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Estimation of additive and nonadditive genetic variances in Hereford, Gelbvieh, and Charolais by Method \mathfrak{R}^1

M. Duangjinda², J. K. Bertrand³, I. Misztal, and T. Druet⁴

Animal and Dairy Science Department, University of Georgia, Athens 30602-2771

ABSTRACT: Parameters for direct and maternal dominance were estimated in models that included non-additive genetic effects. The analyses used weaning weight records adjusted for age of dam from populations of Canadian Hereford ($n = 467,814$), American Gelbvieh ($n = 501,552$), and American Charolais ($n = 314,552$). Method \mathfrak{R} estimates of direct additive genetic, maternal additive genetic, permanent maternal environment, direct dominance, and maternal dominance variances as a proportion of the total variance were 23, 12, 13, 19, and 14% in Hereford; 27, 7, 10, 18, and 2% in Gelbvieh; and 34, 15, 15, 23, and 2% in Charolais. The correlations between direct and maternal additive genetic effects

were -0.30 , -0.23 , and -0.47 in Hereford, Gelbvieh, and Charolais, respectively. The correlations between direct and maternal dominance were -0.38 , -0.02 , and -0.04 in Hereford, Gelbvieh, and Charolais, respectively. Estimates of inbreeding depression were -0.20 , -0.18 , and -0.13 kg per 1% of inbreeding for Hereford, Gelbvieh, and Charolais, respectively. Estimates of the maternal inbreeding depression were -0.01 , -0.02 , and -0.02 kg, respectively. The high ratio of direct dominance to additive genetic variances provided some evidence that direct dominance effects should be considered in beef cattle evaluation. However, maternal dominance effects seemed to be important only for Hereford cattle.

Key Words: Dominance, Genetic Variance

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Introduction

Only additive genetic effects are used in current genetic evaluation of beef cattle. If dominance is ignored, the evaluations of some animals, particularly dams and animals involved in embryo transfer programs, may be inaccurate (Varona et al., 1998). Including dominance effects in the model provides the potential for predicting specific combining abilities in a breeding system (De Stefano and Hoeschele, 1992; Misztal, 1997).

Past estimates of the dominance variance in beef cattle (Cantet et al., 1988; Meyer, 1989; Rodriguez-Almeida et al., 1995) have been derived from very small data sets, although good estimates of dominance variance in field data require large amounts of data

(Chang, 1988). Gengler et al. (1998) estimated the dominance variance for postweaning weight using the animal model, Method \mathfrak{R} , and a large data set. Estimates for maternally influenced traits from field data were not available because Method \mathfrak{R} did not fully support maternal models. Also, the properties of Method \mathfrak{R} under selection were not well known. Druet et al. (2001) extended Method \mathfrak{R} to support animal models containing maternal additive and dominance effects. Duangjinda et al. (2001) showed that estimates by Method \mathfrak{R} were unbiased for large data sets in which phenotypic selection was not practiced across contemporary groups. Both studies showed that direct and maternal dominance variances expressed as a proportion of the total variance can be estimated from large data sets using single-trait models. However, only ad hoc formulas exist for estimation of residual variances in Method \mathfrak{R} (Reverter et al., 1994b).

The objectives of this study were to estimate genetic parameters for direct and maternal dominance effects and to estimate individual and maternal inbreeding depression for weaning weight in several breeds of beef cattle.

Materials and Methods

Data Description

Records of weaning weight adjusted for age-of-dam and age-of-calf were obtained from the Canadian Here-

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²Current address: Dept. of Anim. Sci. Khon Kaen Univ., Khon Kaen 40002, Thailand.

³Correspondence: 356 Animal and Dairy Science Complex (phone: 706-542-0964; fax: 706-583-0274; E-mail: jkbert@arches.uga.edu).

⁴Current address: Anim. Sci. Unit, Gembloux Agricultural Univ., B-5030 Gembloux, Belgium.

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Table 1. Characteristics of the data on weaning weight of Hereford, Gelbvieh, and Charolais

Item	Hereford	Gelbvieh	Charolais
Total no. of animals	467,814	501,552	314,552
No. of animal with records	255,790	381,389	252,456
No. of contemporary groups	20,761	57,050	32,660
No. of dominance subclasses	1,219,123	1,070,024	942,791
No. of full-sib animals	63,084	42,738	40,204
Average weaning weight, kg	246.7	271.6	268.4
Average inbreeding, %	0.102	0.134	0.160

ford Association, American Gelbvieh Association, and American International Charolais Association. Age-of-dam, age-of-calf, and contemporary group definitions were assigned according to each association’s genetic evaluation program. Contemporary groups were defined by herd, management code, sex, and weigh date, and by pasture code if present. Details of the data sets are summarized in Table 1.

Model

The data sets were analyzed separately for each breed using two single-trait animal models. Model I included effects of direct and maternal additive genetic, maternal permanent environmental, and direct and maternal dominance. Model II was as Model I except that the dominance effects were removed. Both models included regressions on individual and maternal inbreeding. The models can be written as follows:

$$\text{Model I: } \mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\mathbf{b}_i\Delta_i + \mathbf{Z}\mathbf{b}_m\Delta_m + \mathbf{Z}\mathbf{a} + \mathbf{Z}\mathbf{m} + \mathbf{Z}\mathbf{d} + \mathbf{Z}\mathbf{q} + \mathbf{W}\mathbf{p} + \mathbf{e},$$

$$\text{Model II: } \mathbf{y} = \mathbf{X}\beta + \mathbf{Z}\mathbf{b}_i\Delta_i + \mathbf{Z}\mathbf{b}_m\Delta_m + \mathbf{Z}\mathbf{a} + \mathbf{Z}\mathbf{m} + \mathbf{W}\mathbf{p} + \mathbf{e},$$

where \mathbf{y} was the vector of weaning weight records, β was the vector of fixed effects (contemporary groups), \mathbf{b}_i was the vector of inbreeding of individuals, \mathbf{b}_m was the vector of inbreeding of dams, Δ_i was the regression coefficient for individual inbreeding depression, Δ_m was the regression coefficient for maternal inbreeding depression, \mathbf{a} was the vector of random direct additive genetic effects, \mathbf{m} was the vector of random maternal additive genetic effects, \mathbf{d} was the vector of random direct dominance effects, \mathbf{q} was the vector of random maternal dominance effects, \mathbf{p} was the vector of random maternal permanent environmental effects, and \mathbf{X} , \mathbf{Z} , and \mathbf{W} were known incidence matrices relating records to their respective fixed and random effects.

The variances were as follows:

$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{d} \\ \mathbf{q} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & 0 & 0 & 0 & 0 \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{D}\sigma_d^2 & \mathbf{D}\sigma_{dq} & 0 & 0 \\ 0 & 0 & \mathbf{D}\sigma_{dq} & \mathbf{D}\sigma_q^2 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_p^2 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix},$$

where σ_a^2 , σ_m^2 , σ_p^2 , σ_d^2 , σ_q^2 , and σ_e^2 , were direct additive, maternal additive, maternal permanent environmental, direct dominance, maternal dominance, and residual variances, respectively, σ_{am} was the covariance between direct and maternal additive effects, σ_{dq} was the covariance between direct and maternal dominance effects, \mathbf{A} was the numerator relationship matrix for direct and maternal genetic effects, and \mathbf{D} was the numerator relationship matrix for direct and maternal dominance genetic effects.

Data Analyses

Estimates of variance components were obtained by Method \Re (Reverter et al., 1994a) using an acceleration method described by Druet et al. (2001). Data from each breed were analyzed 10 times with different 50% partial data subsets selected randomly. The convergence criterion was $r_i = 1 \pm 0.0001$, where r_i is regression for variance component i . Sampling standard deviations of the estimates were calculated as SD of the estimates from different subsamples.

Results and Discussion

Estimates of Variance Components and Genetic Parameters

Estimates of additive and nonadditive genetic variances as a proportion of the total variance of weaning weight for each breed and Models I and II are shown in Tables 2 and 3. For Model I, the estimates of heritability for direct genetic effects (h^2) were 0.23, 0.27, and 0.34 for Hereford, Gelbvieh, and Charolais, respectively. For Model II, these estimates were 0.24, 0.28, and 0.33 for Hereford, Gelbvieh and Charolais, respectively. Previous h^2 estimates for Hereford were in the

Table 2. Parameter estimates for Hereford, Gelbvieh, and Charolais using Model I

Parameter ^a	Hereford		Gelbvieh		Charolais	
	Mean	SD	Mean	SD	Mean	SD
h^2	0.23	0.03	0.27	0.02	0.34	0.01
m^2	0.12	0.01	0.07	0.01	0.15	0.01
c^2	0.13	0.01	0.10	0.01	0.15	0.01
d^2	0.19	0.03	0.18	0.01	0.23	0.01
q^2	0.14	0.03	0.02	0.01	0.02	0.01
d^2/h^2	0.79	0.16	0.65	0.03	0.68	0.02
q^2/h^2	0.62	0.13	0.08	0.02	0.07	0.05
$r(a, m)$	-0.30	0.05	-0.23	0.04	-0.47	0.03
$r(d, q)$	-0.38	0.14	-0.02	0.11	-0.04	0.13
Δ_i	-0.20	0.08	-0.18	0.03	-0.13	0.08
Δ_m	-0.01	0.05	-0.02	0.02	-0.02	0.02

^a h^2 = direct additive genetic variance as a proportion of the total variance, m^2 = maternal additive genetic variance as a proportion of the total variance, c^2 = maternal permanent environmental variance as a proportion of the total variance, d^2 = direct dominance variance as a proportion of the total variance, q^2 = maternal dominance variance as a proportion of the total variance, $r(a, m)$ = correlation between direct and maternal additive effects, $r(d, q)$ = correlation between direct and maternal dominance effects, Δ_i = regression coefficient for individual inbreeding depression (kg/%), and Δ_m = regression coefficient for maternal inbreeding depression (kg/%).

range of 0.18 to 0.24 (Meyer, 1992; Dodenhoff et al., 1998; De Mattos et al., 2000). In addition, Dodenhoff et al. (1998) reported h^2 of 0.27 for Gelbvieh, and Koots et al. (1994) reported h^2 of 0.31 for Charolais.

The estimates of maternal heritability (h_m^2) and maternal permanent environmental variance as a proportion of the total variance (c^2) from Models I and II were within the range of previous reports using equivalent models (Meyer, 1992; Koots et al., 1994; Snelling et al., 1996). The estimates of h_m^2 from Model I were 0.12, 0.07, and 0.15 and from Model II were 0.14, 0.08, and 0.15 for Hereford, Gelbvieh, and Charolais, respectively. The estimates for Hereford seemed lower when compared to those of Koots et al. (1994) and De Mattos et al. (2000), who reported 0.20 and 0.16, respectively. However, these estimates were similar to the weighted estimate of 0.13 from various studies reviewed by Mohiuddin (1993). In addition, Dodenhoff et al. (1998) reported h_m^2 of 0.10 in Gelbvieh and 0.14 in Charolais. The estimates of c^2 from Model I were 0.13, 0.10, and

0.15 and from Model II were 0.17, 0.09, and 0.14 in Hereford, Gelbvieh, and Charolais, respectively.

The results showed that ignoring dominance and maternal dominance effects only slightly influenced the estimates of heritability. These results supported previous studies that showed accounting for dominance effects had little influence on the estimates of additive genetic variances (Tempelman and Burnside, 1991; Fuerst and Solkner, 1994; Rodriguez-Almeida et al., 1995).

The direct dominance variance estimates for weaning weight expressed as a ratio of the direct genetic variance (d^2/h^2) was greater than 64% in all breeds, which may be interpreted as suggesting that dominance effects should be considered in beef cattle evaluation. The estimates of dominance variance as a proportion of the total variance (d^2) were 0.19, 0.18, and 0.23 in Hereford, Gelbvieh, and Charolais, respectively. These estimates were within the range of the estimates from previous reports in beef cattle. Hohenboken and Brinks (1971) and Cantet et al. (1988) found

Table 3. Parameter estimates for Hereford, Gelbvieh, and Charolais using Model II

Parameter ^a	Hereford		Gelbvieh		Charolais	
	Mean	SD	Mean	SD	Mean	SD
h^2	0.24	0.02	0.28	0.02	0.33	0.01
m^2	0.14	0.01	0.08	0.01	0.15	0.01
c^2	0.17	0.01	0.09	0.01	0.14	0.01
$r(a, m)$	-0.32	0.05	-0.31	0.02	-0.46	0.03
Δ_i	-0.22	0.11	-0.20	0.02	-0.16	0.01
Δ_m	-0.02	0.05	-0.01	0.06	-0.02	0.02

^a h^2 = direct additive genetic variance as a proportion of the total variance, m^2 = maternal additive genetic variance as a proportion of the total variance, c^2 = maternal permanent environmental variance as a proportion of the total variance, $r(a, m)$ = correlation between direct and maternal additive effects, Δ_i = regression coefficient for individual inbreeding depression (kg/%), and Δ_m = regression coefficient for maternal inbreeding depression (kg/%).

d^2 of 0.09 to 0.13 using ANOVA methods, whereas Rodriguez-Almeida et al. (1995) reported d^2 of 0.29 using REML with small data sets and animal models. However, maternal dominance did not seem to be important in all breeds. The estimates of maternal dominance variance as a proportion of the total variance (q^2) were 0.14, 0.02, and 0.02 in Hereford, Gelbvieh, and Charolais, respectively. This result implied that a model including maternal dominance may not be needed for Gelbvieh and Charolais because the estimates of maternal dominance were very small with a ratio of q^2/h^2 less than 10%.

Negative correlations between direct and maternal effects were found in all breeds. The estimates were -0.30 , -0.23 , and -0.47 in Model I and -0.32 , -0.31 , and -0.46 in Model II for Hereford, Gelbvieh, and Charolais, respectively. The estimates from Model II agreed with recent reports that used similar models (Waldron et al., 1993; Robinson, 1997; De Mattos, et al., 2000). A previous study by Rodriguez-Almeida et al. (1995) reported that dominance and epistatic effects had no influence on the correlation between direct and maternal genetic effects. However, the result from this study showed that the inclusion of direct and maternal dominance effects had a slight effect.

The estimate of the correlation between direct and maternal additive effects in Canadian Hereford was similar to the estimates of -0.29 reported by Meyer (1997), which was produced by analyzing Polled Hereford data using a model that included maternal phenotype as a fixed covariate. The negative correlation implies a tendency for animals with high genetic merit for weaning weight growth to have low genetic merit for maternal ability. This would suggest that genes that partition nutrients for growth are partly antagonistic with genes that partition nutrients for lactation (Garrick, 1990.) Another reason for negative correlation could be sire \times year interaction effects (Robinson, 1996) or a negative environmental correlation between dam and offspring (Meyer, 1997; Doderhoff et al., 1998).

The estimates of the correlation between direct and maternal dominance effects were -0.38 , -0.02 , and -0.04 in Hereford, Gelbvieh, and Charolais, respectively. The negative correlation in Hereford showed that animals with high weaning weight due to direct dominance effect tend to have a lower maternal ability due to maternal dominance effects. Subsequently, the choice of combination of their parents could adversely affect the maternal dominance ability of their offspring. For Herefords, the inclusion of the maternal dominance effect may be justified. However, for Gelbvieh and Charolais, the maternal dominance effects do not seem to be important.

Estimates of Inbreeding Depression

The estimates of inbreeding depression from Model I were -0.20 , -0.18 , and -0.13 kg for every 1% increase

in inbreeding in Hereford, Gelbvieh, and Charolais, respectively. For every 1% increase in inbreeding in dams, calves will lose 0.01, 0.02, and 0.02 kg of weaning weight in the same breeds, respectively. The estimates of inbreeding depression were similar in Models I and II. The estimates from this study seemed to be lower than those of Snelling et al. (1996), who reported -0.49 and -0.38 for individual and maternal inbreeding depression in American Hereford weaning weight. However, these estimates were obtained from four closely related herds with fewer than 10,000 animals in the data set.

Implications

The inclusion of the dominance effects in the model had a slight impact on the estimates of additive and permanent environmental variances. The high ratio of d^2/h^2 in all breeds suggested the direct dominance effect is important for weaning weight. However, the weaning weight maternal dominance effect seems only to be important for Hereford cattle.

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