Sire carcass breeding values affect body composition in lambs - 2. Effects on fat and bone weight and their distribution within the carcass as measured by computed tomography.

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Abstract

This study assessed the effect of **paternal** Australian Sheep Breeding Values for post weaning c-site eye muscle depth (PEMD) and fat depth (PFAT), and post weaning weight (PWWT) on **the composition of lamb carcasses**. **Composition** was measured using computed tomography scans of 1665 lambs which were progeny of 85 Maternal, 115 Merino and 155 Terminal sires. Reducing sire PFAT decreased carcass fat weight by 4.8% and increased carcass bone by 1.3% per unit of PFAT (range 5.1**mm**). Increasing sire PEMD reduced carcass fat weight by 3.8% in Maternal and 2% in Terminal sired lambs per unit of PEMD (range 7.8**mm**), with no impact on bone. Increasing sire PWWT reduced carcass fat weight, but only at some experimental locations. Differences in composition varied between sire types with Maternal sired lambs having the most fat and Merino sired lambs the greatest bone weight. Genetic effects on fatness were greater than the environmental or production factor effects, with the converse true of bone.

Keywords: lamb, fat, bone, breeding value, computed tomography

1. Introduction

A high proportion of saleable meat in the carcass is an important determinant of carcass value, as it reduces the processing costs associated with fat and bone trim (Hopkins, 1989; Jones, Simm, & Young, 2002) and meets consumer preferences for leaner cuts of meat (Banks, 2002; Pethick, Hopkins, D'Souza, Thompson, & Walker, 2005). Producers can select for these carcass types indirectly using three Australian Sheep Breeding Values (ASBVs): increased post weaning weight (PWWT) and eye muscle depth (PEMD), and reduced post weaning fat depth (PFAT). Previous studies have shown the impact of these ASBVs on carcass fatness, but have relied on fat depths (Hopkins, Stanley, Martin, Ponnampalam, & van de Ven, 2007), or the weight of specific fat depots (Gardner et al., 2010) to “indicate” these effects. The use of indicator measurements is inaccurate and importantly may be biased in circumstances where tissue has been redistributed within the carcass, particularly due to genetic selection. Previous studies have assessed whole carcass composition using technologies such as dual energy absorbtometry (Dunshea et al., 2007; Pearce et al., 2009; Ponnampalam et al., 2007) or computed tomography (CT) (Bunger et al., 2011; Gardner et al., 2010; Young, Simm, & Glasbey, 2001). This study has used CT technology to investigate the impact of ASBVs on carcass weights of fat and bone and their distribution within the carcass.

Selecting sires for low PFAT breeding values has been shown to reduce fatness at the c-site of measurement in their offspring (45 mm from the midline over the 12th rib) (Hall, Gilmour, Fogarty, & Holst, 2002; Hegarty, Hopkins, Farrell, Banks, & Harden, 2006). Work in pigs has shown that selection for decreasing back fat can alter the distribution of fat (Trezona-Murray, 2008; Wood, Whelehan, Ellis, Smith, & Laird, 1983), decreasing it at the site of measurement and partially redistributing it to other subcutaneous fat depots. However, studies in sheep have demonstrated that reducing sire PFAT has a more uniform impact across

the carcass (Gardner et al., 2010; Hopkins, Stanley, Martin, Ponnampalam, et al., 2007; Kadim, Purchas, Rae, & Barton, 1989). This reduced fatness is likely to be offset by increased proportions of bone tissue, as demonstrated by Gardner et al. (2010) who showed an increase in carcass hind limb bone weight and carcass bone %.

Increasing sire PEMD has been shown to produce lambs with reduced c-site fat (Hall et al., 2002; Hegarty, Hopkins, et al., 2006) and less trimmable carcass fat (Hegarty, Hopkins, et al., 2006). Yet contrary to these studies Gardner et al. (2010) found that the PEMD breeding value reduced fat depths at the c-site but did not change the proportion of whole carcass fat. The result of Gardner et al. (2010) is possibly more reliable than these earlier studies, as the experiment contained 5-fold more sires and was measured using CT. The impact of PEMD on bone is less well described, however, Gardner et al. (2010) also demonstrated that PEMD had no impact on whole carcass bone %. Therefore the impact of increasing sire PEMD is likely to reduce carcass fat, but only in the region around its point of measurement, and have little impact on carcass bone.

In sheep, the PWWT breeding value exerts its influence on carcass composition through its impact on mature size (Huisman & Brown, 2008), resulting in lambs of faster growth (Kelman *pers comm*). Given carcass fat is late maturing and bone early maturing (Berg & Butterfield, 1968; Butterfield, Griffiths, Thompson, Zamora, & James, 1983), sires of high PWWT should produce lambs that are less mature at the same slaughter weight, containing less fat and more bone. Work by Gardner et al. (2010) supported this notion showing that lambs from high PWWT sires had decreased CT fat % and increased bone % indicating a whole carcass effect on these tissues. There is no evidence of PWWT causing redistribution of fat or bone tissue within the carcass.

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79 Sire type has been shown to impact on the proportion of fat and bone. Lambs sired by
80 maternal breeds such as the Border Leicester have more carcass fat and less muscle than
81 Terminal sire breeds (e.g. Dorset Horns) when compared at the same carcass weight (Fogarty,
82 Hopkins, & van der Ven, 2000; Thompson, Atkins, & Gilmour, 1979b). Ponnampalam et al.
83 (2007) demonstrated a similar effect comparing Border Leicester sired lambs to Poll Dorset
84 and Merinos. Sire type has also been shown to impact on bone composition, with Merino
85 sired lambs having heavier bone weights than Maternal and Terminal sired lambs (Cake,
86 Boyce, Gardner, Hopkins, & Pethick, 2007). Based on these studies it is expected that lambs
87 sired by Maternal breeds will have the greatest proportion of fat, while Merino sires will
88 produce lambs with an increased proportion of bone. The impact of sire type on the
89 distribution of these two tissues throughout the lamb carcass has not previously been reported.

90

91 This paper describes the association of non-genetic and genetic factors on the carcass
92 composition of fat and bone in lambs as measured by CT, with the results of these factors on
93 lean described in Anderson et al.(2015). We hypothesised that selection for decreasing sire
94 PFAT will result in decreased carcass fat across all carcass regions, and increased carcass
95 bone, with a preferential increase in hind section bone. Increasing sire PEMD will have a site
96 specific effect on fat, decreasing it in the saddle region only, while having no impact on bone.
97 Additionally, through its impact on mature size, we hypothesised that increasing sire PWWT
98 will decrease whole carcass fat and increase carcass bone weight. Lastly, Maternal sired
99 lambs are expected to have greater carcass fat % and the Merino sired lambs an increase in
100 bone % compared to Terminal sired lambs.

101

2. Material and methods

2.1. Experimental design and slaughter details.

Complete details of the experimental design, slaughter details are presented in Anderson et al. (2015) and more briefly in this paper. 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, Banks, van de Werf, Ball and Gibson (2007). Within each year, at each of the six research stations, a subset of lambs were chosen from 1-2 sites each year for CT scanning of their carcasses following slaughter. The lambs were divided into groups based on live weights, with each group killed separately (kill groups) at a target carcass weight of 23 kg.

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 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 were 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). 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).

(insert table 1 near here)

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129 2.2. *Computed tomography scanning*

130 Carcasses were transported for CT scanning to either Murdoch University (Picker PQ
131 5000 spiral CT scanner) or the University of New England (Picker, Bavaria, Germany) within
132 72 hours of slaughter to determine the proportions of fat, lean and bone. Prior to scanning the
133 carcasses were split into three primal components to enable more rapid post scanning
134 processing of the CT images for the distribution analysis: fore-section, saddle and hind
135 section. The fore section was separated from the saddle by a cut between the fourth and fifth
136 rib. The hind section was separated from the saddle by a cut through the mid-length of the
137 sixth lumbar vertebrae. The method used for determination of muscle, fat and bone was
138 similar to that described by Gardner et al. (2010) with the discrimination between fat, lean
139 and bone adapted from work by Alston et al. (2005). Precision for predicting dissectable fat
140 ($R^2=0.718$; RMSE=0.713), and bone ($R^2=0.789$; RMSE=0.439) has previously been reported
141 by Gardner, Pearce, and Smith (2007). A more detailed description of the CT scanning
142 protocol and image analysis are presented in Anderson et al. (2015).

143

144 2.3. *Data used*

145 CT scanning data from a total of 1665 carcasses from the 9 site-year combinations was
146 available for analysis of fat and bone composition within the carcass (Table 1). The 111
147 carcasses from Katanning in 2007 were not scanned in sections, therefore when analysing
148 distribution of lean between carcass sections, 1554 carcasses were included in the analysis.
149 The mean weight (and range) of the lamb carcasses in this experiment was 23.3kg (13.3-40.0
150 kg), with weights (and range) of fat, lean and bone, 6.3kg (2.1-15.3), 13.3kg (7.4-20.8), and
151 3.8kg (2.4-5.7). The full description of carcass weights of fat lean and bone across the three
152 sections are reported in Anderson et al. (2015).

153

Of the 85 Maternal, 119 Merino and 155 Terminal sires, 70, 109 and 154 had ASBV values for PWWT, PEMD, and PFAT available, with the mean and range of these sire breeding values shown in Anderson et al. (2015). The breeding values for PEMD and PFAT are based upon live ultrasound measurements at the c-site, located at the 12th rib, 45mm from the midline, and PWWT is based upon live weight, all measured at the post weaning time point (about 240 days of age). The ASBV values were all sourced from Sheep Genetics, Australia's national sheep genetic evaluation database (Brown et al., 2007). The sire breeding values were generated within 3 separate data-bases for Terminal, Maternal, and Merino sired progeny and were from an analysis completed in April 2013.

2.4. Statistical analyses

2.4.1. Data transformation

An allometric approach allows the relative rates of development of carcass tissue types to be determined. All data are converted to natural logarithms in order to utilise Huxley's allometric equation, $y = ax^b$ in its $\log_e$ linearised form (Huxley & Teissier, 1936). By transforming all of the values to natural logarithms, ($\log_e y = \log_e a + b \cdot \log_e x$) the data are linearised and solved by least squares regression. A significant advantage of using the $\log_e$ 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 the above allometric equation 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 fat (or bone) and will be either: early maturing ($b < 1$), late maturing ($b > 1$) or maturing at the same rate as that of x ($b = 1$). In this paper, the b coefficient describes the rate

of development of either fat (or bone) in the whole carcass or the development of fat (or bone) within each section of the carcass (fore, saddle and hind) relative to the whole carcass weight of fat (or bone). 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 lean tissue in the same set of lambs was taken (Anderson et al., 2015) so that the model could be constrained, meaning in the analysis of whole carcass composition, reported increases or decreases in fat, lean and bone are offset by each other.

2.4.2. *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). When whole body composition was assessed, the $\log_e$ weight of carcass fat or bone was used as the dependent variable, and $\log_e$ carcass weight was the covariate. A similar analysis was performed for lean tissue (Anderson et al., 2015) with the models constrained such that they maintained the exact same form across all tissue types, enabling the addition of differences in fat, bone and lean to approximately off-set each other and thus the addition of the tissues can still approximate carcass weight. To assess the distribution of fat or bone between the fore, saddle, and hind sections, the $\log_e$ weight of fat (or bone) within each of the 3 carcass regions was used as the dependent variable, and the $\log_e$ total fat (or bone) weight within the carcass was used as the covariate. Within a tissue type (fat or bone) these models were constrained such that they maintained the exact same form across all three carcass sections (fore, saddle and hind), enabling the addition of differences in section fat (or bone) to approximately off-set each other and thus the addition across the 3 carcass regions can still approximate total fat (or

bone) weight. The results for carcass composition and distribution of lean is reported in Anderson et al. (2015).

For all the models described above, we tested a standard set of fixed effects, and random terms which denotes the base model. 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 x Merino (BLM)) 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 to derive a base model. 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 2).

(insert table 2 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 the fixed effects. This included the interaction between ASBVs and sire type, which was particularly relevant given that the breeding values were derived from 3 separate data-bases for Terminal, Maternal, and Merino

sired progeny, and thus their magnitudes may not be directly comparable. 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. Impact of production and management on carcass fat and bone

3.1.1. Impact on whole carcass fat and bone

There was considerable variation between site-year combinations in the weight of fat and bone within the carcass ($P < 0.01$, Table 3). The weight of carcass fat varied by as much as 15% (Table 4) and the weight of carcass bone varied by as much as 19.3% (Table 5).

(insert table 3, 4 and 5 near here)

Within each site-year there was variation in the fat and bone percentage of the carcass between kill groups ($P < 0.01$, Table 3). The largest variation in carcass fat weight was 12.4% (results of individual kill groups not shown), with the younger kill groups generally containing less carcass fat than the older kill groups. The largest variation in carcass bone weight between kill groups was 17.8% (results of individual kill groups not shown), however in contrast to the impact of kill group on fat, there was no consistent effect of kill group on carcass bone weight.

A comparison between sexes was only possible within the Terminal sired lambs where there were marked differences in the amount of fat and bone within the carcass. ($P < 0.01$,

Table 3). On average the ewe lambs had 6.9% more fat (Table 4) and 2.8% less bone (Table 5) in the carcass than the wether lambs.

3.1.2. *Impact on fat and bone distribution*

The distribution of fat and bone between sections of the carcass varied between sites ($P < 0.05$, Table 3) with Hamilton 2009 showing the greatest variation in carcass fat weight between sections, with the least fore and one of the least hind section fat but the most saddle fat. Kirby in 2007 had the most variation in the distribution of bone between sections, with the most fore-section bone and least hind-section bone (Table 5).

The distribution of fat and bone varied between the sexes ($P < 0.05$, Table 3). Carcasses of ewe lambs had less fat and bone (2.2% and 1%) in the fore section, less hind section fat (2.1%), and more fat and bone (2.7% and 2.3%) in the saddle section when compared to the wether lambs (Table 4 and 5).

The birth-type rear-type did not impact on the proportion of fat or bone in the carcass but did impact on tissue distribution in the saddle and hind-sections ($P < 0.05$, Table 3). The lambs born and raised as triplets had the most saddle bone and the least hind-section bone, (Table 5) when compared to the other birthing and rear type combinations. Lambs that were born as triplets and reared as singles had the least saddle fat and the most hind section fat (Table 4).

3.2. *Impact of genetics on carcass fat and bone*

3.2.1. *Impact of sire, sire type and dam breed*

3.2.1.1. *Impact on whole carcass fat and bone*

When evaluating whole carcass fat and bone in the base model there were marked differences between sires ($P < 0.01$). For fat, 95% of the sire estimates for all three sire types ranged between $\pm 8.6\%$ and for bone between $\pm 5.6\%$ at any given carcass weight.

Sire type comparisons could be made in the wether lambs born to Merino dams. There were significant differences between sire types for whole carcass fat and bone ($P < 0.01$, Table 3), with **Terminal sired lambs having the least carcass fat. The Maternal and Merino sired lambs had 9.6% and 6.3% respectively more carcass fat** than the Terminal sired lambs (Table 4). Alternatively, the Merino sired lambs had the most bone, with 3.9 and 4.1% more than the Maternal and Terminal sired lambs (Table 5).

The impact of dam breed could be assessed in the Terminal sired lambs where BLM dams produced progeny with more carcass fat than those of the Merino dams ($P < 0.01$, Table 3). This effect was strongest in ewe lambs where progeny from BLM dams were 4.1% fatter than lambs from Merino dams (Table 4). In contrast this difference was only 1.9% in wether lambs (Table 5).

3.2.1.2. *Impact on distribution of carcass fat and bone*

The distribution of these tissues between carcass sections differed between sires ($P < 0.05$). The sire estimates for fat within a section varied, with 95% lying between $\pm 3.2\%$, $\pm 1.8\%$ and $\pm 3.7\%$ for the fore, saddle and hind sections respectively at any given weight of whole-carcass fat. For bone, 95% of the sire estimates from the saddle and hind lay between $\pm 2.8\%$ and $\pm 3.7\%$ at any given weight of whole-carcass bone.

There were differences in the distribution of fat and bone between carcass sections ($P < 0.01$, Table 3). The Terminal sired lambs had the least fore section fat, with the carcasses of lambs sired by Maternal and Merino breeds 2.0% and 2.2% fatter than the carcasses from Terminal sires (Table 4). Additionally, the carcasses of lambs born to Terminal sires had similar levels of saddle fat to the Maternal sired lambs, although lambs from Merino sires had 1.9% less saddle fat than the Terminal sired lambs (Table 4). In the hind section, the Maternal sired lambs had the most carcass fat, and the Terminal sired lambs the least (Table 4). The carcasses from Terminal sired lambs had less fore-section bone, with the Merino and Maternal sired lambs having 1.0% and 1.5% more fore section bone (Table 5). There was no difference in carcass bone distribution in the saddle and hind sections between sire types.

There was only a small impact of dam breed on bone distribution with only the hind section of ewe lambs impacted ($P < 0.05$, Table 3). The ewe lambs born to BLM dams had 1.1% more hind section bone than those from Merino dams (Table 5).

3.2.2. Impact of Australian Sheep Breeding Values on carcass fat and bone

3.2.2.1. Post weaning fat depth Australian Sheep Breeding Value

Decreasing sire PFAT had a marked impact on whole carcass fat and bone weight ($P < 0.01$, Table 6). Carcass fat was reduced by 24.7% (Table 7) across the 5.1 mm PFAT sire range. By contrast carcass bone increased by 6.5% across this same PFAT range (Table 8). Sire PFAT did not impact on the distribution of fat or bone within the carcass.

(insert table 6, 7 and 8 near here)

3.2.2.2. *Post weaning eye muscle depth Australian Sheep Breeding Value*

Increasing sire PEMD resulted in a decrease in carcass fat ($P < 0.01$, Table 6), but only in Maternal and Terminal sired lambs and not in Merino lambs. In Maternal sired lambs carcass fat decreased by 16.3% and in Terminal sired lambs by 15.4% (Table 7) across their respective ranges of sire PEMD (4.3 and 7.8 mm). On a per unit PEMD basis this difference was even more marked, with carcass fat decreasing by 3.8% in Maternal and 2% in Terminal sired lambs per unit of sire PEMD. The PEMD ASBV did not impact on whole carcass bone or the distribution of either fat or bone within the carcass.

3.2.2.3. *Post weaning weight Australian Sheep Breeding Value*

The PWWT ASBV influenced total carcass fat, although the direction and magnitude of the changes varied between sites and years ($P < 0.05$, Table 6), with no main effect. For those effects that were significant, the greatest decrease in carcass fat was 20.5% (Table 7) and the greatest increase was 9.6% (Table 7) across the 24.1 kg PWWT range.

Sire PWWT ASBV also had an impact on carcass bone weight but this varied between kill groups at some sites in some years such that on average there was no overall effect ($P < 0.05$, Table 6). The largest variation in bone weight was 13%, with individual kill group data not shown.

The only breeding value to influence tissue distribution of fat and bone was PWWT ($P < 0.05$, Table 6). When compared at the same weight of carcass fat, an increasing sire PWWT had at times opposing effects (Table 7). At many sites, alterations to proportions of fat in the saddle region were offset by the opposite effect in the hind section (Table 7).

Increasing sire PWWT on average increased hind section bone but this varied between sites ($P<0.05$, Table 6). The greatest increase in hind section bone across the 24.1 unit PWWT range was 8.4% (Table 8), with this increase in hind section bone largely offset by a decrease in saddle bone weight.

In both the whole body and tissue distribution analysis, when the three breeding values were included in the models one at a time, as opposed to all three simultaneously, there was no change to the effects described above.

3.3. Allometric (b) coefficients

There were no significant interactions between fixed effects and the b coefficient. Compared to the growth rate of the whole carcass, carcass fat was relatively late maturing and bone early maturing ($P<0.01$, Table 3), with allometric coefficients 1.48 for fat (Table 4), and 0.73 for bone (Table 5). The rate of maturation of the fat tissue differed between sections with the fat in the fore section developing earliest, followed by the hind and saddle sections with allometric coefficients of 0.85 (fore), 0.92 (hind) and 1.15 (saddle) (Table 4). Similarly the rate of bone development differed between sections, with bone in the hind section developing earliest, followed by the fore and saddle sections with allometric coefficients of 0.82, 1.03 and 1.23 (Table 5).

4. Discussion

4.1. Genetic influences on carcass fat and bone

4.1.1. Post weaning fat depth Australian Sheep Breeding Value

In support of our hypothesis, selection for decreasing sire PFAT reduced the weight of fat uniformly across the three carcass sections for all three sire types. This indicates that the use of this breeding value, which is based on fat depth measurement at the c-site, effectively

decreases whole carcass fat and that its impact is not solely localised around its point of measurement – an effect previously identified in pigs (Trezona-Murray, 2008; Wood et al., 1983). This associated reduction in CT fat % by decreasing sire PFAT had previously been reported by Gardner et al. (2010), using a subset of lambs from this study (those slaughtered in 2007), and was further reflected in the point measurements of fat depth all located within the saddle region (C5 fat, GR and c-site). Yet in contrast to these early results, the magnitude of the whole carcass fat effect was far greater in the current study. Hopkins, Stanley, Martin, Ponnampalam, et al. (2007) reported reduced point measures of fat at the c-site, rump and GR, and decreased fat % as measured by dual energy x-ray absorptiometry, however utilised only Terminal sired lambs over a limited range of PFAT values.

In partial support of our hypothesis, a reduction in sire PFAT increased bone weight for all three sire types, however the lack of an effect on bone distribution suggests that this increase in bone was not proportionally greater in the hind-section as we were expecting. This redistribution hypothesis was based on an earlier study by Gardner et al. (2010) in which a small but significant increase in measured hind limb bone weights of lambs of similar weights and ages was observed.

The effect of PFAT on fat and bone weights may be due to an increased mature size, which would also account for the increase in lean weight reported in Anderson et al. (2015). However analysis of the growth of these lambs indicated that PFAT only has a small effect on lamb weight (Kelman, *pers comm* 2015) and has little genetic or phenotypic correlation with adult weight in Merino lambs (Huisman & Brown, 2008). Therefore the alternative explanation is that PFAT is influencing mature composition. To confirm this theory a

longitudinal study of the growth and carcass composition of lambs from birth through to maturity would be required.

4.1.2. *Post weaning eye muscle depth Australian Sheep Breeding Value*

Increasing sire PEMD was hypothesised to decrease carcass fat in the saddle only, however its effect was more far-reaching, uniformly reducing fat in the fore, saddle, and hind sections. This effect was greatest in the Terminal sired lambs, with a smaller effect in the Maternal sired lambs, and no effect in Merino lambs. Although erroneous, the original hypothesis was based on previous work by Gardner et al. (2010) who suggested a site specific effect of this breeding value after observing a decrease in fat depth at the c-site, but no change in total weight of short-loin fat or whole carcass fat. There is some basis for the reduction in whole carcass fatness, with previous work by Martin, McGilchrist, Thompson, and Gardner (2011) demonstrating that animals with high PEMD were more responsive to adrenalin within their adipose tissue, and less responsive within muscle. This catabolic mechanism may explain the reduced adiposity observed at a whole carcass level. Alternatively, the lack of impact of PEMD on the fat of Merino sired lambs is difficult to explain.

In support of our hypothesis, sire PEMD did not impact on carcass weight of bone or bone distribution between sections. This is in contrast, Cake, Boyce, Gardner, Hopkins and Pethick (2007), who demonstrated that increasing sire PEMD caused a decrease in the length of most limb bones and a decrease in carcass length. Increasing sire PEMD has been shown to increase whole carcass lean and distributed this lean to the saddle region (Anderson et al., 2015). The current study shows no increase in bone weight as a result of increasing sire PEMD, which indicates the mechanism for the increase in muscle appears to be due to muscle hypertrophy rather than an impact on mature size, lamb maturity or bone weight.

4.1.3. *Post weaning weight Australian Sheep Breeding Value*

Consistent with our hypothesis, increasing sire PWWT decreased whole carcass fat %, however this effect was small and not consistent across all experimental sites and years. Lambs of high PWWT have been shown to have a larger mature size (Huisman & Brown, 2008), and therefore when slaughtered at the same age these lambs would be leaner as they are at an earlier stage of maturity. Furthermore, several studies have demonstrated that the genetic potential for growth with increasing sire PWWT is limited when lambs are on low nutrition (Gardner et al., 2006; Hegarty, Hopkins, et al., 2006; Hegarty, Shands, et al., 2006), which may account for the variation in carcass composition observed between sites within this study.

Contrary to our hypothesis, increasing sire PWWT had no significant effect on the percentage of bone in the carcass. There was a small effect of PWWT at some sites, in some years but this was highly variable and only evident within certain kill groups. Our result is in contrast to previous work which has shown that an increase in weaning weight (Thompson, Butterfield, & Perry, 1985) and post weaning weight (Gardner et al., 2010) resulted in a proportionately heavier skeleton.

When compared at the same bone weight, lambs of high PWWT sires having increased proportions of hind section bone. However in contrast, little change in bone distribution was observed between high and low growth Merino lambs (Butterfield & Thompson, 1983; Perry, Thompson, & Butterfield, 1992). If PWWT increases mature size (Huisman & Brown, 2008), it may account for the increased hind limb bone as this region of bone is early maturing (b coefficient <1). The impact of PWWT on the other carcass sections was small, which may explain the lack of impact on whole carcass bone %.

4.1.4. *The impact of sire type and dam breed on carcass fat and bone*

In support of our hypothesis, Maternal sired lambs contained the most carcass fat when compared to the Merino and Terminal sired lambs at the same carcass weight (wether lambs born to Merino dams). The dam breed was also consistent with this sire type effect, with the BLM dams producing lambs with increased fat compared to Merino dams. These results are similar to previous studies in which lambs from Border Leicester sires produced lambs with increased point measures of fat (Atkins & Thompson, 1979; Fogarty et al., 2000) or whole carcass fat (Ponnampalam et al., 2007) compared to the lambs of other sires, and aligns well with this breeds improved reproductive capacity (Ferguson et al., 2010). The Terminal sired lambs had the least carcass fat and the highest portion of lean (Anderson et al., 2015). This lean/fat profile is consistent with the selection focus for fast-lean-growth within these breeds, which is likely to impact on mature size. Therefore at the same carcass weight, the Terminal sired lambs would be less mature and therefore have less carcass fat.

In support of our hypothesis, at any given carcass weight the Merino sired lambs had a greater proportion of bone than the Maternal and Terminal sired lambs, aligning well with work by Cake et al. (2007). This is unlikely to be associated with mature size as Merino's are smaller at maturity than Maternal or Terminal sired lambs (Hopkins, Stanley, Martin, & Gilmour, 2007), hence the differences are more likely to reflect variation in their composition at maturity.

The Terminal sired lambs had the least fore section bone compared to the Merino and Maternal sired lambs. These lambs also had the most fore section lean (Anderson et al., 2015), which supports the notion that lambs selected for muscling, such as the Terminal sired lambs, undergo bone hypotrophy (Cake et al., 2007). However, if this were true then we would also expect lambs from sires with high PEMD to have less bone which was not evident

in the current study. The decreased fore section bone in Terminal sired lambs is not likely due to maturity, with fore section bone maturing at the same rate as total bone in lambs sired by all sire types.

The Terminal sired lambs had the least fore section fat, with maturity a possible explanation given fat in this section is relatively early maturing. However the small differences in fat distribution between sire types in other carcass sections make this explanation less tenable. The variation in carcass fat and bone distribution in lambs from different sire types has not been previously reported.

4.2. Production factors affecting carcass fat and bone.

The differences between carcass composition of ewes and wethers in this study are similar to previous studies, with reports of ewes having the greatest weight of fat (Afonso & Thompson, 1996; Butterfield, 1988) and least bone (Thompson, Atkins, & Gilmour, 1979a) when compared at the same carcass weight. These castrate male and female differences can be partly attributed to differences in mature size (Hopkins, Stanley, Martin, & Gilmour, 2007) and mature composition. Alternatively, the differences may also relate to fat distribution between the main fat depots: subcutaneous, intermuscular, abdominal and intramuscular. Butterfield (1988) showed in Merinos that both sexes are likely to have similar total body fat weights, with rams having less subcutaneous fat but more intermuscular and mesenteric fat. Differences in bone may be due to wethers having longer, and thicker bones compared to ewes (Wood, MacFie, Pomeroy, & Twinn, 1980). Finally, the rate maturation of fat and bone may differ in females compared to males but the lack of sex interaction with the b coefficient makes this scenario less significant.

The carcasses of wether lambs had more bone in the fore section and less bone in the saddle than ewe lambs which is similar to results found by Thompson, Atkins, and Gilmour (1979b). This earlier study showed Merino wethers had more forelimb bone when compared at the same total bone weight, which may be due to increased forelimb thickness. Our wether lambs also had increased fore section lean (Anderson et al., 2015), perhaps due to the need for more dominant male behaviour as suggested by Butterfield (1988), explaining the need for an increase in supporting fore section bone.

Differences in carcass fat and bone between sites, and kill groups, are likely to be reflective of a range of processing, environmental, nutritional, age effects, or CT measurement error – all of which this study was not specifically designed to address. Conflict exists with respect to the impact of a high plane of nutrition on carcass fat, with some studies showing that animals on a high plane of nutrition have a higher proportion of fat in the carcass (Berg & Butterfield, 1968), while others have shown no change in carcass fat (Lee, Harris, Ferguson, & Jelbart, 1990). Compared at the same carcass weight there was a trend for the site-years with the lowest proportion of bone to have the largest proportions of fat, with the remainder of the weight difference accounted for by lean (Anderson et al., 2015).

Within a site, animals in the younger kill groups generally had less carcass fat, although carcasses from two sites have results contrary to this trend. Lamb carcasses from earlier kill groups represent faster growing animals that reach slaughter weights earlier. These lambs were likely to be on a growth path to larger mature size and would be at a smaller portion of their mature weight. Alternative explanations could be associated with variation in nutrition, i.e. ewe milk output and pasture conditions, or worm burdens (ewe and lamb impacts). Given

there was no consistent trend between carcass bone weight and kill group (age) there appears to be no obvious association between age and proportion of carcass bone.

Lambs born as triplets and raised as singles had carcasses with low saddle section fat and high hind section fat, which may indicate a distributional effect of compensatory growth. However there were only 11 animals within this category, which is too few to draw conclusive interpretations. The reasons for lambs born and raised as triplets having carcasses with altered bone distribution are unclear. These lambs may be late maturing given the saddle and hind sections are late and early with respect to their rate of maturation of bone which may be the cause of the high and low weight of bone in these sections.

4.3. Allometric coefficient

Previous studies assessing allometric coefficients used manual dissection rather than CT, and the allometric coefficients within this study align well with previous experiments (Afonso & Thompson, 1996; Berg & Butterfield, 1968; Butterfield et al., 1983; Butterfield, Zamora, Thompson, Reddacliff, & Griffiths, 1984), demonstrating the well known principles that fat is a late maturing tissue and bone an early maturing tissue. There were no significant interactions of the b coefficients with any fixed effects, which is in contrast to studies by Fourie, Kirton, and Jury (1970), and Thompson, Parks, and Perry (1985) who showed the maturation rate of fat to be earlier in ewes compared to rams. Thompson, Parks, and Perry (1985) also showed bone to be earlier maturing in ewes compared to rams. Alternatively, Afonso and Thompson (1996) and Thompson, Atkins, and Gilmour (1979a) both demonstrated no difference in the rate of fat development between sexes. The lack of difference in our study may be explained by the fact that our animals were wethers and not rams or that the age range in this experiment did not provide sufficient sensitivity to detect

differences (24-60 weeks of age) compared to birth to 102 weeks of age in the study of Thompson, Butterfield, and Perry (1985).

There are fewer studies that assess the rate of development of fat and bone between the fore, saddle, and hind sections. The fore section fat was earliest to develop followed by the hind and saddle section. The early development of the fore section fat negates the potential to manipulate fatness in this region simply by slaughtering lambs at earlier ages. The rate of maturation of the bones within the three sections also varied, with the hind section earliest to mature; the fore section maturing at the same rate as total carcass bone and saddle bone being late maturing. These results for fat and bone are similar to those of earlier studies based on manual dissection (Butterfield & Thompson, 1983; Thompson et al., 1979b).

4.4. Comparison of effects

4.4.1. Genetic effects on carcass fat and bone

The impact of the ASBVs on carcass fat was far greater than that of the non-genetic effects. Among these ASBV effects, the impact of PFAT was about 60% greater than the impact of PEMD on carcass fat, however the latter was not consistent across all sire types with no effect observed in the Merino sired lambs. The PWWT ASBV also had a substantial impact on carcass fat, but only at some sites making its use in carcass fat reduction less important.

The magnitude of the ASBV effects on bone was less than that observed for fat. Of the genetic effects, decreasing sire PFAT had the greatest influence on the proportion of carcass bone and was approximately 1.6 times greater than that of the sire type effect. The PWWT effect was variable and only observed in some years at certain sites with individual kill groups

showing no consistent effect. There was no impact of PEMD on carcass bone weight or its distribution.

Therefore we can conclude that sire PFAT had the most impact on fat composition within the carcass, having a magnitude of impact at least 50% greater than the effect of PEMD or PWWT. Similarly, PFAT also had the most marked impact on bone composition, with neither PEMD nor PWWT having any impact on whole carcass bone. All three ASBVs had minimal impact on fat and bone distribution, with increased sire PWWT resulting in only small increases in hind section bone.

Sire type impacted carcass fat and bone composition, however the magnitude of these effects was less than those of the ASBVs. Maternal sired lambs were fatter and Merino sired lambs had more carcass bone. In contrast to the whole carcass effects, there was a greater impact of sire type and dam breed on fat and bone distribution compared to the ASBVs.

4.4.2. Production factors affecting carcass fat and bone

Among the production and management effects, site and kill group had the largest impact on carcass fat and its distribution between sections. Site had more than double the impact of the sex and birth-type rear-type effects, demonstrating the potential for nutrition, and other environmental factors to impact on carcass fat and its distribution.

In contrast to fat, the greatest impact on bone was seen with site, year and kill groups, having up to three times the magnitude of impact compared to the strongest genetic effects observed with PFAT. Of the other non genetic effects, sex had less impact on carcass bone and its distribution.. Similarly, birth type-rear type had minor impacts on bone with its distribution only impacted in lambs born and raised as triplets.

606

607 4.5. *Conclusions*

608 The effectiveness of using the PFAT and PEMD breeding values to reduce carcass fat is
609 well demonstrated by this study. Furthermore, the impact of these ASBVs has been shown to
610 impact not only at the site of measurement in the saddle region, but across all regions of the
611 carcass. The PFAT breeding value was also shown to increase the proportion of carcass bone,
612 however this was a comparatively small effect relative to the decrease in carcass fat and
613 increase in carcass muscle attributed to this breeding value, suggesting an overall positive
614 impact on carcass value. The PWWT breeding value does not appear to have a strong
615 influence on whole carcass fat, with any effects heavily influenced by lamb nutrition and
616 environmental conditions. The impact of PWWT and PEMD on carcass bone weight or its
617 distribution throughout the carcass was minimal. This is an important finding as it implies that
618 selection for improved lean meat yield does not negatively impact carcass composition by
619 increasing the proportion of bone, which is considered undesirable by the consumer.

620

621 There are marked differences between sire types with respect to the amount of fat and
622 bone within the carcass, with Merino sired lambs having the most carcass bone, and Maternal
623 sired lambs the most carcass fat. Production factors and environmental effects were also
624 shown to impact both fat and bone in the carcass, with sex having a marked effect on carcass
625 fat, and environmental effects like site and killgroup having marked effects on bone. Further
626 analysis of the data from this experiment will help determine the economic implications of
627 these changes.

628

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788

789 Table 1. Total number of lamb carcasses scanned using computed tomography at each
790 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	25	-	1665

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Table 2. Number of lamb carcasses 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

792

BLM: Border Leicester x Merino

Table 3. F-values and numerator and denominator degrees of freedom of factors affecting fat and bone weight of lamb in the whole carcass and the distribution of fat and bone between the fore, saddle and hind sections of the lamb carcass.

Effect	Whole carcass analysis			Fat distribution between sections				Bone distribution between sections			
	NDF, DDF	Carcass fat	Carcass bone	NDF, DDF	Fore- section	Saddle- section	Hind- section	NDF, DDF	Fore- section	Saddle- section	Hind- section
		F-values			F-values				F-values		
Site-year	8,177	27.35**	60.79**	7,170	25.19**	94.75**	100.38**	7,169	31.42**	8.96**	43.89**
Sex(sire type)	1,177	124.61**	36.89**	1,170	23.91**	55.93**	17.5**	1,169	8.1**	15.08**	2.58
Birth-type rear-type	NA	NA	NA	5,170	2.04	5.04**	2.46*	5,169	0.78	2.51*	7.46**
Sire type	2,177	13.58**	13.63**	2,170	10.41**	18.77**	2.71	2,169	11.52**	2.57	3.58*
Kill group (site-year)	16,177	7.51**	13.19**	15,170	9.7**	13.78**	8.6**	15,169	7.75**	4.01**	7.68**
Dam breed (sire type)	1,177	11.22**	1.02	NA	NA	NA	NA	1,169	0.71	1.98	6.66*
Site-year x sire type	13,177	2.78**	1.27	12,170	1.58	4.23**	4.23**	NA	NA	NA	NA
Site-year x dam breed (sire type)	5,177	4.48**	1.18	NA	NA	NA	NA	NA	NA	NA	NA
Log _e x ¹	1,177	3638.16**	1855.03**	1,170	8357.13**	25459.4**	7738.26**	1,169	7218.74**	3335.74**	4751.55**

NDF, DDF: numerator and denominator degrees of freedom.

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

¹ Where carcass fat and bone were analysed, the covariate (x) was carcass weight (kg), and when fat and bone distribution was analysed either whole carcass fat or whole carcass bone was the covariate (x).

* P < 0.05, **P < 0.01

Table 4. The relative change (% change in weight) for site-year, sex dam breed(sire type) and birth-type rear-type impact on lamb carcass fat weight and the distribution of fat between the fore, saddle and hind sections of the lamb carcass.

Effect	Level	Carcass fat weight	Section fat weight (fat distribution between sections)		
		% change in weight	Fore- section % change in weight	Saddle- section % change in weight	Hind- section % change in weight
Site-year ¹	Kirby 2007	0.81^a	-0.38^{de}	5.47^c	-9.31^{bc}
	Kirby 2008	12.64^c	-7.48^b	11.80^e	-14.76^a
	Rutherglen 2010	13.64^c	-8.08^{ab}	1.19^{ab}	8.47^e
	Hamilton 2009	5.71^b	-9.82^a	13.0^e	-13.32^{ab}
	Struan 2010	14.98^c	-0.62^{de}	0.63^{ab}	0.06^d
	Turretfield 2009	7.64^b	-1.93^d	1.39^b	0.33^d
	Katanning 2007	6.68^b	NA	NA	NA
	Katanning 2008	8.56^b	-5.34^c	8.19^d	-8.68^c
	Katanning 2011	0.00^a	0.00^e	0.00^a	0.00^d
SexDambreed (sire type) ²	Maternal x Merino M	9.55^l	1.97^k	-0.69^j	-1.62^{ijk}
	Merino x Merino M	3.23^{jk}	2.22^k	-1.89ⁱ	-0.44^{kl}
	Terminal x BLM F	9.88^l	-1.80ⁱ	2.49^k	-2.81ⁱ
	Terminal x Merino F	5.81^k	-2.33ⁱ	2.75^k	-2.32^{ij}
	Terminal x BLM M	1.86^{ij}	0.34^j	0.03^j	-1.05^{jkl}
	Terminal x Merino M	0.00ⁱ	0.00^j	0.00^j	0.00^l
Birth-type rear-type ³	Born and raised as single	NA	-0.34	-1.35^x	2.72^x
	Born twin, raised single	NA	-0.26	-0.92^{xy}	1.89^x
	Born and raised as twin	NA	-1.48	0.12^z	1.32^{wx}
	Born triplet, raised single	NA	0.96	-3.09^w	4.23^y
	Born triplet, raised twin	NA	-2.11	0.25^z	1.47^x
	Born and raised as triplet	NA	0.00	0.00^{yz}	0.00^w
<i>b coefficient (±SE)</i>					
log x ⁴		1.48 ±0.025	0.85 ±0.010	1.15 ±0.007	0.92 ±0.011

% change in weight: the difference in log_e y 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 x Merino

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

^{1 a-e} 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 sex-dambreed (sire type), % change in weight values without a common superscript differ significantly at $P < 0.05$.

^{3 w-z} Within columns for birth-type rear-type, % change in weight values without a common superscript differ significantly at $P < 0.05$.

815 ⁴Where carcass fat was analysed, carcass weight was the covariate (x) and when fat distribution was
816 analysed whole carcass fat was the covariate (x)

Table 5. The relative change (% change in weight) for site-year, sex dam breed(sire type) and birth-type rear-type impact on carcass bone weight and the distribution of bone between the fore, saddle and hind sections of the lamb carcass.

Effect	Level	Carcass bone weight	Section bone weight (bone distribution between sections)		
		% change in weight	Fore-section	Saddle-section	Hind-section
		% change in weight	% change in weight	% change in weight	% change in weight
Site year ¹	Kirby 2007	-6.34^{de}	6.30^d	0.40^{abc}	-6.58^a
	Kirby 2008	-10.93^{bc}	1.66^{bc}	4.69^e	-4.31^{bc}
	Rutherglen 2010	3.68^g	1.75^{bc}	3.25^{de}	-3.99^{bcd}
	Hamilton 2009	-8.16^{cd}	0.88^{ab}	3.47^{de}	-2.58^d
	Struan 2010	-15.68^a	2.73^c	3.07^{cde}	-4.80^b
	Turretfield 2009	-10.37^{bc}	0.11^a	-1.02^a	0.89^e
	Katanning 2007	-4.73^e	NA	NA	NA
	Katanning 2008	-12.18^b	2.17^{bc}	2.02^{bcd}	-3.20^{cd}
	Katanning 2011	0.00^f	0.00^a	0.00^{ab}	0.00^e
Sex dam breed (sire type) ²	Maternal x Merino M	0.19^k	0.95^l	-0.24^{ij}	-0.90ⁱ
	Merino x Merino M	4.10^l	1.45^l	-1.41ⁱ	-0.65ⁱ
	Terminal x BLM ⁷ F	-3.19ⁱ	-1.24ⁱ	1.30^{jk}	0.43^j
	Terminal x Merino F	-1.73^j	-0.95^{ij}	2.45^k	-0.65ⁱ
	Terminal x BLM M	0.47^k	-0.33^{jk}	-0.70^{ij}	0.79^j
	Terminal x Merino M	0.00^k	0.00^k	0.00^{ij}	0.00^{ij}
Birth-type rear-type ³	Born and raised as single	NA	-1.69	-4.69^w	4.87^y
	Born twin, raised single	NA	-1.69	-3.86^{wx}	4.23^{xy}
	Born and raised as twin	NA	-1.39	-3.09^{wx}	3.46^x
	Born triplet, raised single	NA	-2.14	-3.13^{wx}	3.87^{xy}
	Born triplet, raised twin	NA	-2.03	-2.81^x	3.97^{xy}
	Born and raised as triplet	NA	0.00	0.00^y	0.00^w
<i>b</i> coefficient (±SE)					
log x ⁴		0.729 ±0.017	1.030 ±0.012	1.235 ±0.021	0.816 ±0.012

% change in weight: the difference in log_ey 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 x Merino

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

¹ ^{a-e} 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 bone weight was analysed, carcass weight was the covariate (x) and when bone distribution was analysed whole carcass bone was the covariate (x)

832 Table 6. F-values, and numerator and denominator degrees of freedom in lambs for Australian Sheep Breeding Values affecting fat and bone weight in the
833 whole carcass and distribution of fat and bone between the fore, saddle and hind sections of the lamb carcass.

Effect	Whole carcass analysis			Fat distribution between sections				Bone distribution between sections			
	NDF,	Carcass	Carcass	NDF,	Fore-	Saddle-	Hind-	NDF,	Fore-	Saddle-	Hind-
	DDF	fat	bone	DDF	section	section	section	DDF	section	section	section
		F-values			F-values				F-values		
PWWT	1,156	2.55	0	1,166	0.06	0.95	0.96	1,166	3.06	0.03	4.13*
PWWT x site-year	8,156	3.14**	1.24	7,166	1.15	2.2*	2.72*	7,166	0.34	2.35*	3.25**
PWWT x kill group (site-year)	16,156	2.16**	1.78*	NA	NA	NA	NA	NA	NA	NA	NA
PFAT	1,156	91.81**	11.09**	NA	NA	NA	NA	NA	NA	NA	NA
PEMD	1,156	24.58**	1.5	NA	NA	NA	NA	NA	NA	NA	NA
PEMD x sire type	2,156	4.54*	0.4	NA	NA	NA	NA	NA	NA	NA	NA

834 NDF, DDF: numerator and denominator degrees of freedom.

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

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

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

838 Table 7. Percentage change in weight per unit of Australian Sheep Breeding Values on lamb carcass
839 fat weight and fat distribution between the fore, saddle and hind sections of the lamb carcass.

Effect	Level	Carcass fat weight	Section fat weight (fat distribution between sections)		
		% change in weight	Fore- section % change in weight	Saddle- section % change in weight	Hind- section % change in weight
PWWT		-0.19	-0.02	0.06	-0.09
PWWT x	Kirby 2007	-0.85	-0.22	0.00	0.33
site-year	Kirby 2008	-0.07	0.05	-0.17	0.18
	Rutherglen 2010	-0.54	0.16	0.29	-0.68
	Hamilton 2009	0.30	0.08	-0.06	-0.21
	Struan 2010	-0.05	-0.23	0.12	0.05
	Turretfield 2009	0.40	-0.15	0.26	-0.23
	Katanning 2007	-0.20	NA	NA	NA
	Katanning 2008	-0.48	0.21	-0.02	-0.20
	Katanning 2011	-0.23	-0.08	0.10	0.01
PFAT		4.84	NA	NA	NA
PEMD		-2.13	NA	NA	NA
PEMD x	Maternal	-3.80	NA	NA	NA
sire type	Merino	-0.63	NA	NA	NA
	Terminal	-1.96	NA	NA	NA

840 % Change in weight is per unit of the relevant Australian Sheep Breeding Value
841 PWWT: post weaning weight; PFAT: post weaning c-site fat depth; PEMD: post weaning eye muscle depth
842 NA: term was not retained in the final model as was not significant for any section (fore, saddle, hind)
843 Significant effects are in bold ($P<0.05$).

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

Effect	Level	Carcass bone weight	Section bone weight (bone distribution between sections)		
		% change in weight	Fore-section	Saddle-section	Hind-section
		% change in weight	% change in weight	% change in weight	% change in weight
PWWT		0.01	-0.10	-0.02	0.12
PWWT x	Kirby 2007	0.20	-0.07	-0.40	0.34
site-year	Kirby 2008	-0.03	-0.06	0.00	0.06
	Rutherglen 2010	0.08	-0.07	-0.38	0.35
	Hamilton 2009	0.03	-0.13	0.23	-0.04
	Struan 2010	-0.19	-0.11	-0.23	0.23
	Turretfield 2009	-0.28	-0.04	0.38	-0.20
	Katanning 2007	0.10	NA	NA	NA
	Katanning 2008	-0.06	-0.26	0.24	0.17
	Katanning 2011	0.21	-0.06	0.01	0.06
PFAT		-1.27	NA	NA	NA
PEMD ¹		-0.39	NA	NA	NA

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

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

¹This term was included in the model as it was significant in the analysis of carcass fat and lean.

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

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