



## Intramuscular fat in the *longissimus* muscle is reduced in lambs from sires selected for leanness<sup>☆</sup>

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### ABSTRACT

Selection for lean growth through Australian Sheep Breeding Values (ASBVs) for post weaning weight (PWWT), eye muscle depth (PEMD) and c-site fat depth (PFAT) raises concerns regarding declining intramuscular fat (IMF) levels. Reducing PFAT decreased IMF by 0.84% for Terminal sired lambs. PEMD decreased IMF by 0.18% across all sire types. Female lambs had higher IMF levels and this was unexplained by total carcass fatness. The negative phenotypic association between measures of muscling (shortloin muscle weight, eye muscle area) and IMF, and positive association between fatness and IMF, was consistent with other literature. Hot carcass weight increased IMF by 2.08% between 12 and 40 kg, reflective of development of IMF as lambs approach maturity. Selection objectives with low PFAT sires will reduce IMF, however the lower impact of PEMD and absence of a PWWT effect, will enable continued selection for lean growth without influencing IMF. Alternatively, the negative impact of PFAT could be off-set by inclusion of an IMF ASBV.

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### 1. Introduction

Premium quality and value for money are crucial consumer expectations when purchasing prime lamb meat (Pethick, Banks, Hales, & Ross, 2006). While consumers maintain a desire for flavoursome meat, they are increasingly seeking lower fat/healthier food options (Harper & Pethick, 2004); two important consumer drivers which are linked through the level of intramuscular fat (IMF) (Harper & Pethick, 2004). Intramuscular fat has an important influence on meat palatability due to its specific contribution to juiciness, flavour and tenderness (Neely et al., 1998; Pannier et al., 2014; Thompson, 2004; Wheeler, Cundiff, & Koch, 1994) and it has been found to contribute 10–15% of the variance in palatability of beef (Dikeman, 1987). Indeed, work on lamb has estimated that a threshold of 4–5% IMF is required to achieve consumer satisfaction for palatability (Hopkins, Hegarty, Walker, & Pethick, 2006).

The impact of nutritional, environmental and production factors on IMF has previously been quantified as well as their subsequent influence on meat eating quality. This includes the impact of

different dietary treatments (Pethick, Davidson, Hopkins, Jacob, D'Souza, Thompson and Walker, 2005), sex (Craigie et al., 2012; Santos, Silva, Mena, & Azevedo, 2007), and carcass weight (Craigie et al., 2012; Pethick, Hopkins, D'Souza, Thompson, & Walker, 2005). Genetic factors also influence IMF deposition, and various studies have shown differences between genotypes. Hopkins, Stanley, Martin, Toohey, and Gilmour (2007) and McPhee, Hopkins, and Pethick (2008) demonstrated higher IMF levels when the proportion of Border Leicester (Maternal) within a breed type increased. Furthermore, a recent study has demonstrated the heritability of IMF in lamb was high, which was estimated at  $0.47 \pm 0.04$  (Mortimer et al., 2014), indicating a potential for genetic manipulation of the trait.

Genetic selection for lean growth has been linked to declining IMF levels with subsequent detrimental effects on meat eating quality (Hopkins, Hegarty, & Farrell, 2005). The improvements in leanness and growth, in combination with greater muscling have also led to improvements in carcass qualities (Banks & Ross, 2003) which will be more efficient for on-farm production and result to an increase in lean meat yield for processors and retailers (Pethick et al., 2006). Australian lamb producers can select indirectly for increased lean meat yield through the use of Australian Sheep Breeding Values (ASBVs) for post weaning weight (PWWT), eye muscle depth (PEMD) and c-site fat depth (PFAT; defined here as 4.5 mm from the midline over the 12th rib). Lambs selected from sires with reduced PFAT have reduced whole carcass fatness and increased loin muscle weight (Gardner et al., 2010). Similarly, lambs selected from sires with higher PEMD breeding values have

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increased muscling in high valued cuts mainly located in the animal's saddle region (Gardner et al., 2010). Lambs selected for high PWWT will be faster growing due to a larger mature size (Huisman & Brown, 2008) and will therefore be less mature and leaner at the same slaughter weight. It is likely that these impacts on lean growth will reduce IMF.

The Australian Cooperative Research Centre (CRC) for Sheep Industry Innovation established an Information Nucleus Flock (INF). Commencing in 2007, it produced approximately 2000 slaughter lambs each year over a 5 year period. Some of the INF objectives are to measure a diverse range of phenotypic traits, and to produce heritability estimates and genetic correlations for a range of new traits such as IMF (Mortimer et al., 2014). This paper describes the associations between genetic and non-genetic factors such as site (research station), year of birth, sex, birth-rearing type, dam breed, sire type, kill groups, and carcass composition traits such as muscle and carcass fat with IMF in the lamb *longissimus* muscle from diverse genetic backgrounds. Given that the INF lamb flocks are maintained across different production regions in Australia (Fogarty, Banks, van der Werf, Ball, & Gibson, 2007; van der Werf, Kinghorn, & Banks, 2010), the environmental impact can also be quantified. Results from three years of progeny (2007–2009) from the INF are presented in this paper. We hypothesised that lambs from sires with reduced PFAT, and increased PEMD and PWWT breeding values would have decreased IMF levels, and that this would be reflected through the correlation between IMF and the phenotypic expression of leanness (shortloin fat weight and GR tissue depth), muscling (shortloin muscle weight and eye muscle area) and growth (at a given weight) that these ASBVs deliver. Furthermore, we hypothesised that lambs sired from Maternal breeds will have higher IMF levels compared to those sired by Merino and Terminal breeds.

## 2. Material and methods

### 2.1. Experimental design and slaughter details

The design of the Sheep CRC INF is detailed elsewhere (Fogarty et al., 2007; van der Werf et al., 2010). Briefly, approximately 6000 lambs were produced over a 3 year period (2007–2009) at eight research sites across Australia (Katanning WA, Cowra NSW, Trangie NSW, Kirby NSW, Struan SA, Turretfield SA, Hamilton VIC, and Rutherglen VIC), which represent a broad cross-section of Australian production systems. The lambs (Merino × Merino, Maternal × Merino, Terminal × Merino and Terminal × Border Leicester–Merino) were the progeny of 279 key industry sires, representing the major production types in the Australian sheep industry. The sires included Terminal sires (Hampshire Down, Ile De France, Poll Dorset, Southdown, Suffolk, Texel, White Suffolk), Maternal sires (Bond, Booroola, Border Leicester, Coopworth, Corriedale, Dohne Merino, East Friesian, Prime SAMM, White Dorper), and Merino sires (Merino, Poll Merino). Lambs were mainly maintained under extensive pasture grazing conditions, but were fed grain, hay or feedlot pellets when feed supply was limited at some sites (Ponnampalam et al., 2014). Lambs were yarded the day before slaughter, held for 6 h and then weighed and transported to one of the five commercial abattoirs, where they were held in lairage overnight and slaughtered the following day at an average carcass weight of 22.9 kg. For each site lambs were consigned to smaller groups which were killed at the same day (kill groups) to enable carcass weight targets to be achieved. All carcasses were subjected to a medium voltage electrical stimulation (Pearce et al., 2010) and trimmed according to AUS-MEAT specifications (Anonymous, 1992). Carcasses were chilled overnight (3–4 °C) before sampling. All lambs were measured and sampled for a wide range of live animal, carcass, meat and growth traits.

### 2.2. Sample collection and measurements

Hot carcass weight (HCWT) was measured after slaughter and GR tissue depth (11 cm from the midline to the lateral surface of the 12th

rib) and eye muscle area (between 12 and 13th rib) were measured on the carcass. At 24 h post-mortem the entire *longissimus lumborum* muscle (shortloin muscle) (up to the 12th rib) was excised from the carcass and weighed (shortloin muscle weight). Subcutaneous loin fat was dissected and weighed (shortloin fat weight) and silver skin was removed. Approximately 40 g of diced loin muscle was collected in 50 ml tubes. Samples were stored at –20 °C until subsequent freeze drying. Samples were commercially freeze-dried using a Cuddon FD 1015 freeze dryer (Cuddon Freeze Dry, NZ). The IMF content was determined using a near infrared procedure (NIR) in a Technicon InfraAnalyzer 450 (19 wavelengths) (Perry, Shorthose, Ferguson, & Thompson, 2001). NIR readings were validated with chemical fat determinations using solvent extraction. IMF was expressed as percentage fat.

### 2.3. Statistical analysis

IMF levels were analysed using linear mixed effects models (SAS Version 9.1, SAS Institute, Cary, NC, USA). The base model included fixed effects for site (Kirby, Trangie, Cowra, Rutherglen, Hamilton, Struan, Turretfield, Katanning), year (2007, 2008, 2009), sex (male, female), birth-rearing type (term representing animals born as single, twin or triplet and reared as single, twin or triplet; 11, 21, 22, 31, 32, 33), sire type (Merino, Maternal, Terminal), dam breed within sire type (Merino × Merino, Maternal × Merino, Terminal × Merino, Terminal × Border Leicester–Merino) and kill group within site by year. Sire identification, and dam identification by year were included as random terms. All relevant first order interactions between fixed effects were tested and non-significant ( $P > 0.05$ ) terms were removed in a stepwise manner.

The same approach was taken to test the impact of age at slaughter on IMF, however in this case the kill group within site by year term was removed as a fixed effect and used as a random term. This is because within each site by year, age was confounded by kill group (i.e. there were no lambs of the same age within a separate kill group, and the range in age within each kill group was less than 10 days). Thus kill group accounted for the slaughter-age effect, and removing this term as a fixed effect enabled the impact of age at slaughter to be estimated.

The associations between IMF and sire ASBVs for PWWT, PEMD and PFAT were also tested in the base model. Initially all 3 ASBVs were included as covariates in the model, as well as their first order interactions with other terms and their quadratic effects. Non-significant ( $P > 0.05$ ) terms were removed in a stepwise manner. Due to the correlations that exist between these ASBVs in this data set (PWWT vs PEMD = 0.3; PWWT vs PFAT = –0.3; PFAT vs PEMD = 0.2) this process was repeated with the ASBVs included one at a time to test the independence of their effects.

The base and ASBV models described above were also tested with the inclusion of HCWT as a covariate to assess whether the observed effects were associated with their correlated impacts on HCWT. Likewise, to test for associations between IMF and carcass composition traits such as muscling and fatness were incorporated as phenotypic covariates (one at a time) such as shortloin fat weight, GR tissue depth, shortloin muscle weight and eye muscle area in the base and ASBV models with HCWT. These models included all relevant first order interactions between fixed effects and covariates, as well as the quadratic effects for each covariate. Non-significant ( $P > 0.05$ ) terms were removed in a stepwise manner.

## 3. Results

### 3.1. Levels of intramuscular fat

The average IMF level for all lambs ( $n = 5,867$ ) for the three years was  $4.23 \pm 0.01\%$  ( $\pm$  SE), with 44.6% of all lambs having IMF levels lower than 4%.

### 3.2. Effect of genetic and non-genetic factors on intramuscular fat

The data analysed in the IMF base model has been summarised in Tables 1 and 2. The base model outcomes are presented in Table 3. The model used 5642 observations of the total 5867 available (after dropping animals with missing data) and described 52% of the total variance in IMF.

Females ( $4.20 \pm 0.04$ ) had on average about 0.10% more IMF ( $P < 0.01$ ) than males ( $4.10 \pm 0.04$ ), although this difference was not consistent across the eight sites, with no difference between sexes at the Turretfield and Hamilton sites, and females having more IMF than males by as much as 0.22% at the Rutherglen site. Single raised lambs, born as single ( $4.30 \pm 0.03$ ) or twins ( $4.19 \pm 0.04$ ) had 0.30% and 0.19% more IMF ( $P < 0.01$ ) than lambs born as triplets ( $4.00 \pm 0.13$ ). Within the Terminal sired lambs, those from Border Leicester–Merino dams ( $4.22 \pm 0.05$ ) had 0.20% more IMF ( $P < 0.01$ ) compared to lambs from Merino dams ( $4.02 \pm 0.05$ ).

IMF levels differed between sites ( $P < 0.01$ ), with lambs from Kirby and Katanning having the highest IMF across all years compared to all other sites and Rutherglen and Cowra having the lowest IMF levels. There were differences between years ( $P < 0.01$ ) although this demonstrated no consistent pattern for one particular year to always have the highest IMF across all sites. But for the most part lambs from year 2009 had the lowest IMF levels (Fig. 1). The variation between years differed between sites from as little as 0.22% for the Katanning site, to as much as 1.24% IMF for the Rutherglen site. Within each year at each site there were marked differences between kill groups ( $P < 0.01$ ) which varied by as much as 2.09% for the Katanning site. Overall there was a general trend for IMF to increase in the older kill groups, aligning well with the impact of age at slaughter which was associated with an average 2.0% increase in IMF across the age range (Fig. 2). This was reflected in a 2.4, 2.1 and 1.5% increase in IMF for the Maternal, Merino and Terminal sired lambs.

When HCWT was included in the model as a covariate, heavier carcasses had more IMF ( $P < 0.01$ ), with IMF increasing by about 2.08% across the 28 kg range in HCWT. This relationship differed between sites ( $P < 0.05$ ), sire types ( $P < 0.01$ ) and dam breeds within sire types ( $P < 0.05$ ) although these differences were small. In the HCWT corrected model, the effect of birth-rear type was no longer significant and the magnitude of the effect of dam breed halved. Alternatively, sire type became significant with Terminal ( $4.17 \pm 0.04$ ) sired lambs having 0.32 and 0.27% less IMF ( $P < 0.05$ ) than the Merino ( $4.49 \pm 0.07$ ) and Maternal ( $4.44 \pm 0.05$ ) sired lambs. All other production effects described above remained relatively unchanged by the inclusion of the HCWT covariate.

### 3.3. Effect of muscling and carcass fatness phenotypic traits on intramuscular fat

The phenotypic measures of fatness, shortloin fat weight and GR tissue depth values varied between 10–745 g and 0.5–31 mm. Both measures in the HCWT corrected model, demonstrated a positive

relationship with IMF ( $P < 0.01$ ), with levels increasing by about 1.21% IMF between 10 and 500 g shortloin fat, and by about 1.57% IMF between 0.5 and 25 mm GR tissue depth. In both cases IMF plateaued beyond 500 g of shortloin fat weight and 25 mm GR tissue depth.

The phenotypic measures of muscling, shortloin muscle weight and eye muscle area values varied between 140–670 g and 7.5–25 cm<sup>2</sup>. Compared to the fat measurements, the opposite relationship was seen for shortloin muscle weight and eye muscle area ( $P < 0.01$ ). IMF decreased by about 1.42% between a shortloin muscle weight range of 200 to 550 g, reaching a plateau beyond this point, and decreased by about 0.60% between 10 and 20 cm<sup>2</sup> eye muscle area values. The inclusion of these covariates in the base model, which also contained HCWT, had minimal impact on the significance of the other terms within the model.

### 3.4. Effect of sire and sire breeding values on intramuscular fat

In the base model, sire as a random term was significant ( $P < 0.01$ ) with sire estimates for IMF varying between 3.48 and 4.87% within Terminal, 3.93 and 4.77% within Maternal, and 3.58 and 4.64% within Merino sires.

When the sire ASBVs for PWWT, PEMD and PFAT were included simultaneously as covariates in the base linear mixed effects model, PFAT and PEMD demonstrated a significant effect ( $P < 0.05$ ). Across the 5 mm PFAT range, reducing PFAT was associated with a reduction in IMF of 0.84%, although this response was only evident in Terminal sired lambs (Fig. 3). The magnitude of this relationship was the same when PFAT was tested individually within the base model.

Between 0 and 5 mm PEMD, IMF decreased by 0.56%. However, there were relatively few sires represented above values of +3 ( $n = 6$ ) (Fig. 4). Increasing PEMD from 0 mm to +3 mm values was associated with a decrease of about 0.18% IMF (Fig. 4) and at PEMD values below 0 mm there was no impact on IMF. This effect remained fairly unchanged, although slightly diminished, when PEMD was included alone in the base model.

PWWT had no impact on IMF, and this remained the case when it was tested individually within the base model.

When the 3 ASBV model was corrected for HCWT, all of the effects described above remained unchanged. However, when either shortloin muscle weight or shortloin fat weight was included in the ASBV model, the magnitude of the PFAT effect was diminished by about one third. Likewise, the magnitude of the PEMD effect was almost halved when shortloin muscle weight was included as a covariate. The mean and range for these ASBVs are summarised in Table 4.

## 4. Discussion

### 4.1. Association of sire PFAT ASBV and phenotypic fatness and muscling on intramuscular fat

In support of our hypothesis, decreasing PFAT ASBV was associated with reduced IMF levels, although only in the progeny of Terminal

**Table 1**

Number of progeny analysed in the base model at each site according to year, sex, sire type, birth-rearing type and dam breed within sire type.

Site	Year			Sex		Sire type			Birth-rearing type					Dam breed (sire type)				
	07	08	09	F	M	Maternal	Merino	Terminal	11	21	22	31	32	33	MATM	MM	TM	TBLM
Kirby	233	392	376	313	688	193	199	609	526	100	357	6	11	1	193	199	275	334
Trangie	<sup>a</sup>	215	194	144	265	74	77	258	89	22	249	2	16	31	74	77	126	132
Cowra	284	144	197	200	425	101	86	438	145	59	311	7	52	51	101	86	252	186
Rutherglen	291	213	172	232	444	87	103	486	186	29	393	8	22	38	87	103	33	453
Hamilton	190	191	168	193	356	89	79	381	290	62	186	3	3	5	89	79	308	73
Struan	269	121	169	192	367	99	62	398	175	46	283	4	29	22	99	62	78	320
Turretfield	260	220	213	227	466	136	116	441	232	37	367	4	17	36	136	116	327	114
Katanning	387	397	346	354	776	259	194	677	438	102	524	7	48	11	259	194	677	0

07: year 2007; 08: year 2008; 09: year 2009; F: Females; M: Male wethers; MATM: Maternal × Merino; MM: Merino × Merino; TM: Terminal × Merino; TBLM: Terminal × Border Leicester–Merino.

<sup>a</sup> No animals were produced.

**Table 2**  
Raw mean  $\pm$  s.d. (min–max) for intramuscular fat and each phenotypic covariate tested within the base model.

	Intramuscular fat (%)	Hot carcass weight (kg)	Slaughter age (days)	Shortloin muscle weight (kg)	Eye muscle area (mm <sup>2</sup> )	Shortloin fat weight (g)	GR fat depth (mm)
<i>Site</i>							
Kirby	4.6 $\pm$ 1.0 (2.4–9.0)	25.5 $\pm$ 5.0 (15.4–40.0)	328 $\pm$ 56.5 (230–427)	389 $\pm$ 78.4 (140–670)	15.0 $\pm$ 2.8 (8.2–22.7)	270 $\pm$ 157 (30.0–745)	17.1 $\pm$ 6.7 (3.0–30.0)
Trangie	3.8 $\pm$ 0.9 (1.5–7.7)	23.3 $\pm$ 3.3 (16.2–34.7)	208 $\pm$ 65.6 (148–346)	360 $\pm$ 62.7 (227–582.5)	14.7 $\pm$ 2.3 (9.1–21.8)	124 $\pm$ 55.4 (30.0–330)	12.8 $\pm$ 4.4 (2.0–25.0)
Cowra	3.9 $\pm$ 0.7 (1.6–7.1)	23.4 $\pm$ 3.3 (14.0–35.3)	195 $\pm$ 54.3 (134–329)	363 $\pm$ 65.0 (160–585)	15.3 $\pm$ 2.3 (8.0–22.1)	148 $\pm$ 64.4 (20.0–385)	12.5 $\pm$ 4.0 (1.0–25.0)
Rutherglen	3.8 $\pm$ 0.9 (1.8–7.1)	22.3 $\pm$ 2.9 (14.2–31.8)	270 $\pm$ 50.9 (208–396)	335 $\pm$ 58.6 (157–558)	13.6 $\pm$ 2.1 (8.2–19.5)	190 $\pm$ 70.4 (46.0–590)	12.1 $\pm$ 4.2 (2.0–30.0)
Hamilton	4.2 $\pm$ 0.9 (2.0–7.7)	21.7 $\pm$ 3.0 (13.4–32.2)	296 $\pm$ 57.8 (225–460)	341 $\pm$ 59.6 (160–525)	13.9 $\pm$ 2.1 (8.0–20.9)	176 $\pm$ 72.9 (10.0–412)	12.8 $\pm$ 4.4 (2.0–26.0)
Struan	4.0 $\pm$ 1.0 (1.6–8.2)	22.0 $\pm$ 3.3 (12.8–29.8)	260 $\pm$ 50.4 (205–430)	337 $\pm$ 72.1 (155–590)	14.7 $\pm$ 2.1 (8.4–20.5)	193 $\pm$ 111 (21.0–543)	11.2 $\pm$ 4.2 (2.0–25.0)
Turretfield	4.0 $\pm$ 0.9 (1.9–8.4)	21.6 $\pm$ 2.6 (14.6–29.8)	256 $\pm$ 51.3 (184–364)	336 $\pm$ 57.6 (190–558)	14.5 $\pm$ 2.0 (9.6–21.1)	199 $\pm$ 107 (20.0–555)	10.1 $\pm$ 3.5 (1.5–24.5)
Katanning	4.5 $\pm$ 1.1 (1.5–9.8)	22.3 $\pm$ 3.6 (13.6–36)	274 $\pm$ 84.6 (173–504)	364 $\pm$ 72.0 (173–661)	14.9 $\pm$ 2.7 (7.5–25.2)	213 $\pm$ 88.2 (15.0–560)	13.0 $\pm$ 6.0 (0.5–31.0)
<i>Year</i>							
2007	4.2 $\pm$ 0.9 (1.5–9.0)	22.4 $\pm$ 3.1 (12.8–36.0)	257 $\pm$ 63.4 (152–460)	350 $\pm$ 62.4 (140–661)	14.6 $\pm$ 2.3 (8.3–23.7)	203 $\pm$ 86.8 (11.0–543)	12.4 $\pm$ 4.6 (1.0–31)
2008	4.4 $\pm$ 0.9 (1.8–9.5)	22.9 $\pm$ 4.3 (13.6–40.0)	288 $\pm$ 90.6 (134–504)	359 $\pm$ 75.9 (173–670)	14.6 $\pm$ 2.5 (7.5–22.7)	207 $\pm$ 113 (15.0–745)	12.9 $\pm$ 6.0 (0.5–30.0)
2009	3.9 $\pm$ 1.1 (1.5–9.8)	23.4 $\pm$ 3.9 (13.4–40.0)	260 $\pm$ 58.5 (148–365)	360 $\pm$ 71.1 (155–620)	14.6 $\pm$ 2.5 (8.0–25.2)	187 $\pm$ 125 (10.0–720)	13.7 $\pm$ 5.7 (1.5–30.0)
<i>Sex</i>							
Female	4.1 $\pm$ 0.9 (1.8–9.8)	23.0 $\pm$ 3.7 (12.8–40.0)	250 $\pm$ 57.1 (134–427)	362 $\pm$ 64.0 (165–625)	15.1 $\pm$ 2.1 (9.2–23.7)	212 $\pm$ 111 (31.0–745)	14.2 $\pm$ 5.4 (2.0–31)
Male	4.2 $\pm$ 1.0 (1.5–9.7)	22.8 $\pm$ 3.9 (13.4–40.0)	277 $\pm$ 79.0 (134–504)	353 $\pm$ 72.8 (140–670)	14.4 $\pm$ 2.5 (7.5–25.2)	193 $\pm$ 108 (10.0–720)	12.4 $\pm$ 5.4 (0.5–30.0)
<i>Sire type</i>							
Maternal	4.3 $\pm$ 1.1 (1.6–9.7)	21.8 $\pm$ 3.5 (14.0–36.6)	252 $\pm$ 60.5 (136–425)	324 $\pm$ 60.2 (155–565)	13.5 $\pm$ 2.2 (8.0–23.7)	196 $\pm$ 106 (20.0–585)	12.8 $\pm$ 5.3 (2.0–30.0)
Merino	4.5 $\pm$ 1.2 (1.8–9.0)	21.0 $\pm$ 3.6 (12.8–33.8)	374 $\pm$ 59.7 (220–504)	324 $\pm$ 65.8 (140–580)	12.9 $\pm$ 2.1 (7.5–20.7)	156 $\pm$ 106 (10.0–610)	9.94 $\pm$ 5.3 (0.5–30.0)
Terminal	4.1 $\pm$ 0.9 (1.5–9.8)	23.6 $\pm$ 3.7 (14.8–40.0)	246 $\pm$ 55.3 (134–427)	373 $\pm$ 67.9 (193–670)	15.4 $\pm$ 2.2 (9.2–25.2)	211 $\pm$ 109 (28.0–745)	13.8 $\pm$ 5.3 (1.0–31.0)
<i>BTRT</i>							
11	4.3 $\pm$ 1.0 (1.6–9.7)	23.3 $\pm$ 3.9 (13.4–40.0)	272 $\pm$ 74.2 (135–503)	363 $\pm$ 73.4 (155–670)	14.6 $\pm$ 2.5 (7.5–25.2)	207 $\pm$ 110 (10.0–720)	13.0 $\pm$ 5.7 (0.5–30.0)
21	4.2 $\pm$ 1.0 (1.9–8.4)	22.8 $\pm$ 3.9 (13.8–37.0)	274 $\pm$ 79.7 (134–504)	359 $\pm$ 68.5 (171–573)	14.6 $\pm$ 2.4 (8.3–22.1)	197 $\pm$ 117 (21.0–745)	12.8 $\pm$ 5.7 (0.5–31.0)
22	4.2 $\pm$ 1.0 (1.5–9.8)	22.7 $\pm$ 3.7 (13.4–40.0)	267 $\pm$ 71.6 (134–503)	353 $\pm$ 67.7 (140–670)	14.6 $\pm$ 2.4 (7.8–23.7)	198 $\pm$ 109 (11.0–720)	13.1 $\pm$ 5.4 (0.5–30.0)
31	3.9 $\pm$ 0.9 (2.0–5.9)	23.1 $\pm$ 4.2 (15.0–32.4)	258 $\pm$ 72.9 (156–500)	357 $\pm$ 72.6 (214–515)	14.8 $\pm$ 2.4 (8.3–19.5)	203 $\pm$ 110 (37.0–510)	12.9 $\pm$ 5.7 (2.0–25.0)
32	4.0 $\pm$ 1.0 (2.0–7.2)	22.0 $\pm$ 3.7 (12.8–33.4)	266 $\pm$ 87.0 (137–501)	339 $\pm$ 72.0 (165–661)	14.6 $\pm$ 2.5 (8.8–22.1)	178 $\pm$ 99.1 (29.0–540)	12.4 $\pm$ 5.3 (2.0–30.0)
33	3.9 $\pm$ 0.9 (1.5–7.7)	21.9 $\pm$ 2.9 (15.2–30.6)	241 $\pm$ 58.4 (139–454)	338 $\pm$ 60.1 (196–516)	14.3 $\pm$ 2.1 (10.0–20.8)	162.8 $\pm$ 91.6 (34.0–540)	12.1 $\pm$ 4.0 (4.0–30.0)
<i>Dam breed (sire type)</i>							
MATM	4.3 $\pm$ 1.1 (1.6–9.7)	21.8 $\pm$ 3.5 (14.0–36.6)	252 $\pm$ 60.5 (136–425)	324 $\pm$ 60.2 (155–565)	13.5 $\pm$ 2.2 (8.0–23.7)	196 $\pm$ 106 (20.0–585)	12.8 $\pm$ 5.3 (2.0–30.0)
MM	4.5 $\pm$ 1.2 (1.8–9.0)	21.0 $\pm$ 3.6 (12.8–33.8)	374 $\pm$ 59.7 (220–504)	324 $\pm$ 65.8 (140–580)	12.9 $\pm$ 2.1 (7.5–20.7)	156 $\pm$ 106 (10.0–610)	9.9 $\pm$ 5.3 (0.5–30.0)
TM	4.1 $\pm$ 0.9 (1.5–9.8)	22.7 $\pm$ 3.4 (14.8–38.8)	244 $\pm$ 55.3 (134–424)	369 $\pm$ 66.1 (193–661)	15.3 $\pm$ 2.3 (9.2–25.2)	202 $\pm$ 99.8 (28.0–695)	13.1 $\pm$ 5.1 (2.0–31.0)
TBLM	4.0 $\pm$ 0.9 (1.5–7.6)	24.8 $\pm$ 3.8 (15.4–40.0)	249 $\pm$ 55.3 (138–427)	378 $\pm$ 70.0 (193–670)	15.5 $\pm$ 2.2 (9.2–22.7)	221 $\pm$ 119 (35.0–745)	14.7 $\pm$ 5.4 (1.0–30.0)

MATM: Maternal  $\times$  Merino; MM: Merino  $\times$  Merino; TM: Terminal  $\times$  Merino; TBLM: Terminal  $\times$  Border Leicester–Merino.

sires. This result implies that current selection objectives for lean growth using Terminal sires with low PFAT is likely to reduce the IMF content in lamb meat. This response (0.17% IMF per mm PFAT) supports the study of Hopkins, Stanley, Toohey, Gardner, Pethick and van de Ven (2007) who also found a decrease in IMF with decreasing PFAT breeding value (0.1% IMF per mm PFAT). The lack of impact of PFAT within the Maternal and Merino sired progeny is difficult to explain, however minimal selection pressure for leanness has been applied to these breeds

traditionally. Within the Australian sheep industry, it is mainly the Terminal sires that have been selected for meat production, with the PFAT breeding value used extensively for the last 15 years to drive genetic gain for meat production. Such continued selection pressure may be required to elicit the response in IMF (Ball, Banks, Brown, & Field, 2011).

Previous studies have indicated the relationship of PFAT ASBV and carcass composition, in particular increasing shortloin muscle weight and decreasing shortloin fat weight (Gardner et al., 2010). As hypothesised,

**Table 3**  
F-values, and numerator and denominator degrees of freedom for the effects of the base linear mixed effects model of intramuscular fat (%) of the *m. longissimus lumborum* of lambs.

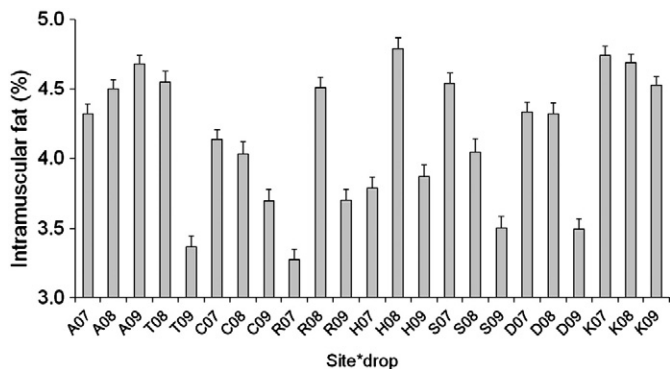
Effect	Base model not corrected for HCWT		Base model corrected for HCWT	
	NDF, DDF	F-value	NDF, DDF	F-value
Site	7, 975	62.06**	7, 945	5.35**
Year	2, 4288	56.85**	2, 4230	57.53**
Sex	1, 975	11.33**	1, 945	28.54**
Sire type	na	na	2, 945	4.28*
Birth-rearing type	5, 975	4.07**	na	na
Dam breed (sire type)	3, 975	11.11**	1, 945	5.98*
Kill group (Site * year)	64, 975	21.25**	64, 945	14.16**
Site * year	13, 975	49.75**	13, 945	42.53**
Site * sex	7, 975	3.68**	7, 945	2.90*
HCWT			1, 945	187.82**
HCWT * site			7, 945	2.64*
HCWT * sire type			2, 945	11.30**
HCWT * dam breed (sire type)			15, 945	4.56*

NDF, DDF: numerator and denominator degrees of freedom; HCWT: hot carcass weight; na: not applicable.

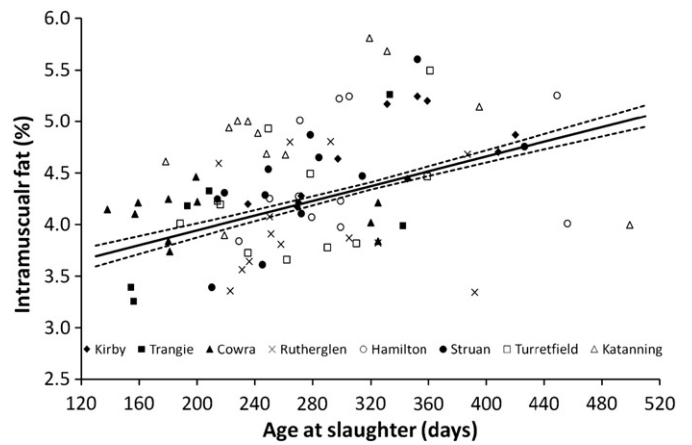
\*  $P < 0.05$ .  
\*\*  $P < 0.01$ .

these phenotypic covariates were strongly associated with IMF in the progeny of all sire types in our study. Thus, when compared at the same HCWT, IMF increased with increasing shortloin fat weight, and decreasing shortloin muscle weight by a similar magnitude for each. These associations have been well established previously and are dependent upon the relative rates of fat deposition and muscle growth (Pethick, Barendse, Hocquette, Thompson, & Wang, 2007). Furthermore, McPhee et al. (2008) demonstrated that IMF in sheep is early maturing in relation to total carcass fat – thus the proportion of IMF relative to total carcass fat decreases as animals mature (McPhee et al., 2008). This was also evident in our data given that IMF levels reached a maximum level at higher shortloin fat weights, with the shortloin fat depot crudely indicative of whole body fatness. This could imply that extended feeding schemes for lambs to high levels of total carcass fatness may not greatly promote elevated IMF levels as the genetic predisposition for development of other fat depots relative to IMF adipocytes is of higher relevance (McPhee et al., 2008).

Thus it is conceivable that the association of the PFAT ASBV and IMF is delivered entirely through its correlated impacts on whole body muscling and adiposity. Computer tomography was used to determine whole carcass muscle and fat weights on the same animals, and this data demonstrated that shortloin muscle weight was strongly correlated with whole carcass muscle weight (0.84) and shortloin fat weight was strongly correlated with whole carcass fat weight (0.83)



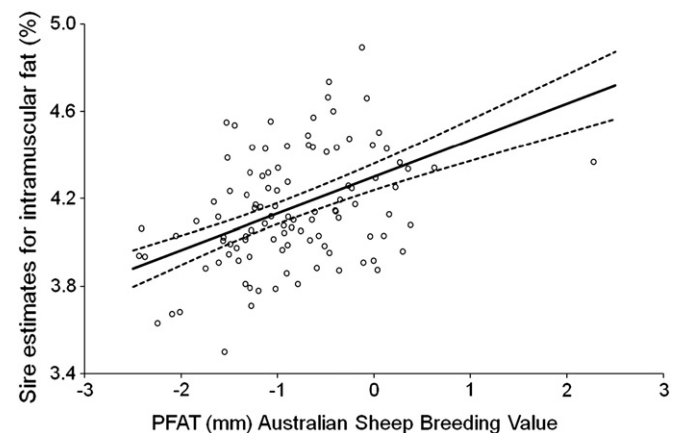
**Fig. 1.** Effect of site by year on intramuscular fat (%) levels obtained from the base model. 07: year 2007; 08: year 2008; 09: year 2009; A: Kirby; T: Trangie; C: Cowra; R: Rutherglen; H: Hamilton; S: Struan; D: Turretfield; K: Katanning.



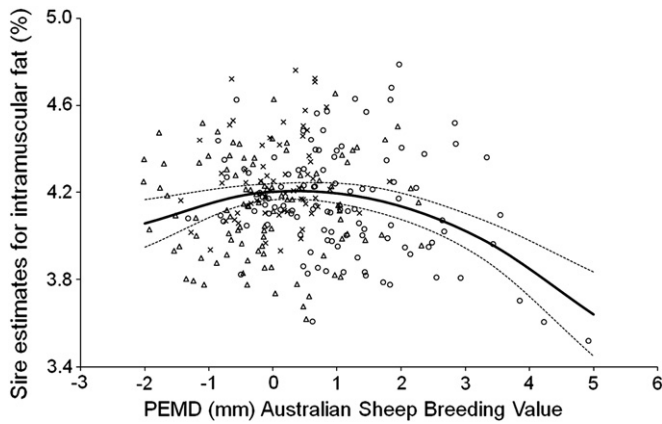
**Fig. 2.** Relationship between intramuscular fat (%) and slaughter age (days). Symbols represent kill group least squares means from the base model for each site. Lines represent least squares means for slaughter-age ( $\pm$ SE) from the base model with kill group term as a random term.

(Anderson, unpublished data). As such, these measurements are good indicators of whole carcass muscling and adiposity and would therefore be expected to account for the impact of PFAT when included in the same model. Yet contrary to this assertion, the inclusion of these two covariates simultaneously only reduced the PFAT effect within the Terminal sired progeny by less than half. This suggests that the impact of PFAT upon IMF is delivered through mechanisms other than just the correlated impact on whole body adiposity and muscling. Furthermore, if the impact of PFAT on IMF was entirely dependent upon muscling and adiposity then it should have impacted within the progeny of Maternal and Merino sired lambs where the phenotypic association between IMF and both shortloin muscle weight and fat weight was evident. Thus we can conclude that selecting for reduced PFAT ASBV will reduce IMF, impacting through mechanisms beyond just its affect on whole body muscling and adiposity.

Importantly, the sire estimates shown in Fig. 3 clearly demonstrate that there are sires within the Terminals that have low PFAT ASBVs (i.e. less than 0) and yet produce progeny with relatively high IMF levels. This highlights the potential for an IMF breeding value to be used in conjunction with PFAT ASBV enabling continued selection for leanness while maintaining IMF levels.



**Fig. 3.** Relationship between sire estimates for intramuscular fat (%) and subcutaneous post-weaning c-site fat depth (PFAT) for the Terminal sires. Lines represent least squares means for the Terminal sires for PFAT ( $\pm$ SE) from the ASBV model. Terminal sire estimates (○) plus the least squares means for the Terminal sire type are obtained from the ASBV model in which PFAT was removed.



**Fig. 4.** Relationship between sire estimates for intramuscular fat (%) and post weaning eye muscle depth (PEMD) ( $\pm$ SE). Icons represent sire estimates as (x) Maternal, ( $\Delta$ ) Merino and ( $\circ$ ) Terminal sires plus the least squares means for their respective sire type, and are obtained from the ASBV model in which PEMD was removed. Lines represent least squares means for PEMD ( $\pm$ SE) from the ASBV model.

#### 4.2. Association of sire PEMD ASBV on intramuscular fat

The PEMD sire breeding value also demonstrated a negative association with IMF, however, this effect was driven mainly by a few sires with extreme PEMD values (Fig. 4). When these sires were removed from the model, there was no significant PEMD effect, which is contrary to our initial hypothesis of increased PEMD resulting in lower IMF levels. Previous studies have shown the effect of PEMD on decreasing IMF levels, with a 0.11% decrease per mm of PEMD (Hegarty, Warner, & Pethick, 2006; Hopkins et al., 2005). However in these previous studies relatively few sires were used ( $n = 9$ ) and the PEMD was strongly correlated with PFAT (correlation coefficient = 0.55) and may have been reflecting the PFAT effect. This contrasts to our study in which 279 sires were used. As such our results indicate that there is potential for selecting for lean meat yield using PEMD without incurring the negative impact on IMF, although more sires with PEMD values higher than 3 are needed to understand the impact of this breeding value at these extremes.

#### 4.3. Sire PWWT ASBV

The PWWT ASBV was not associated with IMF, which is contrary to our initial hypothesis, and demonstrates that the selection of sires with higher PWWT would not cause any IMF differences. It has been well documented that PWWT increases growth rate as well as mature size (Huisman & Brown, 2008). Thus when killed at the same age (i.e. kill group corrects for age – see Fig. 2) these lambs were expected to be less mature and leaner but clearly this effect on IMF is too small to be detected in this analysis.

#### 4.4. Phenotypic associations with intramuscular fat

The positive association between IMF and HCWT was expected (Pethick, Harper, & Oddy, 2004), with HCWT at a constant slaughter age (i.e. kill group corrects for age – see Fig. 2) reflecting growth rate within our study. This emphasises the importance of growth rate as a

strong driver of IMF. Previous studies in lamb have confirmed this relationship in which a high phenotypic correlation coefficient (0.57) was reported between IMF and HCWT (Craigie et al., 2012).

The difference in growth rate is likely to be a reflection of environment (i.e. worm burden, feed intake, ewe milk production) rather than a genetic/mature size effect. Hence the faster growing lambs would be closer to their mature size and therefore proportionately fatter with more IMF, aligning well with results evidenced in this study. The alternative is that the lambs were growing faster due to a larger mature size. However this would imply that they would be less mature at the same carcass weight, and therefore leaner with less IMF – the opposite of what was shown in this study. In addition PWWT is known to impact mature size (Huisman & Brown, 2008), however it had no effect on IMF.

Thus at an applied level, an improved nutrition to achieve heavier weights at slaughter could be used to increase IMF levels. However, the relative improvements are poor compared to the sire effects on IMF. Every kilo of HCWT only delivers a 0.07% improvement in IMF relative to the difference between sires which was as much as 1.39% IMF (total sire range). Increased carcass weight would also be offset against a reduced lean meat yield percentage which decreases by 0.25% lean meat yield percentage units per kilo increase in HCWT (Gardner, unpublished data). Hence, given the high heritability for IMF (Mortimer et al., 2014), genetic manipulation for shifting the emphasis towards the IMF depot might be a better option for maintaining and increasing IMF levels than finishing to heavier weights.

#### 4.5. Production and management effects on intramuscular fat

The Katanning and Kirby sites had on average consistently higher IMF levels compared to the other sites and also had very similar IMF levels across the three years. Results from the other sites indicated greater variation over the three years, and varied by as much as 1.24% IMF between years for the Rutherglen site. These effects remained unchanged when HCWT was included in the model, suggesting that the differences were not simply a reflection of weight. As such the source of their site variation remains unclear, although it is likely to reflect differences in nutrition, dam genetics or slaughter age differences between sites. Nutritional effects have been shown in previous studies which demonstrated reduced levels of IMF in lambs assigned to a straw-fed finishing system for the last 12–16 days, compared to lambs fed on pasture and pellet finishing systems (Pethick, Davidson, Hopkins, Jacob, D'Souza, Thompson and Walker, 2005). Furthermore, in cattle it has been shown that grain feeding promotes more IMF development compared to grass finishing due to the increased rate of net energy needed for fat synthesis (Pethick et al., 2004). Age may also partly explain the site differences, however this seems less likely given that the site effects were unchanged when the model was corrected for age or kill group.

The differences between kill groups within each year at each site partly reflects animal age, as IMF increased in the older kill groups (see Fig. 2). One confounding factor for this interpretation could be that the older kill groups at each site consisted predominantly of Merino sired lambs because of their slower growth to target slaughter weight. As such, the age effect could have been a Merino sire type effect (average slaughter age for Merino's = 374 days; average slaughter age for Terminal and Maternal sired lambs = 249 days). However the

**Table 4**

Number of sires and mean (min, max) of Australian Sheep Breeding Values for each sire type.

Sire type	No. of sires	PFAT (mm)	PEMD (mm)	PWWT (kg)
Maternal	65	−0.08 (−1.61, 2.56)	0.06 (−1.44, 1.82)	5.19 (−3.66, 10.5)
Merino	109	−0.22 (−1.89, 1.50)	−0.10 (−2.02, 2.32)	1.81 (−5.00, 8.39)
Terminal	105	−0.85 (−2.44, 2.27)	1.07 (−1.33, 4.92)	12.1 (1.13, 18.1)

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

association with age was confirmed by excluding all kill groups which consisted of only Merino sired lambs from the analysis. In this case the magnitudes of the effect of age at slaughter were 4.9, 4.1 and 5.3 for the Maternal, Terminal and Merino sired lambs respectively. These magnitudes increased compared to the magnitudes when the Merino kill groups were included. This confirms that age is an important determinant of IMF, although the Merino sired lambs appear to follow a faster developmental pattern for IMF compared to Maternal and Terminal sired lambs. This was previously demonstrated by [McPhee et al. \(2008\)](#) who found a higher increase in IMF proportion in the *longissimus* muscle across their age range (4–22 months) for both wether and ewe Merino sired lambs compared to Maternal and Terminal sired lambs.

Female lambs demonstrated significantly higher IMF levels than male lambs, irrespectively of the HCWT correction. The mature size of female lambs is smaller, and thus when compared to males at the same average weight, they are expected to be fatter reflecting their more mature state. However, the higher female IMF levels were still present when our model was also corrected for shortloin fat weight or GR tissue depth, other measures of whole carcass body fatness, indicating that the IMF difference is due to more than just maturity and total carcass adiposity. [Craigie et al. \(2012\)](#) also found females to have higher IMF levels compared to males however entire rams were used instead of wethers. Nonetheless, when wethers and ewes were compared of different genotypes and age groups, wethers demonstrated more IMF than ewes however the age range was much larger (4–22 months) and animal numbers were much lower ( $n = 595$ ) compared to our study ([McPhee et al., 2008](#)) and hence it is hard to make direct comparisons. In contrast, [Tejeda, Peña, and Andrés \(2008\)](#) did not find a significant effect of sex on IMF levels, however this comparison was only made within Merino lambs of a small dataset ( $n = 48$ ).

The comparison of the birth-rearing types indicated that lambs born as single or twins had more IMF compared to triplet lambs reared as single animals. However these birth-rear type differences were largely a reflection of differences in HCWT as they were not significant in the HCWT corrected model.

There were no differences in IMF between sire types, contrasting with our hypothesis that Maternal sired lambs would deposit more IMF. However, when compared at the same HCWT (i.e. model corrected for HCWT) the Merino sired progeny had the highest IMF levels and the Terminal sired progeny the lowest. For Terminal sired lambs this response likely reflects the current selection objectives for rapid lean growth within this sire group making them leaner at the same weight and age. Alternatively, for Merino lambs this response is likely to reflect the combined association of IMF with both HCWT and age, thus the slower growing Merino lambs are older at a given HCWT resulting in elevated IMF.

In contrast to the sire type effect, lambs from Border Leicester–Merino dams had more IMF compared to lambs from Merino dams. This effect was only partly explained by the differences in HCWT. This contrast with the sire type result may highlight the importance of maternal nutrition for expressing this trait in lambs. These results align well with previous studies by [Hopkins, Stanley, Martin, Toohey and Gilmour \(2007\)](#) and [McPhee et al. \(2008\)](#), which reported a dam effect, whereby lambs from Border Leicester–Merino dams had higher IMF levels compared to pure Merino dams regardless of age.

#### 4.6. Comparison of effects on intramuscular fat

Hot carcass weight and differences between kill groups demonstrated the largest non-genetic effects with a magnitude more than twice that of the differences between sites and the effect of PFAT. The PFAT effect was about one third greater than the PEMD and year effects, and the impact of sex, dam breed within sire type and birth-rearing type were minimal. Therefore, while the selection for increased lean meat yield using ASBVs does impact on IMF in the *longissimus* muscle, the effect is small compared to the impact of the

other production and environmental effects. However the genetic responses do suggest some potential for genetic manipulation of IMF using breeding values.

#### 4.7. Levels of intramuscular fat in prime lamb

The average level of IMF for all INF lambs of the three years tested over all sites was 4.23%, thus higher than the minimum Australian palatability target for IMF of 4%, however there is room for improvement given that still a substantial amount of lambs had IMF levels below 4%. However these estimates for minimum levels differ for different species. For pork a minimum level of 2–2.5% was estimated ([Bejerholm & Barton-Gade, 1986](#)) while a level of 3.5% is thought to achieve optimal consumer acceptability ([Fernandez, Monin, Talmant, Mourot, & Lebret, 1999](#)). To claim a source of 'low fat' meat cuts, the fat content should be equal to or less than 3% (Food Standards Australia & New Zealand, 2004), however higher levels are required to achieve consumer satisfaction ([Hopkins et al., 2006](#); [Savell & Cross, 1988](#)). [Savell and Cross \(1988\)](#) suggested that within a broad range of IMF an impact on the palatability of meat is observed. Generally, as the IMF content increases the palatability increases and the authors stated that a meat fat content between 3 and 7.3% is generally considered acceptable. Furthermore, it has been shown that consumer sensory scores of lamb meat continuously improved when IMF levels increased between 2.5 and 7.0% ([Pannier et al., 2014](#)). Based on the studies above, we can conclude that the IMF levels of the lambs tested in this study are acceptable as they fall within this range, however ensuring that IMF levels in lamb do not decrease should be a key concern when selecting for lean meat yield.

Furthermore, the reduction of IMF driven by PFAT (within the Terminal sires) and PEMD reached minimum IMF levels around 4% ([Figs. 3, 4](#)), and the association analysis of the consumer sensory traits (tenderness, overall liking, juiciness, flavour and odour) for the INF lambs indicates a strong positive effect of IMF on all of these scores ([Pannier et al., 2014](#)), further highlighting the importance of this trait in maintaining consumer satisfaction. In addition, the negative impact of these breeding values could be off-set by inclusion of an ASBV for IMF in future breeding programmes.

## 5. Conclusions

This study demonstrated that both genetic and non-genetic factors had significant effects on IMF. Selection for lean meat yield through sires with reduced PFAT and to an extent increased PEMD breeding values decreased IMF levels in lamb meat, and therefore emphasises the current concerns of selecting for lean growth and its impact on meat quality. Growth rate was shown to be a strong driver of IMF, with the observed effects likely to be due to environmental effects. The average level of IMF in the *longissimus* muscle reached the Australian target of IMF to maintain consumer satisfaction. However, continued selection for leanness should be carefully monitored to avoid IMF levels dropping below the critical 4% threshold required to underpin consumer acceptance. Alternatively, selection programmes could incorporate a measure of IMF for inclusion within the selection index to off-set the strong negative impact of the PFAT ASBV, and part of the Sheep CRC objectives is to estimate new ASBV for traits such as IMF within the INF.

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