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Methane, growth and carcase considerations when breeding for more efficient Merino sheep production

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ABSTRACT

Feed intake, methane and feed efficiency have important genetic correlations with growth, carcase weights and mature size that need to be considered when breeding for production whilst reducing feed requirements and methane production in the Australian sheep industry. Live weight, growth, fat and muscle have significant antagonistic relationships with feed intake, which may make simultaneous selection for efficiency traits and, growth and meat quality slower. For example, selecting animals that grow faster is known to reduce meat-eating quality. Therefore, we estimated the genetic and phenotypic correlations between feed intake, residual feed intake, methane, carbon dioxide, oxygen, live weight, growth, fat and muscle depth traits. Fat and muscle depth were corrected for live weight. Traits were recorded on Merino sheep (n = 2 717) in Western Australia between 2010 and 2016. Sheep were measured at post-weaning (range 753–2 717 records across traits), hogget (~18 months old; range 602–1 046) and adult ages (>2 years old; range 269–443). Live weight and growth rate had significant moderate to high positive genetic correlations with feed intake, residual feed intake, methane and carbon dioxide at postweaning, hogget and adult ages. Fat and muscle depth measured at the start and finish of the feed intake measurement period generally had negative genetic correlations with residual feed intake, feed intake and methane. These genetic correlations with feed intake and residual feed intake were more negative with fat and muscle measured at the start of the measurement period than at the end. Furthermore, in young sheep, selecting for lower feed intake and residual feed intake will mean a lower change in fat between the start and finish of the intake period. Fat and muscle had significant correlations with feed efficiency and greenhouse gas traits and should therefore be considered when estimating residual feed intake, particularly in young animals.

Implications

Sheep farmers often select for animals that grow faster with more muscle and fat. We found that selecting for animals that grow faster and are heavier will also increase the amount of feed intake and methane produced by these animals, because of high genetic correlations between these traits. Also, if farmers select animals for higher fat and muscle depth corrected for live weight, this can also impact feed intake, residual feed intake and methane production. Therefore, sheep breeding programmes should consider these correlations when selecting for more production in their sheep.

Introduction

An efficient and environmentally responsible sheep industry should consider the balance between productivity and the environmental impact of production. The Australian sheep industry is investigating ways to produce meat and wool more efficiently while simultaneously decreasing environmental wastage through methane and carbon dioxide production (Cottle et al., 2009). Efficient production can include increasing production while decreasing feed intake. Paganoni et al. (2017) showed that Merino sheep

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that eat less and are more feed-efficient produce less methane and carbon dioxide. However, Johnson et al. (2022) showed in a composite breed of sheep that increased feed intake was associated with greater methane and carbon dioxide production, but these were dependent on how the traits were expressed.

Selection for feed efficiency is one way to increase production whilst reducing feed intake. Feed efficiency can be measured using residual feed intake. Residual feed intake is the difference between actual feed intake and expected feed requirements based on BW and live weight gain (Koch et al., 1963). Therefore, more feed-efficient animals will have a more negative residual feed intake. In addition, Knott et al. (2008) found that the fit of models when estimating residual feed intake could be improved by including whether live weight gain was due to either increased fat or muscle. Many sheep breeders in Australia include fat and muscle depth in their breeding objectives to improve the quality and quantity of meat production (Mortimer et al., 2010) and possibly reproduction (Walkom and Brown, 2016). Fat and muscle depth in Australian breeding programmes is corrected for live weight. This correction is so that fat and muscle depth can be selected mostly independently of live weight. Live weight and feed intake have high correlations, therefore, we expect it is also possible that fat and muscle depth corrected for live weight should also be selected independent of live weight and feed intake. Therefore, the genetic correlations between fat and muscle and feed efficiency need to be explored more.

Selecting for production and efficiency simultaneously depends on the strength and direction (positive or negative) of genetic and phenotypic correlations between traits. Increasing production and efficiency (decreasing waste, feed intake) are difficult if production and efficiency traits have high positive correlations. Strong genetic correlations have been shown between feed intake and both live weight and growth (Snowder and Vleck, 2003). Sheep that eat less and are more feed efficient have also been shown to produce less methane (Paganoni et al., 2017). Therefore, there are potentially important interactions between live weight, growth and methane production given the important interactions between live weight and growth with feed intake and feed efficiency.

This study tested the hypothesis that live weight and growth will have significant positive genetic correlations with greenhouse gas production traits in sheep. Additionally, we tested the hypothesis that fat and muscle depth measured using ultrasound and corrected for live weight have lower genetic relationships with residual feed intake and methane than live weight and growth. These hypotheses were tested across three age groups representing different levels of maturity.

Material and methods

Experimental design

Feed intake, gas and growth traits were measured on 2 800 Merino sheep between 2010 and 2016. The pedigree structure included four generations with 116 sires and 1 452 dams (Paganoni et al., 2017). The number of matings ranged from 1 to 4 per dam. All sheep were born between 2009 and 2014 and managed at the University of Western Australia Future Farm, 'Ridgefield', in West Pingelly, Western Australia (32°32′S, 117°05′E).

Feed intake and gas production were measured on animals in 28 groups of up to 225 sheep at the Department of Agriculture and Food Research Station at Medina, Perth (32°13′S, 115°48′E) (Paganoni et al., 2017). After adapting to the pellet diet in outdoor pens, sheep were stratified by sire into a feedlot comprising up to 15 indoor pens (up to 15 sheep per pen) and fed the pellet diet for 35 days (Paganoni et al., 2017). More detailed information about sheep numbers, sheep management, feed intake and greenhouse gas trait measurement are reported by Paganoni et al. (2017).

Description of traits

A description of each trait is in Table 1. Sheep were measured for all traits at three ages when in the feedlot; postweaning (mean 223 days), hogget (mean 607 days) and adult (mean 1080 days). More records were measured at postweaning age (range 753–2 717 records across traits) than hogget age (range 602–1 046) and adult age (range 269–443; Table 2). The same animals are measured at weaning, hogget and adult age. For example, all the animals in the adult analysis are also in the hogget and weaning analyses. The pedigree structure is four generations with 117 unique sires and 1 939 unique dams. Of the animals with measurements, 184 had an unknown dam only, 199 had an unknown sire only, and 162 had both unknown sire and dam.

The sheep were weighed twice a week. The Live weight trait was the average live weight over the 35-day period. The chutes leading to the feeders in the pens were adjusted so that only one sheep could enter the feeder at a time. This chute allowed for the measurement of individual feed intake using a radio frequency identification aerial that recorded the sheep's electronic tag. Feed intake was recorded daily for 35 days. Sheep had their fat and eye muscle depth at the C-site (45 mm along the spine at the 12th rib) measured via ultrasound scanning at the start and end of the feed intake period. These traits are an indication of the fat and muscle deposition in sheep only. Currently in Australia, ultrasound scanning is used by breeders as it is the most cost-effective and practical way to measure fat and muscle depth. Analysis of fat and muscle data included live weight fitted as a covariate at the time they were measured. This correction accounted for heavier sheep that were more likely to have higher fat and muscle depth. Methane, oxygen and carbon dioxide production were measured using an individual portable accumulation chamber during the last 14–21 days of the feed intake measurement period. Detailed description of the individual portable accumulation chamber and measurements taken are reported by Paganoni et al. (2017). All individual portable accumulation chamber measurements were adjusted for the size of the animal. Residual feed intake was estimated using multiple linear regression. Average daily feed intake over 35 d was adjusted by fitting midweight and average daily gain as covariates. Daily gain was estimated by modelling live weights over time separately for each animal using a random coefficient regression including a cubic spline for time (Verbyla et al., 1999).

Table 1
Units and description of intake, gas and growth traits measured on sheep.

Trait	Units	Description
Intake	kg DM/day	Average daily feed intake over 35 days
RFI	kg DM/day	Residual feed intake
CH_4	g/day	Methane (standard temperature and pressure)
CO_2	%	Carbon dioxide
O_2	%	Oxygen
BW	kg	Average live weight over 35 days
Growth	kg/day	Average daily gain over 35 days
EMD1	mm	Eye muscle depth at start of the 35-day feed intake period
EMD2	mm	Eye muscle depth at end of the 35-day feed intake period
CF1	mm	[1]C-site fat at start of the 35-day feed intake period
CF2	mm	[1]C-site fat at end of the 35-day feed intake period
ΔEMD	mm	Change in eye muscle depth over the 35-day feed intake period
ΔCF	mm	Change in C-site fat depth over the 35-day feed intake period

[1] The C-site is 45 mm from the spine at the 12th/13th rib.

Table 2
Number of animals recorded (*N*), mean value and SD for intake, gas and growth traits for sheep measured at postweaning, hogget and adult ages.

	Postweaning age			Hogget age			Adult age		
Trait[1]	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD
Intake	1 476	1.4	0.30	1 046	2.03	0.31	443	2.17	0.39
RFI	1 470	−0.009	0.21	1 046	−0.00	0.18	443	0.0006	0.24
CH_4	2 665	31.7	10.3	964	37.1	−12.0	436	32.7	8.43
CO_2	753	2.49	0.38	969	3.31	0.51	439	3.18	0.42
O_2	755	18.8	0.38	970	17.9	0.51	439	17.8	0.42
BW	2 717	40.6	9.12	1 046	59.0	7.85	443	71.1	7.76
Growth	2 714	0.23	0.06	1 043	0.27	0.08	442	0.28	0.08
EMD1	1 936	21.9	4.64	973	24.4	3.58	443	27.4	3.66
EMD2	2 032	26.9	3.33	996	31.1	2.46	442	33.3	2.30
CF1	1 934	2.17	1.08	972	2.21	0.97	443	2.87	1.07
CF2	2 024	3.69	1.14	995	4.63	1.29	442	5.26	1.55
ΔEMD		5.56[1]	3.43		6.66[1]	2.98		5.86[1]	3.01
ΔCF		1.61*	0.96		2.37*	1.08		2.39*	1.23

Abbreviations: Intake = feed intake, RFI = residual feed intake, CH_4 = methane, CO_2 = carbon dioxide, O_2 = Oxygen, EMD1 = eye muscle depth measured at the start of the feed intake period, EMD2 = eye muscle depth at the end of the feed intake period, CF1 = C-site fat depth at the start of the feed intake period, CF2 = C-site fat depth at the end of the feed intake period, ΔEMD is the change in eye muscle throughout the feed intake period of 35 days and ΔCF is the change in C-site fat depth throughout the feed intake period of 35 days.

[1] These are estimates because the genetic parameters for change in fat and muscle were estimated using the traits measured at the start and end of the feed intake period. These traits had different numbers of records within each age.

The model fitted was live weight = μ + day + animal + animal.day + spline(day) + animal.spline(day). The term "day" was fitted as a fixed effect, whereas all other terms were fitted as random effects, with a covariance between the animal intercept (animal) and slope (animal.day). The likelihood ratio test was used to assess any spline effects after the previously mentioned terms (day, animal, and animal.day) had been fitted. Average daily gain was the slope from this model, and the live weight was estimated for each animal halfway through the feed intake measurements.

The unexplained variation after fitting the model of average daily feed intake with midweight and average daily gain fitted as covariates was the residual feed intake. Feed intake measured early in the experiment were excluded because they were unreliable. Consequently, modifications to the feed intake systems were made, and a weekly calibration procedure using meal-size weights was introduced.The sheep were stratified by sire into up to 15 indoor pens (up to 15 sheep per pen). Sheep at postweaning age were also stratified by live weight so that there was less than a 5-kg difference between the heaviest and lightest sheep in each pen. This was to reduce bullying and shy feeding, which was not necessary for older sheep. More information about how feed intake and residual feed intake were measured are in Paganoni et al. (2017). A weighting for the number of records was included for methane, oxygen and carbon dioxide traits that were measured 2 or 3 times per sheep.

Description of critical methods

The heritability of traits was estimated using univariate models;

$$y = Xb + Z_a a + e \quad (1)$$

$$y = Xb + Z_a a + ZQ_g g + e \quad (2)$$

where y are the observations for the traits, b is the vector of fixed effects, a is the vector of animal genetic effects, g is the genetic group effects defined by breed and strain, and e is the vector of error effects. X and Z are the incidence matrices that relate observations to particular levels of fixed effects and additive genetic effects, and Q_g is the matrix describing the proportion of genes in each animal that originate from each genetic group. The random effects of e are normally distributed with a mean of zero.

Likelihood ratio tests were used to test if fitting genetic groups significantly improved the fit of the traits. Genetic groups are defined by a flock of the origin or sheep type (Swan et al., 2016). None of the traits had significant effects on genetic groups ($P > 0.05$). Genetic groups were not significant because only 4% of sheep had contributions of more than 25% from genes of breeds other than Merino.

All other models tested excluded genetic groups. The other models used were;

$$y = Xb + Z_a a + Z_m m + e \quad (3)$$

where m are the maternal genetic effects due to the dam, and Z_m relates the m vectors to the traits (y).

$$\text{where var}\begin{bmatrix} a \\ m \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_a & A\sigma^2_{ma} & 0 \\ A\sigma^2_{am} & A\sigma^2_m & 0 \\ 0 & 0 & I\sigma^2_{ae} \end{bmatrix}.$$

I is the identity matrix, a is the additive genetic relationship matrix between animals is the maternal genetic relationship matrix between animals

The genetic correlations (r_g) between traits were estimated using a bivariate model which estimated the variance of traits and the covariance between trait 1 (tr1) and trait 2 (tr2);

$$\begin{bmatrix} y_{tr1} \\ y_{tr2} \end{bmatrix} = \begin{bmatrix} X_{tr1} & 0 \\ 0 & X_{tr2} \end{bmatrix} \begin{bmatrix} b_{tr1} \\ b_{tr2} \end{bmatrix} + \begin{bmatrix} Z_{a\ tr1} & 0 \\ 0 & Z_{a\ tr2} \end{bmatrix} \begin{bmatrix} a_{tr1} \\ a_{tr2} \end{bmatrix} + \begin{bmatrix} Z_{m\ tr1} & 0 \\ 0 & Z_{m\ tr2} \end{bmatrix} \begin{bmatrix} m_{tr1} \\ m_{tr2} \end{bmatrix} + \begin{bmatrix} e_{tr1} \\ e_{tr2} \end{bmatrix}$$

where y_{tr1} and y_{tr2} are the observations for the first trait and second trait in the analysis, b_i is the vector of fixed effects, a_i is the vector of additive genetic effects, m_i is the vector of maternal genetic effects and e_i is the vector of error effects. X_i and $Z_{a\ i}$ and $Z_{m\ i}$ are the incidence matrices (i = tr1 and tr2). Variance components and their SEs were estimated using ASReml software (Gilmour et al., 2006). The estimation of genetic parameters was done the same way as the research by Paganoni et al. (2017). We estimated maternal genetic variance and the covariance between both traits when maternal genetic effects were significant for both traits. When only one of the traits in the bivariate model had significant maternal genetic effects, we included maternal genetic effects for that trait only.

Genetic correlations for live weight, fat and muscle change

We estimated the genetic parameters for the change in fat and muscle between the start and finish of the feed intake period.

These new traits were change in muscle depth (ΔEMD = EMD2 − EMD1) and change in fat depth (ΔCF = CF2 − CF1). These two traits were estimated from the variance components estimated individual fat and muscle traits instead of first estimating the change and fitting in the model. The variance components of ΔEMD and ΔCF were then calculated by estimating the covariance between both measurements. For example, the additive genetic variance of change in muscle ΔEMD ($\sigma^2_{a\ \Delta EMD}$) was;

$$\sigma^2_{a\Delta EMD} = \sigma^2_{aEMD2} + \sigma^2_{aEMD1} - 2 \times cov_a(EMD2,EMD1)$$

where $\sigma^2_{a\ EMD2}$ is the additive genetic variance of EMD2, $\sigma^2_{a\ WEMD1}$ is the additive genetic variance of EMD1 and cov_a(EMD2,EMD1) is the additive genetic covariance between EMD2 and EMD1.

We estimated the variance components for ΔCF and ΔEMD as separate traits and estimating variance components postanalysis because all records for fat and muscle could be included in the analysis. For example, if an animal had only one record for muscle, then when a change in muscle is calculated, this record is not included in the analysis. Table 2 shows differences in available measurements for CF1, CF2, EMD1 and EMD2. Additionally, fixed effects are estimated for both the start and end measurements independently, improving the accuracy of the analysis.

The genetic correlations between fat and muscle change with intake and gas traits were calculated from the covariances between the two fat or muscle traits and the intake and gas traits, and the variances of all three traits. For example, the genetic correlation between muscle change and Intake ($r_{g\ \Delta EMD,Intake}$) was;

$$r_{g\ \Delta EMD,Intake} = \frac{cov_a(EMD2, Intake) - cov_a(EMD1, Intake)}{\sigma_{a\ Intake} \times \sqrt{\sigma^2_{a\ \Delta EMD}}}$$

To test if this genetic correlation was significantly greater than zero, a likelihood ratio test was used to compare the fit of two models. Both models were bivariate fitting EMD1 and EMD2. The first model had no restrictions on the estimates for variance and covariance, and the second model required the covariance between EMD2 and Intake to be equal to the covariance between EMD1 and Intake. Making the covariances between each muscle and intake equal makes the numerator for the correlation zero. The second model therefore reflects our null hypothesis that the genetic correlation is equal to zero.

Fixed effects

For all traits, we fitted fixed effects for the management group, birth type, rear type, sex, pen and age of measurement. Fat and muscle were also corrected for live weight. All significant interactions between fixed effects were also included.

Validation and quality assurance

Variance components for each trait were estimated first with a univariate model. The results of these univariate models were used as starting values in the bivariate analysis. Extreme outliers of data were removed if they were more than four times the SD from the mean across all data.

Statistical analysis of results

We used likelihood ratio tests to test model 3 against model 1 to see if adding maternal genetic effects significantly improved the fit of the traits. There were no significant ($P > 0.05$) permanent environmental effects caused by the dam in all traits, but maternal genetic effects were significant ($P < 0.05$) for most traits (Table 3).

To test if the genetic correlations between traits were significantly greater than zero, we used likelihood ratio tests to compare the fit of two models. The first model was with no restrictions on the estimates for variance and covariance, and the second model restricted the covariance between the two traits to zero. The second model therefore reflects our null hypothesis that the genetic correlation is equal to zero. We also tested if genetic correlations were significantly different to 1 or −1 using likelihood ratio tests.

Results

Trait means and heritabilities

Live weight, growth, muscle and fat increased with sheep age (Table 2). Hoggets tended to produce more CH_4, CO_2 and O_2 than sheep at postweaning and adult ages (Table 2). The phenotypic variance of these traits increased as sheep aged (Table 3). Most traits did not have any significant maternal genetic effects and those that did were mostly low even when they were significantly greater than zero (Table 3).

On average, live weight was more heritable (range 0.47–0.58) than fat (range 0.27–0.54), change in fat (0.32–0.47), growth (range 0.21–0.34), muscle (range 0.07–0.30) and change in muscle (range 0.04–0.09; Table 3).

Correlations

Live weight and growth had moderate to high positive phenotypic correlations with intake, carbon dioxide and methane (range 0.33–0.67; Table 4). Phenotypic correlations were low with residual feed intake (range −0.02 to 0.12; Table 4) and moderate to high and negative with oxygen (range −0.46 to −0.64; Table 4). Live weight and growth had significant positive genetic correlations with intake at all ages (range 0.50–0.94; Table 4). Growth rate

Table 3
Phenotypic variance (σ^2_p), heritability (h^2) and maternal heritability (m^2) of growth and intake traits for sheep at postweaning, hogget and adult ages. SEs are presented in brackets. Missing maternal heritabilities (–) were not significant. See Table 1 for definitions of traits.

Traits	Age[1]	σ^2_p	h^2	m^2
BW	P	21.1 (0.83)	0.48 (0.07)	0.02 (0.04)
	H	40.3 (2.18)	0.58 (0.09)	0.00 (0.00)
	A	60.7 (4.80)	0.47 (0.15)	–
Growth	P	0.003 (0.00)	0.21 (0.05)	–
	H	0.005 (0.00)	0.34 (0.08)	–
	A	0.005 (0.00)	0.25 (0.12)	–
EMD1	P	3.65 (0.15)	0.30 (0.08)	0.00 (0.04)
	H	6.87 (0.37)	0.18 (0.08)	0.00 (0.00)
	A	7.71 (0.71)	0.24 (0.16)	0.00 (0.00)
EMD2	P	3.08 (0.13)	0.26 (0.07)	0.02 (0.03)
	H	4.10 (0.20)	0.18 (0.08)	0.00 (0.00)
	A	5.25 (0.38)	0.07 (0.09)	0.13 (0.11)
CF1	P	0.59 (0.02)	0.54 (0.05)	0.08 (0.03)
	H	0.80 (0.04)	0.43 (0.11)	0.03 (0.05)
	A	0.82 (0.07)	0.27 (0.17)	–
CF2	P	0.75 (0.03)	0.41 (0.06)	0.02 (0.03)
	H	1.49 (0.08)	0.46 (0.09)	0.00 (0.00)
	A	1.70 (0.16)	0.49 (0.21)	0.06 (0.16)
ΔEMD	P	0.59 (0.02)	0.04 (0.03)	–
	H	0.80 (0.05)	0.05 (0.05)	–
	A	0.82 (0.07)	0.09 (0.08)	–
ΔCF	P	0.75 (0.03)	0.32 (0.04)	–
	H	1.49 (0.08)	0.34 (0.08)	–
	A	1.70 (0.16)	0.47 (0.13)	–

Abbreviations: EMD1 = eye muscle depth measured at the start of the feed intake period, EMD2 = eye muscle depth at the end of the feed intake period, CF1 = C-site fat depth at the start of the feed intake period, CF2 = C-site fat depth at the end of the feed intake period, ΔEMD is the change in eye muscle throughout the feed intake period of 35 days and ΔCF is the change in C-site fat depth throughout the feed intake period of 35 days.

[1] P = postweaning, H = hogget age, A = adult.

Table 4
Phenotypic and genetic correlations between live weight and growth traits with intake, residual feed intake (RFI), methane (CH_4), carbon dioxide (CO_2) and oxygen (O_2) traits for sheep at postweaning, hogget and adult ages.

Trait	Intake	RFI	CH_4	CO_2	O_2
Phenotypic correlations					
Postweaning age					
BW	0.52 (0.02)	0.12 (0.02)	0.40 (0.01)	0.67 (0.02)	−0.64 (0.02)
Growth	0.46 (0.02)	0.09 (0.02)	0.41 (0.01)	0.53 (0.02)	−0.46 (0.02)
Hogget age					
BW	0.61 (0.02)	−0.00 (0.03)	0.48 (0.02)	0.54 (0.02)	−0.51 (0.02)
Growth	0.61 (0.02)	0.04 (0.03)	0.49 (0.02)	0.56 (0.02)	−0.54 (0.02)
Adults					
BW	0.47 (0.03)	−0.02 (0.04)	0.33 (0.04)	0.46 (0.03)	−0.52 (0.03)
Growth	0.67 (0.02)	0.01 (0.04)	0.50 (0.03)	0.63 (0.02)	−0.61 (0.03)
Genetic correlations					
Postweaning age					
BW	0.50 (0.10)[a]	0.12 (0.17)	0.62 (0.09)[a]	0.85 (0.06)[a]	−0.80 (0.07)[a]
Growth	0.61 (0.13)[a]	0.35 (0.20)	0.63 (0.12)[a]	0.45 (0.18)[a]	−0.44 (0.18)[a]
Hogget age					
BW	0.76 (0.06)[a]	0.42 (0.16)[a]	0.71 (0.10)[a]	0.72 (0.08)[a]	−0.71 (0.08)[a]
Growth	0.74 (0.07)[a]	0.48 (0.16)[a]	0.84 (0.09)[a]	0.78 (0.08)[a]	−0.83 (0.07)[a]
Adults					
BW	0.94 (0.09)[a]	0.37 (0.51)	−0.01 (0.41)	0.30 (1.67)	−0.16 (3.18)
Growth	0.83 (0.12)[a]	0.58 (0.51)	0.55 (0.29)	0.79 (0.33)	−0.60 (0.30)

Values within a row with a superscript 'a' differ significantly from zero ($P < 0.05$).

Table 5
Genetic correlations between muscle and fat traits with intake, residual feed intake (RFI), methane (CH_4), carbon dioxide (CO_2) and oxygen (O_2) for sheep at postweaning, hogget and adult ages.

Trait[1]	Intake	RFI	CH_4	CO_2	O_2
Postweaning age					
EMD1	−0.49 (0.15)[a]	−0.57 (0.17)[a]	−0.22 (0.17)	−0.60 (0.17)[a]	0.30 (0.19)
EMD2	−0.37 (0.17)[a]	−0.38 (0.19)	−0.38 (0.17)[a]	−0.13 (0.23)	−0.05 (0.20)
CF1	−0.63 (0.11)[a]	−0.50 (0.15)[a]	−0.29 (0.13)[a]	−0.62 (0.14)[a]	0.46 (0.14)[a]
CF2	−0.16 (0.16)	−0.14 (0.18)	−0.46 (0.13)[a]	−0.35 (0.20)	0.33 (0.18)
Hogget age					
EMD1	−0.24 (0.18)	−0.19 (0.23)	−0.33 (0.24)	0.00 (0.22)	0.01 (0.22)
EMD2	−0.39 (0.16)[a]	−0.06 (0.25)	−0.35 (0.25)	−0.19 (0.22)	0.09 (0.23)
CF1	−0.34 (0.14)[a]	−0.21 (0.18)	−0.43 (0.19)[a]	−0.18 (0.17)	0.30 (0.16)
CF2	−0.17 (0.13)	−0.06 (0.17)	0.01 (0.20)	−0.06 (0.16)	−0.01 (0.16)
Adult age					
EMD1	−0.69 (0.19)[a]	−0.17 (0.64)	−0.73 (0.32)	−0.92 (0.59)	0.65 (0.35)
EMD2	0.89 (0.29)[a]	0.04 (0.71)	0.08 (0.63)	0.68 (0.67)	−0.84 (0.43)
CF1	−0.41 (0.29)	0.02 (0.77)	−0.29 (0.45)	−0.08 (3.35)	0.89 (0.32)
CF2	−0.23 (0.22)	−0.00 (0.47)	−0.03 (0.34)	−0.60 (0.29)	0.53 (0.26)

Abbreviations: Intake = feed intake, RFI = residual feed intake, CH_4 = methane, CO_2 = carbon dioxide, O_2 = Oxygen, EMD1 = eye muscle depth measured at the start of the feed intake period, EMD2 = eye muscle depth at the end of the feed intake period, CF1 = C-site fat depth at the start of the feed intake period, CF2 = C-site fat depth at the end of the feed intake period.
Values within a row with a superscript 'a' differ significantly from zero ($P < 0.05$).

and live weight had significant positive genetic correlations with residual feed intake at hogget age only (range 0.42–0.48; Table 4). Growth rate and live weight also had significant positive genetic correlations with carbon dioxide and methane (range 0.45–0.85; Table 4), and significant negative genetic correlations with oxygen (range −0.44 to −0.71; Table 4) at postweaning and hogget ages. All other genetic correlations were not significantly different from zero or associated with high SEs.

Muscle measured at the start had significant negative genetic correlations with intake at postweaning age (−0.49) and adult age (−0.69), residual feed intake at postweaning age (−0.57) and carbon dioxide at postweaning age (−0.60; Table 5). Muscle measured at the end of the feed intake period also had significant negative genetic correlations with intake at postweaning (−0.37) and hogget age (−0.39) and methane at postweaning age (−0.38), but a significant positive correlation with intake as adults (0.89; Table 5). Fat measured at the start of the feed intake period had significant negative genetic correlations with intake at postweaning (−0.63) and hogget age (−0.34), residual feed intake at postweaning age (−0.50), methane at postweaning (−0.29) and hogget age (−0.43), and carbon dioxide at postweaning age (−0.62). However, fat measured at the start of the feed intake period had a significant positive genetic correlation with oxygen at postweaning age (0.46; Table 5). Fat measured at the end of the feed intake period had a significantly negative genetic correlation with methane only at postweaning age (−0.46; Table 5).

Feed intake and residual feed intake had significant positive genetic correlations with change in fat at postweaning age (range 0.48–0.50; Table 6). Carbon dioxide had a significant positive genetic correlation (0.67; Table 6) with change in muscle for postweaning age. Feed intake had a positive significant genetic correlation (0.64; Table 6) with change in muscle at adult age.

Discussion

Merino sheep selected for high growth rates have higher feed intake and production of methane and carbon dioxide. Therefore,

Table 6
Phenotypic and genetic correlations between change in eye muscle depth (ΔEMD) and change in C-site fat depth (ΔCF) in sheep at postweaning, hogget and adult ages from the start to the finish of the feed intake period with intake, residual feed intake (RFI), methane (CH_4), carbon dioxide (CO_2) and oxygen (O_2) traits.

Trait	Intake	RFI	CH_4	CO_2	O_2
Phenotypic correlations					
Postweaning age					
ΔEMD	0.09 (0.02)	0.04 (0.02)	0.02 (0.02)	0.09 (0.03)	−0.04 (0.03)
ΔCF	0.22 (0.03)	0.22 (0.03)	−0.02 (0.02)	0.11 (0.04)	−0.09 (0.04)
Hogget age					
ΔEMD	0.02 (0.03)	0.14 (0.03)	0.11 (0.03)	0.04 (0.03)	−0.03 (0.03)
ΔCF	0.09 (0.03)	0.03 (0.03)	0.12 (0.03)	0.06 (0.03)	−0.09 (0.03)
Adult age					
ΔEMD	0.39 (0.04)	0.35 (0.04)	0.26 (0.04)	0.27 (0.04)	−0.22 (0.04)
ΔCF	0.04 (0.05)	0.08 (0.04)	0.03 (0.05)	–	–
Genetic correlations					
Postweaning age					
ΔEMD	0.42 (0.32)	0.63 (0.35)	−0.31 (0.33)	0.67 (0.29)[a]	−0.44 (0.33)
ΔCF	0.50 (0.14)[a]	0.48 (0.17)[a]	−0.08 (0.15)	0.24 (0.18)	−0.09 (0.17)
Hogget age					
ΔEMD	0.18 (0.35)	0.41 (0.39)	0.29 (0.40)	−0.12 (0.36)	0.00 (0.37)
ΔCF	0.11 (0.15)	0.15 (0.20)	0.45 (0.19)	0.11 (0.18)	−0.30 (0.17)
Adult age					
ΔEMD	0.64 (0.27)[a]	0.41 (0.63)	0.80 (0.42)	0.49 (0.62)	−0.34 (0.67)
ΔCF	0.15 (0.25)	−0.06 (0.44)	0.31 (0.36)	–	–

Abbreviations: Intake = feed intake, RFI = residual feed intake, CH_4 = methane, CO_2 = carbon dioxide, O_2 = Oxygen, ΔEMD is the change in eye muscle throughout the feed intake period of 35 days and ΔCF is the change in C-site fat depth throughout the feed intake period of 35 days.
Values within a row with a superscript 'a' differ significantly from zero ($P < 0.05$).

we accepted the hypothesis that live weight and growth have significant antagonistic correlations with greenhouse gas traits in sheep. Nevertheless, selection for increased growth rate and improved feed efficiency is easier in young animals where growth is potentially more important than in older ages because the genetic correlations between growth and residual feed intake are weaker. The correlations estimated in young animals included more records and were more accurate than those measured in older animals. Therefore, more records are required for animals at hogget and adult age to increase the reliability of these estimates.

The genetic correlations suggest that selecting for increased fat and muscle depth corrected for live weight would decrease feed intake, residual feed intake and methane production. These negative genetic correlations tended to be stronger when fat and muscle were measured at the start of the measurement period compared to the end. These differences in correlations between the start and end of the feed intake period also influence the correlations for the change in fat and muscle across the measurement period. Furthermore, the initial condition (fat and muscle) of animals at the beginning of the measurement period could influence how much feed is eaten during the feed intake measurement period. Additionally, these negative correlations could be because selecting for higher fat and muscle corrected for live weight may also indirectly reduce live weight which in turn decreases feed intake. This is because fat and muscle corrected for live weight can increase by increasing fat and muscle or by decreasing live weight. Therefore, the selection pressure for fat and muscle could also impact the selection for live weight indirectly. The correlations, however, were not consistent across ages and were impacted by the timing of measurement which also needs to be considered. In most cases, they were weaker than the correlations between live weight and growth with feed intake, residual feed intake and methane but also had higher errors. These results generally agree with those reported for Romney sheep by Johnson et al. (2022) for fat depth, however, the correlations for lean tissue deposition tended to be in the opposite direction but with higher errors to those present from the current study. Johnson et al. (2022) measured lean tissue using computed tomography to assess body composition. Therefore, it is difficult to compare the two studies.

Residual feed intake had lower genetic correlations with live weight and growth compared to intake and was not significantly different from zero at postweaning and adult age. This is expected because residual feed intake is corrected for live weight and average daily gain. This also explains why the phenotypic correlations between residual feed intake with live weight and average daily gain are almost zero. Therefore, it is easier to select animals that grow faster and are more feed efficient than reducing feed intake. The genetic correlations between feed intake and residual feed intake with change in fat depth were positive. Accordingly, selecting for lower feed intake and residual feed intake will reduce fat depth. Additionally, less feed-efficient sheep at postweaning age will also gain more fat during the feed intake period. These significant correlations between intake, feed efficiency and change in fat suggest that including only growth as a predictor of feed intake in feed efficiency equations does not consider all of the variation of energy deposition. Therefore, a fat-adjusted residual feed intake could improve the interpretation of residual feed intake for energy use efficiency and by default reduce the variation that you have to work with.

This study found genetic correlations that suggested sheep that were genetically fatter and more muscled at the start and finish of the feed intake periods ate less than genetically less fat and less muscular sheep at the same live weight. Fat and muscle were scanned and used as an indicator of body fat and energy in field conditions. Further work is required to understand the biological implications of these correlations. Furthermore, young animals that have more increase in muscle depth will also produce more carbon dioxide, due to increases in feed intake during the feed intake period. Perhaps the sheep that had less fat ate more to compensate on the high-quality diet. The genetic correlations between fat and muscle with intake were more negative at the start of the feed intake period than in the finish. Therefore, change in fat and muscle had positive correlations with intake because the covariance between the first measurement and intake was lower than the covariance between the second measurement and intake. Less muscular and fat sheep at the start of the feed intake period ate more and gained more fat and muscle than fatter and more muscular sheep. This is supported by Blumer et al., (2016) who found that Merino ewes with more fat may not have a lower residual feed

intake. Therefore, these types of sheep may be more productive and profitable during periods where extra feed is required. Additionally, the feed intake period of 35 days may not be long enough to express the change in fat and muscle depth. Additionally, there will be a lag between feed intake and changes in tissue deposition that could be considered in future analyses.

Fat and muscle are included in Australian sheep breeding programmes corrected for live weight because larger animals tend to have more fat and muscle (Huisman and Brown, 2009; Huisman et al., 2008). Therefore, comparing residual feed intake, which is the residual from fitting live weight and weight change against feed intake, with fat and muscle, which is also corrected for live weight, can be complicated. For example, van der Werf (2004) suggested that feed intake and production traits should be used for optimal selection as opposed to feed efficiency. This could also be the case for including feed intake with live weight, fat and muscle, particularly if fat and muscle are not included as covariates when estimating residual feed intake.

The composition of weight gain in animals depends also on the type of live weight gain. Compensatory growth in animals after restricted feeding could be from decreased maintenance requirements, increased protein deposition or increased feed intake (Ryan et al., 1993). Additionally, once compensatory growth has stopped, animals may eat more and produce more CO_2.

We used a high-quality pellet in our experiments. However, most Merino sheep in Australia are managed outdoors in Mediterranean climatic zones (Squires, 2006). These areas have high variation in pasture quality and quantity during the year (Rossiter, 1966) and animals are supplemented with high-quality feed during periods of low pasture quality and quantity. Therefore, future work should seek to understand if the relationships between fat, muscle and live weight with intake, residual feed intake, methane and other gas traits are consistent on different types of feed. However, the genotype by environmental interactions when sheep consume different types of feed would have to be high to change these correlations. This study did not consider different types of feed that should be considered in future work.

Pinares-Patiño et al. (2013) found positive genetic correlations between methane and weaning weight when animals were fed a fixed amount of feed based on their live weight (0.88), postweaning weight (0.89) and eye muscle depth (0.64), similar to our results. However, the genetic correlations between intake and fat and muscle were negative when fat and muscle are corrected for live weight. Therefore, sheep that are fatter or more muscular when corrected for live weight eat less. The high correlations between fat and muscle with live weight mean that including live weight as a covariate is important to disentangle the real effects of fat and muscle on feed intake and feed efficiency. These differences in feed efficiency were also reflected in the methane production that also decreased when fat and muscle increased at the same live weight.

Additionally, the proportion of fat and muscle in the gain or loss of live weight can change the efficiency of feed utilisation for weight gain (Cameron, 1998). Selecting animals at postweaning age that gain more fat at the same live weight will make them genetically less feed efficient. At all ages, the genetic correlation between change in muscle corrected for live weight and residual feed intake was higher than the correlation between change in fat and residual feed intake. Therefore, selecting animals to gain more muscle would make them genetically less feed efficient than those selected for more fat. Fat deposition requires more energy than protein deposition (Freer et al., 2007). Once stored, however, fat requires less energy to maintain than protein (Herd and Arthur, 2009). Therefore, once stored, fat is an accessible store of energy for biological demands such as reproduction and immunity (Blumer et al, 2016). Therefore, efficiencies gained in selecting animals to deposit more fat than muscle are unlikely to be measurable in finishing systems but should be more evident in the extensive breeding systems where lambs are generated.

Our heritability estimates for live weight (0.27) were low compared to Huisman et al. (2008) (0.75) but our phenotypic variance (0.20) was similar (0.22). The estimates of heritability for growth rate were slightly lower (0.20) than Snowder and Vleck (2003) (0.25–0.39). Heritabilities for eye muscle (0.21 and 0.25) were similar to Maximini et al., (2012) (0.25) but lower for fat (0.10 and 0.18 compared to 0.40).

Conclusions

The results presented here suggest breeding for higher live weight and growth will increase feed intake and methane production but also make hogget age animals more feed efficient. Breeding for increased fat and muscle per kg of live weight will impact feed intake, residual feed intake and methane production in different ways depending on when it is measured. The interactions between all of these traits means that appropriate selection across all traits is needed to ensure that overall responses are favourable. Finally, high correlations between feed intake, methane production, live weight, growth, fat and muscle will reduce simultaneous selection responses when trying to select for feed efficiency in Merino sheep.

These correlations are important for the Australian Sheep industry because it shows the consequence of current selection for growth, fat and muscle on feed intake, methane production and feed efficiency. In the future, if feed intake and methane production are included in breeding programmes, more work will be required to estimate appropriate weightings for selection indexes to ensure a balanced response to selection.

Ethics approval

This research was approved by the Animal Ethics Committee of the Department of Agriculture and Food Western Australia. All procedures were conducted in accordance with the Australian code of practice for the care and use of animals for scientific purposes, and the Australian Animal Welfare Act 2002. The relevant permit numbers included 01-09-08 and 06-11-27.

Data and model availability statement

None of the data were deposited in an official repository. The access rights to data, software or model are confidential.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

None.

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