Genetic correlations between meat quality traits and growth and carcass traits in Merino sheep[1]

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ABSTRACT: Genetic correlations between 16 meat quality and nutritional value traits and live weight at various ages, live ultrasound fat and muscle depth, carcass measures, and carcass dissection traits were estimated for Merino sheep in the Information Nucleus (IN). Genetic correlations between live weight at various ages and the carcass traits are also reported. The IN comprised 8 genetically linked flocks managed across a range of Australian sheep environments. Meat quality traits included between 1,200 and 1,300 records for progeny from over 170 sires for intramuscular fat (**IMF**), lean meat yield (**LMY**), shear force (**SF5**), pH, meat color, and meat nutritional value traits including iron and zinc levels and long-chain omega-3 and omega-6 polyunsaturated fatty acid levels. The genetic correlations indicated that selection of Merino sheep to either reduce fat or increase muscle using ultrasound assessments will result in little change in IMF and SF5. Myoglobin levels would tend to be reduced following selection for reduced ultrasound fat depth (0.35 ± 0.21, 0.43 ± 0.14), whereas increases in myoglobin levels would occur due to selection for increased ultrasound muscle depth (0.25 ± 0.24, 0.38 ± 0.15). Selection for increased live weight will result in favorable correlated responses in hot carcass weight (0.76 to 0.97), dressing percentage (0.13 to 0.47), and carcass muscle (0.37 to 0.95), but unfavorable responses of increases in carcass fatness (0.13 to 0.65) and possible small reductions in muscle oxidative activity (−0.13 ± 0.14 to −0.73 ± 0.33) and iron content (−0.14 ± 0.15 to −0.38 ± 0.16), and a possible deterioration of shear force from selection at later ages (0.15 ± 0.26, 0.27 ± 0.24). Negligible changes are generally expected for LMY and meat color traits following selection for increased live weight (most genetic correlations less than 0.20 in size). Selection for increased LMY would tend to result in unfavorable changes in several aspects of meat quality, including reduced IMF (−0.27 ± 0.18), meat tenderness (0.53 ± 0.26), and meat redness (−0.69 ± 0.40), as well as reduced iron levels (−0.25 ± 0.22). These genetic correlations are a first step in assisting the development of breeding values for new traits to be incorporated into genetic evaluation programs to improve meat production from Merino sheep and other dual-purpose sheep breeds.

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INTRODUCTION

Processors and retailers are concerned with carcass quality and lean meat yield, whereas consumers are increasingly focused on eating quality and nutritional value (Pethick et al., 2011). However, for dual-purpose breeds, such as the Merino, genetic improvement of meat traits has traditionally involved selection on live weight and ultrasound measures of fat and muscle depth (Brown and Swan, 2016). As selection for increased muscling and lean meat yield, and to a lesser extent growth, has been suggested to adversely affect eating quality (Hopkins et al., 2011; Hopkins and Mortimer, 2014; Pannier et al., 2014a), knowledge of the size of these relationships among meat quality, carcass, and growth traits is critical to developing effective breeding programs to improve productivity without compromising carcass or meat quality (Pethick et al., 2011).

There is considerable genetic variation for growth and ultrasound traits (Safari et al., 2005; Huisman et al., 2008; Brown et al., 2016; Mortimer et al., 2017a), with generally smaller, although fewer and less reliable, estimates of heritability for carcass and meat quality traits in sheep (Greeff et al., 2008; Hopkins et al., 2011; Mortimer et al., 2017b, 2017c). In contrast, few estimates of the genetic and phenotypic correlations of meat quality traits with growth and carcass traits have been published. This study completes a series reporting genetic parameter estimates for wool and meat production traits of Merino lambs from the Information Nucleus (**IN**) (Fogarty et al., 2007; van der Werf et al., 2010) managed in a range of environments. Earlier papers reported genetic correlations of wool traits with live weight and ultrasound traits (Mortimer et al., 2017a), of wool and ultrasound traits with carcass traits and among the carcass traits (Mortimer et al., 2017b), and of wool traits with meat quality traits and among the meat quality traits (Mortimer et al., 2017c). This paper reports genetic and phenotypic correlations between meat quality and nutritional value traits and growth and carcass traits in the Merino breed.

MATERIALS AND METHODS

Animals

The Merino progeny were born over 5 yr (2007 to 2011) as part of the IN breeding program of the Cooperative Research Centre for Sheep Industry Innovation (**Sheep CRC**). The design of the IN, including procedures used to select the sires for artificial insemination of the base ewes, and the management procedures are described by van der Werf et al. (2010) and Geenty et al. (2014). Eight genetically linked flocks, located in each of the major sheep growing areas of Australia (Armidale, NSW; Trangie, NSW; Cowra, NSW; Rutherglen, VIC; Hamilton, VIC; Struan, SA; Turretfield, SA; and Katanning, WA), formed the IN. The lambs were tail docked and the males castrated at marking. Following weaning, the lambs were managed to achieve target growth rates of 150 g/d and a target carcass weight of 21.5 kg. A random half of the wether lambs (balanced for sire) was slaughtered in their first year. The ewe lambs and the remainder of the wethers were retained for yearling and adult wool production measurements. The lambs usually grazed extensive pastures available at the sites, but were supplemented with grain, hay, or feedlot pellets when the pasture supply was restricted. The details of the nutritional background of sheep reared under 8 production sites for 3 consecutive years are described elsewhere by Ponnampalam et al. (2014). The data from a maximum of 9,135 progeny born to 184 Merino sires and 4,614 Merino dams were analyzed. Each flock was managed by a Sheep CRC partner organization, with all activities approved by the Animal Ethics Committee for each site. Research and data collection activities used a common protocol across the IN sites.

Live Weight and Ultrasound Traits

Live weights recorded included birth weight (**bWT**), weaning weight (**wWT**, range of 62 to 117 d), post weaning weight (**pwWT**, range of 204 to 316 d), yearling weight (**yWT**, range of 289 to 393 d), and adult weight (**aWT**, range of 531 to 633

d). Live animal ultrasound measurements were obtained for subcutaneous fat depth (**FATUS**) and eye muscle depth (**EMDUS**) at the C site (over the 12th rib, 45 mm from the midline). Measurements were conducted at post weaning (**pw**, range 124 to 305 d) and/or yearling (**y**, range 298 to 554 d) ages by accredited ultrasound scanners. Weaning weight records were available from 7,007 animals, progeny of 182 sires and 4,113 dams, with over 2,650 and 3,590 progeny records for the ultrasound traits at weaning and yearling ages, respectively. Numbers of records and unadjusted means for these traits are shown in Table 1, as well as estimates of phenotypic variance and heritability reported by Mortimer et al. (2017a).

Carcass Traits

Measurement procedures for the carcass traits, described by Gardner et al. (2010), occurred following slaughter of the lambs at commercial abattoirs. Briefly, all carcasses were subjected to medium-voltage electrical stimulation and trimmed according to AUS-MEAT specifications (AUS-MEAT, 2006). Hot carcass weight (**HCW**) and carcass fat at the GR site (**FATGR**, total tissue depth measured with a GR knife at the 12th rib, 110 mm from the midline) were recorded on the hot carcass. Dressing percent (**DP**) was calculated as the ratio of HCW to live weight recorded the day prior to slaughter.

After carcasses were chilled overnight (3–4 °C), subcutaneous fat depth at the 5th rib (**FAT5**, 110 mm from the midline) was measured. At a cut between the 12th and 13th ribs of each carcass, eye muscle (M. longissimus thoracis et lumborum, **LL**) depth (**EMD**) and eye muscle width (**EMW**) were measured, as well as fat depth at the C site (**FATC**, depth of fat over the maximum depth of the eye muscle). Eye muscle area (**EMA**) was calculated as 80% of the product of depth and width (Plant and Maden, 1996). After excising the LL muscle from the carcass at 24-h post mortem, trimmed subcutaneous fat (**FATLL**) and the total weight of denuded (epimysium removed) LL (**WTLL**) were recorded. The topside was removed from the hind leg (HAM No. 5073, (AUS-MEAT, 2006)), trimmed of external fat and weighed (**WTTOP**). The knuckle (HAM No. 5072, (AUS-MEAT, 2006)) was also removed and weighed (**WTRND**), as well as the bone of the hind leg (**BONE**). An algorithm, based on HCW, FATGR, FATLL, FAT5, EMA, WTLL, WTTOP, WTRND, and BONE, was used to predict lean meat yield (**LMY**) for each animal (Gardner et al., 2010). There were over 1,249 progeny records for each of the carcass traits from over 176 sires and 1128 dams. Table 2 shows the numbers of records and unadjusted means and estimates of phenotypic variance and heritability for these traits reported by Mortimer et al. (2017b).

Meat Quality Traits

Within 2 h of slaughter, a sample (1 g) was taken from the LL and frozen in liquid nitrogen to assay isocitrate dehydrogenase activity (**ICDH**) using a procedure described by Gardner et al. (2006). Following the cut made between the 12th and 13th ribs, the meat color of the LL was measured after exposure to the air at ambient temperature for 30–40 min (Warner et al., 2010). Minolta Chroma meters (Models CR-300 and CR-400) were used that were set on the L^*, a^*, b^* system,

Table 1. Number of records and means for live weight and ultrasound traits[1] and estimates of phenotypic variances and heritability (h^2)[2]

Trait	No.	Mean	Phenotypic variance	CV (%)	Heritability (h^2)
Live weight					
bWT, kg	9,135	4.58	0.66	17.7	0.22 ± 0.04
wWT, kg	7,007	23.80	11.06	14.0	0.14 ± 0.04
pwWT, kg	6,082	38.28	20.43	11.8	0.31 ± 0.06
yWT, kg	5,304	41.01	20.75	11.1	0.38 ± 0.07
aWT, kg	4,276	53.91	32.41	10.6	0.59 ± 0.06
Ultrasound					
pwFATUS, mm	2,655	2.28	0.31	24.4	0.11 ± 0.06
pwEMDUS, mm	2,653	21.36	6.23	11.7	0.14 ± 0.07
yFATUS, mm	3,590	2.65	0.45	25.3	0.26 ± 0.05
yEMDUS, mm	3,590	23.83	5.65	10.0	0.20 ± 0.06

[1]bWT = birth weight; wWT = weaning weight; pwWT = post weaning weight; yWT = yearling weight; aWT = adult weight; pwFATUS = post weaning live ultrasound fat; pwEMDUS = post weaning live ultrasound eye muscle depth; yFATUS = yearling live ultrasound fat; yEMDUS = yearling live ultrasound eye muscle depth.

[2]Source: Mortimer et al. (2017a).

Table 2. Number of records and means for carcass dissection and measures traits[1] and estimates of phenotypic variances and heritability (h^2)[2]

Trait	No.	Mean	Phenotypic variance	CV (%)	Heritability (h^2)
Carcass measures					
HCW, kg	1331	21.1	5.03	10.6	0.35 ± 0.10
DP, %	1262	43.6	6.53	5.9	0.21 ± 0.11
FATGR, mm	1336	10.7	10.95	30.9	0.23 ± 0.11
FATC, mm	1281	3.3	2.58	49.1	0.29 ± 0.10
FAT5, mm	1288	5.6	4.60	38.0	0.21 ± 0.08
EMW, mm	1289	59.5	14.51	6.4	0.29 ± 0.09
EMD, mm	1289	27.4	8.38	10.6	0.12 ± 0.08
EMA, cm^2	1289	13.1	3.18	13.6	0.19 ± 0.08
Carcass dissection					
LMY, %	1249	58.4	3.891	3.4	0.29 ± 0.11
WTLL, g	1292	319.4	2205.9	14.7	0.46 ± 0.10
WTTOP, g	1291	541.3	3700.5	11.2	0.34 ± 0.11
WTRND, g	1293	426.9	2054.0	10.6	0.38 ± 0.11
FATLL, g	1290	159.0	3015.9	34.5	0.17 ± 0.10
BONE, g	1289	912.4	7757.5	9.7	0.29 ± 0.11

[1]HCW = hot carcass weight; DP = dressing percent, FATGR = carcass fat depth at the GR site; FATC = carcass fat depth at the C site; FAT5 = carcass fat depth at the 5th rib; EMW = eye muscle width; EMD = eye muscle depth; EMA = eye muscle area; LMY = lean meat yield; WTLL = loin muscle weight; WTTOP = topside weight; WTRND = round weight; FATLL = weight of fat trim of the loin; BONE = hind leg bone weight.

[2]Source: Mortimer et al. (2017b).

where *L** (**cf*L****) measures relative lightness, *a** (**cf*a****) relative redness, and *b** (**cf*b****) relative yellowness. These meters had closed cones and used illuminant D65, with a standard observer of 2°. The pH of the LL (**pH_{24}LL**) and the M. semitendinosus (**ST**) (**pH_{24}ST**) were measured at approximately 24 h after slaughter using a number of different pH meters linked to pH electrodes calibrated at chiller temperatures (3–4 °C) (Pearce et al., 2010). From the excised denuded LL muscle, two 40 g samples of diced muscle were collected, frozen, and stored. While iron (IRON) and zinc (ZINC) levels were measured on one sample (Pannier et al., 2010), fatty acid composition was measured on the other sample (Ponnampalam et al., 2010). These included the long-chain omega-3 fatty acids, eicosapentaenoic acid (**EPA**, 20:5n-3), docosapentaenoic acid (**DPA**, 22:5n-3), and docosahexaenoic acid (**DHA**, 22:6n-3) and omega-6 fatty acids, linoleic acid (**LA**, 18:2n-6) and arachidonic acid (**ARA**, 20:4n-6). On a sample (1 g) taken from the loin, myoglobin levels (**Myo**) were measured using methods described by Trout (1991). Intramuscular fat (**IMF**) of the LL (50 g) was measured using a Technicon Infralyser 450 and near-infrared procedure (Perry et al., 2001). A section of the LL (65 g) was aged for 5 d at 3–4 °C and stored frozen prior to shear force testing (**SF5**). Testing was conducted, using a Lloyd texture analyzer (Model LRX, Lloyd Instruments, Hampshire, UK) with a Warner–Bratzler type shear blade fitted as described by Hopkins et al. (2010), on samples which had been cooked from frozen for 35 min in plastic bags at 71 °C in a water bath. Numbers of records and unadjusted means and estimates of phenotypic variance and heritability for these traits, as reported by Mortimer et al. (2017c), are shown in Table 3.

Statistical Analysis

Covariance components were estimated using linear mixed animal models and restricted maximum likelihood methods with ASReml software (Gilmour et al., 2015). Phenotypic and genetic (co) variances were estimated using a series of bivariate analyses. To also aid in achieving convergence, nonestimable (co)variance components were removed from the mixed models in the instances where convergence did not occur. Appropriate (co)variances for the trait combinations then were used to estimate phenotypic and genetic correlations and their SE. The residual covariance for each combination of carcass and meat quality traits with adult live weight was fixed at zero and phenotypic correlations were not estimated, as no males were measured for both carcass and adult traits. The correlations involving EPA, DPA, and EPA+DPA+DHA were not estimable due to the absence of genetic variance for these traits

Table 3. Number of records and means for meat quality and nutritional value traits[1] and estimates of phenotypic variances and heritability (h^2)[2]

	No.	Mean	Phenotypic Variance	CV (%)	Heritablity (h^2)
Meat quality					
IMF (%)	1236	4.6	0.827	19.6	0.58 ± 0.11
SF5 (N)	1135	31.04	69.15	26.8	0.10 ± 0.09
$pH_{24}LL$	1292	5.72	0.011	1.8	0.15 ± 0.07
$pH_{24}ST$	1295	5.84	0.032	3.1	0.20 ± 0.10
ICDH (μmol/min/g tissue)	727	5.21	0.932	18.5	0.06 ± 0.10
Myo (mg/g tissue)	1292	7.45	1.77	17.9	0.31 ± 0.09
cf*a**	1262	18.54	1.96	7.6	0.07 ± 0.07
cf*b**	1264	3.64	1.11	28.9	0.08 ± 0.08
cf*L**	1262	34.07	4.42	6.2	0.14 ± 0.08
Nutritional value					
IRON (mg/kg wet tissue)	1289	22.1	9.72	14.1	0.20 ± 0.09
ZINC (mg/kg wet tissue)	1290	25.9	18.35	16.6	0.11 ± 0.09
EPA (mg/ 100 g tissue)	1277	14.7	15.83	27.0	0.00 ± 0.00
DPA (mg/100 g tissue)	1279	24.5	30.47	22.5	0.00 ± 0.00
DHA (mg/100 g tissue)	1279	7.3	4.36	28.4	0.01 ± 0.07
EPA+DHA (mg/ 100 g tissue)	1277	22.1	30.83	25.1	0.00 ± 0.00
EPA+DPA+DHA (mg/100 g tissue)	1277	46.6	108.92	22.4	0.00 ± 0.00
LA (mg/100 g tissue)	1277	161.2	942.50	19.0	0.14 ± 0.07
ARA (mg/100 g tissue)	1279	55.3	108.91	18.9	0.00 ± 0.00
LA+ARA (mg/100 g tissue)	1277	216.4	1419.1	17.4	0.10 ± 0.07

[1]IMF = intramuscular fat; SF5 = shear force after 5 days ageing; pH_{24} = pH at 24 h after slaughter for LL and ST muscles; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cf*a** = fresh meat redness; cf*b** = fresh meat yellowness; cf*L** = fresh meat lightness; IRON = iron content; ZINC = zinc content; EPA = eicosapentaeonic acid content; DPA = docosapentaeonic acid content; DHA = docosahexaeonic acid content; EPA+DHA = sum of EPA and DHA; EPA + DPA + DHA = sum of EPA, DPA and DHA; LA = linoleic acid content; ARA = arachidonic acid content; LA + ARA = sum of LA and ARA.

[2]Source: Mortimer et al. (2017c).

(Mortimer et al., 2017c). Details of the fixed effect and random models have been reported for live weight and ultrasound traits by Mortimer et al. (2017a), carcass traits by Mortimer et al. (2017b), and meat quality traits by Mortimer et al. (2017c).

Briefly, the fixed effects, plus their significant ($P < 0.05$) two-way interactions, and random effects for the live weight, ultrasound, carcass, and meat quality traits had been derived from univariate models. A mixed linear sire model was fitted initially to each trait which included the following fixed effects: site (8 levels), year of birth (5 levels), sex (2 levels, live animal traits only), sheep type (3 levels, ultra/super fine, fine fine/medium, and medium/strong to account for sires being from different types of Merino; Swan et al., 2016), type of birth and rearing (6 levels: 11, 21, 22, 31, 32, or 33 for numbers of lambs born and reared, respectively), and dam age (7 levels: 2 to greater than or equal to 8 yr of age). Age of the lamb at measurement was fitted as a linear covariate to the data. Management group nested within site was fitted to the live animal traits, whereas for the carcass and meat quality traits, slaughter group was fitted. Testing laboratory (2 levels) was fitted to the data for SF5 only. No other covariates were fitted to the data for the ultrasound traits (such as live weight), the carcass composition traits (such as carcass weight), and the meat quality traits (such as carcass weight or pH). This was done in order to evaluate the maximal amount of the genetic variation in the traits and genetic covariation with other traits. The fitting of live weight as a covariate in models for ultrasound eye muscle and fat depths has been found to alter the partitioning of variance between genetic effects and overcorrect the genetic relationship between traits (Mortimer et al., 2014a).

For all models, random effects included animal and genetic groups, with the genetic group effect defined by Merino flock of origin (bloodline) or sheep type (Swan et al., 2016). Significant random effects of sire x site interaction and dam (representing a maternal effect comprising both maternal genetic and maternal environmental effects) were included in the models for the live animal and carcass traits (Mortimer et al., 2017a, 2017b), but not the meat quality traits (Mortimer et al., 2017c).

RESULTS AND DISCUSSION

Live Weight Traits

Meat quality traits. There tended to be negligible (less than 0.2 in size) to low (between 0.2 and 0.4 in size) negative genetic correlations (favorable) between live weight at various ages and $pH_{24}LL$, as well as for live weights after weaning for $pH_{24}ST$ (Table 4). These estimates were associated with relatively large SE. The estimates tended to be consistent with reports by Fogarty et al. (2003) for Merino rams and de Hollander et al. (2014) for terminal x Merino crossbred progeny, although Greeff et al. (2008; Merino rams), Ingham et al. (2007; crossbred progeny of maternal breed sires), Payne et al. (2009; terminal sire progeny), Mortimer et al. (2010; an earlier multibreed sampling of the IN progeny), and Brito et al (2017; terminal sire progeny) reported correlations close to zero. There were also moderate (between 0.4 and 0.6 in size) to low negative genetic correlations for live weight with ICDH and to a lesser extent Myo, which were associated with large SE. In contrast, significant positive regressions of sire estimated breeding values (EBV), also known as Australian Sheep Breeding Values (**ASBV**), for pwWT on ICDH and Myo observed in an earlier multibreed sampling of the IN progeny (Kelman et al., 2014) and no association of this sire EBV effect with Myo observed in crossbred ewe lambs of Poll Dorset sires (Hopkins et al., 2005) have been reported. Myoglobin concentration and ICDH activity, an oxidative enzyme of muscle tissue, can be used as indicators of oxidative capacity of muscle of lamb, which is linked to muscle fiber type (Gardner et al., 2006). These indicators have been associated with reduced redness and increased lightness and yellowness of lamb loins (Calnan et al., 2016), as well as increased iron and zinc levels (Pannier et al., 2014b). The genetic correlations for live weight with the other meat quality traits tended to be negligible, which was consistent with reported genetic correlations for meat color (Fogarty et al., 2003; Greeff et al., 2008; Mortimer et al., 2010; Brito et al., 2015, 2017), IMF (Brien et al., 2013, an earlier multibreed sampling of the IN progeny; Mortimer et al., 2010), and shear force (Brien et al. 2013; Brito et al., 2015, 2017). Also, no effect has been observed of sire pwWT EBV on meat color (Calnan et al., 2017), except L^* (Hopkins et al., 2005), or IMF (Hopkins et al., 2007a; Pannier et al., 2014c; Anderson et al., 2015) and shear force (Hopkins et al., 2005; Allingham et al., 2006). However, low-positive genetic correlation between shear force and live weight at later

Table 4. Estimates of genetic and phenotypic correlations (±SE) between live weight[1] and meat quality traits[2]

	bWT	wWT	pwWT	yWT	aWT
Genetic correlations					
IMF	−0.05 ± 0.13	−0.09 ± 0.14	0.02 ± 0.12	−0.04 ± 0.12	−0.05 ± 0.11
SF5	0.00 ± 0.25	−0.11 ± 0.28	0.02 ± 0.25	0.15 ± 0.26	0.27 ± 0.24
$pH_{24}LL$	−0.37 ± 0.20	−0.14 ± 0.21	−0.19 ± 0.19	−0.17 ± 0.19	−0.19 ± 0.17
$pH_{24}ST$	0.01 ± 0.18	0.04 ± 0.19	−0.23 ± 0.17	−0.23 ± 0.17	−0.20 ± 0.15
ICDH	−0.31 ± 0.27	−0.73 ± 0.33	−0.35 ± 0.25	−0.50 ± 0.27	−0.46 ± 0.23
Myo	−0.22 ± 0.14	−0.31 ± 0.15	−0.15 ± 0.14	−0.13 ± 0.14	−0.17 ± 0.13
cfa^*	−0.19 ± 0.26	−0.30 ± 0.28	−0.06 ± 0.25	−0.06 ± 0.24	0.11 ± 0.23
cfb^*	−0.08 ± 0.22	−0.03 ± 0.24	−0.22 ± 0.21	−0.07 ± 0.21	−0.05 ± 0.20
cfL^*	0.23 ± 0.18	−0.01 ± 0.20	−0.19 ± 0.18	−0.24 ± 0.18	−0.16 ± 0.16
Phenotypic correlations					
IMF	−0.04 ± 0.03	0.01 ± 0.03	0.16 ± 0.03	0.16 ± 0.03	
SF5	0.01 ± 0.03	−0.04 ± 0.03	−0.13 ± 0.03	−0.11 ± 0.04	
pH24LL	−0.02 ± 0.03	0.01 ± 0.03	−0.11 ± 0.03	−0.12 ± 0.03	
pH24ST	−0.03 ± 0.03	−0.02 ± 0.03	−0.07 ± 0.03	−0.09 ± 0.03	
ICDH	−0.07 ± 0.04	−0.14 ± 0.04	−0.09 ± 0.04	−0.04 ± 0.04	
Myo	−0.08 ± 0.03	−0.02 ± 0.03	0.14 ± 0.03	0.11 ± 0.03	
cfa^*	−0.01 0.03	0.00 ± 0.03	0.08 ± 0.03	0.03 ± 0.04	
cfb^*	0.03 ± 0.03	0.01 ± 0.03	0.02 ± 0.03	−0.01 ± 0.04	
cfL^*	0.08 ± 0.03	0.01 ± 0.03	−0.06 ± 0.03	−0.03 ± 0.04	

[1] bWT = birth weight; wWT = weaning weight; pwWT = post weaning weight; yWT = yearling weight; aWT = adult weight.

[2]IMF = intramuscular fat; SF5 = shear force after 5 days ageing; pH_{24} = pH at 24 h after slaughter for LL and ST muscles; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cfa^* = fresh meat redness; cfb^* = fresh meat yellowness; cfL^* = fresh meat lightness.

ages may exist as shown by the present study and reported by Mortimer et al. (2010). The phenotypic correlations between live weight and the meat quality traits were all negligible (Table 4).

There were low to negligible negative genetic correlations (unfavorable) between live weight at various ages and IRON (−0.38 ± 0.16 to −0.14 ± 0.15), whereas those for ZINC were negligible (Table 5). Pannier et al. (2014b) reported no relationship between sire pwWT ASBV and both iron and zinc contents of lamb. There were moderate negative genetic correlations for yWT and aWT with the omega-3 fatty acids (EPA + DHA), albeit with high SE. The genetic correlations for the omega-6 fatty acids (LA and ARA) tended to be low and negative for yWT and aWT (−0.17 ± 0.33 to −0.35 ± 0.21), but were moderately positive for bWT (0.39 ± 0.21, 0.56 ± 0.49). The phenotypic correlations between live weight and the meat nutritional value traits were all negligible (Table 5).

Carcass traits. The estimates of genetic and phenotypic correlations between live weight and the carcass traits are shown in Table 6. As would be expected, the genetic correlations for HCW with live weights from weaning were highly positive (0.76 ± 0.08 to 0.97 ± 0.03) and consistent with other studies in Merinos (Greeff et al., 2008) and other mixed breed populations (Ingham et al., 2007; Payne et al., 2009; Mortimer et al., 2010; Brito et al., 2015, 2017). The correlations for DP were moderate and positive for live weights after weaning (0.35 ± 0.15 to 0.47 ± 0.17), which were at the upper end of the range of published estimates for DP (−0.22 to 0.28; Fogarty et al., 2003; Ingham et al., 2007; Greeff et al., 2008; Mortimer et al., 2010; Brito et al., 2017), but was negative for bWT (−0.32 ± 0.15). There were also moderate to high genetic correlations for live weight after weaning with measures of carcass fat (0.34 ± 0.13 to 0.63 ± 0.16) and eye muscle (0.38 ± 0.14 to 0.70 ± 0.15), which were generally consistent with Ingham et al. (2007), Greeff et al. (2008), and Brito et al. (2017; fat depth at the GR site only), although the correlations were negligible from other studies (Fogarty et al., 2003) or negative (Mortimer et al., 2010). It should also be noted that there were low to moderate negative correlations between bWT and carcass fat measures (−0.26 ± 0.14 to −0.42 ± 0.17), as were also reported by Brien et al. (2013). The phenotypic correlations were generally consistent with the corresponding genetic correlations, although smaller in magnitude.

The estimates of genetic and phenotypic correlations between live weight and the carcass dissection traits are shown in Table 7. There were high genetic correlations for live weight from weaning onwards with carcass dissected muscle (0.55 ± 0.11 to 0.95 ± 0.04), which were consistent with estimates reported by Brito et al. (2017) for 6-mo live weight with a range of primal cut weights, FATLL (0.25 ± 0.18 to 0.65 ± 0.13) and

Table 5. Estimates of genetic and phenotypic correlations (±SE) between live weight[1] and meat nutritional value traits[2]

	bWT	wWT	pwWT	yWT	aWT
Genetic correlations					
IRON	−0.19 ± 0.15	−0.38 ± 0.16	−0.14 ± 0.15	−0.23 ± 0.14	−0.18 ± 0.14
ZINC	−0.14 ± 0.17	−0.08 ± 0.19	−0.06 ± 0.16	−0.15 ± 0.16	−0.02 ± 0.15
DHA	0.13 ± 0.21	0.31 ± 0.23	0.09 ± 0.21	−0.09 ± 0.20	−0.03 ± 0.19
EPA + DHA	0.10 ± 0.45	0.13 ± 0.49	−0.31 ± 0.47	−0.55 ± 0.55	−0.42 ± 0.46
LA	0.39 ± 0.21	−0.06 ± 0.23	−0.12 ± 0.21	−0.35 ± 0.21	−0.33 ± 0.19
ARA	0.56 ± 0.49	0.07 ± 0.39	0.17 ± 0.37	−0.21 ± 0.36	−0.17 ± 0.33
LA + ARA	0.45 ± 0.24	−0.04 ± 0.25	−0.08 ± 0.23	−0.35 ± 0.24	−0.33 ± 0.21
Phenotypic correlations					
IRON	−0.06 ± 0.03	−0.05 ± 0.03	0.11 ± 0.03	0.03 ± 0.03	
ZINC	−0.06 ± 0.03	−0.04 ± 0.03	0.07 ± 0.03	0.07 ± 0.04	
DHA	−0.01 ± 0.03	0.02 ± 0.03	0.02 ± 0.03	−0.02 ± 0.03	
EPA + DHA	−0.03 ± 0.03	−0.02 ± 0.03	−0.03 ± 0.03	−0.09 ± 0.03	
LA	0.02 ± 0.029	−0.03 ± 0.03	0.08 ± 0.03	0.08 ± 0.03	
ARA	−0.02 ± 0.03	−0.06 ± 0.03	0.02 ± 0.03	−0.03 ± 0.03	
LA + ARA	0.01 ± 0.03	−0.04 ± 0.03	0.07 ± 0.03	0.05 ± 0.03	

[1]bWT = birth weight; wWT = weaning weight; pwWT = post weaning weight; yWT = yearling weight; aWT = adult weight.

[2]IRON = iron content; ZINC = zinc content; DHA = docosahexaeonic acid content; EPA = eicosapentaeonic acid content; EPA + DHA = sum of EPA and DHA; LA = linoleic acid content; ARA = arachidonic acid content; LA + ARA = sum of LA and ARA.

Table 6. Estimates of genetic and phenotypic correlations (±SE) between live weight[1] and carcass measures traits[2]

	bWT	wWT	pwWT	yWT	aWT
Genetic correlations					
HCW	0.16 ± 0.12	0.76 ± 0.08	0.97 ± 0.03	0.94 ± 0.03	0.91 ± 0.06
DP	−0.32 ± 0.15	0.13 ± 0.18	0.42 ± 0.16	0.47 ± 0.17	0.35 ± 0.15
FATGR	−0.40 ± 0.14	0.23 ± 0.15	0.58 ± 0.11	0.57 ± 0.12	0.52 ± 0.13
FATC	−0.26 ± 0.14	0.16 ± 0.16	0.40 ± 0.12	0.37 ± 0.13	0.34 ± 0.13
FAT5	−0.42 ± 0.17	0.13 ± 0.19	0.63 ± 0.16	0.53 ± 0.17	0.48 ± 0.16
EMW	0.01 ± 0.15	0.15 ± 0.16	0.38 ± 0.14	0.45 ± 0.13	0.39 ± 0.14
EMD	0.26 ± 0.21	0.41 ± 0.23	0.58 ± 0.16	0.65 ± 0.17	0.50 ± 0.18
EMA	0.21 ± 0.19	0.37 ± 0.19	0.61 ± 0.14	0.70 ± 0.15	0.58 ± 0.16
Phenotypic correlations					
HCW	0.13 ± 0.03	0.47 ± 0.02	0.80 ± 0.01	0.83 ± 0.01	
DP	−0.10 ± 0.03	0.06 ± 0.03	0.18 ± 0.03	0.13 ± 0.03	
FATGR	−0.11 ± 0.03	0.14 ± 0.03	0.41 ± 0.03	0.42 ± 0.03	
FATC	−0.04 ± 0.03	0.12 ± 0.03	0.35 ± 0.03	0.33 ± 0.03	
FAT5	−0.05 ± 0.03	0.13 ± 0.03	0.32 ± 0.03	0.32 ± 0.03	
EMW	0.08 ± 0.03	0.18 ± 0.03	0.29 ± 0.03	0.26 ± 0.03	
EMD	0.11 ± 0.03	0.21 ± 0.03	0.28 ± 0.03	0.30 ± 0.03	
EMA	0.13 ± 0.03	0.25 ± 0.03	0.35 ± 0.03	0.35 ± 0.03	

[1] bWT = birth weight; wWT = weaning weight; pwWT = post weaning weight; yWT = yearling weight; aWT = adult weight.

[2]HCW = hot carcass weight; DP = dressing percent, FATGR = carcass fat depth at the GR site; FATC = carcass fat depth at the C site; FAT5 = carcass fat depth at the 5th rib; EMW = eye muscle width; EMD = eye muscle depth; EMA = eye muscle area.

Table 7. Estimates of genetic and phenotypic correlations (±SE) between live weight[1] and carcass dissection traits[2]

	bWT	wWT	pwWT	yWT	aWT
Genetic correlations					
LMY	0.52 ± 0.15	−0.03 ± 0.18	−0.21 ± 0.15	−0.18 ± 0.15	−0.21 ± 0.14
WTLL	0.08 ± 0.13	0.55 ± 0.11	0.72 ± 0.07	0.74 ± 0.07	0.69 ± 0.09
WTTOP	0.33 ± 0.12	0.74 ± 0.09	0.95 ± 0.04	0.91 ± 0.05	0.83 ± 0.07
WTRND	0.33 ± 0.12	0.65 ± 0.10	0.90 ± 0.05	0.88 ± 0.05	0.82 ± 0.07
FATLL	−0.42 ± 0.16	0.25 ± 0.18	0.65 ± 0.13	0.62 ± 0.13	0.62 ± 0.14
BONE	0.56 ± 0.11	0.85 ± 0.08	0.91 ± 0.05	0.93 ± 0.05	0.90 ± 0.07
Phenotypic correlations					
LMY	0.13 ± 0.03	0.02 ± 0.03	−0.14 ± 0.03	−0.12 ± 0.03	
WTLL	0.09 ± 0.03	0.36 ± 0.03	0.59 ± 0.02	0.62 ± 0.02	
WTTOP	0.15 ± 0.03	0.41 ± 0.03	0.67 ± 0.02	0.69 ± 0.02	
WTRND	0.16 ± 0.03	0.41 ± 0.02	0.67 ± 0.02	0.69 ± 0.02	
FATLL	−0.05 ± 0.03	0.19 ± 0.03	0.43 ± 0.03	0.45 ± 0.03	
BONE	0.28 ± 0.03	0.51 ± 0.02	0.70 ± 0.01	0.72 ± 0.02	

[1]bWT = birth weight; wWT = weaning weight; pwWT = post weaning weight; yWT = yearling weight; aWT = adult weight.

[2]LMY = lean meat yield; WTLL = loin muscle weight; WTTOP = topside weight; WTRND = round weight; FATLL = weight of fat trim of the loin; BONE = hind leg bone weight.

BONE (0.85 ± 0.08 to 0.93 ± 0.05). The genetic correlations for LMY tended to be low and negative for live weights after weaning (−0.18 ± 0.15 to −0.21 ± 0.15), but was moderate and positive for bWT (0.52 ± 0.15). These estimates agreed generally with similar genetic correlations presented by Mortimer et al. (2010) for live weights at later ages, except for the directions of the correlations differing between estimates for live weight and FATLL, and by Brien et al. (2013) for birth weight. Where examined, the regressions of the sire ASBV for pwWT on carcass composition traits have only been significant and consistent with the sign of our genetic correlation estimates on WTTOP (Gardner et al., 2010), hind bone weight (Gardner et al., 2010; Anderson et al., 2016), and saddle lean weight (Anderson et al., 2015). The phenotypic correlations were generally consistent with

the corresponding genetic correlations, although smaller in magnitude.

Overall, based on the genetic correlations estimated by this study and Mortimer et al. (2017a), expected changes from selection to increase live weight in Merinos would include possible small reductions in iron content and oxidative capacity of muscles (reduced levels of Myo and ICDH), whereas more substantial increases would occur in HCW, carcass fatness traits, muscle weights, and bone weight and small increases in ultrasound muscle and fat depths, DP, and carcass eye muscle dimensions. Negligible changes would occur generally in LMY and the objective eating quality and meat color traits, though selection on yearling and adult weights could result in slight unfavorable changes in meat tenderness.

Ultrasound and Meat Quality Traits

For both ultrasound traits, the genetic correlations were negligible with IMF at both ages (all estimates less than 0.20 in size, Table 8) and associated with relatively large SE, which agrees with other studies that have found no or little relationship between sire ASBV for post weaning ultrasound traits and IMF in Poll Dorset–sired progeny (Hopkins et al., 2005; Hopkins et al., 2007b; Pannier et al., 2014c), though Brito et al. (2015, 2017) reported a moderate positive genetic correlation between ultrasound fat depth and marbling score. Genetic correlations between ultrasound fat and eye muscle depth and SF5 at post weaning age were moderate and negative, and at yearling age were negligible, but these correlations had relatively large SE. This is generally consistent with negligible genetic correlations estimated by Brito et al. (2015, 2017), and no effects of sire EBV for the ultrasound traits on shear force have been found (Hopkins et al. 2005, 2007b). There were low to moderate negative genetic correlations between meat pH in both muscles and ultrasound measurements of fat and muscle depth in live animals (−0.10 ± 0.29 to −0.53 ± 0.29). This is in contrast with low and positive genetic correlations for pH with ultrasound fat depth (0.07 ± 0.10) and eye muscle depth (0.26 ± 0.10) in Merino rams (Greeff et al., 2008). Similarly, low genetic correlations between these traits that were not significantly different from zero have also been reported (Mortimer et al., 2010; Brito et al., 2015, 2017). These estimates agree with the lack of the effect of the sire EBV for ultrasound muscle and fat depths

Table 8. Estimates of genetic and phenotypic correlations (±SE) between ultrasound traits[1] and meat quality traits[2]

	pwFATUS	pwEMDUS	yFATUS	yEMDUS
Genetic correlations				
IMF	0.20 ± 0.19	0.04 ± 0.22	0.01 ± 0.14	−0.18 ± 0.13
SF5	−0.57 ± 0.41	−0.49 ± 0.43	−0.02 ± 0.27	−0.11 ± 0.27
pH_{24}LL	−0.10 ± 0.29	−0.32 ± 0.33	−0.31 ± 0.21	−0.43 ± 0.20
pH_{24}ST	−0.23 ± 0.25	−0.53 ± 0.29	−0.23 ± 0.18	−0.29 ± 0.18
ICDH	−0.07 ± 0.40	−0.25 ± 0.44	−0.23 ± 0.28	−0.56 ± 0.29
Myo	0.35 ± 0.21	0.25 ± 0.24	0.43 ± 0.14	0.38 ± 0.15
cf*a**	−0.06 ± 0.36	0.28 ± 0.44	0.49 ± 0.34	0.57 ± 0.35
cf*b**	0.13 ± 0.31	0.13 ± 0.37	0.10 ± 0.25	0.15 ± 0.25
cf*L**	−0.05 ± 0.26	−0.52 ± 0.31	−0.36 ± 0.20	−0.31 ± 0.19
Phenotypic correlations				
IMF	0.17 ± 0.03	0.11 ± 0.03	0.14 ± 0.04	0.14 ± 0.05
SF5	−0.12 ± 0.04	−0.11 ± 0.04	−0.07 ± 0.04	−0.12 ± 0.05
pH_{24}LL	−0.01 ± 0.03	−0.04 ± 0.03	−0.12 ± 0.05	−0.33 ± 0.05
pH_{24}ST	0.00 ± 0.03	−0.03 ± 0.03	−0.07 ± 0.05	−0.06 ± 0.06
ICDH	0.06 ± 0.05	0.04 ± 0.05	−0.05 ± 0.05	−0.17 ± 0.06
Myo	0.10 ± 0.03	0.16 ± 0.03	0.18 ± 0.04	0.22 ± 0.05
cf*a**	0.04 ± 0.03	0.03 ± 0.03	0.02 ± 0.05	0.20 ± 0.05
cf*b**	0.09 ± 0.03	0.06 ± 0.03	0.01 ± 0.05	0.07 ± 0.06
cf*L**	0.00 ± 0.03	−0.10 ± 0.03	−0.08 ± 0.05	−0.05 ± 0.06

[1]pwFATUS = post weaning live ultrasound (C site, measured over the 12th rib, 45 mm from the midline) fat; pwEMDUS = post weaning live ultrasound eye muscle depth; yFATUS = yearling live ultrasound fat; yEMDUS = yearling live ultrasound eye muscle depth.

[2]IMF = intramuscular fat; SF5 = shear force after 5 days ageing; pH_{24} = pH at 24 h after slaughter for LL and ST muscles; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cf*a** = fresh meat redness; cf*b** = fresh meat yellowness; cf*L** = fresh meat lightness.

on pH (Hopkins et al., 2005; Gardner et al., 2006; Hopkins et al., 2007b; Gardner et al., 2010). There tended to be also generally low to moderate positive genetic correlations for FATUS and EMDUS with Myo (0.25 ± 0.24 to 0.43 ± 0.14) and cf*a** (−0.06 ± 0.36 to 0.57 ± 0.35), and negative with cf*L** (−0.05 ± 0.26 to −0.52 ± 0.31). Genetic correlation estimates for these traits from other studies are variable (Greeff et al., 2008; Mortimer et al., 2010; Brito et al., 2015, 2017), with sire EBV for the ultrasound traits having no (Gardner et al., 2006) to a small positive (Kelman et al., 2014) effect on Myo and no (Hopkins et al. 2005, 2007b) to small effects on the meat color traits (positive of muscle depth on redness, and negative of fat depth on redness and lightness in Merinos; Calnan et al., 2017). However, our results suggest that selection to increase FATUS and EMDUS in Merinos may result in increased Myo and meat redness (cf*a**), but decreased meat brightness (cf*L**), although any correlated changes would be small. The phenotypic correlations were smaller in magnitude and generally consistent in sign to the corresponding genetic correlations. There were small but significant phenotypic correlations in the desirable directions for FATUS and EMDUS with IMF, SF5, pH_{24}LL, and Myo.

The estimates of genetic and phenotypic correlations between ultrasound traits and meat nutritional value traits are shown in Table 9. There were low to moderate negative genetic correlations (−0.10 ± 0.40 to −0.61 ± 0.30) for FATUS and EMDUS with the long-chain omega-6 polyunsaturated fatty acids (LA, ARA, and LA + ARA). Although there were low to moderate genetic correlations with some of the other meat nutritional value traits, they were not consistent between ultrasound measures at post weaning and yearling ages, and associated with relatively large SE. No estimates of these genetic correlations are available from the literature, but a sire EBV effect on these traits has only been found in the case of a positive effect of the sire ASBV for pwFATUS on iron content (Pannier et al., 2014b).There were low significant positive phenotypic correlations for FATUS and EMDUS with IRON and also for yEMD with DHA, LA, and LA + ARA.

As well as selection to increase live weight, meat sheep breeding programs generally place emphasis on selection to increase muscle and reduce fat (Fogarty, 2009). The genetic correlations estimated by Mortimer et al. (2017b) and this study, though SE are often high, suggest that selection to reduce ultrasound fat depth in Merinos could result in slight increases in LMY, whereas carcass fatness and Myo would be reduced, together with smaller reductions in HCW, DP, carcass eye muscle dimensions, muscle weights, and bone weights.

Table 9. Estimates of genetic and phenotypic correlations (±SE) between ultrasound traits[1] and meat nutritional value traits[2]

	pwFATUS	pwEMDUS	yFATUS	yEMDUS
Genetic correlations				
IRON	0.23 ± 0.22	0.03 ± 0.26	0.14 ± 0.16	0.18 ± 0.16
ZINC	0.22 ± 0.24	−0.03 ± 0.29	−0.29 ± 0.18	−0.38 ± 0.18
DHA	0.32 ± 0.29	0.59 ± 0.37	0.00 ± 0.22	0.13 ± 0.22
EPA + DHA	0.42 ± 0.67	0.36 ± 0.75	−0.41 ± 0.51	−0.09 ± 0.41
LA	−0.34 ± 0.30	−0.30 ± 0.36	−0.46 ± 0.25	−0.30 ± 0.22
ARA	−0.21 ± 0.53	0.23 ± 0.59	n.e.	−0.10 ± 0.40
LA + ARA	−0.34 ± 0.33	−0.22 ± 0.40	−0.61 ± 0.30	−0.28 ± 0.25
Phenotypic correlations				
IRON	0.07 ± 0.03	0.10 ± 0.03	0.018 ± 0.05	0.13 ± 0.05
ZINC	0.02 ± 0.03	0.03 ± 0.03	−0.01 ± 0.05	0.03 ± 0.05
DHA	0.04 ± 0.04	0.02 ± 0.03	0.00 ± 0.04	0.14 ± 0.05
EPA + DHA	0.00 ± 0.04	0.01 ± 0.04	−0.07 ± 0.04	−0.01 ± 0.05
LA	0.02 ± 0.03	0.02 ± 0.03	0.05 ± 0.05	0.16 ± 0.06
ARA	−0.02 ± 0.03	0.01 ± 0.03	n.e.	−0.03 ± 0.06
LA+ARA	0.01 ± 0.03	0.02 ± 0.03	0.03 ± 0.05	0.16 ± 0.06

[1]pwFATUS = post weaning live ultrasound (C site, measured over the 12th rib, 45 mm from the midline) fat; pwEMDUS = post weaning live ultrasound eye muscle depth; yFATUS = yearling live ultrasound fat; yEMDUS = yearling live ultrasound eye muscle depth.

[2]IRON = iron content; ZINC = zinc content; DHA = docosahexaeonic acid content; EPA = eicosapentaeonic acid content; EPA+DHA = sum of EPA and DHA; LA = linoleic acid content; ARA = arachidonic acid content; LA+ARA = sum of LA and ARA.

n.e. = not estimable.

In contrast, selection to increase ultrasound muscle depth is expected to increase HCW, muscle weights, carcass fatness, eye muscle dimensions, and bone weights, with smaller increases in DP, meat redness, and Myo. Small reductions in meat lightness also are expected. The impact on shear force of selection on ultrasound eye muscle depth is unclear, as this study indicates that slightly reduced values (more tender meat) may result, vs. the small positive relationship (0.15 ± 0.17) reported by Mortimer et al. (2010) that suggests increased values (less tender meat) may result. However, negligible responses in LMY would occur.

Carcass and Meat Quality Traits

The estimates of genetic and phenotypic correlations between carcass measures and meat quality traits are shown in Table 10. Apart from the genetic correlation of HCW with ICDH (−0.49 ± 0.29), the genetic correlations of HCW with the meat quality traits were negligible to low in size, had relatively large SE, and generally were similar to those estimated by Mortimer et al. (2014b). With SE estimates being relatively large across the studies, our estimates were reasonably consistent with those published for HCW with shear force (Johnson et al., 2015; Brito et al., 2015, 2017), pH (Ingham et al., 2007; Brito et al., 2015, 2017; Johnson et al., 2015), fresh meat *a** and *b** (Brito et al., 2015, 2017), and fresh meat *L** (Ingham et al., 2007; Brito et al., 2015, 2017). The genetic correlations of carcass fatness traits with SF5 were low to moderate and negative (−0.08 ± 0.33 to −0.53 ± 0.32) and low and positive with IMF (0.10 ± 0.17 to 0.26 ± 0.20), consistent with low negative estimates for FATGR with marbling score (Brito et al., 2015, 2017). This suggests that the meat quality traits could be under the control of different genetic mechanisms to those influencing the carcass fatness traits. Based on detailed phenotyping of an extensive range of carcass composition traits of lambs of the IN breeding program combined with a multitrait genome-wide association analysis, the SNP groups influencing fatness were found to differ from the SNP groups that affect eating quality traits (IMF, tenderness) of lamb (Bolormaa et al., 2016). The genetic correlations for ICDH with DP, FATGR, and FAT5 were also low to moderate and negative (−0.29 to −0.53), but were associated with relatively large SE. There were generally moderate positive relationships of cf*a** and cf*b** with the various carcass fat measures (0.13 ± 0.29 to 0.52 ± 0.35), but generally negligible relationships with muscle measurements.

Table 10. Estimates of genetic and phenotypic correlations (±SE) between carcass measures[1] and meat quality traits[2]

	HCW	DP	FATGR	FATC	FAT5	EMW	EMD	EMA
Genetic correlations								
IMF	0.04 ± 0.15	0.15 ± 0.19	0.16 ± 0.17	0.10 ± 0.17	0.26 ± 0.20	−0.06 ± 0.18	−0.13 ± 0.25	−0.10 ± 0.21
SF5	−0.09 ± 0.29	−0.20 ± 0.36	−0.53 ± 0.32	−0.08 ± 0.33	−0.39 ± 0.40	0.17 ± 0.35	−0.02 ± 0.47	0.00 ± 0.41
pH_{24}LL	0.19 ± 0.22	−0.33 ± 0.29	0.09 ± 0.28	−0.06 ± 0.27	0.16 ± 0.33	−0.30 ± 0.27	−0.27 ± 0.38	−0.38 ± 0.32
pH_{24}ST	−0.24 ± 0.19	−0.03 ± 0.25	−0.49 ± 0.21	−0.05 ± 0.23	−0.56 ± 0.24	−0.01 ± 0.24	−0.27 ± 0.33	−0.20 ± 0.28
ICDH	−0.49 ± 0.29	−0.53 ± 0.37	−0.44 ± 0.36	−0.14 ± 0.37	−0.29 ± 0.43	−0.45 ± 0.36	0.21 ± 0.50	−0.05 ± 0.43
Myo	−0.25 ± 0.17	0.12 ± 0.22	0.07 ± 0.19	0.19 ± 0.19	−0.25 ± 0.24	−0.41 ± 0.20	−0.04 ± 0.28	−0.32 ± 0.23
cf*a**	0.23 ± 0.29	0.35 ± 0.39	0.48 ± 0.34	0.38 ± 0.34	0.43 ± 0.39	0.03 ± 0.35	0.06 ± 0.48	0.11 ± 0.42
cf*b**	0.27 ± 0.25	0.27 ± 0.34	0.49 ± 0.29	0.13 ± 0.29	0.52 ± 0.35	0.26 ± 0.31	−0.11 ± 0.41	0.14 ± 0.37
cf*L**	−0.19 ± 0.21	−0.30 ± 0.26	−0.16 ± 0.24	−0.51 ± 0.25	−0.07 ± 0.29	0.32 ± 0.26	−0.27 ± 0.36	0.02 ± 0.30
Phenotypic correlations								
IMF	0.18 ± 0.03	0.10 ± 0.03	0.23 ± 0.03	0.15 ± 0.03	0.14 ± 0.03	−0.03 ± 0.03	0.01 ± 0.03	−0.01 ± 0.03
SF5	−0.15 ± 0.03	−0.09 ± 0.03	−0.18 ± 0.03	−0.10 ± 0.03	−0.14 ± 0.03	0.00 ± 0.03	−0.05 ± 0.03	−0.04 ± 0.03
pH_{24}LL	−0.12 ± 0.03	−0.03 ± 0.03	−0.11 ± 0.03	−0.11 ± 0.03	−0.02 ± 0.03	0.04 ± 0.03	−0.05 ± 0.03	−0.03 ± 0.03
pH_{24}ST	−0.08 ± 0.03	0.05 ± 0.03	−0.07 ± 0.03	−0.10 ± 0.03	−0.09 ± 0.03	−0.01 ± 0.03	−0.03 ± 0.03	−0.04 ± 0.03
ICDH	−0.04 ± 0.04	−0.13 ± 0.04	0.00 ± 0.04	−0.01 ± 0.04	0.01 ± 0.04	0.07 ± 0.04	−0.02 ± 0.04	0.01 ± 0.04
Myo	0.12 ± 0.03	0.14 ± 0.03	0.20 ± 0.03	0.14 ± 0.03	0.15 ± 0.03	−0.02 ± 0.03	0.08 ± 0.03	0.06 ± 0.03
cf*a**	0.07 ± 0.03	0.05 ± 0.03	0.08 ± 0.03	0.04 ± 0.03	0.06 ± 0.03	0.02 ± 0.03	0.06 ± 0.03	0.05 ± 0.03
cf*b**	0.03 ± 0.03	0.02 ± 0.03	0.06 ± 0.03	0.04 ± 0.03	0.02 ± 0.03	−0.04 ± 0.03	0.00 ± 0.03	−0.02 ± 0.03
cf*L**	−0.03 ± 0.03	−0.08 ± 0.03	−0.06 ± 0.03	0.01 ± 0.03	−0.01 ± 0.03	−0.05 ± 0.03	−0.03 ± 0.03	−0.04 ± 0.03

[1]HCW = hot carcass weight; DP = dressing percent, FATGR = carcass fat depth at the GR site; FATC = carcass fat depth at the C site; FAT5 = carcass fat depth at the 5th rib; EMW = eye muscle width; EMD = eye muscle depth; EMA = eye muscle area.

[2]IMF = intramuscular fat; SF5 = shear force after 5 days ageing; pH_{24} = pH at 24 h after slaughter for LL and ST muscles; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cf*a** = fresh meat redness; cf*b** = fresh meat yellowness; cf*L** = fresh meat lightness.

The genetic correlation between meat color brightness (cf*L**) and FATC was −0.51 ± 0.25, which was similar to estimates reported by Fogarty et al. (2003) for Merino rams and Ingham et al. (2007). However, these results contrast with those of Greeff et al. (2008), who reported low to moderate negative genetic correlations between meat color and muscle (−0.07 to −0.47) and negligible correlations between meat color and fatness traits in Merino rams. Although the genetic correlations between pH_{24}LL and carcass fat measures were negligible and consistent with other reports (Fogarty et al., 2003; Ingham et al., 2007; Greeff et al., 2008; Brito et al., 2015, 2017), the correlations for pH_{24}ST with FATGR (−0.49 ± 0.21) and FAT5 (−0.56 ± 0.24) were moderately negative, which may indicate that the pH may be dependent on fat levels in some muscles.

The estimates of genetic and phenotypic correlations between carcass measures and meat nutritional value traits are shown in Table 11. Genetic correlations of HCW with the nutritional value traits were generally negligible and had relatively large SE, apart from a low negative correlation with IRON (−0.27 ± 0.17) and a moderate positive correlation with ARA (0.38 ± 0.45). These estimates were generally consistent with those reported by Mortimer et al. (2014b). Although minimal changes in the meat quality traits following selection for HCW are expected to occur, iron and myoglobin levels, and ICDH activity may be reduced and result in reduced oxidative capacity of the loin muscle. There was a general trend for the genetic correlations for the long-chain omega-6 polyunsaturated fatty acids (LA, ARA, and LA + ARA) to be moderately negative with FATGR and FATC (−0.40 to −0.70) and moderately positive with muscle traits (0.25 to 0.73), though all these genetic correlations had relatively large SE.

The estimates of genetic and phenotypic correlations between carcass dissection traits and meat quality traits are shown in Table 12. LMY tended to have unfavorable genetic correlations with IMF (−0.27 ± 0.18) and SF5 (0.53 ± 0.36), whereas FATLL was favorably correlated with these traits (IMF, 0.25 ± 0.19 and SF5, −0.68 ± 0.42). LMY was negatively correlated with Myo, cf*a**, and cf*b**, but positively with cf*L**, which similarly contrasted with the signs of the correlations with FATLL. These genetic correlations were associated with relatively large SE. Negligible negative genetic correlations of WTLL and WTTOP with IMF were similar to estimates for these trait combinations in a line of Norwegian White sheep (Lorentzen and Vangen, 2012). BONE was also moderately negatively correlated with ICDH (−0.54 ± 0.31) and Myo (−0.42 ± 0.17). The generally negligible genetic correlations for WTLL with meat color (−0.01 ± 0.22 to −0.24 ± 0.29) were consistent with results of Lorentzen and Vangen (2012), but in contrast to our results, they reported high-positive correlations for WTLL with pH (0.69 ± 0.41). These

Table 11. Estimates of genetic and phenotypic correlations (±SE) between carcass measures[1] and meat nutritional value traits[2]

	HCW	DP	FATGR	FATC	FAT5	EMW	EMD	EMA
Genetic correlations								
IRON	−0.27 ± 0.17	0.08 ± 0.23	−0.10 ± 0.21	0.03 ± 0.20	−0.25 ± 0.25	−0.25 ± 0.20	−0.10 ± 0.29	−0.19 ± 0.25
ZINC	−0.04 ± 0.20	−0.10 ± 0.26	−0.21 ± 0.24	0.03 ± 0.23	−0.17 ± 0.29	−0.13 ± 0.25	−0.12 ± 0.33	−0.25 ± 0.30
DHA	0.00 ± 0.25	0.39 ± 0.32	−0.02 ± 0.29	−0.27 ± 0.28	0.07 ± 0.33	−0.15 ± 0.28	0.02 ± 0.40	−0.05 ± 0.35
EPA + DHA	−0.08 ± 0.50	0.56 ± 0.83	−0.03 ± 0.58	−0.22 ± 0.58	−0.07 ± 0.65	−0.50 ± 0.58	−0.19 ± 0.77	−0.32 ± 0.67
LA	0.11 ± 0.24	0.20 ± 0.31	−0.40 ± 0.31	−0.49 ± 0.31	0.01 ± 0.33	0.25 ± 0.28	0.52 ± 0.39	0.57 ± 0.33
ARA	0.38 ± 0.45	−0.12 ± 0.54	−0.70 ± 0.77	−0.40 ± 0.58	−0.26 ± 0.60	0.39 ± 0.52	0.27 ± 0.74	0.58 ± 0.73
LA + ARA	0.18 ± 0.26	0.15 ± 0.34	−0.48 ± 0.36	−0.51 ± 0.36	−0.03 ± 0.36	0.30 ± 0.32	0.70 ± 0.44	0.73 ± 0.38
Phenotypic correlations								
IRON	0.03 ± 0.03	0.05 ± 0.03	0.09 ± 0.03	0.07 ± 0.03	0.07 ± 0.03	0.02 ± 0.03	0.03 ± 0.03	0.04 ± 0.03
ZINC	0.06 ± 0.03	−0.02 ± 0.03	0.02 ± 0.03	0.03 ± 0.03	0.04 ± 0.03	0.06 ± 0.03	0.01 ± 0.03	0.04 ± 0.03
DHA	0.00 ± 0.03	0.05 ± 0.03	−0.02 ± 0.03	−0.04 ± 0.03	−0.04 ± 0.03	0.02 ± 0.03	−0.01 ± 0.03	0.01 ± 0.03
EPA + DHA	−0.07 ± 0.03	0.00 ± 0.03	−0.08 ± 0.03	−0.07 ± 0.03	−0.09 ± 0.03	0.01 ± 0.03	−0.05 ± 0.03	−0.02 ± 0.03
LA	0.07 ± 0.03	0.02 ± 0.03	0.02 ± 0.03	0.00 ± 0.03	−0.03 ± 0.03	0.08 ± 0.03	0.00 ± 0.03	0.03 ± 0.03
ARA	−0.06 ± 0.03	−0.04 ± 0.03	−0.11 ± 0.03	−0.08 ± 0.03	−0.12 ± 0.03	0.08 ± 0.03	−0.09 ± 0.03	−0.02 ± 0.03
LA + ARA	0.04 ± 0.03	0.00 ± 0.03	−0.01 ± 0.03	−0.02 ± 0.03	−0.06 ± 0.03	0.09 ± 0.03	−0.03 ± 0.03	0.02 ± 0.03

[1]HCW = hot carcass weight; DP = dressing percent, FATGR = carcass fat depth at the GR site; FATC = carcass fat depth at the C site; FAT5 = carcass fat depth at the 5th rib; EMW = eye muscle width; EMD = eye muscle depth; EMA = eye muscle area.

[2]IRON = iron content; ZINC = zinc content; DHA = docosahexaeonic acid content; EPA = eicosapentaeonic acid content; EPA + DHA = sum of EPA and DHA; LA = linoleic acid content; ARA = arachidonic acid content; LA + ARA = sum of LA and ARA.

Table 12. Estimates of genetic and phenotypic correlations (±SE) between carcass dissection traits[1] and meat quality traits[2]

	LMY	WTLL	WTTOP	WTRND	FATLL	BONE
Genetic correlations						
IMF	−0.27 ± 0.18	−0.06 ± 0.15	−0.07 ± 0.15	0.00 ± 0.15	0.25 ± 0.19	−0.01 ± 0.15
SF5	0.53 ± 0.36	−0.05 ± 0.29	−0.02 ± 0.31	0.23 ± 0.31	−0.68 ± 0.42	0.15 ± 0.32
$pH_{24}LL$	−0.18 ± 0.30	−0.15 ± 0.23	0.03 ± 0.25	−0.22 ± 0.23	0.16 ± 0.32	−0.09 ± 0.24
$pH_{24}ST$	0.20 ± 0.24	−0.05 ± 0.20	−0.13 ± 0.20	−0.27 ± 0.19	−0.32 ± 0.25	−0.06 ± 0.20
ICDH	0.21 ± 0.40	−0.29 ± 0.30	−0.25 ± 0.32	−0.52 ± 0.30	−0.24 ± 0.40	−0.54 ± 0.31
Myo	−0.27 ± 0.20	−0.19 ± 0.17	−0.30 ± 0.17	−0.25 ± 0.17	0.26 ± 0.22	−0.42 ± 0.17
cf*a**	−0.69 ± 0.40	−0.24 ± 0.29	0.01 ± 0.30	0.05 ± 0.30	0.58 ± 0.43	0.43 ± 0.33
cf*b**	−0.32 ± 0.32	0.15 ± 0.26	0.03 ± 0.26	0.16 ± 0.26	0.53 ± 0.35	0.30 ± 0.27
cf*L**	0.49 ± 0.26	−0.01 ± 0.22	−0.05 ± 0.22	0.06 ± 0.22	−0.25 ± 0.28	−0.14 ± 0.22
Phenotypic correlations						
IMF	−0.25 ± 0.03	0.06 ± 0.03	0.07 ± 0.03	0.05 ± 0.03	0.22 ± 0.03	0.07 ± 0.03
SF5	0.15 ± 0.03	−0.10 ± 0.03	−0.12 ± 0.03	−0.05 ± 0.03	−0.15 ± 0.03	−0.04 ± 0.03
$pH_{24}LL$	0.02 ± 0.03	−0.12 ± 0.03	−0.12 ± 0.03	−0.10 ± 0.03	−0.11 ± 0.03	−0.06 ± 0.03
$pH_{24}ST$	−0.02 ± 0.03	−0.07 ± 0.03	−0.12 ± 0.03	−0.14 ± 0.03	−0.08 ± 0.03	−0.05 ± 0.03
ICDH	0.03 ± 0.04	0.03 ± 0.04	0.00 ± 0.04	−0.05 ± 0.04	−0.01 ± 0.04	−0.05 ± 0.04
Myo	−0.14 ± 0.03	0.14 ± 0.03	0.10 ± 0.03	0.03 ± 0.03	0.22 ± 0.03	−0.01 ± 0.03
cf*a**	−0.05 ± 0.03	0.05 ± 0.03	0.06 ± 0.03	0.06 ± 0.03	0.09 ± 0.03	0.05 ± 0.03
cf*b**	−0.05 ± 0.03	0.02 ± 0.03	0.00 ± 0.03	0.02 ± 0.03	0.07 ± 0.03	0.00 ± 0.03
cf*L**	0.01 ± 0.03	−0.03 ± 0.03	−0.08 ± 0.03	−0.03 ± 0.03	−0.04 ± 0.03	−0.01 ± 0.03

[1]LMY = lean meat yield; WTLL = loin muscle weight; WTTOP = topside weight; WTRND = round weight; FATLL = weight of fat trim of the loin; BONE = hind leg bone weight.

[2]IMF = intramuscular fat; SF5 = shear force after 5 days ageing; pH_{24} = pH at 24 h after slaughter for LL and ST muscles; ICDH = isocitrate dehydrogenase activity; Myo = myoglobin concentration; cf*a** = fresh meat redness; cf*b** = fresh meat yellowness; cf*L** = fresh meat lightness.

authors also reported positive genetic correlations between WTTOP and the meat color traits, vs. our estimates of negligible genetic correlation between these traits. Our estimates of genetic correlations of meat quality traits with muscle weight traits were consistent with those reported for similar carcass weight traits by Brito et al. (2017).

The estimates of genetic and phenotypic correlations between carcass dissection traits and meat nutritional value traits are shown in Table 13. The genetic correlations for IRON were low and negative for LMY, muscle, and BONE (−0.15 ± 0.18 to −0.48 ± 0.17). ZINC also had low negative genetic correlations with muscle (−0.17 ± 0.21 to −0.35 ± 0.21). There was a tendency for ARA to be positively genetically correlated with muscle weight (0.38 to 0.68), although the estimates had high SE. The correlations for the omega-3 fatty acids (DHA and EPA+DHA) were inconsistent and generally less than their SE.

LMY is regarded as an important component of lamb meat productivity (Pethick et al., 2011), with selection for increased LMY expected to result in unfavorable changes in several aspects of meat eating quality. Although SE for the genetic correlations were large, this expectation is supported by the genetic relationships involving LMY presented here and by Mortimer et al. (2017b). In particular, IMF and meat tenderness would tend to be reduced. Muscle oxidative activity, through lower myoglobin levels, and iron levels also could be reduced, as well as meat redness being affected. Reductions in live weight, HCW, and DP would also occur. However, selection for improved LMY would result in meat yellowness and carcass fatness being reduced while small increases would occur in ICDH, meat brightness (cf*L**), muscle weights, carcass eye muscle dimensions, and bone weight.

CONCLUSIONS

This study, together with the preceding studies in the series, has presented genetic parameter estimates for a wide range of carcass and meat quality traits, including several novel traits, live weight, and wool traits of Merino sheep. These estimates are critical for the design of effective breeding programs for dual-purpose production systems that aim to produce both wool and meat products that meet desired quality specifications. However, the present estimates of genetic correlations involving the carcass and meat quality traits are based on low numbers of records and are not well estimated. Further data are needed to validate the estimates presented in this series, as

Table 13. Estimates of genetic and phenotypic correlations (± SE) between carcass dissection traits[1] and meat nutritional value traits[2]

	LMY	WTLL	WTTOP	WTRND	FATLL	BONE
Genetic correlations						
IRON	−0.25 ± 0.22	−0.15 ± 0.18	−0.32 ± 0.18	−0.48 ± 0.17	−0.11 ± 0.24	−0.32 ± 0.18
ZINC	−0.12 ± 0.25	−0.35 ± 0.21	−0.24 ± 0.21	−0.17 ± 0.21	−0.01 ± 0.26	−0.03 ± 0.21
DHA	−0.17 ± 0.30	0.22 ± 0.27	−0.03 ± 0.26	−0.26 ± 0.25	0.32 ± 0.34	−0.31 ± 0.25
EPA + DHA	−0.59 ± 0.70	0.32 ± 0.78	−0.22 ± 0.52	−0.68 ± 0.64	0.50 ± 0.92	−0.64 ± 0.74
LA	0.11 ± 0.31	0.03 ± 0.25	0.05 ± 0.25	0.13 ± 0.25	−0.13 ± 0.33	0.10 ± 0.26
ARA	n.e.	0.68 ± 0.58	0.38 ± 0.48	0.38 ± 0.48	−0.05 ± 0.53	0.46 ± 0.52
LA + ARA	0.27 ± 0.36	0.15 ± 0.27	0.12 ± 0.28	0.19 ± 0.28	−0.13 ± 0.36	0.18 ± 0.29
Phenotypic correlations						
IRON	−0.04 ± 0.03	0.07 ± 0.03	0.07 ± 0.03	−0.02 ± 0.03	0.10 ± 0.03	0.00 ± 0.03
ZINC	0.00 ± 0.03	0.03 ± 0.03	0.05 ± 0.03	0.04 ± 0.03	0.07 ± 0.03	0.05 ± 0.03
DHA	0.04 ± 0.03	0.00 ± 0.03	0.03 ± 0.03	0.01 ± 0.03	−0.04 ± 0.03	−0.00 ± 0.03
EPA + DHA	0.07 ± 0.03	−0.04 ± 0.03	−0.03 ± 0.03	−0.03 ± 0.03	−0.07 ± 0.03	−0.01 ± 0.03
LA	−0.02 ± 0.03	0.03 ± 0.03	0.08 ± 0.03	0.06 ± 0.03	0.03 ± 0.03	0.05 ± 0.03
ARA	n.e.	−0.04 ± 0.03	0.00 ± 0.03	−0.02 ± 0.03	−0.10 ± 0.03	−0.01 ± 0.03
LA + ARA	0.01 ± 0.03	0.01 ± 0.03	0.06 ± 0.03	0.04 ± 0.03	0.00 ± 0.03	0.04 ± 0.03

[1]LMY = lean meat yield; WTLL = loin muscle weight; WTTOP = topside weight; WTRND = round weight; FATLL = weight of fat trim of the loin; BONE = hind leg bone weight.

[2]IRON = iron content; ZINC = zinc content; DHA = docosahexaeonic acid content; EPA = eicosapentaeonic acid content; EPA + DHA = sum of EPA and DHA; LA = linoleic acid content; ARA = arachidonic acid content; LA + ARA = sum of LA and ARA.

n.e. = not estimable.

well as to expand the range of genetic relationships to include those with other traits that influence profitability of dual-purpose production systems, such as feed efficiency, reproduction, and disease resistance traits. Nonetheless, these genetic parameters will assist in the development of EBV for new traits (e.g., Brown et al. (2007)) and indexes for breeding objectives which include emphasis on meat quality (Swan et al., 2015) to be incorporated into national sheep genetic evaluation programs. Many of the meat quality traits are difficult or expensive to measure commercially and developments in phenotyping of body composition and meat quality via noninvasive methods on live animals and carcasses are occurring to remove these impediments (Maltin et al., 2015). Additionally, genomic information is being generated to increase the accuracy of selection and to include these traits in breeding programs (Daetwyler et al., 2010, 2012; Jacob and Pethick, 2014).

As many of the genetic correlations are small or negligible, selection for the major meat production traits will have little effect on many of the traits associated with meat quality, particularly where breeding programs are based on suitably defined breeding objectives and effective selection indexes. However, the study has confirmed the potential adverse effects on IMF, tenderness, color, and iron levels of lamb meat that may be expected to occur following selection emphasizing either one of the key traits currently used in dual purpose breeding programs (live weight, and ultrasound fat and muscle depths). Similar adverse effects on meat quality also were identified following selection for increased LMY, as well as on carcass fatness. As the Merino has low fat levels (Fogarty et al., 2000; Ponnampalam et al., 2007) and is used as a dual-purpose breed, for some production systems increasing fat is desirable as it is associated with higher reproduction and farm profit (Ferguson et al., 2010; Brown and Swan, 2016). It may be that directly incorporating LMY into breeding programs, rather than through component live animal traits, may offer the opportunity to develop more effective and flexible selection strategies that improve maternal traits and lean meat production while addressing consumer preferences for tender, flavorsome, and nutritious lamb. Assessment of this opportunity awaits further development of breeding objectives for dual purpose production systems and modeling of a range of selection strategies, as well as availability of more accurate estimates of genetic parameters.

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