Parameter Estimation for Carcass Traits Including Growth Information of Simmental Beef Cattle Using Restricted Maximum Likelihood with a Multiple-Trait Model

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ABSTRACT: (Co)variance component estimates were computed for retail cuts per day of age (kilograms per day), cutability (percentage of carcass weight), and marbling score (1 through 11) using a multiple-trait sire model. Restricted maximum likelihood estimates of (co)variance components were obtained via an expectation-maximization algorithm. Carcass data consisted of 8,265 progeny records collected by U.S. Simmental producers. Growth trait information (birth weight, weaning weight, and/or postweaning gain) for those progeny with carcass data and an additional 5,405 contemporaries formed the complete data set for analysis. A total of 420 sires were represented. Three models differing in number of traits were investigated: 1) carcass traits with growth traits, 2) carcass traits only, and 3) single trait. The final models did not include postweaning gain because of convergence problems. Parameter estimates for all three models were essentially the same. Heritability estimates were .30, .18, and .23 for retail cuts per day, cutability, and marbling score, respectively. Correlations between growth and carcass traits were low except for those with retail cuts per day, which were moderate and positive. The additional information gained by adding growth traits to the carcass-traits-only evaluation lowered prediction error variances most for retail cuts per day. Little change in prediction error variances was found for cutability and marbling score. Inclusion of growth traits in future sire evaluations for carcass traits will benefit the evaluation of retail cuts per day but have considerably less effect on cutability and marbling score.

Key Words: Variance Components, Genetic Parameters, Carcass Traits, Correlated Traits, Simmental, Beef Cattle

Introduction

Recent reports by the National Research Council (NRC, 1988) and others on necessary changes in the American diet as related to red meat consumption and, more specifically, to reducing fat intake, have prompted an increasing interest in studies involving carcass traits. Attainment of some of these dietary changes will occur as consumers' access to leaner red meat at the retail level increases. The production of leaner red meat may be achieved in part through genetic selection provided that consumer demand dictates change through the entire market chain back to the producer and that packers buy fed cattle in a manner that will reward producers for putting selection emphasis on carcass traits (i.e., according to individual carcass lean and fat content).

To "trim" carcasses genetically, bulls must be identified who sire progeny that, when fed out, have the desired carcass characteristics. Currently, sires are evaluated for carcass traits based on carcass information of their progeny. However, research is being conducted that may someday allow the evaluation of bulls for carcass traits based on live-animal measurements of feedlot cattle and/or breeding animals.
Parameter estimates are a very important part of any genetic evaluation because they describe the population being evaluated. The BLUP methodology developed by Henderson (1963, 1973, 1974) has been widely used for animal evaluation. The assumptions and properties of BLUP require that the unknown (co)variance components be substituted with the most accurate estimates available for the population and traits being studied. Henderson (1975a) pointed out that use of inaccurate estimates of (co)variance components results in decreased accuracy of evaluation and, if selection has occurred, this use may bias the predictors.

The main objective of this project was to estimate (co)variance components for carcass and growth traits using REML with a multiple-trait sire model. In doing so, we considered a model with carcass and growth traits vs the traditional carcass-trait-only model. Aside from comparing the resulting parameter estimates, we were interested in determining whether including weight data resulted in increases in accuracy and reduction in selection bias.

### Data

Growth and carcass data for this study were collected by Simmental producers for calves born during the period 1971 to July 1988. Previous Simmental sire evaluations for carcass characteristics have included the following: 1) percentage of cutability, 2) retail cuts per day of age, and 3) marbling score. Due to the lack of a more recent equation for estimating percentage of cutability, the USDA standard equation which was developed for English breed cattle by Murphey et al. (1960) was used. That equation is Percentage of cutability = 51.34 - 2.277 × fat thickness (cm) - .462 × KPH % - .0205 × hot carcass weight (kg) + .1147 × longissimus muscle area (cm²), where KPH % is a subjective measure of the amount of kidney, pelvic, and heart fat as a percentage of the carcass. Cutability is an estimate of closely trimmed, boneless retail cuts from the round, loin, rib, and chuck as a percentage of carcass weight. Using this same equation for Simmental F₁ calves may not induce a serious bias because the upgrading process in the U.S. involved primarily Angus and Hereford cows. However, it is not known how well the equation estimates cutability for higher percentage of Simmental and other Continental breeds with larger frame sizes.

Retail cuts per day of age is an indicator of preslaughter growth rate and composition of gain. It is computed as carcass weight times percentage of cutability divided by slaughter age in days. Finally, marbling score is a subjective measure of the amount and distribution of intramuscular fat in the longissimus muscle located between the 12th and 13th ribs. Scores may range from 1 to 11, with 1 corresponding to no fat in the muscle and 11 implying a very abundant amount of intramuscular fat (BIF, 1990). Marbling score is the major factor in determining USDA carcass quality grade (maturity of the animal is also considered).

Initially, a carcass data set was constructed and consisted of usable (those records remaining after preliminary edits) progeny records with carcass weights between 177.3 and 500 kg and slaughter ages between 270 and 900 d. The final carcass-data-only data set contained 8,265 records (Table 1) and 385 connected sires. This data set was then merged with the growth data file to make one complete record for each calf from birth to slaughter containing all usable information reported. At the same time, any progeny record in the growth data set in the same growth contemporary group as two or more progeny with carcass data was added to the combined data set, resulting in an additional 5,405 records (Table 2) and 35 sires. Growth traits originally included in the multiple-trait model were birth weight, weaning weight, and postweaning gain.

To account for management and herd effects, a contemporary group is established for each trait. Contemporary groups for all traits have the

Table 1. Number of progeny with carcass data for each sex and percentage of Simmental of calf subclass

<table>
<thead>
<tr>
<th>Sex</th>
<th>Percentage of Simmental</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>50</td>
<td>2,505</td>
</tr>
<tr>
<td></td>
<td>75</td>
<td>2,774</td>
</tr>
<tr>
<td></td>
<td>≥ 87.5</td>
<td>431</td>
</tr>
<tr>
<td>Heifers</td>
<td>5,710</td>
<td>1,741</td>
</tr>
</tbody>
</table>

*aSex at weaning.

Table 2. Number of progeny records gained by adding growth trait information to the existing carcass data set

<table>
<thead>
<tr>
<th>Sex</th>
<th>Percentage of Simmental</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>50</td>
<td>1,204</td>
</tr>
<tr>
<td>Steers</td>
<td>705</td>
<td>117</td>
</tr>
<tr>
<td>Heifers</td>
<td>571</td>
<td>621</td>
</tr>
<tr>
<td>Total</td>
<td>2,480</td>
<td>1,848</td>
</tr>
</tbody>
</table>

*aSex at weaning.*
following in common: 1) breeder number, 2) herd code, 3) sex at the time the record is measured, and 4) percentage of Simmental. Because of the nested structure of the way contemporary groups are defined, all other traits will have the same contemporary group for traits measured previously in the life of the animal. All three carcass traits have the same group number.

In a data set consisting of measurements on progeny from birth to slaughter, there are plenty of opportunities for selection/culling decisions to prevent the entire birth contemporary group from being slaughtered together. Realistically, there may be situations in which data are only collected on a subset of the animals that are slaughtered, possibly resulting in more bias. One would hope that this occurs only randomly. Such decisions may be motivated by genetic improvement policies, management abilities, available facilities, cost factors, and so forth. Regardless of the reasons, analyses of traits from the remaining selected animals may lead to biased parameter and EPD estimates as a result of the selection that occurred. To supplement the small number of observations available on carcass traits and to help overcome selection bias, growth traits on calves that have carcass measurements and their contemporaries (without carcass measurements) may be included in evaluating sires. These other traits provide additional information about sires through the genetic correlations among carcass and growth traits when used in a multiple-trait analysis.

The final data set consisted of 13,670 records with at least one of six traits observed and a minimum of two carcass records in each contemporary group. The number of records for each trait is given in Tables 3 and 4 for each sex and percentage of Simmental category. The numbers of observations decrease as percentage of Simmental increases because most of the data were

### Table 3. Number of observations and means* for growth traits by sex and percentage of Simmental of calf

<table>
<thead>
<tr>
<th>Sex</th>
<th>Percentage of Simmental</th>
<th>Progeny with birth weights, kg</th>
<th>Progeny with weaning weights, kg</th>
<th>Progeny with postweaning gains, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50</td>
<td>75</td>
<td>≥ 87.5</td>
<td>Overall</td>
</tr>
<tr>
<td>Bulls</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3,554</td>
<td>2,060</td>
<td>1,261</td>
<td>6,875</td>
</tr>
<tr>
<td></td>
<td>41.6</td>
<td>43.7</td>
<td>44.7</td>
<td>42.8</td>
</tr>
<tr>
<td>Heifers</td>
<td>994</td>
<td>1,017</td>
<td>556</td>
<td>2,587</td>
</tr>
<tr>
<td></td>
<td>38.2</td>
<td>39.9</td>
<td>41.3</td>
<td>39.5</td>
</tr>
<tr>
<td>Steers</td>
<td>2,664</td>
<td>418</td>
<td>61</td>
<td>3,141</td>
</tr>
<tr>
<td></td>
<td>38.6</td>
<td>42.5</td>
<td>41.4</td>
<td>39.2</td>
</tr>
<tr>
<td>Overall</td>
<td>7,212</td>
<td>3,493</td>
<td>1,878</td>
<td>12,583</td>
</tr>
<tr>
<td></td>
<td>40.0</td>
<td>42.4</td>
<td>43.6</td>
<td>41.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 4. Number of observations and means* for carcass traits by sex and percentage of Simmental of calf

<table>
<thead>
<tr>
<th>Sex</th>
<th>Percentage of Simmental</th>
<th>Progeny with retail cuts per day of age, kg/d</th>
<th>Progeny with cutability, %</th>
<th>Progeny with marbling scores, 1-11</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50</td>
<td>75</td>
<td>≥ 87.5</td>
<td>Overall</td>
</tr>
<tr>
<td>Bulls</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2,503</td>
<td>969</td>
<td>520</td>
<td>3,992</td>
</tr>
<tr>
<td></td>
<td>.36</td>
<td>.39</td>
<td>.39</td>
<td>.37</td>
</tr>
<tr>
<td>Heifers</td>
<td>431</td>
<td>398</td>
<td>214</td>
<td>1,043</td>
</tr>
<tr>
<td></td>
<td>.32</td>
<td>.33</td>
<td>.34</td>
<td>.33</td>
</tr>
<tr>
<td>Steers</td>
<td>2,754</td>
<td>357</td>
<td>76</td>
<td>3,187</td>
</tr>
<tr>
<td></td>
<td>.35</td>
<td>.37</td>
<td>.34</td>
<td>.35</td>
</tr>
<tr>
<td>Overall</td>
<td>5,688</td>
<td>1,724</td>
<td>810</td>
<td>8,222</td>
</tr>
<tr>
<td></td>
<td>.35</td>
<td>.37</td>
<td>.38</td>
<td>.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Observations adjusted for age of calf and age of dam.
collected during the middle 1970s, when most calves were 50% Simmental due to upgrading. Tables 3 and 4 also contain means of the observations adjusted for age of calf and age of dam (within sex and percentage of Simmental) for growth traits and age of calf at slaughter for carcass traits.

It is surprising to see that more bulls are slaughtered than steers because most fed cattle in the United States are steers, followed by heifers and, finally, bulls. Some producers probably recorded all males as bulls without regard to whether they were castrated. This classification system is not thought to present a real problem because most of the time the entire contemporary group will be either bulls or steers. In the early years of record keeping, there was no provision for producers to report that a bull was castrated after weaning.

Trait Combinations. To use as much of the data as possible, a transformation procedure (i.e., canonical, sequential) to uncorrelate the residuals was not used because such procedures generally require a certain data structure that is not often attained in field data sets without loss of data. The remaining choice is to do no transformation at all. Usually, 2^t - 1 possible combinations of measured and unmeasured traits for each progeny exist. However, in the data set used in this study, only 23 trait combinations were possible (22 observed) because postweaning gain cannot occur without a weaning weight measurement and retail cuts per day cannot occur without a cutability measurement (Table 5). Subsequent removal of postweaning gain from all models eliminated seven trait combinations, leaving a total of 15.

Statistical Methodology

Accurate estimates of (co)variance components are important in evaluating animals regardless of the traits of interest. In the past, the available computing facilities and the size of the data as well as the model dictated which statistical method would be used for estimating (co)variance components. Today, REML is the estimation procedure predominantly used for animal breeding problems. The IBM 3090-600E supercomputer was used to meet the computational demands of this problem.

Model

The multiple-trait linear mixed model (sire model) used was

\[ y = X\beta + Zu + e \]

where \( y \) is a vector of \( N_t \) observations of \( t \) traits measured on \( n_i \) progeny of sire \( i \) such that the sum of the \( n_i \) for all \( q \) sires is \( N \); \( \beta \) is a vector of \( b \) unknown fixed contemporary group effects for all traits; \( u \) is a vector of \( q_t \) unknown random sire effects (one effect for each sire-trait combination) for \( q \) sires. Within \( u \) these effects are ordered by trait within each sire; \( X \) is a \( N \times b \) known incidence matrix relating observations to fixed effects, \( X \) having full column rank; \( Z \) is a \( N \times q_t \) known incidence matrix relating observations to sire effects for each trait; and \( e \) is a vector of \( N_t \) unknown random residual effects not explained by \( X\beta \) and \( Zu \).

A sire model was used because 89.1% of the carcass data set are records from 50% Simmental calves. The maternal grandsires for these calves are therefore unknown. Only 30.5% of the calves with carcass information had known maternal grandsires. In addition, Garrick et al. (1989) reported a small maternal variance for birth weight (2.2) and an extremely small maternal variance for postweaning gain (0.8). Ignoring the random maternal effect for weaning weight (120 according to Garrick et al., 1989) probably only results in a slight increase in prediction error variance (Henderson, 1975b).

Contemporary group effects for each trait were

<table>
<thead>
<tr>
<th>Number of records</th>
<th>BWT</th>
<th>WWT</th>
<th>PWG</th>
<th>RC</th>
<th>CU</th>
<th>MB</th>
</tr>
</thead>
<tbody>
<tr>
<td>559</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>146</td>
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<tr>
<td>2,510</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
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<td>X</td>
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<td>X</td>
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<td>13</td>
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<tr>
<td>1</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>87</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
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<td>1</td>
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<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<td>558</td>
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<td>218</td>
<td>X</td>
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<td>91</td>
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<tr>
<td>2,598</td>
<td>X</td>
<td>X</td>
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<td></td>
<td>X</td>
</tr>
<tr>
<td>13,670</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

\[ \text{BWT} = \text{birth weight (kg)}, \text{WWT} = \text{weaning weight (kg)}, \text{PWG} = \text{postweaning gain (kg)}, \text{RC} = \text{retail cuts per day of age (kg/d)}, \text{CU} = \text{cutability (%)}; \text{MB} = \text{marbling score (1-11)}. \]

Table 5. Number of progeny records for each trait combination occurring in the data
the only fixed effects fit during the analysis. Other nongenetic effects were adjusted for prior to analyzing the data. The only trait not adjusted at all was retail cuts per day of age because it is already essentially adjusted for age of calf at slaughter.

Weaning weights were adjusted for age of calf at weaning using a linear version of the age-of-calf adjustment developed for Simmental calves by Woodward et al. (1989). Yearling weights were adjusted according to BIF (1990). The same type of bias Woodward et al. (1989) reported in age-adjusted weaning weights (according to BIF) may also occur when using the BIF-recommended yearling weight age adjustment. Age of dam adjustment factors for birth weight, weaning weight, and yearling weight and linear regression coefficients for age of calf at weaning were taken from the 1989 Simmental sire evaluation.

Percentage of cutability and marbling score records were adjusted for age of calf at slaughter using linear regression coefficients estimated in the 1989 evaluation of sires for carcass traits. Separate linear regressions were estimated for each sex by percentage of Simmental category.

To account for those progeny records without observations on all traits (i.e., missing data) zero may be used as the missing observation with the corresponding row of X and Z being null. Use of null values simplifies the notation. For the current discussion, the no-missing-data case is assumed. The following distributional assumptions are made when using the linear model in (II):

\[
E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix}
\]

\[
\text{var} \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & ZG & R \\ GZ' & G & 0 \\ R & 0 & R \end{bmatrix}
\]

where \( V = \text{var}(y) = ZGZ' + R \) with order equal to the number of progeny records times the number of traits and \( G = \text{var}(u) = A \otimes G_o \) with \( G \), being a \( t \) by \( t \) matrix of genetic (co)variances of sire effects (one-fourth the additive genetic (co)variance matrix) for the \( t \) traits in the analysis; \( A \) is the numerator relationship matrix for sires and \( \otimes \) denotes the direct product operator. The inverse of \( G \), \( G^{-1} = A^{-1} \otimes G_o^{-1} \) is easily computed following procedures developed by Henderson (1975b,c, 1978) and Henderson and Quaas (1976).

Finally, \( R \) is the residual (co)variance matrix. \( R = \text{diag} \{R_i\} \), \( i = 1,...,N \), where \( R_i \) is a \( t \) by \( t \) matrix of residual (co)variances for progeny \( i \). If we let \( R_i \) denote the residual variance-covariance matrix for a progeny with all traits recorded, \( R_i \) for animals with missing data can be formed from \( R_i \) by substituting values of zero into those rows and columns of \( R_i \) corresponding to missing data. There are as many \( R_i \) as there are different trait combinations existing in the data.

Estimation of (Co)variance Components

(Co)variance components were estimated using REML and computed via an expectation-maximization (EM) algorithm. The REML and EM methods were first developed by Patterson and Thompson (1971) and Dempster et al. (1977), respectively.

Complete details regarding the derivation of the estimators for the sire model using all possible trait combinations used in this study may be found in the dissertation by Woodward (1990). Henderson (1984) presented the general theory behind this type of approach to estimating (co)variance components. More recently, Mantysaari and Van Vleck (1989) provided more theory and explanation for the case in which no transformation is used in the analysis of reproductive trait data of dairy cattle.

Postweaning gain records were few and caused convergence problems when they were left in the model. All attempts to determine the cause of these problems failed to result in a satisfactory answer. Therefore, postweaning gain was removed from the final model. Eliminating this trait from the analysis resulted in convergence of estimates for all other traits within 35 to 40 rounds of iteration. To ensure that convergence had actually been attained, the program was run one more time for the model including all correlations among the remaining five traits with Round 40 variance component estimates used as starting values. The program was set up to stop when the average absolute deviation over all estimates of the genetic variance components was less than .0001, which occurred at Round 79 (previous 40 rounds plus 39 more). All estimates remained the same as in Round 40.

(Co)variance Component Priors

First-round values for variances and covariances among growth and among carcass characteristics were those currently being used to evaluate Simmental sires (Table 6). Covariances between growth and carcass traits were started at zero because literature values were not available for Simmentals. In fact, very little information exists across all breeds for the specific combination of traits in this study. Research has been published for many growth and carcass traits, but
few studies have included all five traits examined in this study.

Priors for growth traits are the average of those parameter estimates for 50% males and females used in the 1989 national Simmental evaluation. Values of 50% calves are used because 60.0% of all 13,670 progeny records in the current data set are from 50% Simmental calves.

The same general program was used for all analyses and the same priors were also used. Different models were obtained by setting appropriate covariances to zero each round of iteration.

Comparing Sire Evaluations

After the same data have been analyzed with one or more different models, a decision must be made about whether the addition of growth traits produces a better evaluation sufficient enough to warrant the extra computations. Additional trait information has an impact on the analysis (aside from the increased computational difficulty) in at least three areas: 1) lower prediction error variances, 2) decrease bias that is a factor in the mean square error, and 3) cause the variance of EPD to increase.

First, the fact that additional information on a sire, be it from more progeny records or correlated trait information, decreases the prediction error variance of a sire’s evaluation has already been established. Thus, intuitively, the carcass and growth trait model should be better in terms of having lower prediction error variances.

Second, if selection has occurred, such that the carcass data collected are from a selected group of calves, adding growth trait information from their contemporaries will help to account for the bias as a result of using BLUP techniques. As a result of accounting at least partially for this bias, the mean square error (equal to the prediction error variance plus bias squared) should be decreased. There is no exact method to test this theory when analyzing field data. One can only assume a decrease has occurred if there is little change in the variance component estimates.

Third, an increase in the spread of EPD for all bulls can be ascertained by comparing the distribution of EPD obtained from each model. Depending on the amount of information added, the increase in the variance of EPD may be too small to detect in this way.

There is no obvious single definitive way to show the amount of improvement for all bulls. We expect the added information to be more important for those bulls with little progeny information for carcass traits only, in the situation in which equal information is added for all sires. That is to assume that those bulls have enough progeny with growth trait information to have an impact when using the combination of traits.

To compare the results from these models with respect to the resulting sire evaluations, sires were grouped by accuracy of evaluation value for each carcass trait based on their accuracy value from the carcass-traits-only evaluation. The 10 accuracy categories were 1) 0 to < .1, 2) .1 to < .2, ..., 10) .9 to 1.0. Note that the accuracy value used is that recommended by the BIF (1990). It is 1 minus the square root of (prediction error variance divided by the sire variance).

Resulting prediction error variances are dependent on the variances and covariances used to form the mixed-model equations. To compare each model, prediction error variances need to be based on the same variance components. Therefore, the final round estimates from the full model were used as the starting values for a single round of iteration of each reduced model. The single round of iteration was used to form and solve the mixed-model equations and to obtain the prediction error variances.

A ratio of prediction error variances from each model for each carcass trait and bull was then calculated for each of the 385 bulls having progeny with carcass measurements. The ratio was calculated as the prediction error variance from the full model divided by the prediction error variance from the reduced model. The expectation is then that the ratio should be < 1. These ratios were averaged over all bulls in each accuracy group mentioned above for each trait.
Some concern in using this method may be warranted because the accuracy value for each bull is dependent on the prediction error variance for a particular trait. One could regress the prediction error variance from one model on that for another within age groups for sires. That is certainly possible, but the age groups would also be confounded to some extent with prediction error variance in the sense that younger bulls generally have much less progeny information reported than older bulls. Because age of the sires was not readily available, this approach was not used.

Results and Discussion

(Covariance components for all three models, carcass and growth traits, carcass traits only, and single trait (Table 7), were essentially the same. These results indicate that the calves having carcass data seem to be a random sample of calves from these contemporary groups because selection would most likely have resulted in biased estimates in the carcass-trait-only analysis. It is only necessary then to discuss the results from the full model because it includes all traits and respective parameter estimates.

Heritabilities

Comparing heritability values currently used for genetic evaluation of Simmental sires for carcass traits (Table 6) with final-round heritability estimates in Table 7, one immediately notices that the current estimates are all higher. These larger heritability estimates are due to the larger genetic variance component estimates. The largest increase occurred for marbling score, which is three times larger than the prior (.09 vs .03), resulting in doubling of the heritability estimate. Nevertheless, all are lower than the heritability estimates of other researchers (Table 8). Average heritability values shown are .40, .48, and .37 vs .30, .18, and .23 found in this study for retail cuts per day, cutability, and marbling score, respectively. Note that in Table 8 retail cuts is measured on a weight basis, whereas it is measured on the basis of weight per day of age in this study. Although the current estimates are dissimilar to the averages, they are not so different from the lower estimates in Table 8.

Table 7. Genetic and residual (co)variance components and heritabilities for various models

<table>
<thead>
<tr>
<th>Trait</th>
<th>BWT</th>
<th>WWT</th>
<th>RC</th>
<th>CU</th>
<th>MB</th>
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</table>

Results and Discussion

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Heritabilities

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Table 8. Heritability estimates from several literature sources

<table>
<thead>
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*Upper triangle = genetic (co)variances, lower triangle = residual (co)variances.

Caution should be taken in using many of the literature values for comparisons because most of the data sets available for those studies were small and consisted of records generally from English breeds of cattle. Dunn et al. (1970) estimated heritabilities for growth and carcass characteristics using purebred English cattle and crosses among those breeds. Their estimates from these two data sets for the same traits varied by as much as a factor of two. The heritability estimates from this study are not too low to prevent genetic progress; however, progress may be more rapid if one selects for correlated traits. Much lower additive genetic variance estimates for carcass traits, in comparison to growth traits, also suggest that slow genetic progress in carcass traits would result if major emphasis were put on carcass traits in a selection program.

Correlations

Genetic, residual, and phenotypic correlations among carcass traits only were low (Table 9). Correlations between cutability and marbling score were all negative as well as low with genetic and phenotypic correlations of -.12 and -.15 compared with -.20 and -.17, average values from the literature (see Table 10). Correlations between retail cuts per day and marbling score were essentially zero. This relationship implies that increasing the weight of high-priced cuts per day would not adversely affect marbling score. Cundiff et al. (1971) reported genetic and environmental correlations of -.16 and .12, respectively, for marbling score and retail product. Their estimates of these two parameters for cutability and retail product are similar to cutability and retail cuts per day in this study, .08 and .23 vs .03 and .21, respectively. If average carcass weight is maintained at a reasonable level by slaughtering at younger ages, genetic progress can be made in the amount of retail product, fat trim, and bone based on expected direct response for growth (measured by carcass weight adjusted for age) and correlated response in carcass composition (Cundiff et al., 1971). The statement by Cundiff et al. is partially supported by the current results because retail product and retail cuts per day are functions of each other and retail cuts per day was shown to be correlated to growth traits (Table 9).

### Table 9. Genetic (G), residual (E), and phenotypic (P) correlations for various models

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### Table 10. Genetic and phenotypic correlations among carcass and growth traits from several literature sources

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<td>.26</td>
<td>-.20</td>
<td>.37</td>
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</table>

*Genetic correlations are in the first row and phenotypic in second for each pair of traits.

| Values > .10 were excluded from average.
| BWT = birth weight (kg), WWT = weaning weight (kg), RC = retail cuts per day (kg/d), CU = cutability (%), MB = marbling score.
| Source 1 reported actual cutability rather than estimated.
Correlations between carcass and growth traits may be seen in Table 9. The moderate correlations found between retail cuts per day and birth weight and weaning weight indicate that this information is beneficial in selection programs as well as in evaluating sires. Similar results were also reported for genetic correlations between growth traits and carcass weight by Wilson et al. (1976), Koch et al. (1982), and Benyshek et al. (1988).

Genetic correlations between total retail cuts (kilograms) and feedlot daily gain, 12th rib fat thickness, and marbling score were reported to be .48, -.88, and .02, respectively, by Dinkel and Busch (1973). Their results along with those from the present study suggest that selection for weight traits may result in calves that yield more weight of retail cuts at younger ages with less external fat without deleteriously affecting marbling, thus maintaining carcass quality. This may be easier for Continental breeds of cattle given their faster growth rates compared with English breeds.

Correlations between other pairs of growth and carcass traits are low. Correlations between birth weight and cutability are all close to zero but positive, whereas those for weaning weight and cutability are all small but negative. This may be explained by realizing that as weight increases in the calf, weight of retail cuts also increases, but when put on a percentage of carcass weight basis, cutability decreases because of the increase in other components of the carcass. Not fitting separate direct and maternal effects for weaning weight may also have had an impact here. Genetic and phenotypic correlations between birth weight and cutability reported by Koch et al. (1982) are similar to those estimated for these data (.05 and .05 vs .14 and .04, respectively).

The phenotypic correlation between birth weight and marbling score is slightly < 0 (-.04), similar to the value Koch et al. (1982) estimated (-.02). Their genetic and residual correlations, for this same pair of traits, are larger than those estimated here (.31 and -.25 vs .05 and -.05, respectively). Correlations between weaning weight and marbling score were also very small and positive, in contrast to literature values (Table 10), but were not very different from those of Koch (1978) in magnitude.

Correlations from this study are generally similar to or less than average correlations presented in the literature (Table 10), with the exception of those for weaning weight and retail cuts per day, for which the current estimates are higher. The direction of the correlations for each pair of traits corresponds to that reported by others with the exception of the correlations between weaning weight and marbling score, between retail cuts per day and marbling score, and to a lesser extent

![Figure 1. Ratio of prediction error variances (PEV) for the combined carcass- and growth-traits model and carcass-traits-only model (calculated as combined model PEV divided by carcass only PEV). RC = retail cuts per day of age, CU = percentage of cutability, and MB = marbling score.](image-url)
between birth weight and marbling score. Correlations involving marbling score varied considerably from one study to the next, possibly because they were measured subjectively with less accuracy than other subjective measurements.

Comparison of Sire Evaluations

The additional information obtained by using correlated traits for sires having progeny with carcass measurements results in lower prediction error variance than without that information (Figure 1). As expected, the average ratios are < 1 because the ratios were calculated as the prediction error variances from the full model divided by the prediction error variances from the carcass-trait-only model. Final-round estimates from the full model were used as the starting values for a single round of iteration in the carcass-trait-only model, resulting in a comparison based on the same (covariance) components. Most of the 385 sires having progeny with carcass measurements had accuracy values of < .3 for retail cuts per day (274), cutability (307), and marbling score (288) in the carcass-trait-only model.

The prediction error variance ratios for cutability and marbling score indicate that there was very little change in the accuracy of prediction between the two models because none of the average prediction error variance ratios were < .98. Prediction error variances for retail cuts per day are different (ranging from .883 to .867) for the two models, varying by accuracy group. The results for retail cuts per day indicate that the inclusion of growth traits in the carcass trait analysis led to significantly lower prediction error variance for this trait.

Surprisingly, the results for retail cuts per day indicate that the benefit of correlated growth traits increases as the amount of carcass information from a bull’s progeny and/or relative information increases. Normally, added information is most important for sires with lower accuracy values. The main reasons are probably the moderate to high correlations between retail cuts per day and birth weight and weaning weight. The potential for those sires having greater numbers of progeny with carcass data also to have greater numbers of progeny with growth-trait data, some of whom would have been contemporaries to those progeny with carcass data, may also play a role.

Consistency of Parameter Estimates Among Models

Some recent studies have compared genetic parameter estimates obtained for the same data using single- and multiple-trait models and found that estimates differ in certain situations (Walter and Mao, 1985; Lin and Lee, 1986; Buttazzoni and Mao, 1989; Moore, 1990). Some of the differences in estimates were quite large. Each of these studies involved data with no missing trait observations. The most recent study by Moore (1990) used simulation to estimate genetic parameters and root mean square errors for numerous combinations of traits, in which the magnitude of heritabilities and correlations were varied, as were the number of traits involved. Residual correlations were .5 across all 12 combinations, and, within each combination, genetic correlations were the same for all pairs of traits. Her final conclusions were that no significant biases occurred in heritability estimates. Genetic correlation estimates tended to be biased downward under stronger negative correlations and biased upward when traits were weakly, negatively correlated. Precision in covariance estimation tended to increase as heritabilities increased for all levels of genetic correlations (both positive and negative). When weak genetic correlations were used, precision of covariance estimation also tended to increase as the number of traits in the multiple-trait model increased.

The results for the three- and five-trait models from this study were very similar. A single-trait analysis was performed in addition to evaluate possible single-trait vs multiple-trait differences in estimates. The heritability and variance component estimates for the single-trait model are given in Table 7. Only slight difference existed between those estimates and their counterparts (also in Table 7). Traits in this study were not equally correlated and all heritabilities were low in contrast to those of Moore (1990).

Summary and Conclusions

Parameter estimates for carcass traits from all models were almost identical. Neither number of traits nor level of relationship among traits seemed to affect the estimates, in contrast to some other studies. Heritability estimates from this study were higher than the estimates currently being used in the national Simmental sire evaluation for carcass traits. Correlations were almost without exception lower than average literature values from the past 26 yr, probably due to differences in breed, sample size, and method of estimation.

The decrease in prediction error variance is evident upon examining the ratio of prediction error variances obtained for the carcass-trait-only and full models. The change in prediction error variance for cutability and marbling score was very slight and might be interpreted as insignifi-
cant in relation to the increased number of computations encountered when adding correlated traits.

The decrease in prediction error variance was much larger for retail cuts per day. The reason the lines are so different for cutability and marbling score vs retail cuts per day is the amount of weight the growth trait information receives in terms of the correlations involved. The correlations among the growth traits, cutability, and marbling score are all close to zero or low, whereas the correlations among the growth traits and retail cuts per day are moderate to high.

The EPD were small for all three traits, as expected given the data. Rather than publish retail cut EPD on a weight per day basis, the EPD should be scaled to give an indication that they are not so close to zero. One reasonable scaling method would be to multiply them by a slaughter age of, for example, 500 d (average for these data is 497.5 d) so that the EPD would be on a weight of retail cuts basis.

The benefits of this sophisticated analysis of carcass characteristics may be questionable in light of 1) the limited amount of data being reported because of the management and cost problems associated with maintaining and collecting carcass data and 2) the relative ease of selecting for growth in a manner to obtain genetic progress in carcass traits (to a limited extent given low correlations, except with retail cuts per day) as a result of correlated response due to selection. Most of the literature reviewed on carcass trait analyses in combination with some growth traits indicates that selection emphasis placed on some combination of growth traits is probably more effective than selection on carcass traits (Cundiff et al., 1964, 1971; Dinkel and Busch, 1973; Wilson et al., 1976; Koch, 1978). Results from this study of birth weight, weaning weight, retail cuts per day of age, cutability, and marbling score indicate that the same statement holds for the Simmental population.

Implications

Evaluation of Simmental sires for carcass traits by including growth trait information in a multiple-trait model indicated that evaluation of retail cuts per day benefited the most from including growth trait information. The low heritabilities and correlations estimated and the difficulty in obtaining carcass data suggest that Simmental producers should continue to put primary selection emphasis on growth (direct and maternal) and reproductive traits. In the future, producers may need to increase their selection emphasis on carcass characteristics when the beef cattle industry changes to allow them to realize some added profit from the superior carcasses eventually produced as a result of genetic selection.

Literature Cited


