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Models with nuclear, cytoplasmic, and environmental effects for production traits of Columbia sheep¹

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ABSTRACT: Statistical models (16) were compared for birth weight of 24,741 Columbia lambs recorded at the U.S. Sheep Experiment Station (USSES; 1950 to 1998). The goal was to estimate fractions of variance due to cytoplasmic line (c^2 ; $n = 590$) and sire \times cytoplasmic line interaction (sc^2 ; $n = 12,831$) with other nuclear and environmental effects included in the model. The basic model included direct genetic (fractional variance, a^2 ; $n = 26,623$), maternal genetic (m^2 , with direct-maternal correlation r_{am}), and maternal permanent environmental (p_m^2 ; $n = 6,385$) effects. The model with sc^2 was significantly ($P < 0.05$) better than the basic model with c^2 , but with other random effects added, sc^2 became zero. Significant ($P < 0.05$) variance components were associated with random dam \times year (dy^2) and dam \times number born (dn^2) interaction effects. Estimates with all effects in the model were: a^2 , 0.26; m^2 , 0.24; r_{am} , -0.05; p_m^2 , 0.02; c^2 , 0.00; dn^2 , 0.04; dy^2 , 0.08; sd^2 , 0.04; sc^2 , 0.00. Estimates for a^2 , m^2 , and r_{am} were the same for all models. Estimate of p_m^2 changed when other effects were added to the model. The largest

estimates for nongenetic effects were: p_m^2 , 0.06; c^2 , 0.00; dy^2 , 0.14; sd^2 , 0.13; and sc^2 , 0.04. Parameter estimates were similar regardless of whether fixed genetic groups ($n = 84$) were in the model. For weaning weight (120 d, $n = 23,903$), estimates of variances of effects added to the basic model were all near zero (a^2 , 0.14; m^2 , 0.09; r_{am} , 0.23; p_m^2 , 0.04). For fleece weight (FW, $n = 29,024$) and number born (NB, $n = 29,688$), animal permanent environmental effects were added to the model (p_a^2 ; $n = 7,741$ and 7,840) and r_{am} was dropped. For these traits, effects not in the basic model had small variances. For FW, estimates with the full model were: a^2 , 0.52; m^2 , 0.01; p_m^2 , 0.00; p_a^2 , 0.06; c^2 , 0.00; dy^2 , 0.00; sd^2 , 0.02; and sc^2 , 0.06, and for NB they were: a^2 , 0.08; m^2 , 0.00; p_m^2 , 0.00; p_a^2 , 0.02; c^2 , 0.00; dy^2 , 0.00; sd^2 , 0.00; and sc^2 , 0.01. Cytoplasmic effects were not important. Unusual random effects in the model did not change estimates for basic parameters. Although some effects were significant, especially for BW, effects on genetic evaluations are likely to be small.

Key Words: Cytoplasmic Inheritance, Genetic-Environment Interaction, Genetic Variation, Heritability

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Introduction

Recent studies on quantitative traits of cattle have not found cytoplasmic effects to be important, in contrast to earlier, less critical studies—for example, on dairy cattle (Bell et al., 1985; Boettcher and Gibson, 1997; Albuquerque et al., 1998) and on beef cattle (Tess et al., 1987; Tess and Robison, 1990; Tess and MacNeil, 1994). Kennedy (1986), in a classic study by simulation, showed that not accounting for genetic relationships would result in overestimation of variance due to cytoplasmic effects. Southwood et al. (1989), through simu-

lation, showed that under an additive maternal genetic model, a small cytoplasmic variance was estimated, although none was present. Specific mitochondrial types may influence milk production in dairy cattle (Faust et al., 1990; Schutz et al., 1994; Boettcher et al., 1996), carcass traits of Japanese Black cattle (Mannen et al., 1998), and litter size in pigs (Robison, 1998). Some interactions of mitochondrial and nuclear genomes have been identified in humans (Wolz et al., 1997) and cattle (Seelan and Grossman, 1992). Maniatis and Pollott (2002) recently found no evidence of cytoplasmic effects on weight traits of Suffolk lambs. Four traits (birth, weaning and fleece weights, and number of lambs born) of a Targhee sheep population, with records from 1950 to 1998, were unaffected by cytoplasmic effects (Van Vleck et al., 2002).

Quantitative traits of sheep might not be expected to be influenced by cytoplasmic effects, but only one study of a meat-type breed (Maniatis and Pollett, 2002) and

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Table 1. Summary of number of records, means, and of levels by factor for four traits of Columbia sheep^a

Item	Birth weight, kg	Weaning weight, kg	Fleece weight, kg	No. born
Records ^b	24,741	23,903	29,024	29,688
Mean	4.89	35.7	5.31	1.29
SD	0.86	6.5	1.04	0.73
Animals with records	24,741	23,903	7,741	7,840
Sires	1,020	1,020	904	905
Dams	6,385	6,318	4,098	4,140
Cytoplasmic line	590	587	346	352
Average animals/line	41.9	40.7	22.4	22.3
Dam × year	18,336	18,089	7,017	7,099
Sire × dam	17,773	17,536	6,966	7,047
Sire × cytoplasmic line	12,831	12,698	5,828	5,892
Dam × No. born	9,836	—	—	—

^aNumber of animals in pedigree file = 26,623, number of genetic groups = 84, up to 17 generations to founder dam.

^bMeans and standard deviations not adjusted for model effects.

one study of a dual-purpose synthetic breed (Van Vleck et al., 2002) have been fully reported. The purpose of this study was to compare estimates of variance due to nuclear, cytoplasmic, and environmental effects, and due to genotype × cytoplasmic effects for birth weight, weaning weight, fleece weight, and number of lambs born for Columbia sheep with those from a study of Targhee sheep (Van Vleck et al., 2002).

Materials and Methods

Data were records collected from 1950 to 1998 at the U.S. Sheep Experiment Station (USSES) in Dubois, Idaho, from the station's Columbia flock. As in the previous study with Targhee records (Van Vleck et al., 2002), Hanford (2001) had previously edited the data for estimation of genetic change over the 49-yr period. Ercanbrack and Knight (1991) have described the origin of the Columbia flock and its general management, as well as how weaning weight was adjusted to the standard 120-d age.

Means and levels of random factors describing the data for birth weight, weaning weight (120 d), fleece weight of ewes, and number of lambs born per ewe are in Table 1. Fixed factors for the analyses were the same

Table 2. Number of levels for fixed factors in models for analysis of four traits (birth weight, BWT; weaning weight, WWT; fleece weight, FLW; number born, NB)

Factor	BWT	WWT	FLW	NB
Year	49	49	46	47
Age dam (ewe)	12	12	(12)	(12)
Gender	2	3	—	—
Type birth (TB) ^a	4	—	—	—
TB and rearing ^b	—	8	—	—
No. weaned	—	—	4	—

^aFour types of birth; single, twin, triplet, quadruplet.

^bEight TB and rearing levels; single-single, single-twin, twin-single, twin-twin, triplet/quadruplet-single, triplet/quadruplet-twin, triplet/quadruplet-triplet, quadruplet-any type of rearing (used 1983 to 1992).

(Table 2) as those for the Targhee study (Van Vleck et al., 2002).

Cytoplasmic lines were defined by tracing all animals through the female line of descent to unique founding dams, which ranged from 346 to 590, depending on the trait. The data were truncated in 1950 so pedigrees ending in 1950 might, if extended, be traced to fewer founding dams (Roughsedge et al., 2001). Rambouillet ewes were the source of all cytoplasmic effects in the creation of the Columbia breed, in contrast to the Targhee breed, which was not exclusively derived from Rambouillet ewes (Terrill, 1947). The interaction of genotype × cytoplasmic line effects or the interaction of nuclear and mitochondrial genomes was modeled by including a random effect for sire × cytoplasmic line combination since sires were mated to ewes with various cytoplasmic origins.

Birth weight was the first trait analyzed. Initial models included direct and maternal genetic (with covariance), maternal permanent environmental, and residual environmental effects, as well as cytoplasmic line effects. The final part of the initial model was to include a dam × year interaction effect because sires were not repeated over years. The intent was to determine if including such a factor would affect estimates of genetic parameters including the direct-maternal genetic correlation.

In agreement with the previous Targhee study (Van Vleck et al., 2002) for birth weight, the estimate of the component of variance for dam × year effects was large (approximately 12% of phenotypic variance). The only way a dam could have more than one measure in a year was to have multiple births in at least one year. Therefore, dam × number born and sire × dam terms were added to the model. These effects are highly confounded and also confounded with levels of dam × year (Table 1). As with the previous Targhee report (Van Vleck et al., 2002), cytoplasmic line effects were found to be unimportant for birth weight, and more emphasis was put on the interaction of dam with year, number born, and sire in the model comparisons.

Table 3. Possible random factors in models for analyses of four traits (birth weight, BWT; weaning weight, WWT; fleece weight, FLW; number born, NB)

Factor	BWT	WWT	FLW	NB
Animal genetic, a^2	✓	✓	✓	✓
Maternal genetic, m^2	✓	✓	✓	✓
Correlation, r_{am}	✓	✓	—	—
Maternal permanent environmental, p_m^2	✓	✓	✓	✓
Animal permanent environmental, p_a^2	—	—	✓	✓
Cytoplasmic line, c^2	✓	✓	✓	✓
Dam \times year, dy^2	✓	✓	✓	✓
Dam \times number born, dn^2	✓	—	—	—
Sire \times dam, sd^2	✓	✓	✓	✓
Sire \times cytoplasmic line, sc^2	✓	✓	✓	✓

Fewer models were used for the other traits because cytoplasmic line effects had essentially zero variances. For traits with repeated measures, (number born and fleece weight), animal and maternal permanent environmental effects were both included in some models.

Analyses with founder genetic groups ($n = 84$) included as fixed effects were compared with analyses without founder groups (Westell et al., 1988). These groups were based on an animal's year of birth for sires and dams whose own records were not found in the database (Hanford, 2001). As with the Targhee study (Van Vleck et al., 2002), whether groups were in the model resulted in similar estimates for genetic parameters. Therefore, only the full and usual models were used with founder genetic groups in the model. Random factors included in models for the four traits are presented in Table 3.

Estimates of variance components were obtained by derivative-free REML (Smith and Graser, 1986) using the MTDFREML programs (Boldman et al., 1995). Standard errors for genetic parameters and for fractions of variance due to other factors were based on the delta method and average information matrix at convergence (e.g., Dodenhoff et al., 1998). Likelihood ratio tests (LRT) were used as a statistical comparison of models.

Results

Birth Weight

Estimates of components of variance and fractions of phenotypic variance from 16 models for birth weight are in Table 4. The phenotypic variance ranged from 0.5381 to 0.5500 kg^2 . The general pattern of variance components estimates was similar to that for the Targhee breed (Van Vleck et al., 2002), which is another dual-purpose synthetic breed. The results will be summarized briefly. Models with and without fixed genetic group effects gave similar results (Models 1 vs. 3 and Models 2 vs. 15). Estimates of direct and maternal heritabilities and the direct-maternal genetic correlation were essentially the same for all models. Variance due to cytoplasmic lines was zero and was not significant

in all models including cytoplasmic effects (Models 4, 10 to 12, 15, and 16). Adding dam \times year interaction accounted for an additional 14% of the total variance (Model 5; e^2 , the fraction of variance due to residual effects, was reduced from 0.45 to 0.33) with only a slight reduction (from 0.06 to 0.04) in fraction of variance due to maternal permanent environmental effects (p_m^2). When the maternal permanent environment effect was dropped, the fraction of variance due to the dam \times year interaction did not change (Model 6). Following the Targhee study (Van Vleck et al., 2002), dam \times number born was then included as a random factor (Model 7). The fit of the model with dam \times number born in the model (Model 7) was better than without the effect (Model 3), but added alone, it was not as good as with only dam \times year effects added in the model (Models 5 and 6). The model was improved significantly by including both dam \times year and dam \times number born effects compared with models with only one of these factors (Model 8 vs. Models 5 and 7). The variance due to dam \times number born was partitioned about equally from variance due to maternal permanent environmental effects and variance due to dam \times year effects. The basic model was improved with sire \times dam effects in the model (Model 9), as was expected due to obvious confounding with dam \times year effects. The improvement in the log likelihood was not as great as with the addition of dam \times year effects to the basic model (Model 5). The estimate of fractional variance due to sire \times dam effects of 0.13, which would correspond to a fractional estimate of dominance variance of about 0.50, is much too large. When in the model with dam \times year (Model 13) or with dam \times year and dam \times number born effects (Model 14), the estimate of fractional variance due to sire \times dam effects was reduced to 0.04, similar to the 0.05 reported for the Targhee study (Van Vleck et al., 2002). With sire \times cytoplasmic line effects added to the basic model (Model 11), the LRT was significant, but the improvement was less than that found by adding other interaction effects. The relative estimate of 0.04 was reduced to zero when any of the other interaction effects with dam were in the model (Models 12, 15, and 16). The model with all three interactions with dam effects, in addition to the

Table 4. Estimates of genetic parameters for birth weight with 16 models with standard errors (SE) for the complete model in bottom row^{ab}

Model	Parameters										
	a ²	r _{am}	m ²	p _m ²	c ²	dy ²	dn ²	sd ²	sc ²	e ²	2logL
Models with genetic groups											
1	0.27	-0.05	0.25	0.05	—	—	—	—	—	0.45	0.00 ^c
2	0.27	-0.04	0.24	0.04	0.00	0.10	—	0.04	0.00	0.33	228.64 ^c
Models without genetic groups											
3	0.26	-0.05	0.24	0.06	—	—	—	—	—	0.45	0.00 ^d
4	0.26	-0.05	0.24	0.06	0.00	—	—	—	—	0.45	0.02 ^d
5	0.26	-0.05	0.24	0.04	—	0.14	—	—	—	0.33	226.66 ^d
6	0.25	-0.05	0.29	—	—	0.14	—	—	—	0.33	207.72 ^d
7	0.27	-0.06	0.24	0.02	—	—	0.07	—	—	0.42	88.74 ^d
8	0.26	-0.05	0.24	0.02	—	0.12	0.04	—	—	0.33	251.92 ^d
9	0.26	-0.05	0.24	0.04	—	—	—	0.13	—	0.34	211.02 ^d
10	0.26	-0.04	0.24	0.04	0.00	—	—	0.13	—	0.34	211.02 ^d
11	0.26	-0.04	0.24	0.05	0.00	—	—	—	0.04	0.42	52.36 ^d
12	0.26	-0.05	0.24	0.04	0.00	—	—	0.13	0.00	0.34	211.02 ^d
13	0.26	-0.05	0.24	0.04	—	0.10	—	0.04	—	0.33	228.79 ^d
14	0.26	-0.05	0.24	0.02	—	0.08	0.04	0.04	—	0.33	251.92 ^d
15	0.26	-0.05	0.24	0.04	0.00	0.10	—	0.04	0.00	0.33	228.79 ^d
16	0.26	-0.05	0.24	0.02	0.00	0.08	0.04	0.04	0.00	0.33	251.92 ^d
	(0.019	0.051	0.018	0.011	0.002	0.025	0.008	0.025	0.006	0.014	SE) ^b

^aProportion of variance: a², direct genetic; m², maternal genetic; p_m², maternal permanent environmental; c², cytoplasmic line; dy², dam × year; dn², dam × number born; sd², sire × dam; sc², sire × cytoplasmic line; e², temporary environmental; r_{am}, direct-maternal genetic correlation; phenotypic variance: 0.5381 to 0.5500 kg².

^bSE for model not including genetic groups.

^cDifference in 2log likelihood (2logL) from usual model (a², r_{am}, m², p_m²) with genetic groups in model.

^dDifference in 2log likelihood from usual model (a², r_{am}, m², p_m²) with genetic groups not in model.

basic direct-maternal model, was not significantly different from the model including only dam × year and dam × number born effects (Model 14 vs. 8). The sire × dam fraction seems to come entirely from the dam × year component of variance. Cytoplasmic line and sire × cytoplasmic line effects contribute little to nothing to variation in birth weight.

Al-Shorepy and Notter (1998) reported that litter effects (comparable to the dam × year effect) account for about 17% of variation in birth weight. Notter (personal communication) indicated that unpublished analyses of birth weights of Targhee, Suffolk, and Polypay lambs included in the National Sheep Improvement Program have shown large and significant variance components for litter effects. A reviewer of the Targhee study (Van Vleck et al., 2002) suggested that much of the variance due to dam × year and dam × number born effects may be due to year-specific effects on lambs in the same litter in that, if the effects result in light (or heavy) birth weight for one member of the litter, weights of others in the litter will be similar.

Weaning Weight

Estimates of fractional variances for weaning weight are in Table 5. The phenotypic variances ranged from 27.27 to 27.73 kg². The pattern of estimates for weaning weight did not follow the same pattern as estimates for birth weight. As with the Targhee study (Van Vleck et

al., 2002), none of the four effects added to the basic model improved the likelihood. Estimates of fractional contributions of each of the four “extra” factors were zero.

Estimates of fractional variances from models with and without genetic groups (Model 1 vs. 3 and Model 2 vs. 11) were only slightly different, indicating the main difference was in the estimate of the direct-maternal genetic correlation.

Lack of evidence for cytoplasmic or genotype × cytoplasmic effects is in agreement with the similar study of Targhee weaning weights (Van Vleck et al., 2002). Also, Maniatis and Pollott (2002) found no evidence for cytoplasmic effects for 8-wk and 146-d weights.

Fleece Weight

Estimates of fractional variances for fleece weight are in Table 6. The phenotypic variances ranged from 0.8374 to 0.8617 kg². Although variances due to maternal genetic and permanent environmental effects were small, these analyses resulted in a significant LRT for the model including both maternal effects compared to a model without maternal effects (Model 3 vs. 5). Even though the estimate of maternal heritability was low (about 0.01), for consistency with the other traits, the factor was included in most models. The variance due to maternal permanent effects was near zero, so that factor was dropped from further analyses. The direct-

Table 5. Estimates of genetic parameters for weaning weight with 11 models with standard errors for the complete model in bottom row^{ab}

Model	Parameters									
	a ²	r _{am}	m ²	p _m ²	c ²	dy ²	sd ²	sc ²	e ²	2logL
Models with genetic groups										
1	0.16	0.35	0.09	0.03	—	—	—	—	0.68	0.00 ^c
2	0.16	0.35	0.09	0.03	0.00	0.00	0.00	0.00	0.68	0.00 ^c
Models without genetic groups										
3	0.14	0.23	0.09	0.04	—	—	—	—	0.71	0.00 ^d
4	0.14	0.23	0.09	0.04	0.00	—	—	—	0.71	0.00 ^d
5	0.14	0.23	0.09	0.04	—	0.00	—	—	0.71	0.00 ^d
6	0.13	0.24	0.13	—	—	0.00	—	—	0.71	-21.38 ^d
7	0.14	0.23	0.09	0.04	—	—	0.00	—	0.71	0.00 ^d
8	0.14	0.23	0.09	0.04	0.00	—	—	0.00	0.70	0.00 ^d
9	0.14	0.23	0.09	0.04	0.00	—	0.00	—	0.71	0.00 ^d
10	0.14	0.23	0.09	0.04	0.00	—	0.00	0.00	0.71	0.00 ^d
11	0.14	0.23	0.09	0.04	0.00	0.00	0.00	0.00	0.71	0.00 ^d
	(0.014	0.094	0.012	0.009	0.002	0.033	0.032	0.017	0.016	SE) ^b

^aProportion of variance: a², direct genetic; m², maternal genetic; p_m², maternal permanent environmental; c², cytoplasmic line; dy², dam × year; dn², dam × number born; sd², sire × dam; sc², sire × cytoplasmic line; e², temporary environmental; r_{am}, direct-maternal genetic correlation; phenotypic variance: 27.27 to 27.73 kg².

^bSE for model not including genetic groups.

^cDifference in 2log likelihood (2logL) from usual model (a², r_{am}, m², p_m²) with genetic groups in model.

^dDifference in 2log likelihood from usual model (a², r_{am}, m², p_m²) with genetic groups not in model.

maternal genetic covariance was not included in the model because of the low maternal heritability. Estimates of direct and maternal heritabilities were the same no matter what other effects were included in the model. Similarly, estimates of fractional variances were the same regardless of whether genetic groups were in the models (Model 1 vs. 3 and 2 vs. 10). Variance due

to cytoplasmic lines was near zero (Model 10). The estimate of fraction of variance due to sire × dam effects was 0.02, which was not significantly different from zero. Adding a dam × year interaction accounted for 11% of the total variance (Model 6). All of the variance due to this effect seems to be partitioned from variance due to individual permanent environmental effects.

Table 6. Estimates of genetic parameters for fleece weight with 10 models with standard errors for the complete model in bottom row^{ab}

Model	Parameters									
	a ²	m ²	p _m ²	p _a ²	c ²	dy ²	sd ²	sc ²	e ²	2logL
Models with genetic groups										
1	0.51	0.02	0.00	0.13	—	—	—	—	0.33	0.00 ^c
2	0.52	0.01	0.00	0.06	0.00	0.01	0.00	0.06	0.33	32.78 ^c
Models without genetic groups										
3	0.53	0.01	0.02	0.12	—	—	—	—	0.33	0.00 ^d
4	0.53	—	0.02	0.12	—	—	—	—	0.33	-1.32 ^d
5	0.53	—	—	0.14	—	—	—	—	0.33	-11.40 ^d
6	0.55	0.01	—	0.00	—	0.11	—	—	0.32	-1.29 ^d
7	0.55	0.01	—	—	—	0.11	—	—	0.32	-1.31 ^d
8	0.52	0.01	—	0.08	0.00	—	—	0.06	0.33	33.73 ^d
9	0.52	0.01	—	0.06	0.00	0.02	—	0.06	0.33	34.37 ^d
10	0.52	0.01	0.00	0.06	0.00	0.00	0.02	0.06	0.33	34.43 ^d
	(0.019	0.009	0.009	0.022	0.004	0.041	0.041	0.013	0.006	SE) ^b

^aProportion of variance: a², direct genetic; m², maternal genetic; p_m², maternal permanent environmental; p_a², animal permanent environmental; c², cytoplasmic line; dy², dam × year; dn², dam × number born; sd², sire × dam; sc², sire × cytoplasmic line; e², temporary environmental; r_{am}, direct-maternal genetic correlation; phenotypic variance: 0.8374 to 0.8617 kg².

^bSE for model not including genetic groups.

^cDifference in 2log likelihood (2logL) from usual model (a², m², p_m², p_a²) with genetic groups in model.

^dDifference in 2log likelihood from usual model (a², m², p_m², p_a²) with genetic groups not in model.

Table 7. Estimates of genetic parameters for number born with five models with standard errors for the complete model in bottom row^{ab}

Model	Parameters									
	a ²	m ²	p _m ²	p _a ²	c ²	dy ²	sd ²	sc ²	e ²	2logL
Models with genetic groups										
1	0.08	0.00	0.00	0.03	—	—	—	—	0.89	0.00 ^c
2	0.08	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.89	1.69 ^c
Models without genetic groups										
3	0.08	0.00	0.00	0.03	—	—	—	—	0.89	0.00 ^d
4	0.08	—	—	0.03	—	—	—	—	0.89	0.67 ^d
5	0.08	0.00	0.00	0.02	0.00	0.00	0.00	0.01	0.89	1.36 ^d
	(0.009)	0.005	0.005	0.013	0.001	0.023	0.024	0.007	0.006	SE) ^b

^aProportion of variance: a², direct genetic; m², maternal genetic; p_m², maternal permanent environmental; p_a², animal permanent environmental; c², cytoplasmic line; dy², dam × year; sd², sire × dam; sc², sire × cytoplasmic line; e², temporary environmental; phenotypic variance: 0.4147 to 0.4152.

^bSE for model not including genetic groups.

^cDifference in 2log likelihood (2logL) from usual model (a², m², p_m², p_a²) with genetic groups in model.

^dDifference in 2log likelihood from usual model (a², m², p_m², p_a²) with genetic groups not in model.

Adding sire × cytoplasmic line effects to the model increased the likelihood (Model 8). Much of the variance due to this effect also seems to be partitioned from variance due to individual permanent environmental effects. Addition of the dam × year effect to the sire × cytoplasmic line effect did not significantly improve the model (Model 9). When both maternal effects are dropped from the model, the variances of those effects seemed also to go to the direct permanent environmental variance (Model 5). The small maternal genetic variance for fleece weight might be attributed to the influence of postnatal nutrition of lambs on the capacity of wool follicles to produce fiber (Corbett, 1979).

Number Born

Estimates of fractional variances for number of lambs born are in Table 7. The phenotypic variances ranged from 0.4147 to 0.4152. As with the other traits and estimates from the Targhee analyses (Van Vleck et al., 2002), estimates of variance due to cytoplasmic effects were near zero. Estimates of fractional variance were the same whether or not genetic groups were included in the model (Model 1 vs. 3 and 2 vs. 5). Direct heritability was the same with all models. No other sources of variation were significant. Including sire × cytoplasmic line effects partitioned variance from the relatively small component of variance due to animal permanent environmental effects (Model 5). The estimate of fractional variance was about the same size as the standard error. A model with direct genetic value and animal permanent environmental effects would seem to be adequate for genetic evaluation (Model 4). The estimates of variance components and estimates of variances are nearly the same as those reported by Rao and Notter (2000) and in the parallel study of Targhee sheep (Van Vleck et al., 2002).

Discussion

Cytoplasmic line effects were not important for any of the four traits analyzed. The variance component due to the interaction of nuclear and cytoplasmic genomes modeled as sire × cytoplasmic line effects was near zero for all traits except fleece weight, which could be due to confounding with other interaction effects. For genetic evaluations of weaning weight, the standard maternal effects model would be optimal. For fleece weight, a model with direct animal and maternal genetic effects and with an animal permanent environmental effect would be adequate. For number born, a model with direct animal genetic and permanent environmental effects would be sufficient.

The results for birth weight are puzzling but agree with other studies with litter effects in the model (Al-Shorepy and Notter, 1998) and with a similar study of birth weight of Targhee lambs (Van Vleck et al., 2002). Of the nontraditional factors added to the model, only cytoplasmic effects did not improve the model. The four interaction effects are highly confounded, but only the variance of sire × cytoplasmic line effects becomes zero when all four effects are in the model. The other three jointly reduce residual variance by about one-quarter, from 0.45 to 0.33 of phenotypic variance. The maternal (dam) permanent environmental variance was decreased from 0.06 to 0.04 or 0.02 of phenotypic variance when the interaction of dam with year or dam with number born was included in the model. Including sire × dam effects in the model slightly reduced the proportion of total variance from maternal permanent environmental effects from 0.06 to 0.04. Including dam × year effects reduced the sire × dam component of variance from 0.13 to 0.04 of phenotypic variance in much the same pattern as for Targhee birth weights (Van Vleck et al., 2002). The non-zero estimate for the sire

× dam component of variance with other effects in the model is not significant but also was non-zero and significant in the Targhee analysis (Van Vleck et al., 2002). For birth weight, estimates of the basic genetic parameters were not affected by adding nontraditional factors to the model. Although further study is needed, this result, in agreement with the Targhee study (Van Vleck et al., 2002), suggests that the standard model with addition of dam × year (or litter) effects (Al-Shorepy and Notter, 1998) would be relatively robust for ranking on EBV. Further investigation to explain why modeling the covariance between littermates (which exists only with more than one lamb in a litter) improves the likelihood is warranted.

Implications

For Columbia sheep, cytoplasmic effects seem unimportant for birth and weaning weight, fleece weight, and number of lambs born. Models for genetic evaluation of ewes for weaning weight and fleece weight and number of lambs born would not need to include interactions between dams and years or dams and sires. Standard models including direct and maternal genetic effects and, as appropriate, either direct or maternal permanent environmental effects are adequate. Further study may be needed to understand why interactions of dam with year and with number born, and possibly, with sire are important.

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