Genetic correlations between body weight change and reproduction traits in Merino ewes depend on age[1]

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ABSTRACT: Merino sheep in Australia experience periods of variable feed supply. Merino sheep can be bred to be more resilient to this variation by losing less BW when grazing poor quality pasture and gaining more BW when grazing good quality pasture. Therefore, selection on BW change might be economically attractive but correlations with other traits in the breeding objective need to be known. The genetic correlations (r_g) between BW, BW change, and reproduction were estimated using records from approximately 7,350 fully pedigreed Merino ewes managed at Katanning in Western Australia. Number of lambs and total weight of lambs born and weaned were measured on approximately 5,300 2-yr-old ewes, approximately 4,900 3-yr-old ewes, and approximately 3,600 4-yr-old ewes. On a proportion of these ewes BW change was measured: approximately 1,950 2-yr-old ewes, approximately 1,500 3-yr-old ewes, and approximately 1,100 4-yr-old ewes. The BW measurements were for 3 periods. The first period was during mating period over 42 d on poor pasture. The second period was during pregnancy over 90 d for ewes that got pregnant on poor and medium quality pasture. The third period was during lactation over 130 d for ewes that weaned a lamb on good quality pasture. Genetic correlations between weight change and reproduction were estimated within age classes. Genetic correlations were tested to be significantly greater magnitude than 0 using likelihood ratio tests. Nearly all BW had significant positive genetic correlations with all reproduction traits. In 2-yr-old ewes, BW change during the mating period had a positive genetic correlation with number of lambs weaned (r_g = 0.58); BW change during pregnancy had a positive genetic correlation with total weight of lambs born (r_g = 0.33) and a negative genetic correlation with number of lambs weaned (r_g = –0.49). All other genetic correlations were not significantly greater magnitude than 0 but estimates of genetic correlations for 3-yr-old ewes were generally consistent with these findings. The direction of the genetic correlations mostly coincided with the energy requirements of the ewes and the stage of maturity of the ewes. In conclusion, optimized selection strategies on BW changes to increase resilience will depend on the genetic correlations with reproduction and are dependent on age.

Key words: body weight change, genetic correlations, Merino ewes, reproduction

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INTRODUCTION

Most Merino sheep in Australia are farmed in Mediterranean climate regions and they generally lose BW during summer and autumn and regain BW during late winter and spring (Adams and Briegel, 1998). Managing the extent and timing of BW loss and gain in relation to pasture supply and animal requirements can affect whole farm profit (Young et al., 2011). Management of BW of ewes will become more difficult if length of annual periods of drought during summer and winter become longer and harder to predict (IPCC, 2007). One way to make sheep production systems more resilient to uncertain pasture supply is to se-

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lect sheep that lose less BW when the supply and quality of paddock feed is low (Rose et al., 2013).

Phenotypically, Merino ewes that are heavier at mating have a higher reproductive rate (Ferguson et al., 2011). Additionally, there are positive phenotypic correlations between BW gain during pregnancy and birth and weaning weight in lambs, with heavier lambs more likely to survive both before and after weaning (Oldham et al., 2011; Thompson et al., 2011).

Genetic correlations between BW change and reproduction depend on correlations between BW at all times during the reproductive cycle and reproduction traits. Therefore, it is important to know the genetic correlations between BW at key times during the reproductive cycle and reproduction traits. Ewe BW before mating has a positive genetic correlation with fertility (Owen et al., 1986; Cloete and Heydenrych, 1987). Borg et al. (2009) estimated positive genetic correlations between number of lambs born and BW change during late lactation but correlations during the mating period and pregnancy are still unknown. Based on these correlations the hypothesis that increases in ewe BW during the mating and pregnancy periods would have significant positive genetic correlations with reproduction traits was tested.

MATERIALS AND METHODS

Records from 7,346 Merino ewes were used from 697 sires and 4,724 dams using pedigree records from 17,836 sheep over 10 generations. These sheep were from the Merino Resource flocks of the Department of Agriculture and Food Western Australia located at Katanning (33°41′ S, 117°35′ E, elevation 310 m). Katanning is in a Mediterranean climatic region with hot dry summers and mild wet winters. This combination of temperature and rainfall means that there is a period of no pasture growth during summer and autumn, typically extending from November to May each year. All ewes were managed on 1 farm under conditions typical for commercial farms in the area. The amount of supplement fed varied between years but on average ewes were fed 100 g of an oats and lupin grain mixture per head per day in late December increasing gradually to 800 g per head per day at lambing in July. Hay was fed ab libitum during lambing. More information about how the flock was managed can be found in Greeff and Cox (2006).

Body Weight Change

To estimate change in BW of ewes, BW data from ewes aged 2, 3, and 4 yr old was used and treated BW at each age as different traits, using the same data as used by Rose et al. (2013). The age groups were 2, 3, and 4 yr old at lambing in July. The ewes were weighed 4 times during the year. The average dates for each BW were January 13 for premating weight (**WT1**), February 24 for postmating weight (WT2), May 23 for prelambing weight (**WT3**), and October 2 for weaning weight (**WT4**). The timing of measurements varied between years with WT1, WT2, and WT4 all measured within a week of each other while WT3 was measured within a month. Body weights were corrected for wool weight by estimating wool growth from shearing to the day the BW was measured. These estimates were based on the greasy fleece weight of ewes and assumed that wool growth was linear across the year. Conceptus weight was estimated using equations from the GRAZPLAN model (Freer et al., 1997) and subtracted from WT2 and WT3.

Body weight change was then split into 3 parts of the reproduction cycle: mating, pregnancy, and lactation. For BW change during the mating period all ewes that were mated were included, for pregnancy only ewes that gave birth to lambs were included, and for lactation only ewes that weaned at least 1 lamb were included. Therefore, new BW traits were created that only included the relevant ewes. These traits were for mating (premating BW of all ewes that were mated [**WT1mate**] and postmating BW of all ewes that were mated [**WT2mate**]), for pregnancy (postmating BW for ewes that got pregnant [**WT2preg**] and prelambing BW for all ewes that got pregnant [**WT3preg**]), and for lactation (prelambing BW for ewes that weaned lambs [**WT3lact**] and BW at weaning for ewes that weaned lambs [**WT4lact**]). These 3 groups were derived because ewes that did not bear or rear lambs have different energy and protein requirements compared with ewes that were pregnant and lactating. Therefore, BW change in ewes that do not bear or rear lambs may be genetically different than BW change in ewes that do bear or rear lambs.

Using these new BW the genetic parameters for BW change during mating period (ΔWTmate = WT2mate – WT1mate), during pregnancy (ΔWTpreg = WT3preg – WT2preg), and during lactation (ΔWTlact = WT4lact – WT3lact) could be estimated. Change in BW during mating for all ewes that were mated (**ΔWTmate**) was measured in summer when pasture was dry, change in BW during pregnancy for ewes that got pregnant (**ΔWTpreg**) was measured in autumn when pasture was dry and the start of winter when pasture started growing, and change in BW during lactation for ewes that reared lambs (**ΔWTlact**) was measured during winter and spring when pasture growth was most rapid.

The variance components of these BW change traits were calculated by estimating the covariance between both BW. The additive genetic variance of change in BW (**ΔWT**) ($\sigma^2_{a(\Delta WT)}$) is

$$\sigma^2_{a\,(\Delta WT)} = \sigma^2_{a\,WT2} + \sigma^2_{a\,WT1} - 2 \times cov_a(WT2, WT1), \qquad [1]$$

in which $\sigma^2_{a\,WT2}$ is the additive genetic variance of WT2, $\sigma^2_{a\,WT1}$ is the additive genetic variance of WT1, and $cov_a(WT2, WT1)$ is the additive genetic covariance between WT2 and WT1.

Body weights were used instead of calculating BW change because the number of records for the 4 traits was different. Therefore, only including records from animals with both traits would bias the estimates for BW change. Additionally, the fixed effects can be fitted to each BW trait separately.

Reproduction Data

Reproduction traits at 2 (first lambing opportunity), 3 (second lambing opportunity), and 4 yr of age (third lambing opportunity) were used. These traits were total weight of lambs born (**TBW**) and total weight of lambs weaned (**TWW**) in each age group. These traits incorporate most of the aspects of reproduction such as fecundity, mothering ability, and ease of birth into 1 composite trait (Snowder and Fogarty, 2009). Variances and covariances for total number of lambs born (**NLB**) in each year and total number of lambs weaned (**NLW**) in each year were also estimated. Both NLB and NLW were estimated as linear traits including ewes that had no lambs born or weaned. Traits TBW and TWW were only measured in ewes that gave birth to or weaned lambs. The genetic correlations between BW change and reproduction traits were estimated in the same year at the same age.

Genetic Correlations between Number of Lambs Born and Weaned with BW Change

The genetic correlations (r_g) between BW during the mating, pregnancy, and lactation periods and NLB and NLW were calculated by estimating the genetic covariance between the 2 BW and each reproduction trait using Eq. [2]. This equation was used to estimate the genetic correlations between BW change during pregnancy and lactation and NLB and NLW. Equation [2] is

$$\begin{bmatrix} y_{\text{trait}} \\ y_{\text{wt}_a} \\ y_{\text{wt}_b} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{trait}} & 0 & 0 \\ 0 & \mathbf{X}_{\text{wt}_a} & 0 \\ 0 & 0 & \mathbf{X}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{trait}} \\ \mathbf{b}_{\text{wt}_a} \\ \mathbf{b}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{trait}} & 0 & 0 \\ 0 & \mathbf{Z}_{\text{wt}_a} & 0 \\ 0 & 0 & \mathbf{Z}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{trait}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{trait}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix}, \qquad [2]$$

in which y_{trait} are the observations for NLB and NLW, y_{wt_a} are the observations for the first BW used to calculate BW change, and y_{wt_b} are the observations for the second BW used to calculate BW change; $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{a}_i$ is the vector of additive genetic effects, and $\mathbf{e}_i$ is the vector of error effects; and $\mathbf{X}_i$ and $\mathbf{Z}_i$ are the incidence matrices (i = reproduction trait, wt_a = first BW measurement, and wt_b = second BW measurement). The random effects $\mathbf{a}_i$ and $\mathbf{e}_i$ are trivariate normally distributed with mean 0 and variance:

$$\text{var}\begin{bmatrix} \mathbf{e}_{\text{trait}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I}, \text{ in which}$$

$$\mathbf{R} = \begin{bmatrix} \acute{o}^2_{e\,\text{trait}} & \acute{o}^2_{e\,\text{trait wt}_a} & \acute{o}^2_{e\,\text{trait wt}_b} \\ \acute{o}^2_{e\,\text{wt}_a\,\text{trait}} & \acute{o}^2_{e\,\text{wt}_a} & \acute{o}^2_{e\,\text{wt}_a\,\text{wt}_b} \\ \acute{o}^2_{e\,\text{wt}_b\,\text{trait}} & \acute{o}^2_{e\,\text{wt}_b\,\text{wt}_a} & \acute{o}^2_{e\,\text{wt}_b} \end{bmatrix} \text{ and}$$

$$\text{var}\begin{bmatrix} \mathbf{a}_{\text{trait}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A},$$

$$\text{in which } \mathbf{G} = \begin{bmatrix} \sigma^2_{a\,\text{trait}} & \sigma^2_{a\,\text{trait wt}_a} & \sigma^2_{a\,\text{trait wt}_b} \\ \sigma^2_{a\,\text{wt}_a\,\text{trait}} & \sigma^2_{a\,\text{wt}_a} & \sigma^2_{a\,\text{wt}_a\,\text{wt}_b} \\ \sigma^2_{a\,\text{wt}_b\,\text{trait}} & \sigma^2_{a\,\text{wt}_b\,\text{wt}_a} & \sigma^2_{a\,\text{wt}_b} \end{bmatrix},$$

in which **I** is the identity matrix and **A** is the additive genetic relationship matrix between ewes.

Variance components and their standard errors were estimated using ASReml (Gilmour et al., 2006). For all traits fixed effects were for year (1982–2005), the age of the dam of the ewe (years), birth and rearing type of the ewe (single or multiple), and birth date as a fixed covariate.

Reproductive performance of a ewe affects BW change during pregnancy and lactation, as more lambs will cause a higher fetal and lactation burden. Ewes that produce larger litters are expected to lose more BW during pregnancy and lactation. Therefore, correlations between BW change during pregnancy and lactation and reproduction were calculated with and without fixed effects fitted for number of lambs born and reared by the ewes in the year of measurement. Differences in correlations using both methods are in Appendix I for number of lambs born and weaned and Appendix II for total weaning weight and total birth weight.

The genetic correlations between BW change and reproduction traits were calculated from the covariances between the 2 BW and the reproduction trait and the variances of all 3 traits. For example, the genetic correlation between BW change and NLB ($r_{g\,\Delta WT,\,NLB}$) is

$$r_{g\,\Delta\text{WT, NLB}} = \left[\text{cov}_a(\text{WT2,NLB}) - \text{cov}_a(\text{WT1,NLB})\right] \Big/ \left\{\sigma_{a\,\text{NLB}} \times \left[\sigma^2_{a\,\text{WT2}} + \sigma^2_{a\,\text{WT1}} - 2 \times \text{cov}_a(\text{WT1, WT2})\right]^{1/2}\right\}. \qquad [3]$$

To test if this genetic correlation was significantly greater magnitude than 0 a likelihood ratio test was used to compare the fit of 2 models. The first model was with no restrictions on the estimates for variance and covariance and the second model required the covariance between WT2 and NLB to be equal to the covariance between WT1 and NLB. Making the covariances between each BW and NLB equal makes the numerator for the correlation 0. The second model therefore reflects our null hypothesis that the genetic correlation is equal to 0.

Genetic Correlations Between Total Birth and Weaning Weights with BW Change

Removing the ewes that did not give birth to or wean a lamb from the analysis would bias the estimates for variance of TBW and TWW and the covariance between these traits and other traits (Thompson, 1973). Therefore, when TBW was analyzed a binary trait was included for ewes that were mated and did (1) or did not (0) give birth to any lambs (**HAVELAMB**). When TWW was analyzed a binary trait was included for ewes that were mated and did (1) or did not (0) wean any lambs (**WEANLAMB**). These binary traits were included in multivariate analyses with reproduction traits (TBW or TWW) and the 2 BW traits used to estimate the BW change trait at ages 2, 3, and 4 using Eq. [4]:

$$\begin{bmatrix} y_{\text{bin}} \\ y_{\text{repro}} \\ y_{\text{wt}_a} \\ y_{\text{wt}b} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{bin}} & 0 & 0 & 0 \\ 0 & \mathbf{X}_{\text{repro}} & 0 & 0 \\ 0 & 0 & \mathbf{X}_{\text{wt}_a} & 0 \\ 0 & 0 & 0 & \mathbf{X}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{bin}} \\ \mathbf{b}_{\text{repro}} \\ \mathbf{b}_{\text{wt}_a} \\ \mathbf{b}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{bin}} & 0 & 0 & 0 \\ 0 & \mathbf{Z}_{\text{repro}} & 0 & 0 \\ 0 & 0 & \mathbf{Z}_{\text{wt}_a} & 0 \\ 0 & 0 & 0 & \mathbf{Z}_{\text{wt}_b} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{bin}} \\ \mathbf{a}_{\text{repro}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{bin}} \\ \mathbf{e}_{\text{repro}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix}, \quad [4]$$

in which y_{bin} are the observations for the binary reproduction traits HAVELAMB or WEANLAMB, y_{repro} are the observations for the reproduction traits TBW or TWW, y_{wt_a} are the observations for the first BW used to calculate BW change, and y_{wt_b} are the observations for the second BW used to calculate BW change; $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{a}_i$ is the vector of additive genetic effects, and $\mathbf{e}_i$ is the vector of error effects; and $\mathbf{X}_i$ and $\mathbf{Z}_i$ are the incidence matrices (i = binary trait, reproduction trait, wt$_a$, and wt$_b$). The random effects $\mathbf{a}_i$ and $\mathbf{e}_i$ are multivariate normally distributed with mean 0 and variance:

$$\text{var}\begin{bmatrix} \mathbf{e}_{\text{bin}} \\ \mathbf{e}_{\text{repro}} \\ \mathbf{e}_{\text{wt}_a} \\ \mathbf{e}_{\text{wt}_b} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I}, \text{ in which}$$

$$\mathbf{R} = \begin{bmatrix} 1 & 0 & \sigma^2_{e\,\text{bin wt}_a} & \sigma^2_{e\,\text{bin wt}_b} \\ 0 & \sigma^2_{e\,\text{repro}} & \sigma^2_{e\,\text{repro wt}_a} & \sigma^2_{e\,\text{repro wt}_b} \\ \sigma^2_{e\,\text{wt}_a\,\text{bin}} & \sigma^2_{e\,\text{wt}_a\,\text{repro}} & \sigma^2_{e\,\text{wt}_a} & \sigma^2_{e\,\text{wt}_a\,\text{wt}_b} \\ \sigma^2_{e\,\text{wt}_b\,\text{bin}} & \sigma^2_{e\,\text{wt}_b\,\text{repro}} & \sigma^2_{e\,\text{wt}_b\,\text{wt}_a} & \sigma^2_{e\,\text{wt}_b} \end{bmatrix}, \text{ and}$$

$$\text{var}\begin{bmatrix} \mathbf{a}_{\text{bin}} \\ \mathbf{a}_{\text{repro}} \\ \mathbf{a}_{\text{wt}_a} \\ \mathbf{a}_{\text{wt}_b} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A}, \text{ in which}$$

$$\mathbf{R} = \begin{bmatrix} \sigma^2_{a\,\text{bin}} & \sigma^2_{a\,\text{bin repro}} & \sigma^2_{a\,\text{bin wt}_a} & \sigma^2_{a\,\text{bin wt}_b} \\ \sigma^2_{a\,\text{repro bin}} & \sigma^2_{a\,\text{repro}} & \sigma^2_{a\,\text{repro wt}_a} & \sigma^2_{a\,\text{repro wt}_b} \\ \sigma^2_{a\,\text{wt}_a\,\text{bin}} & \sigma^2_{a\,\text{wt}_a\,\text{repro}} & \sigma^2_{a\,\text{wt}_a} & \sigma^2_{a\,\text{wt}_a\,\text{wt}_b} \\ \sigma^2_{a\,\text{wt}_b\,\text{bin}} & \sigma^2_{a\,\text{wt}_b\,\text{repro}} & \sigma^2_{a\,\text{wt}_b\,\text{wt}_a} & \sigma^2_{a\,\text{wt}_b} \end{bmatrix},$$

For HAVELAMB and WEANLAMB traits a LOGIT link function was used and the residual variance was set to 1. The residual covariance between the binary and reproduction traits was set to 0. The implicit residual variance on the underlying scale for the logit link is $\pi^2/3 \sim 3.3$ (Gilmour et al., 2006). The genetic correlations between BW change and the reproduction traits (TWW and TBW) were calculated using Eq. [3].

RESULTS

Trait Information and Heritability

Two-year-old ewes had the lowest BW and BW increased as ewes got older (Table 1). Two-year-old ewes were still growing to maturity and gained the most BW between lambing and weaning (Table 1). At all ages, ewes were on average heaviest at weaning (WT2lact). Weight differences between ages were significant ($P < 0.05$). The heritability of BW was moderate to high (0.47–0.72) and decreased with age (Table 1). Within each age group the heritability of BW at different weight measurements were different (Table 1). For ewes aged 2 yr, heritabilities were highest for prelambing weights (WT3preg and WT3lact) while for older ewes (aged 3 and 4 yr) heritabilities were highest for postmating weights (WT2mate and WT2preg; Table 1). For ewes aged 2 and 3 yr, heritability was lowest for weaning weight (WT4lact) while for ewes aged 4 yr, heritability was lowest for prelambing weights (WT3preg and WT3lact; Table 1).

At all ages ewes on average lost BW during mating period (ΔWTmate) and gained weight during lactation (ΔWTlact; Table 2). During pregnancy (ΔWTpreg), 2-yr-old pregnant ewes gained weight, 3-yr-old ewes slightly gained weight, and 4-yr-old ewes slightly lost

Table 1. Weight measurements by age, number of observations, mean, phenotypic variance (σ_p^2) and h^2 (standard errors are in parentheses)

Weight trait[1]	Records	Mean, kg	σ_p^2, kg	h^2
Age 2				
WT1mate	1,940	50.4	8.64	0.70 (0.05)
WT2mate	1,940	48.2	25.10	0.68 (0.05)
WT2preg	1,540	48.7	21.53	0.68 (0.06)
WT3preg	1,540	50.7	33.33	0.72 (0.05)
WT3lact	1,290	50.8	20.19	0.72 (0.06)
WT4lact	1,280	55.3	34.54	0.60 (0.07)
Age 3				
WT1mate	1,520	58.8	7.89	0.52 (0.06)
WT2mate	1,520	58.2	20.20	0.63 (0.06)
WT2preg	1,330	58.5	21.70	0.58 (0.06)
WT3preg	1,330	58.7	26.35	0.57 (0.06)
WT3lact	1,150	58.5	22.06	0.53 (0.07)
WT4lact	1,140	61.2	25.69	0.52 (0.07)
Age 4				
WT1mate	1,110	62.1	8.03	0.56 (0.07)
WT2mate	1,110	61.2	15.70	0.58 (0.07)
WT2preg	960	61.4	21.59	0.59 (0.08)
WT3preg	960	61.1	24.25	0.47 (0.08)
WT3lact	850	61.1	22.75	0.47 (0.08)
WT4lact	840	62.5	25.77	0.53 (0.09)

[1]WT1mate = premating BW of all ewes that were mated; WT2mate = postmating BW of all ewes that were mated; WT2preg = postmating BW for ewes that got pregnant; WT3preg = prelambing BW for all ewes that got pregnant; WT3lact = prelambing BW for ewes that weaned lambs; WT4lact = BW at weaning for ewes that weaned lambs.

Table 2. Body weight measurements by age, mean, phenotypic variance (σ_p^2) and h^2 (standard errors are in parentheses)

Weight change trait[1]	Mean, kg	σ_p^2, kg	h^2
Age 2			
ΔWTmate	–2.20	6.43	0.14 (0.04)
ΔWTpreg	2.00	8.82	0.13 (0.04)
ΔWTlact	4.60	22.8	0.36 (0.06)
Age 3			
ΔWTmate	–0.50	11.5	0.15 (0.05)
ΔWTpreg	0.20	9.14	0.16 (0.06)
ΔWTlact	2.70	29.5	0.24 (0.06)
Age 4			
ΔWTmate	–0.90	10.8	0.12 (0.06)
ΔWTpreg	–0.3	11.1	0.18 (0.07)
ΔWTlact	1.4	32.1	0.24 (0.07)

[1]ΔWTmate = change in BW during mating for all ewes that were mated; ΔWTpreg = change in BW during pregnancy for ewes that got pregnant; ΔWTlact = change in BW during lactation for ewes that reared lambs.

weight (Table 2). Differences in changes in body weight between ages were significant ($P < 0.05$). The heritability of BW change was highest at all ages for lactating ewes (ΔWTlact; Table 2). For ewes aged 2 yr the heritability of BW change was lowest for pregnant ewes (ΔWTpreg), while for ewes aged 3 and 4 yr old heritability of BW change during mating period was lowest (Table 2).

Ewes gave birth to more lambs (NLB) as they aged and the total weight of those lambs at birth (TBW) increased ($P < 0.05$; Table 3). In addition, as ewes aged they weaned more lambs (NLW) and the total weight of those lambs at weaning (TWW) increased ($P < 0.05$; Table 3). The heritability of reproduction traits NLB, NLW, TBW, and TWW was low to moderate (0.08–0.17; Table 3). Heritabilities of birth traits (NLB and TBW) decreased when age of ewes increased while heritabilities of weaning traits (NLW and TWW) were highest at age 2 yr and lowest at age 3 yr (Table 3). Although some differences in heritability were substantial, they were generally not statistically significant due to the relatively large approximated standard errors.

Genetic Correlations BW and Reproduction

All genetic correlations between all BW and reproduction traits were positive. The highest genetic correlations were between BW and total weaning weight (TWW; Table 4). At age 2 TBW and TWW had the highest genetic correlation with WT1 mate while NLB and NLW had the highest genetic correlation with WT2preg (Table 4). At age 3 TBW had the highest genetic correlation with WT1mate while TWW and NLW had the highest genetic correlation with BW pre lambing for ewes that weaned lambs (**WT3wean**) and NLB had the highest genetic correlation with WT2mean (Table 4). For 4-yr-old ewes TBW had the highest genetic correlation with WT3preg while TWW, NLB, and NLW had the highest genetic correlation with WT3wean (Table 4). All reproduction traits had lowest genetic correlations with BW at weaning for ewes that weaned lambs at all ages except for TWW at age 3, which had the lowest genetic correlation with BW pre mating (Table 4).

Genetic Correlations BW Change and Reproduction

The genetic correlations between BW change and reproduction traits ranged between –0.49 and 0.58 (Table 5) but only 4 out of 26 were significantly greater magnitude from 0. These significant genetic correlations were at age 2 between NLW and ΔWTmate (0.58), between NLW and ΔWTpreg (–0.49), and between TBW and ΔWTpreg (0.33; Table 5). The other genetic correlation significantly different from 0 was at age 4 between TBW and ΔWTlact (–0.42; Table 5). For 3-yr-old ewes some correlations were close to significance with a P-value less than 0.10. These were between ΔWTmate and NLB, between ΔWTmate and NLW,

Table 3. Reproduction trait measurements by age, mean, phenotypic variance (σ_p^2) and h[2] (standard errors are in parentheses)

Reproduction trait[1]	Units	Age	Number	Mean	σ_p^2	h[2]
NLB	Lambs	2	6,756	0.78	0.26	0.15 (0.02)
NLB	Lambs	3	5,585	1.05	0.33	0.12 (0.02)
NLB	Lambs	4	4,360	1.11	0.41	0.10 (0.02)
TBW	kg	2	4,699	4.85	0.75	0.17 (0.02)
TBW	kg	3	4,609	5.13	1.07	0.15 (0.02)
TBW	kg	4	3,551	5.36	1.32	0.12 (0.03)
NLW	Lambs	2	4,699	0.64	0.27	0.11 (0.02)
NLW	Lambs	3	4,609	0.87	0.36	0.08 (0.02)
NLW	Lambs	4	3,551	0.94	0.41	0.09 (0.02)
TWW	kg	2	4,092	26.5	22.2	0.17 (0.03)
TWW	kg	3	4,089	27.6	29.7	0.13 (0.03)
TWW	kg	4	3,363	28.10	36.3	0.15 (0.03)

[1]NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

Table 4. Genetic correlations between BW and reproduction traits at ages 2, 3, and 4 with standard errors in parentheses. Correlations in bold are significantly larger than 0.

Weight trait[2]	Reproduction traits[1]			
	TBW	TWW	NLB	NLW
Age 2				
WT1mate	0.40 (0.09)	0.76 (0.09)	0.36 (0.09)	0.29 (0.11)
WT2mate	0.37 (0.09)	0.75 (0.09)	0.46 (0.09)	0.46 (0.11)
WT2preg	0.27 (0.10)	0.65 (0.10)	0.48 (0.09)	0.47 (0.11)
WT3preg	0.33 (0.09)	0.64 (0.10)	0.37 (0.10)	0.31 (0.11)
WT3wean	0.37 (0.10)	0.63 (0.10)	0.32 (0.10)	0.26 (0.12)
WT4wean	0.24 (0.11)	0.50 (0.11)	0.28 (0.12)	0.29 (0.13)
Age 3				
WT1mate	0.34 (0.11)	0.39 (0.12)	0.36 (0.13)	0.27 (0.16)
WT2mate	0.31 (0.10)	0.45 (0.11)	0.49 (0.11)	0.41 (0.15)
WT2preg	0.21 (0.11)	0.46 (0.13)	0.43 (0.12)	0.36 (0.16)
WT3preg	0.24 (0.11)	0.49 (0.13)	0.40 (0.13)	0.45 (0.16)
WT3wean	0.24 (0.12)	0.55 (0.14)	0.40 (0.13)	0.52 (0.16)
WT4wean	0.15 (0.12)	0.52 (0.14)	0.19 (0.15)	0.24 (0.18)
Age 4				
WT1mate	0.39 (0.14)	0.66 (0.14)	0.23 (0.16)	0.29 (0.16)
WT2mate	0.48 (0.13)	0.73 (0.13)	0.33 (0.15)	0.41 (0.15)
WT2preg	0.52 (0.14)	0.76 (0.14)	0.35 (0.16)	0.37 (0.16)
WT3preg	0.53 (0.16)	0.75 (0.15)	0.32 (0.18)	0.33 (0.18)
WT3wean	0.47 (0.16)	0.78 (0.16)	0.42 (0.18)	0.49 (0.18)
WT4wean	0.12 (0.16)	0.60 (0.16)	0.19 (0.19)	0.26 (0.19)

[1]NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

[2]WT1mate = premating BW of all ewes that were mated; WT2mate = postmating BW of all ewes that were mated; WT2preg = postmating BW for ewes that got pregnant; WT3preg = prelambing BW for all ewes that got pregnant; WT3wean = prelambing BW for all ewes that weaned lambs; WT4wean = weaning BW for all ewes that weaned lambs.

between ΔWTpreg and NLW, between ΔWTlact and NLW, and between ΔWTlact and NLB (Table 5).

DISCUSSION

In this study, the genetic correlations between body weight change during mating and pregnancy and reproduction traits in Merino ewes varied. The only significant positive genetic correlations estimated were between body weight change during mating period and number of lambs weaned and between body weight change during pregnancy and total birth weight for 2-yr-old ewes. Moreover, there was a significant negative genetic correlation between body weight change during pregnancy and number of lambs weaned in 2-yr-old ewes. However, there were suggestive positive genetic correlations between body weight change during mating period and number of lambs born and weaned and between body weight change during pregnancy and number of lambs weaned in 3-yr-old ewes. Overall, the hypothesis that body weight change during mating and pregnancy would have significant positive genetic correlations with reproduction traits in Merino ewes was rejected.

For 2- and 3-yr-old mated ewes, number of lambs weaned had a larger genetic correlation with body weight postmating than body weight premating. These correlations made the genetic correlation between body weight change during mating period and number of lambs weaned positive and significantly greater than 0 for 2-yr-old ewes. Body weight during the mating period and energy balance affects fertility (Forcada and Abecia, 2006). Therefore, ewes that gain weight during mating period would be expected to wean more lambs because they have a positive energy balance.

For pregnant ewes, the correlations were not as clear as for mated ewes, with 2-yr-old ewes having different correlations than 3-yr-old ewes. For 2-yr-old pregnant ewes, number of lambs weaned had a larger genetic correlation with body weight postmating than body weight prelambing. For 3-yr-old pregnant ewes, number of lambs weaned had a larger genetic correlation with body weight prelambing than with body weight postmating. These correlations meant that for 2-yr-old ewes, total birth weight had a genetic correlation with body weight change during pregnancy significantly less than 0, while for 3-yr-old ewes the correlation was in the opposite direction. Additionally, for 2-yr-old ewes, total birth weight had a larger genetic correlation with body weight prelambing than body weight postmating. These correlations made the genetic correlation between body weight change during pregnancy and total birth weight significantly greater than 0. These genetic correlations meant that 2-yr-old ewes that gained weight during pregnancy gave birth to a higher total birth weight but weaned fewer lambs while 3-yr-old ewes that gained more weight during pregnancy weaned more lambs. These different

Table 5. Genetic correlations between BW change and reproduction traits at ages 2, 3, and 4 with standard errors in parentheses. Correlations in bold are significantly larger than 0.

Weight change trait[2]	Reproduction traits[1]			
	TBW	TWW	NLB	NLW
Age 2				
ΔWTmate	−0.26 (0.16)	−0.20 (0.17)	0.27 (0.17)	**0.58 (0.17)**
ΔWTpreg	**0.33 (0.17)**	0.24 (0.20)	−0.34 (0.17)	**−0.49 (0.19)**
ΔWTlact	−0.15 (0.13)	−0.1 (0.14)	−0.08 (0.14)	0.00 (0.16)
Age 3				
ΔWTmate	−0.1 (0.16)	0.24 (0.19)	0.39 (0.20)	0.48 (0.23)
ΔWTpreg	0.21 (0.19)	0.16 (0.21)	0.15 (0.24)	0.53 (0.27)
ΔWTlact	−0.09 (0.16)	0.06 (0.18)	−0.35 (0.18)	−0.46 (0.20)
Age 4				
ΔWTmate	0.26 (0.24)	0.13 (0.23)	0.27 (0.29)	0.33 (0.29)
ΔWTpreg	−0.07 (0.22)	−0.22 (0.21)	−0.15 (0.25)	−0.21 (0.25)
ΔWTlact	**−0.42 (0.20)**	0.00 (0.20)	−0.21 (0.22)	−0.20 (0.22)

[1]NLB = number of lambs born; TBW = total weight of lambs born; NLW = total number of lambs weaned; TWW = total weight of lambs weaned.

[2]ΔWTmate = change in BW during mating for all ewes that were mated; ΔWTpreg = change in BW during pregnancy for ewes that got pregnant; ΔWTlact = change in BW during lactation for ewes that reared lambs.

correlations between ages are perhaps due to differences in physiology between young and older ewes.

There were differences in body weight and reproductive performance between 2- and 3-yr-old ewes that could affect the physiology of the 2 age groups. Two-year-old ewes were still growing to maturity and were 10 to 12 kg lighter at the start of mating than 3- and 4-yr-old ewes. Additionally, 3-yr-old ewes gave birth to and weaned more twin lambs than 2-yr-old ewes. This may explain why weight change during pregnancy for pregnant 2-yr-old ewes had a positive genetic correlation with total birth weight but a negative correlation with number of lambs weaned. Because 2-yr-old ewes mostly had 1 lamb, number of lambs weaned indicates if the ewes got pregnant. The total birth weight indicates how big the lamb was at lambing. Getting pregnant is probably more related to energy balance during mating period while lamb growth is probably related to energy balance during pregnancy. Therefore, if 2-yr-old ewes are selected to gain body weight during mating and pregnancy periods, the correlated response will be to wean a lamb that has a higher birth weight. In 3-yr-olds, more ewes weaned multiple lambs than 2-yr-old ewes. This was because 2 lambs require more resources from the ewe for successful weaning of lambs, with resource requirements peaking after lambing. Therefore, 3-yr-old ewes require positive energy balance during mating and during pregnancy to ensure that lambs can survive to weaning. So despite the differences in physiology and genetic correlations between 2- and 3-yr-old ewes, selecting ewes to gain weight during mating and pregnancy periods will have a favorable correlated response in number of lambs weaned.

For 4-yr-old lactating ewes, total birth weight had a larger genetic correlation with body weight prelambing than body weight at weaning. This was also the case for 3-yr-old ewes with number of lambs born and number of lambs weaned both having larger genetic correlations with body weight prelambing than body weight at weaning. These genetic correlations suggest that these ewes needed to be heavier at lambing to have enough energy for milk production but then lose that weight during lactation. Therefore, losing body weight during lactation period will increase the number of lambs born and weaned in 3-yr-old ewes and increase total birth weight in 4-yr-old ewes. These genetic correlations are supported by 3- and 4-yr-old lactating ewes weaning more lambs than young ewes.

Including fixed effects for lambs born and reared for body weight change during pregnancy and lactation changed the interpretation of the body weight traits. Our results showed that ewes that gained body weight during pregnancy gave birth to a higher total birth weight but weaned fewer lambs. When body weight change during pregnancy was corrected for number of lambs born and reared, the genetic correlation with number of lambs weaned became less negative and not greater magnitude than 0. This change means that correcting for number of lambs weaned reduces the importance of the correlation. The correlation became less negative because of a reduced covariance between body weight change and number of lambs weaned. Therefore, correcting body weight change for number of lambs weaned reduced the influence of body weight change on number of lamb weaned. Additionally, including number of lambs born and weaned had more effect on the correlations between body weight change with number of lambs weaned and born than the correlations with total birth and weaning weight. To best test the hypothesis that body weight change during pregnancy and lactation is genetically correlated with reproduction traits, body weight change uncorrected for reproduction provides the best interpretation of the trait to account for changes in reproduction. This is the best interpretation because the covariance between body weight change and reproduction is not altered by correcting body weight for reproduction at the same time.

The genetic correlations between body weight change during all periods and both total weaning weight and number of lambs born were not significant. Genetic correlations between total weaning weight and body weights and most of the genetic correlations between total birth weight and body weights were all similar during mating period, pregnancy, and lactation. When the genetic correlations between 2 body weights and reproduction are similar, then the covariance between body weight change and reproduction will tend towards 0. This meant that the genetic correlations between total weaning weight and total birth weight and body weight change were near 0 because heavy ewes at any time during the reproductive cycle weaned a higher total weight of lambs. Ewes that weaned multiple lambs had a higher total weaning weight ($P < 0.05$) than ewes that weaned 1 lamb, but the weight of each lamb was lower ($P < 0.05$). Therefore, the positive genetic correlations between body weight and total weaning weight are mainly due to higher number of lambs weaned. Furthermore, maternal genetic effects might be confounded with direct genetic effects on weaning weight of each lamb Separation of these effects is difficult because each ewe has 1 record for weaning weight at each age. Additionally, ewes on average did not lose a lot of weight during mating and pregnancy periods. Mating period was short, and pregnancy period was perhaps too long to accurately describe changes in body weight. The pregnancy period perhaps should be split into 2 periods, early pregnancy and late pregnancy, as ewes generally lose weight during early pregnancy and gain weight during late pregnancy in Mediterranean environments (Ferguson et al., 2011). Therefore, the physiology of the animals would be different during these periods, as animals that lose weight during early pregnancy and gain weight during late pregnancy would be treated the same as those that did not lose or gain any weight during pregnancy.

The heritability of traits estimated in our study are similar to those estimated in previous studies and range from 0.47 to 0.72 for body weight, 0.10 to 0.15 for number of lambs born, and 0.08 to 0.11 for number of lambs weaned. Huisman et al. (2008) estimated a heritability of 0.44 for body weight, 0.09 for number of lambs born, and 0.07 for number of lambs weaned for 2-yr-old Merino ewes. Cloete et al. (2002) estimated a heritability of 0.04 for total weaning weight, which was much smaller than the range found in this study, 0.13 to 0.17. Additionally, Owen et al. (1986) estimated a positive genetic correlation (0.40) between body weight premating and prolificacy in Cambridge sheep, similar to our estimates between body weights pre- and postmating and number of lambs born. Cloete and Heydenrych (1987) estimated low positive genetic correlations between body weight premating and number of lambs born (0.24) and number of lambs weaned (0.20) in 2-yr-old Tygerhoek Merino ewes. These estimates had higher error than our estimates, which were higher and significantly greater than 0. Borg et al. (2009) estimated a low positive genetic correlation (0.12) between adult body weight postweaning and number of lambs born. These estimates were smaller than our estimates between weaning body weight and number of lambs born. It is reasonable to conclude that our heritabities are in the range of other studies, suggesting our dataset is appropriate to study correlations between body weight change and reproduction.

These results are important because ewes on sheep farms in Mediterranean regions of Australia are mated during periods of low nutrition availability (Pitta et al., 2005; Demmers et al., 2011; Ferguson et al., 2011). This means farmers put a high emphasis on nutrition of ewes during the mating period to increase ovulation rate and during pregnancy to increase lamb survival. Selecting for ewes that lose less weight during pregnancy will have mostly favorable correlated responses in reproductive traits. Therefore, the advantage of breeding 2- and 3-yr-old ewes to be robust to this low nutrition is that they are both easier to manage during the mating period and are genetically more fertile.

Optimal selection strategies on body weight changes to increase resilience depend on the genetic correlations with reproduction and are dependent on age. Index selection could be used to minimize undesired effects on total weaning weight and number of lambs born. This means that Australian sheep farmers and breeders can select for body weight change to make adult ewes more robust to uncertain feed supply and increase reproduction simultaneously.

Conclusion

Body weight change during mating period, pregnancy, and lactation had significant genetic correlations with number of lambs weaned and total birth weight. These genetic correlations are caused by different strengths of genetic correlations between body weights and reproduction. The interpretation of the genetic correlations implies gaining weight during certain stages of reproduction will affect how many lambs are weaned and the total weight of lambs born.

The direction of the genetic correlations mostly coincided with the energy requirements of the ewes and the stage of maturity of the ewes. Body weight change during mating period was most important for 2-yr-old ewes, which were still growing to maturity and required energy during mating period to get pregnant. Body weight change during pregnancy was more important for 3-yr-old ewes, which gave birth to and weaned more lambs and required more energy at the end of pregnancy and during lactation.

Therefore, optimized selection strategies on body weight changes to increase resilience will depend on the genetic correlations with reproduction and are dependent on age.

Appendix I. Comparing genetic correlations between BW change and birth and wean weight traits with and without fixed effects for number lambs born and reared in current year and previous year. Correlations are forages 2, 3, and 4 with standard errors in parentheses. Correlations in bold are significantly larger than 0.

Weight change trait[2]	Birth and wean weight traits[1]			
	TBW		TWW	
	Without	With	Without	With
Age 2				
ΔWTpreg	**0.33 (0.17)**	**0.34 (0.17)**	0.24 (0.20)	0.26 (0.20)
ΔWTlact	−0.15 (0.13)	−0.15 (0.13)	−0.10 (0.14)	−0.10 (0.14)
Age 3				
ΔWTpreg	0.21 (0.19)	0.27 (0.19)	0.16 (0.21)	0.15 (0.21)
ΔWTlact	−0.09 (0.16)	0.01 (0.17)	0.06 (0.18)	0.05 (0.19)
Age 4				
ΔWTpreg	−0.07 (0.22)	−0.07 (0.23)	−0.22 (0.21)	−0.21 (0.22)
ΔWTlact	**−0.42 (0.20)**	−0.33 (0.19)	0.00 (0.20)	0.05 (0.19)

[1]TBW = total weight of lambs born; TWW = total weight of lambs weaned.

[2]ΔWTmate = change in BW during mating for all ewes that were mated; ΔWTpreg = change in BW during pregnancy for ewes that got pregnant; ΔWTlact = change in BW during lactation for ewes that reared lambs.

Appendix II. Comparing genetic correlations between BW change and number lambs born and weaned traits with and without fixed effects for number lambs born and reared in current year and previous year. Correlations are forages 2, 3, and 4 with standard errors in parentheses. Correlations in bold are significantly larger than 0.

Weight change trait[2]	Number born and weaned traits[1]			
	NLB		NLW	
	Without	With	Without	With
Age 2				
ΔWTpreg	−0.34 (0.17)	−0.22 (0.19)	**−0.49 (0.19)**	−0.42 (0.19)
ΔWTlact	−0.08 (0.14)	−0.09 (0.14)	0.00 (0.16)	0.09 (0.16)
Age 3				
ΔWTpreg	0.15 (0.24)	0.25 (0.24)	0.53 (0.27)	0.53 (0.26)
ΔWTlact	−0.35 (0.18)	−0.32 (0.19)	−0.46 (0.20)	−0.37 (0.24)
Age 4				
ΔWTpreg	−0.15 (0.25)	−0.02 (0.27)	−0.21 (0.25)	−0.13 (0.26)
ΔWTlact	−0.21 (0.22)	0.06 (0.23)	−0.20 (0.22)	0.06 (0.22)

[1]NLB = number of lambs born; NLW = total number of lambs weaned.

[2]ΔWTmate = change in BW during mating for all ewes that were mated; ΔWTpreg = change in BW during pregnancy for ewes that got pregnant; ΔWTlact = change in BW during lactation for ewes that reared lambs.

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