

REVISITING TOTAL WEANING WEIGHT AS A SELECTION CRITERION

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SUMMARY

Data from a single prolific Merino flock (N=10705 joining records) recorded over 10 years were used to estimate genetic parameters for annual total weight weaned (TWW) of ewes which weaned lambs (N=8615), treated as a ewe trait, and the accompanying reproductive traits. TWW was the sum of individual weights of weaned lambs to birth ewe. An alternative trait definition included ewes which lambled and lost, which received zero trait values (TWW0, N=9509). Both TWW and TWW0 were lowly heritable (range h^2 : 0.06-0.11). Most of the phenotypic variation in these traits resulted from variation in the number of lambs weaned. Trait definition significantly influenced both the observable variation in the ewe weaning weight traits (eg. TWW vs TWW0) and correlations with reproductive traits. Because total weight weaned traits combine direct and maternal effects, and multiple non-genetic sources of variation, prediction of response to selection for total weight weaned and its components depends on the trait definition used and accompanying population characteristics and genetic parameters. We conclude that selection on an index which combines breeding values for reproductive performance, and both direct and maternal contributions to weaning weight traits, should be considered to improve ewe productivity in a more predictable manner under dual purpose breeding goals. This index is provided by Sheep Genetics, which also appropriately analyses individual animal reproductive and weight data while accounting for systematic effects and multiple records.

INTRODUCTION

Total lamb weight weaned per ewe joined has been proposed as a simple selection criterion for increasing reproduction and ewe productivity in dual purpose sheep (Snowder and Fogarty 2009). Total lamb weight weaned can reflect the full complement (or a subset) of traits important to ewe productivity, such as conception, ewe survival, litter size and lamb survival, along with the ewe's maternal contributions (genetic and non-genetic) to lamb weaning weight(s). However, lamb weaning weights are also influenced by genes of the lamb (the direct genetic effect), half of which were received from the sire. Individual lamb weaning weights are also significantly influenced by a number of non-genetic factors, such as season, age of dam, birth and rear type, lamb gender, and weaning age (Ch'ang and Rae 1961). Therefore, trait values for total weight weaned combine many sources of variation, several of which are non-genetic in origin. In this study we estimated parameters for weaning weight traits defined as traits of the ewe in a prolific Merino population, particularly with respect to illustrating the effect of using alternative trait definitions and correction for non-genetic effects, to investigate potential implications of using a complex selection criterion such as total lamb weight weaned.

MATERIALS AND METHODS

Data were obtained from a prolific (high fertility, high litter size) Merino population recorded over 10 years for reproductive performance, as described in Bunter *et al.* (2014). Ewes with reproductive records (N=7457) were daughters of 308 sires and 3540 dams. A subset of individual lamb weaning weights was obtained over 8 years. Lambs recorded with weaning weights were progeny of 4197 ewes and 136 service sires.

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Trait definitions. Reproductive traits for ewes included fertility (FERT), the number of lambs born (NLB) and weaned (NLW) per ewe joined, along with litter size at birth (LSIZE) and at weaning (LSIZEW) for lambing ewes. Weaning weight traits were defined as the average (AVWW) and total weaning weight (TWW) calculated annually for each ewe from weaning weight records on their lambs. For comparison, ewes which lambing but failed to wean a lamb had records augmented with trait values of zero (AVWW0, TWW0). Infertile ewes which did not lamb within a year had (zero) records for FERT, NLB and NLW only.

Models for analyses. All traits were treated as repeated measures of the ewe under an animal model, with additional variation due to service sire effects (σ^2_s). The additive direct genetic contribution to lamb weaning weight was approximated as $4\sigma^2_s/\sigma^2_p$ using parameters for AVWW. Systematic effects for ewe reproductive traits included year (10 levels) combined with lambing contemporary group (CGP: 30 levels), with CGP defining conception method (AI vs natural), ewe age group (3 levels) and breeder defined management groups. Models for weaning weight traits included year (8 levels) and weaning CGP (58 levels), where CGP included ewe age group and breeder defined management groups for weaning traits. Parameters were first estimated in univariate analyses using models without any covariates. Litter size at lambing, the number of lambs weaned and weaning age were then added as linear covariates for weaning weight traits (AVWW and TWW) for comparison. For zero augmented traits (eg TWW0 and AVWW0) no weaning contemporary group was defined and the covariate for lamb age at weaning was excluded from models for analyses. The relative contributions of each covariate to phenotypes for AVWW and TWW were approximated as the squared correlation between the weaning weight trait and each covariate, calculated as $(b \cdot SD_X / SD_Y)^2$, where b is the partial regression coefficient, SD_X and SD_Y are the SD of each covariate (X) and the dependent trait (Y), with both X and Y pre-adjusted for year-CGP effects. Correlations between specific traits were estimated from a series of bivariate analyses using ASReml (Gilmour *et al.* 2006), excluding all covariates from models for analyses.

RESULTS AND DISCUSSION

Ewe average weaning weight of lambs at approximately 107 days of age was 25.6 kg (Table 1). Total weaning weight averaged 34.3 kg and was highly variable (CV=32%) relative to AVWW (CV=16%). Mean values decreased, while phenotypic variance and CV for both traits increased when the data were augmented for ewes which lambing and lost (ie 0 kg weight weaned).

Parameter estimates. Heritability estimates were low and close to expectation for ewe reproductive traits. Variation due to service sire (σ^2_s) was significant for FERT but not litter size. Direct heritability for lamb weaning weight (as calculated from σ^2_s) was moderate regardless of litter size: 0.23 ± 0.04 estimated for single born lambs versus 0.21 ± 0.04 across all lambs weaned. Direct heritability was lower than the 0.29 ± 0.01 reported by Safari *et al.* (2007) from a more diverse Merino population. Variance due to the permanent environmental effect of the ewe was similar across these studies (0.04, derived from values in Table 1, vs 0.05). In our analyses, when service sire was not fitted in models for analyses, service sire variance was mostly repartitioned to the residual variance (not presented).

Parameter estimates for AVWW ($h^2=0.10 \pm 0.02$, $pe^2=0.04$) were relatively low. The expectation for component(s) contributing to the calculated ewe AVWW is $1/4\sigma^2_a + \sigma^2_m + \sigma_{am} + \sigma^2_c$, where: σ^2_a is the additive genetic variance (direct effect), σ^2_m is the additive maternal genetic variance, σ_{am} is the direct-maternal covariance, and σ^2_c is the common litter effect. Using parameters for individual lamb weaning weights estimated by Safari *et al.* (2007), assuming $\sigma_{am}=0$ and accurate partitioning for σ^2_c , the heritability for AVWW could be approximated as $0.25 \times 0.26 + 0.10 = 0.17$, which is higher than the value of 0.10 ± 0.02 obtained here. Compared to phenotypic variance of individual lamb weaning weights, the phenotypic variance of AVWW is also reduced. Heritability and repeatability for TWW were similar to estimates for

AVWW, but the phenotypic variance was approximately doubled. Each TWW record is equivalent to AVWW $\times n$, where n was the number of progeny recorded at weaning, but additional variation is also expected due to ewe genetic contributions to n and (co)variances between the reproductive and weaning weight traits. Relative to AVWW and TWW, phenotypic variances were greatly increased by the zero enrichment of AVWW0 and TWW0. However, contemporary groups and a covariate for weaning age cannot sensibly be applied across values for these trait definitions.

Table 1: Raw data characteristics, along with estimates of heritability (h^2), repeatability (r), and service sire (σ^2_s), residual (σ^2_e) and phenotypic (σ^2_p) variances from univariate analyses (*line 1: no covariates; line 2: covariates included, with % reduction of variance in brackets)

Trait	N	Mean (SD)	h^2	r	σ^2_s	σ^2_e	σ^2_p
FERT	10705	0.95 (0.22)	0.02 \pm 0.01	0.03 \pm 0.01	0.05 \pm 0.01	0.042	0.046
NLB	10705	1.58 (0.69)	0.07 \pm 0.01	0.13 \pm 0.01	0.02 \pm 0.01	0.381	0.450
NLW	10705	1.18 (0.66)	0.03 \pm 0.01	0.09 \pm 0.01	0.02 \pm 0.00	0.361	0.406
LSIZE	10139	1.66 (0.60)	0.10 \pm 0.02	0.15 \pm 0.01	0.01 \pm 0.00	0.289	0.347
LSIZEW	10139	1.28 (0.63)	0.03 \pm 0.01	0.10 \pm 0.01	0.01 \pm 0.00	0.334	0.374
AVWW	8615	25.6 (4.20)	0.08 \pm 0.02	0.13 \pm 0.01	0.05 \pm 0.01	14.3	17.4
			0.10 \pm 0.02	0.14 \pm 0.01	0.05 \pm 0.01	9.55 (34)	11.9 (32)
AVWW0	9509	23.2 (8.47)	0.06 \pm 0.01	0.14 \pm 0.02	0.02 \pm 0.00	58.5	69.7
			0.04 \pm 0.01	0.07 \pm 0.01	0.02 \pm 0.00	44.5 (24)	49.0 (30)
TWW	8615	34.3 (11.0)	0.06 \pm 0.01	0.11 \pm 0.01	0.04 \pm 0.01	101	119
			0.11 \pm 0.02	0.12 \pm 0.01	0.05 \pm 0.01	19.9 (80)	25.4 (79)
TWW0	9509	31.1 (14.5)	0.05 \pm 0.01	0.12 \pm 0.01	0.02 \pm 0.00	173	199
			0.08 \pm 0.01	0.12 \pm 0.01	0.07 \pm 0.01	20.3 (88)	24.9 (87)

$h^2 = \sigma^2_a / \sigma^2_p$ and $r = (\sigma^2_a + \sigma^2_{pe}) / \sigma^2_p$, where σ^2_a is the additive genetic variance and σ^2_{pe} is variance due to permanent environmental effects of the ewe; *covariates relevant for ewe weaning weight traits only

The importance of weaning age, litter size and lambs weaned. Models without covariates explained <5% of the variation in all ewe weaning weight traits. When all covariates were included in the models for analyses, phenotypic variances were greatly reduced: by 30-32% for AVWW and AVWW0 and by 79-87% for TWW and TWW0 (Table 1). Variation in weaning age and litter size at birth explained about 13-15% each of the variation in AVWW. The number of lambs weaned explained the bulk of variation in TWW ($r^2 \sim 82\%$) (results not tabulated). Birth-rearing class and weaning age are the main factors affecting individual weaning weights of lambs (Ch'ang and Rae 1961) and consequently traits derived from lamb weights for their dams. Since weaning dates are generally fixed, variation in weaning age mostly resulted from how early ewes conceived in the joining period. In these data, heritability from an additional analysis for the number of days until lambing, after the commencement of lambing, was only 0.03 \pm 0.01 ($r = 0.05 \pm 0.01$). Therefore, for accurate comparisons amongst ewes, ewe weaning weight traits should also be corrected for lamb age at weaning.

Correlations between reproductive and weaning weight traits. Correlations between traits at the genetic and phenotypic level indicate that fertility is favourably correlated with all weaning weight traits (Table 2). Both TWW and TWW0 also had consistently positive correlations with reproductive traits (NLB, NLW, LSIZE and LSIZEW), being larger in magnitude for reproductive traits representing only lambs alive at weaning. This is partly because only weaned lambs generate non-zero weaning weight records. In contrast, some unfavourable correlations were evident between the reproductive traits and AVWW or AVWW0, demonstrating that individual lamb weights are decreased for lambs weaned in larger litters. Genetic correlations between AVWW and TWW or AVWW0 and TWW0 were 0.61 \pm 0.04 and 0.80 \pm 0.07 (not tabulated). These results

suggest overall that selection for (unadjusted) TWW would most strongly favour litter size at weaning in this prolific Merino flock, thereby increasing total weight weaned, but individual weaning weights would suffer. The latter has implications for lamb marketability at weaning and/or post-weaning survival of lambs.

Table 2. Additive genetic (ra) and phenotypic (rp) correlations between reproductive and weight traits (ne: not estimable)

Trait	Correlation	AVWW	AVWW0	TWW	TWW0
FERT*	ra	0.09±0.17	0.81±0.21	0.10±0.17	0.22±0.18
NLB	ra	-0.20±0.14	-0.32±0.13	0.51±0.11	0.18±0.14
	rp	-0.38±0.01	-0.18±0.01	0.53±0.00	0.36±0.00
NLW	ra	0.12±0.21	0.68±0.12	0.89±0.04	0.92±0.03
	rp	-0.52±0.01	0.42±0.01	0.93±0.00	0.94±0.00
LSIZE	ra	-0.22±0.12	-0.45±0.11	0.51±0.10	0.09±0.14
	rp	-0.34±0.01	-0.21±0.06	0.48±0.01	0.31±0.00
LSIZEW	ra	0.23±0.24	0.57±0.15	0.88±0.06	0.80±0.07
	rp	-0.53±0.07	0.39±0.01	0.87±0.00	0.84±0.00

*residual and therefore phenotypic correlations are not estimable

While simple in concept, total weaning weight is an exceptionally complex trait. Trait values for ewes represent both direct and maternal effects, correlations between traits, non-genetic factors influencing both ewe and lamb performance, the possibility of unaccounted for environmental covariance between dam and offspring, and a potentially high degree of variance inflation due to inclusion of somewhat arbitrary zero values. This can create quite large fluctuations in genetic parameters (eg see correlations between LSIZE and TWW or TWW0, which are affected by lamb survival). Therefore, choice of trait definition and the ability to adjust for systematic effects will impact on the expected response to selection for total weaning weight, and correlated response in the sub-traits of economic importance. Studies to date have typically not made these calculations.

CONCLUSION

Selection for total weaning weight is simple at face value, but the response to selection for contributing traits will vary depending on population characteristics, the trait definition used, the corrections for non-genetic effects applied and therefore underlying genetic parameters. Further work is required to evaluate whether index selection combining ewe reproductive traits with both direct and maternal components for weaning weight, as is included in the existing Sheep Genetics dual purpose Merino index, delivers a more optimal and predictable improvement in response to selection for ewe reproductive traits and productivity, and individual lamb weaning weights, when compared to selection based on TWW alone.

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