will be relatively in-effective.

4.2. *Genetic influences on carcass lean tissue*

4.2.1. *PWWT ASBV*

To partially support our hypothesis, increasing sire PWWT had no main effect on carcass lean tissue when adjusted to the same carcass weight, however at some sites in some years an increase in lean was observed. This contradicts previous findings from smaller studies where PWWT had no effect (Gardner et al., 2010; Hegarty, Hopkins, et al., 2006; Ponnampalam, Hopkins, Dunshea, et al., 2007), though it does support the general principle that lambs selected for high post weaning weights would have a larger mature size (Huisman & Brown, 2008) and therefore they will be physiologically less mature when compared at the same weight (Berg & Butterfield, 1968; Butterfield et al., 1983; Hegarty, Shands, et al., 2006)

demonstrated a reduced PWWT response when lambs were on depressed nutrition, potentially explaining the lack of response at low nutrition sites. Therefore the variation in response to increasing sire PWWT across different sites and years may be due to variation in nutrition which has previously been documented for this experiment (Ponnampalam et al., 2014).

An unexpected finding was that PWWT resulted in increased lean in the saddle, which was largely offset by a reduction in fore section lean. This redistribution effect may be explained by maturity as spinal musculature is relatively early maturing (Butterfield, Reddacliff, et al., 1984), yet contrary to this assertion the *b* coefficients in our analysis indicate that lean tissue in all sections developed at a similar rate, suggesting that maturity is unlikely to explain the redistribution of lean to the saddle. Our findings are in contrast to those of Gardner et al (2010) who showed that with increasing sire PWWT, the topside muscle weight increased, with no impact of this breeding value on muscles of the saddle section.

4.2.2. PEMD ASBV

In support of our initial hypothesis, more lean had been distributed to the saddle region of the carcass. This appears to align with suggestions made in previous studies, where selection for increased PEMD resulted in an increase in loin depth and weight (Gardner et al., 2010; Hegarty, Shands, et al., 2006; Hopkins, Stanley, Martin, Ponnampalam, et al., 2007), and little effect elsewhere in the carcass. Alternatively, these previous experiments were unable to clearly demonstrate redistribution of lean to the saddle as fore section lean was not recorded and only a small number of indicator muscles (e.g. Round and top side) were collected from the hind section. The redistribution of lean may be due to a change in muscle fibre type, with a shift towards more type IIX muscle fibres within the saddle region leading to an increased

cross-sectional area and muscle hypertrophy (Greenwood, Gardner, & Hegarty, 2006). In support of this notion, there is evidence of a decrease in isocitrate dehydrogenase activity in the *M. longissimus lumborum* associated with selection for increased sire PEMD (Kelman, Pannier, Pethick, & Gardner, 2014). Further experiments detailing oxidative capacity on the fore and hind sections may elicit the cause of lean redistribution effects.

Contrary to our expectations, selecting for increasing sire PEMD increased whole carcass lean, the first time that this effect has been reported across Merino and Maternal sire types. This finding is at odds with a previous analysis of a much smaller subset of the data used in this experiment (Gardner et al., 2010), however it aligns well with work by Hopkins et al (2007) who reported an increase in lean % with an increase in sire PEMD. None-the-less the magnitude of the effect in the Hopkins et al (2007) study was markedly smaller than that reported here, and pertained only to a small number of Poll Dorset sires (n=20). One explanation for this result could be associated with a larger mature size, leading to proportionately more muscle when compared at the same weight (Berg & Butterfield, 1968; Butterfield et al., 1983). However if maturity was implicated then there should also have been proportionately more bone (Berg & Butterfield, 1968; Butterfield, Zamora, Thompson, Reddacliff, & Griffiths, 1984; Fourie et al., 1970). Furthermore, Huisman & Brown (Huisman & Brown, 2008) have demonstrated no phenotypic or genetic correlation between PEMD and mature weight. Therefore the more muscular composition appears to be independent of maturity.

In contrast to the PWWT effects, the impact of PEMD on muscle did not vary between sites, suggesting that this breeding value is less affected by nutritional variation. This would support work by Hegarty et al. (2006) which showed that the depth of loin muscle from animals with high PEMD was similar under high and low nutritional regimes. Of course

under a “non-industry relevant” severe starvation scenario, it is likely that the magnitude of the PEMD effect would eventually be affected. But clearly the effects of this ASBV on composition appear to be more environmentally resilient compared to the PWWT ASBV.

4.2.3. PFAT ASBV

Consistent with our hypothesis, selection for reduced PFAT increased lean weight within the carcass. This change in body composition may be suggestive of low PFAT animals having a larger mature size, however, previous research has demonstrated little genetic or phenotypic correlation between sire PFAT and adult weight (Huisman & Brown, 2008) or growth rate (Kelman et al. unpublished). Thus it seems likely that these compositional differences will still be present when the animals reach their mature size. These results are consistent with previous studies. Hopkins et al (2007) showed an association between reducing PFAT and an increase in lean within the carcass, as measured by dual energy x-ray absorbiometry. However this was only demonstrated in the progeny of Poll Dorset sires, and the magnitude of the effect was smaller. Similarly, Gardner et al. (2010) showed increased weights of specific muscles in the saddle (loin) and hind section (round) in response to reducing PFAT, however in contrast to this study there was no increase in whole carcass lean measured using CT.

The redistribution of lean to the saddle section from the fore section as sire PFAT decreased was an unexpected and previously unreported finding. This may be attributable to the PFAT measurement being taken from a single site in the saddle section, placing more emphasis on reducing fat (offset by increasing lean) in this region as suggested by Gardner et al. (2010).

4.2.4. Impact of sire type and dam breed

The wether progeny of Terminal sired lambs had the greatest proportion of lean when compared to the wether progeny of Maternal and Merino sired lambs. Based on the relative rate of maturation of lean tissue it is likely that the Terminal sired animals were less mature when compared at the same weight or age, resulting in proportionately more lean tissue in the carcass (Berg & Butterfield, 1968). This is in contrast to Ponnampalam et al (2007) who showed that Merinos had a greater lean % than Poll Dorset sired lambs at the same age, however this observation was based on only 4 sires. The other key difference between sire types was the distribution of lean tissue. At the same lean weight the Terminal sired lambs had a greater proportion of lean tissue in the saddle and hind sections compared to the Merino and Maternal sired animals. A similar result has previously been suggested through assessment of indicator muscles such as the loin and *M. semitendinosus* (Ponnampalam, Hopkins, Butler, et al., 2007), however in this study lambs were compared at the same age, rather than the same lean weight. The reason for altered lean distribution is unclear though may be associated with the emphasis on selection for muscling in the Terminal sires. This selection has been on-going for generations using both visual methods, and in recent years using a site specific measurement of muscle depth in the saddle region which may account for the observed redistribution.

The dam breed results align well with the sire type results with the lambs born to Merino dams having more lean than those from the Border Leicester x Merino dams. Lambs from Border Leicester x Merino dams have previously been shown to have less lean and more carcass fat (Ponnampalam et al., 2008) and produce lambs with a greater amount of intramuscular fat (Hopkins, Stanley, Martin, Toohey, & Gilmour, 2007; Pannier et al., 2014). This aligns well with this breeds improved reproductive capacity, which is linked to whole

carcass fatness (Ferguson et al., 2010). Alternatively, this may be a reflection of their relative maturation rates, with Merinos dams producing lambs that mature slower (Hopkins, Stanley, Martin, Ponnampalam, et al., 2007).

4.3. *Production and management effects on carcass lean.*

In support of our hypothesis, at any given carcass weight, Terminal sired wether lambs had more lean than ewes. This aligns well with previous studies (Butterfield, Thompson, & Reddacliff, 1985; Fourie et al., 1970) and partly reflects that rams and wethers grow to a larger mature size than ewes (Thompson, Parks, & Perry, 1985), and at the same carcass weight will be leaner. A similar result was observed by Ponnampalam et al (2007) where wethers had increased lean % compared to ewes, even though these lambs were compared at the same age rather than the same carcass weight. In terms of lean distribution, Terminal sired wether lambs had more lean in the fore section compared to the ewes, a result that is similar to work performed by Perry et al (1988) in Merino rams and ewes. In the latter study, the rams had increased neck and forelimb musculature, speculated to be consistent with the need for males to enforce dominant behaviour and support a larger head and horns. This reasoning may still be valid despite the males in the current study being castrated.

There was no difference in the rate of development of lean between wethers and ewes (i.e. no sex interaction with the b coefficient), which is in contrast to other studies who showed rams to have a higher impetus for muscle growth compared to ewes (Fourie et al., 1970; Thompson, 1983). McClelland et al (1976) showed that at approximately 50 to 60% of maturity ram and female composition was similar which may account for the lack of difference between sexes seen in our analysis. This result was emulated in another analysis (Thompson, Butterfield, & Perry, 1985), although in this case a cross-over effect was seen in

tissue maturation rate between rams and ewes which may explain the variability seen in some of the studies.

The birth-type and rear-type had no impact on carcass lean and little impact on the distribution of carcass lean. The lambs born and raised as triplets had least hind section lean which was significantly less than the single born and raised, the twin born and raised or twin born single raised lambs. The reason for this difference is difficult to explain with the current data.

Although this study was not designed to assess nutritional impacts on carcass composition, the differences between sites, and to a lesser degree kill groups, are likely to be reflective of nutritional variation. However the between-site variations in the amount of carcass lean and the distribution of lean between the three sections (fore, saddle and hind) may be due to differences in the dam genetics between sites. Alternative explanations could be associated with variation in nutrition (Ponnampalam et al., 2014) associated with ewe milk output and pasture conditions, or worm burdens (ewe and lamb impacts). Within a site, kill group reflects to some extent lamb age. The increased proportion of carcass lean in the earlier kill groups may be a reflection of lamb maturity and the early maturation of lean (allometric coefficient < 1). A maturity explanation is difficult to ascribe to the changing proportion of lean between kill groups, with all sections tending to develop at the same rate (allometric coefficient = 1)

4.4. *Comparison of effects*

Compared to the non-genetic effects, the impact of the ASBVs on lean tissue is much more profound. PFAT demonstrated the greatest impact on total carcass lean an effect that

was 20% greater in magnitude than PEMD. The impact of PWWT was lower than both PFAT and PEMD and was heavily influenced by the different sites making its role for improvements to lean percentage within the carcass more limited.

The results of this study provide a better understanding of the compositional changes caused by the carcass breeding values, allowing more accurate assessment of their impact on carcass value. The weighting of breeding values in industry indexes are performed on the basis of their economic impact. In particular, this may be underestimating the value of PEMD because of its substantial impact on the high value loin musculature. Hence the data from this paper will enable improved precision for arriving at more accurate economic weightings for the carcass.

The differences between sites and kill groups had the greatest impact of the non-genetic effects on total carcass lean tissue and distribution. There was about 2.5 times the variation in lean between the sites and kill groups when compared to the impact of sex and birth-type rear-type. This demonstrates the substantial influence that nutrition and other environmental factors can have on carcass composition. Some caution is required in this interpretation given that we cannot separate the influence of dam genetics from the observed site differences. Additionally, we cannot discount the fact that differences between sites may in part be due to different CT scanners being used.

4.5. *Conclusions*

CT scanning of the 1665 lambs in this study has provided precise whole-body quantification of the impact of decreasing sire PFAT and increasing sire PEMD on the weight of lean in the carcass, which increased by 9.5% and 7.7% across the range of these ASBVs

when lambs were compared at the same carcass weight. Additionally, these breeding values have been shown to redistribute lean from the fore section to the saddle section, which will likely increase carcass value as the saddle region is more highly valued. Similarly, PWWT ASBV increased the weight of lean in the carcass, however this effect was not consistent across different sites/environments. PWWT also redistributed lean to the more valued saddle region, without decreasing hind section lean. These results indicate targeted selection for sires of decreased PFAT and increased PEMD, have the ability to improve the value of the lamb carcass through the manipulation of lean tissue. This experiment has for the first time allowed these breeding value effects to be quantified at a whole body level, rather than just using cut weights and carcass tissue depths to indicate these trends. The results of this experiment will be used to determine the financial gains of using carcass ASBVs to improve carcass composition in addition to the improvements in hot carcass weight that they provide (Gardner et al., 2015).

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Table 1. Total number of lambs scanned using computed tomography at each site.

Site-Birth Year	Kill group number	Average age at slaughter (days)	Number of lambs
Kirby 2007	1	235	72
	2	270	63
	3	352	96
Kirby 2008	1	269	97
	2	345	99
	3	408	99
	4	420	96
Rutherglen 2010	1	198	55
	2	254	59
Hamilton 2009	1	229	53
Struan 2010	1	260	67
	2	287	67
	3	322	27
Turretfield 2009	1	235	58
	2	262	63
	3	310	29
Katanning 2007	1	177	59
	2	248	52
Katanning 2008	1	235	20
	2	242	29
	3	319	28
Katanning 2011	1	168	87
	2	238	96
	3	280	99
	4	355	95
Total	-	-	1665

Table 2. Raw means \pm standard deviation, (minimum and maximum) values in lamb for the weight (kg) of fat, lean, bone within the whole carcass, and the fore, saddle and hind sections.

	All components		Fat		Lean		Bone	
	Mean \pm SD	Min-Max	Mean \pm SD	Min-Max	Mean \pm SD	Min-Max	Mean \pm SD	Min-Max
Whole carcass weight (kg)	23.3 \pm 4.39	13.3-40.0	6.3 \pm 2.19	2.1-15.3	13.3 \pm 2.05	7.4-20.8	3.8 \pm 0.56	2.4-5.7
Fore section weight (kg)	7.7 \pm 1.39	4.4-13.1	1.9 \pm 0.57	0.8-4.4	4.3 \pm 0.74	2.3-7.1	1.5 \pm 0.23	0.9-2.4
Saddle section weight (kg)	7.5 \pm 1.82	3.7-14.0	2.9 \pm 1.24	0.8-8.1	4.3 \pm 0.74	2.3-7.1	0.9 \pm 0.19	0.4-1.5
Hind section weight (kg)	8.0 \pm 1.34	4.8-13.2	1.4 \pm 0.45	0.4-3.3	5.3 \pm 0.84	2.9-8.6	1.4 \pm 0.18	0.9-2.0

Table 3. Number of sires of lambs and mean (min, max) for the Australian Sheep Breeding Values for post weaning weight (PWWT), post weaning c-site fat depth (PFAT) and post weaning eye muscle depth (PEMD) for each sire type.

Sire type	No. of sires	PWWT (kg)	PFAT (mm)	PEMD (mm)
Maternal	70	4.7 (-6.1, 12.4)	-0.3 (-2.1, 2.6)	0.1 (-2.5, 1.8)
Merino	109	1.9 (-5.0, 10.8)	-0.2 (-1.9, 1.9)	0.0 (-2.6, 2.6)
Terminal	154	12.7 (5.3, 18.6)	-0.7 (-2.5, 2.3)	1.2 (-2.8, 5)

Table 4. Number of lambs analysed in the base model according to sex, sire type, birthing and rearing type and dam breed.

	Sex		Birth type-rearing type					Dam breed		
	Female	Wether	Single born and raised	Born as twin-raised as single	Born as twin-raised as twin	Born as triplet-raised as single	Born as triplet-raised as twin	Born and raised as triplet	Merino	BLM
Maternal	0	373	172	31	155	2	8	5	373	0
Merino	0	251	129	38	79	1	0	4	251	0
Terminal	507	534	413	96	472	8	30	22	527	514
Total	507	1158	714	165	706	11	38	31	1151	514

BLM: Border- Leicester x Merino

Table 5. F-values, and numerator and denominator degrees of freedom of factors affecting lean weight of lamb in the whole carcass and the distribution of lean in the fore, saddle and hind sections of the lamb carcass.

Effect	Whole carcass lean		Lean distribution between sections (F-values)			
	NDF, DDF	F-value	NDF, DDF	Fore-section	Saddle-section	Hind-section
site-year	8,177	30.0**	7,170	124.8**	59.3**	29.7**
sex (sire type)	1,177	115.4**	1,170	47.0**	4.7*	23.2**
birth-type rear-type	NA	NA	5,170	1.8	0.9	2.9*
Sire type	2,177	22.1**	2,170	34.2**	6.6**	13.4**
kill group(site-year)	16,177	12.0**	15,170	8.2**	9.1**	3.8**
dam breed(sire type)	1,177	11.6**	1,170	0.15	0.1	0.0
site-year x sire type	13,177	2.8**	12,170	2.0*	1.7	1.5
site-year x dam breed (sire type)	5,177	4.3**	5,170	3.1*	1.2	1.4
log x ¹	1,177	8660.7**	1,170	6966.0**	4846.2**	11412**

NDF, DDF: numerator and denominator degrees of freedom.

NA: term was not retained in the final model as was not significant for any component (fat, lean, bone)

¹ Where carcass lean was analysed, carcass weight was the covariate (x) and when lean distribution was analysed whole carcass lean was the covariate (x)

* $P < 0.05$, ** $P < 0.01$

Table 6. Relative change (% Change in weight) for site-year, sex dam breed(sire type) and birth-type rear-type on lamb carcass lean weight and the lean distribution between the fore, saddle and hind sections of the lamb carcass.

Factor	Level	Carcass lean weight %	Section lean weight (Lean distribution between sections)		
			Fore-section % Change in weight	Saddle-section % Change in weight	Hind-section % Change in weight
Site year ¹	Kirby 2007	1.80^f	11.47^f	-9.83^a	-2.97^a
	Kirby 2008	-3.02^b	6.25^e	-7.60^b	0.24^c
	Rutherglen 2010	-6.98^a	6.21^e	-2.19^{cd}	-3.51^a
	Hamilton 2009	0.24^e	3.55^d	-3.23^c	-0.41^c
	Struan 2010	-2.26^{bc}	1.54^c	-0.97^{def}	-0.58^c
	Turretfield 2009	-0.10^{de}	-0.62^a	-1.10^{de}	1.21^d
	Katanning 2007	-1.29^{cd}	NA	NA	NA
	Katanning 2008	-0.16^{de}	1.08^{bc}	1.06^f	-1.67^b
	Katanning 2011	0.00^e	0.00^{ab}	0.00^{def}	0.00^c
Sex Dambreed (sire type) ²	Maternal x Merino M	-4.41ⁱ	2.29^k	-1.68ⁱ	-0.76^{ij}
	Merino x Merino M	-2.83^{jk}	2.59^k	-1.24^{ij}	-1.28ⁱ
	Terminal x BLM F	-3.61^{jk}	-1.68ⁱ	0.76^l	0.78^k
	Terminal x Merino F	-2.15^k	-1.93ⁱ	0.53^{kl}	1.18^k
	Terminal x BLM M	-0.85^l	0.45^j	-0.30^{jk}	-0.17^k
	Terminal x Merino M	0.00^l	0.00^j	0.00^{kl}	0.00^k
Birth-type rear-type ³	Born and raised as single		-1.39	-1.51	2.20^y
	Born twin, raised single		-1.75	-1.05	2.16^y
	Born and raised as twin		-1.64	-1.27	2.20^y
	Born triplet, raised single		-1.94	-0.87	1.99^{yz}
	Born triplet, raised twin		-0.09	-1.78	1.16^{yz}
	Born and raised as triplet		0.00	0.00	0.00^z
<i>b</i> coefficient (± SE)					
log <i>x</i> ⁴		0.86 ±0.009	1.003 ±0.012	1.045 ±0.015	0.967 ±0.009

% Change in weight: the difference in logy values for each fixed effect compared to the fixed effect with coefficient 0.00 expressed as a percentage.

M = wether; F = ewe; BLM: Border Leicester-Merino

¹ a-f Within columns for site year, % Change in weight values without a common superscript differ significantly at $P < 0.05$.

² i-l Within columns for sexdambreed(sire type), % Change in weight values without a common superscript differ significantly at $P < 0.05$.

³ w-y Within columns for birth-type rear-type, % Change in weight values without a common superscript differ significantly at $P < 0.05$.

⁴ Where carcass lean weight was analysed, carcass weight was the covariate (*x*) and when lean distribution was analysed whole carcass lean was the covariate (*x*)
Significant effects are in bold ($P < 0.05$)

Table 7. F-values, and numerator and denominator degrees of freedom for Australian Sheep Breeding Values affecting lamb lean weight in the whole carcass and lean distribution between the fore, saddle and hind sections of the lamb carcass.

Effect	Whole carcass lean		Lean distribution between sections (F-values)			
	NDF, DDF	F-value	NDF, DDF	Fore-section	Saddle-section	Hind-section
PWWT	1,156	3.56	1,166	4.29*	5.4*	0.18
PWWT x site-year	8,156	2.3*	7,166	1.41	2.32*	1.45
PWWT x kill group(site-year)	16,156	2.14**	NA	NA	NA	NA
PFAT	1,156	96.6**	1,166	3.89*	7.57**	1.54
PEMD	1,156	38.02**	1,166	12.24**	8.37**	0.14
PEMD x sire type ¹	2,156	2.83	NA	NA	NA	NA

NDF, DDF: numerator and denominator degrees of freedom.

NA: term not retained in the final model as was not significant for any section

PWWT: post weaning weight; PFAT: post weaning c-site fat depth; PEMD: post weaning eye muscle depth

¹This interaction was included in the model as it was significant in the analysis of carcass fat

* $P < 0.05$, ** $P < 0.01$.

Table 8. Percentage change in weight per unit of Australia Sheep Breeding Values on lamb carcass lean weight and lean distribution between the fore, saddle and hind sections of the lamb carcass.

Effect	Level	Carcass lean weight	Section lean weight (Lean distribution between sections)		
		% Change in weight	Fore-section % Change in weight	Saddle-section % Change in weight	Hind-section % Change in weight
PWWT		0.08	-0.11	0.16	-0.02
PWWT*	Kirby 2007	0.27	-0.14	0.08	0.10
site year	Kirby 2008	0.06	-0.01	0.01	0.01
	Rutherglen 2010	0.25	-0.12	0.07	0.06
	Hamilton 2009	-0.12	-0.04	0.03	0.00
	Struan 2010	0.00	-0.20	0.25	-0.01
	Turretfield 2009	-0.07	-0.16	0.38	-0.15
	Katanning 2007	0.06	NA	NA	NA
	Katanning 2008	0.23	-0.23	0.44	-0.10
	Katanning 2011	0.08	0.03	0.02	-0.04
	PFAT		-1.86	0.40	-0.73
PEMD		0.99	-0.45	0.49	0.04

% Change in weight is per unit of the relevant Australian Sheep Breeding Value

NA: term was not retained in the final model as was not significant for any section (fore, saddle, hind)

PWWT: post weaning weight; PFAT: post weaning c-site fat depth; PEMD: post weaning eye muscle depth

Significant effects are in bold ($P < 0.05$)

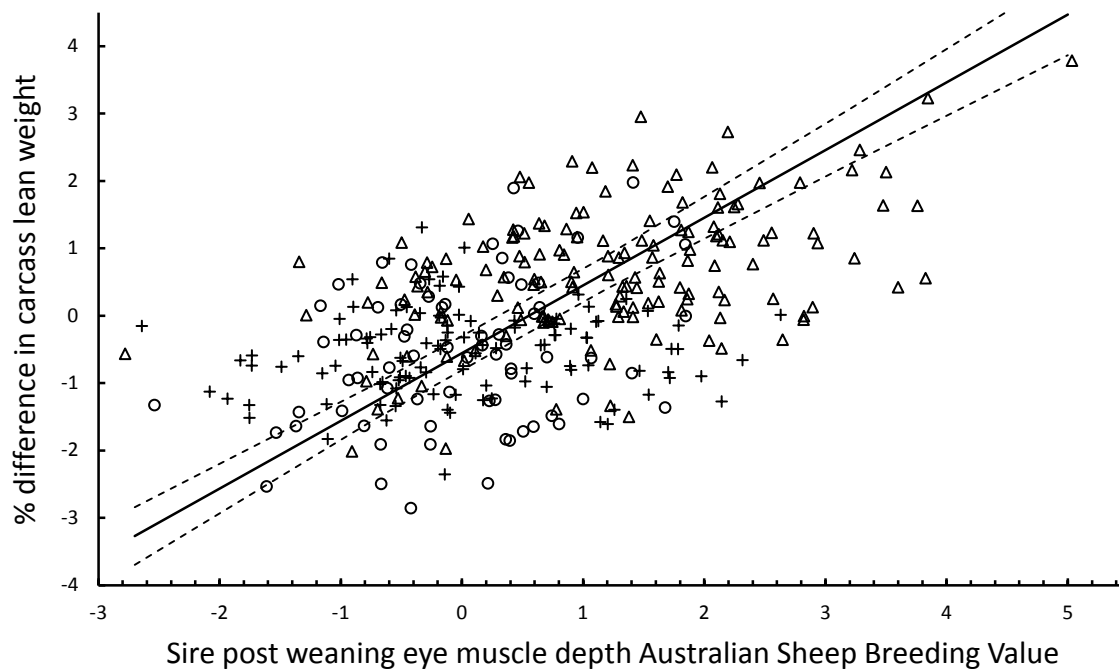


Figure 1

Figure captions

Figure 1. The relationship between lamb sire estimates for percentage of lean and post-weaning eye muscle depth (PEMD). Symbols represent sire estimates plus the least squared means for (o) Maternal, (+) Merino (Δ) Terminal sired lambs and are obtained from the ASBV model in which PEMD was removed. The line represents least squared means (\pm SE as dashed lines) for PEMD from the model containing the Australian Sheep Breeding Values.

Implications

- Sires with increased muscling and reduced carcass fat will increase carcass lean.
- Selection for increased growth may increase carcass lean %.
- Selection for lean yield preferentially distributes lean to the highly valued saddle region.
- Selection for increased yield using breeding values will increase carcass value.