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Genotypic Expression at Different Ages: I. Prolificacy Traits of Sheep[1]

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ABSTRACT: Genetic parameters for prolificacy traits for Columbia (COLU), Polypay (POLY), Rambouillet (RAMB), and Targhee (TARG) breeds of sheep were estimated with REML using animal models. Traits were number of live births (LAB), litter size at birth (LSB) and weaning (LSW), and litter weight weaned (LWW). Numbers of observations ranged from 5,140 to 7,095 for prolificacy traits and from 5,101 to 8,973 for litter weight weaned for the four breeds. For single-trait analyses, ewes were classified as young (1 yr old), middle-aged (2 and 3 yr old), or older (> 3 yr old). After single-trait analyses, three-trait analyses were done for each characteristic with traits defined by age class. Generally, heritability estimates from single-trait analyses were low and ranged from .01 to .17 for LAB and LSB and from .00 to .10 for LSW. Heritability estimates obtained for LWW ranged from low to moderate (.00 to .25) and were less for older ewes. Heritability estimates from the three-trait analyses were generally similar to estimates from single-trait analyses. Heritabilities for LAB and LSB were similar, and, for three-trait analyses, they ranged across age groups from .07 to .13 for COLU, .13 to .16 for POLY, .10 to .16 for RAMB, and .01 to .16 for TARG. Estimates for LSW from three-trait analyses ranged from .07 to .12 for COLU, .04 to .09 for POLY, .01 to .11 for RAMB, and .03 to .11 for TARG. For LWW, heritabilities ranged from .00 to .21 for COLU, .05 to .08 for POLY, .12 to .15 for RAMB, and .18 to .29 for TARG. Genetic correlations for LAB, LSB and LSW among age-defined traits ranged from .25 to 1.00. Genetic correlations for LAB and LSB between young and middle and between young and older age classes were less than .80 in COLU, POLY, and RAMB breeds. Only genetic correlations between middle and older age classes for these breeds were greater than .80. For TARG, genetic correlations among all age classes were greater than .80 (.88 to 1.00) for those traits. All genetic correlations among ages for LSW were greater than .80 for POLY and TARG. For RAMB, only the correlation between young and older age classes for LSW was less than .80 (.45). None was greater than .80 for COLU. For LWW, genetic correlations among all age classes in POLY and RAMB were greater than .80 (.82 to 1.00). For COLU, genetic correlation between young and middle was low (.07), between young and older was high (.88), and between middle and older classes was moderately high (.54). For TARG, genetic correlations were .49, .65, and .98 for young-middle, young-older, and middle-older age classes, respectively. Results indicate that more progress could be made in selection programs for prolificacy traits in some sheep breeds by considering age of ewe as a part of the trait rather than by simply adjusting for ages of ewes.

Key Words: Heritability, Genetics, Breeds, Genotypes

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Introduction

Estimates of heritability for prolificacy traits of sheep generally have been low (Bunge et al., 1990; Al-Shorepy and Notter, 1996; van Zyl, 1998), and few reports are available for traits such as litter size at weaning and litter weight weaned. Some breeds, such as Columbia and Targhee, have low reproductive rates

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Table 1. Summary by breed and age of dam class of number of measurements (n) with unadjusted means (X) and standard deviations (SD) for number born alive (LAB), litter size at birth (LSB), litter size at weaning (LSW), and litter weight weaned (LWW)

	Numbers		LAB		LSB		LSW		Numbers			LWW, kg	
Breed and age group	Litters	Ewes	X	SD	X	SD	X	SD	Litters	Ewes	Mating sires	X	SD
Columbia													
Young	666	666	1.16	.37	1.16	.37	.80	.48	508	508	31	38.8	8.8
Middle	2,512	1,667	1.57	.56	1.58	.55	1.28	.62	2,281	1,546	213	52.9	15.9
Older	1,962	928	1.78	.61	1.78	.61	1.44	.63	1,820	878	194	57.3	16.8
Polypay													
Young	1,998	1,998	1.43	.53	1.43	.53	.98	.55	1,674	1,674	67	39.8	10.8
Middle	3,002	2,172	1.92	.62	1.92	.62	1.53	.61	2,830	2,051	238	56.4	16.2
Older	2,095	1,102	2.11	.70	2.11	.70	1.58	.64	1,965	1,032	214	59.0	17.2
Rambouillet													
Young	960	960	1.15	.36	1.15	.36	.79	.43	750	750	42	35.9	10.8
Middle	2,365	1,663	1.60	.55	1.60	.55	1.29	.62	2,156	1,570	361	48.1	14.7
Older	2,370	1,203	1.85	.59	1.85	.59	1.45	.63	2,195	1,135	310	52.5	15.8
Targhee													
Young	757	757	1.12	.33	1.12	.32	.76	.47	559	559	34	34.2	6.3
Middle	3,091	2,033	1.53	.55	1.53	.55	1.22	.61	2,785	1,882	419	47.1	14.4
Older	2,604	1,247	1.76	.57	1.76	.57	1.37	.65	2,364	1,171	364	51.6	16.0

(Abdulkhaliq et al., 1989), and selection could play an important role in increasing the prolificacy rate in such breeds. Hence, reliable estimates of (co)variance components are needed to aid in establishing an efficient selection program for ewe productivity.

For estimation of variance components and genetic parameters, ages of ewes are usually considered fixed effects with measurements simply adjusted for age (e.g., Notter, 1998). If repeated observations on an animal were available in subsequent years, combining all genetic and nongenetic information would increase the accuracy of genetic evaluation. Observations for traits in later years often are assumed to be due to the same genetic effects that influence the traits in earlier years (i.e., the genetic correlation is assumed to be unity). Improving female prolificacy by selection is important to increase profitability (e.g., Abdulkhaliq et al., 1989). Planning optimum designs for selection programs, however, requires knowledge of genetic parameters for all age classes for prolificacy traits. The objective of this study was to estimate parameters necessary to determine whether in a selection program more progress can be made by considering the age of the ewe as a part of the trait (Falconer, 1952), rather than with the usual method of adjusting for the age of the ewe under the assumption of perfect genetic correlation between expression at different ages.

Materials and Methods

Data and Traits

Data for this study were collected at the United States Sheep Experiment Station, Dubois, ID, during the period 1974 to 1996 for Columbia (**COLU**), Polypay (**POLY**), Rambouillet (**RAMB**), and Targhee (**TARG**) breeds. Basic statistics of the data are shown in Table 1. Prolificacy traits used in this study were number of lambs alive at birth (**LAB**), litter size at birth (**LSB**), and litter size at weaning (**LSW**). These measures were based on all ewes lambing. In addition, total litter weight weaned (**LWW**) per ewe was analyzed separately as a composite trait of litter size at weaning and weaning weight. Details on management have been presented by Ercanbrack and Knight (1998). The data were previously analyzed by van Zyl (1998) to estimate correlations among and between prolificacy, wool, and weight traits.

Initially, the data for each trait within each of the four breeds were split into 10 data sets by age of ewe. Therefore, 40 data sets were created and 160 single-trait analyses (4 breeds × 10 age groups × 4 traits) were performed. Parameter estimates were not reasonable for certain age groups for some breeds, in particular for age 5 and older groups, because of small data sets for those ages. Therefore, the data were divided according to three ages of ewe: young ages (age 1 yr), middle ages (ages 2 and 3 yr), and older ages (age greater than 3 yr). Then, a total of 48 single-trait analyses (4 breeds × 3 age groups × 4 traits) were performed to obtain starting values for three-trait analyses.

The composite trait, litter weight weaned, was the total 120-d weight of all lambs present at weaning that a ewe bore and raised. The model for the composite trait included adjustment for sex using a combination of sex and number of the lambs in the litter as covariates (van Zyl, 1998). The covariates were the fractions of male, female, and wether lambs produced by a ewe within a production year for each possible birth type (single, twins, triplets, and quadruplets). For example, if a ewe had triplets and two of the lambs were rams that were kept intact and the third lamb was a ewe lamb, the covariate would be 2/3 for the male triplet entry, 1/3 for the female triplet entry, and .00 for the wether entry for the triplet birth type and zero for the sex categories for single, twin, and quadruplet births for a specific year. For example, if one of the ram lambs had been castrated, the covariates would have been one 1/3 for each of the three triplet entries and zero for all others.

After the single-trait analyses, new data sets were created for three-trait analyses with the traits defined by age class of the ewe when the trait was measured. All pedigree information from 1974 to 1996 was used. Levels of random and fixed effects that were included in the linear mixed model for single-trait analysis by age group were included for the new data sets. The new data sets for each trait were created with three fields for measurements depending on age of ewe when measured at young, middle, and older ages.

This pattern for the data allowed use of all relationships including animals in all subsets of the data. A ewe could be measured at most once at the young age and twice in the middle age group. Outliers (> 4.5 SD) were discarded from data sets to reduce possible influence on estimates of variance.

Statistical Analysis

Estimates of variance components with REML were obtained using a derivative-free algorithm (Graser et al., 1987) with the computer programs of Boldman et al. (1993). Convergence was considered to have been obtained when the variance of the −2log likelihoods in the simplex was less than 1×10^{-6}. Restarts were performed to ensure global convergence.

Depending on the trait, variations of the following linear animal model for single traits were used:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u}_{\mathrm{a}} + \mathbf{S}\mathbf{u}_{\mathrm{ms}} + \mathbf{P}\mathbf{u}_{\mathrm{pe}} + \mathbf{e}$$

where $\mathbf{y}$ is vector of observations, $\boldsymbol{\beta}$ is the vector of unknown fixed effects, $\mathbf{u}_{\mathrm{a}}$ is the vector of direct additive genetic effects of the ewe, $\mathbf{u}_{\mathrm{ms}}$ is the vector of uncorrelated random effects associated with mating sires, and $\mathbf{u}_{\mathrm{pe}}$ is the vector of uncorrelated permanent environmental effects associated with the ewe with association matrices $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{S}$, and $\mathbf{P}$; $\mathbf{e}$ is a vector of random residual effects. The $\mathbf{Z}$ matrix is augmented with columns of zeros for animals in the pedigree that do not have records.

The first and second moments are $E(\mathbf{y}) = \mathbf{X}\boldsymbol{\beta}$ and

$$\mathbf{V}\begin{pmatrix}\mathbf{u}_{\mathrm{a}}\\ \mathbf{u}_{\mathrm{ms}}\\ \mathbf{u}_{\mathrm{pe}}\\ \mathbf{e}\end{pmatrix} = \begin{pmatrix}\mathbf{A}\sigma^2_{\mathrm{a}} & 0 & 0 & 0\\ 0 & \mathbf{I}_{\mathrm{ms}}\sigma^2_{\mathrm{ms}} & 0 & 0\\ 0 & 0 & \mathbf{I}_{\mathrm{pe}}\sigma^2_{\mathrm{pe}} & 0\\ 0 & 0 & 0 & \mathbf{I}_{\mathrm{n}}\sigma^2_{\mathrm{e}}\end{pmatrix}$$

The mixed model equations (**MME**) multiplied by σ^2_{e}, the residual variance, are as follows:

$$\begin{bmatrix}\mathbf{X'X} & \mathbf{X'Z} & \mathbf{X'S} & \mathbf{X'P}\\ \mathbf{Z'X} & \mathbf{Z'Z} + \mathbf{A}^{-1}\mathrm{k}_{11} & \mathbf{Z'S} & \mathbf{Z'P}\\ \mathbf{S'X} & \mathbf{S'Z} & \mathbf{S'S} + \mathbf{I}_{\mathrm{ms}}\mathrm{k}_{22} & \mathbf{S'P}\\ \mathbf{P'X} & \mathbf{P'Z} & \mathbf{P'S} & \mathbf{P'P} + \mathbf{I}_{\mathrm{pe}}\mathrm{k}_{33}\end{bmatrix}\begin{bmatrix}\boldsymbol{\beta}\\ \mathbf{u}_{\mathrm{a}}\\ \mathbf{u}_{\mathrm{ms}}\\ \mathbf{u}_{\mathrm{pe}}\end{bmatrix} = \begin{bmatrix}\mathbf{X'y}\\ \mathbf{Z'y}\\ \mathbf{S'y}\\ \mathbf{P'y}\end{bmatrix}$$

with $\mathrm{k}_{11} = \sigma^2_{\mathrm{e}}/\sigma^2_{\mathrm{a}}$, $\mathrm{k}_{22} = \sigma^2_{\mathrm{e}}/\sigma^2_{\mathrm{ms}}$ and $\mathrm{k}_{33} = \sigma^2_{\mathrm{e}}/\sigma^2_{\mathrm{pe}}$, and where $\mathbf{A}$ is the numerator relationship matrix among animals; $\mathbf{I}_{\mathrm{ms}}$, $\mathbf{I}_{\mathrm{pe}}$, and $\mathbf{I}_{\mathrm{n}}$ are appropriate identity matrices; and σ^2_{a}, σ^2_{ms}, σ^2_{pe}, and σ^2_{e} are variances due to additive genetic effects of ewes, mating sires (for LWW only), permanent environmental effects of ewes, and residual effects, respectively.

Two somewhat different animal models were used for single-trait analyses of the prolificacy traits. For LAB and LSB, both year and age of ewe at lambing (age only for middle and older age classes) were included as fixed effects. Additive genetic effects and permanent environmental effects (the latter only for middle and older age classes) of ewes were random effects in the model. For LSW and LWW, however, foster codes and mating sires were added to the model as fixed and random effects, respectively. The proportion of variance due to mating sires for LSW was found to be less than .005 and was subsequently removed from the model for LSW. For LWW, from 5 to 12 covariates (fractions by sex for single, twin, triplet, and quadruplet litters) were included in the model to account for sex of lambs in the litter but without adjusting for litter size. The number of covariates depended on the age class and breed.

For the three-trait analyses, records of ewes in each of three age groups (young, middle, and older) of the same trait were considered to be different traits and were analyzed with a three-trait animal model. The same fixed and random effects, with permanent environmental included for all age classes, included in the single-trait analyses were considered for the three-trait models with non-zero covariances possible among all effects across age classes. Residual covariances were zero and forced any environmental covariance across age classes into the permanent environmental covariance and environmental correlations among repeated measures in the same age class into the corresponding component of variance due to permanent environmental effects.

Although environmental covariance due to dams across age classes can be forced into the permanent environmental effects, interpretation requires some caution when one class, such as the young age of dam class, cannot have repeated measures. Because of the complete confounding between the permanent environmental and residual effects, variance due to those effects can go to either component of variance, and this makes interpretation of the correlations among permanent environmental effects difficult.

One way to interpret the residual and permanent environmental variances and covariances is 1) to calculate a combined environmental variance from the sum of the original residual and permanent environmental variance components and 2) to calculate an environmental correlation as in the following formula for the environmental correlation between measures in the young and middle age classes:

$$r_{e_{ym}} = \left[r_{pe_{ym}}\left(pe_y^2 \times pe_m^2\right)^{.5}\right] \div \left[\left(pe_y^2 + e_y^2\right)\left(pe_m^2 + e_m^2\right)\right]^{.5}$$

where $r_{pe_{ym}}$ is the correlation between permanent environmental effects, pe_y^2 and pe_m^2 are fractions of variance due to permanent environmental effects, and e_y^2 and e_m^2 are fractions of variance due to residual effects for the young and middle age classes.

Results

Single-Trait Analyses

Table 2 shows estimates of variance components, heritability, and fractional variance due to permanent environmental effects for the single-trait animal models for LAB, LSB, and LSW by breed. Table 3 shows corresponding estimates for LWW. Generally, heritability estimates for these traits were low and ranged from .01 to .17 for LAB and LSB and from .00 to .10 for LSW across ages and breeds.

Estimates of heritability for LAB and LSB had a similar pattern over the four breeds and three age groups, although estimates for LAB and LSB for TARG were quite variable; the lowest and highest heritabilities for LAB and LSB (.01 and .17) were obtained for this breed. However, POLY was the only breed for these two traits for which the heritability estimates for each of three age classes were greater than .10 (.12 to .17). Heritability estimates differed across age classes and tended to decrease with age (.06 to .12 and .08 to .14) for COLU and RAMB, respectively. Heritability estimates averaged over age groups were identical for both LAB and LSB: .09, .14, .12, and .08 for COLU, POLY, RAMB, and TARG, respectively.

Estimates of heritability for LSW were somewhat lower than for LAB and LSB. Estimates for COLU for LSW were slightly greater than those for other breeds. The lowest estimates of heritability for LSW were zero for POLY for the middle age class and for TARG for the young age class. The largest estimates were for COLU and RAMB at young and middle age classes, respectively (.10 and .10). Only for TARG did the heritability estimate increase as age class of ewe became older (.00, .03, and .09 for young, middle, and older age classes, respectively).

The proportions of variance due to permanent environmental effects of ewe for LAB and LSB were

Table 2. Estimates of components of variance and fractions[a] of total variance for Columbia, Polypay, Rambouillet, and Targhee breeds for prolificacy traits with single-trait analyses

	Young age				Middle ages						Older ages					
Traits	σ_a^2	σ_e^2	σ_p^2	h^2	σ_a^2	σ_{pe}^2	σ_e^2	σ_p^2	h^2	pe^2	σ_a^2	σ_{pe}^2	σ_e^2	σ_p^2	h^2	pe^2
Lambs alive at birth (LAB)																
Columbia	.02	.12	.14	.12	.02	.00	.27	.29	.08	.00	.02	.02	.32	.36	.06	.05
Polypay	.04	.24	.27	.13	.04	.00	.32	.37	.12	.00	.08	.01	.39	.47	.17	.02
Rambouillet	.02	.11	.12	.14	.04	.00	.23	.27	.14	.01	.03	.01	.30	.34	.08	.02
Targhee	.00	.10	.11	.01	.05	.00	.23	.28	.17	.01	.02	.02	.28	.32	.07	.05
Litter size at birth (LSB)																
Columbia	.02	.12	.14	.12	.02	.00	.27	.29	.08	.00	.02	.02	.32	.36	.06	.05
Polypay	.04	.28	.31	.12	.04	.00	.32	.37	.12	.00	.08	.00	.39	.47	.17	.00
Rambouillet	.02	.11	.12	.14	.04	.00	.23	.27	.14	.01	.03	.01	.30	.34	.08	.02
Targhee	.00	.10	.10	.01	.05	.00	.23	.28	.17	.01	.02	.02	.28	.32	.07	.05
Litter size at weaning (LSW)																
Columbia	.02	.20	.22	.10	.02	.00	.34	.36	.06	.00	.03	.00	.36	.39	.09	.00
Polypay	.01	.27	.29	.05	.00	.03	.32	.36	.00	.09	.03	.00	.36	.39	.09	.00
Rambouillet	.00	.18	.18	.01	.04	.00	.31	.35	.10	.01	.03	.02	.34	.39	.08	.04
Targhee	.00	.21	.22	.00	.01	.03	.30	.34	.03	.10	.04	.01	.36	.41	.09	.03

[a] σ_a^2, additive genetic variance; σ_{pe}^2, permanent environmental variance; σ_e^2, residual variance; σ_p^2, total variance; h^2, fraction of total variance represented by σ_a^2; pe^2, fraction of total variance represented by σ_{pe}^2.

Table 3. Estimates of components of variance and fractions[a] of total variance for litter weight weaned (kg) from single-trait analyses

Age of ewes and breed	σ^2_a	σ^2_{ms}	σ^2_{pe}	σ^2_e	σ^2_p	h^2	ms^2	pe^2
Young								
Columbia	11.0	.5	—	45.8	56.9	.19	.00	—
Polypay	5.4	9.6	—	68.8	83.7	.06	.11	—
Rambouillet	4.4	.4	—	22.0	26.8	.17	.01	—
Targhee	7.8	.0	—	23.9	31.7	.25	.00	—
Middle								
Columbia	.3	8.2	.9	129.4	138.8	.00	.06	.00
Polypay	9.9	13.8	10.9	127.1	161.7	.06	.09	.07
Rambouillet	14.1	6.9	2.5	92.9	116.5	.12	.06	.02
Targhee	17.8	3.3	2.9	91.7	115.6	.15	.03	.03
Older								
Columbia	2.4	5.7	10.9	129.9	148.9	.02	.04	.07
Polypay	9.0	18.8	6.9	130.6	165.2	.05	.11	.04
Rambouillet	20.7	1.1	7.4	126.7	155.9	.13	.01	.06
Targhee	12.4	3.5	6.6	105.9	127.8	.10	.03	.05

[a] σ^2_a, additive genetic variance; σ^2_{ms}, variance due to mating sire; σ^2_{pe}, permanent environmental variance; σ^2_e, residual variance; σ^2_p, total variance; h^2, fraction of total variance represented by σ^2_a, ms^2, fraction of total variance represented by σ^2_{ms}, pe^2, fraction of total variance represented by σ^2_{pe}.

generally less than those for direct genetic effects. In most cases, the proportions of variance due to permanent environmental effects of ewe for the older age class were greater than those for the middle age class. Generally, more than 80% of the phenotypic variance was associated with temporary environmental effects for LAB and LSB.

Estimates of heritability for LWW ranged from low to moderate (.00 to .25). Heritability estimates for this trait generally decreased as ewes became older. The smallest and largest heritability estimates were for COLU for the middle age (.00) and for TARG for the young age class (.25). Heritabilities for LWW estimated for RAMB and TARG were greater than those estimated for POLY. All estimates obtained for RAMB and TARG were .10 or larger, whereas estimates for POLY were less than .07. Heritability estimates for COLU were highest for the young age class (.19) but negligible at older ages (.00 and .02). The average estimates of heritability for LWW over age groups were .07, .06, .14, and .17 for COLU, POLY, RAMB, and TARG, respectively.

Estimates of variance components for mating sire and permanent environmental effects of ewe for LWW varied considerably with an indication of importance for some age groups in all breeds. For POLY, the proportion of variance due to mating sire effects was greater than the proportion due to direct genetic effects for all age groups and for COLU for middle and older age groups. The highest estimates of proportion of variance due to mating sire were obtained for POLY (.11, .09, and .11 for young, middle, and older age classes, respectively). This result suggests that selection of mating sire could improve litter weight weaned. The highest estimates of proportion due to permanent environmental effects of ewes were .07 for POLY for the middle age and for COLU for the older age class. The proportion of variance due to permanent environmental effects on the ewe tended to be smaller than heritability.

Three-Trait Analyses

(Co)variance components and genetic parameters estimated with three-trait analyses for LAB, LSB, and LSW traits are shown in Table 4 and for LWW in Table 5. In general, estimates of direct genetic variance from three-trait analyses were similar to estimates from single-trait analyses. Estimates of heritability for LAB and LSB ranged across age groups from .07 to .13 for COLU, from .13 to .16 for POLY, from .10 to .17 for RAMB, and from .01 to .17 for TARG. As with estimates obtained from single-trait analyses, heritability estimates of LSW with multiple-trait analyses were somewhat less than estimates for LAB and LSB. Estimates for LSW with three-trait analyses ranged from .07 to .12 for COLU, from .04 to .09 for POLY, from .01 to .11 for RAMB, and from .03 to .11 for TARG.

Following the guideline of Robertson (1959), genetic correlations between age classes larger than .80 will be assumed to indicate that similar genetic influences affect that trait across ages. Genetic correlations less than .80 between age classes will be assumed to be important to consider in selection programs.

Estimates of genetic correlations of LAB, LSB, and LSW between pairs of age classes were positive and ranged from .25 to 1.00. Direct genetic correlations for LAB and LSB between young and middle and young

Table 4. Estimates[a] of heritability, fractional variances, and correlations by age-trait and breed from three-trait (age class) analyses

	Lambs alive at birth[b]				Litter size at birth[c]				Litter size at weaning[d]			
Parameter	COLU[e]	POLY[e]	RAMB[e]	TARG[e]	COLU	POLY	RAMB	TARG	COLU	POLY	RAMB	TARG
h^2_{ay}	.13	.15	.12	.01	.11	.15	.14	.01	.12	.09	.01	.03
h^2_{am}	.09	.13	.16	.16	.08	.13	.17	.17	.07	.04	.11	.08
h^2_{ao}	.07	.16	.10	.09	.07	.16	.10	.11	.08	.08	.09	.11
r_{aym}	.59	.78	.55	.91	.62	.76	.69	.93	.76	.96	.81	.96
r_{ayo}	.46	.78	.49	.88	.34	.79	.54	.92	.25	.92	.45	1.00
r_{amo}	.99	1.00	1.00	1.00	.95	1.00	.98	1.00	.72	.99	.89	.97
pe^2_y	.11	.00	.00	.00	.02	.00	.01	.00	.00	.00	.00	.01
pe^2_m	.00	.00	.00	.00	.00	.00	.01	.00	.00	.07	.02	.00
pe^2_o	.04	.00	.00	.02	.04	.00	.01	.02	.00	.01	.01	.00
r_{eym}	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	–.00	.00
r_{eyo}	–.04	.00	.00	.00	–.01	.00	.00	.00	.00	.00	.00	.00
r_{emo}	.01	.00	.00	.00	.00	.00	.01	.00	.00	.00	.01	.00
e^2_y	.76	.84	.88	.99	.87	.84	.85	.99	.88	.91	.99	.96
e^2_m	.91	.87	.84	.84	.92	.87	.82	.83	.93	.90	.88	.92
e^2_o	.88	.84	.90	.89	.88	.84	.89	.87	.92	.92	.90	.89

[a] $h^2_{a(j)}$ = direct heritability for age class j (y = young, m = middle, and o = older); $r_{a(j,k)}$ = direct genetic correlation between expression in age class j and k; $pe^2_{(j)}$ = fractional variance due to permanent environmental effects in age class j; $r_{e(j,k)}$ = correlation between environmental effects in age classes j and k; and $e^2_{(j)}$ = fractional residual variance for trait j.

[b] Phenotypic variances for young, middle, and older ages of live births for COLU, .14, .29, .37; for POLY, .27, .37, .47; for RAMB, .12, .30, .34; for TARG, .11, .28, .32.

[c] Phenotypic variances for young, middle, and older ages of litter size at birth for COLU, .14, .29, .36; for POLY, .27, .36, .47; for RAMB, .12, .27, .34; for TARG, .11, .28, .32.

[d] Phenotypic variances for young, middle, and older ages of litter size at weaning for COLU, .22, .36, .39; for POLY, .30, .36, .40; for RAMB, .18, .35, .39; for TARG, .21, .34, .41.

[e] COLU = Columbia; POLY = Polypay; RAMB = Rambouillet; TARG = Targhee.

and older age classes were less than the guideline of .80 in COLU, POLY, and RAMB. Only estimates of genetic correlations between middle and older age classes for those breeds were greater than .80. For TARG, however, genetic correlations among all pairs of age classes were greater than .80 (.88 to 1.00) for LAB, LSB, and LSW. Estimates of genetic correlations for LSB are generally greater than those previously reported by Snowder (1987), whose estimates ranged from .00 to .62 across six age-specific groups in Rambouillet sheep. Estimates of genetic correlations among pairs of age classes for LSW were greater than the guideline of .80 (.92 to 1.00) for POLY and TARG. For RAMB, correlations between young and middle and middle and older age classes were greater than .80. For COLU, however, estimates of direct genetic correlations among all age classes were less than .80 and ranged from .25 to .76.

The estimated proportions of variance due to permanent environmental effects of ewe for LAB, LSB, and LSW generally were small, most less than 1%. The environmental correlations after combining permanent environmental and residual variances were near zero for all pairs of age classes.

Heritability estimates from three-trait analyses for LWW were almost the same as those for single-trait analyses, except for larger estimates for TARG. Heritability estimates for COLU ranged from .00 to .21, for POLY from .05 to .08, for RAMB from .12 to .15, and for TARG from .18 to . 29, which were greater than those for other breeds. Heritability estimates for both single and multiple traits showed the same pattern. Heritability of LWW tended to decrease as ewes became older.

Estimates of genetic correlations for LWW between all pairs of age classes for POLY and RAMB were greater than .80 (.82 to 1.00). For COLU, the correlation between young and middle age classes was low (.07), between young and older age classes was high (.88), and between middle and older age classes was moderately high (.54). For TARG, estimates of direct genetic correlations were .49, .65, and .98 between young and middle, young and older, and middle and older age classes, respectively. The proportions of variance due to mating sire and permanent environmental effects of ewe were generally less than those for direct genetic effects for LWW. These proportions were within ranges of .00 to .06 and .00 to .15 for middle and older age groups, respectively. The estimated variance due to effects of mating sire were similar across age classes for all breeds, whereas the permanent environmental effects associated with the ewe declined with age class of ewes. If the fraction of variance attributed to permanent environmental effects is added to that for temporary environmental effects for the young age, the fractions of variance due to environmental effects are similar for all breeds and all age classes. Correlations between all pairs of age classes within and across breeds for mating sire effects ranged from –.05 to 1.00, with most near zero. Small estimates of variance due to mating sires are likely the reasons for the higher estimates. After combining permanent environmental and residual variances to calculate environment correlations across age classes, the estimates were near zero, except for the –.13 between the middle and older age classes for Targhee.

Discussion

The most obvious result is that phenotypic variance was considerably larger for the medium and older age groups for LAB, LSB, and LSW, as expected, because of the differences in means. Similarly, the phenotypic variance for medium and older classes was two to four times larger than that for the young age class for LWW, also as expected, because of the influence of LSW on variation in LWW.

Previous estimates of heritability for prolificacy traits in sheep have not been consistent. Ranges of estimates are from .00 to .35 (Al-Shorepy and Notter, 1996), which are similar to estimates obtained from this study (.00 to .29). However, for Rambouillet, Bunge et al. (1990) reported an estimate of .15 for LSW, which is greater, and an estimate of .07 for LWW, which is smaller, than the estimates from this study. The estimates of direct genetic heritability with

Table 5. Estimates[a] of fractional variances and correlations for litter weight weaned from three-trait (age class) analysis

	Direct genetic effect					
Breed	h^2_{ay}	h^2_{am}	h^2_{ao}	r_{aym}	r_{ayo}	r_{amo}
Columbia	.21	.00	.03	.07	.88	.54
Polypay	.05	.08	.07	.96	.98	1.00
Rambouillet	.14	.12	.15	.82	.89	.99
Targhee	.29	.21	.18	.49	.65	.98
	Mating sire effect					
	ms^2_y	ms^2_m	ms^2_o	r_{msym}	r_{msyo}	r_{msmo}
Columbia	.00	.01	.01	.00	.99	.00
Polypay	.02	.06	.02	.00	–.05	.00
Rambouillet	.01	.02	.02	.00	.18	.00
Targhee	.01	.02	.01	.00	1.00	.00
	Permanent environmental effect					
	pe^2_y	pe^2_m	pe^2_o	r_{eym}	r_{eyo}	r_{emo}
Columbia	.26	.04	.03	.00	.00	–.01
Polypay	.00	.00	.01	.00	.00	.00
Rambouillet	.56	.04	.02	.00	.00	.00
Targhee	.14	.06	.15	.00	.00	–.13
	Temporary environmental effect and phenotypic variance					
	e^2_y	e^2_m	e^2_o	σ^2_{py}	σ^2_{pm}	σ^2_{po}
Columbia	.53	.96	.92	55.0	129.2	135.2
Polypay	.93	.85	.91	71.4	140.9	138.0
Rambouillet	.29	.82	.82	26.4	125.8	167.6
Targhee	.56	.62	.66	33.1	105.2	127.1

[a] y = young; m = middle; o = older age class; $h^2_{a(j)}$ = direct heritability for age class j; $r_{a(j,k)}$ = direct genetic correlation between expression in age class j and k; $ms^2_{(j)}$ = fractional variance due to mating sire for age class j; $r_{ms(j,k)}$ = correlation between mating sire effects in age classes j and k; $pe^2_{(j)}$ = fractional variance due to permanent environmental effects in age class j; $r_{e(j,k)}$ = correlation between environmental effects in age classes j and k; $e^2_{(j)}$ = fractional variance due to residual effects for age class j; and $\sigma^2_{p(j)}$ = phenotypic variance for age class j.

three-trait analyses agreed well with those of single-trait analyses for LAB, LSB, LWS, and LWW. The heritability estimates for, and estimates of correlations between, LAB and LSB as reported by van Zyl (1998) from traditional analyses of these records indicate that these two traits are essentially the same.

The low heritability estimates for LSW indicate that direct genetic effects for this trait are relatively less important than for other prolificacy traits. This result suggests that LAB and LSB should be used as measures of prolificacy at birth, rather than LSW.

The average heritability estimates for LWW from single-trait analysis across breeds were .07 for COLU, .06 for POLY, .14 for RAMB, and .17 for TARG. Heritability estimates over age groups and breeds of .00 to .25 are within the range of previous estimates of –.05 to .50 cited by Abdulkhaliq et al. (1989), although most of those estimates ranged from .03 to .20. The range of estimates reviewed by Fogarty (1995) was .08 to .26, with an average of .15, mostly from paternal half-sib information. Abdulkhaliq et al. (1989) reported heritability estimates of .13 and .25 for TARG and COLU based on variance components due to sire and ewe effects.

Heritability estimates for LWW for the young age classes for COLU, RAMB, and TARG are greater (.19, .17, and .25) than those for other age classes of the same breeds. The numbers of animals in the young age classes, however, were small compared with other age classes and may not allow a reasonable comparison. The number of animals of the young age class in POLY is considerable, and the heritability estimate for this group was equal to that of the middle age class and similar to that of the older age class. The averages over all breeds for LWW suggest that direct additive genetic effects are relatively less important as ewes become older. Estimates of variance due to effects of mating sire were relatively small. The estimates of variance due to permanent environmental effects of ewes were somewhat variable but large enough to be considered in genetic evaluation for LWW. The artifact described in the Materials and Methods section when including a permanent environmental effect in the model for the young age class can be seen in Table 4 for LAB for COLU and especially in Table 5 for COLU, RAMB, and TARG for LWW. The sums of the fractions of variances for permanent and temporary environmental effects are similar across breeds for LWW, although the individual variances seem to be quite different from breed to breed. The prolificacy traits seem sensitive to temporary environment.

For TARG, the genetic correlations among all age groups for LAB, LSB, and LSW were high (ranging from .88 to 1.00). These results indicate that similar genetic effects are involved in expression of these traits for a ewe at different ages, so expression in young, middle, and older age classes of ewes in TARG may be considered one trait rather than two or three traits for genetic evaluation. The same statement would hold for LSW for POLY, and possibly for RAMB. Direct genetic correlations between young and middle and young and older age classes for LAB and LSB for COLU were considerably less than .80, which indicates that those traits may need to be defined by age of ewes.

In general, and as expected, heritability estimates obtained for LWW with multiple-trait analyses were within the range of those obtained with single-trait analyses. In particular, for COLU and TARG, direct genetic heritability for LWW tended to decrease as ewes became older, indicating that environmental effects have more influence on older ewes than on young ewes for this composite trait. Genetic correlations among all pairs of age classes for POLY and RAMB were greater than .80. Similarly, genetic correlations between middle and old age classes for TARG and between young and old classes for COLU also were greater than .80 for LWW. The average genetic correlation between young and older age classes was .85 and between medium and older age classes was .88. Although the average between young and medium was only .58, that average was influenced by the small estimate of .07 for COLU. Expression in middle and older age groups seems to be essentially the same for LWW, so LWW can be considered a single trait rather than more than one trait in a selection program.

For all breeds, only non-zero estimates of the genetic correlations between effects of mating sire were for young and middle age classes, but the amount of variance due to mating sire is so small that the correlations have little meaning.

Implications

For litter weight weaned, performance of a ewe at a young age may not be the same trait as performance at older ages. A two-trait analysis for genetic evaluation should be considered, because heritability at a young age seems larger and phenotypic variance seems smaller than for later ages. For litter size at birth and at weaning, genetic correlations suggest no need to consider middle and older age performance to be different traits. Correlations between performance at young and older ages suggest theoretical calculations be done before deciding whether young and older age performance might be considered as two traits for genetic evaluation and selection. Due to the small number of measurements for young ewes of some breeds, caution is recommended in interpreting average genetic correlations between young and middle or older age classes. The small fraction of variance associated with genetic and permanent environmental effects of ewes suggests that previous performance is not very indicative of subsequent reproduction.

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