Effect of Including Relationships in the Estimation of Genetic Parameters of Beef Calves

*Department of Animal and Poultry Science, University of Arkansas, Fayetteville 72701

ABSTRACT: Variances and covariances for birth weight, gain from birth to weaning (ADG), and 205-d weight were obtained from a sire-dam model and a sire-maternal grandsire model for a herd of Angus and a herd of Hereford cattle. Estimates of direct additive genetic variance ($\sigma^2_A$), maternal additive genetic variance ($\sigma^2_M$), covariance between direct and maternal additive genetic effects ($\sigma_{AM}$), permanent environmental variance ($\sigma^2_{PE}$), and residual variance ($\sigma^2_e$) were obtained both with and without the inverse of the numerator relationship matrix ($A^{-1}$) included. Estimates of heritability for direct genetic effects ($h^2_A$), maternal genetic effects ($h^2_M$), and the correlation between direct and maternal effects ($r_{AM}$) for birth weight were .37, .18, and -.01 in Angus and .53, .23, and -.19 in Herefords, respectively, for the analyses without $A^{-1}$. For the analyses with $A^{-1}$, estimates of $h^2_A$, $h^2_M$, and $r_{AM}$ were .42, .22, and -.12 for Angus and .58, .22, and -.13 for Herefords, respectively. Estimates of $h^2_A$, $h^2_M$, and $r_{AM}$ for ADG were .43, .15, and -.44 in Angus and .52, .38, and -.03 in Herefords, respectively, without $A^{-1}$. With $A^{-1}$, estimates of $h^2_A$, $h^2_M$, and $r_{AM}$ were .57, .15, and -.32 for Angus and .58, .39, and -.05 for Herefords, respectively. Estimates of $h^2_A$, $h^2_M$, and $r_{AM}$ for 205-d weight were .49, .15, and -.46 for Angus and .58, .43, and -.06 for Herefords, respectively, without $A^{-1}$. With $A^{-1}$, estimates of $h^2_A$, $h^2_M$, and $r_{AM}$ were .63, .16, and -.36 for Angus and .68, .43, and -.08 for Herefords, respectively. Estimates of $h^2_A$ were higher with $A^{-1}$ than without $A^{-1}$, but estimates of $h^2_M$ were similar. Using variances and covariances obtained from analyses including $A^{-1}$ generally gave higher estimates of direct breeding values than using variances and covariances obtained from analyses not including $A^{-1}$. Both Pearson product-moment and Spearman rank correlations were high (.99) between estimates of breeding values from the two analyses, although some changes in rank did occur.

Key Words: Beef Cattle, Preweaning Period, Growth, Variance, Genetic Parameters, Breeding Value


Introduction

Knowledge of the relative importance of direct and maternal additive genetic effects for growth traits is important to beef producers when they formulate breeding plans. Bertrand and Benyshek (1987) presented procedures for estimating genetic and environmental variances and covariance with beef cattle field data. Including the inverse of
the numerator relationship matrix \((A^{-1})\) in the 
estimation procedure should improve the accuracy of estimates. The objectives of this study were 1) to estimate variances and covariance for birth weight, preweaning ADG, and 205-d weight both with and without \(A^{-1}\) for a herd of Angus and a herd of Hereford cattle 2) to use these estimates in a reduced animal model (RAMI) for a maternally influenced trait for prediction of direct and maternal breeding values for these traits, and 3) to compare estimates of breeding values obtained from analyses using variances and covariance estimated by including \(A^{-1}\) with those obtained from analyses using variances and covariance estimated without \(A^{-1}\).

**Materials and Methods**

Data were birth and 205-d weight records for Angus and Hereford calves born on the University of Arkansas Experiment Station farm near Fayetteville, AR from 1965 through 1988. Cattle were not used for management and/or production type experiments, and herd management stayed the same during these years. All calves were born in the spring and weaned in the fall, usually the 1st wk of October. After heifer calves were weaned, each received an average of 2 to 4 kg/d of supplemental grain in addition to pasture and/or hay free-choice until grass was available the following spring. Heifers were bred as 2-yr-olds to calve at approximately 3 yr of age. Heifers and cows grazed pastures that were mixed stands of tall fescue and bermudagrass with some clover and native grasses. Supplemental feeding of cows and 2-yr-old heifers was limited to the winter season and consisted of prairie hay and range cubes. The amount of daily supplement was determined by the herdsman to maintain moderate body condition and provide adequate nutrients for production.

Mating was by natural service between May 20 and July 20 each year; two to four sires per breed were used each breeding season. Cows were checked for pregnancy by rectal palpation when calves were weaned, and all nonpregnant cows were culled. The majority of females were kept as replacements, and no females from outside the herds were added. Approximately one-third of the bulls used originated outside the herds. In both cases, structural soundness and records of preweaning gain, postweaning gain, and feed conversion were considered in choosing herd sires.

Birth and weaning weight records were adjusted for age of dam using additive adjustment factors (BIF, 1986). The ADG from birth to weaning was calculated from these adjusted weights. There were 2,039 birth weight records and 1,835, 205-d weight records representing 54 sires and 604 dams in the Hereford data. In the Angus data there were 2,514 birth weight records and 2,309, 205-d weight records representing 35 sires and 672 dams. There were 48 contemporary groups in each herd defined by birth year and sex of calf (24 yr and two sexes).

Thirty of the 35 Angus sires were also maternal grandsires, and 18 were sons of sires. In the Hereford herd, 39 of the 54 sires were also maternal grandsires, and 23 were sons of sires used previously. Complete pedigrees of all animals born into the herd could be traced back to the base population with the exception of descendants of sires that originated outside the herd. These pedigrees could be traced back to that sire. The base population would be parents born before 1965 that had progeny born in 1965 or later.

Variances and covariances were estimated using two models: a sire-dam model and a sire-maternal grandsire model with and without including relationships among sires and dams. This procedure was described by Bertrand and Benyshek (1987) for the case without relationships.

The sire-dam model expressed in matrix notation is

\[
y = Xc + Z_1s_1 + Z_2d + e_1,
\]

where \(y\) is a vector of progeny records, \(c\) is a vector of unknown fixed contemporary group effects, \(s_1\) and \(d\) are vectors of unknown random sire and dam effects, respectively, and \(e_1\) is the random error. The \(X, Z_1,\) and \(Z_2\) are incidence matrices of zeros and ones assigning each record to the appropriate contemporary group, sire, and dam. Mixed-model equations are as follows:

\[
\begin{bmatrix}
XX & XZ_1 & XZ_2 \\
Z_1'Z_1 + A^{-1}_s & Z_1'Z_2 & \\
\text{symmetric} & Z_2'Z_2 + A^{-1}_d \end{bmatrix}
\begin{bmatrix}
c \\
d_1 \\
d_2 \\
\end{bmatrix} =
\begin{bmatrix}
y \\
Z_1'y \\
Z_2'y \\
\end{bmatrix}
\]

where \(A^{-1}_s\) is the inverse of relationships among sires, not accounting for dams, and \(A^{-1}_d\) is the inverse of relationship among dams, not accounting for sires, and \(k_1\) and \(k_2\) are the ratios of error variance to sire and dam variances, respectively.
Relationships among sires and dams were assumed zero for this analysis. The $A^{-1}$ were calculated using the noninbred population method of Henderson (1976). Occasionally, matings were made that resulted in inbreeding; however, these were relatively small in number, and average inbreeding coefficients were less than 5% (Buddenberg et al., 1990). For analyses without relationships included, $A^{-1}_{s1}$ and $A^{-1}_{d}$ were replaced with the appropriate identity matrix (I). Solutions for $c$, $s1$, and $d$ were obtained, and sire ($c^2_{s1}$), dam ($c^2_{d}$), and error ($c^2_{e}$) variances were calculated by REML with an expectation maximization (EM) algorithm as follows:

$$
\sigma^2_{c1} = (y'y - \hat{c}X'y - \hat{s1}'Z_1'y - \hat{d}'Z_2'y)/(N - CG)
$$

$$
\sigma^2_{s1} = (s1'A^{-1}_{s1}s1 + tr(A^{-1}_{s1}T_{ss}))/NS
$$

$$
\sigma^2_{d} = (d'A^{-1}_{d}d + tr(T_{dd}))^2_{e1})/ND.
$$

Variances without $A^{-1}$ were estimated as follows:

$$
\sigma^2_{c1} = (y'y - \hat{c}X'y - \hat{s1}'Z_1'y - \hat{d}'Z_2'y)/(N - CG)
$$

$$
\sigma^2_{s1} = (s1' + tr(T_{ss}))^2_{e1})/NS
$$

$$
\sigma^2_{d} = (d'd + tr(T_{dd}))^2_{e1})/ND.
$$

where $NS$ = number of sires, $ND$ = number of dams, $N$ = total number of records, and $CG$ = number of contemporary groups. The terms $T_{ss}$ and $T_{dd}$ are submatrices of the inverse of the coefficient matrix (Henderson, 1973) corresponding to the sire or dam portion as illustrated below:

$$
\begin{bmatrix}
XX & XZ_1 & XZ_2 \\
Z_1Z_1 + A^{-1}_{s1}k_1 & Z_1Z_2 \\
\text{symmetric} & Z_2Z_2 + A^{-1}_{d}k_2
\end{bmatrix}^{-1}
$$

These equations are similar to the REML estimators presented by Lin (1988).

An iterative solution was required. Convergence for birth weight and 205-d weight variances was assumed when the new estimates were within .02 kg$^2$ of the previous estimates. Convergence for ADG was assumed when the new estimates were within .00002 kg$^2$ of the previous estimates.

Expectations of variances and covariances were assumed (Bertrand and Benyshek, 1987) to be as follows:

$$
E(\sigma^2_{c1}) = (1/4) \sigma^2_{A},
$$

$$
E(\sigma^2_{d}) = (1/4) \sigma^2_{A} + \sigma_{AM} + \sigma^2_{M} + \sigma^2_{PE},
$$

and

$$
E(\sigma^2_{e}) = (1/2) \sigma^2_{A} + \sigma^2_{e},
$$

where $\sigma^2_{A}$ is the additive genetic variance of the direct effect, $\sigma_{AM}$ is the covariance between direct and maternal genetic effects, $\sigma^2_{M}$ is the additive genetic variance of the maternal effect, $\sigma^2_{PE}$ is the variance of the maternal permanent environment effect, and $\sigma^2_{e}$ is the variance of temporary environmental influence.

The sire-maternal grandsire model expressed in matrix notation is

$$
y = Xc + Z_1s2 + Z_2mgs + e_2,
$$

where $y$ is a vector of progeny records, $c$ is a vector of unknown fixed contemporary group effects, $s2$ and $mgs$ are vectors of unknown random sire and maternal grandsire effects, respectively, and $e_2$ is the random error. The $X$, $Z_1$, and $Z_2$ are incidence matrices of zeros and ones assigning each record to the appropriate contemporary group, sire, and maternal grandsire. The vectors $s2$ and $mgs$ included the same animals in the same order. Individuals that were only a sire and not a maternal grandsire had all zeros in the corresponding column in $z_2$. Because no females were added from outside the herds, all maternal grandsires were also sires; therefore, $Z_1$ did not have any zero columns. Again, an iterative procedure was followed, and convergence was as defined above.

Mixed-model equations including relationships are as follows:

$$
\begin{bmatrix}
XX & XZ_1 & XZ_2 \\
Z_1Z_1 + A^{-1}_{s1} & Z_1Z_2 + A^{-1}_{d} & Z_2Z_2 + A^{-1}_{d}
\end{bmatrix}
\begin{bmatrix}
c \\
s2 \\
mgs
\end{bmatrix}
$$

where $A^{-1}$ is the same for sires and maternal grandsires and is the same as $A^{-1}_{s1}$ in the previous analysis, because the same sires were present in both analyses. For the analyses without relationships each $A^{-1}$ was replaced by an identity matrix (I).
Sire ($\sigma^2_s$), maternal grandsire ($\sigma^2_{mgs}$), and error ($\sigma^2_e$) variances and covariance between sire and maternal grandsire ($\sigma_{smgs}$) were estimated as follows at each round of iteration:

$$\sigma^2_s = (y'y - \hat{c}X'y - \hat{s}Z'y - \hat{mgs}Z'y)/(N - CG)$$

$$\sigma^2_e = (\hat{s}A^{-1}\hat{s} + tr(A^{-1}T_{ss}\sigma^2_e))/NS$$

$$\sigma^2_{smgs} = (\hat{mgs}A^{-1}\hat{mgs} + tr(A^{-1}T_{mgs}\sigma^2_e))/NS$$

where $NS = \text{number of sires} = \text{number of maternal grandsires}$, $N = \text{total number of records}$, and $CG = \text{number of contemporary groups}$. The terms $T_{ss}$, $T_{mgs}$, and $T_{smgs}$ are the appropriate segments of the inverse of the coefficient matrix. For analyses without $A^{-1}$, $A^{-1}$ was replaced with $I$ in the above equations.

The $\alpha$ were calculated from the following $2 \times 2$ matrix:

$$\begin{bmatrix} \sigma^2_{s2} & \sigma^2_{smgs} \\ \sigma^2_{smgs} & \sigma^2_{mgs} \end{bmatrix}^{-1} = \begin{bmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{12} & \alpha_{22} \end{bmatrix}$$

Expectations of the variances and covariances were assumed (Bertrand and Benyshek, 1987) to be the following:

$$E(\sigma^2_s) = (1/4) \sigma^2_A,$$

$$E(\sigma^2_{mgs}) = (1/8) \sigma^2_A + (1/4) \sigma^2_{AM},$$

$$E(\sigma^2_{smgs}) = (1/16) \sigma^2_A + (1/4) \sigma^2_{AM} + (1/4) \sigma^2_{M}, \text{ and}$$

$$E(\sigma^2_e) = (11/16) \sigma^2_A + (3/4) \sigma^2_{AM} + (3/4) \sigma^2_M + \sigma^2_{PE} + \sigma^2_e.$$

Genetic variances and covariance needed to set up the mixed-model equations to predict direct and maternal breeding values using RAM for a maternally influenced trait were computed (Bertrand and Benyshek, 1987) as follows:

- additive variance: $\sigma^2_A = 2 (\sigma^2_{s1} + \sigma^2_{s2});$
- additive x maternal variance: $\sigma^2_{AM} = 4 (\sigma^2_{smgs} - \sigma^2_A/8);$
- maternal variance: $\sigma^2_M = 4 (\sigma^2_{mgs} - \sigma^2_A/16 - \sigma^2_{AM}/4);$
- permanent maternal environmental variance: $\sigma^2_{PE} = \sigma^2_e - \sigma^2_{e1} - (3/16) \sigma^2_A - (3/4) \sigma^2_{AM} - (3/4) \sigma^2_M$ and

- temporary environmental variance: $\sigma^2_e = \sigma^2_{e2} - \sigma^2_{PE} - (3/4) \sigma^2_M - (3/4) \sigma^2_{AM} - (11/16) \sigma^2_A.$

Estimates of heritability of additive and maternal effects were obtained as follows:

$$h^2_A = \sigma^2_A/\sigma^2_{AM}, \sigma^2_{AM} = \sigma^2_{M} + \sigma^2_{PE} + \sigma^2_e,$$

and the correlation between additive and maternal effects was estimated as $r_{AM} = \sigma_{AM}/\sqrt{\sigma^2_A \sigma^2_M}$

Direct and maternal breeding values for each trait were estimated for each breed using a RAM for a maternally influenced trait as described by Quaas and Pollak (1980) and Pollak and Quaas (1983). Further description of this model was given by Benyshek et al. (1988). The permanent environmental effect of the dam was not included in this analysis because all estimates of this variance were negative, except for Hereford birth weight. Solutions were obtained for parents from this analysis. Back-solutions for nonparents are given by the following:

$$u_i = 1/2u_{disire} + 1/2u_{ddam} + [1/(1 + \alpha_1D_i^{-1})] (Y_i - CG - u_{mdam} - 1/2u_{disire} - 1/2u_{ddam})$$

and

$$u_{mi} = 1/2u_{msire} + 1/2u_{mmdam} + [\alpha_1/\alpha_2] (u_i - 1/2u_{disire} - 1/2u_{ddam}),$$

where $u_i$ is the direct breeding value for growth for individual $i$, $u_{mi}$ is the maternal breeding value for individual $i$, $u_{disire}$ is the direct breeding value of the sire, $u_{ddam}$ is the direct breeding value of the dam, $u_{msire}$ is the maternal breeding value of the sire, and $u_{mmdam}$ is the maternal breeding value of the dam.

The value of $\alpha_1 = \sigma^2_{e2}/\sigma^2_A$, $\alpha_2 = \sigma^2_e/\sigma^2_{AM}$, $CG = \text{estimate for contemporary group for individual } i$, and the value of $D_i$ is 1/2 or 3/4 depending on whether one or both parents are known. In this analysis pedigrees were known for all individuals born into the herd; therefore, parents were always known.

Two sets of breeding values were estimated for each trait for each breed: 1) using variances and covariances obtained by including $A^{-1}$ and 2) using variances and covariances obtained without including $A^{-1}$. Predicted breeding values by year of birth are presented graphically. Relationship between estimates of breeding values from the two analyses were examined by Pearson product-moment correlations and Spearman rank correlations.
Results and Discussion

Estimates of variances and covariances for both the sire-dam model and the sire-maternal grandsire models, with and without $A^{-1}$ included, are presented in Table 1 for all traits for both breeds. Sire components of variance for Angus were consistently smaller than for Herefords. Wilson et al. (1986) also reported smaller sire components of variance for Angus than for Herefords. As expected, dam components of variance were larger than sire components of variance except for ADG and 205-d weight of Angus. Larger dam than sire components of variance for birth weight and weaning weight were also reported by Wilson et al. (1986).

Sire components were larger in the analyses with $A^{-1}$ included than in the analyses without $A^{-1}$. Van Vleck and Hudson (1982), using Henderson's Method 3, reported that estimates of sire components were increased by 2 to 5% when relationships were considered. Components of variance for dam, maternal grandsire, and error were similar with or without $A^{-1}$ included.

Additive direct and maternal estimates of variance are presented in Table 2. Estimates of direct additive genetic variance were larger than maternal variance for all three traits for both breeds. Both additive and maternal variances were larger for Herefords than for Angus. Numerous reports have documented that direct and maternal additive effects differ among breeds (MacNeil et al., 1982; Dearborn et al., 1987; Trus and Wilton, 1988). Analyses including $A^{-1}$ gave larger additive and maternal variances than analyses omitting $A^{-1}$.

The covariance between additive and maternal genetic effects was negative for all traits in both breeds (Table 2). Trus and Wilton (1988) also reported negative covariances between direct and maternal effects for birth weight and preweaning gain in Angus, Hereford, Shorthorn, Charolais, and Simmental. They stated that negative covariances would suggest a genetic antagonism between a heifer's prenatal growth potential and the subsequent quality of her intrauterine environment. Others (Koch and Clark, 1955; Deese and Koger, 1967; Hohenboken and Brinks, 1971) have also shown large negative correlations between

---

Table 1. Estimates of variances and covariances [kg²] from analyses of preweaning growth traits of Angus (A) and Hereford (H) cattle using two models

<table>
<thead>
<tr>
<th>Item</th>
<th>Birth wt</th>
<th>ADG</th>
<th>205-d Wt</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>H</td>
<td>A</td>
</tr>
<tr>
<td>Sire-dam model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{a1}$</td>
<td>1.09</td>
<td>2.51</td>
<td>.0010</td>
</tr>
<tr>
<td>$\sigma^2_d$</td>
<td>1.88</td>
<td>4.18</td>
<td>.0012</td>
</tr>
<tr>
<td>$\sigma^2_{e1}$</td>
<td>13.42</td>
<td>9.77</td>
<td>.0086</td>
</tr>
<tr>
<td>Sire-maternal grandsire model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{a2}$</td>
<td>1.33</td>
<td>2.42</td>
<td>.0009</td>
</tr>
<tr>
<td>$\sigma^2_{mgs}$</td>
<td>.91</td>
<td>1.38</td>
<td>.0003</td>
</tr>
<tr>
<td>$\sigma^2_{mg}$</td>
<td>.60</td>
<td>.92</td>
<td>.0002</td>
</tr>
<tr>
<td>$\sigma^2_{e2}$</td>
<td>11.11</td>
<td>14.80</td>
<td>.0077</td>
</tr>
<tr>
<td>Sire-dam model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{a2}$</td>
<td>1.25</td>
<td>2.73</td>
<td>.0014</td>
</tr>
<tr>
<td>$\sigma^2_d$</td>
<td>1.91</td>
<td>4.10</td>
<td>.0011</td>
</tr>
<tr>
<td>$\sigma^2_{e1}$</td>
<td>13.29</td>
<td>9.61</td>
<td>.0087</td>
</tr>
<tr>
<td>Sire-maternal grandsire model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{a2}$</td>
<td>1.55</td>
<td>2.82</td>
<td>.0013</td>
</tr>
<tr>
<td>$\sigma^2_{mgs}$</td>
<td>.98</td>
<td>1.53</td>
<td>.0005</td>
</tr>
<tr>
<td>$\sigma^2_{mg}$</td>
<td>.58</td>
<td>1.17</td>
<td>.0009</td>
</tr>
<tr>
<td>$\sigma^2_{e2}$</td>
<td>11.11</td>
<td>14.79</td>
<td>.0094</td>
</tr>
</tbody>
</table>
Table 2. Estimates of genetic and environmental variances and covariances (kg$^2$) of preweaning growth traits of Angus (A) and Hereford (H) cattle

<table>
<thead>
<tr>
<th>Trait and breed</th>
<th>$\sigma_A^2$</th>
<th>$\sigma_{AM}$</th>
<th>$\sigma_M^2$</th>
<th>$\sigma_{PE}^2$</th>
<th>$\sigma_e^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>4.85</td>
<td>-.02</td>
<td>2.43</td>
<td>-5.03</td>
<td>11.00</td>
</tr>
<tr>
<td>H</td>
<td>9.86</td>
<td>-1.27</td>
<td>4.34</td>
<td>-.88</td>
<td>4.84</td>
</tr>
<tr>
<td>Preweaning ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.0039</td>
<td>-.0010</td>
<td>.0014</td>
<td>-.0018</td>
<td>.0067</td>
</tr>
<tr>
<td>H</td>
<td>.0065</td>
<td>-.0002</td>
<td>.0048</td>
<td>-.0021</td>
<td>.0035</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>209.40</td>
<td>-53.15</td>
<td>62.49</td>
<td>-114.69</td>
<td>320.20</td>
</tr>
<tr>
<td>H</td>
<td>344.05</td>
<td>-16.54</td>
<td>251.43</td>
<td>-118.54</td>
<td>131.19</td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>5.60</td>
<td>-.48</td>
<td>2.92</td>
<td>-5.07</td>
<td>10.49</td>
</tr>
<tr>
<td>H</td>
<td>11.09</td>
<td>-.88</td>
<td>4.25</td>
<td>.58</td>
<td>4.06</td>
</tr>
<tr>
<td>Preweaning ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.0054</td>
<td>-.0099</td>
<td>.0015</td>
<td>-.0024</td>
<td>.0060</td>
</tr>
<tr>
<td>H</td>
<td>.0075</td>
<td>-.0003</td>
<td>.0051</td>
<td>-.0025</td>
<td>.0032</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>282.75</td>
<td>-51.51</td>
<td>71.51</td>
<td>-140.66</td>
<td>287.80</td>
</tr>
<tr>
<td>H</td>
<td>400.02</td>
<td>-23.48</td>
<td>258.93</td>
<td>-103.29</td>
<td>107.90</td>
</tr>
</tbody>
</table>

Genetic parameters of beef calves

additive and maternal effects for weaning weight. Herefords had larger covariance between additive and maternal effects than Angus for birth weight, but Angus had larger covariances between additive and maternal effects for preweaning ADG and 205-d weight. Covariances were similar for analyses including or not including $A^{-1}$ for preweaning ADG and 205-d weight; however, for birth weight, including relationships increased the covariance for Angus (-.48 vs -.02) and decreased the covariance for Hereford (-.88 vs -.127).

The variance component associated with permanent environmental effects was negative in all cases except birth weight of Herefords in the analysis without $A^{-1}$ included (Table 2). The extent to which the negative estimates were the result of sampling or the result of some unknown source of bias was not clear. A negative estimate of $\sigma_{PE}^2$ for Brangus birth weight was reported by Bertrand and Benyshek (1987). Estimates of $\sigma_e^2$ were larger for Angus than for Hereford and were larger in the analyses without $A^{-1}$ than in the analyses with $A^{-1}$ included (Table 2).

Estimates of $h_A^2$, $h_M^2$, and $r_{AM}$ are presented in Table 3. Estimates of heritability were larger in magnitude for Hereford than for Angus for all three traits, although differences were not as great for preweaning ADG and 205-d weight as for birth weight. Wilson et al. (1986), using a sire-dam model with field data, also reported larger heritability of birth weight in Hereford than in Angus (.41 vs .19) and little difference in estimates of heritability for weaning weight of the two breeds (.13 for Hereford and .16 for Angus). Heritabilities of birth weight and weaning weight reported by Wilson et al. (1986) were smaller than those reported in this study. Typically, analyses of data

Table 3. Heritability estimates and genetic correlation between direct and maternal effects for preweaning growth traits of Angus (A) and Hereford (H) cattle

<table>
<thead>
<tr>
<th>Trait and breed</th>
<th>$h_A^2$</th>
<th>$h_M^2$</th>
<th>$r_{AM}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.37</td>
<td>.18</td>
<td>-.01</td>
</tr>
<tr>
<td>H</td>
<td>.53</td>
<td>.23</td>
<td>-.19</td>
</tr>
<tr>
<td>Preweaning ADG</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.43</td>
<td>.15</td>
<td>-.44</td>
</tr>
<tr>
<td>H</td>
<td>.52</td>
<td>.38</td>
<td>-.03</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.49</td>
<td>.15</td>
<td>-.46</td>
</tr>
<tr>
<td>H</td>
<td>.58</td>
<td>.43</td>
<td>-.06</td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.42</td>
<td>.22</td>
<td>-.12</td>
</tr>
<tr>
<td>H</td>
<td>.59</td>
<td>.22</td>
<td>-.13</td>
</tr>
<tr>
<td>Preweaning ADG</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.57</td>
<td>.15</td>
<td>-.32</td>
</tr>
<tr>
<td>H</td>
<td>.58</td>
<td>.39</td>
<td>-.05</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>.63</td>
<td>.16</td>
<td>-.36</td>
</tr>
<tr>
<td>H</td>
<td>.66</td>
<td>.43</td>
<td>-.08</td>
</tr>
</tbody>
</table>
collected at experiment or research stations produce heritabilities larger than estimates from field data (Wright et al., 1987).

Cantet et al. (1988) reported estimates of heritability for direct effects of .16 to .27 for birth weight and of .26 to .32 for weaning weight for Hereford calves using 17 different covariances among relatives. Estimates of heritability for direct additive effects for breeds analyzed at the University of Georgia ranged from .24 to .33 for birth weight and from .16 to .28 for weaning weight (Benyshek et al., 1988). Trus and Wilton (1988) reported heritability estimates for direct additive effects of .37 and .39 for birth weight and .3d and .30 for preweaning gain for Angus and Herefords, respectively.

Estimates of heritability for maternal effects of .18 to .63 for birth weight and .27 to .67 for weaning weight were reported by Cantet et al. (1988). Benyshek et al. (1988) reported that heritabilities of breeds analyzed at the University of Georgia ranged from .06 to .15 for maternal additive effects for birth weight and from .13 to .26 for maternal additive effects for weaning weight. Trus and Wilton (1988) reported heritability estimates for maternal additive effects of .13 and .21 for birth weight and .21 and .27 for preweaning gain for Angus and Herefords, respectively.

Table 4. Mean, standard deviation, minimum, and maximum for direct and maternal breeding values [kg] for preweaning growth traits of Angus and Hereford cattle

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Direct breeding values - Angus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2741</td>
<td>0.24</td>
<td>1.20</td>
<td>-5.28</td>
<td>5.04</td>
</tr>
<tr>
<td>With A-1</td>
<td>2741</td>
<td>0.30</td>
<td>1.36</td>
<td>-5.46</td>
<td>5.50</td>
</tr>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2536</td>
<td>0.226</td>
<td>0.0364</td>
<td>-1.229</td>
<td>1.452</td>
</tr>
<tr>
<td>With A-1</td>
<td>2536</td>
<td>0.261</td>
<td>0.0458</td>
<td>-1.450</td>
<td>1.786</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2536</td>
<td>5.12</td>
<td>9.05</td>
<td>-29.90</td>
<td>32.72</td>
</tr>
<tr>
<td>With A-1</td>
<td>2536</td>
<td>5.78</td>
<td>10.53</td>
<td>-38.80</td>
<td>38.44</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Direct breeding values - Hereford</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2249</td>
<td>0.38</td>
<td>2.21</td>
<td>-8.06</td>
<td>7.32</td>
</tr>
<tr>
<td>With A-1</td>
<td>2249</td>
<td>0.47</td>
<td>2.42</td>
<td>-8.97</td>
<td>8.13</td>
</tr>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2045</td>
<td>0.0132</td>
<td>0.0557</td>
<td>-1.627</td>
<td>2.040</td>
</tr>
<tr>
<td>With A-1</td>
<td>2045</td>
<td>0.0132</td>
<td>0.0600</td>
<td>-1.753</td>
<td>2.229</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2045</td>
<td>3.05</td>
<td>13.46</td>
<td>-39.54</td>
<td>49.30</td>
</tr>
<tr>
<td>With A-1</td>
<td>2045</td>
<td>3.44</td>
<td>14.87</td>
<td>-43.49</td>
<td>55.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Material breeding values - Angus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2741</td>
<td>-0.52</td>
<td>0.75</td>
<td>-2.76</td>
<td>2.51</td>
</tr>
<tr>
<td>With A-1</td>
<td>2741</td>
<td>-0.58</td>
<td>0.80</td>
<td>-2.85</td>
<td>2.68</td>
</tr>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2536</td>
<td>-0.059</td>
<td>0.160</td>
<td>-0.713</td>
<td>0.427</td>
</tr>
<tr>
<td>With A-1</td>
<td>2536</td>
<td>-0.056</td>
<td>0.161</td>
<td>-0.725</td>
<td>0.452</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2536</td>
<td>-1.74</td>
<td>3.41</td>
<td>-14.88</td>
<td>8.59</td>
</tr>
<tr>
<td>With A-1</td>
<td>2536</td>
<td>-1.74</td>
<td>3.56</td>
<td>-15.67</td>
<td>9.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maternal breeding values - Hereford</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2249</td>
<td>0.03</td>
<td>1.20</td>
<td>-4.71</td>
<td>5.51</td>
</tr>
<tr>
<td>With A-1</td>
<td>2249</td>
<td>0.01</td>
<td>1.18</td>
<td>-4.69</td>
<td>5.45</td>
</tr>
<tr>
<td>ADG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2045</td>
<td>0.0086</td>
<td>0.0348</td>
<td>-1.330</td>
<td>0.152</td>
</tr>
<tr>
<td>With A-1</td>
<td>2045</td>
<td>0.0083</td>
<td>0.0349</td>
<td>-1.380</td>
<td>0.158</td>
</tr>
<tr>
<td>205-d Wt</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without A-1</td>
<td>2045</td>
<td>2.03</td>
<td>8.12</td>
<td>-29.11</td>
<td>40.54</td>
</tr>
<tr>
<td>With A-1</td>
<td>2045</td>
<td>1.91</td>
<td>8.13</td>
<td>-30.18</td>
<td>41.95</td>
</tr>
</tbody>
</table>
Heritability estimates for direct additive effects were larger when relationships were included than when they were omitted; the largest difference occurred for preweaning ADG and 205-d weight in the Angus, for which a difference of 14% was observed. Estimates of heritability for maternal effects were similar when using A⁻¹ or not using A⁻¹ in the analysis. The largest difference observed was for birth weight in Angus (.22 vs .18). Van Vleck and Hudson (1982) showed for Henderson's Method 3 that including relationships among sires for a sire model would increase the estimate of heritability. Dong and Van Vleck (1989) reported that heritabilities of survival and calving interval in first-lactation Holstein cows were slightly larger using REML with an animal model than results in the literature that did not use REML with an animal model.

All estimates of \( r_{AM} \) were negative (Table 3). This correlation was greater for Angus for preweaning ADG and 205-d weight than for Herefords but was similar for the two breeds for birth weight when A⁻¹ was considered. Trus and Wilton (1988) also reported negative genetic correlations between direct and maternal additive genetic effects for birth weight and preweaning gain but did not observe a difference between Angus and Herefords. Garrick et al. (1989), for Simmental-sired calves, reported negative correlations between direct and maternal effects for birth weight and weaning weight for both males and females. Wright et al. (1987) reported a positive \( r_{AM} \) of .16 for weaning weight of American Simmental cattle. Bertrand and Benyshek (1987) reported a negative \( r_{AM} \) for Limousin and Brangus cattle for birth and weaning weights.

<table>
<thead>
<tr>
<th>Trait and breed</th>
<th>Avg change in rank</th>
<th>Max. change in rank</th>
<th>Avg absolute difference in EBV, kg</th>
<th>Max. absolute difference in EBV, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Birth wt, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>42</td>
<td>295</td>
<td>.0881</td>
<td>.4547</td>
</tr>
<tr>
<td>H</td>
<td>25</td>
<td>157</td>
<td>.2034</td>
<td>1.0132</td>
</tr>
<tr>
<td><strong>Preweaning ADG, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>66</td>
<td>362</td>
<td>.0075</td>
<td>.0428</td>
</tr>
<tr>
<td>H</td>
<td>16</td>
<td>96</td>
<td>.0037</td>
<td>.0189</td>
</tr>
<tr>
<td><strong>205-d Wt, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>56</td>
<td>338</td>
<td>1.4925</td>
<td>8.8979</td>
</tr>
<tr>
<td>H</td>
<td>20</td>
<td>140</td>
<td>1.2249</td>
<td>6.2760</td>
</tr>
<tr>
<td><strong>Birth wt, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>50</td>
<td>387</td>
<td>.0811</td>
<td>.3890</td>
</tr>
<tr>
<td>H</td>
<td>27</td>
<td>205</td>
<td>.0528</td>
<td>.3404</td>
</tr>
<tr>
<td><strong>Preweaning ADG, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>60</td>
<td>394</td>
<td>.0014</td>
<td>.0068</td>
</tr>
<tr>
<td>H</td>
<td>20</td>
<td>125</td>
<td>.0012</td>
<td>.0078</td>
</tr>
<tr>
<td><strong>205-d Wt, kg</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>60</td>
<td>384</td>
<td>3.110</td>
<td>1.4536</td>
</tr>
<tr>
<td>H</td>
<td>27</td>
<td>200</td>
<td>.3627</td>
<td>2.8483</td>
</tr>
</tbody>
</table>

Using variances and covariances obtained from the analyses including A⁻¹ gave larger mean estimates of direct breeding values for all three traits than using variances and covariances obtained from analyses not including A⁻¹ for both Angus and Herefords (Table 4).

Both Pearson product-moment and Spearman rank coefficients of correlation were > .99 between the two estimates of breeding values for direct additive genetic value for all traits for both breeds. Estimates of coefficients of correlation between estimates of maternal breeding values were also > .99 for all traits for both Angus and Herefords. The magnitude of these correlations indicates that ranking of animals for direct or maternal breeding value would be similar regardless of which set of variances and covariances was used.

Changes in rank did occur between the two sets of breeding values (Table 5). Maximum changes in rank ranged from 96 to 362 for direct breeding
values and from 125 to 394 for maternal breeding values. These changes may not be great considering the number of animals evaluated; however, one Angus bull did change as much as 8.9 kg and one Hereford bull as much as 6.28 kg in estimated breeding value for 205-d weight. These changes were the lowest ranked Angus and the highest ranked Hereford for both estimates of breeding value; therefore, ranking did not change for the maximum absolute differences in estimated breeding values for 205-d weight for these extreme animals. Maximum absolute differences in estimated breeding values were 1.01 kg or less for birth weight.

Direct breeding values for birth weight increased when plotted against year of birth, whereas maternal breeding values for birth weight tended to decrease for both Angus and Herefords (Figure 1). Direct breeding values for ADG increased in both Angus and Herefords when plotted against year of birth (Figure 2). Maternal breeding values for Angus ADG decreased when plotted against year of birth, whereas those for Herefords were variable and tended to increase (Figure 2). Direct breeding values also increased over time for both Angus and Hereford 205-d weight (Figure 3). Maternal breeding values for 205-d weight decreased over time for Angus and tended to increase slightly for Herefords (Figure 3).

Benyshek et al. (1988) discussed effects of using improper genetic covariances in RAM analyses. They reported that predictions of breeding values for direct additive genetic value for weaning weight of sires, dams, and nonparents were not affected by the presence of a covariance between direct and maternal effects. In their study, predictions of maternal breeding value for sires were most affected by the use of an improper covariance. Use of a negative correlation when a

![Figure 1. Trends over time for direct and maternal breeding values for birth weight of Angus and Hereford cattle. Breeding values were estimated from variances and covariances obtained from analyses with A^{-1} included (solid symbols) and without A^{-1} included (open symbols).](image1)

![Figure 2. Trends over time for direct and maternal breeding values for preweaning ADG of Angus and Hereford cattle. Breeding values were estimated from variances and covariances obtained from analyses with A^{-1} included (solid symbols) and without A^{-1} included (open symbols).](image2)
correlation did not exist resulted in the smallest accuracy of prediction for sires. They suggested using a zero covariance if accurate estimates of the true value are not available.

In summary, preweaning growth in beef cattle is influenced by an individual's genotype for growth (direct genetic effects), by the dam's genotype for maternal characters, and by environmental effects. Genetic antagonism between direct and maternal effects on preweaning growth reported in this study suggest that loss in maternal performance due to intense selection for individual growth could be large and should be of concern to producers in their selection programs. Including $A^{-1}$ in estimation of heritabilities increased estimates of $h^2_A$ by 5 to 8% in the Hereford and by 5 to 14% in the Angus. Estimates of $h^2_M$ were increased by 0 to 4% by including $A^{-1}$. Bertrand and Kriese (1989) reported that little was gained in variance component estimation by including only sire-son, half-sib, and grandsire-grandson relationships.

Using variances and covariances obtained from the analyses including $A^{-1}$ generally gave higher estimates of direct breeding values than using variances and covariances obtained from analyses not including $A^{-1}$. Both Pearson product-moment and Spearman rank correlations were large (.99) between estimates of breeding values for all traits; however, some changes in rank did occur. The maximum change in rank for the three traits in Angus was 394 and in Hereford was 205.

**Implications**

Direct and additive maternal effects and the correlation between them differ among breeds. The genetic antagonisms between direct and maternal effects on preweaning growth reported in this study should be of concern to producers in their selection programs. Including the relationship matrix in the procedure for estimation of genetic parameters should improve accuracy of estimates; however, under conditions of this study, few changes in ranking of individual animals with respect to breeding values occurred. Thus, in some situations, procedures that do not make use of the relationship matrix would be acceptable for estimation of genetic parameters to be used in reduced animal model analyses.

**Literature Cited**


and environmental (co)variances for first lactation milk yield, survival, and calving interval. J. Dairy Sci. 72:978.


