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INVESTIGATION OF SIRE BY BREED OF DAM INTERACTION WITHIN PERCENTAGE SIMMENTAL GROUPS FOR BIRTH WEIGHT AND 205D WEIGHT IN THE U.S. SIMMENTAL POPULATION

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Bruce Edward Cunningham

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by

Bruce Edward Cunningham

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ABSTRACT

INVESTIGATION OF SIRE BY BREED OF DAM INTERACTION WITHIN PERCENTAGE SIMMENTAL GROUPS FOR BIRTH WEIGHT AND 205D WEIGHT IN THE U. S. SIMMENTAL POPULATION

By

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Because of the "grading up" process used to introduce the Simmental breed into the U. S., Simmental bulls were mated to a diverse population of cows. As a result, Simmental sires could be evaluated based on progeny of dams of varying breed composition. Performance records of 905,118 Simmental calves were supplied by the American Simmental Association. Breeds of dam included in the study were Angus, Hereford, and Polled Hereford. Dams with Polled Hereford breeding were pooled with the Hereford group. The variance components for sire, interaction of sires with breeds of dam, and error were estimated within three dam groups: foundation, F_1 Simmental, and 75% Simmental. The variance components were used to estimate heritabilities across and within breeds of dam and genetic correlations between sires' breeding values across breeds of dam. The evaluation and ranking of bulls were studied by computing expected progeny differences within breeds of dam for each sire. For both birth weight and 205d weight, the variance for the interaction of sires with breeds of dams in calves from foundation Angus and Hereford dams accounted for only 1.5% of the total variance. The reduction in the magnitude of the interaction variance was caused by decreased influence of the base breed of dam through successive generations of repeat backcrossing. Heritability estimates for both traits increased with increased levels of

Simmental breeding. The agreement of evaluation and ranking across groups with Angus or Hereford breeding improved with increased percentage Simmental breeding. For all percentage Simmental groups, the rank correlations between sires' EPD's across breeds of dams were .90 or greater for 205d weight. The results indicated that an interaction of sires and breeds of dam was not important in the U. S. Simmental population for birth and 205d weights.

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Introduction

Prior to the mid-1960s, cattlemen in the United States were limited to a few beef cattle breeds. At that time, cattlemen demanded cattle with increased growth potential, muscularity, and leanness which they were not able to obtain from the British breeds. As a result, a search was started for alternative sources of cattle germplasm. This demand for cattle with high growth potential reached its fruition when cattle from several breeds were imported from the European continent to Canada. These new breeds from Western Europe were recognized for their large frame, rapid growth rate, and muscularity compared to the British breeds. The European breeds came to be known as Continental breeds or "Exotics".

The use of artificial insemination (AI) provided many cattlemen in North America access to these new European breeds. Even though imported bulls were under quarantine, semen was collected and sold to cattlemen, primarily through the bull studs. The new breed associations developed open artificial insemination policies and grading-up programs, enabling cattlemen with herds using traditional breeds to establish herds using the imported European breeds. The availability of semen from sires of these new largeframed, breeds with rapid growth potential was a boon to commercial cattlemen using traditional beef breeds. By using these new breeds, they were able to take advantage of high breeding values for growth and muscularity, and the heterosis produced by crossing cattle from different breeds.

The breed associations for these new breeds established performance recording programs, with several associations requiring performance records for registration. The unrestricted use of AI allowed sires to be used in many herds and served as a basis for developing across-herd comparisons between sires. The breed performance programs, open AI, and limited number of sires provided the breed associations with the means to develop national sire evaluation programs.

In analysis of beef cattle field data, environment is usually defined in terms of region of the country, herd, or contemporary group. With extensive use of AI, sires would have progeny distributed in many contemporary groups across the country. Interactions of sires and environments could be caused by different genes affecting the expression of a trait in different environments, by nonrandom mating, and(or) by preferential treatment of progeny groups. If such an interaction is detected in field data, determining the cause of the interaction is very difficult. Ignoring such an interaction would result in increased prediction error variance and biased predictions.

As a result of grading-up programs, sires will have progeny born to cows of different breed compositions. The breed compositions could range from foundation dam to fourth generation backcross. As of 1986, 50 and 75% Simmental calves comprised 30 to 40% of the data being received by the American Simmental Association (Pollack, personal communication). The evaluation of sires could be affected by having progeny born to a cow population with such diversity of breed composition. Benyshek (1979) indicated that an interaction of sires and breeds of dam may be caused by differences in maternal environment or genetic makeup between breeds of dam. Also, nonrandom mating of sires to cows of specific breeds could cause such an interaction (Miller, personal communication; Benyshek, 1979).

Objectives

The objectives of this study were to:

1) investigate the existence of an interaction of sires and breeds of dams in Simmental field data;

2) study the influence of such an interaction on estimates of genetic parameters and evaluation of sires in the Simmental breed; and

3) study the influence of breed of dam on the effects of age of dam and sex of calf on birth weight and 205d weight.

II. Literature Review

II.1. Description of Interactions of Genotype and Environment

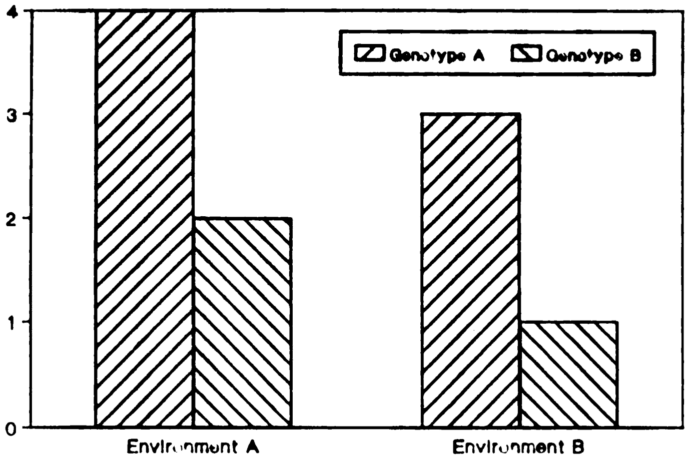
Concerning selection and environment, Lush (1945) stated that animals being selected for certain characters should be kept in an environment which allows the greatest expression of those characters.

Haldane (1946) provided the definition of a interaction of genotypes and environments by using a general example with two genotypes and two environments. He described four types of interaction, which are depicted in Figure 1. If m genotypes and n environments existed, the possible number of types of interactions would equal $(mn)!/m!n!$. Of the four interaction types, Haldane thought that elimination of type 1 interactions was most important so that inferior environments and genotypes would be eliminated.

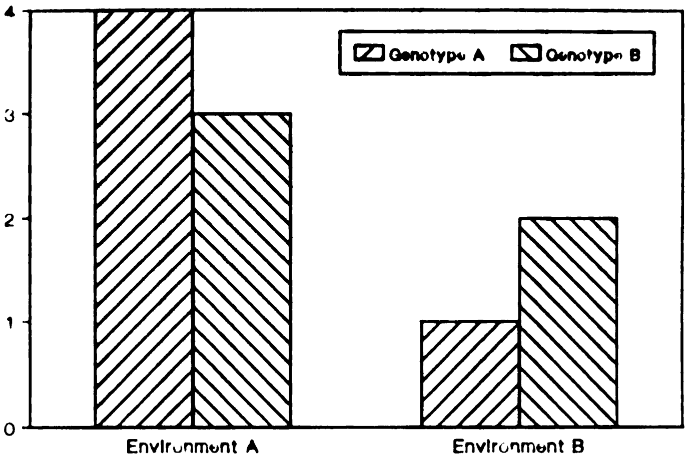
Maximum expression of a trait was the reasoning proposed by Hammond (1947) for practicing selection in the most favorable environment. When the trait is developed, it could be used in other environments, if other traits required in those environments are present in the selected animals. The author stated that variability in quantitative traits is the greatest when the average performance is the greatest.

Hammond's proposal was criticized by Falconer (1952) who indicated for selection of a trait in the most favorable environment to be most effective when the trait is expressed in other environments, no genotype x environment interactions could exist. His recommendation was that selection be performed in the environment in which the selected population is expected to live.

Figure 1. Four Types of Genotype by Environment Interactions



Interaction 1



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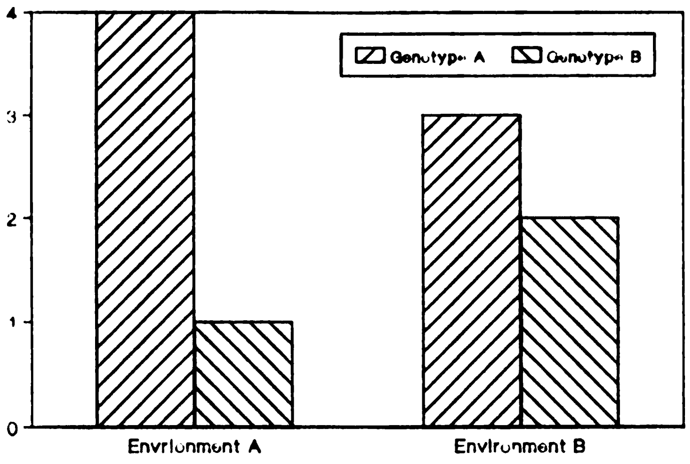
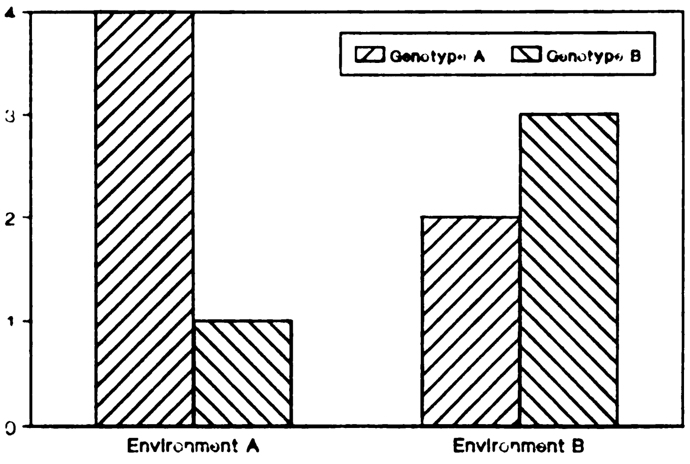


Interaction 3



Interaction 4

If two genotypes and two environments exist, the interaction of genotype and environment could be expressed as a genetic correlation if the performance in each environment is regarded as genetically correlated. To practice selection in the secondary environment, the expectation of a higher heritability in the secondary environment is the only reason for not selecting in the primary environment.

A classification of interactions of genotypes and environments, based on types of genetic and environmental differences was presented by McBride (1958). Environments were partitioned into micro- and macro-environments and genetic differences into intra- and inter-population differences. Type A interactions involved intra-population genotype and micro-environment. Interactions of intra-population genotypes and macro-environments were classified as type B. Type B interactions are the most important to animal breeders when performing selection within breeds across several environments. The existence of such interactions implies that selection should be performed in the environment in which the organism is expected to live. Studies of Type B interactions were classified as static or dynamic. Static studies used genotypes (families) in a population across two or more environments. Studies practicing selection under different environmental conditions and estimating the genetic correlation were termed dynamic studies. Type C interactions involved inter-population genotypes and micro-environments. In some ways, heterosis is one form of Type C interaction. Also important to animal breeders are Type D interactions which involve inter-population genotypes and macro-environments.

Dickerson (1962) described types of environmental factors that could modify the phenotype or genetic evaluation, resulting in an interaction of genotype and environment. The types of environments were 1) external physical influences, 2) background genotype, 3) maternal effects, 4) social climate, and 5) economic forces. Interactions of genotype and environment reduce the accuracy in predicting from phenotypes the ranking of genotypes in other environments.

A definition of interaction of genotype and environment presented by Van Vleck (1963), involved no change in rank from one environment to another. This interaction exists because the genetic variance differs from environment to environment. As level of environment changes, genetic variation increases with no change in genotypic ranking. With interactions of this type, the genetic correlation between progeny performance across environments would be close to 1.0.

Bowman (1972) defined interaction of genotype and environment as a change in relative performance of a trait of two or more genotypes measured in two or more environments. Interactions can be expressed as changes in rank order or changes in absolute and relative magnitude of genetic and environmental variances. In most livestock species, extreme differences would have to exist between environments for rank changes to occur.

An interaction of sires and populations of mates was hypothesized by Brun (1982). The interaction would be caused by differences in ranking of sires based on progeny performance and differences in progeny variability depending on mate population of origin. Considering population of mates as an environment, the environment has two components related to genes that the population transmits to progeny and genes responsible for individual effects on progeny. The interaction was modelled by mating sires from population A randomly to females from populations A and B. Parameters defined were the correlation between additive effects of a sire on its purebred and crossbred progeny and variances of these additive effects.

Brun (1985) reviewed literature to study the interaction of sires and populations of mates. Estimated genetic parameters evaluated were genetic correlation between progeny performance in purebred and crossbred populations, purebred heritability, and crossbred heritability. Also, realized parameters from selection experiments involving two populations were compiled. Interactions of sires and populations of mates were more likely to happen when traits were heterotic, lowly heritable, and had experienced long-term selection pressure.

Types of interactions of genotypes and environments in pig breeding programs were discussed by Brascamp et al. (1985). Those interactions were used to describe two different genetic correlations for use in breeding programmes. Breeding values are estimated for growth and carcass traits on the basis of central or on-farm tests. The goal in pig breeding programmes is defined on the commercial level. Because of the breeding structure, interactions of genotypes and environments could involve test versus commercial environments or differences among commercial environments.

II.2. Analysis of Studies of Interaction of Genotypes and Environments

II.2.1. Analysis of Variance Techniques

Robertson (1959) presented techniques for studying interactions of genotypes and environments. Interactions of genotypes and environments may be classified by 1) differences in between-group variances or 2) differences in true ranking of groups. These two classes can be demonstrated by examining the expected genotype x environment and error mean squares which are shown below:

$$E(MS_{GE}) = \frac{\sigma_{e1}^2 + \sigma_{e2}^2}{2} + \frac{n}{2}[(\sigma_{g1} - \sigma_{g2})^2 + 2\sigma_{g1}\sigma_{g2}(1-r_g)] \text{ and}$$

$$E(MS_e) = (\sigma_{e1}^2 + \sigma_{e2}^2)/2.$$

The component of the genotype x environment variance due to differences in variances between groups is $n(\sigma_{g1} - \sigma_{g2})^2/2$. Changes in group ranking from one environment to another equals $n\sigma_{g1}\sigma_{g2}(1-r_g)$. Detection of r_g deviating from 1.0 is more sensitive than detection of differences of variances between groups.

Studies of interactions of genotypes and environments are limited statistically to models where differences of between groups variances do not exist. The detection of interactions results in the measurement of r_g. If r_g is less than .8 then the interaction of genotypes and environments has biological or agricultural importance. If two or more environments exist, r_g is equal to the mean r_g averaged over all pairs of environments. In this case, r_g is expressed as an intra-class correlation or the proportion of between group variance common to all environments. Formulae for genetic correlations and variances of estimates were developed using standard analysis of variance techniques for two environments and for cases of two or more environments.

The concepts presented by Robertson (1959) were extended by Dickerson (1962) for use in studies of interaction of genotypes with a large number of environments. With many environments, the genetic correlation across environments could be expressed as $r_g = \sigma_{g1g2}/\sigma_{g1}\sigma_{g2} = \sigma_G^2/(\sigma_G^2 + \sigma_{GE}^2)$. This method of estimating r_g is biased by scale effects that occur if variances between genotypes differ across environments. The variance caused by interaction of genotypes and environments is inflated by scale effects as shown below:

$$\sigma_{GE}^2 = \frac{(\sigma_{gi} - \sigma_{gj})^2}{2} + \sigma_{gi}\sigma_{gj}(1-r_{Gi}) = V(\sigma_{gi}) + \overline{\sigma_{gi}\sigma_{gj}(1-r_g)} .$$

The mean value of $(\sigma_{gi} - \sigma_{gj})^2/2$ equals $V(\sigma_{gi})$ for many environments. Adjusting for scale effects, the genetic correlation equals $r_g' = \sigma_G^2/(\sigma_G^2 + \sigma_{GE}^2 - V(\sigma_{gi}))$. If r_g is less than zero, σ_G^2 is negative, which is possible since the genotypic variance equals the average genotypic covariance between all environments. Standard analysis of variance is satisfactory for analyzing studies of interaction of genotypes and environments if 1) adjustments are made for scale effects and 2) the variance component for average genetic ranking across all environments is interpreted as the average genetic covariance for same genotype in different environments.

Yamada (1962) equated models that consider a trait under different environments as different traits and models that treat a trait under different environments as the same trait. Robertson's and Dickerson's concepts were extended to random and mixed models using balanced two-way analysis of variance. The equality of genetic correlations from the two types of models for random and fixed models with two environments are:

$$r_g = \hat{\sigma}_{Gii'}/(\hat{\sigma}_{Gi}\hat{\sigma}_{Gi'}) = \hat{\sigma}_G^2/(\hat{\sigma}_G^2 + \hat{\sigma}_{GE}^2) \text{ and}$$

$$r_g = (\hat{\sigma}_G^2 - \tfrac{1}{2}\hat{\sigma}_{GE}^2)/(\hat{\sigma}_G^2 + \tfrac{1}{2}\hat{\sigma}_{GE}^2), \text{ respectively.}$$

By adjusting for scale effects across many environments, the average genetic correlations are:

$$\bar{r}_g = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \hat{\sigma}_{GE}^2 - V(\hat{\sigma}_{Gi})} \text{ for random models and}$$

$$\frac{\hat{\sigma}_G^2 - \frac{1}{k}\hat{\sigma}_{GE}^2}{\hat{\sigma}_G^2 + \frac{k-1}{k}\hat{\sigma}_{GE}^2 - V(\hat{\sigma}_{Gi})} \text{ for mixed models.}$$

Pani and Lasley (1972) presented intra-class correlations (repeatability) for use in studies with a environments, b genotypes, and n individuals per subclass. The repeatabilities of genotype performance evaluated in one environment but used in different environments for random and mixed models are

$$r = \frac{\sigma_B^2}{\sigma_A^2 + \sigma_B^2 + \sigma_{AB}^2 + \sigma_E^2/n}$$

$$\text{and} \qquad \frac{\sigma_B^2}{\sigma_B^2 + \sigma_{AB}^2 + \sigma_E^2/n}, \text{ respectively.}$$

Repeatabilities of average performance of genotypes over all environments for random and mixed models are

$$r = \frac{\sigma_B^2}{\sigma_A^2/a + \sigma_B^2 + \sigma_{AB}^2/a + \sigma_E^2/an}$$

$$\text{and} \qquad \frac{\sigma_B^2}{\sigma_B^2 + \sigma_{AB}^2/a + \sigma_E^2/an}, \text{ respectively.}$$

Eisen and Saxton (1983) extended the concept of genetic correlation of a trait across environments to two environmental factors B and C, by using analysis of (co)variance. Definitions for three genetic correlations were developed: r_g, correlation across both environmental factors; $r_{G(B)}$, correlation across environment C and within environment B; $r_{G(C)}$, correlation across environment B and within environment C. Corrections factors were developed to remove the effects of heterogeneous genetic variances across environments. The genetic correlations, $r_{G(B)}$ and $r_{G(C)}$, can be biased upward or downward by heterogeneous variances. The three-way genetic correlation, r_G, is always biased upward by heterogeneity of genetic variances. Formulae for estimating variances and calculating correction factors were derived for designs using paternal half-sibs or factorial matings. The genetic correlations between traits were derived for analyses across environments, within environment B and across C, within C and across B, and within both B and C.

II.2.2. Mixed Model Techniques

A method for estimating variances and covariances, presented by

Schaeffer et al. (1978), which allowed for different characters to be measured on different experimental units. Henderson's mixed-model equations were used in a multiple trait setting to estimate genetic and residual variances and covariances. The mixed model used is

$$y = Xb + Zu + e$$

where y is written as $t(N_i x1)$ vectors of observations on t traits. Matrices **X** and **Z** can expressed as

$$\mathbf{X} = \sum_{i=1}^{t}{}^{+} \mathbf{X}_i \quad \text{and } \mathbf{Z} = \sum_{i=1}^{t}{}^{+} \mathbf{Z}_i$$

where Σ^+ is the direct sum operator. The matrix $\mathbf{X}_i$ with dimensions N_i x p_i is assumed to have full column rank. The vectors, **b** and **u**, can be expressed as $\mathbf{b}' = (\mathbf{b}_1',\ldots,\mathbf{b}_t')$ and $\mathbf{u}' = (\mathbf{u}_1',\ldots,\mathbf{u}_t')$. The vector $\mathbf{b}_i$ has length p_i and each random vector, $\mathbf{u}_i$, has only one random factor and the same number of levels, s. The vector $\mathbf{e}' = (\mathbf{e}_1',\ldots,\mathbf{e}_t')$. Expectations for each trait i (i=1,...,t) are

$$E\begin{bmatrix} \mathbf{y}_i \\ \mathbf{u}_i \\ \mathbf{e}_i \end{bmatrix} = \begin{bmatrix} \mathbf{X}_i\mathbf{b}_i \\ 0 \\ 0 \end{bmatrix}.$$

The (co)variance matrices for **u** and **e**, Var(**u**) and Var(**e**), are

$$\begin{bmatrix} \sigma_{11} & \sigma_{1i} & . & . & \sigma_{1t} \\ \sigma_{i1} & \sigma_{22} & . & . & \sigma_{2t} \\ . & . & & & . \\ . & . & & & . \\ \sigma_{t1} & \sigma_{t2} & . & . & \sigma_{tt} \end{bmatrix} \text{ and } \begin{bmatrix} \sigma_{e1}{}^2 & 0 & . & . & 0 \\ 0 & \sigma_{e2}{}^2 & . & . & 0 \\ . & . & & & . \\ . & . & & & . \\ 0 & 0 & & . & \sigma_{et}{}^2 \end{bmatrix},$$

respectively. Cov(**u**,**e**) is assumed to be zero. Variance of **y** is

$$V = \sum_{i \geq j=1}^{t} Z(I^{*}D_{ij})Z'\sigma_{ij} + \sum_{i=1}^{t} D_i\sigma_{ei}{}^2$$

where * is the direct product operator, I is an identity matrix of dimensions s x s, D_{ij} is a t x t matrix with $(i,j)^{th}$ and $(j,i)^{th}$ elements equal to one and all other elements equal to zero, and D_i represents a N x N diagonal matrix where the j^{th} diagonal element equals one if the j^{th} observation comes from the i^{th} trait. The mixed model equations are

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}.$$

The matrices, R^{-1} and G^{-1}, are

$$\begin{bmatrix} I\sigma_{e1}^2 & 0 & . & . & 0 \\ 0 & I\sigma_{e2}^2 & . & . & 0 \\ . & . & . & & . \\ . & . & & . & . \\ 0 & 0 & . & . & I\sigma_{et}^2 \end{bmatrix}^{-1} = \begin{bmatrix} I\tau_1 & 0 & . & . & 0 \\ 0 & I\tau_2 & . & . & 0 \\ . & . & . & & . \\ . & . & & . & . \\ 0 & 0 & . & . & I\tau_t \end{bmatrix}^{-1} \text{ and}$$

$$\begin{bmatrix} \sigma_{11} & \sigma_{12} & . & . & \sigma_{1t} \\ \sigma_{21} & \sigma_{22} & . & . & \sigma_{2t} \\ . & . & . & & . \\ . & . & & . & . \\ \sigma_{t1} & \sigma_{t2} & . & . & \sigma_{tt} \end{bmatrix}^{-1} * I_{txt} = \begin{bmatrix} I\alpha_{11} & I\alpha_{21} & . & . & I\alpha_{1t} \\ I\alpha_{21} & I\alpha_{22} & . & . & I\alpha_{2t} \\ . & . & . & & . \\ . & . & & . & . \\ I\alpha_{t1} & I\alpha_{t2} & . & . & I\alpha_{tt} \end{bmatrix},$$

respectively. Given the structure of genetic and residual variance-covariance matrices, mixed model equations are

$$\begin{bmatrix} \tau_1 X_1'X_1 & 0 & \tau_1 X_1'Z_1 & 0 \\ 0 & \tau_2 X_2'X_2 & 0 & \tau_2 X_2'Z_2 \\ \tau_1 Z_1'X_1 & 0 & \tau_1 Z_1'Z_1 + I\alpha_{11} & I\alpha_{12} \\ 0 & \tau_2 Z_2'X_2 & I\alpha_{21} & \tau_2 Z_2'Z_2 + I\alpha_{22} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ u_1 \\ u_2 \end{bmatrix} =$$

$$\begin{bmatrix} \tau_1 X_1'y \\ \tau_2 X_2'y \\ \tau_1 Z_1'y \\ \tau_2 Z_2'y \end{bmatrix}.$$

The fixed effects can be absorbed into the random effects, resulting in

$$\begin{bmatrix} \tau_1\mathbf{Z}_1'\mathbf{P}_1\mathbf{Z}_1 + \mathbf{I}\alpha_{11} & \mathbf{I}\alpha_{12} \\ \mathbf{I}\alpha_{21} & \tau_2\mathbf{Z}_2'\mathbf{P}_2\mathbf{Z}_2 + \mathbf{I}\alpha_{22} \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \begin{bmatrix} \tau_1\mathbf{Z}_1'\mathbf{P}_1\mathbf{y} \\ \tau_2\mathbf{Z}_2'\mathbf{P}_2\mathbf{y} \end{bmatrix}$$

where $\mathbf{P}_i = \mathbf{I} - \mathbf{X}_i(\mathbf{X}_i'\mathbf{X}_i)^-\mathbf{X}_i'$. Variances and covariances were estimated using a modified maximum likelihood method which is equivalent to iterative minimum-norm quadratic-unbiased estimation (I-MINQUE). The method equated $\hat{\mathbf{u}}_i'\hat{\mathbf{u}}_j$ and $\hat{\mathbf{e}}_i'\hat{\mathbf{e}}_i$ ($i \geq j = 1,\ldots,t$) to their expectations where $\hat{\mathbf{e}}_i = \mathbf{y}_i - \mathbf{X}_i\tilde{\mathbf{b}}_i - \mathbf{Z}_i\hat{\mathbf{u}}_i$. Equations solved for $\hat{\theta}$ are $\mathbf{F}\theta = \mathbf{f}$ where $\mathbf{F}$ is the information matrix of θ and $\mathbf{f}$ is the vector of quadratic forms. An iterative scheme was used with the $(k+1)^{th}$ iterate defined as $\hat{\theta}^{(k+1)} = (\mathbf{F}^k)^{-1}\mathbf{f}^k$.

Fernando et al. (1984) indicated that models for one-way analysis of (co)variance and two-way analysis of variance were not equivalent unless both characters have equal genetic group and residual variances. The model for one-way analysis of (co)variance (model A) is

$$\mathbf{y} = \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{1}_1\mu_1 \\ \mathbf{1}_2\mu_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}$$

where $\mathbf{y}_i$ is the $n_i \times 1$ vector of data for trait i, $i = 1,2$, and n_i is the number of observations for the i^{th} trait; μ is the expected value of trait i and $\mathbf{1}_i$ is a $n_i \times 1$ vector of ones; $\mathbf{u}_i$ is a vector of genetic group effects for trait i with the order of $\mathbf{u}_1$ equal to the order of $\mathbf{u}_2$; $\mathbf{Z}_i$ is a matrix of ones and zeros relating effects in $\mathbf{u}_i$ to observations in $\mathbf{y}_i$, and $\mathbf{e}_i$ is a $n_i \times 1$ vector of residuals for trait i. Expectations of model A are

$$E\begin{bmatrix} \mathbf{y}_i \\ \mathbf{u}_i \\ \mathbf{e}_i \end{bmatrix} = \begin{bmatrix} \mathbf{1}_i\mu_i \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} .$$

Variance-covariance matrices for u_i, e_i, and y_i are

$$\mathrm{Var}\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} I\sigma^2{}_1 & I\sigma_{12} \\ I\sigma_{12} & I\sigma^2{}_2 \end{bmatrix},$$

$$\mathrm{Var}\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I_1\sigma_{e1}{}^2 & 0 \\ 0 & I_2\sigma_{e2}{}^2 \end{bmatrix},$$

$$\text{and}\quad \mathrm{Var}\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} Z_1Z'_1\sigma^2{}_1 + I_1\sigma_{e1}{}^2 & Z_1Z'_2\sigma_{12} \\ Z_2Z'_1\sigma_{12} & Z_2Z'_2 + I_2\sigma_{e2}{}^2 \end{bmatrix},$$

respectively, where I, I_1, and I_2 are identity matrices.

The two-way analysis of variance model (model B) is

$$y = \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} 1_1\mu_1 \\ 1_2\mu_2 \end{bmatrix} + \begin{bmatrix} Z_1 \\ Z_2 \end{bmatrix} u_G + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} u_I + e.$$

where u_g is the vector of genetic-group effects averaged over environments; u_I is a vector of genotype x environment interaction effects, and e is a vector of random residuals. Expected values for model B are

$$E\begin{bmatrix} y_i \\ u_G \\ u_I \\ e \end{bmatrix} = \begin{bmatrix} 1_i\mu_i \\ 0 \\ 0 \\ 0 \end{bmatrix}.$$

Variance-covariance matrices for random effects and y are

$$\mathrm{Var}\begin{bmatrix} u_G \\ u_I \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_G{}^2 & 0 & 0 \\ 0 & I\sigma_I{}^2 & 0 \\ 0 & 0 & I\sigma_e{}^2 \end{bmatrix}$$

$$\text{Var}\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} Z_1Z'_1 & Z_1Z'_2 \\ Z_2Z'_1 & Z_2Z'_2 \end{bmatrix} \sigma_G^2 + \begin{bmatrix} Z_1Z'_1 & 0 \\ 0 & Z_2Z'_2 \end{bmatrix} \sigma_I^2$$

$$+ \begin{bmatrix} I_1 & 0 \\ 0 & I_2 \end{bmatrix} \sigma_e^2.$$

Relationships between models A and B are depicted in Table 1. Models A and B are not equivalent unless σ_1^2 is equal to σ_2^2 and σ_{e1}^2 equals σ_{e2}^2. If variances are not equal then no meaningful relationship exists between models A and B.

The effects of heterogeneity on Best Linear Unbiased Prediction (BLUP) was investigated by Gianola (1986). If the model is correct and the variance-covariance structure is known, then BLUP accounts for heterogeneous variance automatically. Using the model from Schaeffer et al. (1978), an expectation-maximization algorithm for restricted maximum-likelihood (EM-REML) was developed to estimate heterogeneous variances with the genetic correlation across environments not equal to 1. The algorithm allows for non-zero covariance between random effects. The EM-REML algorithm was considered to be less demanding computationally than the I-MINQUE algorithm presented by Schaeffer et al. (1978).

Garrick and Van Vleck (1987) discussed prediction of breeding values when confronted with heterogeneous genetic and residual variances. If the genetic correlation across environments is unity, an interaction of genotypes and environments would be caused by changes in variances across environments. If genetic and residual variances are equal across environments, then mixed model equations would be used with $\text{Var}(u) = A\sigma_g^2$ and $\text{Var}(e) = I\sigma^2$. If additive genetic variance is constant but residual variance is

TABLE 1. RELATIONSHIPS BETWEEN MODEL A AND MODEL B[a]

Parameter	Model A[b]	Model B[c]
σ_{y1}^2	$\sigma_1^2 + \sigma_{e1}^2$	$\sigma_G^2 + \sigma_I^2 + \sigma_e^2$
σ_{y2}^2	$\sigma_2^2 + \sigma_{e2}^2$	$\sigma_G^2 + \sigma_I^2 + \sigma_e^2$
$Cov(u_1,u_1)$	σ_1^2	$\sigma_G^2 + \sigma_I^2$
$Cov(u_2,u_2)$	σ_2^2	$\sigma_G^2 + \sigma_I^2$
$Cov(u_1,u_2)$	σ_{12}	σ_G^2

[a] Fernando et al. (1984).

[b] One-way analysis of (co)variance.

[c] Two-way analysis of variance.

heterogeneous, **R** would be diagonal. The mixed model equations would be weighted by the reciprocals of the residual variances and $\alpha = 1/\sigma_G^2$. Three more-complicated cases exist: 1) additive genetic variances are heterogeneous but residual variances are homogeneous across environments; 2) additive genetic and residual variances are heterogeneous but heritability is constant across environments; and 3) heritabilities are heterogeneous across environments. In these cases multiple trait equations would be used with genetic merit in each environment being a different trait. A singular genetic (co)variance matrix results because breeding values in each environment are linearly related. Mixed model equations are presented which allow for the existance of a singular **G**. If the genetic correlation between breeding values across environments is not unity, multiple trait equations are used, treating performance in each environment as a separate trait. The additive genetic (co)variance matrix is nonsingular. The residual matrix is diagonal since each individual in an environment has only one record, resulting in null residual covariances.

Cameron et al. (1988) used an extension of the work of Yamada (1962) to estimate sire variances and covariances for an interaction of sires and feeding regimes in pigs. A linear model contained environment as a fixed effect, plus sire, sire x environment_1, and sire x environment_2 as random effects. The following variance components were estimated restricted maximum-likelihood (REML): σ_{S12}^2, σ_{S1}^2, and σ_{S2}^2. The interaction variances were expressed as $\sigma_{I1}^2 = \sigma_{S1}^2 - \sigma_{S12}^2$ and $\sigma_{I2}^2 = \sigma_{S2}^2 - \sigma_{S12}^2$. Observations in environment 2 were weighted by $\sigma_{E1}^2/\sigma_{E2}^2$ to account for different residual variances. If σ_{Si}^2 is less than σ_{S12}^2 then σ_{Ii}^2 will be negative. To prevent this from occurring, measurements in environment 2 were scaled by $\beta = \sigma_{S1}/\sigma_{S2}$. The required sire variances and covariances in terms of the scaled σ_{S12}^2 and σ_{Ii}^2 are $\sigma_{S12}^2 = \sigma_{S12}^2/\beta$, $\sigma_{S1}^2 = \sigma_{S12}^2 + \sigma_{I1}^2$, and $\sigma_{S2}^2 = (\sigma_{S12}^2 + \sigma_{I2}^2)/\beta^2$. The genetic correlation was estimated by $r_g = \sigma_{S12}^2/\sigma_{S1}\sigma_{S2}$.

II.2.3. Ad-hoc Techniques

Van Vleck (1963) estimated the genetic correlation across environments using the correlation between daughter averages in different herd levels. Since the variance of daughter averages within each herd contains variation among and within sires, the following term was used to correct the denominator components of the correlation to remove the variance within sires:

$$\frac{1}{s} \sum_{i=1}^{s} \sigma_{ej}^2/n_{ij}$$

where s is the number of sires with daughters in each herd level, n_{ij} is the number of daughters in the j^{th} herd level by the i^{th} sire, and σ_{ej}^2 is the within-sire variance in the j^{th} level.

Blanchard et al. (1983) presented a method of estimating the genetic correlation between traits using sire breeding values to estimate the genetic correlation across environments. If one assumes one record per daughter and that each record is deviated from herd-year-season, then the daughter average for the i^{th} sire is

$$\bar{y}_{i.} = s_i + \bar{e}_{i.}$$

where

$$\bar{e}_i = \sum_{j=1}^{n} e_{ij}/n_i$$

with s_i and e_{ij} being random variables with zero means and variances σ_s^2 and σ_e^2, respectively, and $\mathrm{Cov}(s_i,e_{ij}) = 0$. The variance of the i^{th} sire average equals

$$V(\bar{y}_{i.}) = \sigma_s^2 + \sigma_e^2/n = \sigma_s^2(n_i + \sigma_e^2/\sigma_s^2)/n_i$$

and the regression of s_i on $\bar{y}_{i.}$ is

$$b_i = \sigma_s^2/V(y_{i.}) = n_i/(n_i + \sigma_e^2/\sigma_s^2).$$

Since half of the additive genetic merit of sire $i = s_i$, then

$$4\sigma_s^2 = \sigma_a^2$$

and

$$EBV_i = 2b_i y_i.$$

so

$$\begin{aligned} \mathrm{Var}(EBV_i) &= 4b^2{}_i(\sigma_s^2 + \sigma_e^2/n_i) \\ &= 4b_i\sigma_s^2 \\ &= b_i\sigma_a^2. \end{aligned}$$

The relationships and expectations will be the same for another trait measured on n'_i daughters. The covariance between EBV_i and EBV'_i equals $\mathrm{Cov}(EBV_i,EBV'_i) = 4b_ib'_i\mathrm{Cov}(s_i,s'_i) = b_ib'_i\sigma_{aa'}$ where $\sigma_{aa'}$ is the additive genetic covariance between two traits. If N sires exist, expected values for the population of sires, for $\tau = 1 - 1/N$,

$$\sum_{i=1}^{N} (EBV_i - \sum_{i=1}^{N} EBV_i/N)^2$$

provide an unbiased estimate of

$$\sigma_a^2 \sum_{i=1}^{N} b_i \ .$$

The above would be the same for EBV'_i. Also,

$$\sum_{i=1}^{N} (EBV_i - \sum_{i=1}^{N} EBV_i/N) \cdot \sum_{i=1}^{N} (EBV'_i - \sum_{i=1}^{N} EBV'_i/N)$$

estimates unbiasedly

$$\sigma_{aa'} \sum_{i=1}^{N} b_i b'_i .$$

Pooling variances and covariances across a sample of bulls, the product-moment correlation of sires' EBV across traits is an estimate of

$$\begin{aligned} \sigma_{aa'}\Sigma b_i b'_i/(\sigma_a^2 \Sigma b_i \sigma_{a'}^2 \Sigma b'_i)^{\frac{1}{2}} &= (\sigma_{aa'}/\sigma_a \sigma_{a'})(\Sigma b_i b'_i/(\Sigma b_i \Sigma b'_i)^{\frac{1}{2}}) \\ &= r_{aa}(\Sigma b_i b'_i/(\Sigma b_i \Sigma b'_i)^{\frac{1}{2}}) \end{aligned}$$

where summations for $i = 1,\dots,N$, and $r_{aa'}$ is the genetic correlation. The estimator of $r_{aa'}$ is

$$r_{aa'} = ((\Sigma b_i \Sigma b'_i)^{\frac{1}{2}}/\Sigma b_i b'_i)\ r(EBV_i, EBV'_i) .$$

II.3. Interactions of Sires and Environments

Pani and Lasley (1972) presented an extensive review of studies of interactions of genotypes and environments for beef cattle, dairy cattle, sheep, swine, dogs, laboratory animals, and poultry. This review is limited to studies in beef cattle.

II.3.1. Interaction of sires and breeds of dams

Gregory et al. (1965) performed a crossbreeding experiment using Angus, Hereford, and Shorthorn breeds, and the six reciprocal crosses. Because of the experimental design, sires of each breed were nested within year but cross-classified with breed of dam. The interaction of sire/breed/year and breed of dam was not significant for any of the calf growth traits (birth weight, average daily gain, 200d weight, and conformation score) in either steer or heifer calves. The heterosis expressed for growth traits was due to effects of breeds not those of sires within breeds.

The effects of crossbreeding on heifer postweaning traits were studied by Gregory et al. (1966a). Traits studied were weight at 200, 396, and 550d, and average daily gain from 200 to 396d, from 200 to 550d, and from 396 to 550d. Heifers born from 1960 to 1961 were managed to calve as three-year olds while heifers born from 1962 to 1963 calved as two-year olds. The data were analyzed separately with respect to management scheme. Generally, the interaction of sire/breed/year with breed of dam was insignificant for any trait under either scheme.

The interaction of sire/breed/year and breed of dam was not important for measures of postweaning growth rate and feed efficiency in steers (Gregory et al.,1966b).

For carcass cut-out data, Gregory et al. (1966c) found little evidence to support an interaction of sires and breeds of dams. Any heterosis expressed for carcass traits was not related to the effects of sires within breed.

Dunn (1968) estimated genetic parameters for production traits in purebred and crossbred populations. Data were records from 375 steers and 362 heifers. Angus, Hereford, and Shorthorn breeds were used along with the six reciprocal crosses. Traits evaluated were birth weight, 200-d weaning weight, and weaning score for steers and heifers; final weight, marbling score, final carcass grade, fat thickness, ribeye area, and cutability for steers; and 550-d weight for heifers. Sire variance and covariances were estimated for purebred and crossbred types. No differences in estimates between mating types could be detected. Estimates of heritability for all traits in each mating type were similar in magnitude. Genetic correlations between purebred and crossbred performance for the same trait were high, indicating that selection practiced in purebred populations would improve crossbred performance.

Koger et al. (1975) studied specific combining ability of sires using an interaction of sires and breeds of dams. Angus, Brahman, and Hereford sires were mated to cows of their respective breeds and to crossbred dams to produce backcross calves. Traits studied were condition score, 205-d weight, and postweaning gain. The interaction of sires and breeds of dams was nonsignificant for all analyses. The average genetic correlation between paternal half-sib families from different breeds of dam equaled 0.96. Sire specific combining ability was not large enough to warrant economic consideration.

Benyshek (1979) used 150,000 weaning weight records to study an interaction of sires and breeds of dams in Limousin field data. Nine data sets were created from the original data file to compare different compositions of dam breeds (table 2). Data sets 1 through 5 were used to estimate variance components while data sets 6 through 9 were used to obtain expected progeny differences (EPD) for sires. Variance component estimates from data sets 1 through 5 are shown in table 3. The product-moment and rank correlations for sire EPDs in data sets 6 and 7 were .59 and .58, respectively. Correlations of EPDs in data sets 8 and 9 were .46 and .57. A significant interaction was detected when breeds of dams were Hereford versus Angus, or percentage Limousin versus foundation

TABLE 2. BREED COMPOSITION OF LIMOUSIN CALVES IN DATA SETS USED BY BENYSHEK (1979)

	Breed Composition (%)[a]			
Data set	L	A	H	Other
1	50	50		
	50		50	
2	75	25		
	75		25	
3	50			50
	75			25
4	50		50	
	75		25	
5	50	50		
	75	25		
6	50			50
7	75			25
8	50		50	
9	50	50		

[a] L = Limousin; A = Angus; H = Hereford; Other = Hereford, Angus, Shorthorn, Red Angus, Charolais, Brahman, Hereford x Angus, British cross, dairy crosses.

TABLE 3. ESTIMATES OF SIRE, SIRE X BREED OF DAM, AND ERROR VARIANCES FROM LIMOUSIN FIELD DATA[a]

	Data set[b]				
Variance component, (kg^2)	1	2	3	4	5
Sire	8.5	8.1	6.3	8.4	10.0
%[b]	2.3	2.2	1.5	2.1	2.7
Sire x Breed of dam	3.7	-.4	11.3	15.7	1.0
%	1.0	.0	2.7	4.0	.3
Error	354.8	359.3	404.6	369.1	360.8
%	96.7	97.8	95.8	93.9	97.0

[a] Benyshek (1979).

[b] Percentages of the total variance.

breeds.

The interaction of sire with Angus and Hereford dams was investigated by Massey and Benyshek (1981) using Limousin field data. Estimates of variance components and genetic parameters are shown in table 4. Interaction variance components accounted for a small part of the total variation in birth weight and weaning weight. The heritabilities of birth weight and weaning weight were decreased slightly when the interaction was included.

Cunningham and Magee (1986) investigated the effect of an interaction of sires and types of crossbred dams on estimates of genetic parameters and evaluation of sires. Seventeen Simmental sires were mated to two types of crossbred dams: Charolais x Angus x Hereford and Holstein-Friesian x Angus x Hereford. Differences between types of crossbred dams did not affect prediction of sires' breeding values for birth weight or percentage assisted births. The interaction variance accounted for approximately 1% of the total variation in both traits. For average daily gain and weaning weight, the interaction variance was 1.5 and 2.0 times larger than the sire variance, respectively. Sires tended to be ranked differently in each dam type for weaning traits, possibly reflecting the large maternal difference that existed between the two crossbred types.

II.3.2. Interaction of sires and locations

Location is defined as region of country, herd, contemporary group, or station.

Woodward and Clark (1950) evaluated interactions of sires and stations for birth weight, preweaning and postweaning average daily

TABLE 4. ESTIMATES OF VARIANCE COMPONENTS AND GENETIC PARAMETERS AND GENETIC PARAMETERS INCLUDING A SIRE X BREED OF DAM INTERACTION[a]

Estimates[b]	Birth weight, (kg^2)	205-d Weaning Weight, (kg^2)
σ_s^2	.65 (6.3)[c]	9.50 (2.5)
σ_{sbd}^2	.14 (1.4)	2.30 (.6)
σ_e^2	9.53 (92.3)	366.98 (96.9)
h_1^2	.28	.11
h_2^2	.25	.10
r_g	.81	.78

[a] Massey and Benyshek (1981)

[b] σ_s^2 = sire variance; σ_{sbd}^2 = sire x breed of dam variance; σ^2_e = error variance; h_1^2 = heritability excluding interaction; h_2^2 = heritability including interaction; r_g = genetic correlation for same trait when sire is mated two different breeds of dam.

[c] Percentage of the total variance.

gain, and feedlot efficiency in Hereford cattle. Progeny of 11 Hereford bulls were maintained at two stations in Montana (Havre and Miles City). Bulls were not necessarily progeny tested at both stations during the same year. An interaction of sires and stations did not exist for birth weight and preweaning average daily gain. For feedlot gain and efficiency, a significant interaction was detected, indicating that sires were ranked differently from one station to the other. The interaction, however, was confounded with yearly differences for feedlot traits, so no unbiased estimate of interaction was possible.

Interactions of herds and sires for growth and carcass traits were studied in Angus and Hereford cattle (Wilson et al., 1972). Angus and Hereford sires were replicated in different herds of each breed. Weaning data were from 976 steer calves sired by 55 bulls. Postweaning and carcass data were collected from 486 progeny sired by 30 bulls. Sires were nested within year; breeds were analyzed separately. The interaction was nonsignificant for all live traits and carcass characters in each breed.

Nunn et al. (1978) sorted 12,933 Simmental records into nine regions to study a sire x region interaction for birth weight and weaning weight. Four analyses were made using 1) all regions, 2) Midwest, Oklahoma and Texas, and Montana, 3) Oklahoma and Texas, and Montana, and 4) within Montana. The variance for birth weight associated with interaction of sires and regions accounted for a small percentage of the total variance in each analysis. For weaning weight, interaction of sires and regions was significant in analyses 1, 2 and 3. Even though the interaction was significant, it accounted for a small proportion of the total variation in weaning weight in each regional analysis.

Interactions of sire with region and herd within region were studied using weaning weight records from 15,783 heifers that were 3/4 Simmental (Tess et al., 1979). Regions were Montana, Midwest, and Texas. Each possible combination of regions was analyzed. The interaction of sires and regions was not significant in any of the three analyses. On average, the interaction of sires and herds within regions accounted for 3.0% of the total variation. The average genetic correlations between progeny in different regions and different herds within regions were .60 and .19, respectively.

Buchanan and Nielsen (1979) studied interactions of sires with region, season, herd/region, and sex using field data from Simmental and Maine-Anjou breeds. Simmental birth weight and weaning weight data and Maine-Anjou weaning weight data were sorted into five regions. Two analyses were made using the Simmental data, with analysis 1 using all regions and analysis 2 using data from Texas and Montana. Data from three regions were used in the Maine-Anjou analysis. Interaction of sires and regions was significant for birth weight and weaning weight in both Simmental analyses. Interaction of sires and herds within regions was significant for weaning weight. The estimated genetic correlation between progeny in different herds in the Simmental data was .47. In the Maine-Anjou analysis, interaction of sires and regions was significant for weaning weight with the estimated genetic correlation between progeny performance in different regions equaling .77.

Interactions of sire with region and herd were studied using data on calving ease and birth weight from two-year old Simmental dams (Burfening et al., 1982). Regions were 1) Montana, North Dakota and South Dakota, 2) Kansas and Nebraska, 3) Texas and Oklahoma, and 4) Alabama, Florida, Georgia, Louisiana and Mississippi. Analyses were made for each pair of regions for each trait. Interaction of sires and regions was not significant for calving ease and birth weight. For analyses of region 1 versus 3 and region 1 versus 4, interaction of sires and herds within regions was significant for calving ease. The interaction of sires and herds within regions was important for all analyses containing region 1. On average, the interaction of sires and herds within regions accounted for 3 and 4% of the total variation in calving ease and birth weight, respectively. The average genetic correlation of progeny performance in different herds was .34 for calving ease and .50 for birth weight.

Tess et al. (1984) used progeny of twelve Hereford sires that were managed at three locations in North Carolina. Yearling steer progeny were placed on pasture or feedlot feeding programs until slaughter. An interaction of sires with locations was studied using data on birth weight, preweaning average daily gain, and weaning weight data from 816 calves. Interactions of sires with locations, with diets and with both factors simultaneously were studied using data on postweaning gain, carcass weight, and percentage fat, collected from 355 steers. For all traits, none of the interactions involving sires were significant. When genetic correlations of sire progeny performance were adjusted for differences in sire variances within environments, all correlations were greater than .90.

Polled Hereford weaning weight data were used by Bertrand et al. (1985) to study interactions of sires with regions, with herds within regions, and with contemporary groups within herds. The United States was divided into nine regions; and data were sorted accordingly. Interactions of sires with herds within regions and contemporary groups within herds were evaluated using 19,503 records. The interaction of sires and regions was estimated from 8,659 records. The genetic correlations of sire progeny performance across contemporary groups within herds and across herds and contemporary groups within regions were .59 and .37, respectively. The average correlation of sires' expected progeny differences across regions was .64. The authors concluded that Polled Hereford sire analysis using mixed models should include interactions of sires with herds within regions and with contemporary groups within herds to reduce interaction of sires and environments caused by a single herd or contemporary group and to account for the distribution of progeny across herds and contemporary groups in estimation of prediction error variances.

Silcox (1985) investigated the importance of interactions of sires with regions, with herds within regions, and with contemporary groups within herds for age at first calving in Angus field data. Estimated variances for sires, and the three interactions involving sires were 20.1, -212.7, 293.9, 581.8 and 1532.6 days^2, respectively. Heritability estimates across regions, across herds within regions, within herds, and within contemporary groups were .04, -.35, .18, and 1.23, respectively. The average genetic correlations between sire breeding values were -.10 across regions, .20 across herds within regions and .03 across contemporary groups within herds. Nonrandom treatment of dams may have caused the large interaction variances for age at first calving.

Bertrand et al. (1987) used 109,210 birth weight records and 94,947 weaning weight records to study the importance of interactions of sires with regions and contemporary groups within regions in Limousin field data. The United States was divided into nine regions and data sets were prepared for across and within-region analysis. Within-region expected progeny differences (EPD) for sires were obtained by using a within-region mixed model. The effect of dam was removed by adjusting those records with known dams by the dam's most probable producing ability (MPPA). Estimates of variance components from analyses across and within regions analysis are shown in table 5. Variance components from the within-region analysis, unadjusted and adjusted for dam MPPA, are listed in table 6. Accounting for dam reduced the variance for interaction of sires and contemporary groups within regions by 20 and 38% for birth weight and weaning weight, respectively. The average genetic correlations of sires' EPD across all regions are listed in table 7. The inclusion of dams did not substantially remove the interaction of sires and contemporary groups within regions in the analysis of weaning weight.

The influence of interactions of genotypes and environments on maternal effects was studied by Hanford et al. (1988) who used interactions of maternal grandsires with regions and with herds within regions. Records from two-year old Simmental dams were used.

TABLE 5. ESTIMATED VARIANCE COMPONENTS FROM ACROSS- AND WITHIN-REGIONAL ANALYSES[a]

	Birth Weight, (kg^2)	Weaning Weight, (kg^2)
Across-region[b]		
σ_s^2	.56	9.5
σ_{sr}^2	.10	2.8
σ_{scg}^2	.74	25.4
σ_e^2	9.71	375.4
Within-region[c]		
$\sigma_{s/r}^2$	.70	18.4
σ_{scg}^2	.82	29.9
σ_e^2	9.26	398.4

[a] Bertrand et al. (1987).

[b] σ_s^2 = sire variance; σ_{sr}^2 = sire x region variance; σ_{scg}^2 = sire x contemporary group variance; σ_e^2 = error variance.

[c] $\sigma_{s/r}^2$ = sire within region variance; σ_{scg}^2 = sire x contemporary group variance; σ_e^2 = error variance.

TABLE 6. ESTIMATED VARIANCES FROM WITHIN-REGIONAL ANALYSIS WITH DAMS KNOWN[a]

	Birth Weight (kg^2)		Weaning Weight (kg^2)	
Variances[b]	Unadjusted[c]	Adjusted	Unadjusted	Adjusted
$\sigma_{s/r}^2$	.52	.52	14.9	12.7
σ_{scg}^2	.40	.32	20.9	12.9
σ_e^2	8.89	7.34	367.8	232.8

[a] Bertrand et al. (1987)

[b] $\sigma_{s/r}^2$ = sire within region variance; σ_{scg}^2 = sire x contemporary group variance; σ_e^2 = error variance.

[c] Variances unadjusted and adjusted for dam's most probable producing ability.

TABLE 7. AVERAGE CORRELATIONS OF SIRE EXPECTED PROGENY DIFFERENCES (EPD) ACROSS REGIONS[a]

Analysis[b]	Birth Weight	Weaning Weight
Unadjusted	.73	.55
Dam's MPPA	.78	.66
Dam's MPPA and sire x contemporary group	.81	.69

[a] Bertrand et al. (1987).

[b] Data analysis type.

The data were divided into four regions, as described by Burfening et al. (1982). Analyses were conducted by pairs of regions. Traits studied were calving ease, birth weight, and 205d weight. The interaction of maternal grandsires and regions was not significant in any of the analyses. For birth weight and 205d weight, the interaction of maternal grandsire and herds within regions was significant in four of the six analyses. The interaction of maternal grandsires with herds within regions did not influence calving ease. The genetic correlations from the six analyses for maternal grandsires' progeny performance in different herds were .20 to .74 for birth weight and .04 to .34 for weaning weight.

II.3.3. Interaction of sires and sexes

Tanner et al. (1970) studied interactions of sires and sexes for preweaning growth, feedlot performance and carcass traits in Angus cattle. Preweaning growth data were obtained from 487 calves and feedlot performance and carcass data were gathered from 394 calves. Twenty four sires were represented in both sets of data. No significant interactions were detected for any trait in the study. Sires could be evaluated using different sexes provided adequate sex adjustment factors were available.

An interaction of sires and sexes for preweaning and weaning growth traits in Hereford cattle was studied by Pani et al. (1977). The data were recorded from 902 calves representing 17 sires. For birth weight, the interaction was an important source of variation with the corresponding variance equaling 2.0% of the total variance. The genetic correlation between sire progeny means in each sex was .90. The interaction was significant for average daily gain and weaning weight. As a percentage of the total variation, the interaction variances were larger than the sire variances for both traits. Estimates of heritability within each sex indicated little difference between sexes. These results indicated that sires should be evaluated with an equal number of male and female progeny.

II.3.4. Interaction of sires and testing regimes

Sasaki et al. (1982) studied the interaction of sires and lengths of test periods using performance records from 1,409 Japanese Black bulls sired by 127 sires. Various traits of growth, feed intake, and feed efficiency were evaluated. The interaction was not significant for any trait studied, indicating that sires were evaluated the same, irrespective of length of test period.

The interaction of sire and test regime was investigated using twenty four Friesian sires that were progeny tested in 300 and 600-d tests (Langholz and Thies, 1987). Highly significant interactions of sires and test regimes were obtained for growth and carcass traits. Major changes in sire ranking occurred by lengthing the test period to 600d for all traits. Rank correlations were slightly negative for most traits.

II.3.5. Interaction of sires and years

Pani et al. (1973) used 876 Hereford yearlings sired by 17 sires to investigate interaction of sires and years for postweaning traits. Traits were feedlot gain for bull calves, pasture gain for heifer calves, 392-d weight for bull calves, 550-d weight for heifer calves, and yearling conformation score for bull and heifer calves. Records were deleted if the sire was not used in two or more consecutive years. Data were grouped by sire and years into 18 groups; then each group was analyzed by 2 x 2 or 2 x 3 factorial analysis of variance with sires and years as factors. Averaged across all groups, interaction of sires and years accounted for 13.0, 2.6, 12.5, .5, 8.6 and 1.9% of the total variance for feedlot gain, pasture gain, 392-d weight, 550-d weight, bull and heifer conformation scores, respectively. For bull calves, interaction of sires and years was significant for all traits, whereas it was not for heifer traits. The authors concluded that differences between management practices led to the observed sex differences.

Dinkel and Busch (1973) estimated genetic parameters for production, carcass composition, and carcass quality. Data were collected from 679 grade Hereford steers. The analysis of data included an interaction of years and sires within ranches, but the effect was not important for any characters studied.

Canadian Record of Performance data from Angus and Hereford herds were analyzed, Kennedy and Henderson (1975), to estimate variances for years, sires within herds, interactions of years with herds and sires within herds for weaning weight, preweaning gain, yearling weight, and postweaning gain.Data were divided into four groups based upon breed and creep feed status. Estimated variances are in table 8. For weaning traits, a small interaction of years and sires within herds was detected with the corresponding variance accounting for a greater percentage of the total variance when calves were creep fed. The interaction of years and sires within herds was not important for postweaning traits in any data set. The interaction of year and sires within herds could be caused by

TABLE 8. ESTIMATED VARIANCE COMPONENTS FOR CALF GROWTH TRAITS[a]

		Angus		Hereford	
Trait[b]	Variance	CF[c]	NCF	CF	NCF
WWT	Year	32	2	7	19
	Herd	331	178	222	238
	Sire	21	52	28	45
	Year x Herd	3	58	92	61
	Year x Sire	31	22	32	10
	Error	381	395	515	488
ADG	Year	.0007	.0000	.0002	.0004
	Herd	.0073	.0040	.0054	.0055
	Sire	.0007	.0011	.0007	.0010
	Year x Herd	.0003	.0014	.0020	.0015
	Year x Sire	.0006	.0005	.0007	.0002
	Error	.0087	.0091	.0122	.0116
YWT	Year	45	8	0	42
	Herd	968	761	598	654
	Sire	80	200	138	108
	Year x Herd	146	221	229	282
	Year x Sire	37	-60	-7	10
	Error	911	889	981	982
PADG	Year	-.0004	.0006	-.0002	.0008
	Herd	.0095	.0145	.0113	.0115
	Sire	.0010	.0027	.0022	.0016
	Year x Herd	.0074	.0070	.0065	.0101
	Year x Sire	.0012	-.0012	.0000	.0001
	Error	.0163	.0158	.0166	.0171

[a] Kennedy and Henderson (1975)

[b] **WWT** = weaning weight; **ADG** = preweaning average daily gain; **YWT** = yearling weight; and **PADG** = postweaning average daily gain.

[c] CF = creep feed; NCF = no creep feed;

nonrandom mating of sires within herds.

II.4 Prediction of breeding values

An early representation of mixed model equations was presented by Henderson (1950) using the underlying model

$$y_\alpha = \sum_{i=1}^{p} b_i x_{i\alpha} + \sum_{i=1}^{p} u_i z_{i\alpha} + e_\alpha$$

where b_i are unknown fixed parameters, $x_{i\alpha}$ and $z_{i\alpha}$ are known parameters, u_i are a random sample from a multivariate normal distribution with mean zero and covariance matrix $\|\sigma_{ij}\|$, and e_α are normally and independently distributed with means zero and variances σ_α^2. This model presented three estimation problems: estimation of fixed effects under assumption of model; estimation of random effects; and estimation of variances. Least-squares procedures did not alleviate problems 1 and 2 when u was treated as fixed. A maximum likelihood solution was satisfactory for simultaneous estimation of fixed and random effects. Unbiased estimation of variances could be done by equating expected values to several differences between reduction sums of squares and solving for σ_{ij}.

Henderson et al. (1959) showed that estimation of fixed effects using maximum likelihood techniques and generalized least-squares resulted in the same estimator. The mixed model is

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where $\boldsymbol{\beta}$ is a vector of fixed effects, u and e are independent vectors of variables distributed normally with zero means and variance-covariance matrices $\mathbf{D}\sigma^2$ and $\mathbf{R}\sigma^2$, respectively. The vector y has a multivariate normal distribution with mean $\mathbf{X}\boldsymbol{\beta}$ and variance-covariance matrix $(R + ZDZ')\sigma^2$. The maximum likelihood estimator of β is the solution to

$$\mathbf{X}'(R + ZDZ')^{-1}\mathbf{X}\tilde{\beta} = \mathbf{X}'(R + ZDZ')^{-1}y.$$

Equations for estimating β and u simultaneously are

$$\begin{aligned} \mathbf{X}'R^{-1}\mathbf{X}\hat{\beta} + \mathbf{X}'R^{-1}Z\hat{u} &= \mathbf{X}'R^{-1}y \\ Z'R^{-1}\mathbf{X}\hat{\beta} + (Z'R^{-1}Z + D^{-1})\hat{u} &= Z'R^{-1}y. \end{aligned}$$

In order to show that $\tilde{\beta}$ and $\hat{\beta}$ are the same, is eliminated resulting in

$$\mathbf{X}'\mathbf{W}\mathbf{X}\beta = \mathbf{X}'\mathbf{W}y$$

where $\mathbf{W} = R^{-1} - R^{-1}Z(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}$. If $\mathbf{W} = (R + ZDZ')^{-1}$ then the two estimators are the same and estimates of fixed effects are equivalent. This equality was shown by proving that $(R + ZDZ')\mathbf{W} = I$.

The results of Henderson et al. (1959) were applied to selection index with unequal information and unknown means (Henderson, 1963). It was shown that estimates of fixed effects by maximum likelihood and random effects obtained from selection index were equivalent to estimates obtained from mixed model equations. By setting up least-square equations then adding D^{-1} to the random portion of the coefficient matrix, estimates of fixed effects and selection criteria could be solved for directly.

Henderson (1973) provided an overview of Best Linear Unbiased Prediction (BLUP) and its relationship to Best Prediction (BP) and Best Linear Prediction (BLP). The requirements for BP are knowledge of distribution, means, and variance-covariance matrix. For BLP, the means and variance-covariance matrix must be known but knowledge of distribution is not required. Best Linear Unbiased Prediction does not require knowledge of distribution or means but the variance-covariance matrix must be known. Properties of BLUP are:

1) In the class of linear unbiased predictors, BLUP maximizes the correlation between the predictor and predictand;
2) BLUP of $\mathbf{m}'\hat{\mathbf{w}}$ is $\mathbf{m}'\mathbf{w}$, where $\hat{\mathbf{w}}$ is BLUP of $\mathbf{w}$;
3) Under requirement of normality
   - a) $E(\hat{u}|u) = u$
   - b) $\mathrm{Var}(\hat{u}-u) = \mathrm{Var}(\hat{u}|u)$
   - c) $\hat{\mathbf{w}}$ is maximum likelihood estimator and best linear unbiased estimator of the conditional mean of $\mathbf{w}$
   - d) In the class of linear predictors with means zero, $\hat{u}$ maximizes the probability of correctly ranking the elements u.

The general linear mixed model is

$$y = X\beta + Zu + e$$

where y is the vector of observations,
X is a known, fixed, n x p matrix with rank = $r \leq \min(n,p)$,
β is an unknown vector of fixed effects,
Z is a known fixed matrix,
u and e are non-observable random vectors with zero means
and

$$\mathrm{Var}\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}.$$

If (u,e) are normally distributed, the joint density of (y,u) is maximized for variations in β and u by solutions from the set of equations

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}.$$

Some properties of mixed model equations (MME) are

1) $\mathbf{K}'\tilde{\boldsymbol{\beta}}$ is BLUE of the set of estimable linear functions, $\mathbf{K}'\boldsymbol{\beta}$,

2) $\hat{\mathbf{u}}$ is BLUP,

3) $\hat{\mathbf{u}}$ is unique regardless if the coefficient matrix of the mixed model equations has full rank,

4) $\mathbf{K}'\tilde{\boldsymbol{\beta}} + \mathbf{m}'\hat{\mathbf{u}}$ is BLUP of $\mathbf{K}'\boldsymbol{\beta} + \mathbf{m}'\mathbf{u}$ provided that $\mathbf{K}'\tilde{\boldsymbol{\beta}}$ is estimable,

and 5) variances and covariances: Let some generalized inverse of the coefficient matrix be

$$\begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}$$

then $\mathrm{Var}(\mathbf{K}'\tilde{\boldsymbol{\beta}}) = \mathbf{K}'C_{11}\mathbf{K}$, assuming that $\mathbf{K}'\hat{\tilde{\boldsymbol{\beta}}}$ is estimable. $\mathrm{Cov}(\mathbf{K}'\boldsymbol{\beta},\mathrm{u}) = 0$. $\mathrm{Cov}(\mathbf{K}'\tilde{\boldsymbol{\beta}},\hat{\mathrm{u}}) = -\mathbf{K}'C_{12}$. $\mathrm{Cov}(\mathbf{K}'\tilde{\boldsymbol{\beta}},\hat{\mathrm{u}}-\mathrm{u}) = \mathbf{K}'C_{12}$. $\mathrm{Var}(\hat{\mathrm{u}}) = G - C_{22}$. $\mathrm{Var}(\hat{\mathrm{u}}-\mathrm{u}) = C_{22}$.

Different applications of BLUP and mixed model equations for sire evaluations were discussed and examples presented.

If selection is not taken into account, estimation and prediction of fixed and random effects are biased (Henderson, 1975). Using a conditional model to account for selection, Best Linear Unbiased Estimators and Predictors were derived using a model where selection of certain linear functions of random variables have a joint distribution with the random variables of the usual linear mixed model. The random variables must have a multivariate normal distribution. If selection was performed within fixed effects then obtained from selection model are the solutions to BLUP equations in no selection model. The effects of selection on $\mathbf{y}$, $\mathbf{u}$, $\mathbf{e}$ and sequential selection were discussed and examples presented.

Effects of model misspecification and data deletion on sire evaluation methods were discussed by Henderson (1975). Ignoring fixed effects known to exist resulted in biased estimators and predictors. If random factors are ignored, estimators and predictors from the reduced model are unbiased but sampling variances are increased. The prediction error variance is increased if an incorrect genetic variance-covariance matrix is used in the BLUP equations. The treating of random factors as if they were fixed resulted in a larger variance of prediction error. The variance of prediction error was increased when subsets of data were discarded from analysis.

Gianola et al. (1986) presented a Bayesian inference approach to the problem of prediction of selection criteria and estimation of variance components. From a Bayesian viewpoint, if parameter values are unknown, this state of uncertainty can represented using a prior probability distribution. Combining this distribution with information supplied from the data, a posterior distribution is formed from which needed predictors can be obtained after "nuisances" are integrated out. "Nuisances" are the unknown fixed effects and variances. Prediction of selection criteria under different states of knowledge concerning fixed effects and variances were discussed and solutions presented for each state. An interesting result was presented for prediction with unknown fixed effects and variance components. If prior knowledge of fixed effects and variances is completely vague and distribution is multivariate normal, optimal predictors can be approximated using Henderson's mixed model equations with the unknown variances replaced by EM-REML estimates. This approach leads to empirical Bayes predictors of breeding values.

II.5. Estimation of (co)variances using restricted maximum likelihood

Estimation of variances with analysis of variance for balanced data is a relatively simple task since the expected mean square can be exactly determined for each effect. Variances are estimated by equating the expected mean squares for the random effects with their mean squares and solving for the unknown variances. The variance estimates obtained by using ANOVA estimators are translation invariant and unbiased. Because the estimators are unbiased, the variance estimates can be less than zero. When data are unbalanced, then estimation of variances becomes more difficult since effects in a model are no longer orthogonal. The unbalanced nature of the data causes confounding of fixed and random effects, as a result, the exact expectations of the mean squares are not known.

Henderson (1953) presented three ANOVA-based estimators which were developed for use with unbalanced data sets. The three methods were designated method 1 (HM1), method 2 (HM2), and method 3 (HM3). Method 1 was to be used with random models. The method requires computation of sums of squares for the effects as if the data were balanced, then equating of sums of squares to their expectations and solving for unknown variances. The coefficients for variances in the expected sums of squares are calculated from the distribution of data across subclasses. Biases could exist if fixed effects were considered random effects and included in the analysis. Method 2 attempted to alleviate the problem with treating fixed effects as random effects. Least-square estimates of the fixed effects were obtained then the data were corrected for the fixed effects using the estimates. The corrected data were then analyzed using HM1. Method 2 allowed for a mixed model but no interactions could be included in the model. Method 3 was developed for use with general linear models. Data were analyzed using generalized least squares and reduction sums of squares are obtained for sub-models of the overall linear model. The resulting mean squares were equated to their expectations and solved for the variances. Method 3 allowed the inclusion of interactions between random and fixed factors. If the model included many factors, which of the possible reduction sums of squares should be used is unknown since several different estimators can be obtained with the same data. Also, HM3 can be difficult to use if model has many factors and many levels within each factor. All three methods satisfy the requirement of translation invariance, HM1 by ignoring the fixed effects or calling them random, HM2 by preadjusting the data using estimates of the fixed effects, and HM3 by including the fixed effects directly.

Patterson and Thompson (1971) presented a modified maximum likelihood estimator for inter-block and intra-block weights from experiments using incomplete block designs. The problem of estimating weights is analogous to a general two-way classification model with one fixed factor and one random factor. Instead of maximizing the likelihood of the entire data set, the likelihood of a set of selected error contrasts was maximized. Estimates of weights or variances are obtained using an interative technique. Simultaneous estimation of treatment effects and weights was expressed by using mixed model equations (Henderson et al., 1959). The modified maximum likelihood procedure could be extended to designs with more than one random factor.

Modified maximum likelihood procedures for estimating variances and covariances were presented by Thompson (1973). The likelihood of error contrasts for p variates was maximized instead of the likelihood using the data. Mixed model equations were described for multivariate data.

Henderson (1973) presented an algorithm for obtaining estimable functions, BLUPs, and variances using maximum likelihood directly from the mixed model equations. Starting with a prior value for the variance ratio(s), the mixed model equations are solved for β and . Those results are used to obtain the estimates of variances for random and error effects. Since the algorithm is iterative, those new variance estimates are substituted into the mixed model equations. The process is continued until convergence is reached. The maximum likelihood procedure ignored the fixed effects by using the random portion of the coefficient matrix. Therefore it did not account for the degrees of freedom of the fixed factors. By ignoring the fixed portion of the coefficient matrix, this maximum likelihood procedure is translation invariant.

A detailed review of maximum likelihood (ML) and restricted maximum likelihood (REML) was presented by Harville (1977). Different ML and REML estimators, algorithms, iterative schemes and relationships to other methods were discussed in detail. The author indicated little hope existed of finding an iterative algorithm that would work in all situations. The rate of convergence to a solution is dependent upon the data structure (if convergence is reached at all). With respect to Henderson's ML algorithm, if the prior variance ratio was greater than zero, then estimates of the variances would never become zero. Variances estimated using Henderson's algorithm can never be zero but it is possible to obtain values very close to zero. The ML algorithm described by Henderson (1973) was converted a REML algorithm. Restricted maximum likelihood takes into account the degrees of freedom for the fixed effects by maximizing the likelihood of the set of error contrasts with dimension n - r(**X**) where r(**X**) is the rank of **X**.

Dempster et al. (1977) discussed maximum likelihood estimation using an expectation-maximization (EM) algorithm which was described for several statistical uses. The algorithm is an iterative process that consists of two steps: the expectation step (E-step) and the maximization step (M-step). The E-step calculates the conditional expectations of the sufficient statistics. The calculated sufficient statistics are equated to their expectations. The M-step involves finding solutions to the equations found in the E-step. The estimation of variance components was discussed using a general mixed model with the EM algorithm. The estimates obtained using the EM algorithm were equivalent to restricted maximum likelihood (Ptterson and Thompson, 1971 and Harville, 1977).

Estimation of variance components using the EM-REML algorithm was presented by Taylor and Everett (1985). For a linear model containing additive genetic merit, nonadditive genetic and permanent environment effects, and error, estimators of variance components and computing strategies were presented. Let $\mathbf{K'y}$ be defined as a vector of error contrasts. Let $\mathbf{t}' = (\mathbf{u'A^{-1}u}, \mathbf{p'p}, \mathbf{e'e})$, a vector of quadratic forms, and $\phi' = (\sigma_g^2, \sigma_p^2, \sigma_e^2)$. The vector, ϕ'_k, contains the estimates of the variances in ϕ' after the k^th^ iterate. The E-step is performed to obtain the conditional expectations $t_k = E[\ t \mid \mathbf{K'y}, \phi_k]$. The M-step finds ϕ_k as the solution to $E[\ t \mid \phi] = t_k$. If the additive relationship matrix ($\mathbf{A}$) is not known, estimates of σ_g^2 and σ_p^2 are equal at each iterate k.

Meyer (1987) used EM-REML to estimate variance components in an univariate model with two random factors. The EM-REML algorithm was slow to converge but provided positive estimates if prior values were greater than zero. A reparameterizaton of the EM-REML algorithm was described which speeded up the convergence rate over the original EM algorithm. Computing algorithms were presented for nested and crossclassified designs. Different strategies were described for absorbing fixed effects. Fisher's method of scoring was presented as an alternative to the EM algorithm. The method of scoring is more difficult computationally but has a faster rate of convergence than the EM algorithm.

III. Materials and Methods

Access to the data was kindly provided by the American Simmental Association. The original data file was provided by the Animal Breeding Group of the Department of Animal Science at Cornell University, Ithaca, New York.

III.1. Preparation of Original Data

The original data file consisted of 905,118 records, representing over 12,000 purebred Simmental bulls, collected from 1968 to 1986 by the American Simmental Association. The records represent the most connected data set, with connectedness tested for sire across birth contemporary group. Calf records with erroneous information were deleted from the data file. Values for birth weight, weaning weight, and yearling weight were deleted if they were outside of their respective permissible ranges. Variables included in a calf's record are shown in Table 9. Birth contemporary group was defined as all calves belonging to the same breeder, herd, percent Simmental, sex, and born within 90 days of each other. Weaning contemporary group included all calves in the same birth contemporary group with same preweaning management and weaned on the same date. Yearling contemporary group was defined for calves in same weaning contemporary group that had same postweaning management and same yearling date. These definitions resulted in a nested structure with yearling contemporary group nested in weaning contemporary group which was nested in birth contemporary group.

On each record, the fraction of genes and breed identification code for four different breeds were listed to describe the breed

TABLE 9. VARIABLES LISTED ON A CALF'S RECORD IN ASA DATA FILE

Variable	Code
Breeder Number	IBN
Herd Identification	IHE
Calf Number	IID
Calf Sex	ISX
% Simmental	IPS
Birth Month	IBM
Birth Day	IBD
Birth Year	IBY
Birth Weight	IBW
Weaning Weight Month	IWM
Weaning Weight Day	IWD
Weaning Weight Year	IWY
Weaning Number Contemporaries	NWC
Management Code	IMC
Pasture Unit	IPU
Calf Weaning Weight	IWW
Yearling Weight Month	IYM
Yearling Weight Day	IYD
Yearling Weight Year	IYY
Yearling Number Contemporaries	NYC
Feeding Unit	IFU
Calf Yearling Weight	IYW
Sire Number	ISN
Dam Number	IDI
Calving Ease Trait	ICT
Dam Birth Month	IDM
Dam Birth Day	IDD
Dam Birth Year	IDY
Gestation Length	IGL
Number Calves Born	NCB
Calving Ease	ICE
Maternal Grandsire Number	IMN
Perp. Birth Date	IPB
Perp. Weaning Date	IPW
Perp. Yearling Date	IPY
Dam Perp. Birth Date	IPD
Calf Actual Sex	NSX
Weaning Contemporary Group Number	IWC
Yearling Contemporary Group Number	IYC
Pedigree Number Sire	IQS
Pedigree Number Maternal Grandsire	IQM
Birth Contemporary Group Number	IBC
Birth Weight Status	IST

TABLE 9. CONTINUED

Variable	Code
32nds Breed of Dam 1	MF1
Breed of Dam Code 1	MB1
32nds Breed of Dam 2	MF2
Breed of Dam Code 2	MB2
32nds Breed of Dam 3	MF3
Breed of Dam Code 3	MB3
32nds Breed of Dam 4	MF4
Breed of Dam Code 4	MB4

composition of the calf's dam. The breeds were listed in order from highest to lowest based on contribution of genes. Identification codes were available for 63 breeds of cattle.

III.2. Data Files for Analysis

Birth weight and weaning weight were the traits used in the analysis. For each trait, data files were created containing records of calves with 50, 75, and ≥87.5% Simmental breeding. Within each percentage group, all possible dam breeds and fractions were cross-classified for each part of dam's breed composition. Calves possessing Angus and Hereford backgrounds were the most numerous in all three percentage groups. Thus, those two breeds were used in the analysis. Calves with Polled Hereford breeding were included with Hereford calves. Many calves were eliminated because breed fractions did not match their percentage Simmental classification or breed codes were misclassified. Data files were created for each trait comparing foundation Angus and Hereford dams, F_1 Simmental dams with Angus or Hereford backgrounds, and 75% or greater Simmental dams with Angus or Hereford backgrounds, respectively. Calves with zero values for birth weight or weaning weight were eliminated from their respective data files. Sires were required to have a minimum of 20 progeny with at least two progeny in each dam breed grouping in order to be in a data file. A summary of characteristics for each data file is shown in Table 10. Age of dam was calculated for each calf and used to determine age of dam classification factors. As described by Elzo et al. (1987), age of dam classifications were <2, 2-2.5, 2.5-3, 3-3.5, 3.5-4, 4-4.5, 4.5-5, 5-8, 8-9, 9-10, 10-11, and >11 years of age. In the files

TABLE 10. DESCRIPTION OF MAIN DATA FILES

Data Set	Trait[a]	Number of Sires	Number of Records	Number of Contemporary Groups
Foundation Dams	BWT	303	68,668	22,773
	205D	363	122,268	37,134
F_1 Simmental Dams	BWT	524	86,537	38,530
	205D	663	124,678	52,936
75% Simmental Dams	BWT	903	104,985	56,020
	205D	1,126	122,784	62,254

[a] BWT = Birth Weight; 205D = 205d Weight.

for analysis, some age of dam classes were combined into one class due to small number of calves. The age of dam classes used in all data sets for the study were ≤2, 3-4, 4-5, 5-8, 8-9, 9-10, and >10 years of age. For birth weight, calf sexes were bulls and heifers. Calf sexes for weaning weight were bulls, heifers, and steers. Age•sex•breed subclasses were formed and included on a calf's data record.

III.2.1. Sampling Procedure for Data Files

The inverted coefficient matrix is needed to compute EM-REML estimates of variance components. Direct inversion of matrices requires a considerable amount of memory and CPU time, especially if the matrix is large. At times, the size of the coefficient matrix is so large that inversion is impossible due to memory constraints. Because of the number of sires represented in each of the six data sets, it was determined that the coefficient matrix for each data file would approach or exceed memory limits. To alleviate this problem, a finite population was assumed to exist for each data file with the size of population equal to the number of sires. For each data file, five random samples of 150 sires were taken without replacement for each file described in Table 10. For each sample file, the calf records for each sire in the sample were written onto another file for analysis. The sample files for both weight traits are detailed in Tables 11 and 12, respectively.

III.3. Statistical Analysis

Data were analyzed using a general purpose mixed linear model program (Jensen, personal communication) with capabilities of performing single- or multiple-trait Best Linear Unbiased

TABLE 11. SUMMARY OF SAMPLE DATA SETS FOR ANALYSIS OF BIRTH WEIGHT

Sample #	N[a]	$\hat{\mu}$	$\hat{\sigma}$	n_{ic}
Foundation Angus and Hereford dams				
1	33,435	36.52	5.59	7,287
2	29,351	36.38	5.71	6,877
3	32,254	36.26	5.77	7,004
4	43,080	36.26	5.63	8,084
5	36,011	36.61	5.82	7,370
50% Simmental 50% Angus or Hereford dams				
1	22,908	38.36	5.34	7,972
2	26,174	38.38	5.46	8,548
3	19,920	38.08	5.69	7,101
4	24,611	37.89	5.39	8,475
5	31,344	38.02	5.39	9,814
75% ≥ Simmental 25% ≤ Angus or Hereford dams				
1	14,678	39.63	5.73	6,649
2	13,787	39.67	5.15	6,575
3	16,388	39.10	5.28	7,518
4	13,452	39.98	5.19	5,949
5	20,015	39.02	5.07	9,263

[a] N equals number of records in data set; μ is the mean of sample data set; σ is the standard deviation of sample data set; n_{ic} is the number of contemporary groups in sample data set.

TABLE 12. SUMMARY OF SAMPLE DATA SETS FOR ANALYSIS OF 205d WEIGHT

Sample #	N[a]	$\hat{\mu}$	$\hat{\sigma}$	n_{io}
Foundation Angus and Hereford dams				
1	42,971	208.35	36.97	9,280
2	57,462	206.80	35.98	11,079
3	60,542	208.19	36.20	11,347
4	51,497	207.20	36.12	10,375
5	52,391	207.62	36.06	10,425
50% Simmental 50% Angus or Hereford dams				
1	32,586	234.68	41.00	10,743
2	26,447	233.01	40.82	9,311
3	29,997	231.85	41.41	9,582
4	29,447	233.34	40.74	10,098
5	28,381	235.48	40.24	9,185
75% ≥ Simmental 25% ≤ Angus or Hereford dams				
1	15,267	247.61	39.81	6,800
2	15,297	247.23	40.59	6,347
3	24,845	247.72	40.62	7,518
4	16,526	245.82	39.53	10,419
5	17,146	247.66	40.09	8,294

[a] N equals number of records in data set; μ is the mean of sample data set; σ is the standard deviation of sample data set; n_{io} is the number of contemporary groups in sample data set.

Prediction, estimation of (co)variances using EM-REML, and estimation of fixed factors. Data analyses were performed on an IBM 3090-181 VF computer at Michigan State University.

III.3.1. Model and Expectations

Actual weaning weight was adjusted to a 205d weight basis (Beef Improvement Federation, 1986). If birth weight was zero then the appropriate subclass mean for age-of-dam,sex-of-calf,breed-of-dam was used in the formula. The same model was used to analyze birth weight and 205d weight except that the sexes represented were bulls, heifers, and steers ($k=3$) for 205d weight.

The following linear model was used in the analysis

$$y_{ijklmn} = c_i + asb_{jkl} + s_m + sb_{ml} + e_{ijkmn}$$

where c_i is the fixed effect of the i^{th} contemporary group for $i = 1,\ldots,n_c$;

asb_{jkl} is the fixed effect of the j^{th} age of dam, k^{th} sex of calf, and l^{th} breed of dam subclass where $j=1,\ldots 7$, $k=1,2$ ($k=1,\ldots,3$) and $l=1,2$;

s_m is the random effect of the m^{th} sire which is $N(0, I\sigma_s^2)$ where $m=1,\ldots,150$;

sb_{ml} is the random effect of the m^{th} sire and l^{th} breed of dam subclass which is $N(0, I\sigma_{sb}^2)$;

e_{ijklmn} is the random residual for the n^{th} observation which is $N(0, I\sigma_e^2)$.

The age•sex•breed subclass effect was used in the linear model to account for all main effects, two-way interactions, and the three-way interaction. This is true because $asb_{jkl} = a_j + s_k + b_l + as_{jk} + ab_{jl} + sb_{kl} + asb_{jkl}$. If all main effect, two-way interaction, and the three-way interaction terms were included, seventy five equations for birth weight or ninety five for 205d weight would have to be solved in order to obtain solutions for these fixed effects. Thus, using the subclass effects, the number of equations for subclass effects to be solved was reduced to twenty eight for birth weight and forty two for 205d weight.

In matrix notation, the model was

$$\mathbf{y} = \mathbf{Cc} + \mathbf{Aa} + \mathbf{Z}_1\mathbf{s} + \mathbf{Z}_2\mathbf{i} + \mathbf{e}$$

where **y** is a vector (n x 1) of observations;

C is an incidence matrix (n x c) corresponding to **c**;

c is a column vector (c x 1) of unknown constants for the fixed effect of contemporary groups;

A is an incidence matrix (n x 28 (42)) corresponding to **a**;

a is a column vector (28 (42) x 1) of unknown constants for the fixed subclass effect of age of dam, sex of calf and breed of dam;

$\mathbf{Z}_1$ is an incidence matrix (n x 150) corresponding to **s**;

s is a random vector (150 x 1) containing unknown sire effects;

$\mathbf{Z}_2$ is an incidence matrix (n x 300) corresponding to **i**;

i is a random vector (300 x 1) containing unknown random sire x breed of dam subclass effects;

e is a random vector (n x 1) of residuals pertaining to observations in **y**.

The expectations for the model are

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{s}\\ \mathbf{i}\end{bmatrix} = \begin{bmatrix}\mathbf{Cc} + \mathbf{Aa}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix}.$$

The variance-covariance matrix was

$$V\begin{bmatrix} y \\ s \\ i \\ e \end{bmatrix} = \begin{bmatrix} V_n & Z_1\sigma_s^2 & Z_2\sigma_{sb}^2 & I_n\sigma_e^2 \\ Z_1'\sigma_s^2 & I_p\sigma_s^2 & 0 & 0 \\ Z_2'\sigma_{sb}^2 & 0 & I_q\sigma_{sb}^2 & 0 \\ I_n\sigma_e^2 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

where $V_n = Z_1Z_1'\sigma_s^2 + Z_2Z_2'\sigma_{sb}^2 + I_n\sigma_e^2$.

III.3.2. Computational Procedures

Each sample data set was analyzed using procedures described in the following section irrespective of percentage Simmental or trait.

III.3.2.1. Mixed Model Equations

Henderson's mixed model equations were used to obtain BLUPs for sire and interaction effects, and estimates of variance components. The mixed model equations were

$$\begin{bmatrix} C'C & & \text{Symmetric} & \\ A'C & A'A & & \\ Z_1'C & Z_1'A & Z_1'Z_1 + I_pk_1 & \\ Z_2'C & Z_2'A & Z_2'Z_1 & Z_2'Z_2 + I_qk_2 \end{bmatrix} \begin{bmatrix} c \\ a \\ s \\ i \end{bmatrix} = \begin{bmatrix} C'y \\ A'y \\ Z_1'y \\ Z_2'y \end{bmatrix}$$

where $k_1 = \sigma_e^2/\sigma_s^2$ and $k_2 = \sigma_e^2/\sigma_{sb}^2$.

In each data file, the number of contemporary groups were so numerous that contemporary groups were absorbed while reading the data file using loop absorption. The absorption of contemporary groups was performed as part of the BLUP program used in the analysis.

After absorption of contemporary groups, the mixed model equations were

$$\begin{bmatrix} A'MA & & \text{Symmetric} \\ Z_1'MA & Z_1'MZ_1 + I_p k_1 & \\ Z_2'MA & Z_2'MZ_1 & Z_2'MZ_2 + I_q k_2 \end{bmatrix} \begin{bmatrix} a \\ s \\ i \end{bmatrix} = \begin{bmatrix} A'My \\ Z_1'My \\ Z_2'My \end{bmatrix}$$

where $M = I - C(C'C)^{-1}C'$. Following the completion of contemporary group absorption, a priori values for the variance ratios, k_1 and k_2, augmented the diagonal elements in $Z_1'MZ_1$ and $Z_2'MZ_2$, respectively.

III.3.2.2. Estimation of Variances Using EM-REML

Variance components for sire, interaction, and residual effects were estimated using the Expectation-Maximization Restricted Maximum Likelihood (EM-REML) algortihm (Dempster et al., 1977). The general purpose mixed linear model program (Jensen, personal communication) used the EM-REML algorithm to obtain variance components.

The formulae for sire, interaction, and residual variance components are:

$$\hat{\sigma}_s^2 = [\ \hat{s}'\hat{s} + \hat{\sigma}_e^2 tr(C^{22})\ ]/NS,$$

$$\hat{\sigma}_{sb}^2 = [\ \hat{i}'\hat{i} + \hat{\sigma}_e^2 tr(C^{33})\ ]/NI,$$

and $\hat{\sigma}_e^2 = [\hat{e}'\hat{e} + \hat{\sigma}_e^2(r(C) + r(A) + NS + NI - \hat{k}_1 tr(C^{22}) - \hat{k}_2 tr(C^{33}))]/N$

where tr() is a trace operator, C^{22} is the sire portion of the inverted coefficient matrix, C^{33} is the interaction portion of the inverted coefficient matrix, $\hat{e}'\hat{e}$ is $(y'My - \tilde{a}'A'My - \hat{s}'Z'_1My - \hat{i}'Z'_2My - \hat{k}_1\hat{s}'\hat{s} - \hat{k}_2\hat{i}'\hat{i})$ and $r(C)$ and $r(A)$ are the ranks of $C'C$ and

A'A submatrices, respectively.

The EM-REML algorithm is an iterative procedure which uses the previous round of estimates to estimate variances in the next round of iteration. The procedure iterates until it meets some convergence criterion. Due to computer resource constraints, the algorithm was repeated for a fixed number of iterations. The number of iterations performed for the analyses of birth weight and 205d weight were 150 and 75, respectively. The variance components obtained are not true EM-REML estimates because convergence of estimates was not allowed to occur. The estimated variance components were averaged across samples within each primary data file. The standard error of the mean was computed to provide an empirical estimate of the sampling variance for each component (Banks, 1986).

III.3.2.3. Estimation of Genetic Parameters

To evaluate the magnitude of the interaction of sires and breeds of dams, several genetic parameters were estimated using the estimates of sire, interaction, and error variances. Heritabilities were estimated using the sire intraclass correlation on the bases of across- and within-breeds of dams. The estimate of heritability across-breeds of dams (h^2_A) was computed as follows:

$$\hat{h}_A^2 = 4 \cdot \hat{\sigma}_s^2 \ / \ (\hat{\sigma}_s^2 + \hat{\sigma}_{sb}^2 + \hat{\sigma}_e^2).$$

Heritability within-breeds of dams was estimated by:

$$\hat{h}_W^2 = 4 \cdot (\hat{\sigma}_s^2 + \hat{\sigma}_{sb}^2)/(\hat{\sigma}_s^2 + \hat{\sigma}_{sb}^2 + \hat{\sigma}_e^2).$$

The genetic correlation between sire progeny performance across breed of dam was computed according to Dickerson (1962) and Yamada (1962) as follows:

$$r'_G = \hat{\sigma}_s^2 / (\hat{\sigma}_s^2 + \hat{\sigma}_{sb}^2).$$

For unbalanced data, Fernando et al. (1984) showed that r_G is biased if environments do not have identical genetic and residual variances. In a rebuttal, Yamada et al. (1988) indicated the criticism by Fernando et al. (1984) was unwarranted for the case of unbalanced data. Also, Yamada et al. (1988) showed that r'_G is the lower limit of the true genetic correlation between environments (r_G). As with the estimated variance components, the sample mean and standard error for h_A^2, h_M^2, and r'_G were computed using the five sample estimates within each primary data file.

III.3.2.4. Evaluation of Sires Within Breed of Dam Groups

For each subclass of sire and breed of dam, an expected progeny difference (EPD) was computed as $t_{ml} = s_m + i_{ml}$ where s_m is the m^{th} sire effect and i_{ml} is the interaction effect for the l^{th} dam breed and m^{th} sire. Based upon t_{ml}, sires were ranked from highest to lowest within each breed of dam grouping. A Pearson product-moment correlation (r_P) was computed between sire EPDs within each breed of dam group. Using the sire ranks within dam breed, a Spearman rank correlation (r_s) was computed between sire rankings. To provide further insight into the effects on sire ranking by a sire breed of dam interaction, a top-down correlation (r_K) (Inman and Conover, 1987) was computed using sire rankings.

The Spearman rank correlation gives equal weight to all ranks when testing for no association. There are times when equal weighting of ranks would not be desirable such as evaluating procedures which rank candidates for selection. In selection of individuals for breeding, the highest ranking candidates receive the greatest interest with little regard given to the middle or low ranking candidates. The top-down correlation provides greater emphasis for individuals ranking near the top than middle or low ranking individuals. For each sire within the l^{th} breed of dam group, a Savage score was computed as follows:

$$S_{ml} = \sum_{i=K}^{n} (1/i)$$

where K is the assigned rank of the m^{th} sire within the l^{th} breed of dam. The m^{th} sire will have a pair of ranks and a pair of Savage scores. The top-down correlation is obtained by computing a simple product-moment correlation between the two sets of Savage scores. Within each of the six data files, the estimated r_P, r_S, and r_Ks from the five sample files were used to obtain a sample mean and standard error.

III.3.2.5. Estimation of Age Sex Breed Subclass Effects

For each sample file, solutions to the age•sex•breed subclass effects were computed following estimation of variance components and prediction of random effects. The solutions were used to compute estimates of age of dam effects within sex•breed subclasses for both weight traits. Within each sex•breed category, age of dam effects were deviated from the 5-8 year age group. Within each sex breed subclass, the age of dam effects were averaged across samples and the standard error of the mean was computed.

IV. Results and Discussion

IV.1. Birth Weight

The estimated variance components and heritabilities are listed in Tables 13, 14, and 15, for calves with 50, 75, and 87.5% Simmental breeding, respectively. Estimates of the product-moment, Spearman rank, and top-down correlations are shown in Tables 16, 17, and 18 for the same groups.

IV.1.1. Estimated Variances and Heritabilities

For calves born to foundation Angus and Hereford dams, sire effects were responsible on average for 2.8% of the total variance. Estimates of the sire variance component ranged from .31 to .92 kg^2. When averaged across data sets, the sire variance estimate equaled .58 ± .10 kg^2. The interaction of sires and breeds was responsible for .16 to 3.5% of the total variance for birth weight. The estimated interaction variance component was very small relative to the sire variance in three out of the five samples. In Sample 5, the variance for interaction of sires and breeds of dams was 2.5 times larger than the sire variance. The interaction effect accounted for 2.5% of the total variance in Sample 5. Chance sampling of sires was probably the cause of the two large estimates of the interaction variance. On average, that variance accounted for 1.5% of the total variance. Heritability estimates across breeds of dams ranged from .05 to .16 for calves born to foundation dams. The average heritability was .12 ± .02. When expressed within breeds of dams, estimates varied from .10 for Sample 2 to .26 for Sample 3. On average, that heritability of birth weight was .17 ± .03. The estimated genetic correlation between sires'

TABLE 13. ESTIMATED VARIANCE COMPONENTS AND HERITABILITIES FOR BIRTH WEIGHT OF 50% SIMMENTAL CALVES FROM ANGUS OR HEREFORD FOUNDATION DAMS

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	.674	.038	17.075	.15	.16	.95
2	.480	.040	19.479	.10	.10	.92
3	.913	.592	22.092	.16	.26	.51
4	.542	.028	17.167	.12	.13	.95
5	.307	.846	22.767	.05	.19	.27
Ave[b]	.583	.309	19.716	.12	.17	.74
SEM[c]	.102	.172	1.193	.02	.03	.14

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability.

[b] Average of sample data sets drawn from primary data set.

[c] Standard of mean for sample data sets.

TABLE 14 ESTIMATES OF VARIANCES AND HERITABILITIES FOR BIRTH WEIGHT OF 75% SIMMENTAL CALVES FROM 50% SIMMENTAL DAMS WITH ANGUS OR HEREFORD BASE

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	1.043	.060	16.220	.24	.26	.94
2	.831	.196	15.525	.20	.25	.81
3	.907	.124	17.056	.20	.23	.88
4	1.375	.092	15.779	.32	.34	.94
5	2.229	.123	16.413	.47	.50	.95
Ave[b]	1.277	.119	16.199	.29	.32	.90
SEM[c]	.256	.023	.266	.05	.05	.06

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability; r_G = genetic correlation between sire breeding values across Angus and Hereford dams.

[b] Average of sample data sets drawn from primary data set.

[c] Standard of error of mean for sample data sets.

TABLE 15. ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITIES FOR BIRTH WEIGHT OF 87.5% SIMMENTAL CALVES FROM 75% SIMMENTAL COWS WITH ANGUS OR HEREFORD BASE

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	.932	.167	14.195	.24	.29	.85
2	.623	.215	14.968	.16	.21	.74
3	1.498	.186	15.514	.35	.39	.89
4	1.324	.067	14.859	.33	.34	.95
5	1.687	.075	13.817	.43	.45	.96
Ave[b]	1.213	.142	14.671	.30	.34	.88
SEM[c]	.193	.030	.299	.05	.04	.04

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability; r_G = genetic correlation between sire breeding values across ≥75% Simmental dams with Angus or Hereford base.

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

breeding values, across breeds of dams, ranged from .27 to .95 with an average of .74 ± .14.

Estimates of sire variance expressed in calves born to F_1 Simmental dams with Angus or Hereford base ranged from .83 to 2.23 kg^2. Averaged across samples, the sire variance estimate equaled 1.28 ± .26 kg^2 and accounted for 7.3% of the total variance. The proportion of the total variance associated with interaction of sires and breeds of dams was very small. Except for the estimate obtained from Sample 2, it accounted for less than 1% of the total variance in birth weight. Estimates of the interaction variance ranged from .06 kg^2 for Sample 1 to .19 kg^2 for Sample 2, with average of .12 ± .02, and accounting for .67% of the phenotypic variance. Estimates of heritability across breeds of dams ranged from .20 to .47 for an average of .29 ± .05. Estimates of heritability of birth weight within breeds of dams were slightly higher varying from .23 for Sample 3 to .50 for Sample 5. The average heritability within breeds was .32 ± .05 for calves born to F_1 Simmental dams with Angus or Hereford dams. Estimates of the genetic correlation between sires' breeding values across F_1 Simmental with Angus or Hereford base varied from .81 to .95. The average genetic correlation was .90 ± .06.

The average sire variance measured from progeny born to dams of 75% or greater Simmental breeding and having an Angus or Hereford base was 1.21 ± .19 kg^2. Estimates of the sire variance component ranged from .62 to 1.69 kg^2. As a proportion of the total variance, the sire effect accounted for 4.0 to 10.8% with an average of 7.5%. Effects due to an interaction of sires and breed compositions of dams were small, accounting for less than 1.0% of the total variance on average. Estimates of the interaction variance component ranged from .07 to .21 kg^2. When averaged across samples, the estimated interaction variance was .14 ± .03 kg^2. Estimated heritabilities across breeds of dams ranged from .16 to .43. When averaged across samples, the heritability of birth weight was .30 ± .05. Heritability estimates within breeds of dams varied from .21 to .45. The average heritability within breeds of dams was .34 ± .04 for birth weight. The average genetic correlation between sires' breeding values across 75% Simmental cow groups was .88 ± .04. Estimates of the genetic correlation ranged from .74 in Sample 2 to .96 for Sample 5.

In Limousin field data, Benyshek and Massey (1979) found that variances for sire and interaction of sires with breeds of dams accounted for 6.3 and 1.5% of the total variance in birth weight, respectively. The magnitude of the sire variance was approximately five times larger than the interaction variance. Heritability estimates were .25 and .28 including and excluding the interaction of sires with breeds of dams. Using progeny from Angus or Hereford cows did not appear to seriously affect the evaluation of Limousin sires for birth weight.

When Simmental sires were mated to different types of crossbred dams, the sire effects accounted for 10% of the total variance in birth weight (Cunningham and Magee, 1986). The interaction of sires and types of crossbred dams was responsible for less than 1% of the total variance. When estimated across types of dams, the heritability of birth weight was .41. The heritability within types of dams was slightly higher (.43). The authors concluded that type of crossbred dam did not have an effect on the genetic evaluation of sires for birth weight.

Nunn et al. (1978) found no significant interaction of sire and region for birth weight in Simmental field data. Progeny were 50 to 75% Simmental from twenty-four different breeds of dam, including 50% Simmental cows. Indirectly, an interaction of sires and regions could reflect an interaction of sires with breeds of dams. Estimates of variance associated with the interaction of sires and region accounted for 0 to 1.2% of the total variance in birth weight.

A significant interaction of sires and regions in Simmental field data was detected for birth weight (Buchanan and Nielsen, 1979). The weighted averages of the variances of sire and interactions of sires and regions were similar in magnitude, .36 and .29 kg^2, respectively.

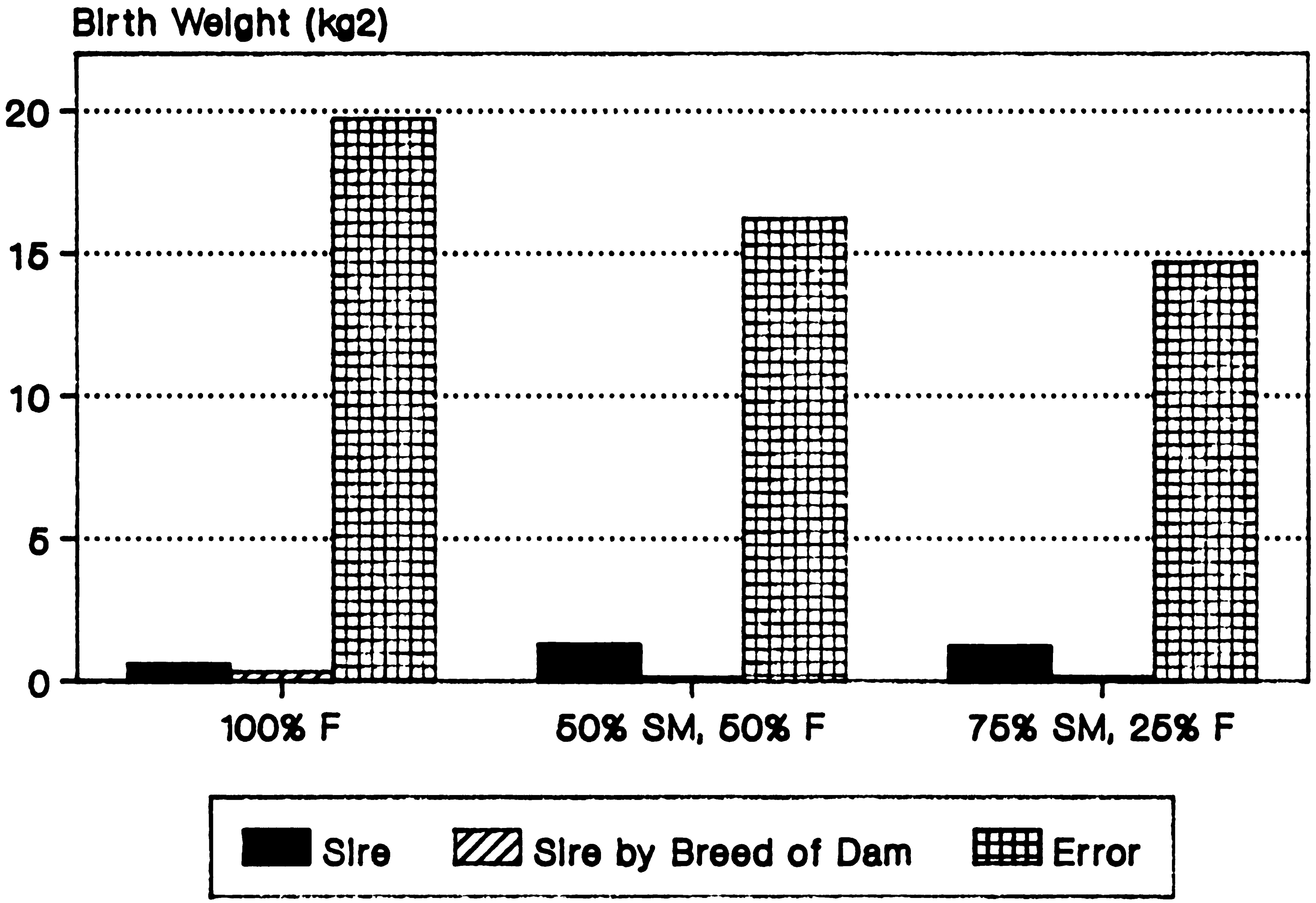
Using Simmental field data, Burfening et al. (1982) found the variance of interaction of sires and herds within regions to be similar in magnitude to the sire variance for birth weight. The weighted averages of the estimated variances were 5.3, .77, .00, .80, and 15.6 kg^2 for herds within regions, sires, interactions of sires with regions and herds within regions, and residual variances, respectively.

The average estimates obtained for heritability of birth weight from the three percent Simmental analyses were within the range of previously reported estimates. In most of the studies using Simmental field records, the data were not analyzed by percent Simmental breeding. Calves from the different Simmental groups were pooled for analysis and percent Simmental breeding was included as a fixed effect. Burfening et al. (1982) obtained a heritability estimate for birth weight of .21 for 50 and 75% Simmental calves. Using data from 50, 75, and 87.5% Simmental calves, Benyshek and Little (1981) estimated the heritability of birth weight to be .18. Heritability estimates for birth weight were .32 and .40 on the bases of inter- and intra-management units, respectively, for 50 and 75% Simmental calves (Burfening et al., 1978). Quass et al. (1985) estimated the heritability of direct and maternal effects for birth weight using Simmental field data. The estimates were .16 and .06 for direct and maternal effects, respectively. Wright et al. (1987), using data obtained from the Canadian Simmental population, obtained heritability estimates of .16 for direct effects and .04 for maternal effects.

As shown in Figure 2, the average phenotypic variance for birth weight decreased, but the sire variance increased as the level of Simmental breeding increased in the dam. Between the F_1 and 75% Simmental groups, little difference was detected between estimates of variance components for sires or for interaction of sires with breeds of dam. Compared to the estimated interaction variance in the 100% foundation group, the two estimates obtained in the F_1 and 75% Simmental group were much smaller and contributed little to the phenotypic variances of birth weight. The error variance component decreased from 19.9 to 14.7 kg^2 with increased level of Simmental breeding in the dam. DeNise et al. (1988) showed that sire and error variance for birth weight increased in Hereford calves as

Figure 2. Estimated Sire, Sire by Breed of Dam, and Error Variance Components for Birth Weight

Estimated Variance Components



range environment improved from poor to good. The estimated heritabilites of birth weight across and within breeds of dams increased as the percent Simmental increased in the calf and dam (Figure 3). The differences between heritability estimates across and within breeds of dams within each percent Simmental group reflected the magnitude of the variance associated with the interaction of sires and breeds of dams. The heritability estimates for birth weight increased as level of Simmental breeding increased (Garrick et al., 1988).

IV.1.2. Effects of Interaction of Sires and Breeds of Dams on Sire Evaluation

For sires evaluated using progeny from Angus and Hereford dams, product-moment correlations (r_P) between sire expected progeny differences indicated that sires tended to be evaluated similarly across breeds of dam. Estimates of r_P were greater than 0.99 for three out of five samples. For Samples 3 and 5, estimates of r_P were .81 and .36, respectively. When averaged across samples, estimated r_P was .83 ± .12. In three of the five samples, sires were ranked virtually the same as indicated by estimated Spearman rank correlations (r_S) greater than .99. In Sample 5, large changes in rank appeared to occur across breeds of dam. The average r_S was .87 ± .09 which indicated that sires were ranked similarly for birth weight across foundation Angus and Hereford dams. Estimates of the top-down correlation (r_K) were used to determine if bulls ranked at the top for one breed of dam were the same for the other breed. For three of five samples, breed of dam did not change ranking of the top bulls as indicated by estimates greater than

Figure 3. Estimated Across- and Within-Breed of Dam Heritabilities for Birth Weight

Estimated Heritability

Birth Weight

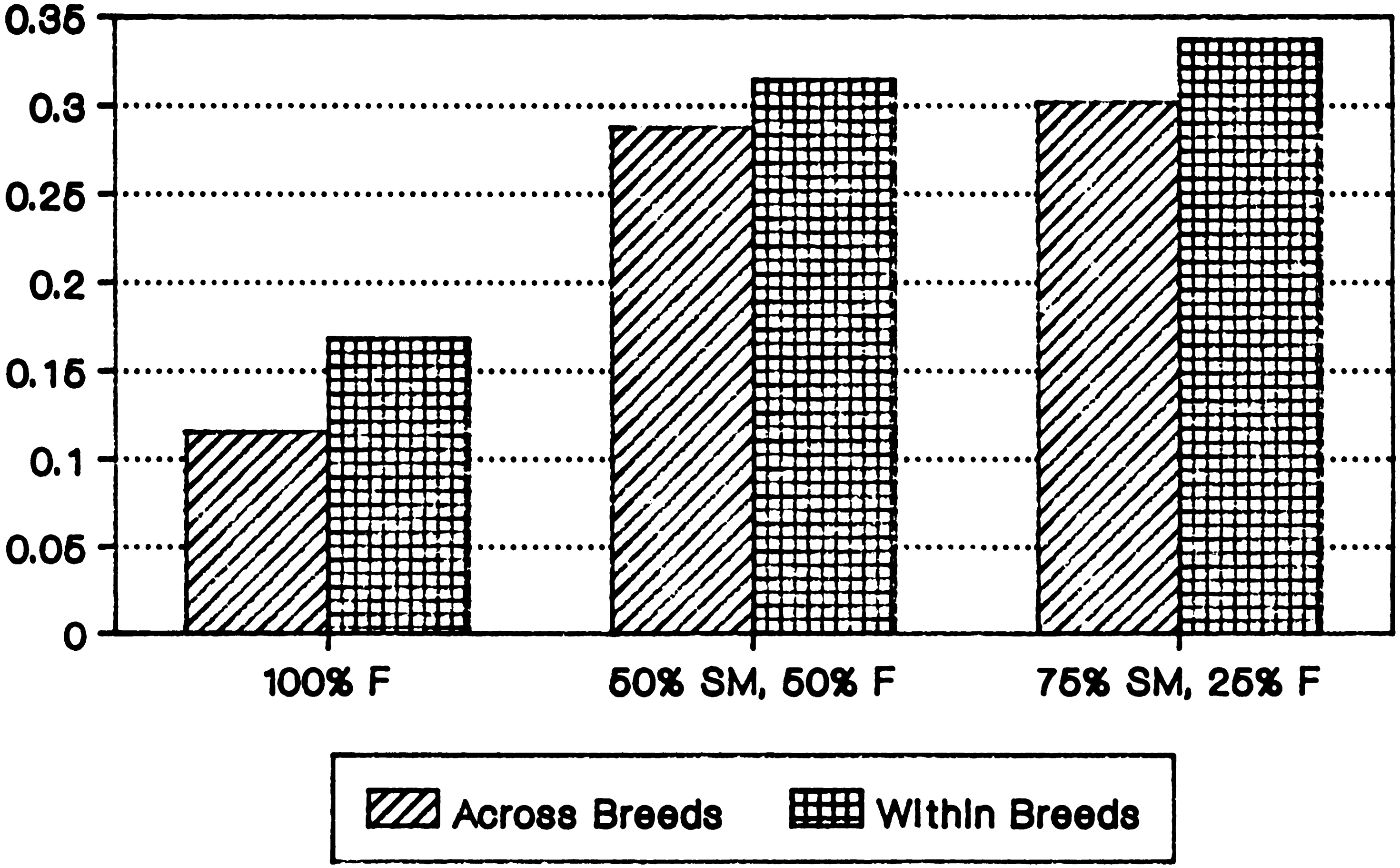


TABLE 16. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR BIRTH WEIGHT ACROSS ANGUS AND HEREFORD FOUNDATION DAMS

Sample #	r_p	r_s	r_k
1	.994	.994	.988
2	.992	.993	.982
3	.808	.828	.794
4	.994	.995	.987
5	.359	.520	.490
Ave[b]	.829	.866	.849
SEM[c]	.123	.092	.097

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 17. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP-DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR BIRTH WEIGHT ACROSS F_1 SIMMENTAL COWS WITH ANGUS OR HEREFORD BASE

Sample #	r_p	r_s	r_k
1	.993	.992	.989
2	.917	.875	.927
3	.968	.965	.961
4	.989	.983	.986
5	.988	.983	.958
Ave[b]	.971	.960	.964
SEM[c]	.014	.022	.011

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 18. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP-DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR BIRTH WEIGHT ACROSS 75% SIMMENTAL DAMS WITH ANGUS OR HEREFORD BASE

Sample #	r_p	r_s	r_k
1	.934	.862	.913
2	.828	.747	.814
3	.964	.927	.910
4	.993	.966	.983
5	.993	.980	.985
Ave[b]	.942	.896	.921
SEM[c]	.031	.043	.031

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

.98. In Sample 5, changes in rank were occurring even with the top sires across the two breeds of dam. On average, the estimated top-down correlation was .85 ± .10. Since results from three of five samples were very similar, estimates obtained in Sample 5 were attributed to chance sampling of sires.

Breed composition of dams did not affect sire EPDs when progeny were born to F_1 Simmental cows with Angus or Hereford backgrounds. Estimates of r_P were greater than .90 for all samples. The estimated correlations varied from .92 to .99 with an average r_P of .97 ± .01. Breed of dam did not affect ranking of sires for birth weight as indicated by an average Spearman rank correlation estimate of .96 ± .02. Spearman rank correlation estimates were greater than .90 for all samples. In four samples, r_S was greater than .95. Top ranking bulls did not change rank across breeds of dam since all estimated top-down correlations were greater than .90. Estimates of r_K ranged from .93 to .99 which indicated ranking of top bulls did not depend on breed composition of dam. When averaged across all samples, the average r_K was .96 ± .01.

The breed composition of 75% and greater Simmental cows did not affect evaluation and ranking of sires. Estimates of product-moment correlations between sire's EPDs across breeds of dam ranged from 0.83 to .99. Four of the five samples had estimates of r_P greater than .90. When averaged across samples, the estimated product-moment correlation was .94 ± .03. The average Spearman rank correlation was .90 ± .04 which indicated that sires tended to be ranked the same within each breed of dam. Estimates varied from .75 to .98 with three sample estimates larger than .90. As indicated by an average r_K of .92 ± .03, the top ranking sires were ranked the same within Angus or Hereford based groups. Top-down correlation estimates ranged from .81 to .98.

The genetic correlation between sire progeny performance across breeds for birth weight was .81 for Limousin sires mated to Angus or Hereford dams (Benyshek and Massey, 1981). Using data from seventeen Simmental sires, Cunningham and Magee (1986) determined that differences in cow breed makeup did not influence evaluation of sires. The simple and Spearman rank correlations between sire EPDs among dam breed type were greater than .99.

Burfening et al. (1982) determined that the genetic correlation between sire progeny performance in different regions of the United States was 1.00 for birth weight. The genetic correlation (weighted average) was .47 for sires' breeding value across regions and 1.22 for sires' breeding values across herds within region (Buchanan and Nielsen, 1979). For the Maine-Anjou breed, the genetic correlation was .77 for sires' breeding value across regions. Nunn et al. (1978) found genetic correlation for sires' progeny performance across regions was at least .86 for birth weight in all analyses. In Limousin field data, Bertrand et al. (1987) determined that average genetic correlation of sires' EPDs across regions were .73, .78, and .81 before adjusting for effects of dams and interaction of sires with contemporary groups, after adjusting for dams, and after adjusting for dams and interaction of sires and contemporary groups, respectively.

IV.1.3. Subclass effects for Combinations of Age of Dam, Sex of Calf, Breed of Dam

Estimates of the subclass effects for combinations of age of dam, sex of calf, and breed of dam are shown in Tables 19, 20, and 21 for calves with 50, 75, and 87.5% Simmental breeding, respectively.

For young cows, calves born to foundation Angus cows required less adjustment to a mature basis than calves born to Hereford cows. Age-of-dam effects ranged from -1.7 to -.2 kg as age increased from ≤2 to 4-5 year groups for Angus females with 50% Simmental bull calves. The age-of-dam effects for bull calves with Angus dams were substantially smaller than those of bull calves with Hereford dams. Angus cows with heifer calves had smaller age effects than Hereford cows with 50% Simmental heifer calves. The age-of-dam effects for young Angus cows relative to a mature base were -1.6, -.6, and -.2 kg for ≤2, 3-4, and 4-5 year groups, respectively. Age effects for young Hereford dams with heifer calves were -2.2, -1.4, and -.6 for ≤2, 3-4, and 4-5 years of age compared to a mature basis, respectively. Differences were difficult to detect for aged cows of either breed with bull or heifer calves. The magnitude of age-of-dam effects tended to increase from 5-8 to ≥10 years of age irrespective of sex or breed. The standard error of age-of-dam effects for aged cows were larger reflecting the greater variation between samples. The number of calves present in those subclasses were less than in subclasses of young foundation dams.

The age-of-dam trends observed in the data from foundation Angus and Hereford dams were evident for F_1 Simmental dams with Angus or Hereford base. The magnitude of the differences between

TABLE 19. SUBCLASS EFFECTS FOR COMBINATIONS OF AGE OF DAM, SEX OF CALF, BREED OF DAM FOR BIRTH WEIGHT FROM CALVES BORN TO FOUNDATION ANGUS OR HEREFORD COWS[a][b]

	Bull		Heifer	
Age of dam	Angus	Hereford	Angus	Hereford
≤2	-1.67	-2.39	-1.59	-2.23
	.25	.25	.20	.06
3-4	-1.08	-1.80	-.60	-1.37
	.17	.08	.12	.06
4-5	-.21	-.82	-.23	-.57
	.13	.07	.02	.03
5-8	0	0	0	0
	0	0	0	0
8-9	-.31	-.11	.01	-.08
	.11	.06	.08	.01
9-10	-.37	-.25	-.65	-.17
	.14	.10	.06	.05
≥10	-.51	-.90	-.43	-.41
	.24	.11	.06	.08

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[a] Subclass effects are expressed as a deviation from the 5-8 yr group.

[b] For each age of dam group, the first line of values is the average effect and the second line is the standard error of the average.

TABLE 20. SUBCLASS EFFECTS FOR COMBINATIONS OF AGE OF DAM, SEX OF CALF, AND BREED OF DAM FOR BIRTH WEIGHT OF CALVES BORN TO F_1 SIMMENTAL COWS WITH ANGUS OR HEREFORD BACKGROUND[a,b]

	Bull		Heifer	
Age of dam	Angus	Hereford	Angus	Hereford
≤2	-2.62	-2.84	-2.53	-2.89
	.19	.18	.16	.06
3-4	-1.43	-1.56	-1.36	-1.40
	.10	.10	.08	.01
4-5	-.20	-.55	-.40	-.58
	.12	.08	.08	.04
5-8	0	0	0	0
	0	0	0	0
8-9	.22	-.36	.04	.16
	.23	.14	.12	.08
9-10	.62	-.08	.43	-.24
	.29	.19	.22	.05
≥10	-.66	-1.19	-.01	-.09
	.37	.11	.13	.16

[a] Subclass effects are expressed as deviation from the 5-8 yr age group.

[b] For each age of dam group, the first line of values is the average effect and the second line is the standard error of the average.

TABLE 21. SUBCLASS EFFECTS FOR COMBINATIONS AGE OF DAM, SEX OF CALF, AND BREED OF DAM FOR BIRTH WEIGHT OF CALVES BORN TO 75 % SIMMENTAL COWS WITH ANGUS OR HEREFORD BACKGROUND[a][b]

	Bull		Heifer	
Age of dam	Angus	Hereford	Angus	Hereford
≤2	-2.75 .13	-2.55 .13	-2.14 .12	-2.24 .08
3-4	-1.34 .17	-1.14 .16	-1.20 .13	-1.16 .11
4-5	-.84 .16	-.45 .15	-.30 .18	-.28 .06
5-8	0 0	0 0	0 0	0 0
8-9	.14 .33	-.07 .20	.05 .31	-.12 .17
9-10	-.02 .55	.12 .17	-.40 .16	-.25 .21
≥10	-1.23 .46	.22 .55	.55 .43	-.53 .06

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[a] Subclass effects are expressed as deviation from the 5-8 yr age group.

[b] For each age of dam group, the first line of values is the average effect and the second line is the standard error of the average.

breeds of dam within sex for young cows was smaller for F_1 Simmental dams compared to foundation dams. Age-of-dam effects for bull calves were -2.6, -1.4, and -.2 for ≤2, 3-4, and 4-5 year old F_1 Simmental cows with an Angus base. For 50% Simmental cows with Hereford breeding, age-of-dam effects were -2.8, -1.6, and -.5 for ≤2, 3-4, and 4-5 year groups for bull calves. Small differences existed for age-of-dam effects for heifer calves of young F_1 Simmental cows with differing genetic background, compared to a mature basis. For young cows with an Angus base, age-of-dam effects were -2.5, -1.4, and -.4 for ≤2, 3-4, and 4-5 year groups, respectively, for heifer calves. Age-of-dam effects for older cows had larger standard errors that made interpretation difficult. Within each combination of sex and breed, trends in age effects for older cows were difficult to detect. The small number of calves within each subclass contributed to the wide range of estimates obtained for older Simmental cows.

The age-of-dam effects for calves from 75% Simmental cows with Angus or Hereford backgrounds were similar in magnitude. For bull calves, age-of-dam effects for young 75% Simmental cows derived from an Angus base were -2.8, -1.3, and -.8 kg for ≤2, 3-4, and 4-5 years compared to a mature basis. The age-of-dam effects for bull calves for 75% Simmental cows from a Hereford base were -2.6, -1.1, and -.5 kg for ≤2, 3-4, and 4-5 years of age, respectively. Age-of-dam effects for heifer calves were very similar across base breed of dam for young 75% Simmental females compared to a mature base. The differences in age-of-dam effects between young Simmental cows with Angus or Hereford base were negligible, being less than .1 kg.

Differences due to base breed for age-of-dam effects were very small for bull and heifer calves when cows were less than five years of age and possessed 75% or greater Simmental breeding. As with foundation and F_1 Simmental groups, age-of-dam effects for older cows within sex and breed were difficult to interpret due to lack of trend as cows grew older. Most of the age-of-dam estimates possessed a standard error larger than the estimate itself.

IV.2. 205 d Weight

IV.2.1. Estimated Variances and Heritabilities

Estimates of variance components and genetic parameters are listed in Tables 22, 23, and 24 for calves with 50, 75, and 87.5% Simmental breeding, respectively.

For 50% Simmental calves born to foundation cows, sire variance ranged from 25.4 to 56.5 kg^2, accounting for 4 to 8% of the total variance in 205 d weight. When averaged across sample files, the sire variance was 40.8 ± 6.3 kg^2. The average variance associated with interaction of sires and breeds of dams was 9.5 ± 1.6 kg^2, or less than a quarter of the magnitude of the sire variance. The interaction variance estimates ranged from 4.8 to 13.87 kg^2. The estimates obtained in Samples 1 and 3 were the largest with each estimate being approximately half as large as the sire variance. The wide range in variance estimates for sires and interaction was attributed to the chance sampling of sires while creating the sample files. For calves born to Angus or Hereford dams, estimates of heritability across breeds of dams varied from .15 to .32, with average of .24 ± .03. When expressed within breeds, the heritability of 205 d weight ranged from .22 to .37, with average of .29 ± .03. The genetic correlation between sire breeding values across breeds of dam reflected the wide range in estimates of variance components. Estimated genetic correlations between sires' breeding values across breeds of dam ranged from .60 for Sample 1 to .91 for Sample 5. The average genetic correlation was .76 ± .06 which indicated that breed of dam may have influenced sire breeding values.

TABLE 22. ESTIMATES OF VARIANCE COMPONENTS, HERITABILITIES AND GENETIC CORRELATION FOR 205d WEIGHT OF 50 % SIMMENTAL CALVES FROM ANGUS OR HEREFORD FOUNDATION DAMS.

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	28.09	13.87	634.51	.166	.248	.604
2	56.48	8.14	631.36	.325	.372	.866
3	25.40	12.17	644.76	.149	.220	.613
4	41.64	8.43	626.99	.246	.296	.816
5	52.37	4.84	652.53	.295	.322	.912
Ave[b]	40.81	9.49	638.03	.236	.292	.762
SEM[c]	6.25	1.60	4.66	.035	.027	.064

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability; r_G = genetic correlation of progeny performance across breed of dam.

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 23. ESTIMATES OF VARIANCE COMPONENTS, HERITABILITIES AND GENETIC CORRELATION FOR 205d WEIGHT OF 75% SIMMENTAL CALVES FROM F_1 SIMMENTAL DAMS WITH ANGUS OR HEREFORD BASE

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	60.38	5.18	665.07	.330	.359	.918
2	64.31	5.88	656.77	.354	.386	.912
3	39.33	10.67	668.08	.219	.278	.761
4	32.74	8.80	675.62	.183	.232	.763
5	44.38	9.13	649.10	.253	.305	.813
Ave[b]	48.23	7.93	662.93	.268	.312	.834
SEM[c]	6.25	1.60	4.66	.035	.027	.035

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability; r_G = genetic correlation of progeny performance across breed of dam.

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 24. ESTIMATES OF VARIANCE COMPONENTS, HERITABILITIES AND GENETIC CORRELATION FOR 205d WEIGHT OF 87.5% SIMMENTAL CALVES FROM 75% SIMMENTAL COWS WITH ANGUS OR HEREFORD BASE

	Estimates[a]					
Sample #	σ_s^2	σ_{sb}^2	σ_e^2	h_1^2	h_2^2	r_G
1	39.11	4.91	552.07	.262	.295	.669
2	80.87	7.63	541.83	.513	.562	.914
3	53.01	4.17	570.03	.338	.365	.927
4	30.77	3.56	548.59	.211	.235	.896
5	70.36	6.17	542.27	.455	.495	.919
Ave[b]	54.82	5.29	550.96	.356	.390	.865
SEM[c]	9.35	.73	5.14	.057	.061	.049

[a] σ_s^2 = sire variance; σ_{sb}^2 = sire by breed of dam variance; σ_e^2 = error variance; h_1^2 = across breed of dam heritability; h_2^2 = within breed of dam heritability; r_G = genetic correlation between progeny performance across breed of dam.

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

Estimates of sire variance varied from 32.7 to 64.3 kg^2, accounting for 4.6 to 8.8% of the total variance in 205d weight for calves born to F_1 Simmental dams. The average sire variance was 48.2 ± 6.2 kg^2 for calves born to F_1 Simmental cows. Variance estimates for interaction of sires and breeds of dams ranged from 5.2 kg^2 in Sample 1 to 10.7 kg^2 in Sample 3, averaging 7.9 ± 1.6 kg^2, and accounting for .7 to 1.5% of the total variance in 205d weight. The average variance component for sires was approximately six times larger than that for interaction. When expressed across breeds, heritability estimates of 205d weight ranged from .18 to .35, averaging .27 ± .03. Estimates of heritability within breed varied from .23 to .39, averaging .31 ± .03. Sample estimates of the genetic correlation between sire breeding values across breeds of dam ranged .76 to .92. Estimates obtained in Samples 3, 4, and 5 were equal or less than .80. For Samples 1 and 2, genetic correlation estimates were greater than .90. The average genetic correlation between sire breeding values across F_1 Simmental dams with Angus or Hereford breeding was .83 ± .03.

As shown in data from calves born to foundation and F_1 Simmental dams, estimates of the sire variance for calves born to 75% Simmental dams were variable, ranging from 30.8 for Sample 4 to 80.9 for Sample 2. The average sire variance was 54.8 ± 9.3 kg^2 and accounted for 9.0% of the variance in 205d weight. Estimates of the variance associated with interaction of sires and breeds of dams ranged from 4.2 to 7.6 kg^2, accounting for .6 to 1.2% of the total variance in 205d weight. Sire variance estimates were 8 to 12 times larger than the interaction variance estimates. When averaged across samples, the interaction variance was 5.3 ± .7 and accounted for .9% of the total variance in 205d weight. When calculated across breeds, heritability of 205d weight varied from .21 to .51, averaging .36 ± .06. Expressing heritability of 205d weight within breeds increased the estimates slightly. The estimates varied from .23 for Sample 4 to .56 for Sample 2, averaging .39 ± .06. All estimates of the genetic correlation between sire breeding values across breeds of dam were greater than .88, ranging from .88 to .93. When averaged across samples, the genetic correlation estimate was .91 ± .01.

Evidence for an interaction of sires and breeds of dams in Limousin field data was found by Benyshek (1979). The interaction of sire and breed of dam was significant when breeds of dam were Angus versus Hereford, and ½ Limousin dams versus miscellaneous foundation breeds. When F_1 Limousin cows with Angus or Hereford base were compared, a negative estimate was obtained for the interaction variance. The interaction variance was 5.6 and 5.4 times larger than the sire variance when sires were mated to miscellaneous foundation breeds versus F_1 Limousin dams and foundation Hereford dams compared to F_1 Limousin dams with Hereford base, respectively. When sires were mated to Angus and F_1 Limousin dams with Angus base, the sire variance component was ten times larger than the interaction variance.

Cunningham and Magee (1986) found the estimate of the variance associated with interaction of sires and types of dams to be approximately two times larger than the sire variance. The heritability estimates for weaning weight were .08 and .23 across and within types of dams, respectively. Differences in maternal ability between the crossbred cow groups appeared to have an effect on sire differences for weaning weight.

Using Limousin field data, Massey and Benyshek (1981) determined that the sire variance was four times larger than the variance associated with the interaction of sires and breeds of dams for 205d weaning weight. For 50% Limousin calves born to Angus or Hereford cows, the interaction variance accounted for less than 1.0% of the total variance. Heritability estimates were .11 and .10, including and excluding the interaction.

The interaction of regions and sires was statistically significant for weaning weight in Simmental field data (Nunn et al., 1978). The associated variance accounted for 0 to 1.8% of the total variance depending on the analysis. The interaction of region and sire was not significant when regions were Eastern and Western Montana. Interaction of sires and breeds of dams may have contributed to the observed interaction of regions and sires.

Effects of interaction of sires and regions were not significant for weaning weight in Simmental field data (Tess et al., 1979). When averaged over all analyses, the variance for interaction of sires and herds within regions accounted for 3.0% of the total variance in weaning weight.

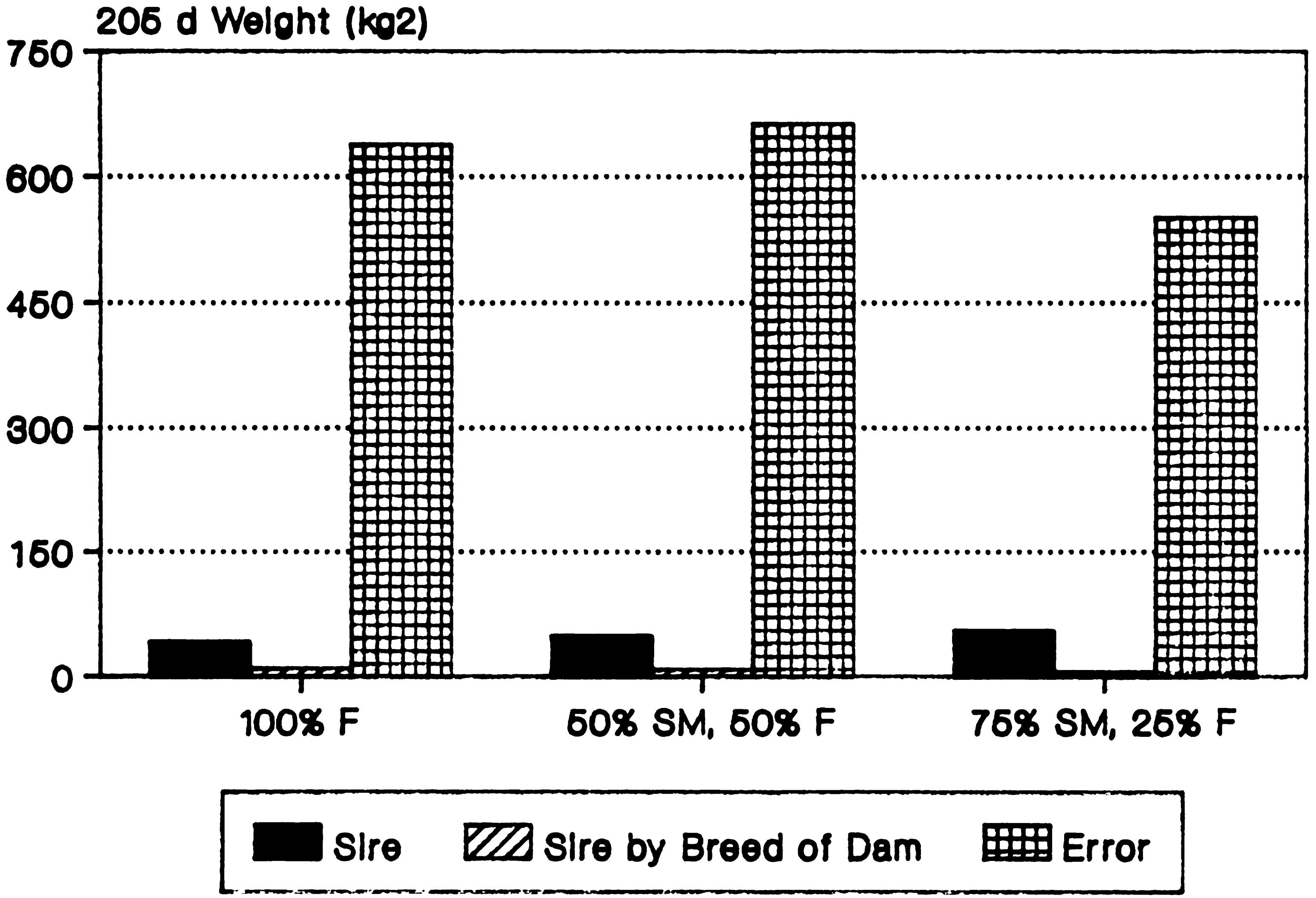
Buchanan and Nielsen (1979) found that the variance associated with interaction of sires and regions was 2.7 times larger than the sire variance for Simmental sires. The variance for interaction of sires and herds was similar in magnitude to the sire variance for weaning weight. In Maine-Anjou field data, the sire variance was approximately 3.5 times larger than the variance for interaction of sires and regions.

The estimates of heritability of 205d weight were within the range of estimates reported in the literature. Using data from calves with 50, 75, and 87,5% Simmental breeding, Benyshek and Little (1981) estimated the heritability of adjusted 205d weaning weight to be .34 ± .12. Heritability estimates of 205d weaning weight were .28 and .51 on the bases of inter- and intra-management units for 50 and 75% Simmental calves (Burfening et al., 1978). Wright et al. (1986) estimated variance components for direct additive genetic effects, maternal additive genetic effects, and permanent environmental effects, and the covariance between direct and maternal effects in American Simmental field data. The estimated heritabilities for direct and maternal contributions to weaning weight were .12 and .09, respectively. The genetic correlation between direct and maternal effects was .16. An analysis using Canadian Simmental field data obtained estimates of the heritabilities of direct and maternal effects for weaning weight of .11 and .05 (Wright et al., 1987). Quass et al. (1985) estimated the heritability for direct and maternal weaning weight in Simmental field data to be .12 and .08, respectively.

For 205d weight, estimates of variance components for sire, interaction of sires and breeds of dams, and error are shown for each % Simmental group in Figure 4. As the percent Simmental increased, the average sire variance increased from 40.8 to 54.8 kg^2. The magnitude of the interaction variance decreased as differences decreased due to breed composition of dam. The average

Figure 4. Estimated Sire, Sire by Breed of Dam, and Error Variance Components for 205d Weight

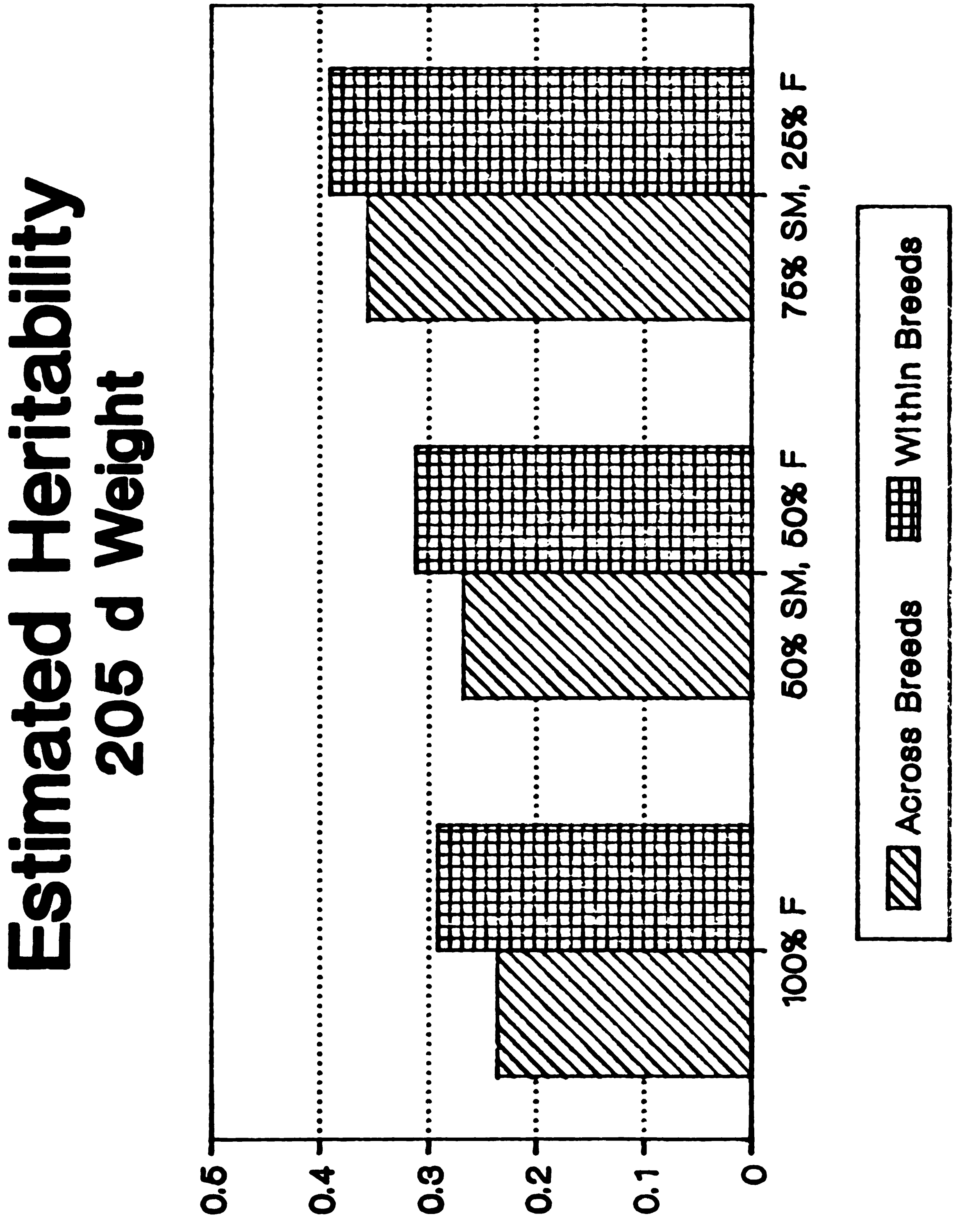
Estimated Variance Components



error variance estimates increased slightly from the 100% foundation group to the F_1 Simmental group. The estimates of error variance decreased from 663 kg^2 in the F_1 Simmental group to 551 kg^2 for the 75% Simmental group. In Figure 5, the estimated heritabilities of 205d weight across and within breeds of dams indicated that as percent Simmental increased, the heritability of 205d weight increased as well. Within each % Simmental group, the differences diminished between average heritability estimates. This decrease was due to the decrease in the magnitude of the interaction variance.

DeNise et al. (1988) determined that estimates of additive-genetic and residual variance for weaning weight increased as environment improved from poor to good for male and female Hereford calves. Garrick et al. (1988) estimated heritabilities for calving ease and weight traits within % Simmental and sex subclasses in the U.S. Simmental population. The estimates of heritability generally increased with increases of % Simmental for male and female calves. They indicated that genetic and residual variances were lower for 50% Simmental calves compared to 75% or greater Simmental calves. Estimates of sire variance, error variance, and heritability should be expected to increase with increased level of performance for both traits. Because differences between base breeds of dam decrease with increased levels of Simmental breeding, the variance for interaction of sires and breeds of dams should decrease accordingly. The error variance decreased as percent Simmental increased in the dam for birth weight. For 205d weight, the error variance was increased somewhat from foundation dams to F_1

Figure 5. Estimated Across- and Within-Breed of Dam Heritabilities for 205d Weight


Estimated Heritability
205 d Weight
0.5
0.4
0.3
0.2
0.1
0
100% F
50% SM, 50% F
75% SM, 25% F
▨ Across Breeds
▦ Within Breeds

Simmental dams but it declined as % Simmental went from 50% to 75% in the dam.

IV.2.2. Effects of Interaction of Sires and Breeds of Dams on Sire Evaluation

Estimates of product-moment, Spearman rank, and top-down correlations for calves of 50, 75, and 87.5% Simmental breeding are listed in Tables 25, 26, and 27, respectively.

On average, sires were similarly evaluated for 205d weight when progeny were from Angus or Hereford foundation dams. The product-moment correlation between sires' expected progeny differences (EPD) across Angus or Hereford dams varied from .81 to .98. Three of the five estimates were greater than .93, indicating strong agreement between evaluations within Angus or Hereford groups. When estimates were averaged, the product-moment correlation was .90 ± .04. Generally, sires tended to be evaluated similarly based on progeny born to Angus or Hereford dams. Estimates of Spearman rank correlation varied from .84 to .97 with Samples 1 and 3 having estimates less than .85. The Spearman rank correlation was .91 ± .03 when averaged across the sample files. It would indicate that progeny's breed of dam did not have a significant effect on sire ranking for 205d weight. Estimates of the top-down correlation in Samples 1 and 3 indicated some changing of rank by high ranking sires across breed of foundation dam. The other three estimates were greater than .90 which indicated very little change in rank was occurring among the sires in the upper percentile groups. Estimated ranged from .76 to .97 with the average top-down correlation equaling .87 ± .05.

TABLE 25. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP-DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR 205d WEIGHT ACROSS ANGUS AND HEREFORD FOUNDATION DAMS

Sample #	r_p	r_s	r_k
1	.808	.838	.758
2	.954	.948	.954
3	.806	.849	.757
4	.935	.934	.909
5	.981	.966	.973
Ave[b]	.897	.907	.870
SEM[c]	.034	.026	.047

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 26. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP-DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR 205d WEIGHT ACROSS F_1 SIMMENTAL DAMS WITH ANGUS OR HEREFORD BASE

Sample #	r_p	r_s	r_k
1	.981	.971	.957
2	.980	.959	.957
3	.895	.846	.871
4	.906	.861	.917
5	.930	.887	.857
Ave[b]	.938	.905	.912
SEM[c]	.003	.026	.021

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

TABLE 27. ESTIMATED PRODUCT-MOMENT, SPEARMAN RANK, AND TOP-DOWN CORRELATIONS BETWEEN SIRE EXPECTED PROGENY DIFFERENCES FOR 205d WEIGHT ACROSS 75% OR GREATER SIMMENTAL DAMS WITH ANGUS OR HEREFORD BASE

Sample #	r_p	r_s	r_k
1	.967	.916	.944
2	.974	.922	.955
3	.984	.973	.981
4	.975	.950	.962
5	.979	.917	.948
Ave[b]	.976	.936	.958
SEM[c]	.003	.011	.007

[a] r_p = product-moment correlation; r_s = Spearman's rank correlation; r_k = top down correlation;

[b] Average of sample data sets drawn from primary data set.

[c] Standard error of sample data set mean.

Prediction of expected progeny differences of sires did not appear to be affected by using progeny from F_1 Simmental dams of differing breed backgrounds. The estimates of the product-moment correlation varied from .89 to .98. When averaged across samples, the product-moment correlation between sire EPDs was .94 ± .003. Spearman rank correlation estimates varied from .85 to .97, indicating ranking of sires were similar across the breed of dam groups. The average Spearman correlation was .91 ± .03. On average, sires evaluated based on progeny from different breed of dam groups appeared to be similarly ranked within each group for 205d weight. Top-down correlation estimates ranged from .86 to .96. The average top-down correlation was .91 ± .02. The average estimate indicated that sires in the upper percentile groups were being similarly ranked irrespective of breed composition of calf's dam.

For progeny born to ≥75% Simmental cows, the base breed appeared to have very little effect on the evaluation of sires for 205d weight. The estimates of product-moment were greater than .95, ranging from .97 to .98. The average product-moment correlation between sires' EPDs was .98 ± .003. It would appear that sires were evaluated very similarly based on progeny from second backcross or higher Simmental cows derived from Angus or Hereford base. The estimates of Spearman rank correlation from .92 to .97. When averaged across samples, the Spearman correlation was .94 ± .01. Although not as large as the average product-moment correlation, the Spearman rank correlation indicated general agreement in rank across breeds of dam. Estimates of the top-down correlation provided further evidence that breed makeup of dam did not influence evaluation of sires for 205d weight. The top-down correlation estimates varied from .94 to .98. When averaged across samples, the top-down correlation was .96 ± .01.

IV.2.3. Estimates of Subclass Effects for Combinations of Age, Sex, and Breed

Estimates of subclass effects for combinations of age-of-dam, sex-of-calf, and breed-of-dam are listed on Tables 28, 29, and 30, for calves with 50, 75, and 87.5% Simmental breeding, respectively.

Bull calves born to Angus dams two years of age required a larger adjustment to a mature basis than did calves nursing Hereford cows. For cows three years of age, age-of-dam effects were very similar in magnitude for bull calves suckling Angus or Hereford dams. The age effect for Angus cows with 50% Simmental bull calves was less than the estimate for calves nursing Hereford cows at 4-5 years of age. The age-of-dam estimates for bull calves were -23.1, -10.2, and -3.8 kg for ≤2, 3-4, and 4-5 yr Angus cows, respectively. For Hereford cows, age-of-dam estimates were -18.4, -10.6, and -7.9 kg for ≤2, 3-4, and 4-5 yr groups, respectively. Calves born to Angus cows required less adjustment to a mature base compared to calves nursing Hereford cows (Tong and Newman, 1980). For purebred Angus and Hereford bull calves, age-of-dam effects for weaning weight were smaller for Angus cows than Hereford cows except for cows four years of age (Chenette and Frahm, 1981). For cows older than eight years of age, bull calves nursing Angus cows required a greater adjustment to the mature base than calves born to Hereford foundation dams.

Generally, age-of-dam effects for 50% Simmental heifer calves

TABLE 28. SUBCLASS EFFECTS FOR COMBINATIONS OF AGE OF DAM, SEX OF CALF, AND BREED OF DAM FOR 205d WEIGHT OF CALVES BORN TO ANGUS OR HEREFORD FOUNDATION COWS

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	-23.07	-18.45	-13.99	-14.19	-19.23	-11.50
	1.08	1.79	1.04	.61	5.34	2.97
3-4	-10.21	-10.61	-6.56	-8.50	-19.02	-11.32
	.92	.69	.90	.11	2.22	1.09
4-5	-3.79	-7.94	-2.90	-3.89	-6.82	-4.00
	1.29	.56	.44	.26	3.07	1.05
5-8	0	0	0	0	0	0
	0	0	0	0	0	0
8-9	-2.75	.08	.30	-.24	-2.22	-.34
	.81	.54	.28	.09	2.16	.63
9-10	-4.60	-3.19	-1.92	-.74	-3.64	-.63
	1.37	.72	.30	.10	2.11	.56
10≤	-5.20	-6.68	-3.77	-4.23	-6.62	-4.75
	2.38	.58	.33	.86	1.13	.90

---

[a] Subclass effects are expressed as a deviation from the 5-8 yr age group within each sex of calf breed of dam group.

[b] The subclass effects are the average of the five sample files. The top line in each age group contains the average effect while the second line contains the standard error of the average effect.

TABLE 29. SUBCLASS EFFECTS FOR COMBINATIONS OF AGE OF DAM, SEX OF CALF, AND BREED OF DAM FOR 205d WEIGHT OF CALVES BORN TO F_1 SIMMENTAL COWS WITH ANGUS OR HEREFORD BACKGROUND[a][b]

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	-19.51	-24.57	-15.06	-18.46	-22.83	-26.29
	1.20	1.12	.48	.37	3.36	2.20
3-4	-10.99	-13.65	-8.90	-10.43	-13.95	-10.54
	1.75	.96	.55	.22	2.80	1.29
4-5	-4.21	-6.11	-1.96	-3.58	-2.55	-3.11
	.63	.57	.98	.98	1.51	1.53
5-8	0	0	0	0	0	0
	0	0	0	0	0	0
8-9	.40	.64	.07	-3.80	.60	2.18
	1.65	.63	1.21	.75	2.59	1.94
9-10	.32	-4.10	-1.89	-6.32	-4.19	-8.86
	1.06	.87	1.39	.96	2.84	2.99
10≤	-6.78	-10.78	-5.66	5.71	-7.83	-9.40
	2.22	1.93	2.03	1.05	2.94	2.18

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[a] Subclass effects are expressed as a deviation from the 5-8 yr age group within each sex of calf breed of dam group.

[b] The subclass effects are the average of the five sample files. The top line in each age group contains the average effect while the second line contains the standard error of the average effect.

TABLE 30. SUBCLASS EFFECTS FOR COMBINATIONS OF AGE OF DAM, SEX OF CALF, AND BREED OF DAM FOR 205d WEIGHT OF CALVES BORN TO 75% SIMMENTAL DAMS WITH ANGUS OR HEREFORD BACKGROUND[a][b]

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	-13.14	-10.15	-9.23	-10.37	-13.89	-12.36
	.27	2.08	.59	.18	1.38	1.11
3-4	-6.33	-6.38	-4.66	-4.83	-7.36	-5.98
	.52	.50	.66	.10	1.45	1.05
4-5	-2.08	-2.69	-1.75	-1.72	-5.39	-2.35
	.31	.21	.40	.28	1.06	1.15
5-8	0	0	0	0	0	0
	0	0	0	0	0	0
8-9	-.21	-1.09	-1.21	-.57	-2.57	-5.18
	.60	2.29	.39	.45	1.88	3.04
9-10	.30	-.69	-1.15	-.37	-4.78	-3.46
	1.33	.52	.28	.47	3.63	2.22
10≤	-1.27	-6.37	-1.48	3.53	-5.72	2.80
	1.95	1.49	.62	3.87	3.64	3.67

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[a] Subclass effects are expressed as a deviation from the 5-8 yr age group within each sex of calf breed of dam group.

[b] The subclass effects are the average of the five sample files. The top line in each age group contains the average effect while the second line contains the standard error of the mean effect.

nursing Angus cows were smaller in magnitude than those for heifers nursing Hereford cows less than five year of age. For heifers suckling Angus cows, age-of-dam effects were -14.0, -6.6, and -2.9 kg for ≤ 2, 3-4, and 4-5 year groups, respectively. The age-of-dam effects for heifers born to Hereford foundation dams were -14.0, -8.5, and -3.9 kg for ≤2, 3-4, and 4-5 years of age, respectively. The 50% Simmental calves born to older cows required a greater adjustment with increased cow age, irrespective of breed of foundation dam. Tong and Newman (1980) found that age-of-dam effects for heifer calves nursing Angus cows were smaller than age effects for heifers with Hereford dams after adjusting for breed of sire. Chenette and Frahm (1981) found that age-of-dam effects were similar for heifer calves nursing Angus or Hereford dams except for heifers born to cows two years of age. The age effect for Angus dams two years of age was less than for Hereford dams, compared to the mature base.

The effects of age-of-dam for steer calves nursing Angus cows were larger for all age groups compared to steers nursing Hereford dams. The difference between breeds of dam for 50% Simmental steers were the same for ≤2 and 3-4 year age groups. Estimates of age effects for steer calves with Angus dams were -19.2 kg for ≤2 yr, -19.0 kg for 3-4 yr, and -6.8 kg for 4-5 yr. For Hereford dams with 50% Simmental steers, age-of-dam effects for young cows were -11.5, -11.3, and -4.0 kg for ≤2, 3-4, and 4-5 yr, respectively. The age of dam effects for older cows increased in magnitude as dams aged, particularly for Angus cows. Estimates of age effects for steers nursing aged Angus cows were -2.2, -3.6, and -6.6 kg for 8-9, 9-10, and ≥10 yr, respectively. For the 8-9 and 9-10 yr groups, steers with Hereford dams required a much smaller adjustment to the mature base. Elzo et al. (1987b) determined the age-of-dam effects for steer calves born to base dams in the Simmental population were generally intermediate between bull and heifer calves.

The age-of-dam effects for 75% Simmental bulls nursing ½ Simmental-½ Angus dams were smaller than those for bulls with ½ Simmental-½ Hereford dams for cows less than five yr of age. The estimates for age effects for bulls with F_1 Simmental cows with an Angus base were -19.5, -11.0, and -4.2 kg for ≤2, 3-4, and 4-5 yr groups, respectively. For bulls nursing ½ Simmental-½ Hereford dams, age-of-dam estimates were -24.6 kg for ≤2 yr, -13.7 kg for 3-4 yr, and -6.1 for 4-5 yr. For cows older than eight years of age raising bull calves, the age-of-dam effects were smaller for cows with an Angus base than for those with a Hereford base. For F_1 Simmental cows with Hereford breeding, age-of-dam effects were .6, -4.1, and -10.8 kg for 8-9, 9-10, and ≥10 yr of age.

The same trends in age effects were found for heifers suckling young F_1 Simmental cows with Angus or Hereford breeding. For 75% Simmental heifers born to ½ Simmental-½ Angus dams, the adjustment to a mature base was less than for heifers nursing F_1 Simmental cows with a Hereford base. Estimates of age effects were -15.0, -8.9, and -2.0 kg for ≤2, 3-4, and 4-5 yr, respectively, for heifers born to ½ Angus cows. The age-of-dam effects for heifers born to F_1 Simmental dams with Hereford breeding were -18.5 kg for ≤2 yr, -10.4 kg for 3-4 yr, and -3.6 kg for 4-5 yr. Age effects on 205d weight for older cows indicated that calves born to ½ Simmental cows with Angus breeding generally required less adjustment than their counterparts born to ½ Simmental cows with Hereford breeding.

The effects of age of cow on 205d weight for bulls and heifers were essentially the same for steers nursing F_1 Simmental cows. Except for the 3-4 yr age group, steers born to young ½ Simmental-½ Angus cows required less adjustment to a mature base than steers nursing ½ Simmental-½ Hereford dams. For 75% Simmental steers with ½ Angus dams, age-of-dam estimates were -22.8, -13.9, and -2.6 kg for ≤2, 3-4, and 4-5 yr, respectively. The age-of-dam effects for steers from ½ Hereford dams were -26.3, -10.5, and -3.1 kg for ≤2, 3-4, and 4-5 yr, respectively. For older ½ Simmental cows, calves nursing cows with Angus breeding required less adjustment back to the mature base than calves with ½ Hereford cows. For calves in all three sex classifications, calves nursing young ½ Simmental-½ Angus dams required less adjustment to a mature base than calves with ½Simmental-½Hereford dams. This would indicate that F_1 Simmental cows with an Angus base were better able to meet the nutritional needs of their 75% Simmental offspring than F_1 Simmental cows with Hereford breeding. Notter et al. (1978) indicated that ½ Simmental-½ Angus dams two years of age had somewhat higher milk production than ½ Simmental-½ Hereford dams over a 187d period.

For young Simmental cows with greater than 75% Simmental breeding and bull calves, few differences were found for age of dam effects between the base breeds of dam. The age-of-dam effects for bulls born to second backcross Simmental cows with an Angus base were -13.1 kg for ≤2 yr, -6.3 kg for 3-4 yr, and -2.1 kg for 4-5 yr. For bulls from Simmental cows of Hereford ancestry, age of dam effects were -10.1, -6.4, and -2.7 kg for ≤2, 3-4, and 4-5 yr of age, respectively. For cows of both breed ancestries over eight years, age-of-dam effects were generally inconsistent and plagued by large standard errors. The overall trend indicated that bull calves born to older cows required a greater adjustment to a mature base, irrespective of base breed.

The age-of-dam effects for heifer calves were similar across dam breed groups. For heifers born to young 75% Simmental cows with an Angus base, age effects were -9.2, -4.7, and -1.7 kg for ≤2, 3-4, and 4-5 yr of age, respectively. The estimates of age effects were -10.4, -4.8, and -1.7 kg for ≤2, 3-4, and 4-5 yr, respectively, for heifer calves nursing Simmental cows with Hereford ancestry. The trends in age-of-dam effects for cows older than eight years of age were variable, reflecting the variation between samples, particularly for heifers nursing cows with some Hereford breeding.

For steers nursing young 75% Simmental dams, calves born to cows with an Angus base required a slightly larger adjustment than calves from Simmental cows with Hereford breeding. Age-of-dam effects were -13.9, -7.4, and -5.4 kg for ≤2, 3-4, and 4-5 yr, respectively, for steers with Simmental dams derived from an Angus base. For steers nursing Simmental dams with Hereford breeding, age of dam effects were -12.4 kg for ≤2 yr, -6.0 kg for 3-4 yr, and -2.3 kg for 4-5 yr relative to the mature base of 5-8 yr. The age effects for older cows indicated that steers born to Simmental cows with Angus breeding required a larger adjustment with increases in age-of-dam. A similar trend could not be detected for cows with

Hereford breeding over eight years of age. For both base breeds, the age-of-dam effect for older dams had large standard errors, reflecting the greater variation between sample estimates. The data indicate that the effects of breed of foundation dam on 205d weight were unimportant for cows with 75% or more Simmental breeding. After two or more consecutive backcrosses, the base breed of dam should have little impact on calf performance. Kress et al. (1984) found no difference in calf performance between 50% Simmental cows and 75% Simmental cows, each group derived from a Hereford base population.

IV.3. Discussion of Interaction of Sires and Breeds of Dams

An interaction between Simmental sires and breeds of dams was not a significant factor influencing birth weight. The average estimates of the interaction variance in data from F_1 and 75% Simmental dams with Angus or Hereford base were less than 1% of the phenotypic variance. Sires tended to be evaluated the same across breeds of dams, particularly when evaluated across the F_1 Simmental groups.

The interaction of sires and breeds of dams accounted for 1.5% of the total variance in birth weight on average. The average sire variance was responsible for 2.9% of the variance and was 1.9 times greater than the interaction variance. The largest variation among sample estimates of the interaction variance component occurred with birth weight of 50% Simmental calves. Estimates of the interaction variance ranged from .03 to .85 kg^2. The largest estimate of the variance for interaction of sires and breeds of dams was almost three times larger than the sire variance for that sample. The results indicate that sampling of sires created two sets of data which contributed to the interaction. Overall, the sire by breed of dam interaction was not an important factor in birth weight of 50% Simmental calves.

For F_1 Simmental dams with Angus or Hereford base, the interaction of sires and breeds of dams did not have a significant effect on birth weight. The average sire variance was almost eleven times larger than the interaction variance and accounted for 7.2% of the phenotypic variance. The interaction variance was very small on average, accounting for only .7% of the total variance. Differences between ½ Simmental dams with Angus or Hereford breeding were not an influential factor on the evaluation of Simmental sires. Estimated correlations between sire EPDs and ranks across breeds of dam all were greater than .95.

The conclusions drawn from the estimates from F_1 Simmental dams were applicable for estimates obtained from 75% Simmental dams. The variance for interaction of sires and breeds of dams was less than 1% of the total variance in birth weight. Compared to the interaction variance, the sire variance was 8.5 times larger in magnitude and accounted for 7.6% of the total variance. The genetic correlation between sires' breeding value across breed groups was strong, equaling .88. The interaction between sires and breeds of dams did not influence the evaluation of sires across groups. The average simple, Spearman rank, and top-down correlations were .94, .90, and .92, respectively.

The interaction of sires and breeds of dams was not important for 205d weight in Simmental field data. As would be expected, the magnitude of the interaction variance component decreased as the percentage Simmental breeding increased in the dams. Within each percentage group, some variability existed between the five sets of sample estimates of variance components, genetic parameters, and correlations between sires' estimated progeny differences and ranks. When sample estimates within each Simmental group were averaged, the average estimates indicated that a interaction of sires and breeds of dams was not an important factor in Simmental field data.

For 50% Simmental calves born to Angus and Hereford dams, the interaction of sires with breed of dam accounted for 1.4% of the total variance in 205d weight. The sire variance accounted 6.0% of the total variance and was 4.3 times larger in magnitude than the interaction variance on average. The genetic correlation was approximately .80 for sires' breeding values across Angus and Hereford dams. The average product-moment correlation between sires' expected progeny differences (EPD) across breeds was .90, indicating that sires tended to be evaluated similarly when progeny were from Angus or Hereford cows. The Spearman rank and top-down correlations were .91 and .87 on average. The rank correlations indicated that gross changes in rank were not occurring across breeds of dam.

On average, the variances for sires and interaction of sires with breeds of dams accounted for 6.7 and 1.0%, respectively, of the total variance in 205d weight for calves born to F_1 Simmental cows. The genetic correlation between sires' breeding values across F_1 Simmental cows with Angus or Hereford base was .85. The average product-moment correlation was .94 between sires' EPDs across ½ Simmental-½ Angus and ½ Simmental-½ Hereford dams. Rankings were similar across breed-of-dam groups, as indicated by a Spearman rank correlation estimate of .91. The average top-down correlation was .91, which indicated that sires in the upper percentile groups tended to be ranked similarly across groups.

For dams with 75% Simmental breeding and Angus or Hereford base, the average of estimates of the variance for interaction of sires and breeds of dams was very small. The interaction variance accounted for less than 1.0% of the phenotypic variance in 205d weight. The sire variance was responsible for 9.0% of the total variance and was 10.4 times larger than the interaction variance. The genetic correlation was .91 between sires' breeding values across breed of dam. The average product-moment correlation between sires' EPDs across 75% Simmental dam groups was .98, which provided evidence that base breed of dam had little influence on sire evaluation for 205d weight. Sires were similarly ranked across breed as shown by a Spearman rank correlation estimate of .94. The average top-down correlation was .96, indicating that ranking of top sires did not change across the two groups of 75% Simmental cows with Angus or Hereford base.

Benyshek (1979) postulated that an interaction of sires and breeds of dams could be caused by interaction of genotypes with environments or with other genotypes. The interaction of genotypes with environments would be caused by differences in maternal environment provided to the calf by the different breeds of dam. Genetic differences between breeds of dam for either weight trait could result in an interaction among genotypes. An interaction among genotypes would be due to effects of dominance or epistatic resulting in different levels of heterosis. If interaction of sires and breeds of dams were important and a result of an interaction among genotypes, then sires could be identified that had higher specific combining ability for one breed of dam than for another. In other words, sires could be found that "nicked" well with specific breeds.

The Angus and Hereford breeds are known to differ in genetic ability for growth and maternal effects. The maternal effects for birth weight would be expressed as part of the uterine environment. For 205d weight, maternal effects would include milk production and possibly other factors. If differences between breeds of dam were important, evaluating sires based on progeny of 50% Simmental breeding from two distinct breeds of dam should reveal those effects on sires' proofs. If maternal ability in one breed simply results in a higher level of calf performance, then sires should be ranked the same across breeds of dam. Scale effects as indicated by differences in sire variances across breeds of dam would probably reflect an interaction. Cundiff et al. (1975) found no significant difference between breeds for genetic variance except for birth weight. An interaction due to different types of gene action is virtually impossible to detect because of the nonrandom mating occurring in field data. Different levels of specific heterotic effects may occur on a breed level due to crossing different breeds of beef cattle (Comerford et al., 1987; Comerford et al., 1988). No evidence exists from experimental herds (Gregory et al., 1965;

Koger et al., 1975) to suggest that specific combining ability occurs among sires. Dunn (1968) showed that the correlation between sires' breeding values across purebred and crossbred progeny for beef cattle performance traits was very high.

For calves of 75% Simmental breeding nursing F_1 Simmental dams with Angus or Hereford base, differences between dam breeds could be caused by differences between levels of maternal ability, or maternal heterosis caused by cows that are F_1 crosses. Indirectly, an interaction of sires and breeds of dams could be caused by nonrandom mating based on sire and maternal grandsire. If differences in maternal ability or levels of maternal heterosis cause changes in level of performance, then sires would be ranked the same across groups. As with comparing Angus and Hereford dam groups, all sires should benefit by an increase in performance across dam groups. If an interaction was important, changes in sire variances across groups should occur. Nonrandom mating of sires and dams does occur, based on analyses of field data from Polled Hereford, Limousin, Simmental and Angus breeds(Bertrand et al., 1985; Bertrand et al., 1987; Elzo et al., 1987a; and Zollinger and Nielsen, 1984). Interactions of sires and contemporary groups have been detected within Polled Hereford, Limousin, and Simmental breeds. (Bertrand et al., 1985; Bertrand et al., 1987; Burfening et al., 1982; and Tess et al., 1979). The investigators have hypothesized that such an interaction could be due to nonrandom mating or preferential treatment of progeny groups. An interaction of sires and breeds of dams may result from mating sires to specific breeds of dam (Miller, 1986).

For progeny born to dams of 75% Simmental breeding, the effects of base breed of dam should decrease sharply after two generations of backcrossing with Simmental. The effects due to maternal environment or different levels of heterosis should not be large enough to cause a large difference in performance between groups. Since the 75% Simmental group contains not only cows with 75% Simmental breeding, but also those with 7/8ths and 15/16ths Simmental breeding. With third and fourth generation backcross Simmental cows, the chance of base breed of dam influencing prediction of sires' breeding values would be very remote.

The analysis of the three groups of dams that an interaction of sires with breeds of dams was the largest for foundation dams and the smallest for 75% Simmental dams. Even for foundation dams, the interaction accounted for only 1.5 and 1.4% of the total variance in birth weight and 205d weight, respectively. If effects of foundation breed of dam were important, the effect on evaluation of sires across breeds should be caused only by changes in scale. The type of analysis used in this study did not allow for estimation of sire variances within breeds so the effects of scale could not be determined. Estimates of correlations between sires' EPDs and ranks indicated generally good agreement across breeds of dams for evaluation of Simmental sires. For both weight traits studied in the American Simmental population, an interaction of sires and breeds of dams was not found to be large enough to merit inclusion in a sire evaluation program.

V. Summary and Conclusions

The introduction of European breeds of cattle resulted in sires being mated to a population of cows with diverse genetic makeup. The process of repeated backcrossing or "grading up" was used to establish purebred herds of these breeds in the United States and Canada. As a result, sires would be evaluated based on progeny of dams of varying breed composition. The purpose of this work was to study the effects of an interaction of sires and breeds of dams on genetic parameters and evaluation of sires for birth weight and 205d weight in Simmental field data.

The performance records of 905,118 Simmental calves were supplied by the American Simmental Association in cooperation with the Animal Breeding Group at Cornell University. The data were used to investigate an interaction of sires and breeds of dams for birth weight and 205d weight in the U. S. Simmental population. Because of the numerous breed combinations, the breeds used in this study were restricted to Angus, Hereford, and Polled Hereford. For this study, dams with Polled Hereford breeding were grouped with those of Hereford based dams. The variance components for sire, interaction of sires and breeds of dams, and error were estimated within three dam groups: foundation, F_1 Simmental and 75% Simmental. The variance component estimates were used to estimate heritabilities across and within breeds of dams and genetic correlations between sires' breeding values across breeds of dams. Also, the evaluation and ranking of bulls across breeds of dams were studied by computing expected progeny differences within breeds of dams for each sire. Subclass effects for combinations of age-of-dam, sex-of-calf, and breed-of-dam were estimated to evaluate differences in effects of age-of-dam and sex-of-calf caused by varying breed composition of dams.

For calves of 50% Simmental breeding born to Angus or Hereford foundation dams, estimated variance components for sires and interaction of sires and breeds of dams accounted for 2.8 and 1.5% of the total variance in birth weight. The heritability estimates across and within breeds of dams were .12 and .17, respectively. The genetic correlation between sires' breeding values across Angus and Hereford dams was .74 on average. The simple correlation between sires' EPDs across foundation breeds of dam was .83. Sire ranking was fairly stable across Angus and Hereford groups as indicated by Spearman rank correlation of .87 and top-down correlation of .85.

The variance components for sires and interaction of sires with breeds of dams were accountable for 7.5 and .67% of the total variance in birth weight when calves were born to F_1 Simmental dams of Angus or Hereford base. When expressed on across and within breeds of dams, estimated heritabilities were .29 and .31, respectively. The genetic correlation was .90 between sires' breeding values across F_1 Simmental groups. The estimates of the simple correlation, Spearman rank, and top down correlation were greater than .95, indicating that sires were evaluated and ranked essentially the same across dam groups.

Estimates of variance components for sires and interaction of sires and breeds of dams in the 75% Simmental dam group accounted for 7.5 and .9% of the total variance in birth weight. Across and within breeds of dams heritability estimates were .3 and .34, respectively. The genetic correlation between sires' breeding values across 75% Simmental groups with Angus or Hereford base was .88. Estimates of the product-moment, Spearman rank, and top down correlations were .94, .90, and .92, respectively, indicating good agreement across 75% Simmental groups for evaluating and ranking of bulls.

Calves born to young foundation Angus cows required less adjustment to a mature base compared to calves born to Hereford females, regardless of sex. The differences in age-of-dam effects between dams of Angus or Hereford breeding decreased as percentage of Simmental breeding in the dam increased from 0 to 75%. Also, differences between cows of Angus or Hereford breeding for age of dam effects were similar for bull and heifer calves.

The variance components for sires and interaction of sires and breeds of dams accounted for 6.0 and 1.4% of the total variance in 205d weight for foundation Angus and Hereford dams. Heritability estimates were well within the range of published values. Estimates across and within breed of dam were .24 and .29, respectively. The genetic correlation between sires' breeding values across Angus and Hereford dams was .76. Evaluation and ranking of sires for 205d weight based on progeny from Angus and Hereford dams agreed well, with the simple, Spearman rank, and top-down correlations being .90, .90, and .87, respectively.

For F_1 Simmental dams with Angus or Hereford base, sire and interaction variances were responsible for 6.7 and 1.1% of the total variance in 205d weight. Heritabilities across and within breeds of dams were .27 and .31, respectively. The estimated genetic correlation was .83 for sires' breeding values across ½Simmental-½Angus and ½Simmental-½Hereford dams. The product-moment, Spearman rank, and top down correlations were .94, .90, and .91, respectively, indicating that sires were evaluated and ranked essentially the same across dam groups.

The sire and interaction variance components for 205d weight in the 75% Simmental group accounted for 8.9 and .85% of the total variance. Compared to estimates obtained in the foundation and F_1 Simmental groups, heritabilities across and within breeds were higher, equaling .36 and .39, respectively. The genetic correlation between sires' breeding values across 75% Simmental cows with Angus or Hereford base was .86. The estimates of the simple, Spearman rank, and top down correlation all were greater than .94.

Age-of-dam effects for 205d weight for calves born to young foundation cows indicated that bull and heifer calves nursing Angus cows required less adjustment to a mature basis than calves with Hereford dams. The exceptions were for bull calves nursing two yr old Angus cows and steers with Angus dams. For F_1 Simmental dams, calves with dams of Angus breeding required less adjustment to a mature base than calves with dams of Hereford breeding. This was true regardless of sex of calf. The effect of base breed of dam had little effect on age-of-dam effects for bull, heifer and steer calves with 75% Simmental dams. Within each combination of sex and breed of dam, age-of-dam effects were similar in magnitude for cows with at least 75% Simmental breeding.

For both weight traits, estimates of the sire variance increased as percentage Simmental breeding increased in the dam. As expected, the magnitude of the variance component for the interaction of sires and breeds of dams decreased with increased levels of Simmental breeding. Reduction in the size of the interaction variance was caused by decreased influence of the base breed of dam through successive generations of repeat backcrossing. Heritability of birth weight and 205d weight increased with increased levels of Simmental breeding in the dam. The agreement of evaluation and ranking of bulls across groups with Angus or Hereford breeding improved with increased percentage Simmental breeding. In the analysis of birth weight, estimates of the error variance decreased as the percent Simmental increased in the dam. The error variance component for 205d weight increased slightly from the foundation dam group to the F_1 Simmental group. When the level of Simmental breeding increased from 50 to 75% in the dam, the average error variance decreased from 663 to 551 kg^2. One would expect the variance to become larger with increased mean performance.The reason for the error variance to decrease as level of mean performance increased is unknown. It may be due to chance sampling or an artifact of the analysis.

Based on these results, if an interaction of sires and breeds of dams was important in Simmental field data, it would probably occur with calves of 50% Simmental breeding born to foundation breed dams. The data indicate that as percent Simmental in the dam increases, the differences due to base breeds of dam decrease. For birth weight and 205d weight, the variance for the interaction of sires and breeds of dams in calves from foundation Angus and

Hereford dams accounted for only 1.5% of the total variance. Bulls were similarly ranked and evaluated across Angus and Hereford groups within each percent Simmental group. From the evidence available, one should conclude that interaction of sires and breeds of dams do not merit inclusion in models for the Simmental sire evaluation system.

TABLE A1. BREEDS OF DAM IN THE AMERICAN SIMMENTAL POPULATION

Breed of Dam	Letter Code	Number Code
Simmental	SM	1
Angus	AN	2
Hereford (Horned)	HH	3
Hereford (Polled)	HP	4
Charolais	CH	5
Africander	AF	6
Red Angus	AR	7
Ayshire	AY	8
Barzona	BA	9
Blonde D' Aquitane	BD	10
Beefalo	BE	11
Buffalo (Bison)	BF	12
Belted Galloway	BG	13
Braford	BO	14
Bos Indicus	BI	15
Beefmaster	BM	16
Brangus	BN	17
Brahman	BR	18
Brown Swiss	BS	19
Bos Taurus	BT	20
Chianina	CA	21
Charbray	CB	22
Devon	DE	23
Dexter	DR	24
Galloway	GA	25
Guernsey	GU	26
Gelbvieh	GV	27
Hayes Converter	HC	28
Holstein	HO	29
Red Holstein	HR	30
Jersey	JE	31
Limousin	LM	32
Lincoln Red	LR	33
Luing	LU	34
Maine-Anjou	MA	35
Murray Gray	MG	36
Meuse-Rhine-Ijssel	MI	37
Marchigiani	MR	38
Milking Shorthorn	MS	39
Mixed	MX	40
Normande	NM	41
Norwegian Red	NR	42

TABLE A1. CONTINUED

Breed of Dam	Letter Code	Number Code
Pinzgauer	PZ	43
Red Brangus	RB	44
Red Dane	RD	45
Romangola	RN	46
Red Poll	RP	47
Romana Red	RR	48
Salers	SA	49
South Devon	SD	50
Santa Gertrudis	SG	51
Scotch Highland	SH	52
Commercial Simmental	CS	53
Polled Shorthorn	SP	54
Shorthorn	SS	55
Sussex	SX	56
Tarentaise	TA	57
Texas Longhorn	TX	58
Welch Black	WB	59
Zebu	ZB	60
Brown Swiss (Milking)	SB	61
Senapole	SE	62
Commercial Simmental	CS	99

TABLE A2. DISTRIBUTION OF CALVES ACROSS AGE OF DAM•SEX OF CALF•BREED OF DAM SUBCLASSES FOR BIRTH WEIGHT: FOUNDATION ANGUS AND HEREFORD DAMS

	Bull		Heifer	
Age of Dam	Angus	Hereford	Angus	Hereford
≤2	134	320	525	1,225
3	361	732	1,223	2,854
4	481	1,250	1,817	4,173
5-8	2,059	5,169	7,206	15,864
8-9	485	1,412	1,466	5,334
9-10	359	1,132	1,083	2,833
10≤	670	1,995	2,180	5,783

TABLE A3. DISTRIBUTION OF CALVES ACROSS AGE OF DAM•SEX OF CALF•BREED OF DAM SUBCLASSES FOR BIRTH WEIGHT: F_1 SIMMENTAL DAMS WITH ANGUS OR HEREFORD BACKGROUND

	Bull		Heifer	
Age of Dam	Angus	Hereford	Angus	Hereford
≤2	2,492	6,185	5,531	11,885
3	1,496	4,115	2,943	7,170
4	1,346	2,410	3,667	5,626
5-8	2,464	6,971	3,690	9,789
8-9	450	1,172	586	1,429
9-10	308	782	426	879
10≤	383	729	532	1,080

TABLE A4. DISTRIBUTION OF CALVES ACROSS AGE OF DAM·SEX OF CALF·BREED OF DAM SUBCLASSES FOR BIRTH WEIGHT: 75% SIMMENTAL DAMS WITH ANGUS OR HEREFORD BACKGROUND

	Bull		Heifer	
Age of Dam	Angus	Hereford	Angus	Hereford
≤2	4,698	10,957	6,842	15,119
3	2,699	5,909	3,655	8,064
4	2,146	4,740	2,878	6,112
5-8	3,566	7,658	4,513	9,794
8-9	472	865	591	1,162
9-10	257	419	314	543
10≤	147	245	240	362

TABLE A5. DISTRIBUTION OF CALVES ACROSS AGE OF DAM•SEX OF CALF•BREED OF DAM SUBCLASSES FOR WEANING WEIGHT: FOUNDATION ANGUS AND HEREFORD DAMS

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	87	330	819	2,421	34	129
3	307	787	2,328	5,563	137	297
4	403	1,224	3,658	8,371	212	544
5-8	1,533	4,745	16,776	31,467	1,069	2,292
8-9	340	1,366	2,765	7,234	250	568
9-10	245	1,005	2,040	5,257	200	475
10≤	404	1,685	3,298	8,473	386	744

TABLE A6. DISTRIBUTION OF CALVES ACROSS AGE OF DAM•SEX OF CALF•BREED OF DAM SUBCLASSES FOR WEANING WEIGHT: F_1 SIMMENTAL COWS WITH ANGUS OR HEREFORD BASE

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	2,525	6,761	9,499	18,705	607	1,214
3	1,461	4,344	5,355	11,436	467	979
4	1,191	3,828	4,047	8,888	418	769
5-8	2,256	7,207	5,705	14,233	726	1,305
8-9	453	1,147	850	2,016	118	173
9-10	327	749	595	1,156	77	119
10≤	353	644	658	1,071	121	125

TABLE A7. DISTRIBUTION OF CALVES ACROSS AGE OF DAM•SEX OF CALF•BREED OF DAM SUBCLASSES FOR WEANING WEIGHT: 75% SIMMENTAL COWS WITH ANGUS OR HEREFORD BASE

	Bull		Heifer		Steer	
Age of Dam	Angus	Hereford	Angus	Hereford	Angus	Hereford
≤2	4,209	10,569	8,334	18,592	688	1,202
3	2,576	6,045	4,640	10,191	352	571
4	2,090	4,788	3,519	7,650	263	473
5-8	3,375	7,617	5,648	12,117	464	748
8-9	409	814	692	1,372	73	92
9-10	198	385	361	656	44	47
10≤	114	187	220	336	29	34

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