EMPIRICAL VALIDATION OF THE DOMINANCE MODEL FOR BEEF CATTLE

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SUMMARY

Data from 770 records of Hereford, 25% Simmental - 75% Hereford, 50% Simmental - 50% Hereford and 75% Simmental - 25% Hereford cows were used to evaluate whether breed group means for maternal traits agreed with expectations based on the dominance model. Cows were managed consistent with practices for western range environments. Cow breed group was significant for 17 of the 18 traits studied. The measure of goodness of fit of the breed group means to the dominance model was the $R^2$ value associated with the linear regression of breed group means on proportion of Simmental for the first three breed groups. Most of the traits agreed with the dominance model expectation (83% of the $R^2$ values were greater than .75).

INTRODUCTION

The dominance model as an explanation for heterosis has been discussed by Cunningham (1982). A basic assumption of the dominance model is a linear relationship between performance and degree of heterozygosity. Experimental evidence presented by McGloughlin (1980) and other studies summarized by Cunningham (1982) have generally supported the linear dependence of performance on heterozygosity.

The objective of this study was to determine if traits measuring maternal performance of Hereford (HH), 25% Simmental - 75% Hereford (1S3H), 50% Simmental - 50% Hereford (1S1H) and 75% Simmental - 25% Hereford (3S1H) cows were in agreement with expectations based on the dominance model.

MATERIALS AND METHODS

The experiment was conducted at the Northern Agricultural Research Center near Havre, Montana. Cow breed groups (HH, 1S3H, 1S1H and 3S1H) ranged from 3 to 8 yr of age. The first three breed groups were all produced from Hereford dams and were raised as contemporaries during the years 1976 to 1979. The fourth breed group was produced from Simmental x Hereford dams and these heifers were purchased at about 10 mo of age from various breeders in Montana. Nine or ten different sires were used to produce each breed group. The same Simmental sires were represented in the two Simmental sire groups and the Simmental x Hereford sire group. Further details regarding design, sires and breeding have been given by Kress et al. (1984a).

Sample halves of each breed group were bred to Charolais or Tarentaise sires by artificial insemination during a 45-d breeding period starting the first week of June. Calves were weaned at an average age of 180d during the first week of October and were not creep-fed. Up to the end of the third calf crop, cows were not culled unless they were open 2 yr in a row. Following the third calf crop, all open cows were culled.

Cows were maintained on native range with sufficient supplemental feeding during the winter to maintain weight. The summer range is 1200 m above sea level and vegetation of the site is a rough fescue (Festuca scabrella), Idaho fescue (Festuca idahoensis), bluebunch

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wheatgrass (Agropyron spicatum) dominated grassland with interspersed areas of ponderosa pine (Pinus ponderosa) overstory. Average annual precipitation was 45 cm and the terrain varied from level to slopes of extreme steepness. The stocking rate was 1.2 ha per cow-calf pair per month.

Table 1 shows the traits studied. Calving difficulty was scored from 1 to 4 (1 = no difficulty, 2 = slight difficulty, some assistance required, 3 = difficult birth, mechanical calf puller required and 4 = Cesarean section). Condition score of cows and calves was subjective and ranged from 1 to 9, with 9 representing the fattest animals. Height was measured at the hips and milk production was estimated by the weigh-suckle-weigh procedure. Cow weights were taken mid-March (precalving), first week of June (prebreeding), third week of July (postbreeding) and first week of October (weaning). Proportion of calves weaned was based on number of cows exposed to breeding. The dependent variable for calf weaning weight per cow exposed to breeding was actual calf weaning weight if the cow weaned a calf and zero if the cow failed to wean a calf. Thus, this trait was not normally distributed and tests of significance were approximate.

Data were analyzed using a fixed model least-squares procedure (Harvey, 1975). Main effects were breed group of cow, year, age of cow (3, 4 and 5 to 8 yr), sex of calf and sire breed of calf. All two-factor interactions were included in preliminary analyses and excluded in final analyses if they were nonsignificant. Birth date was included as a covariate.

The simple dominance model must be expanded to take into account other known or expected genetic components such as maternal effects, maternal heterosis, paternal effects and even recombination loss as shown by Dickerson (1969, 1973). These genetic components were g for additive genetic effects, h for heterotic effects and r for recombination loss. Subscripts for each component denote appropriate breed or crossbreed and superscripts denote individual, maternal or paternal. Other genetic components could be (and perhaps should be) included such as the maternal carry-over effect (gM H , hM H and rM H; Dickerson, 1969). Koch et al. (1985) have reconciled the terminology of Dickerson (1969, 1973), Kinghorn (1980) and Hill (1982).

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:

\[
\begin{align*}
HH &= \frac{1}{2}g_C^T + \frac{1}{2}g_H^T + h_{CH}^T + g_H^P + g_C^P, \\
1S3H &= \frac{1}{2}g_C^T + \frac{3}{8}g_H^T + \frac{1}{8}g_S^T + \frac{3}{4}h_{CS}^T + \frac{1}{4}h_{CH}^T + \frac{3}{4}h_{HS}^T + \frac{1}{4}h_{CS}^T + \frac{1}{4}h_{CH}^T + \frac{1}{2}h_{HS}^T + \frac{1}{4}h_{CS}^T + \frac{1}{4}h_{CH}^T + \frac{1}{2}h_{HS}^T + \frac{1}{2}g_S^P + \frac{1}{2}g_H^P + \frac{3}{4}g_{CS}^T + \frac{1}{2}g_{CH}^T + \frac{1}{2}g_{HS}^T + \frac{1}{2}g_{CS}^P + \frac{1}{2}g_{CH}^P + \frac{1}{2}g_{HS}^P + \frac{1}{2}h_{CS}^P + \frac{1}{2}h_{CH}^P + \frac{1}{2}h_{HS}^P + \frac{1}{2}g_{CS}^M + \frac{1}{2}g_{CH}^M + \frac{1}{2}g_{HS}^M + \frac{1}{2}h_{CS}^M + \frac{1}{2}h_{CH}^M + \frac{1}{2}h_{HS}^M, \\
1S1H &= \frac{1}{2}g_C^T + \frac{1}{2}g_S^T + \frac{1}{2}h_{CS}^T + \frac{1}{2}h_{CH}^T + \frac{1}{2}h_{HS}^T + \frac{1}{2}g_S^P + \frac{1}{2}g_H^P + \frac{3}{4}g_{CS}^T + \frac{1}{2}g_{CH}^T + \frac{1}{2}g_{HS}^T + \frac{1}{2}g_{CS}^M + \frac{1}{2}g_{CH}^M + \frac{1}{2}g_{HS}^M + h_{CS}^T + h_{CH}^T + h_{HS}^T + h_{CS}^P + h_{CH}^P + h_{HS}^P + h_{CS}^M + h_{CH}^M + h_{HS}^M, \\
3S1H &= \frac{1}{2}g_C^T + \frac{1}{2}g_S^T + \frac{1}{2}g_H^T + \frac{1}{2}h_{CS}^T + \frac{1}{2}h_{CH}^T + \frac{1}{2}h_{HS}^T + \frac{1}{2}g_{CS}^P + \frac{1}{2}g_{CH}^P + h_{CS}^T + h_{CH}^T + h_{HS}^T + h_{CS}^P + h_{CH}^P + h_{HS}^P + h_{CS}^M + h_{CH}^M + h_{HS}^M.
\end{align*}
\]

The only genetic components with coefficients that are not linear across HH, 1S3H and 1S1H are those involving recombination loss.

The regression of the three breed group means (HH, 1S3H and 1S1H) on proportion of Simmental breeding (coded as 0 for HH, 1 for 1S3H and 2 for 1S1H) would be linear under the assumption of the dominance model with no recombination loss. The $R^2$ value would deviate from unity due to sampling or recombination loss. Thus, the degree to which the
present data supported the dominance model (the linear dependence of performance on heterozygosity) was measured by the $R^2$ value obtained from the regression of the three breed groups on proportion of Simmental breeding.

RESULTS AND DISCUSSION

The effect of cow breed group was significant for most traits studied (table 2). This was in agreement with the literature, especially where the cow breed groups differed in biological type (Cundiff, 1970; Long, 1980). The only trait not significantly influenced by cow breed group was proportion of calves weaned. However, Kress et al. (1984b) reported that cow breed group had a significant effect on proportion of calves weaned for these same cows as 2-yr-olds and that the trend in breed group means was similar.

Table 1 shows that crossbred cows were superior to straightbred cows for most traits that measured maternal performance. Firstcross cows were generally greater than backcross cows for traits that included components due to reproduction such as calf weaning weight per cow exposed to breeding. These differences are partly due to additive genetic differences and partly due to heterotic differences as previously shown in the composition of the genetic components for each breed group.

The measure of goodness of fit of the breed group means to the dominance model was the $R^2$ value associated with the linear regression of breed group mean on proportion of Simmental (degree of heterozygosity) for the breed groups HH, 1S3H and 1S1H. Table 1 lists the $R^2$ values for each trait. Most of the traits agreed with the dominance model expectation very well (83% of the $R^2$ values were greater than .75, 72% were greater than .85 and 44% were greater than .95). The type of trait that showed good agreement with the dominance model varied, including calf weights, cow weights, skeletal size of cow and calf, cow reproduction and even complex traits like calf weaning weight per cow exposed to breeding.

These results are in good agreement with those summarized by Cunningham (1982). He noted that "Experimental evidence to support the main consequence of the dominance model, the linear dependence of performance on heterozygosity, is not difficult to find." He reviewed results from mice, corn, dogs and beef cattle and concluded that "Experimental evidence, and the opinions of previous reviewers, are broadly supportive of the dominance model."

Koch et al. (1985) studied purebred, F1, backcross and F2 and F3 inter se combinations of Angus and Hereford cattle to examine heterosis retention in advanced generations of inter se matings. Results indicated that net epistatic effects were small for date of calving, birth weight, weaning gain and carcass fat cover. A greater reduction of heterosis in the F3 than expected due to dominance was observed for pregnancy, survival and carcass marbling score. However, there was greater heterosis in the F3 than expected due to dominance for postweaning gain, carcass weight and rib eye area. Koch et al. (1985) pointed out the difficulty of attaining statistically reliable evidence for epistatic effects. Large numbers of animals are required and thus each study should be "considered with evidence from other experiments in reaching conclusions regarding presence or absence of epistasis."

GENERAL DISCUSSION

The most efficient utilization of breed resources in future breeding programs requires knowledge of the genetic basis for heterosis. The genetic basis for heterosis might depend on the trait studied. But, if a particular genetic model proved to be reasonably reliable in explaining performance of different types of crossbred groups for most traits of economic importance, then the genetic model could be used as a basis for predicting the outcome of different breeding programs that utilize breed resources.
As different genetic models for heterosis are evaluated, the dominance model should be
evaluated first. It is relatively easy to predict the outcome of different crossbreeding
systems based on the dominance model. Thus, if the dominance model accurately predicts
performance, it would be the model of choice.

Most traits of the present study, several traits reported by Koch et al. (1985) and
experimental evidence cited by Cunningham (1982) have supported the dominance model.
Thus, in broad terms, the dominance model may be expected to yield relatively accurate
predictions for future breeding programs. However, there are some results showing
deviation from the dominance model such as some traits of the present study and evidence
cited by Cunningham (1982) and Koch et al. (1985).

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Figure 1. Performance of cow breed groups for representative traits illustrating degree to which breed group means support the dominance model. Goodness of fit is measured by size of $R^2$, where an $R^2$ of 1.00 is a perfect fit. The traits are (a) calving difficulty, (b) calf weaning weight, (c) cow postbreeding weight, (d) cow postcalving condition score, (e) calf weaning weight per cow weight at weaning and (f) calf weaning weight per cow exposed to breeding.
### Table 1. List of Traits Studied, Probability Level for Breed Group of Cow from Analyses of Variance. Means for Each Breed Group and a Measure of Goodness of Fit of Breed Group Means to the Dominance Model ($R^2$)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Trait p</th>
<th>HH (140)b</th>
<th>1S3H (157)c</th>
<th>1S1H (143)</th>
<th>3S1H (141)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gestation length, d.</td>
<td>.02</td>
<td>286.4±.45</td>
<td>287.0±.44</td>
<td>286.0±.49</td>
<td>287.0±.49</td>
<td>.16</td>
</tr>
<tr>
<td>Calf birth wt., kg</td>
<td>.00</td>
<td>43.4±.43</td>
<td>44.4±.42</td>
<td>45.5±.47</td>
<td>45.5±.46</td>
<td>1.0</td>
</tr>
<tr>
<td>Calving difficulty</td>
<td>.02</td>
<td>1.54±.080</td>
<td>1.48±.078</td>
<td>1.41±.087</td>
<td>1.30±.086</td>
<td>.98</td>
</tr>
<tr>
<td>Calf weaning wt., kg</td>
<td>.00</td>
<td>211±1.8</td>
<td>227±1.7</td>
<td>240±1.9</td>
<td>244±1.9</td>
<td>1.00</td>
</tr>
<tr>
<td>Calf weaning cond. score</td>
<td>.00</td>
<td>5.1±.06</td>
<td>5.5±.06</td>
<td>5.8±.07</td>
<td>5.9±.07</td>
<td>.97</td>
</tr>
<tr>
<td>Calf weaning ht., cm</td>
<td>.00</td>
<td>109.0±.62</td>
<td>111.0±.60</td>
<td>112.1±.67</td>
<td>113.2±.66</td>
<td>.97</td>
</tr>
<tr>
<td>Milk production, kg</td>
<td>.01</td>
<td>8.8±.53</td>
<td>10.2±.52</td>
<td>12.6±.56</td>
<td>11.3±.54</td>
<td>.98</td>
</tr>
<tr>
<td>Cow wt. precalving, kg</td>
<td>.00</td>
<td>527±4.2</td>
<td>532±4.1</td>
<td>558±4.6</td>
<td>579±4.6</td>
<td>.87</td>
</tr>
<tr>
<td>Cow wt. prebreeding, kg</td>
<td>.00</td>
<td>503±4.1</td>
<td>507±3.9</td>
<td>536±4.4</td>
<td>556±4.4</td>
<td>.84</td>
</tr>
<tr>
<td>Cow wt. postbreeding, kg</td>
<td>.00</td>
<td>522±4.0</td>
<td>530±3.9</td>
<td>554±4.3</td>
<td>575±4.3</td>
<td>.92</td>
</tr>
<tr>
<td>Cow wt. weaning, kg</td>
<td>.00</td>
<td>527±4.0</td>
<td>528±3.8</td>
<td>550±4.3</td>
<td>567±4.2</td>
<td>.78</td>
</tr>
<tr>
<td>Cow ht. weaning, cm</td>
<td>.00</td>
<td>128.3±3.2</td>
<td>129.6±3.1</td>
<td>133.3±3.5</td>
<td>134.6±3.5</td>
<td>.93</td>
</tr>
<tr>
<td>Cow wt./ht. weaning, kg/cm</td>
<td>.00</td>
<td>4.11±.025</td>
<td>4.07±.025</td>
<td>4.12±.027</td>
<td>4.21±.027</td>
<td>.04</td>
</tr>
<tr>
<td>Cow postcalving cond. score</td>
<td>.04</td>
<td>5.0±.08</td>
<td>5.2±.08</td>
<td>5.0±.09</td>
<td>5.3±.09</td>
<td>.06</td>
</tr>
<tr>
<td>Cow weaning cond. score</td>
<td>.00</td>
<td>5.5±.07</td>
<td>5.4±.07</td>
<td>5.1±.08</td>
<td>5.2±.08</td>
<td>.89</td>
</tr>
<tr>
<td>Calf wt./cow wt. weaning</td>
<td>.00</td>
<td>4.01±.0041</td>
<td>4.33±.0040</td>
<td>4.39±.0044</td>
<td>4.32±.0044</td>
<td>.87</td>
</tr>
<tr>
<td>Proportion calves weaned</td>
<td>.47</td>
<td>.75±.03</td>
<td>.78±.03</td>
<td>.79±.03</td>
<td>.72±.03</td>
<td>.97</td>
</tr>
<tr>
<td>Calf wean. wt./cow exposed, kg</td>
<td>.02</td>
<td>158±6.9</td>
<td>177±7.0</td>
<td>193±7.6</td>
<td>175±7.2</td>
<td>1.00</td>
</tr>
</tbody>
</table>

*Level of probability for breed group of cow from analyses of variance.
^Number of observations per breed group except for last two traits.
CNumber of observations per breed group for proportion calves weaned and calf weaning weight per cow exposed to breeding.