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VARIANCE HETEROGENEITY IN DIRECT AND MATERNAL WEIGHT TRAITS BY SEX AND PERCENT PUREBRED FOR SIMMENTAL-SIRED CALVES¹

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ABSTRACT

Phenotypic variances for linear and transformed weight traits were partitioned into residual, direct genetic (D) and maternal genetic (M) components using REML techniques with American Simmental Association data from calves born 1969 to 1985. Variance components were estimated separately from subclasses defined by sex (male, female) and percent Simmental (50, ≥ 75). The model included fixed effects of contemporary group and age-of-dam (<3, 3 to 5, >5 yr). Additive relationships among sires and maternal grandsires were included. Results follow for a sire-maternal grandsire model for $\geq 75\%$ Simmental untransformed data based on 143,280 male and 281,805 female weaning weights (WW) representing 4,763 and 7,406 sires, respectively. Female results are bracketed. For computational simplification, 47,650 [30,909] postweaning gain (PW) records were included in the analysis only for 114,404 [182,255] calves with birth weight (BW). Phenotypic standard deviations (kg) were: BW, 4.5 [4.1]; WW, 26.9 [23.2]; and PW, 25.9 [19.9]. Heritabilities were: BWD, .40 [.45]; WWD, .32 [.39]; PWD, .26 [.32]; BWM, .13 [.15]; WWM, .20 [.16]; and PWM, .01 [.01]. These heritabilities are higher than previously used for genetic evaluations in this breed. Moderate and positive correlations .26 to .50, existed between direct effects and were similar for both sexes. Direct and maternal effects on the same trait were correlated negatively: BW, -.45 [-.31]; and WW, -.27 [-.34]. Genetic correlation between BWM and WWM was .53 [.49]. First-cross progeny exhibited less genetic and residual variation and had lower heritabilities than Simmental calves of higher percent. Correlations between sire evaluations on the subsets were consistent with those expected given a perfect genetic correlation between traits for each sex and percent Simmental. Logarithmic transformed records were no more homogeneous than untransformed records.

(Key Words: Beef Cattle, Maternal Effects, Transformation, Variance, Heterogeneity, Variance Components.)

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Introduction

Genetic evaluations for production traits often assume a linear model; the equation may include fixed effects (e.g., contemporary clas-

sifications and age effects) and random effects (e.g., genetic and residual). Assuming random and residual effects follow a multivariate normal distribution, restricted maximum likelihood (REML) techniques can be used to estimate variances. To minimize the number of parameters to be estimated, it is tempting to assume homogeneous variance.

In beef cattle, phenotypic variance of weight increases with mean; for example, weaning weights have greater variance than birth weights. Typically, males are heavier and more variable than females of the same age. This implies that males and females do not have identical genetic and residual variance.

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TABLE 1. NUMBERS OF OBSERVATIONS AND MEANS (kg) BY CALF SEX FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND YEARLING WEIGHT (YW)

Traits	Sex of calf		
	Bull	Heifer	Steer
BW^a			
No.	220,269	369,933	
Mean	41	36	
WW^b			
No.	205,558	556,448	50,936
Mean	266	228	250
YW^c			
No.	92,208	59,042	4,856
Mean	460	352	397

^aAdjusted for dam age.

^bAdjusted to 205 d.

^cAdjusted to 365 d.

The objective of this study was to quantify heterogeneity for weight traits, by partitioning variation into direct and maternal genetic components, separately for males and females and for first-cross calves compared to later generations of Simmental cattle. Furthermore, it was of interest to investigate power transformations of the observations that may result in homogeneous genetic and residual variance.

Materials and Methods

Description of Data. The American Simmental Association (ASA) made available data on calves born 1969 to 1985 that were used for the genetic evaluation published in the ASA 1987 Sire Selector. These data included birth weights (BW), weaning weights (WW) and yearling weights (YW) (Table 1). To be eligible for registration, a bull must have weaning and yearling weight records; a heifer is required to have a weaning weight record. Accordingly, all calves have weaning weight observations, whereas a lesser number have yearling weights recorded. A large proportion of calves have birth weight records, even though recording is not compulsory, which reflects breeder interest in this trait. Table 2 contains number of records characterized by trait combinations.

Prior to the genetic evaluation, these data had been edited for valid pedigree information and for weights outside ranges considered reasonable (BW, 23 to 64 kg; WW, 91 to 682 kg; YW, 159 to 909 kg). Observations had been assigned to contemporary groups, and

TABLE 2. DISTRIBUTION OF BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND YEARLING WEIGHT (YW) TRAIT COMBINATIONS

Trait combinations	No. of records
WW only	240,863
BW, WW only	377,082
WW, YW only	36,075
BW, WW, YW	158,053
Total	812,073

only records from contemporary groups that were genetically connected with other contemporary groups through common sires were included. Furthermore, within a contemporary group, calves had to be weaned within the range of age (160 to 250 d) defined by the Beef Improvement Federation (BIF). Single-sire contemporary groups had been removed. Further edits were carried out prior to estimating variance components. Records from any bull with more than two progeny or grandprogeny were included. Contemporary groups with no variation in birth weight within sex had BW observations excluded, because such records were assumed to be input standards. These data represented a total of 12,590 bulls appearing as sires, maternal grandsire or pedigree bulls (i.e., sires or maternal grandsires of other bulls, with no recorded progeny.)

Weight traits included in the Cornell genetic evaluation for the ASA and the traits of interest are birth weight, weaning weight adjusted to 205 d (BIF, 1986) and postweaning gain adjusted to 160 d. Adjusted 160-d postweaning gain (PW) is 365-d YW-205-d WW. The computation of variance components using REML was facilitated by transforming the data such that the transformed observations had an identity residual variance-covariance matrix. This required the following four assumptions and edits.

First, joint analysis of 50% and $\geq 75\%$ Simmental calves required different residual variance-covariance matrices by percent Simmental because the residual variance for a calf with sire only known (50% Simmental) includes the maternal grandsire variance. First-cross (50%) and $\geq 75\%$ Simmental calves were analyzed separately with a sire and a sire-maternal grandsire model, respectively.

Second, the model was assumed to include maternal effects for all three traits, BW, WW and PW. This contrasted with the model used for national evaluation of Simmental cattle,

which does not include maternal effects for postweaning gain. There is some evidence for compensatory growth in this population (Elzo et al., 1987) such that Simmental females born out of younger dams have greater postweaning gain than do calves born to older dams. Young dams have lighter calves at weaning than do mature dams, which is due largely to less milk production. A maternal effect for postweaning gain would be expected if the dam effect for postweaning gain were negatively related to preweaning milk production. An objective of this analysis was to confirm the presence or absence of a postweaning maternal effect.

Third, practically all calves with weaning weight and yearling weight records had a birth weight observation (Table 2). Yearling weights from animals without birth weight were excluded to provide a sequential occurrence of trait combinations: WW only, WW and BW, or all three weights.

Fourth, contemporary groups were nested such that PW groups were contained within a single BW group, and the BW group was contained within a single WW group. In reality, from the chronological nature of these traits, a BW contemporary group may include several WW groups. This change in contemporary group nesting resulted in fitting more birth weight contemporary groups than would have been indicated from the actual contemporary groups present at calving. Including unnecessary fixed effects in the model increases the sampling variance of the estimators (Henderson, 1975) but may not be too serious a disadvantage in variance component estimation relative to its computational advantages.

Model for Weight Traits. The model for each weight trait comprised the following terms:

$$y = cg + (\text{sex, age-of-dam, \%Simmental}) + .5u_D(\text{sire}) + .25u_D(\text{mgs}) + .5u_M(\text{mgs}) + \epsilon \quad (1)$$

where

y = BW, 205-d WW, or 160-d PW;
 cg = fixed contemporary group effect;
 (sex, age-of-dam, %Simmental) = fixed effect associated with sex-of-calf, age-of-dam and percent Simmental combination;

$u_D(\text{sire})$ and $u_D(\text{mgs})$ = random direct genetic effects of sire and maternal grandsire;

$u_M(\text{mgs})$ = random maternal genetic effect (environmental effect for the calf); and

ϵ = random residual effect. This includes direct and maternal genetic contributions of the maternal granddam, and Mendelian sampling effects of the dam, direct effect Mendelian sampling of the calf and temporary and permanent environmental effects.

The sire-maternal grandsire model is equivalent to an animal model with direct and maternal effects provided that certain assumptions are satisfied. These include the following: 1) maternal granddams are unrelated and do not have more than one progeny; 2) maternal granddams were mated at random to maternal grandsires; 3) dams do not have more than one progeny; and 4) no information other than maternal grandsire merit was used to select mates for dams. There is some departure from these assumptions in the Simmental population (cows average less than two calvings); however, the sire-maternal grandsire model is a reasonable approximation.

The contemporary groups were defined to group animals that received similar treatment. For animals to be included in the same contemporary group, the following criteria had to be met. All calves had to be identified by the same ASA breeder and herd codes and had to contain the same percent Simmental blood, either 50%, 75% or $\geq 87\%$. These criteria removed the average effects of heterosis that otherwise would bias comparisons among animals of different percent Simmental blood. All contemporary calves were required to have been weighed on the same day. Finally, breeders had to assign identical pasture, management and feeding unit classifications to contemporary calves.

Sex effects for BW included classes for bulls and heifers. Analysis of WW and PW included three sex classes, bulls, heifers and steers. Although sex was not included in the contemporary group definition, 90% or more of contemporary groups contained calves of the same sex. For contemporary groups with mixed-sex calves in the analysis with sexes

pooled, it was assumed that sex differences were constant in all groups.

Age-of-dam categories were <3 yr, 3 to 5 yr, and >5 yr, fewer categories than are used in the national evaluation. Sex by age-of-dam effects were fitted within percent Simmental for analyses that included both 75% and ≥87% Simmental calves. It was assumed that the non-Simmental composition of cross-bred calves did not make any difference to the sex × age-of-dam interaction.

There are two equivalent models for (1) that result in quite different computational efforts to obtain estimates of $u_{D(\text{sire})}$, $u_{D(\text{mgs})}$ and $u_{M(\text{mgs})}$. In matrix notation, defining the vector β to include fixed effects of contemporary group and sex by age-of-dam by percent Simmental interaction, using X to denote the matrix associating effects in β with y , Z_s and Z_m to denote the model matrices corresponding to sire and maternal grandsires, respectively, these two model equations are:

$$y = X\beta + (Z_s + .5Z_m) u_D + Z_m u_M + \epsilon, \quad (2)$$

and

$$y = X\beta + Z_s u_D + Z_m(.5u_D + u_M) + \epsilon. \quad (3)$$

The first expression, (2), involves a vector of direct and a vector of maternal effects. Corresponding to the direct effects are two incidence matrices, one for sires and one for maternal grandsires. The second expression, (3), involves a reparameterization to a sire effect and a maternal grandsire effect. The maternal grandsire effect is a function of direct and maternal effects. In some sense this is a natural parameterization, because an individual observation is affected by the maternal grandsire contribution of direct and maternal genes, which are completely confounded. Relative to Equation (3), fitting model (2) can result in considerable increase in number of nonzero elements in the coefficient matrix for the partition relating to direct effects. This fill increases the cost of forming and iterating mixed model equations. Accordingly, the multiple trait sire-maternal grandsire model equation in (3) was fitted to estimate variance components for ≥75% Simmental calves. First-cross calves had unknown maternal grandsires and were analyzed for direct effects using a

sire model. However, the estimates reported in this paper are causal components, corresponding to an animal equation rather than to sire and maternal grandsire components.

In comparing variance components estimated from 50% and ≥75% Simmental calves, it is difficult to interpret the differences as resulting from the nature of the data (50% vs ≥75%) or from the assumptions relating to the model (sire vs sire-maternal grandsire model). A greater estimated residual variance would be expected from a sire model relative to a sire-maternal grandsire model due to the inadequacy of the sire model to account for assortative mating. Accordingly, the ≥75% data were subjected to analysis with a sire model as well as with a sire-maternal grandsire model.

Restricted Maximum Likelihood. Variance components were estimated using a generalized Expectation-Maximization algorithm (GEM) (Dempster et al., 1977) to obtain a constrained maximum of the restricted log-likelihood function. Computationally, the work required in a single iteration of a GEM algorithm is equivalent to evaluating the first derivative of the restricted log-likelihood function. In general, an evaluation of the first derivative requires obtaining BLUP solutions for random and residual effects and the prediction error variances of random and residual effects, conditional on a current estimate of variance components. Given an estimate of the residual variance-covariance matrix, a matrix can be found to premultiply the data vector such that the resultant vector can be described using a model with uncorrelated residuals. With uncorrelated residuals, the first derivative can sometimes be obtained as a function of the random effects and their prediction error variance, without obtaining solutions for residuals or residual prediction error variance.

Solutions to random effects were obtained after 100 rounds of block Gauss-Seidel iteration using blocks of order 6 defined by the sire and maternal grandsire coefficients corresponding to each bull. Prediction error variances of solutions to random effects were obtained from a second-order approximation based on a Taylor series expansion of a matrix inverse (Garrick, 1988). Iteration of variance components from ≥75% calves was begun using estimates from Elzo et al. (unpublished data) and continued for 90 iterations. There

TABLE 3. NUMBERS OF OBSERVATIONS AND DEGREES OF FREEDOM FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) BY SEX OF CALF WITHIN PERCENT SIMMENTAL

Traits	50% Simmental		≥75% Simmental	
	Female calf	Male calf	Female calf	Male calf
	No. of sires			
	2,554	1,471	7,406	4,763
	No. of observations			
WW	192,272	51,781	281,805	143,280
BW	91,438	37,674	182,255	114,404
PW	12,823	12,106	30,909	47,650
	df			
WW	173,506	46,761	243,361	122,735
BW	82,199	34,137	158,188	98,608
PW	11,652	10,795	27,484	38,750

was no practical or appreciable change in estimates over the last 30 iterations. Subsets of the data were iterated 45 rounds from the converged solution for ≥75% calves. Starting values for estimates of phenotypic variance of log-transformed data were obtained by dividing the phenotypic variance for the untransformed data by the square of the mean. Variance and covariance estimates then were derived using heritabilities and correlations obtained from the analysis of the untransformed data.

Additive genetic relationships among sires and maternal grandsires were included in the analysis by transforming the mixed model equations. Algebraically, the transformation involved premultiplying the left- and right-hand sides of the mixed model equations with a modifying matrix and inserting the modifying matrix and its inverse between the coefficient matrix and the solution vector. The partition of the modifying matrix corresponding to random effects is a Kronecker product involving a Cholesky decomposition of the additive relationship matrix and an identity matrix. In practice, the transformation can be achieved by sequential permutation of the least squares contribution to the mixed model coefficient matrix (Quaas, 1989).

The sampling variance-covariance matrix for estimated variance components was obtained from the inverse of the negative of the estimated matrix of second derivatives. The second derivative matrix was approximated using the method of finite difference (Dennis and Schnabel, 1983).

Definition of Data Subclasses. Distribution of observations and degrees of freedom among the three traits are summarized in Table 3 for data sets partitioned according to calf sex (male, female) within percent Simmental (50, ≥75). Degrees of freedom are the number of observations adjusted for the number of contemporary groups and sex by age-of-dam by percent Simmental effects. A prominent feature of these data was the large proportion of missing observations. Although the majority of the records comprise observations on heifer calves, a higher proportion of postweaning gain records was present for males. Male records can be reported selectively because the ASA registration requirements allow an entire calf record to be submitted by breeders after yearlings have been weighed.

Analysis of records from mixed sexes within percent Simmental subclasses contained 2,922 (50%) and 8,369 (≥75%) sires. Numbers of observations and degrees of freedom can be closely approximated by summing the information in Table 3 within percent Simmental subclass. These sums are approximations because the within-sex subclass data were re-edited for single sire contemporary groups and for sires with ≤2 progeny and ≤2 grandprogeny.

Genetic Correlations between Subclasses. National genetic evaluations for beef cattle in North America assume identical expression of additive genes regardless of calf sex. The evaluation of the American Simmental breed further assumes that the relative performance of first-cross contemporaries is determined by

the same genes that determine relative performance of contemporary cattle from later generations. That is, a unit genetic correlation is assumed to relate performance in each sex-percent Simmental subclass. To investigate this assumption, one would ideally estimate variance components from a multiple-trait system using weights in each sex-percent subclass as different traits. That is computationally difficult because the system of equations to solve for random effects becomes very large and the genetic variance-covariance matrix will approach singularity as the genetic correlation between subclasses approaches one.

An approximate method for validating the assumption of unit genetic correlation between subclasses involves comparing observed and expected correlations of estimated predicted differences obtained in independent data sets. Observed correlations are product-moment correlations between separate evaluations of sires with progeny represented in two subclasses. The expected correlation can be obtained using selection index theory to derive the expression:

$$r_{\hat{g}_1\hat{g}_2} = r_{g_1g_2} \cdot r_{g_1\hat{g}_1} \cdot r_{g_2\hat{g}_2} \quad (4)$$

where subscripts 1 and 2 define subclasses, g_i and \hat{g}_i are actual and predicted merit in subclass i . Assuming a unit genetic correlation between subclasses, $r_{g_1g_2} = 1$, then the expected correlation between evaluations is:

$$r_{\hat{g}_1\hat{g}_2} = r_{g_1\hat{g}_1} \cdot r_{g_2\hat{g}_2} \quad (5)$$

the product of correlations between true and index value in each environment. These terms on the right-hand side of (5) can be obtained from prediction error variances, which are elements of the inverse of the mixed model coefficient matrix.

Investigation of Transformations. Power transformations (y^p for $p \in [-2, 2]$ or $\log(y)$ for $p = 0$) were considered for transforming weight traits to remove variance heterogeneity. Initial investigations involved fitting a single trait fixed effects model to transformed observations for varying p . The model included effects for contemporary groups, sex by age-of-dam by percent Simmental subclasses [INTERCEPT] and date of birth (BW), age at weaning (WW) or gain days (PW) as a covariate [SLOPE]. The absolute values of residuals obtained from the fixed effects model then were analyzed using a model equation containing INTERCEPT and SLOPE effects. If the power transformation removed heterogeneity, one would expect the average magnitude of a residual to be identical regardless of INTERCEPT or SLOPE. Accordingly, for varying p , minimum ratios of mean squares for INTERCEPT and SLOPE relative to error mean square (Table 4) were used to identify a useful transformation. On this basis, log-transformations were considered to be worthy of further investigation using mixed model techniques. Variance components were esti-

TABLE 4. RATIOS OF MEAN SQUARES FOR FIXED EFFECTS ANALYSIS OF ABSOLUTE VALUE RESIDUALS OVER A RANGE OF POWER TRANSFORMATIONS

Model df	Source	Transformation								
		-2.0	-1.5	-1.0	-.5	log	.5	1.0	1.5	2.0
Birth wt										
72	Slope	49.3	34.8	22.6	13.7	9.2	9.6	15.1	25.4	39.8
69	Intercept	1.2	1.1	1.0	1.0	1.1	1.3	1.6	2.0	2.5
Preweaning gain										
109	Slope	36.1	34.4	29.5	23.3	18.7	18.2	23.6	35.4	53.1
105	Intercept	4.3	4.2	3.9	3.5	2.9	2.4	2.2	2.3	2.8
205-d weaning wt										
109	Slope	41.6	34.8	27.0	19.9	15.5	15.3	20.5	31.3	47.4
105	Intercept	4.4	4.1	3.7	3.2	2.7	2.3	2.1	2.2	2.6
Postweaning gain										
108	Slope	3.4	3.2	2.7	2.1	1.9	3.1	1.6	2.0	3.0
103	Intercept	.7	.7	.7	1.4	1.8	2.1	7.9	10.7	10.2

TABLE 5. ESTIMATED DIRECT (D) AND MATERNAL (M) (CO)VARIANCE COMPONENTS (kg^2) AND STANDARD ERRORS (kg) FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) OF $\geq 75\%$ SIMMENTAL CALVES

Traits	Genetic components					
	BWD	WWD	PWD	BWM	WWM	PWM
BWD	7.9 (.7)					
WWD	4.1 (.7)	223 (21)				
PWD	11 (4)	94 (21)	151 (29)			
BWM	-1.6 (.5)	-.3 (2.6)	1 (3)	2.2 (.4)		
WWM	-4.5 (3)	-52 (17)	-3 (19)	7 (2.5)	120 (21)	
PWM	-1.8 (2.5)	-18 (16)	-8 (12)	.8 (1.4)	16 (13)	6 (6)

mated using REML (assuming multivariate normality) for log-transformed BW, WW and PW, using the same model and computational techniques that had been applied to untransformed weights. Effects in both log-transformed and untransformed models cannot follow a multivariate normal distribution; however, there is little statistical methodology available to enable discrimination among possible distributions underlying realizations of random effects in mixed models. In reality, observations may result from processes that include multiplicative and additive effects. In such a case, there is unlikely to be any transformation that removed heterogeneity of genetic and residual effects or a transformation that results in effects that are normally distributed. It is even less likely that such transformations would coincide.

Results and Discussion

Analysis by Percent Simmental with Sexes Pooled

Estimated genetic and residual variance-covariance components are given in Tables 5 and 6 with their (approximate) asymptotic standard errors. Standard errors were small relative to the magnitude of the direct variance estimates for BW and WW. Standard error was relatively larger for the estimate of PW direct effects, probably as a result of missing observations for PW. Compared to relative errors for direct effects, relative errors for maternal variance estimates were larger, which reflects confounding of maternal grandsire contributions of direct and maternal genes. Maternal genetic variance for PW was small relative to its standard error. Table 7 presents

estimated genetic and residual variance components and genetic, residual and phenotypic correlations.

Heritabilities. Heritabilities of BW and WW direct effects were considerably higher than the starting values (Table 7). Relative to starting values, the increased heritabilities resulted from repartitioning residual variance into additive genetic variance. Heritabilities were greater in $\geq 75\%$ Simmental calves relative to first-cross calves. Estimates for $\geq 75\%$ calves from a sire-maternal grandsire model were greater than estimates from a sire model. Heritabilities of maternal effects, defined as the ratio of maternal genetic variance to phenotypic variance, were higher than starting values for BW and WW. Heritability for PW maternal effects was close to zero, confirming that maternal effects for this trait need not be included in genetic evaluations. Strictly speaking, maternal heritability would be defined as the ratio of maternal genetic variance to total maternal variance. However, the model fitted in this analysis did not enable estimation of permanent or temporary maternal environmental variance.

Correlations. Phenotypic correlations (Table 7) were similar to assumed starting values

TABLE 6. ESTIMATED RESIDUAL (CO)VARIANCE COMPONENTS (kg^2) AND STANDARD ERRORS (kg) FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) OF $\geq 75\%$ SIMMENTAL CALVES

Traits	Residual components		
	BW	WW	PW
BW	9.3 (.5)		
WW	10 (2.7)	330 (19)	
PW	6.4 (2.7)	-64 (16)	436 (21)

and did not differ by percent Simmental. Genetic correlations among direct effects were similar to starting values for all subclasses, that is, moderately high and positive. Correlations between direct and maternal effects for the same trait were negative, $-.38$ for BW and $-.32$ for WW. Negative correlations were

expected between direct and maternal effects as a consequence of natural selection for an intermediate optima. The negative correlation was indicative of an incompatibility between genes that enhance an animal's own growth and genes that result in superior maternal performance of a heifer. Correlations between

TABLE 7. VARIANCE COMPONENTS (kg^2), HERITABILITIES AND CORRELATIONS FOR DIRECT (D) AND MATERNAL (M) GENETIC EFFECTS ON BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) BY PERCENT SIMMENTAL

Traits	Random factors:	Percent Simmental			
		50%-100% Sire-MGS ^a	50% Sire	$\geq 75\%$ Sire	$\geq 75\%$ Sire-MGS
Genetic direct (heritabilities)					
BWD		4.3 (.19)	7.7 (.45)	7.5 (.42)	7.9 (.44)
WWD		76 (.14)	159 (.30)	214 (.35)	223 (.36)
PWD		131 (.23)	117 (.21)	122 (.19)	151 (.26)
Genetic maternal (heritabilities)					
BWM		1.5 (.07)			2.2 (.12)
WWM		63 (.11)			120 (.19)
PWM					5.8 (.01)
Residual					
BW		19.3	9.3	10.4	9.3
WW		434	372	394	330
WW		437	438	525	436
Phenotypic					
BW		22.7	17.0	17.9	17.9
WW		562	531	608	621
PW		568	555	648	585
Genetic correlations					
BWD, WWD		.43	.58	.50	.49
BWD, PWD		.39	.32	.32	.32
BWD, BWM		-.48			-.38
BWD, WWM		-.07			-.15
BWD, PWM					-.26
WWD, PWD		.53	.42	.51	.51
WWD, BWM		-.06			-.01
WWD, WWM		-.08			-.32
WWD, PWM					-.49
PWD, BWM		-.01			.06
PWD, WWM		.22			-.02
PWD, PWM					-.28
BWM, WWM		.29			.42
BWM, PWM					.21
WWM, PWM					.60
Residual correlations					
BW, WW		.31	.18	.21	.18
BW, PW		.10	.08	.10	.10
WW, PW		.12	-.11	-.12	-.17
Phenotypic correlations					
BW, WW		.33	.33	.32	.33
BW, PW		.16	.16	.16	.17
WW, PW		.04	.02	.04	.06

^aStarting values from Elzo et al. (unpublished data). MGS = maternal grandsire.

TABLE 8. VARIANCE COMPONENTS (kg²) AND CORRELATIONS FOR DIRECT (D) AND MATERNAL (M) GENETIC EFFECTS ON BIRTH WT (BW) WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW), WITHIN SEX BY PERCENT SIMMENTAL

Traits	Percent Simmental					
	50%		≥75%		≥75%	
	Female	Male	Female	Male	Female	Male
Sex of calves:	Female	Male	Female	Male	Female	Male
Random factors:	Sire	Sire	Sire	Sire	Sire-MGS ^a	Sire-MGS
Genetic direct						
BWD	6.4	7.4	6.6	7.3	7.5	8.0
WWD	107	151	194	208	209	230
PWD	76	136	80	135	126	174
Genetic maternal						
BWM					2.5	2.6
WWM					88	143
PWM					4.8	7.0
Residual						
BW	8.8	13.5	9.7	13.0	7.8	11.4
WW	364	522	340	509	289	399
PW	346	511	428	604	265	497
Phenotypic						
BW	15.2	20.8	16.4	20.4	16.4	20.0
WW	471	674	534	717	539	723
PW	422	647	508	740	394	670
Genetic correlations						
BWD, WWD	.62	.54	.55	.48	.53	.45
BWD, PWD	.38	.37	.37	.26	.29	.26
BWD, BWM					-.31	-.45
BWD, WWM					-.13	-.30
BWD, PWM					-.01	-.34
WWD, PWD	.50	.42	.47	.51	.44	.50
WWD, BWM					-.01	-.07
WWD, WWM					-.34	-.27
WWD, PWM					.00	-.47
PWD, BWM					.01	.10
PWD, WWM					.01	-.06
PWD, PWM					-.03	-.22
BWM, WWM					.49	.53
BWM, PWM					.01	.32
WWM, PWM					-.02	.69
Residual correlations						
BW, WW	.21	.24	.22	.23	.15	.21
BW, PW	.08	.10	.10	.14	.12	.13
WW, PW	-.19	-.02	-.14	-.07	-.22	-.12
Phenotypic correlations						
BW, WW	.33	.32	.35	.31	.36	.31
BW, PW	.16	.17	.16	.17	.18	.18
WW, PW	-.05	.07	.01	.06	.02	.08

^aMGS = maternal grandsire.

maternal effects for different traits were positive. Correlations involving PW maternal effects probably are not meaningful because the covariance estimate was, in most cases, smaller than its estimated standard error (Table 5). Residual correlation between WW and PW was small and negative. A negative residual correlation was expected because WW is the

pivotal weight used in calculating PW. Any error that results in overestimating actual WW results in underestimating PW.

Analysis Within Sex by Percent Simmental Subclass

Variance components and correlations are given in Table 8 for sex by percent Simmental

TABLE 9. DIRECT (D) AND MATERNAL (M) HERITABILITIES FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) BY SEX AND PERCENT SIMMENTAL

Traits	Random factors: Calf sex:	Percent Simmental								
		50% Sire		≥75% Sire		≥75% Sire/MGS ^a				
		Female	All Male	Female	All Male	Female	All Male			
		Heritabilities								
BWD		.42	.45	.35	.40	.42	.36	.45	.44	.40
WWD		.23	.30	.22	.36	.35	.29	.39	.36	.32
PWD		.18	.21	.21	.16	.19	.18	.32	.26	.26
BWM								.15	.12	.13
WWM								.16	.19	.20
PWM								.01	.01	.01

^aMGS = maternal grandsire.

subclasses. Corresponding heritabilities are given in Table 9. There appears to be consistency among estimates of correlations obtained within the subclasses, with the exception of correlations involving PW maternal effects, which are likely to have large estimation errors. There was a consistent increase in phenotypic variance for males relative to females. This increase resulted from greater direct and maternal genetic variance in addition to greater residual variance. However, proportionally, the residual variance showed greater increase in males relative to females than did the genetic variance. This generally resulted in a decrease in heritabilities of direct effects for males compared to females. There was little difference in the maternal heritability for males and females. Estimates from analyses with sexes pooled were, in general, midway between the separate male and females estimates.

Correlations Between Independent Subclasses

Observed and expected correlations were calculated for bulls that had been separately evaluated in two of the subclasses. Correlations were obtained separately for bulls that were accurately evaluated (correlation of true and predicted merit, $r_{g_i\hat{g}_i} \geq .9$ in both subclasses and for all bulls ($r_{g_i\hat{g}_i} \geq .1$). The results are given in Table 10 for correlations between independent evaluations using ≥75%-male and ≥75%-female records. Correlations for direct effects between 50%-male and ≥75%-male subclasses are given in Table 11 and between 50%-female and ≥75%-female subclasses are given in Table 12. The observed and expected correlations for bulls with $r_{g_i\hat{g}_i} \geq .1$ are consistently of similar magnitude with the exception of effects involving postweaning

TABLE 10. CORRELATIONS BETWEEN MALE AND FEMALE EFFECTS FOR DIRECT (D) AND MATERNAL (M) FACTORS FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW)

Traits	No. of bulls	Accuracy ^a of expected progeny differences				
		≥.1 Correlations ^b		≥.9 Correlations		
		Observed	Expected	No. of bulls	Observed	Expected
BWD	1,267	.61	.57	201	.83	.92
WWD	1,216	.50	.54	171	.81	.93
PWD	1,267	.54	.39	85	.76	.91
BWM	1,267	.53	.54	123	.86	.93
WWM	1,246	.47	.45	156	.81	.93
PWM	1,267	.52	.39	79	.72	.91

^aCorrelation between actual and estimated predicted difference, $\text{corr}(g_1, \hat{g}_1)$ and $\text{corr}(g_2, \hat{g}_2)$.

^bCorrelation of expected progeny difference, $\text{corr}(\hat{g}_1, \hat{g}_2)$.

TABLE 11. CORRELATIONS BETWEEN 50% AND $\geq 75\%$ SIMMENTAL EFFECTS FOR DIRECT (D) FACTORS FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) IN MALE CALVES

Traits	No. of bulls	Accuracy ^a of expected progeny differences				
		$\geq .1$ Correlations ^b		No. of bulls	$\geq .9$ Correlations	
		Observed	Expected		Observed	Expected
BWD	297	.59	.61	71	.69	.92
WWD	279	.50	.55	58	.61	.92
PWD	297	.52	.42	18	.71	.93

^aCorrelation between actual and estimated predicted difference, $\text{corr}(g_1, \hat{g}_1)$ and $\text{corr}(g_2, \hat{g}_2)$.

^bCorrelation of expected progeny difference, $\text{corr}(\hat{g}_1, \hat{g}_2)$.

gain, which have a tendency to be more highly correlated than expected. A possible explanation for observed correlations being greater than expected is that the heritability for postweaning gain used in these evaluations was an underestimate of the true heritability. The observed correlations of expected progeny differences from bulls with $r_{g_i, \hat{g}_i} \geq .9$ were

consistently less than the expected correlations. This could result from nonrandom sampling of bulls with high accuracy of evaluation in the subclasses.

A multiple-trait analysis involving postweaning gain by sex as separate traits is worthy of further investigation. However, in the meantime, these results support the assumption that a large fraction of additive genes for weight traits have the same effect with regard to controlling variation in each of the sex-percent Simmental subclasses. That is, the genetic correlation between a random factor in each sex-percent subclass likely is close to unity.

Analysis of Log-Transformed Data

Variance components for sex by percent Simmental subclass are given in Table 13 for analysis of log-transformed weights. Heritabilities from the log analyses are given in Table 14. It is readily apparent that the transformed observations do not have homogeneous variance, although BW and WW transformations may have reduced the level of homogeneity. Transformation for PW increased heterogeneity, such that females had greater phenotypic variance on the transformed scale. This likely is a reflection that the variance of males relative to females did not increase with the mean as rapidly for PW as for BW and WW, because the phenotypic standard deviation for log-transformed records was approximately the ratio of the standard deviation to the mean.

Summary and Conclusions

Estimated variance components for weight traits have moderate to high heritabilities,

TABLE 12. CORRELATIONS BETWEEN 50% AND $\geq 75\%$ SIMMENTAL EFFECTS FOR DIRECT (D) FACTORS FOR BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) IN FEMALE CALVES

Traits	No. of bulls	Accuracy ^a of expected progeny differences				
		$\geq .1$ Correlations ^b		No. of bulls	$\geq .9$ Correlations	
		Observed	Expected		Observed	Expected
BWD	501	.56	.63	122	.84	.94
WWD	484	.47	.59	118	.80	.94
PWD	501	.54	.36	23	.86	.93

^aCorrelation between actual and estimated predicted difference, $\text{corr}(g_1, \hat{g}_1)$ and $\text{corr}(g_2, \hat{g}_2)$.

^bCorrelation of expected progeny difference, $\text{corr}(\hat{g}_1, \hat{g}_2)$.

TABLE 13. VARIANCE COMPONENTS AND CORRELATIONS FOR DIRECT (D) AND MATERNAL (M) EFFECTS OF LOG-TRANSFORMED BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) BY SEX AND PERCENT SIMMENTAL

Traits	Sex of calves: Random factors:	Percent Simmental					
		50% Female	50% All	50% Male	≥75% Female	≥75% All	≥75% Male
		Sire	Sire	Sire	Sire-MGS ^a	Sire-MGS	Sire-MGS
Genetic direct							
BWD		.45	.50	.43	.49	.52	.48
WWD		.20	.26	.26	.36	.38	.36
PWD		.70	.72	.40	.88	.68	.60
Genetic maternal							
BWM					.11	.14	.16
WWM					.14	.20	.23
PWM					.02	.02	.02
Residual							
BW		.70	.71	.89	.62	.62	.69
WW		.93	.93	1.08	.62	.63	.69
PW		5.59	4.05	2.76	4.01	3.12	2.03
Phenotypic							
BW		1.15	1.21	1.32	1.13	1.18	1.21
WW		1.13	1.19	1.34	1.04	1.13	1.21
PW		6.28	4.77	3.16	4.83	3.75	2.58
Genetic correlations							
BWD, WWD		.61	.57	.51	.55	.49	.44
BWD, PWD		.38	.31	.39	.34	.30	.26
BWD, BWM					-.39	-.39	-.44
BWD, WWM					-.18	-.15	-.28
BWD, PWM					-.58	-.40	-.38
WWD, PWD		.48	.42	.48	.42	.44	.47
WWD, BWM					-.02	-.02	-.03
WWD, WWM					-.34	-.32	-.25
WWD, PWM					-.29	-.29	-.27
PWD, BWM					.09	.10	.12
PWD, WWM					.07	.04	-.04
PWD, PWM					-.61	-.56	-.58
BWM, WWM					.43	.43	.52
BWM, PWM					.20	.17	.21
WWM, PWM					.09	.30	.33
Residual correlations							
BW, WW		.23	.22	.25	.19	.18	.21
BW, PW		.06	.08	.09	.08	.09	.11
WW, PW		-.15	-.11	-.02	-.16	-.13	-.10
Phenotypic correlations							
BW, WW		.32	.32	.31	.35	.33	.31
BW, PW		.13	.13	.15	.15	.15	.16
WW, PW		-.06	-.01	.06	.00	.02	.06

^aMGS = maternal grandsire.

indicating likely response to selection on individual performance. However, a breeding objective for beef cattle weight traits is more likely to involve changing the shape of the growth curve rather than increasing weights at

all ages. The moderate positive correlations between weights at different ages implies the existence of sires that, relative to breed average, will enable birth weights to be maintained or reduced while subsequent

TABLE 14. DIRECT (D) AND MATERNAL (M) HERITABILITIES FROM LOG-TRANSFORMED BIRTH WEIGHT (BW), WEANING WEIGHT (WW) AND POSTWEANING GAIN (PW) BY SEX AND PERCENT SIMMENTAL

Traits	Random factors: Calf sex:	Percent Simmental					
		50% Sire			≥75% Sire/MGS ^a		
		Female	All	Male	Female	All	Male
		Heritabilities					
BWD		.39	.41	.32	.44	.44	.40
WWD		.17	.22	.19	.35	.34	.30
PWD		.11	.15	.13	.18	.18	.23
BWM					.10	.12	.14
WWM					.13	.18	.19
PWM					.00	.01	.01

^aMGS = maternal grandsire.

growth rates is increased. Accurate identification of these exceptional sires requires progeny testing.

This study had quantified heterogeneous phenotypic variance by sex-percent Simmental subclass and demonstrated that increased phenotypic variance arose from increased direct genetic, maternal genetic and residual partitions. Furthermore, the increase in direct genetic variance in males relative to females is not in proportion to the increase in residual variance, such that heritability is lower in males than in females. First-cross progeny exhibit less variation and lower heritability than later generations of Simmental cattle. No evidence has been found to suggest that the genetic correlation between different sex-percent subclasses is significantly different from unity.

Power transformers of the weight traits (including log-transformations) have the effect of reducing, but not removing, heterogeneous variance in birth and weaning weight. There remains a tendency for males to exhibit more variation than females for log-transformed birth and weaning weight. Transformations of postweaning gain did not reduce heterogeneity and resulted in male records exhibiting less variation than female records. It is unlikely that a transformation could be found that concurrently will stabilize direct genetic, maternal genetic and residual components of variance.

Models that have a single random factor can be easily modified to account for heterogeneous genetic and residual variances by scaling the observations to standardize the genetic variance, then using heterogeneous residual

TABLE 15. PERCENT OF HEIFER RECORDS BY PROGENY NUMBERS FOR 50% AND ≥75% SIMMENTAL BULLS

No. of progeny	No. of sires	Percent Simmental						
		50%			No. of sires	≥75%		
		Percent heifer calves				Percent heifer calves		
		Minimum	Mean	Maximum		Minimum	Mean	Maximum
90-99	24	44	69	92	85	40	64	100
100-199	107	41	67	97	327	39	63	100
200-299	34	49	74	95	100	43	63	100
300-399	23	46	72	90	45	48	64	84
400-499	12	57	75	88	26	48	65	94
500-599	13	61	73	89	13	46	66	79
600-699	14	60	78	94	15	50	63	82
700-799	2	72	80	88	10	54	64	71
800-899	9	57	78	88	10	58	68	79
900-999	3	79	81	83	11	52	65	79
≥1000	42	71	83	95	68	55	66	80

parameters. This is not possible for models with two or more random factors, unless the random factors can all be scaled by the same constant. In general, evaluations to account for heterogeneous genetic and residual effects require transforming the model (incidence) matrices for random effects, in addition to accounting for heterogeneous residual parameters (Garrick, 1988; Quaas et al., 1989).

If heterogeneous variance can be ignored in evaluations, in the absence of selection, the prediction error variance will be increased but the predictors will remain unbiased. However, the regression of predicted merit on actual merit generally will not be unity, resulting in under- or over-evaluations of individual animals, depending on subclass. Evaluations of sires will be misleading when progeny are unevenly distributed by subclass. The proportions of heifer records for Simmental bulls are given in Table 15, categorized by sire usage. Sires with wide use have variable reporting of progeny records by sex of calf. Evaluation using homogeneous parameters would underestimate superior bulls' evaluations based on predominantly female records, or predominantly 50% Simmental records.

Beginning in July 1988, national genetic evaluations of American Simmental cattle (using the sire-maternal grandsire model for birth weight direct and maternal effects, weaning weight direct and maternal effects and postweaning gain direct effects) account for

heterogeneous genetic residual variances by sex-percent Simmental subclass.

Further research to investigate the adequacy of currently applied models, particularly with respect to the suitability of variance components, is recommended. Heterogeneous variance by age-of-dam and by herd are possible areas of interest for fine-tuning genetic evaluation systems.

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