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Genetic relationship between milk score and litter weight for Targhee, Columbia, Rambouillet, and Polypay sheep[1]

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ABSTRACT: This study was conducted to evaluate the relationship between milk score (MS) and litter weight at 70 d (LW) for four sheep breeds in the United States. Milk score is a subjective measure of milk production used to assess milk production of range ewes when milk yield cannot be quantitatively determined. Variance components for MS and LW were estimated for each of Targhee, Columbia, Rambouillet, and Polypay breeds. Data collected from 1990 through 2000 at the U.S. Sheep Exp. Stn. in Dubois, ID, were analyzed with an animal model using REML. There were 13,900 records of MS and LW for 5,807 ewes. Records were grouped according to parity as first, second, and greater (mature), and all records (lifetime). Estimates of heritability for MS were in the range of 0.05 to 0.18 for first, 0.01 to 0.27 for second, 0.05 to 0.10 for mature, and 0.08 to 0.13 for all lifetime parity groups. Estimates of genetic correlation between MS at first and second parities ranged from 0.74 to 1.00. Similarly, mature MS was highly correlated genetically with MS at first (0.83 to 1.00) and at second (0.60 to 1.00) parities, suggesting that additive genetic value for milking ability at maturity could be evaluated as early as at first parity. Heritability estimates for LW ranged from 0.00 to 0.18 over all breeds and parity groupings. The genetic correlation between LW at first and second parity groups ranged from 0.43 to 1.00. Estimates of genetic correlation between LW at first or second parity with mature LW were mostly high and positive, except for Targhee (–0.10) and Polypay (0.14) at first parity. Litter weight for mature ewes could be improved by selection at first or second parity. Estimates of genetic correlation at first parity between MS and LW were high (1.00) for Rambouillet and Polypay, and near zero for Columbia and Targhee. At second parity, estimates of genetic correlation between MS and LW were positive and moderate for Rambouillet and Polypay but more variable for Columbia and Targhee. Estimates of genetic correlation between MS and LW were mostly positive and may be favorable with smaller estimates of standard errors using all lifetime records rather than first or second parity records. Although estimates are variable, the average of the estimates of the genetic correlation suggests that LW can be improved by selecting ewes for favorable MS.

Key Words: Heritability, Genetic Correlations, Lactation, Reproduction

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Introduction

The growth of suckling lambs is influenced by the milk production of their dams (Neidig and Iddings, 1919; Burris and Baugus, 1955), but it may be impractical to accurately quantify milk production of ewes under range conditions. Milk score (**MS**) is a subjective measure of milk production of ewes that can be qualitatively determined by palpating the ewe's udder and observing her lambs' fill within a few hours of lambing. Snowder et al. (2001a,b) investigated the usefulness of a subjective MS as an alternative to directly quantifying milk yield of nursing range ewes. They estimated the correlation of ewes' MS with litter weight weaned at 120 d of age for four sheep breeds and suggested the possibility of utilizing MS to select for increased litter weight weaned at different parities. Nonetheless, some of their estimates of the genetic correlation between MS and litter weight weaned were so low that it might be impractical to use MS in a selection program to improve litter weight.

Although lambs are typically weaned at 90 to 150 d of age, litter weight at 70 d (**LW**) may be an economically important trait for sheep production under U.S. Western range production systems. Maternal ability of the

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Table 1. Number of sires, total number of records, and proportion of records for each breed by milk score and parity group

		Parity			
Breed	Milk score	First	Second	Mature	Lifetime
Targhee	High, %	12.8	31.3	36.4	28.6
	Average, %	78.4	66.3	61.2	67.1
	Low, %	8.8	2.5	2.5	4.2
	Total No.	888	688	1,579	3,155
	No. of sires	180	184	258	297
Columbia	High, %	25.7	41.6	42.8	37.2
	Average, %	70.7	57.0	56.1	60.8
	Low, %	3.6	1.4	1.2	2.0
	Total No.	802	570	1,211	2,583
	No. of sires	137	130	163	196
Rambouillet	High, %	6.1	25.6	42.8	29.6
	Average, %	82.6	72.7	56.0	66.5
	Low, %	11.3	1.7	1.3	3.9
	Total No.	1,185	1,101	2,445	4,731
	No. of sires	196	199	269	314
Polypay	High, %	2.5	21.7	25.5	17.1
	Average, %	85.4	75.0	72.1	77.1
	Low, %	12.1	3.3	2.4	5.8
	Total no.	1,112	840	1,479	3,431
	No. of sires	205	182	183	245

dams may have a greater effect on early preweaning weight of suckling lambs than on later preweaning performance. Torres-Hernandez and Hohenboken (1980) and Snowder and Glimp (1991) reported greater and highly significant coefficients of correlation for preweaning growth of lambs with milk production of the ewes during early stages of lactation than toward the end of the lactation as may be expected due to the natural decrease of lamb dependence on milk and increased consumption of forage and/or creep feed.

The objective of this study was to investigate the relationship between MS and LW for Targhee, Columbia, Rambouillet, and Polypay sheep breeds. Estimates of variance components were obtained for MS and LW for ewes at first, second, mature, and all lifetime parities. Estimates of genetic and environmental correlations also were obtained for and between MS and LW at and among the four parity groups.

Materials and Methods

Data for Targhee, Columbia, Rambouillet and Polypay sheep were from the U.S. Sheep Exp. Stn., Dubois, ID. Management of the animals was similar to the management for most Western sheep production systems. Newborn lambs and their mothers were placed in individual lambing sheds for approximately 2 d before being moved to larger pens with other ewes and newborns. Lambs were supplemented with a standard lamb creep feed of ground corn or barley grain on an ad libitum basis for approximately 4 wk postpartum. Ewes had ad libitum access to a 20% whole corn or barley and 80% pelleted alfalfa diet (as-fed basis) until they were moved to grazing pastures. On grazing pastures, a trace mineral salt mix (Redmond Salt, Salt Lake City, UT) was provided for ewes and lambs. A randomly bred control population and two to four selection lines for different traits were maintained within each breed. Selection for total litter weight weaned at 105 d postpartum was a selection trait common for all breeds. No direct selection for MS had been imposed. Management, feeding protocols, and selection lines for this flock were previously described in more detail by Ercanbrack and Knight (1998) and Snowder et al. (2001a).

Traits studied were MS and total LW for ewes lambing from 1990 through 2000. All ewes were classified by the scorer as having low, average, or high MS based on the fill of the udder and the suckling lamb(s). Milk score was used at the U.S. Sheep Exp. Stn. as a management tool to determine the number of lambs a ewe would be allowed to rear. The LW were calculated as a function of birth weight and ADG from birth to an average 70-d lamb weight. Total litter weight at 70 d was the sum of weights of lambs reared by a ewe at approximately 70 d after lambing. Only ewes rearing their own single or twin lambs were included in the analyses.

Only spring-born lambs, typically born from late March through early May, were included in the analyses. Records were grouped according to parity. Four parity groups were used: first, second, and greater (mature), and all records (lifetime). The total number of ewes in the final dataset was 5,807, with a total of 13,900 lambing records. Table 1 shows the number of records for each breed by parity grouping and MS classification.

The MS and LW records were first analyzed with a single-trait animal model for each parity group within

Table 2. Estimates of components of variance for milk score for first and second parities[a]

	Targhee		Columbia		Rambouillet		Polypay	
Parameter	First	Second	First	Second	First	Second	First	Second
σ_a^2	0.02	0.03	0.04	0.00	0.01	0.03	0.01	0.06
σ_e^2	0.16	0.20	0.17	0.26	0.14	0.17	0.13	0.16
σ_p^2	0.18	0.23	0.20	0.26	0.15	0.20	0.13	0.22
h^2	0.12	0.13	0.18	0.01	0.06	0.16	0.05	0.27
SE of h^2	0.06	0.08	0.07	0.07	0.04	0.06	0.05	0.08

[a]Additive genetic variance (σ_a^2), residual environmental variance (σ_e^2), total phenotypic variance (σ_p^2), heritability (h^2), and standard error of heritability (SE of h^2).

a breed. All models for MS and LW at different parity groupings included fixed factors of year of record, age of ewe, and selection line of ewe. Litter size at birth was included as a fixed factor for analyses of MS. Effects of gender of lambs within a litter on LW were accounted for by including three covariates for gender of lambs (ewe lamb, ram lamb, and wether). The codes were constructed as fractions of each individual lamb within a litter as described by Hanford (2001). For example, the covariate code would be the same for lambs of the same sex regardless of whether the lambs were reared as singles or twins (a value of 1 for that particular gender classification and 0 for the other two). If a wether and a ram lamb were reared in the same litter, then the covariate value for each type would be 0.5, with 0 for the ewe lamb. This procedure allowed for the adjustment of LW for the gender of lambs, without adjusting for the number of lambs within the litter. This procedure was followed because LW is a composite trait, and litter size is a major component.

The models for all parity groups included animal additive genetic effect as a random factor. Mature and lifetime records had the possibility of having repeated measures. A random permanent environmental factor was included in the models for analysis of mature and lifetime records.

Two-trait analyses were used to estimate genetic and environmental covariance parameters among different parity groups for MS and LW. These traits were recorded once a year for lambing ewes. One pair of those records was available for each ewe at first and second parities. Multiple records for ewes were contained in the dataset for traits at maturity. Two-trait analyses of first or second parity with mature parity groups could result in confounded estimates of residual and permanent environmental variances and covariances for animals in the first and second parity groups. Consequently, the residual covariance between records for first or second parity with mature parity groups was set to 0, while including permanent environmental effects for all traits including traits corresponding to first and second parities. Caution should be taken in interpreting the resulting permanent environmental variances and covariances for traits with single measurements. Alternatively, an overall estimate of environmental correlation could be used instead (Bromley et al., 2000). The relationship between MS and LW also was investigated, utilizing estimates of correlation among the two traits for the four different parity groups.

Data were analyzed using a derivative free REML algorithm (Graser et al., 1987) with the computer program of Boldman et al. (1995). Local convergence was considered to be met if the variance of the –2 log likelihoods in the simplex was less than 1×10^{-6}. The values of –2 log likelihood and estimates of variance components were compared for the consecutive restarts. Global convergence was assumed when the values of the –2 log likelihood and the estimates of variance components did not change to the second decimal for at least three consecutive restarts.

Results and Discussion

Milk Score

Estimates of heritability of MS at first parity were variable ranging from 0.05 to 0.18 for different breeds (Table 2). Estimates of heritability of MS at second parity were more variable by breed and were in the range of 0.01 to 0.27. Except for the Columbia breed, estimates of heritability for MS were greater for second parity than for first parity, although not significantly different ($P > 0.05$). The average estimates of heritability at first and second parities suggest the opportunity to improve MS, especially for the breeds with large estimates of heritability.

Estimates of additive genetic variance were greater for second parity records than for first parity records for all breeds except for the Columbia. Similarly, estimates of total phenotypic variance were always greater for second parity than for first parity records for the four breeds. This result may be due to an asymmetric frequency of MS classifications for the first parity (Table 1). Larger proportions of ewes at first parity were classified with low MS (4 to 12%) than at second parity (1 to 3%). In addition, the incidence of high MS was more frequent for second parity records than for first parity records (22 to 42% at second parity compared with 3 to 26% at first parity). The distributions of MS for first

Table 3. Estimates of components of variance for milk score using mature and all lifetime records[a]

	Targhee		Columbia		Rambouillet		Polypay	
Parameter	Mature	Lifetime	Mature	Lifetime	Mature	Lifetime	Mature	Lifetime
σ^2_a	0.01	0.02	0.02	0.03	0.03	0.02	0.02	0.02
σ^2_{pe}	0.02	0.01	0.02	0.01	0.02	0.02	0.01	0.01
σ^2_e	0.23	0.20	0.21	0.21	0.21	0.19	0.19	0.16
σ^2_p	0.26	0.24	0.25	0.24	0.26	0.22	0.21	0.19
h^2	0.05	0.10	0.10	0.13	0.10	0.08	0.10	0.12
SE of h^2	0.04	0.03	0.05	0.03	0.03	0.02	0.04	0.03
pe^2	0.08	0.05	0.09	0.02	0.07	0.07	0.04	0.03
SE of pe^2	0.05	0.03	0.06	0.03	0.04	0.02	0.04	0.03

[a]Additive genetic variance (σ^2_a), permanent environmental variance (σ^2_{pe}), residual environmental variance (σ^2_e), total phenotypic variance (σ^2_p), heritability (h^2), standard error of heritability (SE of h^2), fraction of total phenotypic variance due to permanent environmental effects (pe^2), and standard error of the fraction of total variance due to permanent environmental effects (SE of pe^2).

and second parities agree with the expected increase in milk production from first to second parity. El Saied et al. (1999) reported a significant increase ($P < 0.05$) in daily milk yield from first to second parity for Spanish Churra sheep.

Snowder et al. (2001b) reported a trend for estimates of variance components for MS to increase from first to second parity. Their estimates of heritability of MS for first and second parities for Targhee, Columbia, Rambouillet, and Polypay sheep were larger than the estimates from the present study. Sakul and Boylan (1992), in a study that included Targhee and Rambouillet among other sheep breeds, concluded that substantial variation for milk production exists among and within U.S. sheep breeds.

Estimates of heritability for MS using records at maturity were similar for Columbia, Rambouillet, and Polypay breeds (0.10), which were larger than the estimate for Targhee (0.05; Table 3). Estimates of heritability using all lifetime records (0.08 to 0.13) were slightly greater than estimates using mature records, except for the Rambouillet breed. Estimates of standard errors of the heritability estimates using mature and lifetime records were in the range of 0.02 to 0.05. Estimates of the fraction of variance due to permanent environmental effects of the ewe were small for all breeds and ranged from 0.04 to 0.09 for records at maturity and 0.02 to 0.07 for all lifetime records. Generally larger estimates of heritability have been previously reported for MS at mature ages for the same four breeds (Snowder et al., 2001b). Legarra and Ugarte (2001) reported an estimate of heritability of 0.20 for Latxa dairy sheep using 120-d repeated lactation records. Baro et al. (1994) and El Saied et al. (1999) estimated heritability to be 0.34 and 0.18 for multiple-lactation, test-day milk yield of Spanish Churra milking sheep, respectively. El Saied et al. (1999) reported an estimate of 0.36 for the proportion of total variance of test day milk yields due to permanent environmental effects across lactations.

Milk scores at first parity were highly genetically correlated with second-parity scores (Table 4). The smallest estimate was 0.74 for Targhee breed. Similarly, the estimates of genetic correlations for MS at first or second parity with records at maturity also were large, with many estimates near unity. The near unitary estimates of genetic correlations suggest that MS at all parities are controlled by the same or similar gene effects. If so, selection to increase MS for first or second parity would also result in improvement of MS for later parities. Snowder et al. (2001b) reported estimates of genetic correlation of near unity for MS for first with second parities. They also obtained large estimates (0.69 to 1.00) for genetic correlations of MS at first or second parity with scores at mature parities.

Estimates of environmental correlation between MS for first and second parities were all positive and small (0.02 to 0.09, Table 4). Estimates of environmental correlations for MS for first or second parities with scores at maturity were also small with one negative estimate (–0.08 to 0.11). Standard errors of estimates of correlation at different parities were not estimated due to a limitation in the statistical package, which does not allow for such estimates when some data are missing. The small estimates of environmental correlations may not be different from zero and may be attributed to the long timespan between the measurements of MS at different parities, in most cases, at least 1 yr. The permanent environmental correlation did not have a large influence on the estimates of overall environmental correlation, which is due to the small estimates of permanent environmental variance relative to the estimates of residual environmental variance as may be seen from the single trait analyses (Table 3). Snowder et al. (2001b) reported similar small estimates (0.02 to 0.17) of environmental correlations of MS at first or second parity with scores at maturity.

Litter Weight at 70 d

Average LW was always less at early parities for all breeds. Columbia and Polypay dams tended to have

Table 4. Estimates of genetic and environmental correlations for milk score by breed among first, second, and mature records[a]

Parity group	Parameter	Targhee	Columbia	Rambouillet	Polypay
First and second	r_g	0.74	1.00	0.94	1.00
	r_e	0.06	0.08	0.02	0.09
First and mature[b]	r_g	1.00	0.83	0.92	0.97
	r_{pe}	1.00	−0.31	0.58	0.01
	r_e	0.00	−0.08	0.03	0.00
Second and mature[b]	r_g	1.00	1.00	0.61	1.00
	r_{pe}	0.37	0.54	0.47	0.58
	r_e	0.05	0.07	0.11	0.04

[a]Additive genetic correlation (r_g), environmental correlation (r_e), and permanent environmental correlation (r_{pe}).

[b]The estimate of overall environmental correlation between traits i and j was obtained as: $r_e = r_{pe} \sqrt{\sigma^2_{pe_i} * \sigma^2_{pe_j}} / \sqrt{(\sigma^2_{e_i} + \sigma^2_{pe_i})*(\sigma^2_{e_j} + \sigma^2_{pe_j})}$, where r_{pe} is estimate of correlation among the ith and jth permanent environmental effects; $\sigma^2_{pe_i}$ and $\sigma^2_{pe_j}$ are estimates of the permanent environmental variances for ewes for the ith and jth parity groups, respectively; and $\sigma^2_{e_i}$ and $\sigma^2_{e_j}$ are estimates of the residual environmental variances for ewes for the ith and jth parity groups, respectively.

greater LW than Targhee or Rambouillet (Table 5). Estimates of heritability of LW for first parity were in the range of 0.05 to 0.18, and for second parity, were mostly smaller than estimates for first parity (0.00 to 0.12; Table 6). The generally small estimates of heritability for LW may be due to the complex composite nature of the LW trait, which may be affected by numerous environmental influences from breeding to weaning (Snowder, 2002). Estimates of phenotypic variance for LW for second parity were almost twice as large as estimates for first parity. This increase may be explained by the generally larger litter size reared at second parity for most ewes. Okut et al. (1999) reported estimates of heritability in the range of 0.00 to 0.25 for Targhee, Columbia, Rambouillet, and Polypay breeds using records of ewes 1 to 3 yr of age. Fogarty (1995) reported a moderate mean estimate (51%) of CV for weaned litter weight based on several studies in a review article, which suggests the possibility of positive response to selection even with small estimates of heritability.

Estimates of heritability for LW for mature and all lifetime records were in the ranges of 0.03 to 0.13 and 0.05 to 0.11, respectively (Table 7). The fractions of phenotypic variance due to permanent environmental effects of the ewes were small for both mature (0.00 to 0.08) and all lifetime records (0.00 to 0.05). Except for Polypay, estimates of additive genetic variance were smaller with all lifetime records than with records at maturity. Estimates of phenotypic variance were always less with all lifetime records than with mature records, which may be due to smaller litter sizes at early parities which are included with the all lifetime records. Abdulkhaliq et al. (1989) reported estimates of heritability for litter weight weaned at 90 d of age of 0.13 for Targhee and 0.28 for Columbia sheep. Bromley et al. (2001) reported small estimates of heritability for lifetime annual litter weight weaned at 120 d for Targhee, Columbia, Rambouillet, and Polypay breeds (0.02 to 0.11). They also reported small estimates of fraction of total variance due to permanent environmental effects for the four sheep breeds (0.00 to 0.10). In a review of estimates of genetic parameters for litter weight weaned, Safari and Fogarty (2003) reported mean estimates of 0.10 and 0.14 for heritability and repeatability, respectively.

Estimates of genetic correlation of LW between first and second parities were moderate to large (0.43 to 1.00), which suggests that selection for higher LW for first parity may improve the trait for second parity (Table 8). Estimates of genetic correlation of LW between first and mature records were more variable (−0.10 to 1.00). Litter weight at 70 d for second parity was highly genetically correlated with mature records (estimates of 1.00 for all breeds except 0.76 for Rambouillet). If the true genetic correlation is one, LW for

Table 5. Means and standard errors of litter weight at 70 d (kg) for each breed by parity group

Breed	First	Second	Mature	Lifetime
Targhee	28.5 ± 0.3	35.9 ± 0.4	37.5 ± 0.3	34.6 ± 0.2
Columbia	31.1 ± 0.3	38.4 ± 0.5	41.1 ± 0.3	37.4 ± 0.2
Rambouillet	25.9 ± 0.2	35.9 ± 0.3	39.7 ± 0.2	35.4 ± 0.2
Polypay	26.6 ± 0.2	38.3 ± 0.3	41.3 ± 0.3	35.8 ± 0.2

Table 6. Estimates of components of variance for litter weight at 70 d (kg) by breed at first and second parities[a]

	Targhee		Columbia		Rambouillet		Polypay	
Parameter	First	Second	First	Second	First	Second	First	Second
σ_a^2	2.08	0.00	5.61	4.62	4.13	7.44	1.53	8.23
σ_e^2	33.60	65.25	38.81	73.11	18.75	55.48	28.73	60.49
σ_p^2	35.68	65.25	44.42	77.73	22.88	62.92	30.27	68.72
h^2	0.06	0.00	0.13	0.06	0.18	0.12	0.05	0.12
SE of h^2	0.05	0.06	0.07	0.07	0.06	0.05	0.05	0.06

[a]Additive genetic variance (σ_a^2), residual environmental variance (σ_e^2), total phenotypic variance (σ_p^2), heritability (h^2), and standard error of heritability (SE of h^2).

Targhee, Columbia, and Polypay for second and mature parities could be considered genetically to be one trait. Okut et al. (1999) estimated genetic correlations for litter weight weaned at 120 d among young (1-yr-old), middle (2- and 3-yr-old), and older (>3-yr-old) age classes of ewes. They reported ranges of estimates of genetic correlations among the three age classes of 0.49 to 0.98 for Targhee, 0.07 to 0.88 for Columbia, 0.82 to 0.99 for Rambouillet, and 0.96 to 1.00 for Polypay sheep.

Estimates of environmental correlations for LW for first and second parities were in the range of –0.03 to 0.11. Estimates of overall environmental correlations of LW for first or second parity ewes with mature records were also small (–0.03 to 0.09). Estimates of correlation among permanent environmental effects did not have a large influence on estimates of overall environmental correlation. This result may be explained by the smaller estimates of permanent environmental variances compared with the estimates of residual environmental variances (see Table 7). It could be concluded that LW is mostly influenced by different environmental effects at different parties. Similar near to zero positive and negative estimates of environmental correlations have been previously reported among three ewe age classes (1, 2 to 3, and more than 3 yr old) for litter weight weaned at 120 d (Okut et al., 1999).

Relationship Between MS and LW

Estimates of genetic and environmental correlations between MS and LW within the four parity group classes are presented in Table 9. Estimates of genetic correlation between MS and LW within the first parity class were large (1.00) for Rambouillet and Polypay but may not be different from zero for Columbia and Targhee. For the second parity class, Rambouillet and Polypay continued to have favorable estimates of genetic correlations between MS and LW but with a smaller magnitude than for first parity. However, large positive and negative estimates with extreme standard errors were found for genetic correlations between MS and LW for the second parity for Targhee and Columbia sheep, respectively. Generally, estimates of genetic correlations between MS and LW were smaller, but with smaller standard errors, when using mature or all lifetime records than when using first or second parity records. The estimates of genetic correlation between MS and LW were in the range of 0.15 to 0.68, with

Table 7. Estimates of components of variance for litter weight (kg) at 70 d by breed using mature and all lifetime records[a]

	Targhee		Columbia		Rambouillet		Polypay	
Parameter	Mature	Lifetime	Mature	Lifetime	Mature	Lifetime	Mature	Lifetime
σ_a^2	10.83	7.63	11.20	3.94	4.79	3.80	2.08	2.89
σ_{pe}^2	6.55	0.00	0.00	2.91	5.84	2.50	6.38	3.31
σ_e^2	66.29	58.98	80.84	67.09	67.19	54.47	68.62	54.70
σ_p^2	83.67	66.60	92.04	73.94	77.82	60.77	77.08	60.90
h^2	0.13	0.11	0.12	0.05	0.06	0.06	0.03	0.05
SE of h^2	0.05	0.03	0.06	0.03	0.03	0.02	0.03	0.02
pe^2	0.08	0.00	0.00	0.04	0.08	0.04	0.08	0.05
SE of pe^2	0.05	0.03	0.05	0.03	0.03	0.02	0.04	0.02

[a]Additive genetic variance (σ_a^2), permanent environmental variance (σ_{pe}^2), residual environmental variance (σ_e^2), total phenotypic variance (σ_p^2), heritability (h^2), standard error of heritability (SE of h^2), fraction of total phenotypic variance due to permanent environmental effects (pe^2), and standard error of the fraction of total variance due to permanent environmental effects (SE of pe^2).

Table 8. Estimates of genetic and environmental correlations for litter weight at 70 d by breed among first, second, and mature records[a]

Parity group	Parameter	Targhee	Columbia	Rambouillet	Polypay
First and second	r_g	1.00	0.43	0.62	1.00
	r_e	0.11	–0.03	0.07	0.09
First and mature[b]	r_g	–0.10	1.00	0.52	0.14
	r_{pe}	0.47	–0.37	–0.03	0.35
	r_e	0.07	–0.03	0.00	0.05
Second and mature[b]	r_g	1.00	1.00	0.76	1.00
	r_{pe}	0.95	0.15	0.40	0.83
	r_e	0.09	0.04	0.04	0.06

[a]Additive genetic correlation (r_g), environmental correlation (r_e), and permanent environmental correlation (r_{pe}).

[b]The estimate of overall environmental correlation between traits i and j was obtained as: $r_e = r_{pe} \sqrt{\sigma^2_{pe_i} \times \sigma^2_{pe_j}} / \sqrt{(\sigma^2_{e_i} + \sigma^2_{pe_i}) \times (\sigma^2_{e_j} + \sigma^2_{pe_j})}$, where r_{pe} is estimate of correlation among the ith and jth permanent environmental effects; $\sigma^2_{pe_i}$ and $\sigma^2_{pe_j}$ are estimates of the permanent environmental variances for ewes for the ith and jth parity groups, respectively; and $\sigma^2_{e_i}$ and $\sigma^2_{e_j}$ are estimates of the residual environmental variances for ewes for the ith and jth parity groups, respectively.

estimates of standard error in the range of 0.16 to 0.25 using all lifetime records. Snowder et al. (2001b) reported variable estimates of genetic correlation (–0.13 to 1.00) between MS and litter weight weaned at 120 d across breeds and parity groups.

For breeds and parity groups with statistically significant positive estimates of genetic correlations between MS and LW, selection for one of the two traits could simultaneously improve the other. This conclusion may be of practical importance if one of the traits is more difficult or more expensive to measure under commercial range sheep production conditions and if the other correlated trait exhibits genetic variation. Litter weight at 70 d is an economically important trait for sheep production under U.S. Western range production systems. Accurate measurements for this trait are typically not easily obtained. Milk score is a subjective trait and may be easier to obtain during the lambing season. Milk score is heritable and seems to be positively correlated genetically with LW for some breeds within some parity classes. Selection for higher MS could result in heavier litter weights at 70 d if positive estimates of genetic correlation between MS and LW reflect the true correlation for those breeds.

Estimates of temporary environmental correlation between MS and LW were consistently positive and small. These estimates were in the narrow range of 0.08 to 0.19, with estimates of standard error in the range of 0.02 to 0.06 for all four sheep breeds for different parity groups (Table 9). Estimates of permanent environmental correlation between MS and LW were always positive and mostly large using either mature (0.44 to 0.99) or lifetime (0.68 to 0.83) records.

The positive environmental correlation between MS and LW may indicate that ewes had common permanent environmental effects for both traits. The common environmental effects between MS and LW may be due to the relatively short time interval (70 d) between measurements of the two traits. Small and near zero estimates of both temporary and permanent environmental correlations have been reported between MS and litter weight weaned at an older age (120 d) than in the present study for Targhee, Columbia, Rambouillet, and Pol-

Table 9. Estimates of genetic and environmental correlations between milk score and litter weight at 70 d for first, second, mature, and all lifetime records[a]

Parameter	Parity group	Targhee	Columbia	Rambouillet	Polypay
r_g	First	0.27 ± 0.46	–0.02 ± 0.35	1.00 ± 0.36	1.00 ± 0.33
	Second	1.00 ± 2.96	–0.93 ± 5.32	0.67 ± 0.23	0.46 ± 0.25
	Mature	–0.28 ± 0.52	–0.32 ± 3.02	0.37 ± 0.24	0.56 ± 0.42
	Lifetime	0.21 ± 0.21	0.15 ± 0.25	0.51 ± 0.17	0.68 ± 0.16
r_e	First	0.14 ± 0.05	0.14 ± 0.06	0.08 ± 0.05	0.13 ± 0.05
	Second	0.16 ± 0.06	0.15 ± 0.06	0.12 ± 0.05	0.12 ± 0.06
	Mature	0.16 ± 0.03	0.17 ± 0.04	0.10 ± 0.03	0.11 ± 0.04
	Lifetime	0.15 ± 0.02	0.14 ± 0.03	0.11 ± 0.02	0.12 ± 0.02
r_{pe}	Mature	0.91 ± 0.35	0.44 ± 0.31	0.70 ± 0.34	0.99 ± 0.61
	Lifetime	0.68 ± 0.31	0.68 ± 0.71	0.68 ± 0.23	0.83 ± 0.46

[a]Additive genetic correlation (r_g), temporary environmental correlation (r_e), and permanent environmental correlation (r_{pe}).

ypay breeds using first, second, and all lifetime records (Snowder et al., 2001b).

Implications

Milk score and litter weight at 70 d generally seemed to be positively genetically correlated across parities. If so, selection for higher MS and litter weight at 70 d could be effectively initiated as early as at the first-parity measurements. Milk score and litter weight at 70 d also generally seemed to be correlated positively for some sheep breeds within many parity groups. If so, sheep producers could effectively use the subjective milk score to indirectly select for favorable response in litter weight at 70 d for those sheep breeds and parities.

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