

JOURNAL OF ANIMAL SCIENCE

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J Anim Sci 1997. 75:1729-1737.

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Genetic Parameter Estimates for Growth and Fleece Characteristics in Targhee Sheep¹

D. R. Notter* and J. D. Hough[†]

*Department of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg 24061-0306 and [†]American Hereford Association, Kansas City, MO 64108

ABSTRACT: Weaning weights at 60 (WW60) and 120 d (WW120), 60- to 120-d postweaning gains (PWG) for lambs weaned at 60 d, 120- to 365-d postweaning gains (YG) for lambs weaned at 120 d, fleece weights (FWT), and fiber diameters (FD) from 20 Targhee flocks were used to estimate parameters required for multiple-trait genetic evaluation. Flocks from western states (n = 10) recorded primarily WW60 (n = 1,762), WW120 (n = 5,961), YG (n = 2,388), FWT (n = 2,824), and FD (n = 2,000). Eastern flocks primarily recorded WW60 (n = 1,754) and PWG (n = 1,237). Heritability estimates were .01 for WW60 (.00 for western flocks and .07 for eastern flocks), .10 for WW120, .33 for PWG, .20 for YG, .41 for FWT, and .58 for FD. Additive maternal and maternal permanent environmental effects as a proportion of phenotypic variance were .10 and .09,

respectively, for WW60 and .05 and .08 for WW120. In western flocks, maternal additive and permanent environmental effects on WW60 and WW120 were highly correlated (>.81), whereas WW120 and YG had a small positive additive genetic correlation (.19) but a negative residual correlation (-.34). Fleece weight had a genetic correlation of .50 with WW120 and YG. Supplemental analyses suggested that the observed genetic relationship between fleece weight and weaning weight arose primarily from a genetic association between additive direct genetic effects on fleece weight and additive maternal effects on weaning weight. Fiber diameter was nearly independent of body weights but had an undesirable additive correlation of .51 with FWT. In eastern flocks, WW60 and PWG had an additive correlation of .71 and a residual correlation of .15.

Key Words: Sheep, Genetic Parameters, Growth, Fleece, Maternal Effects

J. Anim. Sci. 1997. 75:1729-1737

Introduction

Procedures for multiple-trait genetic evaluation of livestock require accurate estimates of genetic and environmental parameters. Best linear unbiased prediction is the current method of choice for genetic evaluation of continuously distributed traits and assumes that (co)variances are known without error, although in reality this is seldom, if ever, the case. When population (co)variances are not known, the generally accepted current strategy is to estimate necessary (co)variances using REML and use these estimates for BLUP of breeding values. In such a situation, one must also decide whether to estimate (co)variances separately, and often with limited accuracy, for each population or to use pooled values estimated from many populations. Average values for

sheep appropriate to the latter option were given by Fogarty (1995).

The U.S. National Sheep Improvement Program (NSIP) was established in 1986 to provide within-flock genetic evaluations for U.S. sheep producers (NSIP, 1986). The program used single-trait prediction methods with variances derived from literature values. In 1995, the program was extended to provide across-flock, multiple-trait genetic evaluations of body weights and fleece characteristics for the Targhee breed. The purpose of this research was to estimate the necessary (co)variances using NSIP Targhee data and to compare them with literature values.

Materials and Methods

Data

Body weights and fleece data were obtained from 20 NSIP Targhee flocks located in seven states (numbers of flocks are in parentheses): New Hampshire (2), Illinois (1), Michigan (1), Wisconsin (6), South

¹This research was partially funded by the U.S. National Sheep Improvement Program.

Received August 28, 1996.

Accepted February 21, 1997.

Dakota (1), Montana (8), and Washington (1). Data were reported from 1984 through 1993.

Weight Data. In NSIP, body weights can be recorded at 30, 60, 90, 120, 180, or 365 d of age, but individual flocks can report no more than three weights, one of which must be a weaning weight. Other weights may be either pre- or postweaning weights. For this study, preweaning and weaning weights taken at the same age were combined because a preweaning weight can be treated as a potential weaning weight. The ranges in ages that are allowed for each of the six weights are 23 to 37, 30 to 83, 68 to 113, 98 to 143, 150 to 210, and 335 to 395 d, respectively. Numbers of weaning weights in the complete data set were 211, 4,156, 370, and 6,476 at 30, 60, 90, and 120 d, respectively. Numbers of postweaning weights were 2, 237, 1,806, and 3,708 at 60, 90, 120, and 365 d, respectively. From these weights, 60- and 120-d weaning (and preweaning) weights and 120- and 365-d postweaning weights were chosen for analysis.

Weaning weights were adjusted to a standard age of t days by adding t times the preweaning ADG to birth weight, when birth weight was reported, or as t times the preweaning weight per day of age, when birth weight was not reported. Age-adjusted weaning weights were adjusted for dam age, type of birth and rearing, and lamb sex using multiplicative factors from NSIP (1986). Adjusted 120-d postweaning weight was obtained as the sum of the adjusted 60-d weaning weight and 60 times the unadjusted postweaning ADG. Adjusted yearling weight was obtained as the sum of the adjusted 120-d weaning weight and 245 times the unadjusted postweaning ADG.

Fleece Data. The NSIP fleece traits are greasy or clean fleece weight, fiber diameter, and staple length. Fleece traits are to be recorded at approximately 1 yr of age. However, a single fleece record for older animals may also be submitted at the time the flock is enrolled in NSIP to provide baseline data for the entire flock. Producers are encouraged to report actual laboratory-derived fiber diameters but are also permitted to convert visually determined spinning count or blood grade evaluations to fiber diameter measurements in microns using factors given by NSIP (1995).

Greasy fleece weight ($n = 3,578$) and fiber diameter ($n = 2,288$) were chosen for analysis. Only four clean fleece weights and no staple lengths were reported. Fleece weight and fiber diameter had been measured on 1,743 animals. Eighty percent of fleece weight records and 78% of fiber diameters were from yearlings; the remainder were from older animals. In yearlings, 67% of fleece weights and 71% of fiber diameters were from females. In older animals, 97% of fleece weights and fiber diameters were from females. Fleece weights were linearly adjusted to either an initial shearing age of 365 d for yearlings or a shearing interval of 365 d for older animals, assuming

a constant rate of wool growth during the year. Postyearling animals were required to have at least two fleece weight records to allow calculation of a shearing interval. Fiber diameters were not adjusted.

Pedigree Data. A total of 9,161 animals had data for at least one body weight or fleece trait in the final data. Pedigree information was based on NSIP sire and dam records. When all recorded ancestors of animals with data were included, the total number of animals in the analysis was 11,317.

Regional Differences. The traits recorded differed between regions (Table 1). Flocks from eastern states ($n = 10$) generally recorded 60-d weaning and 120-d postweaning weights but rarely recorded 120-d weaning or 365-d postweaning weights. Also, 99% of the lambs in eastern flocks were creep-fed before weaning. In contrast, western flocks ($n = 10$) usually recorded 120-d weaning and 365-d weights, and often recorded 60-d preweaning weights, but normally did not record 120-d postweaning weights. Only 3% of lambs from western flocks were creep-fed before weaning. Also, 81% of fleece weights and 96% of fiber diameters came from western flocks.

Statistical Analyses

Contemporary groups for body weights in NSIP were formed based on flock, management code, date of weighing, and a producer-supplied location code. Four management codes for weaning weights discriminated between lambs that were or were not creep-fed and between dams that were all fed alike or were fed according to the number of lambs being nursed. Two management codes for postweaning weights discriminated between animals fed as market lambs and those fed on a postweaning gain test. Contemporary groups for postweaning weights also included the weaning contemporary group. Animals of different sexes were included in the same contemporary group for weaning weight but were placed in separate contemporary groups for postweaning weights. Animals were excluded from the data if their contemporary group contained only a single litter, if information on ewe age or type of birth and rearing was missing, or if the lamb was reared artificially or by a foster dam. The latter restriction accounted for most of the weaning weights that were discarded. For postweaning weights, animals were also required to have a valid weaning weight. Numbers of records in the final data set for each pair of weights are shown in Table 1 with numbers of flocks, sires, dams, and litters represented.

Contemporary groups for fleece data were based on date of shearing, age at shearing (yearling vs older), sex, and a producer-supplied location code. Animals were excluded from the data if the contemporary group contained only one animal, if age at shearing of yearlings was not between 280 and 510 d, or if shearing interval of older sheep was not between 160 and 550 d. For fleece traits, the final data set

Table 1. Numbers of flocks, animals, sires, dams, and litters for each trait and numbers of animals for each pair of traits by region

Trait	No. of flocks	No. of animals	No. of sires	No. of dams	No. of litters	No. of animals for pairs of traits by region ^a					
						60-d weaning wt	120-d weaning wt	120-d postweaning wt	365-d postweaning wt	Fleece wt	Fiber diameter
60-d weaning wt	11	3,516	64	1,321	2,482	1,762 1,754	1,686	0	908	756	372
120-d weaning wt	9	6,047	107	2,120	4,488	0	5,961 86	0	2,380	2,178	1,488
120-d postweaning wt	2	1,237	19	394	883	1,233	0	0 1,237	0	0	0
365-d postweaning wt	3	2,407	52	1,045	1,884	18	0	0	2,388 19	1,408	785
Fleece wt	13	3,473	212	1,741	2,798	249	0	214	0	2,824 649	1,629
Fiber diameter	7	2,083	149	1,233	1,805	15	0	8	0	83	2,000 83

^aNumbers for western and eastern flocks are shown above and below the diagonal, respectively. Pairs of numbers on the diagonal are numbers of animals for each trait in western (upper value) and eastern flock (lower value).

contained 3,473 fleece weights from 13 flocks and 2,083 fiber diameters from seven flocks. Numbers of animals with fleece and body weight information are shown in Table 1.

(Co)variance components were estimated using derivative-free REML (Boldman et al., 1993). Single-trait analyses were initially used to evaluate the significance of the various random effects considered for each trait and to aid in choosing the set of traits that would be included in the final Targhee across-flock genetic evaluation. Bivariate analyses were then conducted for the chosen traits using variance component estimates from single-trait analyses as starting values. Additive direct and residual covariances were calculated for all pairs of traits (i,j). Additive maternal and permanent environmental covariances between traits were also calculated when final single-trait models for both traits included these effects. All other covariances between different traits were initially assumed to be 0. However, covariances between additive direct effects on trait i and additive maternal effects on trait j were also estimated in supplemental analyses for traits that were influenced by maternal effects. Single-trait analyses used combined data from both eastern and western flocks, but bivariate analyses were conducted separately for western and eastern flocks because specific pairs of traits were usually available from only one region (Table 1). Tests of significance of random effects in single-trait analyses were performed using likelihood ratio tests after deleting each random effect (excluding residual) from the model. In bivariate analyses, significance of

covariances was determined by likelihood ratio tests after fixing each covariance to 0.

Adjusted weaning weights were analyzed with an animal model that included fixed effects of contemporary group and additive direct and maternal random effects as well as a random permanent environmental effect of the dam. Additive direct and maternal effects were assumed to be normally distributed with mean 0 and variances $A\sigma_a^2$ and $A\sigma_m^2$, respectively, where A is the additive numerator relationship matrix and σ_a^2 and σ_m^2 are additive direct and maternal variances, respectively. The additive covariance between direct and maternal effects (σ_{am}) and the associated additive direct-maternal correlation (r_{am}) were also estimated in single-trait analyses. Permanent environmental effects of the dam and residual effects were assumed to be normally distributed with mean 0 and variances $I_d\sigma_{pe}^2$ and $I_n\sigma_e^2$, respectively, where I_d and I_n are identity matrices with orders equal to the number of dams and individual records, respectively, and σ_{pe}^2 and σ_e^2 are maternal permanent environmental and residual variances, respectively. Additive direct, additive maternal, and dam permanent environmental effects were also expressed as proportions of phenotypic variance (h^2 , m^2 , and c^2 , respectively). The total maternal effect, $t_m = m^2 + c^2 + 1/4h^2 + mr_{am}h$, was calculated to estimate repeatability of ewe performance.

Postweaning data were analyzed either as adjusted postweaning weights or as postweaning gains. Analyses of adjusted postweaning weights used the same

Table 2. Genetic parameter estimates for body weights (kilograms) from single-trait analyses

Parameter ^a	60-d weaning weight			120-d weaning weight	120-d postweaning weight	Yearling weight
	All flocks	Western flocks	Eastern flocks			
Mean	24.7	22.2	27.1	36.3	46.1	71.6
σ_a^2	.15	.00	1.25	3.21	9.36	15.22
σ_m^2	1.67	1.50	2.12	1.71	1.67	2.60
σ_{pe}^2	1.47	1.25	1.42	2.64	1.20	3.11
σ_e^2	13.13	11.16	14.07	24.13	24.38	36.75
σ_p^2	16.42	13.92	18.86	31.68	36.61	57.68
h^2	.01	.00	.07*	.10*	.26*	.26*
m^2	.10*	.11*	.11*	.05*	.05 ^b	.05 [†]
c^2	.09*	.09*	.08*	.08*	.03 ^b	.05 [†]
t_m	.19*	.20*	.21*	.16*	.15*	.17*

^a σ_a^2 = additive direct genetic, σ_m^2 = additive maternal genetic, σ_{pe}^2 = maternal permanent environmental variance, σ_e^2 = residual variance, σ_p^2 = phenotypic variance, h^2 = heritability = σ_a^2/σ_p^2 , $m^2 = \sigma_m^2/\sigma_p^2$, $c^2 = \sigma_{pe}^2/\sigma_p^2$, and t_m = maternal repeatability = $(\sigma_m^2 + \sigma_c^2 + 1/4\sigma_a^2)/\sigma_p^2$.

^b $(m^2 + c^2)$ was different from 0 ($P < .05$) but the total effect could not be statistically partitioned into effects of m^2 and (or) c^2 .

[†]Different from 0 ($P < .10$).

*Different from 0 ($P < .05$).

model that was used for weaning weights, whereas analyses of postweaning gains did not consider maternal additive or permanent environmental effects. Fleece data were analyzed with the same model that was used for postweaning gains.

Results and Discussion

Single-Trait Analyses. Variance component estimates for body weights from single-trait analyses are shown in Table 2. At 60 d, the direct additive contribution to weaning weight was small ($h^2 = .01$) and not significant. In contrast, maternal additive and permanent environmental components were larger and similar in size ($m^2 = .10$; $c^2 = .09$), and both were significant; maternal repeatability was .19. The additive direct-maternal covariance for 60-d weaning weight was not estimated because of the very low direct additive variance for this trait. Thus, 60-d weaning weight was controlled primarily by maternal effects.

When 60-d weaning weights were analyzed separately for western and eastern flocks, eastern lambs were heavier, and all variance components were correspondingly larger. Additive effects were more important in the predominantly creep-fed eastern lambs ($h^2 = .07$) than in the predominantly non-creep-fed western lambs ($h^2 = .00$). However, the relative importance of additive and permanent environmental maternal effects was similar across regions. The repeatability of 60-d weaning weight as a trait of the ewe was .20 for western lambs and .21 for eastern lambs.

For 120-d weaning weight, additive effects were more important than at 60 d ($h^2 = .10$; $P < .05$). Additive maternal effects were correspondingly reduced ($m^2 = .05$) but remained important ($P < .05$), whereas maternal permanent environmental effects ($c^2 = .08$; $P < .05$) were of the same magnitude as those observed at 60 d. Maternal repeatability for 120-d weaning weight was .16, slightly less than that observed at 60 d. No significant σ_{am} was observed ($r_{am} = .12$; $P = .75$) for 120-d weaning weight, and this covariance was subsequently excluded from analyses of all weights reported in Table 2. Estimates of t_m for 60- and 120-d weaning weights were thus calculated as $m^2 + c^2 + 1/4 h^2$.

Yearling weights came primarily from western flocks, whereas 120-d postweaning weights came primarily from eastern flocks and generally approximated typical market weights. Heritabilities for these two weights were the same (.26; $P < .05$). Additive and (or) permanent environmental maternal effects remained significant for both postweaning weights. The origin of these maternal carryover effects (additive or permanent environmental) could not be statistically determined for 120-d postweaning weights; models including σ_m^2 , σ_{pe}^2 , or both had essentially the same likelihoods. For yearling weight, additive and permanent environmental maternal effects approached significance ($P < .10$).

Genetic parameter estimates for body weights showed the expected increase in importance of additive effects with increasing compositional maturity, feeding level, and body weight. The importance of maternal effects correspondingly declined with

Table 3. Genetic parameter estimates for postweaning gains and fleece traits from single-trait analyses

Parameter ^a	60- to 120-d postweaning ADG, kg/d	120- to 365-d postweaning ADG, kg/d	Fleece weight, kg	Fiber diameter, μm
Mean	.31	.13	3.8	22.4
σ_a^2	.0012	.0001	.139	1.33
σ_e^2	.0024	.0006	.202	.96
σ_p^2	.0037	.0007	.341	2.29
h^2	.33*	.20*	.41*	.58*

^aSee Table 2 for definition of abbreviations.

*Different from 0 ($P < .05$).

increasing maturity but remained significant through 12 mo of age.

Heritabilities of postweaning ADG (Table 3) indicated that additive effects were more important in relatively intensively fed eastern lambs ($h^2 = .33$) than in the more extensively managed western lambs ($h^2 = .20$). Means were larger and phenotypic variance in postweaning ADG was over three times as large for eastern lambs. Maternal effects on postweaning gains were tested in preliminary analyses but were not significant ($P > .25$). Heritabilities for fleece weight and fiber diameter (Table 3) were relatively large, .41 and .58, respectively.

Covariance Component Estimates. Based on single-trait analyses, final traits chosen for inclusion in the Targhee genetic evaluation were 60- and 120-d weaning weights, 60- to 120-d postweaning gain, 120- to 365-d postweaning gain (hereafter referred to as yearling gain), fleece weight, and fiber diameter. Sixty- to 120-d postweaning gain and yearling gain were calculated as ADG in the period times 60 and 245, respectively. Postweaning gains were analyzed in preference to postweaning weights to avoid the need to fit maternal effects for these traits. Only these traits were included in bivariate analyses. Variance compo-

nents fitted for each trait were those shown in Tables 2 and 3. The σ_{am} for maternally influenced traits was assumed to be equal to 0 based on results of single-trait analyses. Initially, only covariances between additive effects, residual effects, and, if appropriate, additive maternal effects and permanent environmental effects for different traits were fitted. However, covariances between additive effects for trait i and additive maternal effects for trait j were also estimated in supplemental analyses where appropriate.

Results of bivariate analyses are shown in Tables 4 through 7. Heritabilities from bivariate analyses were similar to those from univariate analyses for growth traits and fiber diameter, but heritability of fleece weight was lower when data were restricted to western flocks (.32 vs .41; Tables 3 and 4). This change in part reflects an unreasonably high estimate of .73 for fleece weight that was obtained when the 649 fleece weight records from eastern flocks were analyzed alone.

In western flocks (Table 4), additive genetic correlations involving 60-d weaning weight could not be estimated because h^2 was only .01 for this trait. However, relatively large positive residual correlations were observed between 60-d weaning weight and

Table 4. Additive direct and residual correlations and heritabilities for western flocks from bivariate analyses^a

Trait ^b	Trait ^b				
	WW60	WW120	YG	FWT	FD
WW60	.01	— ^c	— ^c	— ^c	— ^c
WW120	.75*	.10*	.19	.50*	.01
YG	-.02	-.34*	.21*	.50*	.28*
FWT	.54*	.38*	.03	.32*	.51*
FD	.03	.05	-.02	.08	.58*

^aHeritabilities, on the diagonal, are the average of values from all bivariate analyses. Additive genetic and residual correlations are shown above and below the diagonal, respectively.

^bWW60 = 60-d weaning weight, WW120 = 120-d weaning weight, YG = 120- to 365-d ADG, FWT = fleece weight, FD = fiber diameter.

^cNot estimated because of low heritability for WW60.

*Different from 0 ($P < .05$).

Table 5. Additive maternal and maternal permanent environmental correlations and variance component ratios for weaning weights in western flocks^a

Trait ^b	Trait ^b	
	WW60	WW120
WW60	.07*, .12*	.81*
WW120	.97*	.06*, .08*

^aValues on the diagonal are additive maternal and maternal permanent environmental variances, respectively, as proportions of phenotypic variance. The additive maternal correlation is above the diagonal. The maternal permanent environmental correlation is below the diagonal.

^bWW60 and WW120 are 60-d and 120-d weaning weights, respectively.

*Different from 0 ($P < .05$).

120-d weaning weight (.75) and fleece weight (.54). In contrast, residual correlations of 60-d weaning weight with yearling gain and fiber diameter were close to 0.

The 120-d weaning weight had a modest but nonsignificant additive genetic correlation of .19 with yearling gain, whereas the residual correlation between these traits was negative and significant ($-.34$), indicating a compensatory environmental relationship between pre- and postweaning gains in western flocks. A positive additive genetic correlation (.50; $P < .05$) and a somewhat smaller positive residual correlation (.38; $P < .05$) were observed between 120-d weaning weight and fleece weight. The additive and residual correlations between 120-d weaning weight and fiber diameter were small and not significant.

Yearling gain had a positive genetic correlation with fleece weight (.50; $P < .05$) and a smaller positive (unfavorable) correlation with fiber diameter (.28; $P < .05$). Residual correlations between yearling gain and fleece traits were close to 0. An undesirable genetic correlation of .51 ($P < .05$) was observed between fleece weight and fiber diameter. The residual correlation between these traits was also unfavorable, but was much smaller (.08).

Correlations between additive maternal effects and between permanent environmental maternal effects on 60- and 120-d weaning weights (Table 5) were large. The maternal permanent environmental correlation of .97 was not significantly different from 1.0. The additive maternal correlation was also large (.81) but was significantly less than unity.

From Table 4, we conclude that measures of body weight and growth rate in Targhee sheep were favorably correlated genetically and had favorable genetic associations with fleece weight, but were genetically independent of, or slightly unfavorable to, fiber diameter. Additive and permanent environmental maternal effects on weaning weights at 60 and 120 d were highly correlated, indicating that many of the

same genes are involved. The only genetic antagonism of consequence was between fleece weight and fiber diameter. Simultaneous improvement in these traits will require explicit consideration of this antagonism.

Residual correlations between performance traits in western flocks were large between 60- and 120-d weaning weight but were relatively small for other pairs of traits. Residual correlations involving fleece weight were somewhat inconsistent; the largest correlation was with 60-d weaning weight (.54), and the correlation declined for 120-d weaning weight (.38) and for yearling gain (.03). In interpreting differences among these correlations, however, it is wise to recognize that substantially different sets of animals from different flocks were used in their calculation (Table 1).

Effects of correlations between direct additive genetic effects for trait *i* and maternal additive effects for trait *j* are shown in Table 6. Residual and permanent environmental maternal correlations from these models changed by, at most, .05 from those given in Tables 4 and 5 and are not shown. Additive maternal effects on 60-d weaning weight had relatively large favorable associations with additive genetic effects on yearling gain ($r = .63$; $P < .05$) and fleece weight ($r = .51$; $P < .05$), but no significant association with additive genetic effects on fiber diameter ($r = .13$).

Additive maternal effects on 120-d weaning weight were not significantly correlated with additive genetic effects for either yearling gain or fiber diameter. However, the positive genetic relationship between fleece weight and 120-d weaning weight in Table 4 seemed to primarily reflect a positive association between additive maternal effects on 120-d weaning weight and additive genetic effects on fleece weight (.46; $P < .05$). The direct additive genetic relationship between these two traits in Table 6 was not significant. Results in Table 6 generally do not contradict those in Table 4 but suggest a favorable genetic association between fleece weight and maternal ability. No additional genetic antagonisms were evident.

Table 6. Correlations of additive direct and maternal effects on weaning weights with additive direct effects on postweaning gain and fleece traits in western flocks^a

Trait ⁱ	Trait ^j		
	YG	FWT	FD
WW60 ^c	—, .63*	—, .51*	—, .13
WW120	.25*, -.13	.22, .46*	-.20, .24

^aTable entries are correlations of additive direct and maternal effects, respectively, of trait *i* with additive direct effects of trait *j*.

^bSee Table 4 for trait abbreviations.

^cCorrelations involving direct effects of WW60 were not estimated because of low heritability of WW60.

*Different from 0 ($P < .05$).

Table 7. Additive genetic and residual correlations and heritabilities for growth in eastern flocks^a

Trait ^b	Trait ^b	
	WW60	PWG
WW60	.07*	.71*
PWG	.15*	.33*

^aHeritabilities are on the diagonal. Additive direct and residual correlations are above and below the diagonal, respectively. All additive-maternal covariances were assumed to be 0.

^bWW60 = 60-d weaning weight, PWG = 60- to 120-d postweaning ADG.

*Different from 0 ($P < .05$).

Correlations involving 60-d weaning weight and 60 to 120 d postweaning gain in eastern lambs are shown in Table 7. The estimated additive correlation was relatively large (.71; $P < .05$), whereas the residual correlation was smaller but still positive (.15; $P < .05$). Entries in Table 7 assume no covariance between additive maternal effects on weaning weight and direct effects on postweaning gain. When this covariance was included in a supplemental analysis, the correlation between additive genetic effects for these two traits was reduced (.46; $P < .05$) but was still over twice as large as the correlation between additive maternal effects on 60-d weaning weight and additive direct effects on postweaning gain (.21; $P > .05$).

Comparisons with Literature Values. Estimates of genetic parameters for growth, fleece, composition, and reproductive traits in sheep were reviewed by Fogarty (1995). Estimates of heritabilities were listed separately for wool, dual-purpose (including Targhee), and meat breeds. Heritabilities of postweaning weights and yearling weights from Fogarty (1995), when averaged across breed types, were .27 and .32, respectively, and were close to the value of .26 obtained for 120-d and 365-d postweaning weights in these Targhees. In contrast, estimates of heritabilities of weaning weights from Fogarty (1995) were greater than those obtained in the present study, averaging .33, .20, and .21 for wool, dual-purpose, and meat breeds, respectively. In a more recent study, Tosh and Kemp (1994) reported heritabilities for 50- and 100-d weights of .16 and .39, respectively, for Hampshires, .21 and .25 for Polled Dorsets, and .07 and .05 for Romanov lambs from the Canadian Sheep Genetic Evaluation Program. Maria et al. (1993) reported heritabilities of .34 for weaning weight at about 40 d and of .09 for postweaning 90-d weight in Spanish Romanov lambs. N asholm and Danell (1996) reported heritabilities of .10 for preweaning weight at approximately 60 d, .12 for weaning weight at approximately 105 d, and .16 for 120-d weight. Fossceco and Notter (1995) reported heritabilities of .23 for 60-d weaning weight and .23 and .25 for postweaning weights at 90 and 120 d, respectively, in a spring-lambing crossbred flock. Al-Shorepy and Notter (1996) reported herita-

bilities for the same population in fall lambing of .05 for 60-d weaning weight, .09 for 90-d postweaning weight, and .19 for 120-d postweaning weight. Estimates of heritability for postweaning weights from these studies tend to be lower than those summarized by Fogarty (1995) and those obtained in the current study. Heritabilities for weaning weights were also lower than those summarized by Fogarty (1995) but were still considerably above those obtained in the current study. The low heritability estimates for 60-d weaning weight in the western Targhee lambs in particular requires careful consideration, indicating that little additive genetic improvement in this trait may be possible, especially in lambs that are not creep-fed.

Relatively few estimates of variance components for maternal effects on body weights have been reported and maternal effects were not explicitly considered by Fogarty (1995). In addition, interpretation of genetic parameter estimates for maternally influenced traits from animal models is critically dependent on the structure of the data and on the model(s) fitted. Separation of additive maternal and permanent environmental maternal effects requires repeated records on individual ewes and the presence of related ewes in the data. Yet, even when this requirement is met, results are often inconsistent. For example, Al-Shorepy and Notter (1996) fitted a series of animal models to lamb body weights at 60 (weaning), 90, and 120 d. The most complete model included additive direct effects, additive maternal effects, maternal permanent environmental effects, and litter (year within ewe environmental plus nonadditive genetic) effects. Heritability ranged from .04 to .08 for weaning weight in models that contained at least one maternal effect but was .24 in a model that fitted only additive direct effects. Also, for weaning weight, the additive maternal effect fitted alone accounted for 18% of phenotypic variance; the maternal permanent environmental effect fitted alone accounted for 17% of phenotypic variance; the additive maternal and permanent environmental effects fitted together accounted for 10 and 9%, respectively, of phenotypic variance; and additive maternal, permanent environmental and litter effects fitted together accounted for 10, 5, and 11%, respectively, of phenotypic variance. Tosh and Kemp (1994) also found that excluding additive maternal effects from an animal-model analysis of 50-d weights increased the average heritability estimate for three breeds from .14 to .22.

In addition, some authors have reported unreasonably large negative covariance (σ_{am}) between direct and maternal additive effects. Thus, Maria et al. (1993) reported an additive direct-maternal correlation of $-.98$ for weaning weight. In the presence of such estimates, estimates of additive direct and(or) maternal variances may be large and can be accepted only if users also accept and incorporate the additive-maternal covariance into any resulting applications.

Thus, for weaning weight, Maria et al. (1993) estimated $h^2 = .34$ and $m^2 = .25$, even though the total additive variance, $\sigma_a^2 + .5\sigma_m^2 + 1.5\sigma_{am}$ (Willham, 1972), in the presence of the large negative σ_{am} accounted for only 18% of phenotypic variance. It seems clear that smaller absolute values of σ_{am} would have required smaller absolute values of h^2 and (or) m^2 .

Apparent inconsistencies in partitioning of maternal repeatability (t_m) into its components also occur in the literature. Thus, for lamb weaning weights in the current study, $t_m = .20$, $.21$, and $.16$ for 60-d weaning weight in western lambs, 60-d weaning weight in eastern lambs, and 120-d weaning weight, respectively, with $c^2 = .09$, $.08$, and $.08$, and $m^2 = .11$, $.11$, and $.05$, respectively. Likewise, for models fitting σ_a^2 , σ_m^2 , σ_{pe}^2 , and σ_{am} and in other studies, Maria et al. (1993) reported $t_m = .05$ for weaning weight with $m^2 = .25$, $c^2 = 0$, and $r_{am} = -.98$, and $t_m = .07$ for 90-d postweaning weight with $m^2 = .01$, $c^2 = .07$, and $r_{am} = -.97$. For weaning weights, Al-Shorepy and Notter (1996) reported $t_m = .20$ with $m^2 = .10$, $c^2 = .09$, and r_{am} set to 0 (the estimated value was $.01$), and N sholm and Danell (1996) reported $t_m = .22$ with $m^2 = .13$, $c^2 = 0$, and $r_{am} = .47$.

In weaning weight models that also included a litter effect (l^2), Al-Shorepy and Notter (1996) reported that $t_m = .27$ with $m^2 = .10$, $c^2 = .05$, and $l^2 = .11$. Fossceco and Notter (1995) fitted only additive maternal plus litter effects, as did Tosh and Kemp (1994). For Fossceco and Notter (1995), $t_m = .17$ with $m^2 = 0$, $l^2 = .11$, and r_{am} set to 0, whereas for Tosh and Kemp (1994), $t_m = .36$, $.34$, and $.26$ with $m^2 = .14$, $.19$, and $.06$, $c^2 = .27$, $.18$, and $.21$, and $r_{am} = -.57$, $-.42$, and $-.39$ in Hampshire, Polled Dorset, and Romanov, respectively. Burfening and Kress (1993) estimated a number of statistical associations among relatives and solved for additive direct and maternal (co)variances. Resulting estimates of m^2 for 120-d weight ranged from $.07$ to $.48$, and estimates of r_{am} ranged from $-.88$ to $.55$. However, five of six estimates of r_{am} were $-.41$ or less. Taken together, these estimates support the estimate of $t_m = .16$ to $.21$ for weaning weight from the current study, but provide little consistent guidance on the partition of maternal effects into m^2 and c^2 .

In contrast to the current study, Mortimer and Atkins (1994) reported significant maternal effects on greasy ($m^2 = .065$) and clean fleece weights ($m^2 = .054$) in 15- to 16-mo-old Merino hoggets. Maternal effects did not influence fiber diameter in that study. They also reported an additive maternal effect on hogget body weight ($m^2 = .07$) that was consistent with maternal effects on yearling weight from the current study ($m^2 = .05$ and $c^2 = .05$).

Additive genetic correlations from Fogarty (1995) exceeded $.72$ among all pairs of body weights. For the current study, calculated additive correlations were $.62$ between 120-d weaning weight and calculated

yearling weight in western flocks and $.87$ between 60-d weaning and 120-d postweaning weights in eastern flocks. However, the genetic correlation between 120-d weaning weight and 120- to 365-d postweaning gains of $.19$ is considerably less than estimates in previous literature.

Heritabilities of greasy fleece weight from Fogarty (1995) averaged $.34$ for wool breeds and $.36$ for dual-purpose breeds but were lower ($.19$) for meat breeds. Heritability estimates of $.41$ and $.32$ from single- and multiple-trait analyses of the current data are consistent with these estimates. Similarly, the current estimate of the heritability of fiber diameter ($.58$) is only slightly higher than the pooled estimate of $.51$ from Fogarty (1995).

Genetic correlations involving Targhee fleece traits were less consistent with literature values. Fogarty (1995) reported average additive genetic correlations of greasy fleece weight with weaning, postweaning, and yearling weights of $.33$, $.50$, and $.28$, respectively, which are reasonably consistent with the estimated genetic correlations of $.50$ between fleece weight and 120-d weaning weight and yearling gain in Table 4. For fiber diameter, Fogarty (1995) reported average additive genetic correlations of $.04$ and $-.11$ with weaning weight and yearling weight, respectively, but variation among estimates was high, with SD of $.15$ to $.30$. For the current study, only the genetic correlation estimate of $.28$ between fiber diameter and yearling gain would differ much from the literature estimates. Phenotypic correlations of fiber diameter with weaning weight ($.08$) and yearling weight ($.07$) reported by Fogarty (1995) are consistent with the very low residual correlations involving fiber diameter in these Targhee data.

The estimate of the additive correlation between greasy fleece weight and fiber diameter ($.51$) is considerably higher than the mean value of $.17$ reported by Fogarty (1995) and is among the highest reported in the literature. Of the 38 estimates of genetic correlations between fiber diameter and either greasy or clean fleece weight reported by Fogarty (1995), only two (both from Blair, 1981, with Romney sheep) exceed $.50$, and only an additional seven estimates exceeded $.40$. However, Iman et al. (1992) reported a genetic correlation between clean fleece weight and fiber diameter in wool taken from the side of the animal of $.46$ in Rambouillet, Columbia, and crossbred ewes. The corresponding residual correlation was $.10$, whereas Fogarty (1995) reported that the mean phenotypic correlation between greasy fleece weight and fiber diameter ($.28$) was larger than the corresponding additive correlation, indicating a relatively larger residual correlation. For the current Targhee data, the residual correlation between greasy fleece weight and fiber diameter ($.08$) was also much smaller than the corresponding additive correlation ($.51$).

Few estimates of correlations between additive direct and maternal effects on different traits have been reported. However, Näsholm and Danell (1996) reported that additive effects on ewe mature body weight were positively correlated with additive direct (.39) and maternal (.47) effects on 120-d body weight in lambs weaned at approximately 105 d. Intercorrelations among additive direct and maternal effects on birth, 120-d, and slaughter (approximately 180 d) weights from Näsholm and Danell (1996) were likewise all positive.

Implications

Genetic parameters indicate that simultaneous improvement of growth, maternal ability, and fleece characteristics can be achieved in Targhee sheep. Genetic parameters required for best linear unbiased predictions of breeding values have been estimated from Targhee field data and are similar in most, but not all, cases to literature values. Genetic antagonisms among economically important traits seem to exist only between fleece weight and fiber diameter. Improvement in fleece value will likely require explicit attention to this antagonism in development of selection programs.

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