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Snowder, G. D.; Hanford, K. J.; and Van Vleck, L. Dale, "Comparison of models including cytoplasmic effects for traits of Rambouillet sheep" (2004). *Faculty Papers and Publications in Animal Science*. 159.
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Comparison of models including cytoplasmic effects for traits of Rambouillet sheep[☆]

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Received 28 October 2003; received in revised form 22 March 2004; accepted 31 March 2004

Abstract

The objective was to determine appropriate analytical models considering cytoplasmic inheritance for birth weight (BWT, $n=35,604$), weaning weight (WWT, $n=34,114$), fleece weight (FWT, $n=38,113$) and number born (NB, $n=39,029$) for Rambouillet sheep. For BWT, models that included dam by year, dam by number born, and sire by dam effects, in addition to direct and maternal effects, were significantly better than the basic maternal effects model. For WWT, variances due to direct, maternal, and maternal permanent environmental effects (0.05 of variance) were not zero. For FWT, heritability was 0.55 for all models, but models with dam by year (0.02), sire by dam (0.05), and sire by cytoplasmic line (0.02) were jointly significantly better than models with permanent environmental effects. For NB, only direct heritability (0.08) and relative permanent environmental variance (0.04) were not zero. No trait showed evidence of variation due to cytoplasmic effects. Adding seldom considered effects to the model did not change estimates of variance due to direct and maternal genetic effects. Variance due to dominance effects may be important for BWT and FWT. The basic direct–maternal effects model seems sufficient for genetic evaluations for WWT and FWT but models for BWT and NB may need to include other effects.

Published by Elsevier B.V.

Keywords: Birth weight; Weaning weight; Fleece weight; Litter size

1. Introduction

Mammalian mitochondrial DNA codes for only 37 genes (13 protein coding genes, 22 transfer RNA genes, and 2 ribosomal genes; Wolstenholme, 1992). When compared to the estimated 24,500 to 45,000

protein coding genes in the mammalian genome (Pennisi, 2003), the mitochondrial DNA contributes less than 0.01% of the mammalian genome. The influence of mitochondrial DNA on phenotypic variation within some populations may be very small because recombination of parental genes cannot occur. A small number of sperm-derived mitochondria may be transferred to the oocyte during fertilization but these are usually degraded in embryogenesis (Sutovsky et al., 1996). Mitochondrial genes are subject to mutations (Hiendleder, 1998) and mitochondrial polymorphisms have been associated with

[☆] Published as paper no. 14529, Journal Ser., Nebraska Agric. Res. Div., University of Nebraska, Lincoln 68583-0908.

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small differences in production traits of dairy cattle (Boettcher et al., 1996a). Genetic evaluations that ignore significant cytoplasmic effects will bias estimates of heritability and animal breeding values (Boettcher et al., 1996b).

More recent studies of beef cattle (Tess and Robison, 1990) and dairy cattle (Boettcher and Gibson, 1997; Albuquerque et al., 1998) performance have found cytoplasmic effects on important production traits are very small in contrast to preliminary studies (Bell et al., 1985; Tess et al., 1987), which substantiated Kennedy (1986) who showed that failure to account for genetic drift with the numerator relationship matrix would result in overestimation of the importance of cytoplasmic effects. A study of five mitochondrial haplotypes in Japanese Black cattle found no significant differences for carcass traits except for marbling score (Mannen et al., 1998). A review of the effect of cytoplasmic inheritance on economically important traits in cattle concluded that cytoplasmic effects are very small and findings were often biased by the statistical analyses (Gibson et al., 1997).

Studies of cytoplasmic effects on traits of sheep have recently also shown cytoplasmic effects to be of little importance for growth of Suffolk lambs (Maniatis and Pollott, 2002) and for four representative traits (birth weight (BWT), weaning weight (WWT), fleece weight (FWT), and litter size at birth) for Targhee (Van Vleck et al., 2003) and for Columbia (Hanford et al., 2003) sheep. The latter two breeds are dual-purpose composite breeds of Rambouillet descent developed at the U.S. Sheep Experiment Station. Because the Rambouillet breed has a more historical pedigree than the recently developed composite breeds of Columbia and Targhee, the effect of cytoplasmic inheritance may differ in the Rambouillet. The purpose of this paper was to compare estimates of variance components due to cytoplasmic origin and due to the interaction of sire genotype with cytoplasmic origin for the Rambouillet breed with those previously reported for Columbia and Targhee breeds. Another purpose was to estimate components of variance due to interactions of dam with year, number born, and sire genotype, which were found to be important for birth weight in the studies of Columbia and Targhee sheep.

2. Materials and methods

Records available for analysis were collected from 1950 through 1998 at the United States Sheep Experiment Station (USSES), Dubois, Idaho. Hanford (2001) edited the records as part of a study to analyze genetic change over the 49 years. The number of records analyzed ranged from 34,119 to 39,029 depending on the trait of interest. General management of the flock under a western range grazing production system was described by Ercanbrack and Knight (1991).

Four traits were analyzed: birth weight, 120-day weaning weight, annual fleece weight, and number of lambs born. Birth weight and weaning weight were lamb traits, and fleece weight and number born were ewe traits. Table 1 shows number of records, means and number of levels for each trait and associated random factors. Fixed factors shown in Table 2 are the same as were used with the Columbia (Hanford et al., 2003) and Targhee (Van Vleck et al., 2003) analyses.

Female line of descent was traced to founding dams to establish cytoplasmic lines. If pedigrees

Table 1
Summary^a of number of records and of levels by factor for four traits

	Birth weight	Wean weight	Fleece weight	Number born
Number records ^b	35,604	34,114	38,113	39,029
Mean (wt., kg)	4.68	32.3	4.65	1.34
S.D. (wt., kg)	0.77	5.4	0.92	0.70
Animals with records	35,604	34,114	10,420	10,634
Sires	1830	1829	1626	1632
Dams	9484	9384	5687	5787
Cytoplasmic line	1577	1566	769	840
Average animals/line	22.6	21.8	13.6	12.7
Dam × year	26,656	26,259	9594	9785
Sire × dam	25,534	25,161	9408	9599
Sire × cytoplasmic line	20,293	20,059	8278	8454
Dam × number born	14,329	–	–	–

^a Number of animals in pedigree file=38,161, number of genetic groups=84, up to 18 generations to founder dam.

^b Means and standard deviations not adjusted for model effects.

Table 2

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

Factor	BWT	WWT	FLW	NB
Year	49	49	46	47
Age of dam (ewe)	12	12	(13)	(13)
Gender	2	3	–	–
Type of birth (TB) ^a	4	–	–	–
TB and rearing ^b	–	8	–	–
Number weaned	–	–	5	–
Calendar day (covariate)	–	–	✓	–

^a Four types of birth: single, twin, triplet, quadruplet.

^b Eight 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.

before 1950 had been available, fewer lines may have been found (Roughsedge et al., 2001). Columbia sheep all trace to Rambouillet ewes, as do most of the Targhee population (Terrill, 1947). Effects of variance due to effects of sire by cytoplasmic line interaction were used as a measure of the interaction of nuclear and mitochondrial genomes. Recent studies have identified enzymes composed of both nuclear and mitochondrial origin, such as cytochrome *c* oxidase, a mammalian enzyme containing 13 polypeptides of which three are encoded by the mitochondrial genome and 10 encoded in the nucleus (Wolz et al., 1997).

Birth weight was analyzed first with the usual direct–maternal effects model plus cytoplasmic line effects and genotype by cytoplasmic line effects. In addition, a dam by year interaction effect was included to resemble a sire by year interaction effect. (Sires did not repeat over years.) With the previous Targhee and Columbia analyses, the variance component for dam by year effects was relatively large, accounting for 10% to 12% of phenotypic variance. Because multiple births were the only way a dam could have more than one progeny per year, dam by year effects are equivalent to litter effects (Al-Shorepy and Notter, 1998). To determine if that variation could be accounted for by litter size or a full sib effect, dam by number born and dam by sire effects were added to the model. What is apparent (Table 1) is that the various dam by other factor interaction effects are highly confounded. After cytoplasmic effects were found not to be important, separation of variation

due to maternal permanent environmental effects, dam by year, dam by number born, and dam by sire interaction effects was attempted. With other traits, variance due to dam by year effects was small so that fewer models were examined. For the ewe traits of fleece weight and number born with repeated measures, both animal and maternal permanent environmental effects were sometimes both included in the model. Random factors in the models are shown in Table 3.

Analyses were conducted with 84 founder genetic groups and without founder genetic groups (Westell et al., 1988). Founder groups were assigned by Hanford (2001) based on year of birth of an animal for the animal's sire and dam when they did not have a record. Estimates of relative (fraction of phenotypic) variance components were similar with or without groups in the model. Thus, only the full and usual models were used for analyses with groups in the model to reduce computing time and costs.

Variance components were estimated with REML by a derivative-free algorithm (Smith and Graser, 1986) using the MTDFREML programs (Boldman et al., 1995). Approximate standard errors of estimates of the parameters (fractions of phenotypic variance) used the average information matrix (Johnson and Thompson, 1995) and the delta method (e.g., Doderhoff et al., 1998). Likelihood ratio tests (LRT) were used to test whether random effects contributed significantly to the likelihood given the data.

Table 3

Possible random factors in models for analyses of four traits (birth weight, BWT; wean 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 × year, dy^2	✓	✓	✓	✓
Dam × number born, dn^2	✓	–	–	–
Sire × dam, ds^2	✓	✓	✓	✓
Sire × cytoplasmic line, sc^2	✓	✓	✓	✓

3. Results and discussion

In agreement with the previous studies of Columbia and Targhee sheep (Hanford et al., 2003; Van Vleck et al., 2002), which were contemporaries of the Rambouillet at USSES, no evidence was found for effects of cytoplasmic line on any of the four traits (birth weight in Table 4, weaning weight in Table 5, fleece weight in Table 6, and number born in Table 7). These results agreed with the Columbia and Targhee analyses and were not surprising given the preponderance of Rambouillet cytoplasm in the development of the Columbia and Targhee composite breeds. The result also agrees with estimates of Maniatis and Pollott (2002) for Suffolk growth traits.

The only trait that expressed possible effects of interaction of sire genotype and cytoplasmic line was fleece weight (Table 6), which also was in agreement with the Columbia and Targhee analyses. The fraction

of variance due to that interaction was only 0.02. What is surprising is that all three breeds thus far studied have shown significant sire by cytoplasmic line effects for fleece weight only and with no detectable variance due to cytoplasmic effects. The lack of variance due to cytoplasmic effects may indicate that the interaction variance is due to confounding with other effects not in the model.

For all traits and in agreement with the previous analyses with contemporaneous Columbia and Targhee data, whether or not founder genetic groups were in the model resulted in none to little change in estimates of genetic parameters. Thus, with groups in the model, only analyses with the usual model and the full model were done and are reported in the first two rows of Tables 4–7. Various reduced models without group effects were done and are also reported. For all four traits, the estimates of variance components as fractions of phenotypic variance, with minor

Table 4

Estimates of genetic parameters^a for birth weight with 16 models with standard errors (S.E.) for complete model^b

Model	Parameters										
	a^2	r_{am}	m^2	p^2	c^2	dy^2	dn^2	sd^2	sc^2	e^2	2logL
<i>Models with genetic groups</i>											
1	0.27	0.03	0.19	0.07	–	–	–	–	–	0.46	0.00 ^c
2	0.27	0.05	0.19	0.05	0.00	0.08	–	0.03	0.00	0.37	221.09 ^c
<i>Models without genetic groups</i>											
3	0.26	0.02	0.19	0.07	–	–	–	–	–	0.47	0.00 ^d
4	0.27	0.03	0.19	0.07	0.00	–	–	–	–	0.47	0.00 ^d
5	0.26	0.05	0.19	0.06	–	0.11	–	–	–	0.37	216.69 ^d
6	0.25	0.03	0.26	–	–	0.12	–	–	–	0.37	166.63 ^d
7	0.26	0.03	0.20	0.03	–	–	0.06	–	–	0.44	102.99 ^d
8	0.26	0.05	0.19	0.04	–	0.10	0.04	–	–	0.37	247.21 ^d
9	0.26	0.05	0.19	0.05	–	–	–	0.10	–	0.38	200.48 ^d
10	0.26	0.05	0.19	0.05	0.00	–	–	0.10	–	0.38	200.47 ^d
11	0.26	0.05	0.19	0.06	0.00	–	–	–	0.05	0.42	94.79 ^d
12	0.26	0.05	0.19	0.05	0.00	–	–	0.10	0.00	0.38	200.78 ^d
13	0.26	0.05	0.19	0.05	–	0.08	–	0.04	–	0.37	220.34 ^d
14	0.26	0.05	0.19	0.03	–	0.06	0.04	0.04	–	0.37	250.28 ^d
15	0.26	0.05	0.19	0.05	0.00	0.08	–	0.03	0.00	0.37	220.50 ^d
16	0.26	0.05	0.19	0.03	0.00	0.06	0.04	0.03	0.00	0.37	250.46 ^d
S.E.	0.015 ^b	0.046 ^b	0.014 ^b	0.009 ^b	0.003 ^b	0.018 ^b	0.009 ^b	0.019 ^b	0.007 ^b	0.011 ^b	

^a Proportional variance: a^2 , direct genetic; r_{am} , direct–maternal genetic correlation; m^2 , maternal genetic; p^2 , maternal permanent environmental; c^2 , cytoplasmic line; dy^2 , dam by year; dn^2 , dam by number born; sd^2 , sire by dam; sc^2 , sire by cytoplasmic line; e^2 , temporary environmental; phenotypic variance: 0.3968 to 0.4062.

^b Model not including genetic groups.

^c Difference in 2log likelihood from usual model (1: a^2 , r_{am} , m^2 , p^2) with genetic groups in model.

^d Difference in 2log likelihood from usual model (3: a^2 , r_{am} , m^2 , p^2) with genetic groups not in model.

Table 5

Estimates of genetic parameters^a for weaning weight with 11 models with standard errors (S.E.) for complete model^b

Model	Parameters									
	a^2	r_{am}	m^2	p^2	c^2	dy^2	sd^2	sc^2	e^2	2logL
<i>Models with genetic groups</i>										
1	0.20	0.33	0.10	0.04	–	–	–	–	0.60	0.00 ^c
2	0.20	0.33	0.10	0.04	0.00	0.00	0.00	0.00	0.60	2.75 ^c
<i>Models without genetic groups</i>										
3	0.18	0.30	0.10	0.05	–	–	–	–	0.63	0.00 ^d
4	0.18	0.30	0.10	0.05	0.00	–	–	–	0.63	0.01 ^d
5	0.18	0.30	0.10	0.05	–	0.00	–	–	0.63	0.01 ^d
6	0.18	0.30	0.10	0.05	–	–	0.00	–	0.63	0.00 ^d
7	0.18	0.31	0.10	0.05	0.00	–	–	0.00	0.62	0.35 ^d
8	0.18	0.31	0.10	0.05	0.00	–	0.00	–	0.63	0.01 ^d
9	0.18	0.31	0.10	0.05	0.00	–	–	0.00	0.62	0.34 ^d
10	0.18	0.31	0.10	0.05	0.00	–	0.00	0.00	0.62	0.30 ^d
11	0.18	0.31	0.10	0.05	0.00	0.00	0.00	0.00	0.62	0.34 ^d
S.E.	0.012 ^b	0.070 ^b	0.011 ^b	0.008 ^b	0.002 ^b	0.022 ^b	0.021 ^b	0.007 ^b	0.013 ^b	

^a Proportional variance: a^2 , direct genetic; r_{am} , direct–maternal genetic correlation; m^2 , maternal genetic; p^2 , maternal permanent environmental; c^2 , cytoplasmic line; dy^2 , dam by year; sd^2 , sire by dam; sc^2 , sire by cytoplasmic line; e^2 , temporary environmental; phenotypic variance: 19.41 to 19.78 kg².

^b Model not including genetic groups.

^c Difference in 2log likelihood from usual model (1: a^2 , r_{am} , m^2 , p^2) with genetic groups in model.

^d Difference in 2log likelihood from usual model (3: a^2 , r_{am} , m^2 , p^2) with genetic groups not in model.

exceptions, were for practical purposes, the same as with models for Columbia and Targhee records that have been reported and discussed (Hanford et al.,

2003; Van Vleck et al., 2003). Therefore, only exceptions and general patterns will be discussed by trait for the Rambouillet analyses.

Table 6

Estimates of genetic parameters^a for fleece weight with 10 models with standard errors (S.E.) for complete model^b

Model	Parameters									
	a^2	m^2	p_m^2	p_a^2	c^2	dy^2	sd^2	sc^2	e^2	2logL
<i>Models with genetic groups</i>										
1	0.54	0.02	0.01	0.11	–	–	–	–	0.34	0.00 ^c
2	0.54	0.01	0.00	0.04	0.00	0.02	0.04	0.02	0.33	23.03 ^c
<i>Models without genetic groups</i>										
3	0.55	0.02	0.01	0.10	–	–	–	–	0.33	0.00 ^d
4	0.56	–	0.02	0.10	–	–	–	–	0.33	3.57 ^d
5	0.56	–	–	0.11	–	–	–	–	0.33	11.11 ^d
6	0.55	0.02	–	0.03	–	0.08	–	–	0.33	17.73 ^d
7	0.56	0.02	–	–	–	0.10	–	–	0.32	14.66 ^d
8	0.54	0.02	–	0.07	–	–	–	0.04	0.33	13.13 ^d
9	0.55	0.02	–	0.03	–	0.06	–	0.02	0.33	21.84 ^d
10	0.55	0.01	0.00	0.03	0.00	0.02	0.05	0.02	0.33	23.99 ^d
S.E.	0.016 ^b	0.009 ^b	0.008 ^b	0.019 ^b	0.003 ^b	0.035 ^b	0.033 ^b	0.012 ^b	0.005 ^b	

^a Proportional variance: a^2 , direct genetic; m^2 , maternal genetic; p^2 , maternal permanent environmental; c^2 , cytoplasmic line; dy^2 , dam by year; sd^2 , sire by dam; sc^2 , sire by cytoplasmic line; e^2 , temporary environmental; phenotypic variance: 0.5916 to 0.6032 kg².

^b Model not including genetic groups.

^c Difference in 2log likelihood from usual model (1: a^2 , m^2 , p_m^2 , p_a^2) with genetic groups in model.

^d Difference in 2log likelihood from usual model (3: a^2 , m^2 , p_m^2 , p_a^2) with genetic groups not in model.

Table 7

Estimates of genetic parameters^a for number born with eight models with standard errors (S.E.) for complete model^b

Model	Parameters									
	a^2	m^2	p_m^2	p_a^2	c^2	dy^2	sd^2	sc^2	e^2	2logL
<i>Models with genetic groups</i>										
1	0.09	0.00	0.00	0.04	–	–	–	–	0.87	0.00 ^c
2	0.09	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.87	2.51 ^c
<i>Models without genetic groups</i>										
3	0.08	0.00	0.00	0.04	–	–	–	–	0.87	0.00 ^c
4	0.09	–	–	0.04	–	0.00	–	0.00	0.87	–1.54 ^d
5	0.08	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.87	0.01 ^d
S.E.	0.008 ^b	0.004 ^b	0.005 ^b	0.013 ^b	0.001 ^b	0.027 ^b	0.026 ^b	0.008 ^b	0.005 ^b	

^a Proportional variance: a^2 , direct genetic; m^2 , maternal genetic; p_m^2 , maternal permanent environmental; c^2 , cytoplasmic line; dy^2 , dam by year; sd^2 , sire by dam; sc^2 , sire by cytoplasmic line; e^2 , temporary environmental; phenotypic variance: 0.3666 to 0.3668.

^b Model not including genetic groups.

^c Difference in 2log likelihood from usual model (1: a^2 , m^2 , p_m^2 , p_a^2) with genetic groups in model.

^d Difference in 2log likelihood from usual model (3: a^2 , m^2 , p_m^2 , p_a^2) with genetic groups not in model.

3.1. Birth weight

Estimates of direct and maternal heritability and the direct–maternal genetic correlation (0.25 to 0.27, 0.19 to 0.20 and 0.02 to 0.05, respectively) changed negligibly, if at all, when various factors were added to the usual model (Table 4). The estimate of variance due to maternal permanent environmental effects did change some depending on what other factors were in the model (0.07 with no other factors to 0.03 with all other factors in the model). Other factors added singly to the usual model accounted for as much as 0.11 (dam by year) and 0.10 (sire by dam) of the phenotypic variance. The obvious confounding among dam by year, dam by number born, and sire by dam interactions makes partitioning those variances difficult. Together the interactions with dams accounted for 0.13 to 0.14 of phenotypic variance. As with the previous studies, including dam by number born effects in the model added significantly to the likelihood even when dam by year effects were in the model. The variance component for dam by year is equivalent to the covariance of records within a dam by year group. The only way more than one lamb could be in the same dam by year subclass was when the ewe had more than one lamb in the litter. With all random factors in the model, the proportional estimate of variance due to sire by cytoplasmic line was zero, although the estimate was as large as 0.05 when added to the

usual model. The model with sire by dam effects in addition to dam by year and dam by number born effects was not significant with the likelihood ratio test but did account for 0.03 of phenotypic variance with the full model. The total contribution of those three components of 0.13 to the phenotypic variance was similar but a little less than for the Columbia (0.16) and Targhee (0.15) analyses.

3.2. Weaning weight

Estimates of genetic parameters for 120-day weaning weight agreed with the pattern for the Columbia and Targhee analyses that the effects added to the usual direct–maternal effects model did not account for any of the phenotypic variance (Table 5). This result seems surprising for two reasons. Estimates for weaning weight might be expected to follow a pattern similar to that for birth weight. Secondly, for none of the other traits were estimates of the other components uniformly zero or exactly the same for the three breeds.

The estimate of the direct–maternal genetic correlation was larger (0.30) than for the Columbia (0.23) and Targhee (–0.02) analyses. The other estimates of fractional variance were similar for the three breeds. Estimates of direct and maternal heritability were 0.18 and 0.10 and of fraction of variance due to maternal permanent environmental effects was 0.05.

3.3. Fleece weight

As with Columbia and Targhee analyses, direct heritability was large (0.55 vs. 0.53 and 0.57 for Columbia and Targhee, respectively). Although the relatively small maternal heritability (0.01 to 0.02) led to the decision not to try to estimate the direct–maternal genetic correlation, maternal genetic and permanent environmental effects contributed significantly to the phenotypic variance (Model 3 vs. Models 4 and 5). When included in the full model, variance due to dam by year, sire by dam and sire by cytoplasmic line interaction effects accounted for about 0.09 of phenotypic variance in agreement with 0.08 for Columbia and with 0.07 for Targhee. Most of that variance seems to have been partitioned from the animal permanent environmental variance (Model 10 vs. Model 3) as was also true for the Columbia and Targhee analyses. The estimate of fraction of variance due to sire by dam interaction (0.05) was larger than for Columbia (0.02) and Targhee (0.00). The smaller estimates for Columbia and Targhee suggest that the sire by dam component for Rambouillet may be due to sampling variation for a relatively small parameter. The asymptotic standard error was about two-thirds (0.033) the size of the estimate of 0.05.

3.4. Number born

Estimates (Table 7) for the model with animal genetic and animal permanent environmental effects (fractional components of 0.08 and 0.04) agreed with estimates for Columbia (0.08 and 0.03) and Targhee (0.10 and 0.04). Estimates of no other components contributed to the phenotypic variance in contrast to the Columbia and Targhee analyses in which sire by cytoplasmic line variance (0.01 for Columbia and Targhee) and dam by year variance (0.02 for Targhee) were partitioned from the animal permanent environmental variance.

4. Conclusion

For Rambouillet sheep, cytoplasmic effects appear to be unimportant for birth, weaning, and fleece weights, and litter size born. Genetic evaluation models would not need to include cytoplasmic effects or

sire by cytoplasmic effects. For weaning weight at 120 days, a model with direct and maternal genetic and maternal permanent environmental effects should be used for genetic evaluation. For fleece weight of ewes and litter size at birth as traits of the ewe, a sufficient model would include animal genetic and permanent environmental effects (repeatability model). For birth weight, a recommendation is more difficult. The model should include direct genetic and maternal genetic and maternal permanent environmental effects. Interactions of dam with year and with number born account for significant additional variation (about 0.10 of total variation) beyond that by the dam alone. Accounting for that variation may be of biological interest but may not be important for genetic evaluation.

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