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# Genetic analysis of litter size in Targhee, Suffolk, and Polypay sheep<sup>1</sup>

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**ABSTRACT:** Data on litter size, weaning weights at 60, 90, and 120 d, postweaning gains from weaning to 120 or 365 d of age, fleece weight, and fiber diameter from Targhee, Suffolk, and Polypay flocks participating in the U.S. National Sheep Improvement Program were used to estimate genetic parameters for litter size and genetic relationships between early-life traits and future litter size. Records on 7,591 lambings by 3,131 Targhee ewes, 10,295 lambings by 5,038 Suffolk ewes, and 6,061 lambings by 2,709 Polypay ewes were used. Heritability estimates for litter size ranged from .09 to .11 across breeds; repeatability ranged from .09 to .13. Additive genetic effects on litter size were generally positively, and occasionally significantly, correlated with animal additive genetic effects on weaning weights

and postweaning gains. Genetic correlations ( $r_a$ ) ranged from .08 to .48 in Targhee and from .17 to .43 in Suffolk but were close to 0 in Polypay (-.14 to .09). Additive maternal effects on weaning weight were positively associated with litter size in Suffolk and Polypay; this correlation was negative (-.23 to -.35), but not significant, in Targhee. Fleece weight was not strongly associated with litter size; ( $r_a = -.09$  to .21). However, fiber diameter had a significant undesirable correlation with litter size (.30) in Targhee. Estimates of phenotypic correlations of litter size with early-life traits were uniformly small (-.02 to .08). Thus, although occasional genetic antagonisms between litter size and early-life traits were observed in these data, none appeared large enough to prevent simultaneous genetic improvement in both traits.

Key Words: Genetic Correlation, Growth, Heritability, Reproduction, Sheep

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## Introduction

Genetic improvement in reproduction, growth, and fleece traits are major goals in sheep breeding. Dickerson (1970) pointed out that efficiency of livestock production is controlled by reproduction, female production, and growth of offspring and concluded that improvements in reproduction were particularly likely to increase efficiency of sheep production. Among reproductive traits, litter size (number of lambs born per ewe lambing) has most often been used as a selection criterion. Litter size is relatively easy to measure and report, and heritability estimates for litter size are generally higher than those of other reproductive traits such as fertility or lamb survival.

Fogarty (1995), in a summary of genetic parameter estimates for sheep performance traits, reported that

the weighted mean heritability estimate for litter size was .10 but the mean coefficient of variation for litter size was high (36%), indicating potential for genetic improvement.

Most performance recording programs for sheep have focused on growth and fleece characteristics because of their relatively high heritabilities and greater ease of measurement. However, failure to explicitly consider reproductive traits is negligent because of their economic importance and because of potential negative relationships with other performance traits. The U.S. National Sheep Improvement Program (NSIP) records litter size and recently implemented an across-flock, multiple-trait genetic evaluation system (Notter, 1998b). Notter and Hough (1997) and Notter (1998a) estimated genetic parameters for growth and fleece traits for this system. However, because of different data structure (i.e., repeated records), litter size is currently still being evaluated in a single-trait genetic analysis. The objective of this study, was, therefore, to estimate genetic parameters for litter size and study genetic relationships between litter size and other traits in the Targhee, Suffolk, and Polypay breeds.

## Materials and Methods

*Data.* Data on weaning weights, postweaning gains, fleece traits, and litter size were obtained from NSIP.

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**Table 1.** Characteristics of Targhee data

Item	Trait <sup>a</sup>						
	WW60	WW120	PWG	YRG	FWT	FD	LS
No. of records	4,650	7,428	1,406	3,241	5,471	3,908	7,591
No. of animals	4,650	7,428	1,406	3,241	5,471	3,908	3,131
No. of sires	96	148	22	66	311	225	335
No. of dams	1,654	2,621	1,406	1,432	2,841	2,136	2,167
No. of litters	3,620	5,519	1,216	2,881	4,800	3,471	2,747
No. of animals with LS records	510	984	242	408	2,269	1,459	3,131
No. of animals with $\geq 2$ LS records	328	638	195	265	1,481	855	1,961
No. of contemporary groups	117	81	55	68	164	113	182
Mean	25.6	36.8	18.0	32.3	3.8	22.2	1.69

<sup>a</sup>WW60 is 60-d weaning weight, WW120 is 120-d weaning weight, PWG is 60- to 120-d postweaning gain, YRG is 120- to 365-d postweaning gain, FWT is fleece weight, FD is fiber diameter, and LS is litter size. All weights are in kilograms; FD is in micrometers.

Data were collected between 1984 and 1996. Twenty Targhee, 125 Suffolk, and 53 Polypay flocks from throughout the United States were represented.

Characteristics of the data are shown in Tables 1, 2, and 3. For litter size, 7,591 Targhee records from 3,131 ewes, 10,295 Suffolk records from 5,038 ewes, and 6,061 Polypay records from 2,709 ewes were available. Litter size records were adjusted to an adult (4-yr-old) ewe basis before analysis using multiplicative adjustment factors (NSIP, 1986). Mean adjusted litter sizes were 1.69 for Targhee, 1.95 for Suffolk, and 2.09 for Polypay. Coefficients of variation for litter size were characteristically high at 34 to 35%.

Background and rationale for the choice of early-life traits in each breed were given by Notter and Hough (1997) and Notter (1998a). Briefly, most Suffolk and Polypay lambs were produced in relatively intensive management systems, weaned at 60 or 90 d, and evaluated for postweaning gain for 30 to 60 d after weaning. Resulting performance traits were 60- or 90-d weaning weights and 60-d total postweaning gain. Targhee lambs were more often produced under extensive conditions, weaned at 120 d, and then evaluated for growth to 1 yr of age. However, a significant minority of Targhee records came from semi-intensive management systems similar to those of the Suffolk and Polypay, and several Targhee breeders recorded 60-d preweaning

weights (which were included as weaning weights in these analyses), even though lambs were not weaned until 120 d. Thus, growth traits for Targhee included 60- and 120-d weaning weights, postweaning gain, and yearling gain from 120 to 365 d. Typically, Targhee lambs were evaluated for either 60-d weaning weight and postweaning gain or for 120-d weaning weight and yearling gain, although a number of lambs had records for 60- and 120-d weaning weights and yearling gain.

Fleece weights were reported only for Targhee and Polypay, and fiber diameter records were only available for Targhee. Fleece data in NSIP are to be reported only for yearling fleeces, but at the time of enrollment breeders may also report a single set of fleece data for older ewes. See Notter and Hough (1997) for a discussion of NSIP fleece traits.

*Statistical Analysis.* All analyses were conducted using the multiple-trait, derivative-free REML program of Boldman et al. (1993). Genetic parameters for litter size were initially estimated for each breed in single-trait analyses using a repeated-measures model that included a fixed effect of contemporary group and random animal additive genetic and permanent environmental effects. Animal additive effects were assumed to have covariance matrix  $\mathbf{A}\sigma_a^2$ , where  $\sigma_a^2$  is the additive variance for litter size and  $\mathbf{A}$  is the numerator relationship matrix among animals with litter size records and

**Table 2.** Characteristics of Suffolk data

Item	Trait <sup>a</sup>			
	WW60	WW90	PWG	LS
No. of records	12,746	2,853	5,621	10,295
No. of animals	12,746	2,853	5,621	5,038
No. of sires	604	171	384	1,182
No. of dams	4,276	1,221	2,362	3,575
No. of litters	8,251	1,850	4,725	4,386
No. of animals with LS records	1,546	327	926	5,038
No. of animals with $\geq 2$ LS records	890	166	519	2,662
No. of contemporary groups	648	165	722	658
Mean	32.2	47.2	23.5	1.95

<sup>a</sup>WW90 is 90-d weaning weight (kg). See Table 1 for other abbreviations.

**Table 3.** Characteristics of Polypay data

Item	Trait <sup>a</sup>				
	WW60	WW90	PWG	FWT	LS
No. of records	6,561	1,690	3,046	1,099	6,061
No. of animals	6,561	1,690	3,046	1,099	2,709
No. of sires	188	54	95	128	424
No. of dams	2,304	695	1,113	713	1,892
No. of litters	3,988	1,095	2,470	921	2,289
No. of animals with LS records	536	298	265	647	2,709
No. of animals with $\geq 2$ LS records	263	188	139	422	1,620
No. of contemporary groups	274	80	240	74	403
Mean	26.1	29.8	19.4	4.2	2.09

<sup>a</sup>WW90 is 90-d weaning weight (kg). See Table 1 for other abbreviations.

their connecting relatives in the NSIP data base. Animal permanent environment effects were assumed independent with variance  $\sigma_{pe-a}^2$ .

In order to form contemporary groups, the age-adjusted litter size records within each flock were first sorted by lambing date. Then, beginning with the first lambing date, all ewes within a flock that lambed within a 30-d period were placed in the same contemporary group. Any contemporary group that contained only one record was eliminated from the analysis.

Following completion of the univariate litter size analyses, a series of bivariate analyses was conducted for each breed, pairing litter size with each of the other traits shown in Tables 1, 2, and 3. The repeated-measures animal model used for litter size in single-trait analyses was also used in bivariate analyses. Weaning weights were adjusted for type of birth and rearing, age of dam, and lamb sex before analysis using multiplicative adjustment factors (NSIP, 1986). The model for weaning weight included a fixed effect of contemporary group and random animal additive genetic, maternal additive genetic, and maternal permanent environmental effects. Animal and maternal additive genetic effects were assumed to have joint covariance matrix  $\mathbf{G} \otimes \mathbf{A}$ , where  $\mathbf{G}$  is a  $2 \times 2$  genetic covariance matrix with animal and maternal additive genetic variance ( $\sigma_a^2$  and  $\sigma_m^2$ , respectively) on the diagonals and the animal-maternal additive covariance ( $\sigma_{am}$ ) on the off-diagonals. The symbol  $\otimes$  denotes the direct product matrix operator. Maternal permanent environmental effects were assumed independent with variance  $\sigma_{pe-m}^2$ .

For postweaning gains and fleece traits, the weaning weight model was simplified by excluding additive maternal genetic and maternal permanent environmental effects (Notter and Hough, 1997; Notter, 1998a). Fleece weight was adjusted for age of the animal or for shearing interval before analysis (Notter and Hough, 1997). No adjustments were applied to postweaning gain or fiber diameter. Contemporary group definitions for weaning weights, postweaning gains, and fleece traits were likewise given by Notter and Hough (1997).

In addition to the animal-maternal additive covariances for weaning weight, the initial bivariate models

also estimated covariances between animal additive effects on litter size and each of the other traits. Covariances between animal additive effects on litter size and maternal additive effects on weaning weights were also estimated. The most detailed bivariate models thus contained 10 (co)variance components. Covariance components were tested for significance using likelihood ratio tests to compare the full model to reduced models in which these covariance components were individually or jointly set to zero. Tests of significance of variance component estimates were presented by Notter and Hough (1997) and Notter (1998a) and were not repeated here.

The software used to analyze the data did not permit direct estimation of covariances between residual environmental effects on early-life traits and litter size. However, environmental circumstances imposed during growth and development may affect future litter sizes. To assess these covariances, bivariate models were reparameterized by replacing residual effects on early-life traits with a vector of independent animal permanent environmental effects. This equivalent parameterization allowed estimation of covariances between residual environmental effects on early-life traits and subsequent permanent environmental effects on litter size. Results of this model will be discussed as supplemental to the initial bivariate models.

## Results

### Univariate Analyses

Univariate analyses (Table 4) yielded estimates of heritability ( $h^2$ ) for litter size that ranged from .09 to .11 ( $P < .01$  for all breeds). Estimates of phenotypic variance ( $\sigma_P^2$ ) increased with mean litter size, from .33 in Targhee to .46 in Suffolk and .51 in Polypay. Estimates of permanent environmental variance were small and not significant, ranging, as a proportion of  $\sigma_P^2$ , from .00 in Suffolk to .02 in Targhee and .04 in Polypay. Resulting estimates of repeatability for litter size were .13 for Targhee and Polypay and .09 for Suffolk. The estimate of the permanent environmental

**Table 4.** Genetic parameter estimates for litter size from univariate analyses

Item <sup>a</sup>	Breed		
	Targhee	Suffolk	Polypay
$h^2$	.11**	.09**	.09**
$c_a^2$	.02	.00	.04†
$\sigma_p^2$	.33	.46	.51

<sup>a</sup> $h^2$  is heritability,  $\sigma_p^2$  is phenotypic variance, and  $c_a^2$  is the ratio of animal permanent environmental variance to phenotypic variance ( $\sigma_{pe}^2 / \sigma_p^2$ ).

† $P < .10$ .

\*\* $P < .01$ .

variance in Suffolk consistently converged to zero in both univariate and preliminary bivariate analyses, and effects of permanent environment on litter size were therefore removed from bivariate models for Suffolk.

*Bivariate Analyses*

*Targhee.* For Targhee (Table 5), estimates of  $h^2$  and  $m^2$  for 60-d weaning weight were .14 and .22, respectively, and were associated with a large and significant negative correlation between direct and maternal additive effects ( $r_{am}$ ) of  $-.90$ . For 120-d weaning weight,

estimates of  $h^2$  and  $m^2$  were .16 and .06, respectively, but the estimate of  $r_{am}$  was only  $-.10$  ( $P > .10$ ). Estimates of correlations between additive direct effects on litter size and weaning weight ( $r_a$ ) were positive (.22 at 60 d and .48 at 120 d) but significant only at 120 d. Corresponding estimates of the correlation between additive direct effects on litter size and additive maternal effects on weaning weight ( $r_m$ ) were negative ( $-.23$  at 60 d and  $-.35$  at 120 d) but not significant.

Estimates of  $h^2$  for postweaning and yearling gains were .27 and .19, respectively. Additive correlations with litter size were positive for both (.44 for postweaning and .08 for yearling gains) but approached significance ( $P < .10$ ) only for postweaning gain. The  $h^2$  estimate for fleece weight was .41, and fleece weight had a small and nonsignificant additive correlation of  $-.09$  with litter size. For fiber diameter,  $h^2$  was .50 and the additive correlation with litter size was positive and unfavorable (.30;  $P < .01$ ).

Correlations between residual environmental effects on early-life traits and permanent environmental effects on litter size ( $r_{pe}$ ), derived from supplemental bivariate models, were small and not significant ( $P > .10$ ) for 60-d weaning weight, postweaning gain, and fiber diameter. Genetic parameter estimates for these traits in Table 5 were essentially unaffected by including  $r_{pe}$ . For other traits,  $r_{pe}$  was .39 ( $P < .10$ ) for 120-d weaning weight. The estimate of  $r_a$  between 120-d weaning

**Table 5.** Genetic parameter estimates from bivariate analyses for Targhee<sup>a</sup>

Item <sup>b</sup>	Early-life trait <sup>c</sup>					
	WW60	WW120	PWG	YRG	FWT	FD, $\mu\text{m}$
$h_x^2$	.14	.16	.27	.19	.41	.50
$m_x^2$	.22	.06				
$r_{am}$	$-.90^{**}$	$-.10$				
$c_m^2$	.10	.08				
$e_x^2$	.70	.71	.73	.81	.59	.50
$h_l^2$	.11	.11	.11	.11	.11	.11
$c_a^2$	.01	.02	.02	.02	.02	.02
$e_l^2$	.88	.88	.88	.88	.88	.88
$r_a$	.22	.48*	.44†	.08	$-.09$	.30**
$r_m$	$-.23$	$-.35$				
$r_p$	.01	.05	.07	.01	$-.02$	.07
$\sigma_{p_x}^2$	17.23	32.44	13.36	40.96	.34	2.00
$\sigma_{p_l}^2$	.33	.35	.33	.33	.33	.33

<sup>a</sup>Tests of significance were performed only for covariance component estimates. See Notter and Hough (1997) and Notter (1998a) for tests of significance of variance component estimates.

<sup>b</sup> $h^2$  = heritability,  $m^2$  = maternal heritability ( $\sigma_m^2 / \sigma_p^2$ ),  $r_{am}$  = the animal-maternal additive genetic correlation (weaning weights only),  $c_m^2$  = the ratio of maternal permanent environmental variance to  $\sigma_p^2$ ,  $e^2$  = the ratio of residual variance to  $\sigma_p^2$ ,  $c_a^2$  = the ratio of animal permanent environmental variance to  $\sigma_p^2$  (litter size only),  $r_a$  = the animal additive genetic correlation between early-life traits and litter size,  $r_m$  = the correlation between maternal additive effects on early-life traits and animal additive effects on litter size,  $r_p$  = the phenotypic correlation, and  $\sigma_p^2$  = the phenotypic variance. Subscripts  $x$  and  $l$  denote early-life traits and litter size, respectively.

<sup>c</sup>See Table 1 for definitions.

† $P < .10$ .

\* $P < .05$ .

\*\* $P < .01$ .

**Table 6.** Genetic parameter estimates from bivariate analyses for Suffolk<sup>a</sup>

Item <sup>b</sup>	Early-life trait <sup>c</sup>		
	WW60	WW90	PWG
$h_x^2$	.19	.13	.17
$m_x^2$	.06	.04	
$r_{am}$	-.33 <sup>d</sup>	.25	
$c_m^2$	.11	.17	
$e_x^2$	.68	.64	.83
$h_f^2$	.10	.09	.09
$c_a^2$	.00	.00	.00
$e_f^2$	.90	.91	.91
$r_a$	.38*	.43 <sup>e</sup>	.17
$r_m$	.32 <sup>d</sup>	.98**	
$r_p$	.06	.08	.02
$\sigma_{P_x}^2$	30.03	50.61	28.52
$\sigma_{P_1}^2$	.46	.46	.46

<sup>a</sup>Tests of significance were performed only for covariance component estimates. See Notter and Hough (1997) and Notter (1998a) for tests of significance of variance component estimates.

<sup>b</sup>See Table 5 for definitions.

<sup>c</sup>See Table 2 for definitions.

<sup>d</sup>No effect of removing  $r_m$  or  $r_{am}$  alone but removal of both effects produced a significant reduction in likelihood.

<sup>e</sup>Removal of  $r_{am}$  from the model resulted in a significant effect of  $r_a$ .

\* $P < .05$ .

\*\* $P < .01$ .

weight and litter size was reduced to .31 ( $P > .10$ ), and the estimate of  $r_m$  was reduced to  $-.26$  by inclusion of  $r_{pe}$  in the model. Thus, a positive association may exist between 120-d weaning weight and litter size, but its source could not be clearly identified. For fleece weight,  $r_{pe}$  was large and positive (.66;  $P < .01$ ). The estimate of  $r_a$  between fleece weight and litter size was  $-.03$  with  $r_{pe}$  in the model. For yearling gain, the estimate of  $r_{pe}$  was  $-.98$  ( $P < .01$ ); the associated estimate of  $r_a$  increased to .18 but remained nonsignificant.

Estimates of phenotypic correlations ( $r_p$ ) between litter size and other traits were uniformly small in Targhee, ranging from  $-.02$  for fleece weight to .07 for postweaning gain and fiber diameter.

**Suffolk.** In Suffolk (Table 6), positive estimates of  $r_a$  between weaning weights and litter size were observed at both 60 (.38) and 90 d (.43), but  $r_a$  was significant only at 60 d. Associations involving maternal additive genetic effects on weaning weight were less consistent. At 60 d, the estimate of  $r_{am}$  was negative ( $-.33$ ) and the estimate of  $r_m$  was positive (.32); neither of these correlations was significant. However, removal of both maternal covariances from the model resulted in a significant reduction in likelihood, suggesting some association of maternal additive effects on weaning weight with direct additive effects on weaning weight and(or) litter size.

At 90 d, the estimate of  $r_{am}$  was positive (.25) but not significant. Estimates of  $r_a$  and  $r_m$  were both positive, but only the unrealistically large estimate of  $r_m = .98$

was significant. However, if  $r_m$  was removed from the model, the estimate of  $r_a$  became significant. These results suggest that a positive association exists between additive effects on litter size and genetic effects on weaning weight, but that this association could not be adequately partitioned with regard to its source (additive direct or maternal, or both) using these data.

The estimate of  $r_a$  between postweaning gain and litter size was positive (.17) but not significant. Estimated genetic relationships of litter size with weaning weights and postweaning gain in Suffolks were all thus favorable, although not all were significant. Estimates of  $r_p$  in Suffolk were positive but small, ranging from .02 for postweaning gain to .06 for 60-d weaning weight and .08 for 90-d weaning weight.

**Polypay.** For Polypay (Table 7), negative estimates of  $r_{am}$  were obtained for both 60- and 90-d weaning weights ( $-.55$  and  $-.69$ , respectively), but the estimate was not significant for 90-d weaning weight, primarily because of the small estimate of the additive maternal variance at 90 d ( $m^2 = .02$ ).

For weaning weights, estimates of  $r_a$  with litter size were small ( $-.14$  to .09) and not significant. Estimates of  $r_m$  were larger and consistently positive but were likewise not significant. The estimate of  $r_a$  for postweaning gain was very small ( $-.05$ ), whereas the estimate of  $r_a$  for fleece weight of .21 was positive but also not significant. Phenotypic correlations of litter size with early life traits were very small, ranging from  $-.01$  to .04.

Addition of an environmental covariance resulted in essentially no improvement in likelihood for 60- or 90-d weaning weight or postweaning gain. For fleece

**Table 7.** Genetic parameter estimates from bivariate analyses for Polypay<sup>a</sup>

Item <sup>b</sup>	Early-life trait <sup>c</sup>			
	WW60	WW90	PWG	FWT
$h_x^2$	.11	.10	.22	.44
$m_x^2$	.11	.02		
$r_{am}$	$-.55^*$	$-.69$		
$c_m^2$	.15	.22		
$e_x^2$	.69	.69	.78	.56
$h_f^2$	.09	.10	.09	.09
$c_a^2$	.04	.04	.04	.04
$e_f^2$	.87	.87	.87	.87
$r_a$	$-.14$	.09	$-.05$	.21
$r_m$	.21	.65		
$r_p$	$-.00$	.02	$-.01$	.04
$\sigma_{P_x}^2$	19.60	19.45	14.91	.53
$\sigma_{P_1}^2$	.51	.51	.51	.51

<sup>a</sup>Tests of significance were performed only for covariance component estimates. See Notter and Hough (1997) and Notter (1998a) for tests of significance of variance component estimates.

<sup>b</sup>See Table 5 for definitions.

<sup>c</sup>See Table 3 for definitions.

\* $P < .05$ .

weight, an estimate of  $r_{pe}$  of .45 was obtained ( $P < .10$ ), which was consistent with the estimate of .66 obtained in Targhee. Inclusion of  $r_{pe}$  in the model reduced the estimate of  $r_a$  for fleece weight to .03 and increased the estimate of  $r_p$  to .06.

### Discussion

Estimates of  $h^2$  for litter size in these data were consistent among breeds, ranging from .09 in Suffolk and Polypay to .11 in Targhee, and averaging .10. The estimates of  $h^2$  were likewise consistent with previously reported values. Fogarty (1995) summarized 53 reported estimates of  $h^2$  for litter size and obtained a mean estimate of .10 with a SD among estimates of .07. The mean coefficient of variation for litter size in those studies was 36%, which likewise corresponds well to values of 34% for Targhee and Polypay and 35% for Suffolk in our data. More recently, Al-Shorepy and Notter (1996) reported  $h^2$  estimates for litter size in fall and in combined fall and spring lambings of .10 and .05, respectively. Altarriba et al. (1998) obtained an estimate of  $h^2$  for litter size of  $.077 \pm .017$  in Rasa Aragonesa sheep using a threshold model, and Kominakis et al. (1998) reported an estimate of  $h^2$  for litter size of  $.06 \pm .03$  for Boutsico dairy sheep in Greece.

Estimates of repeatability of litter size in Targhee and Polypay of .13 also corresponded to previously reported estimates. Fogarty (1995) summarized 50 estimates of repeatability of litter size. The mean estimate was .14 with SD of .07. Altarriba et al. (1998) also reported an estimate of repeatability of .14 for litter size in Rasa Aragonesa sheep, and Al-Shorepy and Notter (1996) obtained estimates of repeatability of litter size of .11 and .14 in fall and in combined fall and spring lambings, respectively. In Suffolk, however, the estimate of the permanent environmental variance for litter size as a proportion of  $\sigma_p^2$  ( $c_a^2$ ) consistently converged to .00. This result can occur if a negative residual environmental correlation exists between litter size records in adjacent years, such that ewes with large litters in one year tend to produce smaller litters the next year, perhaps because of the stress imposed during gestation and lactation by the initial large litter.

The mean numbers of litter size records in our data were 2.42 for Targhee, 2.04 for Suffolk, and 2.24 for Polypay. The effect of a negative residual covariance between adjacent litter size records on the estimate of repeatability is maximized when there are only two records and declines as the number of records increases. As an example, we may model the phenotype for litter size in year  $i$  ( $P_i$ ) as  $P_i = G + PE + TE_i$ , where  $G$  and  $PE$  are additive direct and true permanent environmental effects on litter size, respectively, and  $TE_i$  is an annual residual effect on litter size. For example, let  $h^2 = .10$  and  $c_a^2 = .05$ , and let correlations among  $TE_i$  be  $-.05$  for adjacent years and  $.00$  for nonadjacent years. The resulting average correlation among  $P_i$  would then increase from .108 with two records to .122, .129, and

.133 with three, four, and five records, respectively. Although Suffolks had the fewest litter size records/ewe, the differences in mean number of records among breeds was not large enough to explain differences in estimates of  $c_a^2$ . These differences, if real, would have to also reflect biological differences among breeds. For these three breeds, litter size in young ewes is more similar to that of adult ewes in Suffolk than in Targhee or Polypay (Notter, 2000). These factors could predispose Suffolk ewes to an antagonistic relationship between litter sizes in adjacent years. However, one could postulate similar heightened liability to negative associations between residual effects on litter size in Polypay ewes in an accelerated lambing system, but such a relationship was not apparent.

These results, coupled with those reviewed by Fogarty (1995), support the contention that  $h^2$  for litter size is consistently close to .10 with a phenotypic coefficient of variation of approximately 35%. Estimates of repeatability of litter size seem generally consistent at .13 to .14, but results in Suffolk raise questions about the covariance structure of repeated litter size records. Further study of intercorrelations among adjacent and nonadjacent records, perhaps using time-series analysis, and consideration of effects of ewe age on patterns of association are needed.

These analyses provided little evidence for meaningful genetic antagonisms between early-life traits and subsequent litter sizes. At weaning, correlations between additive direct genetic effects on weaning weight and litter size were usually positive and often significant. The only exception was the estimate of  $r_a = -.14$  at 60 d in Polypay. Analla and Serradilla (1998) also reported positive estimates of  $r_a$  between litter size and lamb weight at 30 ( $.19 \pm .07$ ), 60 ( $.15 \pm .11$ ), and 90 d ( $.13 \pm .08$ ) in Spanish Merino sheep.

Additive maternal effects on weaning weight were positively correlated with additive effects on litter size in Suffolk and Polypay, but estimates of  $r_m$  were negative for Targhee ( $-.23$  at 60 d and  $-.35$  at 120 d). The total additive maternal contribution of a ewe to the weaning weight of her offspring is the sum of the additive maternal effect plus one-half the additive direct effect. Estimates of the correlation between this total additive maternal contribution to weaning weight and additive effects on litter size were  $-.21$  at 60 d and  $.04$  at 120 d for Targhee,  $.60$  at 60 d and  $.43$  at 90 d for Suffolk, and  $.17$  at 60 d and  $.85$  at 90 d for Polypay. Thus, only in Targhee lambs weaned at 60 d was there a suggestion that selection for total maternal effects on weaning weight might reduce litter size. It is perhaps reasonable that expression of high levels of both prolificacy and maternal ability to 60 d might be most difficult in a range breed. In Spanish Merino sheep, estimates of  $r_m$  between weight at 30, 60, and 90 d and litter size ranged from  $-.05$  to  $.03$  (Analla and Serradilla, 1998). Kominakis et al. (1998) reported an estimate of the additive direct correlation between litter size and actual milk yield of .13 in Boutsico dairy sheep.

Additive genetic correlations between postweaning gain (from either 60 to 120 or 120 to 365 d) and litter size ranged from  $-.05$  for postweaning gain in Polypay to  $.44$  ( $P < .10$ ) for postweaning gain in Targhee. Estimates of  $r_a$  for postweaning gain always had the same sign as estimates of  $r_a$  for 60-d weaning weight, indicating consistent genetic relationships between early growth and litter size within each breed. The estimate of  $r_a$  for yearling gain in Targhee was likewise consistent in sign with, but considerably smaller than, the estimate of  $r_a$  for 120-d weaning weight. Selection for rapid postweaning gain should thus have little impact on genetic merit for litter size.

Additive genetic correlations between fleece weight and litter size were negative, but small ( $-.09$ ), in Targhee and positive ( $.21$ ) in Polypay. Thus, selection for fleece weight is unlikely to have meaningful negative effects on litter size in either breed. An estimate of  $h^2$  for fleece weight in NSIP Polypay flocks has not been previously published, but the current estimate of  $.44$  was consistent with the estimate of  $.41$  obtained in Targhee (Notter and Hough, 1997) and slightly higher than the mean estimate from the literature of  $.36$  for dual-purpose breeds (Fogarty, 1995).

Fiber diameter in Targhee had a positive additive correlation with litter size of  $.30$  ( $P < .01$ ), which is undesirable and indicates that selection to reduce fiber diameter would have a negative genetic impact on litter size. Fogarty (1995) reports only three estimates of this genetic correlation:  $-.01 \pm .16$ ,  $.23 \pm .20$ , and  $.61 \pm .30$ . Although these results are highly variable, the mean value ( $.27$ ) is quite close to our estimate of  $.30$ .

Estimates of correlations between residual environmental effects on early-life traits and permanent environmental effects on litter size were generally not significant, were generally positive, and usually did not change estimates of  $r_a$  from those shown in Tables 5 and 7. There were some exceptions to these generalizations, however. Environmental correlations between fleece weight and litter size were positive and substantial in both Polypay ( $r_{pe} = .45$ ;  $P < .10$ ) and Targhee ( $r_{pe} = .66$ ;  $P < .05$ ). These results suggest that environmental effects that promote wool growth also have positive effects on litter size. Most fleece weight records were taken at approximately 1 yr of age, although some records (generally fewer than 15%) came from older ewes. Yearling fleece weights would normally be measured around the time of first lambing in Polypay and approximately 7 mo before first breeding in Targhee, so environmental factors that support early fleece growth may also have positive effects on litter size. Inclusion of  $r_{pe}$  in the model also changed estimates of  $r_a$  for fleece weight somewhat in both Targhee (from  $-.09$  to  $-.16$ ) and Polypay (from  $.21$  to  $-.03$ ); estimates of  $r_a$  for fleece weight were more consistent for the two breeds when  $r_{pe}$  was included in the model, but they remained non-significant.

The estimate of  $r_{pe}$  for yearling gain in Targhee ( $-.98$ ;  $P < .05$ ) was also very large. Both this estimate and the

estimate of  $r_{pe}$  for fleece weight in Targhee discussed above must be viewed in the context of the small permanent environmental variance for litter size in this breed ( $pe^2 = .02$ ). Thus, these relatively large estimates of  $r_{pe}$  would still correspond to relatively small contributions to covariation. Notter and Hough (1997) reported a residual environmental correlation of  $-.34$  ( $P < .05$ ) between 120-d weaning weight and yearling gain in Targhee. Thus, environmental effects that promote rapid gains from 120 to 365 d in this breed tend to be negatively associated with environmental effects that lead to heavy 120-d weaning weights. Compensatory gain is likely involved, and animals that gain rapidly to 365 d in order to compensate for lower preweaning gain may subsequently produce smaller litters. Yearling weight is the sum of 120-d weaning weight and yearling gain, and the predicted value of  $r_{pe}$  between yearling weight and litter size in Targhee was  $-.54$ . Such a negative environmental relationship is difficult to support biologically and needs to be studied further.

Phenotypic correlations are generally estimated more accurately than correlations among their components and provide reasonable initial estimates of anticipated genetic relationships. For all traits, estimates of  $r_p$  were small, ranging from  $-.02$  to  $.08$  for models that excluded  $r_{pe}$  and from  $-.09$  to  $.08$  for models that included  $r_{pe}$ . Thus early-life traits were all poor phenotypic predictors of future litter size.

Estimates of genetic parameters for early-life traits for Suffolk and Polypay in bivariate analyses were similar to those reported by Notter (1998a). In Targhee, genetic parameter estimates for postweaning gain, yearling gain, fleece weight, and fiber diameter were similar to those reported by Notter and Hough (1997), but parameter estimates for weaning weights, and especially for 60-d weaning weight, were considerably different. The observed consistency between reports reflects the similarity between the data sets that were used. Notter (1998a) used the same Polypay data as the current study, and the number of observations in the current Suffolk data set was about 15% larger than that used by Notter (1998a). For Targhee, numbers of records available from the NSIP database for the current study were larger by 32% for 60-d weaning weight, 23% for 120-d weaning weights, 14% for postweaning gain, 35% for yearling gain, 58% for fleece weight, and 88% for fiber diameter than those used by Notter and Hough (1997).

For Targhee 60-d weaning weights,  $h^2$  was very small ( $.01$ ) in the analysis of Notter and Hough (1997) and was higher in more intensively managed eastern flocks ( $.07$ ) than in the more extensively managed western flocks ( $.00$ ). In the combined data, the estimate of maternal heritability was modest ( $.10$ ), but the low estimates of  $h^2$  precluded estimation of the additive direct-maternal correlation. In contrast, estimates of both  $h^2$  and  $m^2$  were higher in the current data ( $.14$  and  $.22$ , respectively), and the estimate of  $r_{am}$  was significant, very large, and negative ( $-.90$ ). Notter and Hough (1997)

and Notter (1998a) noted that estimates of repeatability of total maternal performance ( $t_m = m^2 + c_m^2 + 1/4 h^2 + mr_{am}h$ ) were generally more consistent than estimates of its components. The same observation was true in this study. Estimates of  $t_m$  for 60- and 120-d weaning weights in Targhee were .20 and .17, respectively, compared to .19 and .16, respectively, in the data of Notter and Hough (1997). For other breeds in the current study,  $t_m$  was .18 for 60-d weaning weight and .26 for 90-d weaning weight in Suffolk and was .23 for both 60- and 90-d weaning weights in Polypay.

Very large, negative estimates of  $r_{am}$  have been frequently reported for weaning weights in beef cattle and sheep. As discussed by Robinson (1996a,b) and Notter and Hough (1997), these estimates seem far too large to represent true biological relationships, but their origin has yet to be definitively identified. In comparing the current data to that of Notter and Hough (1997), there would be both increased numbers of observations and changes in data structure. Because the numbers of flocks involved were similar, more animals in the current data set would be expected to have produced records as both individuals and dams, whereas in the earlier data, fewer dams would have had their own weaning weight records included in the data. Although not enumerated by Notter and Hough (1997), there would likely also be more daughter-dam pairs with performance records in the current data. These changes in data structure could allow more opportunities for nongenetic relationships between performance as an individual and as a dam, or between records of daughter and dam, to influence estimates of  $r_{am}$  (see Meyer, 1992 for additional discussion). Also, Robinson (1996b) and Hagger (1998) found that inclusion of sire  $\times$  year or sire  $\times$  flock effects, respectively, in the analytical models reduced the magnitude of negative estimates of  $r_{am}$ . These results could be important because more use of common sires in different flocks would have occurred in recent years in Targhee. Certainly, further study of these large negative estimates of  $r_{am}$  is required.

### Implications

Significant genetic effects on litter size were observed in Targhee, Suffolk, and Polypay sheep, indicating that genetic improvement is possible for this economically important trait. No major genetic antagonisms were observed between litter size and weaning weight, post-

weaning gain, fleece weight, or fiber diameter. Thus, selection on these early-life traits is unlikely to have noticeable future effects on genetic merit for litter size. Recording of both early-life traits and of reproductive performance will be required to maximize genetic improvement in production efficiency in sheep flocks.

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