

## Genetic parameters for wool traits, live weight, and ultrasound carcass traits in Merino sheep<sup>1</sup>

S. I. Mortimer,\*†<sup>2</sup> S. Hatcher,†‡ N. M. Fogarty,†‡ J. H. J. van der Werf,†§ D. J. Brown,†# A. A. Swan,†# J. C. Greeff,†|| G. Refshauge,†¶ J. E. Hocking Edwards,†\*\* and G. M. Gaunt†,††

\*NSW Department of Primary Industries, Agricultural Research Centre, Trangie NSW 2823, Australia; †CRC for Sheep Industry Innovation, University of New England, Armidale, NSW 2351, Australia; ‡NSW Department of Primary Industries, Orange Agricultural Institute, Orange NSW 2800, Australia; §School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia; #Animal Genetics and Breeding Unit (AGBU),<sup>3</sup> University of New England, Armidale, NSW 2351, Australia; || Department of Agriculture and Food WA, Baron Hay Court, South Perth, WA 6151, Australia; ¶NSW Department of Primary Industries, Centre for Red Meat and Sheep Development, Cowra, NSW 2794, Australia; \*\*South Australian Research and Development Institute, Naracoorte, SA 5271, Australia; ††Department of Economic Development, Jobs, Transport and Resources, Rutherglen, VIC 3685, Australia

**ABSTRACT:** Genetic correlations between 29 wool production and quality traits and live weight and ultrasound fat depth (FAT) and eye muscle depth (EMD) traits were estimated from the Information Nucleus (IN). The IN comprised 8 genetically linked flocks managed across a range of Australian sheep production environments. The data were from a maximum of 9,135 progeny born over 5 yr from 184 Merino sires and 4,614 Merino dams. The wool traits included records for yearling and adult fleece weight, fiber diameter (FD), staple length (SL), fiber diameter CV (FDCV), scoured color, and visual scores for breech and body wrinkle. We found high heritability for the major yearling wool production traits and some wool quality traits, whereas other wool quality traits, wool color, and visual traits were moderately heritable. The estimates of heritability for live weight generally increased with age as maternal effects declined. Estimates of heritability for the ultrasound traits were also higher when measured at yearling age rather than at postweaning age. The genetic correlations for fleece weight with live weights were positive (favorable) and moderate (approximately  $0.5 \pm 0.1$ ), whereas those with FD were approximately 0.3 (unfavorable).

The other wool traits had lower genetic correlations with the live weights. The genetic correlations for FAT and EMD with FD and SL were positive and low, with FDCV low to moderate negative, but variable with wool weight and negligible for the other wool traits. The genetic correlations for FAT and EMD with postweaning weight were positive and high ( $0.61 \pm 0.18$  to  $0.75 \pm 0.14$ ) but were generally moderate with weights at other ages. Selection for increased live weight will result in a moderate correlated increase in wool weight as well as favorable reductions in breech cover and wrinkle, along with some unfavorable increases in FD and wool yellowness but little impact on other wool traits. The ultrasound meat traits, FAT and EMD, were highly positively genetically correlated (0.8), and selection to increase them would result in a small unfavorable correlated increase in FD, moderately favorable reductions in breech cover and wrinkle, but equivocal or negligible changes in other wool traits. The estimated parameters provide the basis for calculation of more accurate Australian Sheep Breeding Values and selection indexes that combine wool and meat objectives in Merino breeding programs.

**Key words:** fat depth, genetic correlations, live weight, Merino sheep, muscle depth, wool

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<sup>2</sup>Corresponding author: sue.mortimer@dpi.nsw.gov.au

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## INTRODUCTION

Breeding programs for Merino sheep have traditionally focused on improvement of wool production and wool quality (Atkins, 1997). Continued demand for sheep meat and changes in the relativities between prices paid for wool and meat in recent years has meant that many Merino breeders now wish to place emphasis on both wool and meat traits in their breeding programs (Banks, 2002; Safari et al., 2006; Brown and Swan, 2016). In Merino flocks, the major production traits for improved wool and meat production include fleece weight, fiber diameter, live weight, and reproduction (Fogarty et al., 2006) and carcass eye muscle depth (Brown and Swan, 2016). Other traits associated with product quality (e.g., wool staple strength, carcass fat) and disease (e.g., worm resistance, fly strike) may also be important contributors to profit. There is considerable genetic variation for the major wool and meat traits (Safari et al., 2005, 2007a; Greeff et al., 2008; Huisman et al., 2008; Brown et al., 2016). However, the development of effective breeding programs that combine these disparate objectives also requires accurate estimates of the genetic relationships between the various traits. Expected responses to selection for a range of Merino breeding objectives have been shown to be sensitive to the magnitude of the genetic correlations between the various traits (Safari et al., 2006). This is the first of a series of papers that provides estimates of genetic correlations between an extensive range of wool and meat traits. This paper estimates the genetic correlations between several wool (production and quality) traits and live estimates of meat (weight and ultrasound) traits at different ages. The estimated parameters provide the basis for calculation of more accurate Australian Sheep Breeding Values, reported by the Sheep Genetics evaluation program (Brown et al., 2007), and selection indexes that combine wool and meat objectives in Merino breeding programs.

## MATERIALS AND METHODS

### *Animals*

All activities and procedures involving the animals were approved by the Animal Ethics Committee for each site of the Information Nucleus breeding program (IN; Fogarty et al., 2007; van der Werf et al., 2010) of the Cooperative Research Centre for Sheep Industry Innovation (Sheep CRC; Armidale, Australia). All animals in the project were managed according to the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC, 2013). Data were collected from the Merino progeny born over 5 yr (2007 to 2011) in the IN, which were managed in a wide range

of Australian sheep environments (Fogarty et al., 2007; Mortimer et al., 2009; van der Werf et al., 2010). The IN consisted of 8 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) and managed by Sheep CRC partner organizations. The design of the IN, including procedures used to select the sires to artificially inseminate the founding dams and the management procedures, have been described (van der Werf et al., 2010; Geenty et al., 2014). All sires were used at 2 sites (Armidale and Katanning) and at least 50% of the sires were used at all the sites. The research and data collection activities used a common protocol at each IN site.

Sires used in the IN were selected from a range of breeds used in the Australian sheep industry (Merino wool and maternal and terminal meat breeds), but only data from progeny of Merino sires  $\times$  Merino dams were used in these analyses. The Merino dams were sourced from pedigreed and/or commercial flocks, depending on the site. The data were generated from records of 9,135 progeny born in 6,915 litters. These lambs were the progeny of 184 Merino sires and 4,614 Merino dams. The lambs were tail docked and the males were castrated at marking (7 to 43 d). After weaning (average age at weaning was 90.7 d [SD 9.7]), the Merino lambs at each site were managed to achieve target growth rates of 150 g/d. Half of the wether lambs, after balancing for sire, were randomly allocated to groups for slaughter, where the slaughter of each group was scheduled to occur at a target carcass weight of 21.5 kg. The ewe lambs and the remainder of the wethers were retained for yearling and adult wool production measurements (except the 2011-born wethers, which had only yearling wool measurements). The lambs usually grazed the extensive pastures available at the sites but were supplemented with grain, hay, or feedlot pellets when the pasture supply was restricted.

### *Wool Traits*

The ewes and wethers were shorn as yearlings (259 to 481 d) and adults (>540 d), when greasy fleece weight (GFW)—the unskirted fleece including belly wool—was recorded (i.e., yearling GFW [yGFW] and adult GFW [aGFW], respectively). Prior to shearing, a mid-side wool sample (75–85 g) was taken from the right side of each animal and forwarded to the Melbourne laboratory of the Australian Wool Testing Authority for measurement of various wool traits (AWTA, 2000). These traits included washing yield (YLD), mean fiber diameter (FD), FD SD (FDSD), FD CV (FDCV), staple strength (SS), staple length (SL), and mean fiber curvature (CUR). Clean fleece weight (CFW) was calculated as the product of

GFW and YLD. Greasy fleece weight and CFW were adjusted pro rata to 365 d growth of wool. Further details of the wool testing procedures have been previously reported (Hatcher et al., 2010). Wool color measurements were performed on the clean scoured and carded samples with the color expressed in terms of 3 tristimulus (**T**) values: X, Y, and Z, which are derived from the reflectance spectrum (IWTO, 2003). These values represent the amounts of the red/orange (X), yellow/green (Y), and blue/indigo/violet (Z) components of the spectrum of white light that are reflected from the sample. Scoured wool color is normally described using the Y tristimulus value as an indicator of brightness (**Y**) and the (**Y-Z**) value as an indicator of yellowness. Merino fleece wool tends to have average values of 75 T units for Y and between 8 and 8.5 T units for (Y-Z; Millington et al., 2011).

Within 1 mo after shearing (yearling and adult), indicator traits for the predisposition of sheep to fly strike (Hatcher and Preston, 2015) were assessed. Scores for breech cover (**BCOV**), breech wrinkle (**BRWR**), and body wrinkle (**BDWR**) were assigned using the 1-to-5 diagrammatic scale in the Visual Sheep Scores guide (AWI and MLA, 2013). The scores depict varying areas of bare skin (wool free) around the breech (**BCOV**) and varying degrees of wrinkling over the breech (**BRWR**) or entire body (**BDWR**). For each trait, a score of 1 depicts the most desirable expression (extensive wool free area or no wrinkles) and a score of 5 depicts the least desirable expression of the trait (no wool free area or extensive wrinkles and skin folds). Breech wrinkle was also assessed at lamb marking.

There were approximately 5,700 records for the yearling wool traits, with the number of records, mean, SD, and the number of sires and dams for each trait shown in Table 1. For the adult wool traits, there were approximately 3,700 records (not shown for conciseness), which are available in Supplementary Table S1 (see the online version of the article at <http://journalofanimalscience.org>).

### Live Weight and Ultrasound Traits

Live weight of the Merino progeny was recorded at birth (birth weight [**bWT**]), weaning (weaning weight [**wWT**]; range of 62 to 117 d), postweaning (postweaning weight [**pwWT**]; range of 204 to 316 d), yearling (yearling weight [**yWT**]; range of 289 to 393 d), and adult (adult weight [**aWT**]; range of 531 to 633 d) ages. Live animal ultrasound measurements were taken at the C site (over the 12th rib, 45 mm from the midline) by accredited (Sheep Genetics) ultrasound scanners for subcutaneous fat depth (**FAT**) and eye muscle depth (**EMD**) at postweaning (range 124 to 305 d) and/or yearling (range 298 to 554 d) ages, with 123 animals having records at both ages. The live weight recorded at the ultrasound

**Table 1.** The number of records, mean, SD, and number of sires and dams for yearling wool traits

Trait <sup>1</sup>	No.	Mean	SD	Sires	Dams
Wool production					
yGFW, kg	5,675	3.97	1.37	184	3,995
yYLD, %	5,749	70.65	6.68	184	3,995
yCFW, kg	5,599	2.79	0.95	184	3,995
Wool quality					
yFD, $\mu\text{m}$	5,796	16.88	1.65	184	3,995
yFDSD, $\mu\text{m}$	5,796	3.13	0.53	184	3,995
yFDCV, %	5,796	18.54	2.69	184	3,995
ySS, N/ktex	5,033	31.53	11.86	184	3,995
ySL, mm	5,035	88.68	17.37	184	3,995
yCUR, degrees/mm	5,795	60.48	9.83	184	3,995
Wool color					
yY, T units	5,795	73.82	2.43	184	3,995
y(Y-Z), T units	5,795	8.22	1.06	184	3,995
Visual scores <sup>2</sup>					
yBCOV	3,389	3.57	0.92	162	2,198
mBRWR	6,035	3.00	1.08	183	3,683
yBRWR	4,629	2.47	0.91	176	2,856
yBDWR	4,768	2.21	0.95	163	2,914

<sup>1</sup>yGFW = yearling greasy fleece weight; yYLD = yearling washing yield; yCFW = yearling clean fleece weight; yFD = yearling fiber diameter; yFDSD = yearling fiber diameter SD; yFDCV = yearling fiber diameter CV; ySS = yearling staple strength; ySL = yearling staple length; yCUR = yearling fiber curvature; yY = yearling brightness; T = tristimulus; y(Y-Z) = yearling yellowness; yBCOV = yearling breech cover; mBRWR = marking breech wrinkle; yBRWR = yearling breech wrinkle; yBDWR = yearling body wrinkle.

<sup>2</sup>Visual traits were scored on a 1-to-5 scale, with 1 the least and 5 the greatest expression of the trait.

measurement was used to adjust the ultrasound measurements for weight. The number of records, mean, SD, and the number of sires and dams for each of the live weight and ultrasound traits are shown in Table 2.

### Statistical Analyses

Fixed effects, variance components, and genetic parameters were estimated using a general linear mixed model and REML methods with ASReML software (Gilmour et al., 2015). Initially, mixed linear sire models were developed to identify those fixed effects influencing the wool traits and the weight and ultrasound traits separately. The fixed effects included site (8 levels), year of birth (5 levels), sex (2 levels), 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 the number of lambs born/reared, respectively), and dam age (7 levels: 2 to greater than or equal to 7 yr of age). For the live weight and ultrasound traits, management group nested within site was also fitted as well as age at observation as a linear covariate. A management group effect was not fitted to the wool traits,

**Table 2.** The number of records, mean, SD, and number of sires and dams for live weight and ultrasound traits

Trait <sup>1</sup>	No.	Mean	SD	Sires	Dams
Live weight					
bWT, kg	9,135	4.58	1.08	182	4,614
wWT, kg	7,007	23.80	5.06	182	4,113
pwWT, kg	6,082	38.28	7.83	182	3,696
yWT, kg	5,304	41.01	8.57	182	3,390
aWT, kg	4,276	53.91	10.49	182	3,002
Ultrasound					
pwFAT, mm	2,655	2.28	0.90	174	1,998
pwEMD, mm	2,653	21.36	3.76	174	1,997
yFAT, mm	3,590	2.65	1.05	181	2,454
yEMD, mm	3,590	23.83	4.05	181	2,453

<sup>1</sup>bWT = birth weight; wWT = weaning weight; pwWT = postweaning weight; yWT = yearling weight; aWT = adult weight; pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth.

as Merino progeny retained for yearling and adult wool production measurements within the IN at each site were generally managed in the same group.

Variance components for each trait were then estimated from univariate mixed animal model analyses. All models included the random effects of animal and genetic group. The genetic group effect represents the proportion of genes from various Merino bloodlines of each animal defined from its pedigree using the method initially described by Quaas (1988) and modified by Swan et al. (2016). For each trait, the genetic groups fitted were derived from the pedigrees of animals with phenotypic records for that trait and ranged in number from 130 to 134 across the traits. Genetic groups were defined first by flock of origin (bloodline) and sheep type (Swan et al., 2016). Dam effects were considered unrelated, as the pedigree about the dams was scarce. Hence, the dam effect represented a maternal effect comprising both maternal genetic and maternal environmental effects. Random effects of sire  $\times$  site interaction, dam, and dam  $\times$  year interaction (representing environmental variation between litters) were then added to the model to assess the importance of these effects in explaining variation in each trait. If its inclusion in the model resulted in a significant increase in the log-likelihood value from that of a reduced model, the random effect was retained. The heritability for each trait was estimated from the univariate analyses, where the phenotypic variance was the sum of the additive genetic, maternal (when fitted), sire  $\times$  site (when fitted), and the residual variances. The ratios of maternal and sire  $\times$  site variances to phenotypic variance were estimated as appropriate for each trait. The ratio of genetic group variance to additive genetic variance was also calculated, representing the relative size of the between genetic group variance to the within genetic group variance. Phenotypic and genetic covariances were estimated us-

ing a series of bivariate analyses involving all combinations of traits at each stage of measurement. Fixed effects and significant 2-way interactions were fitted based on the univariate analyses. The random bivariate models included all significant effects from the univariate models, although in the few instances where convergence did not occur, simpler random models were used. Phenotypic and genetic correlations, and their SE, were estimated from the appropriate covariances using ASReml.

## RESULTS AND DISCUSSION

### Heritability

Heritability estimates were high for the major yearling wool production and wool quality traits, with other wool quality, wool color, and visual traits being more moderately heritable (Table 3). The heritability estimates for yGFW ( $0.57 \pm 0.05$ ) and yearling CFW (yCFW;  $0.52 \pm 0.05$ ) were high. There was also considerable genetic group variation for these traits, and the results are generally consistent with those of Swan et al. (2016). The estimates of heritability for the adult wool traits (available in Supplementary Table S2; see the online version of the article at <http://journalofanimalscience.org>) were generally consistent with the yearling traits shown here. These estimates of heritability for the wool production and wool quality traits are generally consistent with those reviewed by Safari et al. (2005) and more recent reports from large Merino data sets (Asadi Fozi et al., 2005; Safari et al., 2007a; Huisman et al., 2008; Swan et al., 2008, 2016; Brown et al., 2010, 2013). The few reports of estimates for heritability of scoured wool yellowness color (Y-Z) in Merino sheep range from 0.25 for yearlings and 0.29 for adults (Smith and Purvis, 2009) to  $0.42 \pm 0.14$  (James et al., 1990) and  $0.45 \pm 0.08$  (Hebart and Brien, 2009), with estimates from Coopworth and Romney sheep being lower ( $0.13 \pm 0.06$ ; Biggam et al., 1983). A heritability of  $0.55 \pm 0.16$  for scoured wool brightness (yY) has also been reported (James et al., 1990). There is a similar range of estimates of heritability for greasy color measurements (James et al., 1990; Raadsma and Wilkinson, 1990).

There were significant, albeit small, sire  $\times$  site effects for each of the yearling wool production and quality traits, including color (Y-Z) and wrinkle scores. These sire  $\times$  site effects were also small and significant for the adult wool production traits and adult FD and adult SS, as well as adult yellowness (a(Y-Z)) and each of the wrinkle scores and adult BCOV (aBCOV). This indicates the presence of small genotype interaction effects such that the expression of these traits by the progeny of some sires may vary across different environments and ewe genotypes. However, the small size of these effects, 6% or less of the phenotypic vari-

**Table 3.** Estimates of phenotypic variance and the proportions due to additive genetic variance ( $h^2$ ), genetic group<sup>1</sup> ( $b^2$ ), sire  $\times$  site ( $s^2$ ), and maternal effects ( $c^2$ ; SE) for yearling wool traits

Trait <sup>2</sup>	Phenotypic variance	CV, %	Heritability ( $h^2$ )	Genetic group ( $b^2$ )	Sire $\times$ site ( $s^2$ )	Maternal ( $c^2$ )
Wool production						
yGFW	0.48	17.4	0.57 (0.05)	1.32 (1.16)	0.04 (0.01)	0.02 (0.02)
yYLD	18.72	6.1	0.44 (0.04)	0.00 (0.00)	0.03 (0.01)	0.08 (0.02)
yCFW	0.25	17.9	0.52 (0.05)	3.10 (2.41)	0.05 (0.01)	0.03 (0.02)
Wool quality						
yFD	1.64	7.6	0.74 (0.04)	0.39 (0.30)	0.02 (0.01)	–
yFDSD	0.20	14.3	0.42 (0.04)	0.30 (0.23)	0.02 (0.01)	0.07 (0.02)
yFDCV	5.95	13.2	0.34 (0.04)	0.05 (0.06)	0.03 (0.01)	0.09 (0.02)
ySS	84.83	29.2	0.23 (0.04)	0.00 (0.00)	0.03 (0.01)	0.07 (0.02)
ySL	123.53	12.5	0.48 (0.04)	0.29 (0.25)	0.02 (0.01)	0.06 (0.02)
yCUR	75.30	14.4	0.39 (0.04)	0.13 (0.11)	0.02 (0.01)	0.08 (0.02)
Wool color						
yY	2.84	2.3	0.19 (0.03)	0.04 (0.05)	–	0.03 (0.02)
y(Y-Z)	0.92	11.7	0.80 (0.04)	0.26 (0.25)	0.04 (0.01)	–
Visual scores <sup>3</sup>						
yBCOV	0.54	20.6	0.16 (0.03)	0.24 (0.22)	–	0.05 (0.03)
mBRWR	0.88	31.3	0.26 (0.04)	0.03 (0.04)	0.03 (0.01)	0.10 (0.02)
yBRWR	0.52	29.2	0.33 (0.04)	0.00 (0.00)	0.02 (0.01)	–
yBDWR	0.48	31.4	0.34 (0.04)	0.02 (0.03)	0.04 (0.01)	–

<sup>1</sup> $b^2$  = ratio of genetic group to additive genetic variance.

<sup>2</sup>yGFW = yearling greasy fleece weight; yYLD = yearling washing yield; yCFW = yearling clean fleece weight; yFD = yearling fiber diameter; yFDSD = yearling fiber diameter SD; yFDCV = yearling fiber diameter CV; ySS = yearling staple strength; ySL = yearling staple length; yCUR = yearling fiber curvature; yY = yearling brightness; y(Y-Z) = yearling yellowness; yBCOV = yearling breech cover; mBRWR = marking breech wrinkle; yBRWR = yearling breech wrinkle; yBDWR = yearling body wrinkle.

<sup>3</sup>Previously reported by Hatcher and Preston (2015).

ance for each trait, indicate they are unlikely to be of any commercial or practical significance to Merino breeders or commercial producers.

The estimates of heritability for live weight generally increased with age as maternal effects became less important (Table 4). The heritability for wWT was low ( $0.14 \pm 0.04$ ) and it also had a large genetic group effect, whereas that for aWT was high ( $0.59 \pm 0.06$ ). These estimates of heritability for the live weights are consistent with earlier reports (Safari et al., 2005, 2007a; Huisman et al., 2008; Brown and Swan, 2014). Estimates of heritability for the ultrasound traits (FAT and EMD) were higher when measured at the older yearling age than at the postweaning age. There was also a marked increase due to adjustment for live weight, especially at the postweaning age. The estimates of heritability are consistent with the review by Safari et al. (2005) and later reports for Merinos (Safari et al., 2007a; Huisman et al., 2008) and meat sheep (Brown and Swan, 2015; Brown et al., 2016).

### Genetic Correlations

The genetic and phenotypic correlations between the yearling wool production and quality traits and the live weight traits are shown in Table 5, with those for the adult wool traits available in Supplementary Table S3

(see the online version of the article at <http://journalofanimalscience.org>). The genetic correlations for fleece weight (yGFW and yCFW) with live weights were positive (favorable) and moderate (approximately  $0.5 \pm 0.1$ ), except with bWT, which were lower (approximately  $0.3 \pm 0.15$ ). These estimates were consistent with genetic correlations of the yearling fleece weights with wWT, pwWT, and yWT reported by Huisman and Brown (2008), although this study did report negligible and low negative genetic correlations of yearling fleece weights with bWT and aWT, respectively. In contrast, genetic correlations reviewed by Safari et al. (2005) and estimates reported by Safari et al. (2007b) were generally low and positive (of the order of about 0.20 to 0.25) between fleece weight (clean or greasy) and live weights recorded at the range of ages considered in our study. Furthermore, from an examination of responses from divergent selection lines of Merinos, Davis and McGuirk (1987) reported that although responses from direct selection on CFW and live weight (at weaning) were observed, correlated responses in either live weight or fleece weight were negligible. Their conclusion, agreeing with that of Williams (1987), was that selection on CFW was associated more with changes in components of wool production per unit area (expressed through FD, SL, and follicle densities) rather than with changes in

**Table 4.** Estimates of phenotypic variance and the proportions due to additive genetic variance ( $h^2$ ), genetic group<sup>1</sup> ( $b^2$ ), sire  $\times$  flock ( $s^2$ ), and maternal effects ( $c^2$ ; SE) for live weight and ultrasound traits

Trait <sup>2</sup>	Phenotypic variance	CV, %	Heritability ( $h^2$ )	Genetic group ( $b^2$ )	Sire $\times$ flock ( $s^2$ )	Maternal ( $c^2$ )
Live weight						
bWT <sup>3</sup>	0.66	17.7	0.22 (0.04)	0.57 (0.29)	0.01 (0.01)	0.23 (0.02)
wWT	11.06	14.0	0.14 (0.04)	1.26 (0.56)	0.03 (0.01)	0.23 (0.02)
pwWT	20.43	11.8	0.31 (0.06)	0.99 (0.39)	0.04 (0.01)	0.11 (0.02)
yWT	20.75	11.1	0.38 (0.07)	0.76 (0.31)	0.04 (0.01)	0.10 (0.03)
aWT	32.41	10.6	0.59 (0.06)	0.71 (0.24)	0.02 (0.01)	–
Ultrasound						
pwFAT	0.31	24.4	0.11 (0.06)	0.83 (0.82)	0.04 (0.02)	0.08 (0.04)
pwEMD	6.23	11.7	0.14 (0.07)	0.43 (0.55)	0.11 (0.02)	0.08 (0.04)
yFAT	0.45	25.3	0.26 (0.05)	0.32 (0.23)	–	–
yEMD	5.65	10.0	0.20 (0.06)	0.98 (0.59)	–	0.09 (0.03)
Ultrasound – adjusted for live weight						
pwFATadj	0.23	21.0	0.18 (0.06)	0.47 (0.43)	–	–
pwEMDadj	3.80	9.1	0.20 (0.06)	0.10 (0.23)	0.07 (0.02)	–
yFATadj	0.38	23.3	0.27 (0.05)	0	–	–
yEMDadj	4.23	8.6	0.28 (0.05)	0.09 (0.14)	–	–

<sup>1</sup> $b^2$  = ratio of genetic group to additive genetic variance.

<sup>2</sup>bWT = birth weight; wWT = weaning weight; pwWT = postweaning weight; yWT = yearling weight; aWT = adult weight; pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth; pwFATadj = postweaning fat depth adjusted for BW; pwEMDadj = postweaning eye muscle depth adjusted for BW; yFATadj = yearling fat depth adjusted for BW; yEMDadj = yearling eye muscle depth adjusted for BW.

<sup>3</sup>Litter effect was also fitted for BWT, estimate of  $0.14 \pm 0.02$  as a proportion of the phenotypic variance.

components of wool-growing surface area (expressed through live weight and wrinkle). The discrepancy between genetic correlation estimates across studies may be due to a limited ability to account for both maternal permanent environment and genetic effects affecting the traits, particularly in the case of GFW and CFW, where estimates of the maternal permanent environmental variances were much lower than earlier estimates (Safari et al., 2007b; Huisman et al., 2008). Not accounting for important maternal genetic effects when estimating direct genetic correlations was shown by Asadi Fozi et al.

(2005) to increase estimates of yGFW with bWT, wWT, and yWT by 52, 17, and 24%, respectively.

The genetic correlations of yearling FD (**yFD**) were positive (unfavorable) and low with pwWT and later weights ( $0.23 \pm 0.07$  to  $0.37 \pm 0.08$ ) but negligible for bWT and wWT. For yearling SL (**ySL**), the genetic correlations were positive (favorable) with pwWT and later weights ( $0.21 \pm 0.10$  to  $0.22 \pm 0.08$ ) but negligible for bWT and wWT. For yearling FDCV (**yFDCV**), there were negative (favorable) and low genetic correlations with wWT, pwWT, and yWT but positive genetic correlations with bWT. The genetic correlations between

**Table 5.** Estimates of genetic and phenotypic correlations (SE) between yearling wool traits and live weight

Live weight trait <sup>1</sup>	Yearling wool trait <sup>2</sup>								
	yGFW	yYLD	yCFW	yFD	yFDS	yFDCV	ySS	ySL	yCUR
Genetic correlations									
bWT	0.32 (0.15)	0.05 (0.11)	0.30 (0.15)	–0.08 (0.09)	0.21 (0.11)	0.28 (0.10)	–0.04 (0.14)	–0.16 (0.11)	–0.04 (0.11)
wWT	0.46 (0.14)	0.07 (0.11)	0.47 (0.14)	0.11 (0.10)	–0.14 (0.12)	–0.21 (0.11)	0.09 (0.14)	–0.02 (0.12)	–0.14 (0.12)
pwWT	0.46 (0.12)	0.04 (0.10)	0.46 (0.12)	0.28 (0.08)	–0.07 (0.10)	–0.24 (0.10)	0.12 (0.12)	0.21 (0.10)	0.06 (0.11)
yWT	0.48 (0.12)	0.19 (0.10)	0.54 (0.11)	0.37 (0.08)	–0.05 (0.10)	–0.29 (0.09)	0.16 (0.12)	0.21 (0.10)	0.05 (0.10)
aWT	0.56 (0.08)	0.01 (0.08)	0.54 (0.09)	0.23 (0.07)	0.02 (0.09)	–0.12 (0.08)	–0.01 (0.11)	0.22 (0.08)	–0.03 (0.09)
Phenotypic correlations									
bWT	0.24 (0.02)	0.02 (0.02)	0.23 (0.02)	–0.08 (0.02)	0.06 (0.02)	0.11 (0.02)	–0.02 (0.02)	–0.03 (0.02)	–0.04 (0.02)
wWT	0.45 (0.01)	0.06 (0.02)	0.44 (0.01)	0.09 (0.02)	–0.04 (0.02)	–0.10 (0.02)	0.13 (0.02)	0.09 (0.02)	–0.03 (0.02)
pwWT	0.49 (0.01)	0.07 (0.02)	0.48 (0.01)	0.26 (0.02)	–0.06 (0.02)	–0.20 (0.02)	0.11 (0.02)	0.25 (0.02)	0.02 (0.02)
yWT	0.43 (0.02)	0.08 (0.02)	0.43 (0.02)	0.24 (0.02)	–0.06 (0.02)	–0.20 (0.02)	0.08 (0.02)	0.20 (0.02)	0.04 (0.02)
aWT	0.34 (0.02)	0.03 (0.02)	0.33 (0.02)	0.21 (0.02)	–0.04 (0.02)	–0.16 (0.02)	0.06 (0.02)	0.20 (0.02)	0.03 (0.02)

<sup>1</sup>bWT = birth weight; wWT = weaning weight; pwWT = postweaning weight; yWT = yearling weight; aWT = adult weight.

<sup>2</sup>yGFW = yearling greasy fleece weight; yYLD = yearling washing yield; yCFW = yearling clean fleece weight; yFD = yearling fiber diameter; yFDS = yearling fiber diameter SD; yFDCV = yearling fiber diameter CV; ySS = yearling staple strength; ySL = yearling staple length; yCUR = yearling fiber curvature.

**Table 6.** Estimates of genetic and phenotypic correlations (SE) between yearling wool traits and ultrasound traits

Ultrasound trait <sup>1</sup>	Yearling wool trait <sup>2</sup>								
	yGFW	yYLD	yCFW	yFD	yFDSD	yFDCV	ySS	ySL	yCUR
Genetic correlations									
pwFAT	-0.48 (0.17)	0.09 (0.15)	-0.48 (0.17)	0.31 (0.15)	-0.24 (0.14)	-0.56 (0.14)	0.28 (0.17)	0.30 (0.15)	0.26 (0.15)
pwEMD	-0.26 (0.21)	-0.06 (0.17)	-0.37 (0.20)	0.32 (0.18)	-0.25 (0.17)	-0.58 (0.19)	0.15 (0.20)	0.48 (0.18)	0.13 (0.18)
yFAT	0.03 (0.10)	0.07 (0.09)	0.05 (0.10)	0.38 (0.07)	-0.07 (0.09)	-0.38 (0.09)	0.06 (0.11)	0.39 (0.08)	0.21 (0.09)
yEMD	0.00 (0.12)	-0.06 (0.09)	-0.04 (0.12)	0.33 (0.08)	-0.10 (0.09)	-0.33 (0.09)	-0.04 (0.11)	0.32 (0.08)	0.18 (0.09)
Phenotypic correlations									
pwFAT	0.10 (0.02)	0.07 (0.03)	0.12 (0.02)	0.14 (0.02)	-0.07 (0.03)	-0.18 (0.03)	0.13 (0.03)	0.17 (0.03)	0.05 (0.03)
pwEMD	0.17 (0.02)	0.07 (0.03)	0.18 (0.02)	0.16 (0.02)	-0.11 (0.03)	-0.23 (0.02)	0.16 (0.03)	0.23 (0.03)	0.01 (0.03)
yFAT	0.06 (0.02)	0.05 (0.02)	0.08 (0.02)	0.17 (0.02)	-0.06 (0.02)	-0.15 (0.02)	0.03 (0.02)	0.17 (0.02)	0.05 (0.02)
yEMD	0.13 (0.02)	0.06 (0.02)	0.15 (0.02)	0.19 (0.02)	-0.09 (0.02)	-0.19 (0.02)	0.04 (0.02)	0.18 (0.02)	0.05 (0.02)

<sup>1</sup>pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth.

<sup>2</sup>yGFW = yearling greasy fleece weight; yYLD = yearling washing yield; yCFW = yearling clean fleece weight; yFD = yearling fiber diameter; yFDSD = yearling fiber diameter SD; yFDCV = yearling fiber diameter CV; ySS = yearling staple strength; ySL = yearling staple length; yCUR = yearling fiber curvature.

yearling YLD, yearling FDSD, yearling SS, and yearling CUR (**yCUR**) and weights were all negligible. The phenotypic correlations were generally of the same sign as the corresponding genetic correlations but slightly smaller in magnitude. The phenotypic correlations are in agreement with the findings of Hatcher et al. (2004) that at the phenotypic level, live weight and wool production traits were related and that most wool quality traits were independent of live weight.

These genetic correlations for yearling fleece weight and yFD with live weights were generally higher than those reviewed by Safari et al. (2005) and those reported by Safari et al. (2007b) in research flocks, although they were generally close to the estimates reported from industry data (Huisman and Brown, 2008). Our estimates for these wool traits are lower than those reported by Swan et al. (2016) for pwWT using similar data. The other wool traits had lower genetic correlations with the live weights, which is generally consistent with the limited number of traits and magnitude of the SE of the estimates in these other reports. From a small data set, Davis (1987) reported negligible changes in FD of ewes following selection on wWT. The genetic and phenotypic correlation estimates of the live weights with the adult wool traits (available in Supplementary Table S3; see the online version of the article at <http://journalofanimalscience.org>) are generally consistent with relationships for the yearling traits shown here.

The genetic and phenotypic correlations between the yearling wool production and quality traits and the ultrasound traits are shown in Table 6, with those for the adult wool traits available in Supplementary Table S4 (see the online version of the article at <http://journalofanimalscience.org>). The genetic and phenotypic correlations between the yearling wool traits and the ultrasound traits adjusted for weight are available in

Supplementary Table S5 (see the online version of the article at <http://journalofanimalscience.org>).

There were low to moderate positive genetic correlations for FAT and EMD at postweaning and yearling ages with yFD and ySL and low to moderate negative genetic correlations with yFDCV. The corresponding phenotypic correlations were of the same sign and generally about half the magnitude of the genetic correlations for these traits. The genetic correlations for postweaning FAT (**pwFAT**) and postweaning EMD (**pwEMD**) with yGFW and yCFW were negative (low to moderate), although the corresponding genetic correlations with yearling ultrasound traits were close to zero. The smaller number of records and lower heritabilities for the postweaning ultrasound traits contributed to the higher SE for the postweaning traits than for the yearling traits.

These genetic relationships suggest that selection for increased FAT and EMD at either age will generate small correlated increases in FD and SL and decreased FDCV, whereas the correlated effect on wool weight is equivocal. The genetic correlations with the other yearling wool traits were generally negligible. The genetic correlations for FAT and EMD at both ages with the adult wool traits (Supplementary Table S4; see the online version of the article at <http://journalofanimalscience.org>) were similar to those with the yearling wool traits, although the genetic correlations with wool weight were slightly more negative (e.g.,  $-0.65 \pm 0.19$  and  $-0.22 \pm 0.10$  for pwFAT and yearling FAT [**yFAT**], respectively, and  $-0.49 \pm 0.25$  and  $-0.21 \pm 0.10$  for pwEMD and yearling EMD [**yEMD**], respectively, with adult CFW). Irrespective of age of recording, adjustment of FAT and EMD for live weight had little effect on the genetic correlations with the yearling wool traits (Supplementary Table S5; see the online version of the article at <http://journalofanimalscience.org>).

The average genetic correlation between fleece weight and FAT in the review by Safari et al. (2005) was

**Table 7.** Estimates of genetic and phenotypic correlations (SE) between yearling wool color and visual traits and live weight

Live weight trait <sup>1</sup>	Yearling wool color and visual trait <sup>2</sup>					
	yY	y(Y-Z)	yBCOV	mBRWR	yBRWR	yBDWR
Genetic correlations						
bWT	0.00 (0.20)	0.15 (0.13)	-0.02 (0.24)	0.34 (0.16)	0.22 (0.14)	0.42 (0.13)
wWT	0.16 (0.21)	0.30 (0.14)	-0.18 (0.24)	0.13 (0.18)	-0.07 (0.15)	0.02 (0.16)
pwWT	0.08 (0.20)	0.30 (0.11)	-0.47 (0.17)	-0.21 (0.16)	-0.10 (0.13)	-0.17 (0.13)
yWT	0.21 (0.19)	0.38 (0.11)	-0.55 (0.16)	-0.09 (0.16)	-0.27 (0.12)	-0.12 (0.13)
aWT	0.01 (0.14)	0.26 (0.10)	-0.39 (0.25)	0.09 (0.11)	-0.07 (0.11)	-0.11 (0.11)
Phenotypic correlations						
bWT	0.03 (0.02)	0.04 (0.02)	0.00 (0.02)	0.12 (0.02)	0.08 (0.02)	0.12 (0.02)
wWT	0.14 (0.02)	0.08 (0.02)	-0.09 (0.02)	0.05 (0.02)	-0.01 (0.02)	0.04 (0.02)
pwWT	0.06 (0.02)	0.08 (0.02)	-0.14 (0.02)	-0.08 (0.02)	-0.13 (0.02)	-0.09 (0.02)
yWT	0.05 (0.02)	0.10 (0.02)	-0.16 (0.02)	-0.07 (0.02)	-0.15 (0.02)	-0.08 (0.02)
aWT	0.01 (0.02)	0.10 (0.02)	-0.10 (0.02)	-0.07 (0.02)	-0.15 (0.02)	-0.12 (0.02)

<sup>1</sup>bWT = birth weight; wWT = weaning weight; pwWT = postweaning weight; yWT = yearling weight; aWT = adult weight.

<sup>2</sup>yY = yearling brightness; y(Y-Z) = yearling yellowness; yBCOV = yearling breech cover; mBRWR = marking breech wrinkle; yBRWR = yearling breech wrinkle; yBDWR = yearling body wrinkle.

low and negative ( $-0.19$ , from 5 highly variable estimates with a 95% confidence interval of  $-0.50$  to  $0.17$ ), although the average correlation between fleece weight and EMD was low and positive ( $0.23$ ). Huisman and Brown (2009) reported pooled estimates of very low negative and negligible genetic correlations of the fleece weights with adjusted FAT and adjusted EMD, respectively. However, Brown and Swan (2016) reported low negative correlations (range  $-0.13$  to  $-0.26$ ) for yGFW with FAT and EMD at postweaning and yearling ages, with greater negative correlations for aGFW (range  $-0.26$  to  $-0.54$ ). Our estimates of the genetic correlations among the other traits in Table 6 were generally consistent in sign and slightly larger in magnitude than those reported by Brown and Swan (2016) from industry data, who were able to include a maternal genetic effect in models fitted to their data, and pooled estimates of Huisman and Brown (2009), which also were estimated from industry data. The other major study of Merinos from research flocks found low negative genetic correlations for yCFW with yFAT ( $-0.17 \pm 0.07$ ) and yEMD adjusted for weight ( $-0.13 \pm 0.07$ ) and moderate positive correlations with yCUR ( $0.43 \pm 0.12$  and  $0.44 \pm 0.15$ , respectively), whereas the genetic correlations with all the other wool traits were negligible (Greeff et al., 2008).

Li et al. (2008) reported increased ultrasound FAT and EMD at the C site in young Merino wethers (18 mo of age) with high EBV for wool growth (and similar EBV for FD and live weight), together with increased whole body protein turnover and energy retention in wool and wool-free body tissue compared with low wool growth EBV wethers. In contrast, Adams et al. (2006) found genetically high CFW sheep to have lower fat reserves but increased lean tissue and concluded that ewes with high

EBV for wool growth had a lower metabolic energy status. Differences in the methodology used to assess fatness and lean tissue would have contributed to these contrasting findings, as the latter study estimated body composition data from the dilution of deuterated water. Adams et al. (2006) found no differences in body composition between low and high FD EBV sheep.

The genetic and phenotypic correlations between the yearling wool color and visual traits and the live weight traits are shown in Table 7, with those for the adult wool traits available in Supplementary Table S6 (see the online version of the article at <http://journalofanimalscience.org>). The genetic correlations between wool yellowness (yearling [Y-Z]) and live weights from weaning and older ages were positive (unfavorable) and low ( $0.26 \pm 0.10$  to  $0.38 \pm 0.11$ ), although those with wool brightness (yY) were negligible. The corresponding genetic correlations for adult wool yellowness (a[Y-Z]) were higher (more unfavorable) and ranged from  $0.39$  to  $0.63$  and those for adult wool brightness were reduced although generally negligible (range  $-0.03$  to  $-0.27$ ; Supplementary Table S6 [see the online version of the article at <http://journalofanimalscience.org>]). The genetic correlation between wool yellowness and live weight in yearlings, hoggets (16 mo of age), and adults has previously been estimated to be negligible (range of  $0.07$  to  $-0.10$ ; Hebart and Brien, 2009; Smith and Purvis, 2009). No other studies have reported genetic correlations for scoured wool brightness (Y).

The genetic correlations between yearling and adult live weights and yearling BCOV (yBCOV) were moderate and negative (favorable), as were those with aBCOV. This is consistent with other reports (Brown et al., 2010; Scholtz et al., 2011; Pickering et al., 2013;



**Table 8.** Estimates of genetic and phenotypic correlations (SE) between yearling wool color and visual traits and ultrasound traits

Ultrasound trait <sup>1</sup>	Yearling wool color and visual trait <sup>2</sup>					
	yY	y(Y-Z)	yBCOV	mBRWR	yBRWR	yBDWR
Genetic correlations						
pwFAT	-0.36 (0.20)	0.12 (0.16)	-0.45 (0.23)	-0.69 (0.18)	-0.87 (0.19)	-0.82 (0.18)
pwEMD	-0.69 (0.23)	0.25 (0.19)	-0.41 (0.28)	-0.89 (0.22)	-0.87 (0.26)	-0.90 (0.27)
yFAT	-0.07 (0.11)	0.14 (0.10)	-0.34 (0.12)	-0.41 (0.10)	-0.51 (0.09)	-0.47 (0.09)
yEMD	-0.25 (0.12)	0.15 (0.10)	-0.31 (0.13)	-0.50 (0.10)	-0.46 (0.09)	-0.41 (0.09)
Phenotypic correlations						
pwFAT	0.07 (0.03)	0.00 (0.03)	-0.11 (0.03)	-0.08 (0.02)	-0.13 (0.03)	-0.12 (0.03)
pwEMD	0.08 (0.03)	-0.01 (0.03)	-0.10 (0.03)	-0.11 (0.02)	-0.14 (0.03)	-0.12 (0.03)
yFAT	0.01 (0.02)	0.03 (0.02)	-0.08 (0.02)	-0.12 (0.02)	-0.16 (0.02)	-0.15 (0.02)
yEMD	0.01 (0.02)	0.07 (0.02)	-0.12 (0.02)	-0.13 (.02)	-0.19 (0.02)	-0.16 (0.02)

<sup>1</sup>pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth.

<sup>2</sup>yY = yearling brightness; y(Y-Z) = yearling yellowness; yBCOV = yearling breech cover; mBRWR = marking breech wrinkle; yBRWR = yearling breech wrinkle; yBDWR = yearling body wrinkle.

S. Hatcher and J. W. V. Preston, NSW Department of Primary Industries, Orange, Australia, unpublished data) and means that selection for increased area of bare skin around the perineum and breech (low BCOV scores) will result in correlated increases in yearling and adult live weight. For the wrinkle scores, the genetic correlations with bWT were positive (unfavorable) and low to moderate (0.22 to 0.42). However, the wrinkle scores were generally negatively correlated (favorable) with live weights at older ages (negligible to low, 0.13 to -0.27). The adult wrinkle scores were generally more negatively correlated (favorable) with the older live weights (-0.18 to -0.44) than the marking or yearling wrinkle scores. The low favorable genetic relationship overall between wrinkle score and live weight is consistent with other studies (Brown et al., 2010; Scholtz et al., 2011; Swan et al., 2016; S. Hatcher and J. W. V. Preston, NSW Department of Primary Industries, Orange, Australia, unpublished data), with only the study of Lewer et al. (1995) reporting genetic correlations with bWT, which were negligible in size. Although Dun and Wall (1962) initially found that increased wrinkle was associated with higher bWT in a study of divergent selection lines selected for wrinkle score, Crook (1992) later reported realized genetic correlations of about 0.10 to 0.20 between bWT and wrinkle from these lines, although he found that bWT in the high wrinkle line decreased over time. The change in direction of the genetic correlations between bWT and yWT may be due to the growth of the animal and the associated increase in skin surface area that impact on wrinkle. Several studies have shown a reduction in BRWR scores as sheep age, with the largest change occurring between the marking and yearling assessments (Brown et al., 2010; Bird-Gardiner et al., 2014; Greeff et al., 2014; Hatcher and Preston, 2015). Two separate studies have also clearly shown that se-

lection for increased skin folds (wrinkle) resulted in a correlated response of lower live weight (Turner et al., 1970; Crook and James, 1991), with a realized genetic correlation of -0.22 (Crook and James, 1991).

The genetic and phenotypic correlations for the yearling wool color and visual traits with the ultrasound traits are shown in Table 8, with those for the adult wool traits available in Supplementary Table S7 (see the online version of the article at <http://journalofanimalscience.org>). Those between the yearling wool color and visual traits and the ultrasound traits adjusted for weight are available in Supplementary Table S8 (see the online version of the article at <http://journalofanimalscience.org>). The genetic correlations for FAT and EMD at both ages with the wrinkle scores were all moderate to highly negative (range  $-0.41 \pm 0.09$  to  $-0.90 \pm 0.27$ ), as was yBCOV (range  $-0.31 \pm 0.13$  to  $-0.45 \pm 0.23$ ). The corresponding genetic correlations for the visual traits scored as adults (Supplementary Table S7; see the online version of the article at <http://journalofanimalscience.org>) were very similar to those scored at yearling age, although adjustment of FAT and EMD for weight reduced their magnitude (range -0.25 to -0.50; Supplementary Table S8 [see the online version of the article at <http://journalofanimalscience.org>]). Our results of negative genetic correlations between wrinkle scores and FAT and EMD at postweaning and yearling ages are consistent with other reports (Brown and Swan, 2016; Swan et al., 2016). The genetic correlations between yearling wool brightness (yY) and FAT and EMD at both ages were negative and variable, although they were all reduced to nonsignificance when FAT and EMD were adjusted for weight (Supplementary Table S8; see the online version of the article at <http://journalofanimalscience.org>) and also for adult wool (aY; Supplementary Table S7 [see the online version of the article at <http://journalofanimalscience.org>]).

**Table 9.** Estimates of genetic and phenotypic correlations (SE) between live weight and ultrasound traits

Ultrasound trait <sup>1</sup>	Live weight trait <sup>2</sup>				
	bWT	wWT	pwWT	yWT	aWT
Genetic correlations					
pwFAT	-0.07 (0.37)	0.47 (0.24)	0.61 (0.18)	0.35 (0.24)	0.31 (0.23)
pwEMD	0.11 (0.29)	0.77 (0.16)	0.65 (0.11)	0.58 (0.18)	0.50 (0.18)
yFAT	-0.11 (0.16)	0.38 (0.15)	0.63 (0.10)	0.48 (0.12)	0.52 (0.10)
yEMD	-0.11 (0.24)	0.40 (0.22)	0.75 (0.14)	0.53 (0.16)	0.77 (0.08)
Phenotypic correlations					
pwFAT	0.00 (0.02)	0.24 (0.02)	0.40 (0.02)	0.29 (0.03)	0.26 (0.03)
pwEMD	0.05 (0.02)	0.37 (0.02)	0.52 (0.02)	0.41 (0.02)	0.36 (0.03)
yFAT	-0.06 (0.02)	0.14 (0.02)	0.31 (0.02)	0.37 (0.02)	0.32 (0.02)
yEMD	-0.01 (0.02)	0.27 (0.02)	0.44 (0.02)	0.47 (0.02)	0.44 (0.02)

<sup>1</sup>pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth.

<sup>2</sup>bWT = birth weight; wWT = weaning weight; pwWT = postweaning weight; yWT = yearling weight; aWT = adult weight.

org]). Therefore, selection to increase EMD and/or FAT in Merino sheep will have a favorable correlated reduction in wrinkle and BCOV, with little impact on wool color, except for a possible decline in brightness of color for scoured yearling wool.

The genetic and phenotypic correlations between the live weight and the ultrasound traits are shown in Table 9, with those for the live weight traits and the ultrasound traits adjusted for weight available in Supplementary Table S9 (see the online version of the article at <http://journalofanimalscience.org>). The genetic correlations between the ultrasound FAT and EMD at postweaning and yearling ages and pwWT were positive and high ( $0.61 \pm 0.18$  to  $0.75 \pm 0.14$ ). The similar correlations with wWT, yWT, and aWT were positive and moderate to high ( $0.31 \pm 0.23$  to  $0.77 \pm 0.08$ ), whereas those with bWT were negligible. The corresponding phenotypic correlations were generally smaller than the genetic correlations. A trend is evident in Merinos of the genetic correlations between weight and ultrasound traits at yearling age being consistently moderate and positive, whereas there is considerable variation in sign and magnitude at other ages (Huisman and Brown, 2008; Brown and Swan, 2016). In contrast, the genetic correlations between weight and ultrasound traits in meat sheep may be low and negative (Mortimer et al., 2010; Brown and Swan, 2015). The genetic correlations of weight with the ultrasound traits adjusted for weight tended to be negative (Supplementary Table S9; see the online version of the article at <http://journalofanimalscience.org>). A review of genetic correlations among these traits where the ultrasound traits were both unadjusted and adjusted for weight (Maximini et al., 2012) and correlation estimates from a multibreed flock (Mortimer et al., 2014) also indicated that positive genetic correlations were estimated from models that did not include weight as a covariate and generally negative correlations were estimated from models that did include weight as a covariate.

The genetic and phenotypic correlations between the ultrasound traits are shown in Table 10, with the corresponding correlations between the traits adjusted for weight available in Supplementary Table S10 (see the online version of the article at <http://journalofanimalscience.org>). There were high positive genetic correlations between FAT and EMD at both postweaning ( $0.83 \pm 0.11$ ) and yearling ( $0.83 \pm 0.05$ ) ages. The corresponding phenotypic correlations were slightly lower ( $0.57 \pm 0.01$  and  $0.50 \pm 0.01$ , respectively). There were also very high genetic correlations between postweaning and yearling ages for FAT ( $0.84 \pm 0.15$ ) and EMD ( $0.85 \pm 0.35$ ), although only 123 animals had ultrasound records at both ages. There was little effect on the corresponding correlations when weight adjustments were included (Supplementary Table S10; see the online version of the article at <http://journalofanimalscience.org>). These high correlations for the ultrasound traits between ages are consistent with other reports for both Merino (Huisman and Brown, 2009) and meat sheep (Brown and Swan, 2015) breeds. The high correlations between FAT and EMD at both postweaning and yearling ages are consistent with other reports for Merinos (Huisman and Brown, 2009; Swan et al., 2016), although these correlations are low in meat sheep (Brown and Swan, 2015). Although meat sheep breeding programs generally aim at increasing EMD and reducing FAT (Fogarty

**Table 10.** Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations (SE) between the ultrasound traits

Ultrasound trait <sup>1</sup>	pwFAT	pwEMD	yFAT	yEMD
pwFAT	–	0.57 (0.01)	0.29 (0.08)	0.34 (0.07)
pwEMD	0.83 (0.11)	–	0.19 (0.08)	0.27 (0.08)
yFAT	0.84 (0.15)	0.99 (0.24)	–	0.50 (0.01)
yEMD	0.84 (0.17)	0.85 (0.35)	0.83 (0.05)	–

<sup>1</sup>pwFAT = postweaning fat depth; pwEMD = postweaning eye muscle depth; yFAT = yearling fat depth; yEMD = yearling eye muscle depth.

et al., 2006), the Merino has lower subcutaneous fat levels than other breeds (Fogarty et al., 2000), and as a maternal breed, it may not be desirable to reduce fat levels. Hence, the importance of having accurate estimates of the genetic correlations between the various traits to develop appropriate breeding programs.

### Conclusions

These analyses provide a comprehensive range of genetic correlations between a large number of wool (production and quality) traits and meat (live weight and ultrasound) traits in Merino sheep at different ages, many of which have not previously been estimated. The data set covers several years of the IN, which was designed to assess genotypes representative of the industry in a wide range of Australian sheep environments. These analyses update earlier reports that had only subsets of the data available (Hatcher et al., 2010, 2011; Mortimer et al., 2010; Jones and Hatcher, 2013) and also include many additional traits. These genetic relationships indicate that selection for increased live weight will result in a moderate correlated increase in wool weight, as well as favorable reductions in BCOV and wrinkle, along with unfavorable increases in FD and wool yellowness, but will have little impact on other wool traits. The ultrasound meat traits, FAT and EMD at both postweaning and yearling ages, are highly positively genetically correlated, which is generally regarded as unfavorable for meat production, although higher fat levels may be desirable for reproduction and welfare in maternal breeds such as the Merino, which has low carcass fat levels. The genetic relationships found here indicate that selection for increased EMD and/or FAT at either postweaning or yearling age in the Merino will result in a small unfavorable correlated increase in FD, moderately favorable reductions in BCOV and wrinkle, but equivocal or negligible changes in fleece weight and other wool traits. These estimated parameters provide the basis for calculation of more accurate Australian Sheep Breeding Values, reported by the Sheep Genetics evaluation program (Brown et al., 2007), and selection indexes that allow Merino breeders to combine wool and meat objectives in their breeding programs.

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