ABSTRACT: Data from Hereford, 25% Simmental-75% Hereford, 50% Simmental-50% Hereford, and 75% Simmental-25% Hereford dams were used to estimate maternal heterosis and level of agreement with the dominance model. Cows were located at the Northern Agricultural Research Center near Havre, MT and were managed consistent with practices for western range environments. Sample halves of dam breed groups were bred to Charolais and Tarentaise sires to produce calves at 3 to 8 yr of age. There were 766 exposures to breeding that resulted in 581 calves. Breed group means for most traits supported the dominance model. Maternal heterosis was estimated by regression techniques for 22 cow and calf traits. Maternal heterosis was not significant for day of conception, number of services, gestation length, or calving difficulty. Estimates of maternal heterosis for calf growth traits ranged from .7% for weaning height to 5.2% for weaning weight and 7.5% for weaning condition score. Calf weight per unit of cow weight at weaning showed significant maternal heterosis (7.1%). Higher levels of maternal heterosis were exhibited for milk production (8.2 to 11.1%) and the negative, but nonsignificant, estimate of maternal heterosis for early minus late milk production suggested more persistent lactation for crossbred cows. Maternal heterosis was 11.5% for proportion of dams that calved and 10.4% for proportion of dams that weaned calves. Calf weaning weight per cow exposed to breeding, a characteristic combining calf growth and dam reproduction, exhibited 17.9% maternal heterosis.

Key Words: Beef Cattle, Maternal Effects, Heterosis, Dominance

Introduction

Several studies have evaluated the maternal productivity of different breed groups of beef cows, but relatively fewer studies have been designed to estimate maternal heterosis. These present results represent part of a long-term experiment to evaluate productivity of different biological types of beef cattle under range conditions. The objectives of the present study were to evaluate whether the dominance model accurately explained breed group differences and to estimate maternal heterosis from Hereford (HH), 25% Simmental-75% Hereford (1S3H), 50% Simmental-50% Hereford (1S1H), and 75% Simmental-25% Hereford (3S1H) 3- to 8-yr-old cows that raised either Charolais or Tarentaise calves.

Materials and Methods

Experimental Animals. Cows within each breed group (HH, 1S3H, 1S1H, and 3S1H) were sired by 9 or 10 different bulls. Random halves of cows within
these breed groups were mated with Charolais (23) and Tarentaise (8) sires to produce calves at 3 to 8 yr of age. Dam age composition was similar for each breed group. Cows were bred by artificial insemination for 45 d during June and July and no clean-up bulls were used. Cows were culled if they were nonpregnant for two consecutive years up to production of the third calf crop. During the fourth and later calf crops all nonpregnant cows were culled.

Experimental cattle were located at the Northern Agricultural Research Center near Havre, MT. Cows were maintained on native range with sufficient supplemental feed during the winter (January through April) to maintain weight. After calving in March and April, the cows were fed alfalfa hay until the 1st wk of May, when they were placed on a spring pasture that was primarily crested wheat grass (Agropyron cristatum). Starting the 1st wk of June the cows were moved to summer pasture located on the northwestern slopes of the Bear Paw mountains in north central Montana. Annual precipitation is about 480 mm and vegetation of the pasture is represented by rough fescue (Festuca scabrella), Idaho fescue (Festuca idahoensis), and bluebunch wheatgrass (Agropyron spicatum) with interspersed areas of ponderosa pine (Pinus ponderosa). The terrain varied from level to slopes of extreme steepness (45%) at an altitude of 1,200 m and the stocking rate was 1.2 ha per animal unit month. More complete descriptions of management of cows from birth through calving have been given by Lawlor et al. (1984), Kress et al. (1984, 1990a,b), Steffan et al. (1985), Lathrop et al. (1988), and Funston et al. (1991).

Traits of the calves (and in some cases a combination trait of the cow and the calf such as milk production) and reproductive traits of the dams that were analyzed are shown in Table 1. There were 581 calf records from 1979 to 1984 that resulted from 766 exposures of cows to breeding. Calving difficulty was scored as 1 to 5 where 1 = no difficulty; 2 = slight difficulty, some assistance required; 3 = difficult birth, use of a mechanical calf puller usually required; 4 = extreme difficulty (Caesarean section); and 5 = abnormal presentation. Abnormal presentations were excluded from the analyses. Calf weights were taken at birth, at 2 mo (prebreeding), at 3.5 mo (postbreeding), and at weaning at 6 mo of age. Other traits measured at weaning were hip height and a visual condition score (the score ranged from 1 to 9 with 1 representing an extremely thin condition and 9 representing an extremely fat condition). Milk production of 4-yr-old dams was measured by the weigh-suckle-weigh technique at approximately 40 and 130 d of lactation. The separation interval was 6 h for the early estimate and ranged from 6 to 10 h for the second estimate. Milk production was converted to a 24-h basis. Proportion calved and weaned were based on the number of dams exposed to breeding. Calf weaning weight per cow exposed to breeding was based on all cows

### Table 1. R²-Values for regression of least squares breed group mean on proportion of Simmental and estimates of maternal heterosis

<table>
<thead>
<tr>
<th>Trait</th>
<th>R²</th>
<th>Maternal heterosis</th>
<th>Midparent mean (P)</th>
<th>Residual SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day of conception, d</td>
<td>.19</td>
<td>-.98 ± 1.74</td>
<td>172.3</td>
<td>11.12</td>
</tr>
<tr>
<td>Number of services</td>
<td>.48</td>
<td>.05 ± .08</td>
<td>1.23</td>
<td>.404</td>
</tr>
<tr>
<td>Gestation length, d</td>
<td>.08</td>
<td>-.61 ± .76</td>
<td>288.1</td>
<td>4.81</td>
</tr>
<tr>
<td>Calving difficulty, score</td>
<td>.06</td>
<td>.03 ± .15</td>
<td>1.23</td>
<td>.932</td>
</tr>
<tr>
<td>Proportion calving difficulty</td>
<td>.11</td>
<td>.05 ± .08</td>
<td>.13</td>
<td>.397</td>
</tr>
<tr>
<td>Calf birth weight, kg</td>
<td>1.00</td>
<td>1.61 ± .72</td>
<td>44.8</td>
<td>4.61</td>
</tr>
<tr>
<td>Calf prebreeding weight, kg</td>
<td>1.00</td>
<td>4.8 ± 1.8</td>
<td>99</td>
<td>11.5</td>
</tr>
<tr>
<td>Calf postbreeding weight, kg</td>
<td>.98</td>
<td>5.8 ± 2.3</td>
<td>154</td>
<td>14.7</td>
</tr>
<tr>
<td>Calf weaning weight, kg</td>
<td>.98</td>
<td>12.1 ± 3.1</td>
<td>233</td>
<td>20.0</td>
</tr>
<tr>
<td>Calf weaning height, cm</td>
<td>.94</td>
<td>.84 ± 5.4</td>
<td>113</td>
<td>3.4</td>
</tr>
<tr>
<td>Calf weaning weight/height, kg/cm</td>
<td>.96</td>
<td>.097 ± .023</td>
<td>2.07</td>
<td>.146</td>
</tr>
<tr>
<td>Calf weaning condition, score</td>
<td>.94</td>
<td>.43 ± .11</td>
<td>5.7</td>
<td>.70</td>
</tr>
<tr>
<td>Calf weaning weight + cow prebreeding weight</td>
<td>.75</td>
<td>.03 ± .007</td>
<td>.43</td>
<td>.047</td>
</tr>
<tr>
<td>Calf weaning weight + cow weight at weaning</td>
<td>.92</td>
<td>.029 ± .007</td>
<td>.41</td>
<td>.045</td>
</tr>
<tr>
<td>Calf weaning weight + (cow prebreeding weight)</td>
<td>.87</td>
<td>.134 ± .031</td>
<td>2.08</td>
<td>.198</td>
</tr>
<tr>
<td>Calf weaning weight + (cow weight at weaning)</td>
<td>.92</td>
<td>.130 ± .031</td>
<td>2.02</td>
<td>.195</td>
</tr>
<tr>
<td>Early milk production of 4-yr-old dams, kg</td>
<td>.25</td>
<td>1.08 ± 1.29</td>
<td>13.0</td>
<td>4.01</td>
</tr>
<tr>
<td>Late milk production of 4-yr-old dams, kg</td>
<td>.99</td>
<td>1.04 ± 1.33</td>
<td>9.4</td>
<td>3.85</td>
</tr>
<tr>
<td>Early minus late milk production, kg</td>
<td>.38</td>
<td>-.89 ± 1.85</td>
<td>4.5</td>
<td>5.37</td>
</tr>
<tr>
<td>Proportion calved</td>
<td>.96</td>
<td>.082 ± .051</td>
<td>.71</td>
<td>.375</td>
</tr>
<tr>
<td>Proportion weaned</td>
<td>.89</td>
<td>.073 ± .056</td>
<td>.70</td>
<td>.410</td>
</tr>
<tr>
<td>Calf weaning weight per cow exposed, kg</td>
<td>.95</td>
<td>28.5 ± 12.9</td>
<td>159</td>
<td>95.2</td>
</tr>
</tbody>
</table>
exposed to breeding, such that the dependent variable was zero if no calf was weaned and actual weaning weight if a calf was weaned.

**Dominance Model.** The dominance model, as the genetic basis for heterosis, was discussed by Cunningham (1982). In addition to additive genetic and heterotic effects, the genetic model may be expanded to take into account other known or expected genetic components such as maternal effects, paternal effects, and recombination loss, as shown by Dickerson (1969, 1973). The genetic components are as follows:

\[
\begin{align*}
    g_A^I &= \text{additive individual effect,} \\
    g_A^M &= \text{additive maternal effect,} \\
    g_A^{M'} &= \text{additive maternal carryover effect,} \\
    g_A^P &= \text{additive paternal effect, for breed A,} \\
    h_{AB}^I &= \text{individual heterosis,} \\
    h_{AB}^M &= \text{maternal heterosis,} \\
    h_{AB}^{M'} &= \text{maternal carryover heterosis,} \\
    h_{AB}^P &= \text{paternal heterosis, for AB and BA F\text{\textsubscript{1}} cross,} \\
    r_{AB}^I &= \text{individual recombination loss,} \\
    r_{AB}^M &= \text{maternal recombination loss,} \\
    r_{AB}^P &= \text{paternal recombination loss, for AB and BA cross.}
\end{align*}
\]

The genetic components can be defined as deviations from the mean of \( n \) specified purebreds (Dickerson, 1969) or another appropriate base point such as midparent average when considering only two breeds. However, heterotic components should always be expressed as deviations from midparent average.

The genetic components that contribute to the maternal performance (e.g., calf weaning weight) of the four breed groups of cows that vary in amount of Hereford (H) and Simmental (S) breeding when raising Charolais (C) calves are as follows:

\[
\begin{align*}
    HH &= \frac{1}{2}g_C^I + \frac{1}{2}g_H^I + h_{CH}^I \quad \text{+ other effects}, \\
    1S3H &= \frac{1}{2}g_C^I + \frac{3}{5}g_H^I + \frac{1}{5}g_S^I + \frac{3}{5}h_{CH}^I + \frac{1}{5}h_{CS}^I \quad \text{+ other effects}, \\
    1S1H &= \frac{1}{2}g_C^I + \frac{1}{4}g_H^I + \frac{1}{4}g_S^I + \frac{1}{2}h_{CH}^I + \frac{1}{2}h_{CS}^I + \frac{3}{5}g_M^I + h_{HS}^I \quad \text{+ other effects,} \\
    3S1H &= \frac{1}{2}g_C^I + \frac{1}{2}g_H^I + \frac{3}{5}g_S^I + \frac{1}{4}h_{CH}^I + \frac{3}{4}h_{CS}^I + \frac{1}{4}g_M^I + h_{HS}^I + \frac{3}{4}g_M^I + h_{HS}^I \\
    &\quad + \frac{3}{4}g_S^I + \frac{1}{2}h_{HS}^I + \frac{1}{2}h_{HS}^I + \frac{1}{2}g_S^M + h_{HS}^I \\
    &\quad + \frac{g_P^I}{16} + \frac{3}{16}h_{HS}^I + \frac{1}{4}g_M^I.
\end{align*}
\]

The composition of the breed group means in terms of genetic components illustrate that there is a linear relationship between heterosis and the amount of heterozygosity if the dominance model is correct (i.e., if there is no recombination loss) and if the dam breed groups for the respective cow breed groups were HH, HH, HH, and 1S1H, as in the present study. Thus, if the dominance model is correct, there is a linear regression of breed group performance on proportion of Simmental breeding for the three breed groups of HH, 1S3H, and 1S1H. This regression was calculated (codes were 0, 1, and 2 for HH, 1S3H, and 1S1H, respectively) for various traits, and the size of the \( R^2 \)-value associated with this linear regression was used to evaluate whether the data supported the dominance model. This is the same procedure that was used by Kress et al. (1990a).

**Estimating Maternal Heterosis.** The estimation procedure for maternal heterosis was based on the genetic model as described in detail by Robison et al. (1981). After imposing the restriction that the additive effects for Simmental (\( 5g_S^I + g_S^M \)) would be estimated as deviations from Hereford, the model was as follows:

\[
\begin{align*}
    Y_{ijklm} &= \mu + R_i + S_j + A_k + B_l + C_l B_l + R_{Sij} + S_{Bij} + (5g_S^I + g_S^M) k_s + h_{HS}^M k_{HS} + b_D D_n + e_{ijklm},
\end{align*}
\]

where \( k_s \) = proportion of genes in dam from Simmental, \( k_{HS} = \) proportion of loci in dam with one gene from Hereford and the other from Simmental, \( h_{HS}^M = \) maternal heterosis estimated as regression coefficients, and \( R_i, S_j, A_k, B_l, C_l, B_l, R_{Sij}, S_{Bij}, \) and \( b_D \) represent year the calf was born, sex of calf, age of dam (3, 4 and 5+), breed of calf sire, calf sire within breed, appropriate interactions, and regression on calf day of birth (\( D_n \), respectively. Sex of calf, breed of calf sire, calf sire, and regression on calf day of birth were deleted in the analyses for proportion calved and weaned and calf weaning weight per cow exposed. All traits were analyzed as traits of calves, but all estimates of heterosis were called maternal heterosis, even for traits that were not completely calf traits such as gestation length, milk production and proportion calving. Midparent mean (\( \bar{P} \)) was calculated as a linear function of breed group least squares means from Kress et al. (1990b), \( \bar{P} = 1S3H + 3S1H - 1S1H \), and percentage of maternal heterosis was calculated as \( \frac{h_{HS}^M}{\bar{P}} \).
Results and Discussion

**Validity of the Dominance Model.** The R²-values for the regression of least squares breed group means on proportion of Simmental breeding are shown in Table 1. The calf growth traits, proportions calved and weaned, and calf weaning weight per cow exposed had R²-values that were generally ≥ .90. The R²-values were variable for milk production and were low for day of conception, number of services, gestation length, calving difficulty, and proportion calving difficulty. These results are in good agreement with R²-values for 2-yr-old dams (Kress et al., 1990a) except for milk production. Overall, the large R²-values in this study lend strong support for the validity of the dominance model for calf growth traits, proportion calved and weaned, and calf weaning weight per cow exposed. These results agree with the conclusions of McGloughlin (1980) and Cunningham (1982) that experimental evidence supports the dominance model. Koch et al. (1985) studied heterosis retention in advanced generations of crosses among Angus and Hereford cattle and concluded that there was greater reduction of heterotic effects than expected from dominance alone for survival and pregnancy, but that results for date of calving, birth weight, and preweaning gain were in agreement with the dominance model. Morris et al. (1986) reported that epistatic effects were nonsignificant for birth date and weights at birth and weaning. However, Sacco et al. (1989) estimated values for maternal heterosis in F₂ dams for calf weaning weight and height that were smaller than expected based on values in F₁ dams.

**Maternal Heterosis.** Table 1 shows estimates of maternal heterosis for the various traits in units of measurement and Figure 1 shows the estimates as percentages. Maternal heterosis was not significant for day of conception, number of services, gestation length, calving difficulty, or proportion of cows experiencing calving difficulty. The estimate for calving difficulty score was greater than the ~6.3% in 2-yr-olds (Kress et al., 1990a) but slightly smaller than the 3.7% reported by Koch et al. (1985) and the 5.8% reported by Dearborn et al. (1987). MacNeil et al. (1986) reported −2.97 d and Morris et al. (1986) reported −3 d for calving date, whereas the present estimate for day of conception was −.98 d. This apparent disagreement could be caused by the short breeding season (45 d) of the present study. No comparable values were found in the literature for number of services or gestation length, except the .01 d for gestation.
Estimates of maternal heterosis were significant for measures of calf condition (weight/height and condition score) but not for calf height. No comparable estimates were found in the literature.

Calf weights exhibited maternal heterosis of 3.6 to 5.2%. Estimates from 2-yr-old dams tended to be larger (Kress et al., 1990a). When calf weaning weight was expressed relative to cow weight, maternal heterosis ranged from 6.4 to 7.1%. Estimates of maternal heterosis for calf birth weight from studies with Bos taurus crossbred cows of all ages have ranged from -3 to 2.7% (except for one estimate of 5.6% by Morris et al. [1986]) and averaged 1.7% (Cundiff et al., 1974b; Spelbrin et al., 1977a; Gaines et al., 1978; Alenda et al., 1980; Dillard et al., 1980; Knapp et al., 1980; Koch et al., 1985; Olson et al., 1985; MacNeil et al., 1986; Morris et al., 1986; Wyatt and Franke, 1986; Bailey et al., 1988; Hohenboken and Weber, 1989; Sacco et al., 1989). The same authors plus Ellis et al. (1979) and MacNeil et al. (1982) have reported maternal heterosis estimates of .4 to 8.7%, with an average of 4.4%, for weaning weight.

Estimates of maternal heterosis were relatively higher for measures of milk production. The negative estimate for early minus late milk production, though not significant, suggested that crossbred cows maintained milk production at a higher level into later lactation. The estimate from these dams as 2 yr olds was also higher (22 vs 0%) later in lactation (Kress et al., 1990a). Two other studies have shown a similar trend. Cundiff et al. (1974b) estimated maternal heterosis to be 7 and 38% for milk production at 6 wk and weaning, respectively, and Daley et al. (1987) reported estimates of 5, 11, and 19% for milk production at 60, 105, and 150 d of lactation. In contrast, Notter et al. (1978) reported that heterosis for milk production of 3- and 4-yr-old cows decreased during lactation (33% at 128 d, 12% at 156 d, and 10% at 184 d).

The reproductive traits (proportion of cows calving and proportion of cows weaning a calf) exhibited greater maternal heterosis than did the calf growth traits, but an even greater amount of maternal heterosis was shown by a characteristic that combined calf growth and cow reproduction (calf weaning weight per cow exposed to breeding). Estimates of maternal heterosis for proportion calved have ranged from 1.1 to 11.3% and averaged 5.5%, whereas estimates for proportion weaned ranged from 0 to 16.9% and averaged 7.7% (Cundiff et al., 1974a,b; Spelbrin et al., 1977b; Gaines et al., 1978; Ellis et al., 1979; Koch et al., 1985; Olson et al., 1985; Dearborn et al., 1987; Bailey et al., 1988). Thus, the present estimates of maternal heterosis for proportions calved and weaned were higher than previous averages but are within the ranges reported previously. The estimate of maternal heterosis for calf weaning weight per cow exposed was 17.9%, compared with the reported range of 1.6 to 20.4% and average of 11.3% for cows of all ages (Cundiff et al., 1974a; Spelbrin et al., 1977a,b; Olson et al., 1985; MacNeil et al., 1986; Dearborn et al., 1987; Bailey et al., 1988).

The estimates of percentage maternal heterosis are listed from smallest to largest in Figure 1. Proportion calving difficulty and early minus late milk production estimates of percentage maternal heterosis are not listed in Figure 1 because their estimates were high (38.5 and -20.0%, respectively) due to small means. The progression of traits shows that gestation length, day of conception, and calf skeletal size had low maternal heterosis; calf growth, calf condition, and calf growth relative to cow size had intermediate levels of maternal heterosis; and cow reproductive traits and milk production exhibited higher levels of heterosis.

Implications

The dominance model can be used as the basis for accurately predicting outcomes of different crossbreeding systems for most traits. Maternal heterosis influences most productive characteristics of beef cattle in an important and positive way. Maternal heterosis had a moderate effect on calf growth traits and a large effect on cow reproduction and milk production. Thus, commercial beef producers can benefit from maternal heterosis and should consider using crossbred cows whenever possible.

Literature Cited


