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Selection for lean meat yield in lambs reduces indicators of oxidative metabolism in the longissimus muscle☆

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ABSTRACT

Selection for increased lean meat yield using Australian Sheep Breeding Values for reduced post-weaning c-site fat depth (PFAT) and increased post-weaning eye muscle depth (PEMD) reduces the oxidative capacity of muscle. Isocitrate dehydrogenase (ICDH) activity and myoglobin concentration were measured in 3178 and 5580 lambs, respectively, to indicate oxidative capacity. In the progeny of sires with a reduced PFAT, ICDH activity and myoglobin concentration were reduced by 0.46 μmol/min/g tissue and 0.67 mg/g tissue across the 5 and 6 mm PFAT ranges respectively. In the progeny of sires with an increased PEMD, ICDH activity and myoglobin concentration were reduced by 0.50 μmol/min/g tissue and 0.49 mg/g tissue across the 7 and 6 mm PEMD ranges respectively. However, the sites at which the lambs were raised had a larger impact on oxidative capacity than genetic or other production factors.

1. Introduction

Lamb is marketed in Australia as a nutritious red meat and a 'good source' of iron and zinc (Pannier, Pethick, Boyce, et al., 2014a). The qualities of redness and mineral content of meat are highly linked to muscle fibre type and thus oxidative capacity of muscles, with reduced oxidative capacity being associated with reduced levels of iron and zinc (Pannier, Pethick, Boyce, et al., 2014a) and a less red appearance. For this reason oxidative capacity is an important determinant of consumer appeal impacting on both the colour and nutritional content of the product.

Muscle oxidative capacity is intrinsically linked to fibre type (Brandstetter, Picard, & Geay, 1998; Staron & Johnson, 1993) with type I muscle fibres having greater expression of oxidative enzymes (Brandstetter et al., 1998; Peter, Barnard, Edgerton, Gillespie, & Stempel, 1972) and higher levels of myoglobin (Pethick, Hopkins, D'Souza, Thompson, & Walker, 2005), in contrast to type II muscle fibres which express higher levels of glycolytic enzymes (Brandstetter et al., 1998). Therefore the activity of oxidative enzymes such as isocitrate dehydrogenase (ICDH; EC 1.1.1.42) and myoglobin concentration can be used as indicators of oxidative metabolism, an approach previously taken to study the muscle of lamb (Gardner, Pethick, Greenwood and Hegarty, 2006).

Production factors such as lamb nutrition and age have been shown to influence oxidative metabolism. A study by Gardner, Pethick, Greenwood and Hegarty, 2006 demonstrated the impact of plane of nutrition in lambs, with nutritional restriction reducing muscle ICDH activity and myoglobin concentration. In comparison the genotypic effects on these traits were smaller, having only half (for ICDH activity) or a quarter (for myoglobin concentration) the impact of the nutritional effects (Gardner, Pethick, Greenwood and Hegarty, 2006).

Animal age is also a strong driver of muscle oxidative capacity with older more mature lambs having decreased proportions of type IIX glycolytic muscle fibres, and increased proportions of type I and IIA fibres (Greenwood, Harden, & Hopkins, 2007; Suzuki & Cassens, 1983; White, McGavin, & Smith, 1978) leading to an increased ICDH activity (Brandstetter et al., 1998) and myoglobin concentration (Gardner et al., 2007; Pethick et al., 2005).

Fibre type and thus oxidative capacity can also be influenced by genetics. The Australian sheep industry uses sire Australian Sheep Breeding Values (ASBVs) to select for increased growth, muscularity and leanness, which are all likely to impact on oxidative capacity. Selection for increased growth via an increased post-weaning weight (PWWT) has been shown to correlate with an increased mature size (Huisman & Brown, 2008). Thus at the same weight lambs from high PWWT sires will be less mature resulting in reduced oxidative capacity. Increased muscularity in double muscled cattle and increased muscling in lambs, achieved by selection for an increased post-weaning eye muscle depth (PEMD), have been shown to result in a greater proportion of type IIX glycolytic fibres (Greenwood, Gardner, & Hegarty, 2006b;

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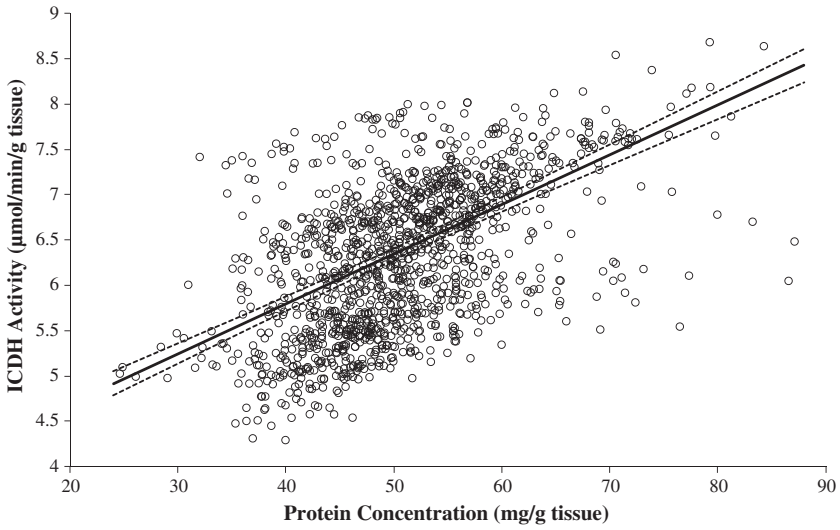

Fig. 1. Linear relationship between muscle sample protein concentration (mg/g tissue) and isocitrate dehydrogenase activity (±s.e.) in µmol/min/g tissue per gramme of protein. Each icon (○) represents an individual lamb.

Wegner et al., 2000). Likewise, selection for leanness via a reduced post-weaning c-site fat depth (PFAT) has been shown to increase eye muscle depth and increase the proportion of type IIX fibres (Greenwood et al., 2006b), reducing ICDH activity and myoglobin concentration (Gardner, Pethick, Greenwood and Hegarty, 2006). Thus current selection for increased PWWT and PEMD and reduced PFAT are all likely to reduce the oxidative capacity of muscle.

As a component of the Information Nucleus Flock (van der Werf, Kinghorn, & Banks, 2010) run by the Australian Cooperative Research Centre for Sheep Industry Innovation numerous measurements, including muscle ICDH activity and myoglobin concentration, were taken on the progeny of sires with divergent ASBVs enabling the effects of genotype and production factors to be determined. We hypothesised that increasing sire PWWT and PEMD ASBVs and reducing sire PFAT ASBVs would all reduce the oxidative capacity of muscle in their progeny. As production factors varied between sites, we also hypothesised that this would cause differences in muscle oxidative capacity and that the magnitude of these effects would be larger than the magnitude of the genotypic effects.

2. Materials and methods

2.1. Experimental design

The design of the Sheep CRC's Information Nucleus Flock was presented in detail by Fogarty, Banks, van der Werf, Ball, and Gibson (2007). Each year a total of approximately 2000 lambs were produced at eight research sites across Australia which represent a broad range of production systems (Kirby NSW, Trangie NSW, Cowra NSW, Rutherglen VIC, Hamilton VIC, Struan SA, Turretfield SA, and Katanning WA). The lambs were progeny of 267 key industry sires, including Merino sires (Merino, Poll Merino), Maternal sires (Border Leicester, Bond, Booroola, Coopworth, Corriedale, Dohne Merino, East Friesian, Prime SAMM, White Dorper), and Terminal sires (Hampshire Down, Ile De France, Poll Dorset, Southdown, Suffolk, Texel, White Suffolk). Lambs were reared under extensive pasture grazing conditions and fed grain, hay or feedlot pellets when feed supply was limited (Ponnampalam et al., 2014) to enable them to reach an average carcass weight of approximately 21.5 kg. The time taken to reach this weight varied between 134 and 504 days. Lambs were yarded for 6 h on the day before slaughter then transported to one of five commercial abattoirs where they were held in lairage overnight. After slaughter, all carcasses were subjected to medium voltage electrical stimulation (Pearce et al., 2010) and dressed according to AUS-MEAT specifications (Anonymous, 1992). Carcasses were chilled overnight (3–4 °C) before a wide range of carcass and meat traits were sampled.

2.2. Collection of phenotypic measurements

Hot carcass weight (HCWT) was measured at slaughter, and within 5 h post-mortem a 1 g sample of m. longissimus lumborum (short loin muscle) was excised from the carcass (over the 12th rib) for every animal. Subcutaneous fat was removed and the samples were snap-frozen in liquid nitrogen and stored at −80 °C until subsequent ICDH determination. The ICDH activity was determined by the method of Briand (1981), which was adapted to run on an Olympus AU400 auto analyser. At 24 h post-mortem the entire short loin muscle was removed and weighed (short loin muscle weight), and additional samples for myoglobin, intramuscular fat and protein determination were collected. Subcutaneous short loin fat was also dissected and weighed (short loin fat). For myoglobin, a 1 g sample of short loin muscle was excised and stored at −20 °C until myoglobin concentration determination by the method of Trout (1991). For lambs born in 2007 only, extractable protein was measured for the ICDH and myoglobin samples by the method of Bradford (1976). For intramuscular fat, a 40 g sample of loin muscle was excised and stored at −20 °C until subsequent freeze drying using a Cuddon FD 1015 freeze dryer (Cuddon Freeze Dry, NZ). The intramuscular fat content was determined using a near infrared (NIR) procedure in a Technicon Infralyser 450 (19 wavelengths) using the method described by Perry, Shorthose, Ferguson, and Thompson (2001).

2.3. Data available

For the ICDH analysis muscle samples for a total of 3178 lambs, which were the progeny of 178 sires across 2 years were available, while for the myoglobin analysis muscle samples for a total of 5580 lambs, which were the progeny of 267 sires across 3 years were available.

3. Statistical analysis

ICDH activity and myoglobin concentration were analysed using linear mixed effects models (SAS Version 9.1, SAS Institute, Cary, NC, USA). Initially, base models for ICDH activity and myoglobin concentration were developed, which included fixed production effects for site (representing research station site; Kirby, Trangie, Cowra, Rutherglen, Hamilton, Struan, Turretfield, Katanning), year of birth (2007 and 2008 for ICDH and

Table 1
NDF, DDF, and F-values for the base models for isocitrate dehydrogenase activity (μmol/min/g tissue) and myoglobin concentration (mg/g tissue).

Effect	Isocitrate dehydrogenase (μmol/min/g tissue)		Myoglobin (mg/g tissue)	
	NDF, DDF	F-value	NDF, DDF	F-value
Site	7, 532	43.32**	7, 972	228.59**
Year of birth	1, 2409	1593.09**	2, 4242	16.76**
Sex	1, 532	8.75**	1, 972	34.81**
Sire type	2, 532	3.17*	2, 972	7.10**
Dam breed (sire type)	1, 532	10.60**	NA	NA
Kill group (site by drop)	38, 532	18.57**	64, 972	40.21**
Site by drop	6, 532	4.22**	13, 972	58.95**

NDF, DDF: Numerator and denominator degrees of freedom.
* $P < 0.05$.
** $P < 0.001$.

2007, 2008 and 2009 for myoglobin), sex (male, female), birth type–rear type (11, 21, 22, 31, 32, 33), age of dam (2, 3, 4, 5, 6, 7 years), sire type (Merino, Maternal, Terminal), dam breed within sire type (Merino ×Merino, Merino × Maternal, Merino × Terminal, Border Leicester–Merino × Terminal) 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 removed in a stepwise manner if non-significant ($P > 0.05$).

To assess the relationship of ICDH activity and myoglobin concentration with aspects of carcass phenotype traits, HCWT, short loin fat weight, short loin muscle weight and intramuscular fat were included as covariates in the above base models. Initially HCWT was included, and then either short loin muscle or fat weight was also included. All models contained all relevant first order interactions between the fixed effects and covariates, including a quadratic effect of the covariate, and were removed in a stepwise manner if non-significant ($P > 0.05$).

To assess the impact of sire PWWT, PFAT and PEMD ASBVs on ICDH activity and myoglobin concentration, the three ASBVs were analysed concurrently as covariates in the base model. Additionally the carcass traits of HCWT, short loin fat weight, short loin muscle weight and intramuscular fat were analysed one at a time within this ASBV model. Each ASBV was also analysed as an individual covariate within the base model. All models contained relevant first order interactions between the fixed effects and covariates, including a quadratic effect of the covariate, and were removed in a stepwise manner if non-significant ($P > 0.05$).

To assess the impact of age at slaughter on ICDH activity and myoglobin concentration, age at slaughter was included as a covariate in the base model. The model contained all relevant first order interactions between the fixed effects and the age at slaughter covariate, including a quadratic effect of age, and these were removed in a stepwise manner if non-significant ($P > 0.05$). The kill group within site by year term was not included in this model as within each site by year the age at slaughter was confounded by kill group. This is because the variation in age within each kill group was less than 10 days. Therefore removing the kill group term allowed the effect of age at slaughter to be estimated.

For lambs born in 2007 only, protein was determined and tested as a covariate within this subset of the data. For both ICDH activity and myoglobin concentration, protein had a large effect, increasing ICDH activity by 1.92 μmol/min/g tissue across the 35 g protein range (Fig. 1) and myoglobin concentration by 3.98 mg/g tissue across the 60 g protein range. However, in both cases the magnitude of the other genotype and environmental effects described within these models did not change whether the models were corrected for protein or not. As the protein correction did not alter the magnitude of the effects, a pragmatic decision was made to reduce assay workload by discontinuing protein determination. Therefore protein was not measured in subsequent years, and the analyses presented are expressed on a per gramme of tissue basis, with no protein correction.

4. Results

4.1. ICDH

4.1.1. Production effects

The phenotypic linear mixed effects model is presented in Table 1. The model utilised ICDH activity for 3178 animals and described 68% of the total variance. The number of progeny analysed in the base model is presented in Table 2 and the raw mean and ranges for ICDH activity and phenotypic covariates are presented in Table 3.

The average activity level of ICDH was 5.17 ± 0.06 μmol/min/g tissue and ranged from 1.02 to 11.40 μmol/min/g tissue. Wethers (5.27 ± 0.03) had on average 0.13 μmol/min/g tissue higher ICDH activity than ewe lambs (5.14 ± 0.05) ($P < 0.01$). Maternal (5.27 ± 0.08) and Merino (5.27 ± 0.12) sired lambs had 0.19 μmol/min/g tissue higher ICDH activity than Terminal (5.08 ± 0.06) sired lambs ($P < 0.05$). Within the Terminal sired lambs, those from Merino dams (5.19 ± 0.07) had 0.23 μmol/min/g tissue higher ICDH activity than lambs from Border Leicester–Merino dams (4.96 ± 0.08) ($P < 0.01$).

ICDH activity was greatest at the Cowra site and least at the Trangie site with activities of 5.76 and 3.99 μmol/min/g tissue ($P < 0.01$). It was also greater in lambs born in 2007 compared to lambs born in 2008 with activities of 6.45 and 4.12 μmol/min/g tissue ($P < 0.01$). However the difference between years varied across sites by as much as 2.69 μmol/min/g tissue at Hamilton to as little as 2.11 μmol/min/g tissue at Kirby ($P < 0.01$) (Fig. 2). Within each site and year there were marked differences between kill groups which varied in ICDH activity by as little as 0.29 μmol/min/g tissue in Hamilton in 2008 to as much a 2.36 μmol/min/g tissue in Katanning in 2007 ($P < 0.01$). ICDH activity generally increased with older kill groups although this trend was not always consistent across all sites. Age at slaughter was associated with an increase in ICDH activity of 0.26 μmol/min/g tissue across the 370 day age range (Fig. 3).

When phenotypic (i.e. short loin muscle weight, short loin fat weight, intramuscular fat, HCWT) or genotypic (PWWT, PFAT, PEMD) covariates were included in this model, the production effects remained unchanged. The only exception to this was for sire type which rarely impacted on ICDH activity in the presence of phenotypic or genotypic covariates.

Table 2
Number of progeny at each site for drop, sex, sire type and dam breed within sire type from the base ICDH activity model.

Site	Year of birth		Sex type		Sire type			Dam breed within sire type			
	2007	2008	Female	Male	Maternal	Merino	Terminal	MATM	MM	TM	TBLM
Kirby	168	298	121	345	105	143	212	102	142	124	85
Trangie	*	218	68	150	43	43	133	43	43	69	63
Cowra	290	157	143	304	65	65	317	64	64	213	101
Rutherglen	298	203	179	322	54	71	376	54	71	0	376
Hamilton	203	194	143	250	61	63	270	61	63	266	0
Struan	89	131	77	143	42	51	128	41	51	38	88
Turretfield	66	184	47	203	64	84	102	64	84	102	0
Katanning	392	409	239	560	184	161	446	184	161	442	0

*No animals were produced. MATM: Maternal × Merino; MM: Merino × Merino; TM: Terminal × Merino, TBLM: Terminal × Border Leicester–Merino.

Table 3
Raw mean ± s.d. (min–max) for ICDH activity and the phenotypic covariates tested within the base model.

	Isocitrate dehydrogenase (μmol/min/g tissue)	Hot carcass weight (kg)	Intramuscular fat (%)	Short loin muscle weight (g)	Short loin fat weight (g)	Slaughter age (days)
Site						
Kirby	4.75 ± 1.62 (1.02–9.01)	26.2 ± 5.3 (16.0–40.0)	4.8 ± 1.0 (2.8–9.1)	404.8 ± 84.7 (140–670)	289.2 ± 166.3 (30–865)	365.4 ± 49.4 (270–420)
Trangie	3.78 ± 1.10 (1.67–7.05)	24.6 ± 3.0 (18.5–34.7)	4.4 ± 0.9 (2.9–7.8)	373.3 ± 62.9 (245–583)	147.8 ± 53.0 (40–330)	226.7 ± 53.3 (193–333)
Cowra	6.07 ± 1.42 (2.67–10.29)	23.4 ± 3.2 (16.3–35.3)	4.0 ± 0.8 (2.3–7.1)	360.1 ± 63.1 (215–565)	159.2 ± 63.1 (28–385)	193.4 ± 57.2 (138–325)
Rutherglen	4.72 ± 1.47 (1.43–8.71)	21.9 ± 2.5 (14.4–31.8)	3.9 ± 1.0 (1.9–7.2)	326.4 ± 53.5 (157–558)	175.6 ± 56.5 (47–429)	266.6 ± 54.6 (215–392)
Hamilton	5.48 ± 1.63 (2.42–11.29)	21.1 ± 2.6 (14.2–32.2)	4.3 ± 1.0 (2.1–7.7)	341.3 ± 55.1 (189–525)	167.4 ± 53.0 (11–354)	313.2 ± 62.3 (270–456)
Struan	4.73 ± 1.58 (2.16–10.46)	20.9 ± 3.2 (12.8–29.0)	4.3 ± 0.9 (2.2–8.0)	317.4 ± 71.7 (165–549)	206.2 ± 84.5 (59–531)	280.6 ± 63.7 (219–426)
Turretfield	5.03 ± 1.53 (2.90–11.27)	20.5 ± 2.8 (14.6–29.8)	4.2 ± 1.2 (2.6–10.5)	332.6 ± 59.2 (211–496)	252.6 ± 78.2 (0–555)	262.7 ± 73.2 (188–361)
Katanning	5.58 ± 1.72 (2.25–11.40)	21.5 ± 3.3 (13.6–31.3)	4.7 ± 1.1 (1.5–9.6)	343.8 ± 66.6 (173–598)	194.9 ± 87.3 (15–560)	280.4 ± 96.8 (178–499)
Year of birth						
2007	6.44 ± 1.35 (2.81–11.40)	21.8 ± 2.8 (12.8–32.2)	4.2 ± 1.0 (1.5–9.1)	339.6 ± 57.7 (140–580)	182.4 ± 73.2 (0–531)	262.9 ± 71.3 (157–456)
2008	4.10 ± 1.06 (1.02–9.54)	23.2 ± 4.4 (13.6–40.0)	4.5 ± 1.0 (1.8–10.5)	359.8 ± 77.5 (173–670)	211.2 ± 115.9 (15–865)	290.0 ± 93.5 (138–499)
Sex						
Female	5.00 ± 1.67 (1.02–11.33)	22.7 ± 3.7 (12.8–39.6)	4.3 ± 0.9 (1.9–8.4)	357.2 ± 65.7 (165–625)	213.4 ± 99.6 (53–865)	250.2 ± 61.0 (138–420)
Male	5.24 ± 1.66 (1.36–11.40)	22.5 ± 3.9 (13.6–40.0)	4.4 ± 1.1 (1.5–10.5)	348.4 ± 72.2 (140–670)	192.3 ± 100.7 (0–740)	289.9 ± 91.4 (138–499)
Sire type						
Maternal	5.15 ± 1.63 (1.70–10.72)	21.6 ± 3.5 (14.3–36.6)	4.4 ± 1.0 (2.2–9.6)	319.8 ± 59.1 (186–565)	206.1 ± 96.1 (63–585)	250.5 ± 64.2 (138–420)
Merino	5.62 ± 1.64 (2.42–11.29)	21.3 ± 3.8 (12.8–33.8)	4.6 ± 1.3 (1.8–10.5)	330.4 ± 65.8 (140–580)	164.6 ± 110.7 (0–610)	394.4 ± 57.0 (178–499)
Terminal	5.02 ± 1.67 (1.02–11.40)	23.3 ± 3.8 (14.8–40.0)	4.2 ± 0.9 (1.5–8.8)	367.5 ± 69.8 (193–670)	207.8 ± 94.4 (53–865)	245.7 ± 60.4 (138–420)
Dam breed within sire type						
MATM	5.15 ± 1.63 (1.70–10.72)	21.7 ± 3.5 (14.3–36.6)	4.4 ± 1.0 (2.2–9.6)	319.9 ± 59.0 (186–565)	206.3 ± 96.3 (63–585)	250.2 ± 63.9 (138–420)
MM	5.61 ± 1.64 (2.42–11.29)	21.3 ± 3.8 (12.8–33.8)	4.6 ± 1.3 (1.8–10.5)	330.6 ± 65.8 (140–580)	164.9 ± 110.6 (0–610)	393.9 ± 58.2 (178–499)
TM	5.21 ± 1.64 (1.90–11.40)	22.6 ± 3.6 (14.8–38.8)	4.3 ± 0.9 (1.5–8.8)	367.1 ± 66.9 (195–598)	204.9 ± 94.1 (53–695)	244.5 ± 61.5 (138–420)
TBLM	4.65 ± 1.66 (1.02–9.41)	24.4 ± 3.9 (16.0–40.0)	4.1 ± 0.9 (1.9–7.0)	368.6 ± 74.5 (193–670)	213.7 ± 95.1 (61–865)	247.6 ± 58.4 (138–420)

MATM: Maternal × Merino; MM: Merino × Merino; TM: Terminal × Merino, TBLM: Terminal × Border Leicester–Merino.

4.1.2. Association between ICDH activity and carcass phenotypic indicators

HCWT varied between 15 and 35 kg and demonstrated an association with ICDH activity, but this was only present at the Turretfield and Kirby sites ($P < 0.05$). At the Turretfield site ICDH activity increased by 1 μmol/min/g tissue across the 20 kg HCWT range while at the Kirby site it decreased by 0.7 μmol/min/g tissue. Short loin muscle weight

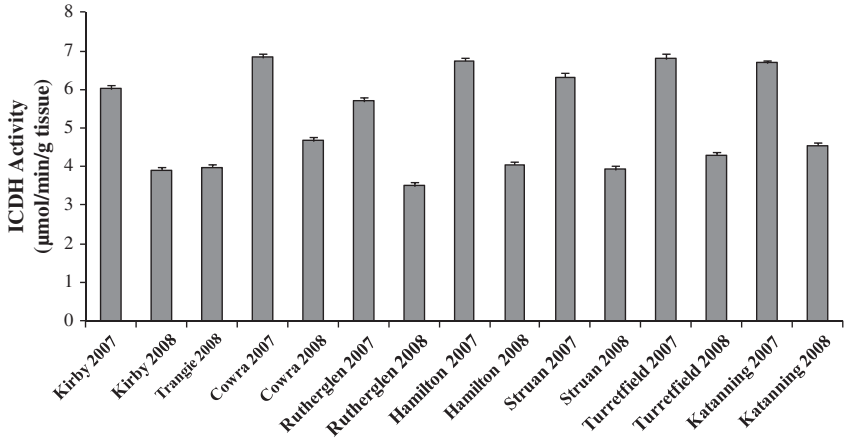

Fig. 2. The effect of site by year of birth on isocitrate dehydrogenase activity (+s.e.) (μmol/min/g tissue) from the base model.

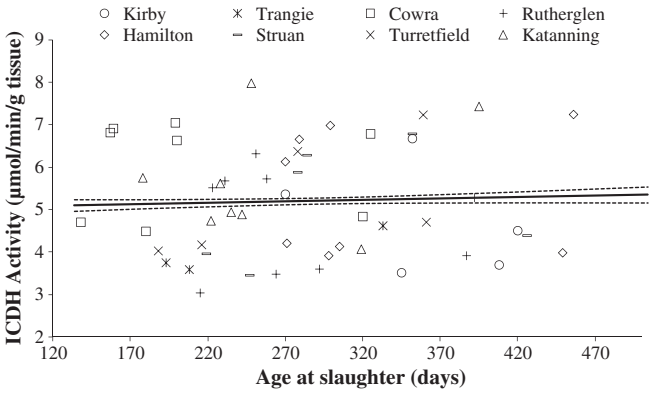

Fig. 3. Linear relationship between isocitrate dehydrogenase (± s.e.) (µmol/min/g tissue) and slaughter age in days. Symbols represent predicted means for kill groups. Lines represent predicted means for age at slaughter (±s.e.) from base model with no kill group term.

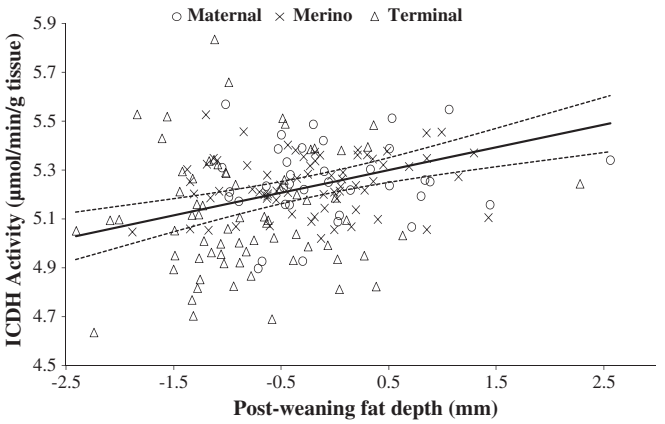

Fig. 5. Relationship between sire estimates for isocitrate dehydrogenase activity (µmol/min/g tissue) and subcutaneous post-weaning c-site fat depth (PFAT) for Maternal, Merino and Terminal sires. Lines represent predicted means for isocitrate dehydrogenase activity (±s.e.) for all sire types combined. Symbols represent individual sire estimates.

varied between 200 and 550 g and demonstrated an association with ICDH activity, but only at some sites. At the Turretfield site, ICDH activity increased by 0.88 µmol/min/g tissue across the 350 g short loin muscle weight range while at the Cowra and Katanning sites it decreased by 0.52 and 0.59 µmol/min/g tissue ($P < 0.05$). This association did not change when HCWT was included in the model. Short loin fat demonstrated no association with ICDH activity. Intramuscular fat demonstrated a curvilinear association with ICDH activity ($P < 0.01$), which increased by 0.72 µmol/min/g tissue between 2 and 6 intramuscular fat percent (Fig. 4). The relationship appeared to plateau beyond 6 intramuscular fat percent. The magnitude of this effect was not changed by the inclusion of the phenotypic covariates short loin fat, short loin muscle weight or HCWT.

4.1.3. Effect of sire and sire breeding values

In the base model sire as a random term was significant with individual sire estimates for ICDH activity varying between 5.04 and 5.54 µmol/min/g tissue for Merino, 4.89 and 5.60 for Maternal and 4.59 and 5.78 for Terminal sires ($P < 0.01$) (Fig. 5).

When PWWT, PFAT and PEMD were included simultaneously as covariates in the base model each had an association with ICDH activity ($P < 0.05$). Across the 21 kg range, increasing PWWT was associated with an increase in ICDH activity of 0.43 µmol/min/g tissue. This effect was no longer significant when the model was corrected for short loin muscle weight, HCWT or intramuscular fat.

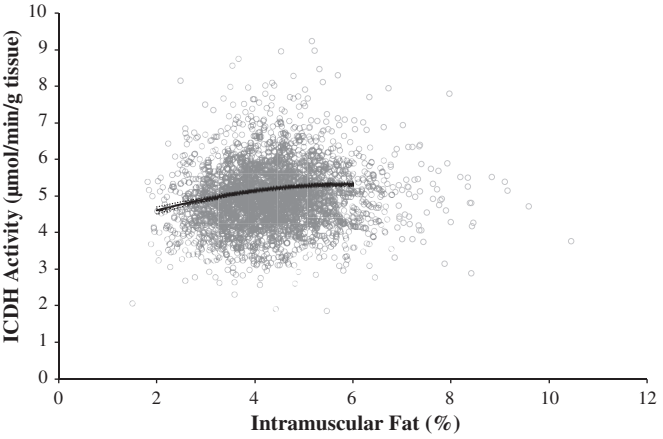

Fig. 4. Curvilinear relationship between intramuscular fat percentage and isocitrate dehydrogenase activity (±s.e.) in µmol/min/g tissue. Symbols (○) represent individual lamb residuals from the intramuscular fat model.

Across the 5 mm range, reducing PFAT was associated with a reduction in ICDH activity of 0.46 µmol/min/g tissue (Fig. 5). This effect was no longer significant when the model was corrected for short loin muscle weight.

Across the 7 mm range, increasing PEMD was associated with a reduction in ICDH activity of 0.50 µmol/min/g tissue. This effect was no longer significant when the model was corrected for short loin muscle weight.

The magnitudes of the PWWT and PEMD responses were similar when analysed as single covariates in the base model, however the PFAT effect was no longer significant.

The mean and ranges for PWWT, PFAT and PEMD are presented in Table 4.

4.2. Myoglobin results

4.2.1. Production effects

The phenotypic linear mixed effects model is presented in Table 1. The model utilised myoglobin concentration for 5580 animals and described 62% of the variance. The number of progeny analysed in the base model is presented in Table 5 and the raw mean and ranges for myoglobin concentration and phenotypic covariates are presented in Table 6.

The average myoglobin concentration was 6.65 ± 0.02 mg/g tissue and ranged from 2.15 to 15.62. Ewe lambs (6.89 ± 0.04) had on average 0.23 mg/g tissue higher myoglobin concentration than wethers (6.66 ± 0.03) ($P < 0.01$). Maternal (6.87 ± 0.06) and Merino (6.84 ± 0.09) sired lambs had higher myoglobin concentrations than Terminal (6.61 ± 0.04) sired lambs ($P < 0.01$).

Myoglobin concentration was greatest at the Kirby site and least at the Struan site with 8.19 and 6.07 mg/g tissue ($P < 0.01$). It was also greater in lambs born in 2008 or 2009 than lambs born in 2007 with values of 6.93, 6.79 and 6.58 mg/g tissue ($P < 0.01$). However these year differences varied across sites by as much as 2.09 mg/g tissue at Hamilton to as little as 0.18 at Trangie ($P < 0.01$) (Fig. 6). Within each site and year there were marked differences between kill groups which varied by as little as 0.40 mg/g tissue in Struan in 2008 to as much as 4.77 in Kirby in 2008 ($P < 0.01$). Myoglobin concentration generally increased with later kill groups and this result aligned well with the age at slaughter effect which was associated with an increase in myoglobin concentration of 5.01 mg/g tissue across the 370 day age range (Fig. 7).

When phenotypic (i.e. short loin muscle weight, short loin fat weight, intramuscular fat, HCWT) or genotypic (PWWT, PFAT, PEMD) covariates were included in this model, the production effects remained unchanged.

Table 4
Number of sires and Australian Sheep Breeding Values mean (min, max) for each sire type from the ICDH activity and myoglobin concentration data.

	Sire type	No. of sires	PFAT (mm)	PEMD (mm)	PWWT (kg)
ICDH activity	Maternal	37	−0.05 (−1.06, 2.56)	0.05 (−1.28, 1.82)	4.79 (−3.66, 10.49)
	Merino	70	−0.25 (−1.89, 1.42)	−0.18 (−2.02, 2.27)	1.45 (−5.00, 7.29)
	Terminal	71	−0.82 (−2.41, 2.27)	1.12 (−1.33, 4.92)	11.92 (1.13, 16.05)
Myoglobin concentration	Maternal	61	−0.07 (−1.61, 2.56)	0.06 (−1.44, 1.82)	5.19 (−3.66, 10.49)
	Merino	101	−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)	12.06 (1.13, 18.08)

PFAT: Post-weaning c-site fat depth, PEMD: Post-weaning eye muscle depth, PWWT: Post-weaning weight.

4.2.2. Association between myoglobin concentration and carcass phenotypic indicators

HCWT demonstrated an association with myoglobin concentration increasing by 1.56 mg/g tissue across the 20 kg HCWT range ($P < 0.01$). This effect varied between sites and sire types ($P < 0.01$). At the Kirby, Cowra, Turretfield, Hamilton, Katanning, Rutherglen, Struan and Trangie sites myoglobin concentration increased by 0.66, 1.23, 1.28, 1.46, 1.72, 1.87, 2.08 and 2.22 mg/g tissue across the 20 kg range in HCWT. Progeny with Merino sires had the largest increase in myoglobin concentration across the HCWT range of 1.90 mg/g tissue, while progeny with Maternal and Terminal sires increased by 1.82 mg/g tissue and 0.97 mg/g tissue across the HCWT range.

Short loin muscle weight did not demonstrate an association with myoglobin concentration.

Short loin fat weight varied between 50 and 400 g and demonstrated an association with myoglobin concentration, increasing by 0.83 mg/g tissue across the 350 g short loin fat weight range ($P < 0.01$). This effect varied between sire types with progeny of Merino sires increasing by 1.29 mg/g, progeny of Terminal sires increasing by 0.64 mg/g tissue and progeny of Maternal sires increasing by 0.57 mg/g tissue across the short loin fat weight range.

Intramuscular fat demonstrated a curvilinear association with myoglobin concentration ($P < 0.01$). Between 2 and 6 intramuscular fat percent myoglobin concentration increased by 0.61 mg/g tissue (Fig. 8). The relationship appeared to plateau beyond 6% intramuscular fat. The association varied between sire types with increases of 0.35, 0.66 and 0.84 mg/g tissue in the progeny of Terminal, Maternal and Merino sires respectively ($P < 0.05$).

When ICDH activity was included as a covariate in the base model it was a significant predictor of myoglobin concentration, which increased by 0.64 mg/g tissue across the 10.05 μmol/min/g tissue ICDH activity range ($P < 0.01$).

4.2.3. Effect of sire and sire breeding values

In the base model sire as a random term was significant with individual sire estimates for myoglobin concentration varying between 6.44 and 7.24 mg/g tissue for Maternal, 6.26 and 7.56 for Merino and 6.03 and 7.49 for Terminal sires ($P < 0.01$) (Fig. 9).

When PWWT, PFAT and PEMD were included simultaneously as covariates in the base model each had an association with myoglobin concentration ($P < 0.05$). Across the 23 kg range, increasing PWWT was associated with an increase in myoglobin concentration of 0.50 mg/g tissue. This effect varied between sites being greatest at the Hamilton and Struan sites where myoglobin concentration increased by 0.89 and 1.00 mg/g tissue across the PWWT range ($P < 0.05$). These effects were no longer significant when the model was corrected for short loin muscle weight, short loin fat weight or intramuscular fat.

Across the 6 mm range, reducing PFAT was associated with a reduction in myoglobin concentration of 0.67 mg/g tissue and this effect varied between sexes with an increase of 0.26 mg/g tissue in wethers and an increase of 1.07 mg/g tissue in ewe lambs. There was no impact to the magnitude of the PFAT effect when short loin muscle weight and short loin fat weight were included separately as covariates. The magnitude of the PFAT effect reduced to 0.58 mg/g tissue when intramuscular fat was included as a covariate.

There was also an association between PEMD and myoglobin concentration however this was only present within the Merino and Terminal sire types ($P < 0.01$). Across the 6 mm range, increasing PEMD was associated with a reduction in myoglobin concentration of 0.49 mg/g tissue in the progeny of Terminal sires and an increase of 1.36 in the progeny of Merino sires (Fig. 9). When short loin muscle weight, short loin fat weight and intramuscular fat were included separately as covariates in the ASBV model there was a reduction of the PEMD effect in progeny of Merino sires to 1.22 mg/g tissue and increase to 0.57 mg/g tissue in the progeny of Terminal sires.

When these ASBVs were analysed as single covariates in the base model the magnitude of the PWWT response increased to 0.74 mg/g tissue and the PFAT response reduced to 0.57 mg/g tissue. The magnitude of the PEMD response remained unchanged.

The mean and ranges for PWWT, PFAT and PEMD are presented in Table 4.

Table 5
Number of progeny at each site for drop, sex, sire type and dam breed within sire type from the base myoglobin concentration model.

Site	Year of birth			Sex		Sire type		
	2007	2008	2009	Female	Male	Maternal	Merino	Terminal
Kirby	247	399	393	324	708	197	203	628
Trangie	*	216	199	145	270	76	77	262
Cowra	291	154	199	208	436	105	90	449
Rutherglen	298	213	172	325	358	88	103	492
Hamilton	198	194	175	196	368	90	80	395
Struan	296	123	177	207	389	108	67	420
Turretfield	269	185	214	207	461	136	119	411
Katanning	399	409	359	364	801	269	199	684

*No animals were produced.

5. Discussion

5.1. Association between carcass breeding values and oxidative capacity

Aligning with our hypothesis, the progeny of sires with an increased PEMD had a reduced oxidative capacity, as indicated by reduced ICDH activity across all sire types and reduced myoglobin concentration within Terminal sired lambs. This aligns well with previous studies, with Gardner, Pethick, Hopkins et al. (2006) demonstrating reduced myoglobin concentration in response to PEMD within Poll Dorset × Merino lambs, and Gardner et al. (2007) demonstrating reduced ICDH activity within Poll Dorset × Merino and Border Leicester × Merino lambs. A further study by Gardner, Pethick, Greenwood and Hegarty (2006) also showed a reduced myoglobin concentration within the progeny of all sire types with increased PEMD but failed to show this effect on ICDH activity. This is likely to be due to the limited number of sires used, 9 compared to 267 in this study, where the PEMD range of 5 mm compared to 7 mm in this study may not have been divergent enough to elicit a response.

The association between PEMD and reduced oxidative capacity may be due to a shift in muscle fibre type with increased PEMD leading to a greater proportion of type IIX fibres (Greenwood et al., 2006a) which have been associated with increased glycolytic

Table 6
Raw mean ± s.d. (min–max) for myoglobin concentration and the phenotypic covariates tested within the base model.

	Myoglobin concentration (mg/g tissue)	Hot carcass weight (kg)	Intramuscular fat (%)	Short loin muscle weight (g)	Short loin fat weight (g)	Slaughter age (days)
Site						
Kirby	8.18 ± 2.03 (3.09–13.65)	25.6 ± 5.1 (15.4–40.0)	4.7 ± 1.0 (2.4–9.1)	388.9 ± 78.6 (140–670)	270.6 ± 160.4 (30–880)	327.3 ± 56.5 (235–420)
Trangie	6.18 ± 1.65 (2.99–12.66)	23.3 ± 3.3 (16.2–34.7)	3.8 ± 1.0 (1.6–7.8)	359.4 ± 62.6 (228–583)	122.6 ± 55.3 (30–330)	208.0 ± 65.3 (154–342)
Cowra	6.13 ± 1.48 (3.17–13.80)	23.4 ± 3.4 (14.0–35.3)	3.9 ± 0.8 (1.7–7.1)	362.3 ± 65.2 (160–585)	147.7 ± 63.8 (20–385)	195.2 ± 54.8 (138–325)
Rutherglen	6.69 ± 1.43 (3.12–13.09)	22.3 ± 2.9 (14.2–31.8)	3.8 ± 0.9 (1.9–7.2)	335.0 ± 58.6 (157–558)	190.2 ± 70.3 (46–590)	270.0 ± 50.9 (215–392)
Hamilton	6.25 ± 1.69 (2.15–11.33)	21.8 ± 3.1 (13.4–32.2)	4.2 ± 0.9 (2.1–7.7)	341.5 ± 59.1 (160–525)	176.3 ± 73.0 (10–412)	295.6 ± 57.5 (229–456)
Struan	5.81 ± 1.50 (2.48–10.75)	22.0 ± 3.3 (12.8–31.4)	4.1 ± 1.0 (1.6–8.2)	336.7 ± 71.8 (155–590)	195.6 ± 112.7 (21–543)	260.4 ± 49.7 (210–426)
Turretfield	5.83 ± 1.58 (2.24–11.57)	21.6 ± 2.7 (14.6–29.8)	4.1 ± 1.0 (1.9–10.5)	335.6 ± 58.3 (190–558)	193.9 ± 107.4 (0–555)	259.9 ± 51.2 (188–361)
Katanning	6.81 ± 1.66 (2.95–15.62)	22.3 ± 3.6 (13.6–35.8)	4.6 ± 1.1 (1.5–9.8)	364.3 ± 72.4 (173–661)	212.6 ± 88.1 (15–560)	274.6 ± 84.4 (178–499)
Year of birth						
2007	6.50 ± 1.97 (2.15–15.62)	22.4 ± 3.1 (12.8–35.8)	4.3 ± 1.0 (1.5–9.1)	349.0 ± 62.3 (140–661)	203.2 ± 87.3 (0–543)	257.7 ± 63.3 (157–456)
2008	6.76 ± 1.85 (2.48–13.66)	23.0 ± 4.4 (13.6–40.0)	4.5 ± 1.0 (1.8–10.5)	359.1 ± 76.5 (173–670)	205.7 ± 115.4 (15–865)	288.9 ± 91.0 (138–499)
2009	6.70 ± 1.70 (2.99–13.80)	23.4 ± 4.0 (13.4–40.0)	4.0 ± 1.1 (1.6–9.8)	360.7 ± 71.3 (155–620)	187.6 ± 126.0 (10–880)	260.3 ± 58.6 (154–359)
Sex						
Female	6.45 ± 1.61 (2.47–12.88)	23.1 ± 3.7 (12.8–40.0)	4.2 ± 1.0 (1.9–9.8)	361.6 ± 64.5 (165–625)	212.5 ± 113.1 (31–880)	250.5 ± 57.2 (138–420)
Male	6.74 ± 1.95 (2.15–15.62)	22.8 ± 3.9 (13.4–40.0)	4.3 ± 1.1 (1.5–10.5)	353.3 ± 72.8 (140–670)	192.2 ± 109.1 (0–740)	277.6 ± 78.9 (138–499)
Sire type						
Maternal	6.55 ± 1.76 (2.24–14.41)	21.9 ± 3.5 (14.0–36.6)	4.4 ± 1.1 (1.6–9.7)	324.1 ± 60.5 (155–565)	194.9 ± 105.9 (20–585)	252.7 ± 60.4 (138–420)
Merino	8.22 ± 2.08 (2.83–15.62)	21.1 ± 3.6 (12.8–33.8)	4.5 ± 1.2 (1.8–10.5)	324.6 ± 66.0 (140–580)	157.1 ± 107.2 (0–610)	373.2 ± 59.7 (178–499)
Terminal	6.27 ± 1.58 (2.15–12.88)	23.7 ± 3.8 (14.8–40.0)	4.1 ± 1.0 (1.5–9.8)	373.0 ± 68.1 (193–670)	210.2 ± 110.0 (28–880)	246.8 ± 55.3 (138–420)

(Gardner, Pethick, Greenwood and Hegarty, 2006) and reduced oxidative enzyme activities (Brandstetter et al., 1998).

The use of the PEMD breeding value within the Australian sheep industry has been shown to increase loin muscle weight (Gardner et al., 2010). As there is an association between increased phenotypic muscle weight and reduced muscle oxidative capacity it could be concluded that the PEMD effect on muscle oxidative capacity is merely a correlate of its impact on short loin muscle weight. However, in this study there was no phenotypic association between short loin muscle weight and myoglobin concentration, and a variable association with ICDH activity. Furthermore, correcting the models for short loin muscle weight had no impact on the association between PEMD and myoglobin concentration. This inconsistent overall phenotypic association between short loin muscle weight and muscle oxidative capacity is unusual and appears to suggest that PEMD is affecting myoglobin concentration through a mechanism other than the phenotype that it directly delivers.

As hypothesised, progeny of sires with a reduced PFAT had a reduced oxidative capacity, as indicated by reduced ICDH activity and myoglobin

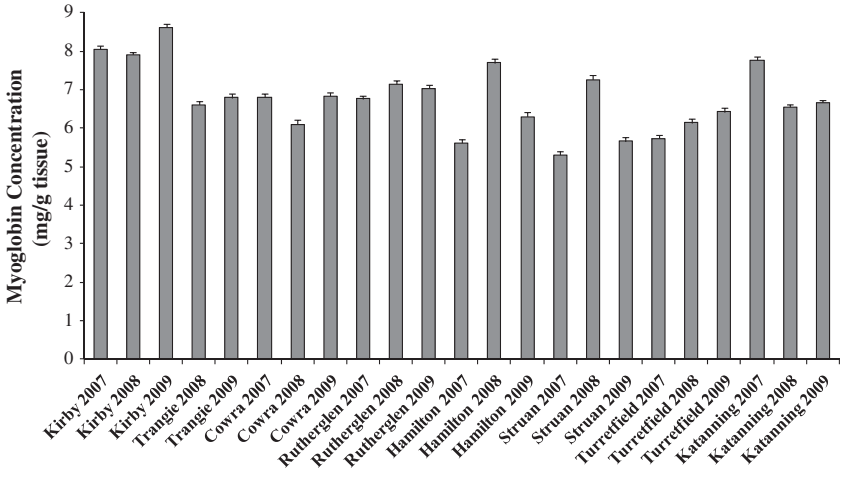

Fig. 6. The effect of site by year of birth on myoglobin concentration (+s.e.) (mg/g tissue) from the base model.

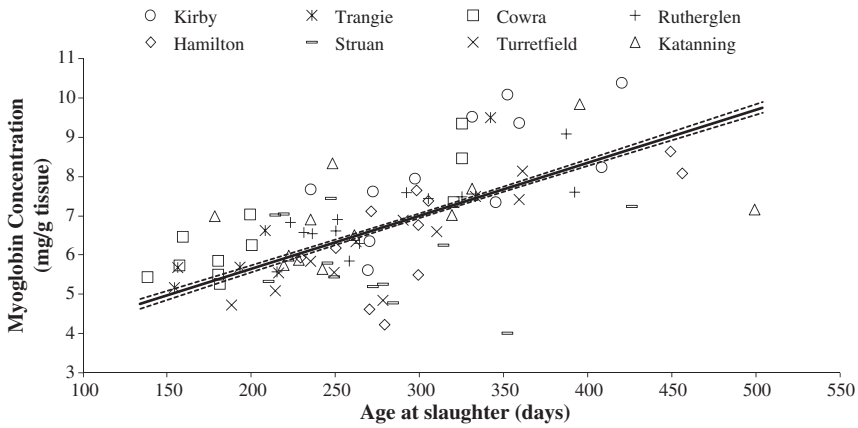

Fig. 7. Linear relationship between myoglobin concentration (±s.e.) in mg/g tissue and slaughter age. Symbols represent predicted means for kill groups. Lines represent predicted means for age at slaughter (±s.e.) from the base model with no kill group term.

concentration. Previous studies have demonstrated similar results, with Gardner, Pethick, Greenwood and Hegarty (2006) and Gardner et al. (2007) both demonstrating reduced ICDH activity in lambs with low PFAT sires, and Greenwood et al. (2006b) showing higher levels of glycolytic type IIX fibres. Although the Gardner, Pethick, Greenwood and Hegarty (2006) study showed a reduction in ICDH activity there was no impact on myoglobin concentration. The study was performed on wether lambs, which in our study had a smaller response to a reduction in PFAT than ewe lambs. As the Gardner, Pethick, Greenwood and Hegarty (2006) study included only 56 wethers this may not have been enough to show an effect.

Intramuscular fat is reduced in the progeny of sires with a reduced PFAT in the animals in this study (Pannier et al., 2014b) however inclusion of intramuscular fat in the ASBV model did not diminish the impact of PFAT on ICDH activity or myoglobin concentration, indicating that the impact of PFAT is not delivered through its correlated impact on intramuscular fat.

Contrary to our initial hypothesis, isocitrate dehydrogenase activity and myoglobin concentration were both increased in the progeny of sires with an increased PWWT. Our hypothesis was based on the assumption that the progeny of high PWWT sires would be less mature and therefore have a lower oxidative capacity at a given slaughter age due to their larger mature size (Huisman & Brown, 2008). However, this effect has clearly been over-ridden by other factors. The samples for ICDH activity and myoglobin concentration were taken from the short loin, and the inclusion of short loin muscle weight as a phenotypic covariate nullified the impact of the PWWT ASBV on both ICDH activity and myoglobin concentration. Evidence from computed tomography scanning of a subset of these same animals suggests an altered tissue distribution within high PWWT lambs. In particular, the weight of muscle within the saddle region of the carcass was 7% higher at any given carcass weight (Gardner et al., 2012). As such the increased growth potential of these tissues would have required greater energy producing capacity, of which the TCA cycle is a vital component. As such it is possible that the impact of PWWT on muscle oxidative capacity is limited to the saddle region.

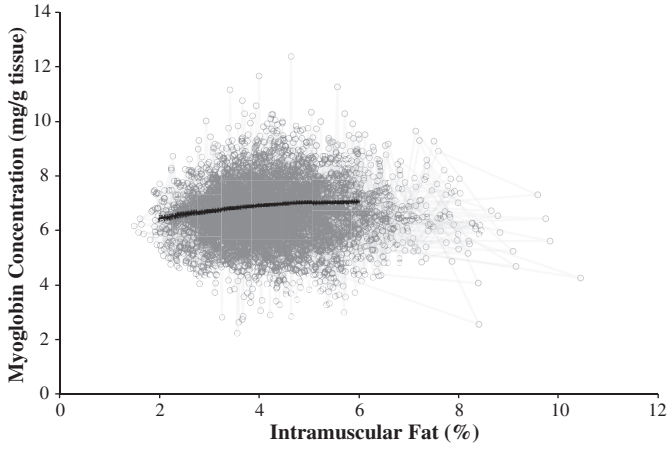

Fig. 8. Curvilinear relationship between intramuscular fat percentage and myoglobin concentration (±s.e.) in mg/g tissue. Symbols (○) represent individual lamb residuals from the intramuscular fat model.

5.2. Associations with carcass phenotype measurements

Heavier carcasses were associated with increased myoglobin concentration, although there was no effect of HCWT on ICDH activity except at the Turretfield and Kirby sites. In this study HCWT at a constant slaughter age (i.e. kill group corrected for age as per Figs. 3 and 7) reflects growth rate, which is most likely delivered through variation in environment and nutrition. As such the faster growing lambs are likely to be closer to their mature size, aligning well with the myoglobin results which have previously been shown to increase as lambs approach maturity (Gardner et al., 2007). Yet this increase in myoglobin concentration may have occurred without a corresponding increase in muscle oxidative capacity, as there was no increase in ICDH activity. Alternatively the higher growth rate may have been due to a larger mature size, in which case faster growing animals slaughtered at the same age would be less mature (Butterfield, 1988), but this seems unlikely as it would have resulted in proportionately less oxidative muscle tissue (Brandstetter et al., 1998), the opposite of what was found here.

The relationship between muscle oxidative capacity and phenotypic carcass muscularity (short loin muscle weight) and adiposity (short loin fat weight) was also assessed. Computed tomography was used to determine whole carcass muscle and fat weights on a subset of the animals used in this study, and these measurements demonstrated that short loin muscle weight was strongly correlated with whole carcass muscle weight (0.84), and short loin fat weight was strongly correlated with whole carcass fat weight (0.83) (Anderson, unpublished data). As such these measurements are good indicators of whole carcass muscularity and adiposity. As mentioned, the muscularity indicator, short loin muscle weight, demonstrated no association with myoglobin and an inconsistent relationship with ICDH. Alternatively the carcass adiposity indicator, short loin fat weight, demonstrated a consistently positive association with myoglobin, although no association with ICDH. Thus phenotypic carcass composition demonstrates some alignment with

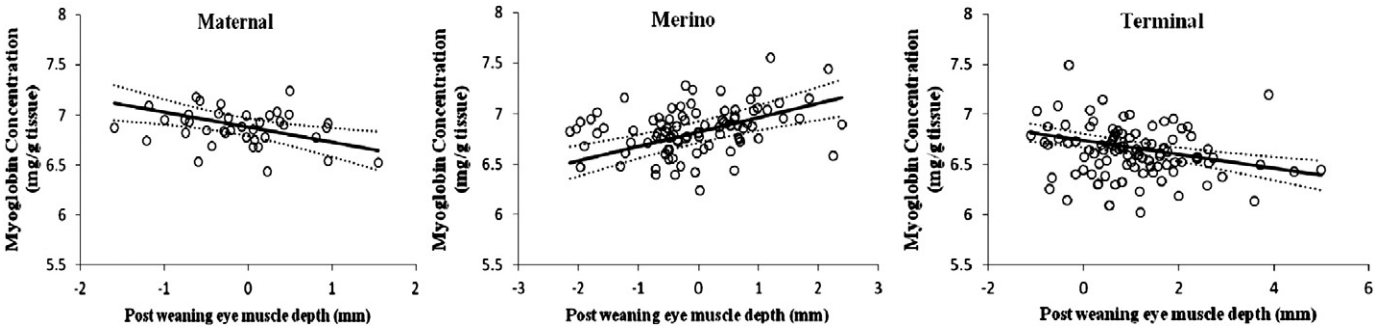

Fig. 9. Relationship between sire estimates for myoglobin concentration (mg/g tissue) and post-weaning eye muscle depth (PEMD) for Maternal, Merino and Terminal sires. Lines represent predicted means for myoglobin concentration (±s.e.) for each sire type. Symbols (○) represent individual sire estimates.

the oxidative capacity of muscle, albeit an inconsistent association. The phenotypic correlation between ICDH activity and myoglobin concentration in this experiment was 0.14 (Mortimer et al., 2014) which may explain some of the variation in response of the oxidative indicators.

In contrast, a far more consistent association was evident for the relationship between muscle oxidative capacity and intramuscular fat. ICDH activity and myoglobin concentration both increased with higher levels of intramuscular fat. Similar effects have been demonstrated in cattle, where the genotypes which expressed higher levels of intramuscular fat also had a more oxidative muscle type, characterised by increased ICDH activity (Hocquette et al., 2003; Jurie et al., 2007; Pethick et al., 2005). Likewise, this has also been demonstrated in pigs (Essén-Gustavsson, Karlsson, Lundström, & Enfält, 1994) and rabbits (Gondret, Mourot, & Bonneau, 1998) in which slow twitch oxidative muscles had higher levels of intramuscular fat. More recently, Pannier, Pethick, Boyce, et al. (2014a) demonstrated a positive association between intramuscular fat and iron and zinc levels.

The association between intramuscular fat and oxidative capacity appears to be independent of maturity, or whole carcass adiposity and muscularity. This was demonstrated by also correcting the ICDH activity and myoglobin models for HCWT, short loin muscle weight and short loin fat weight. In all cases the IMF association with ICDH activity or myoglobin concentration remained unchanged. As such the association between intramuscular fat and muscle oxidative capacity appears to be more than just a correlate of whole carcass fatness or muscularity. It seems unlikely that intramuscular fat would directly mediate the oxidative capacity of adjacent muscle cells, however this result may highlight the presence of some localised control that ensures that more oxidative muscle cells have greater amounts of stored oxidative fuel (fat) in the near vicinity (i.e. intramuscular adipocytes).

5.3. Production effects

As hypothesised, the site at which lambs were reared impacted on oxidative capacity and the magnitude of the effect of site was larger than most other genotypic and production effects. Between sites, the average age at slaughter varied which may explain part of the differences between sites. This was particularly evident in the myoglobin analysis where the Kirby site had the oldest average age at slaughter as well as the highest myoglobin concentration, and of the four sites with the oldest average age, three sites also had higher than average myoglobin concentrations. In line with these findings, a previous study showed a significant increase in chromameter a* values indicating an increase in the relative redness of meat as lambs age (Hopkins, Stanley, Martin, Toohey, & Gilmour, 2007). In the ICDH analysis the site differences appeared to be less age dependant, however this was not entirely unexpected as ICDH activity demonstrated a weaker association with age than myoglobin concentration (Figs. 3 and 7). In addition the effect of age at slaughter on ICDH activity was small compared to the magnitude of the production or breeding value effects while the effect on myoglobin concentration was large compared to all other effects indicating that age was a critical factor in determining myoglobin concentration but not ICDH activity.

The differences between sites are also likely to be partly explained by nutrition. Nutritional variation has been shown to impact on muscle fibre type (Greenwood, Davis, Gaunt, & Ferrier, 2006a; Moody, Kemp, Mahyuddin, Johnston, & Ely, 1980) and subsequently may alter oxidative capacity. Oxidative capacity was highest at the Kirby and Cowra sites after correcting for age and weight (maturity), perhaps indicating an increased plane of nutrition at these sites. However, the Information Nucleus Flock was not designed to control nutrition and thus conclusions regarding the nutritional impact on oxidative capacity are difficult to assess.

There was a difference in oxidative capacity between wether and ewe lambs although ICDH activity was greater in wethers and myoglobin concentration was greater in ewe lambs. Gardner et al. (2007) demonstrated an increased ICDH activity in wether lambs when compared to ewe lambs. Consistent with these results, Greenwood et al. (2007) sampled the same lambs as used in the Gardner et al. (2007) study and demonstrated that wether lambs had reduced proportions of type IIX myofibres. While higher myoglobin levels in ewe lambs were unexpected, a previous study by Ledward and Shorthose (1971) found a similar result, with ewe lambs having a 10% higher myoglobin concentration than wethers. The reason for myoglobin concentration to be increased in ewe lambs is unclear, thus gender demonstrates some alignment with the oxidative capacity of muscle, however the association is inconsistent.

The progeny of Terminal sires had reduced oxidative capacity compared Maternal or Merino sired lambs. This is due to the selection pressure on muscling in these sires (Hall, Gilmour, Fogarty, & Holst, 2002) which has also been shown in this study to reduce oxidative capacity.

Muscle oxidative capacity was influenced by both production and genotypic factors, with site having the largest effect overall. The difference between sites was about three and a half times the magnitude of the effect of PWWT, PFAT or PEMD, and about 10 times the magnitude of the other production effects on ICDH activity and myoglobin concentration. The only exception to this was for year of birth which had a larger effect than site on ICDH activity. Therefore, while sire ASBVs do impact on oxidative capacity in their progeny, the effect is small compared to the impact of the environment.

6. Conclusion

This study demonstrated that both genotypic and production factors had significant effects on oxidative capacity. Selection for leanness and muscling by selection of sires with a reduced PFAT and increased PEMD resulted in a reduction in oxidative capacity in muscle of the progeny. This effect was also seen in the progeny of Terminal sires, which have received greater selection pressure for muscling. Selection

for lambs with a larger mature size using sires with an increased PWWT resulted in increased oxidative capacity however this may be an effect which is localised to the loin region. An increase in intramuscular fat is linked to an increase in oxidative capacity that is independent of its association with PFAT or whole body adiposity or muscularity. Oxidative capacity also increased with age however the effect was more evident on myoglobin concentration than ICDH activity. Increased growth rate, which is heavily influenced by environmental effects at each site, was associated with an increase in oxidative capacity however the effect of growth rate was smaller than the effect of site itself. In conclusion, while selection for leanness, muscling or mature size using ASBVs impacts on oxidative capacity, these effects and those of production factors such as sex and sire type are small compared to the impact of environment.

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