Consideration of Sire Relationships for Estimation of Variance Components with Interaction of Herd and Sire[1]

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ABSTRACT

Effects of sire relationships for sire and interaction of herd and sire were examined using simulation and minimum variance quadratic unbiased estimates of variance components. Data were simulated for 50 herds and 20 sires for five sire relationship matrices, three data structures, and three interaction levels. A total of 1000 replicates were simulated for each combination of relationship matrix, data structure, and interaction level. The minimum variance quadratic unbiased estimates were calculated for the true (simulation) model, for models ignoring relationships for sires and interaction, and for models excluding interaction of herd and sire. Interaction variance was underestimated when relationships were ignored. Underestimation increased with sire relatedness. Sire variance and heritability estimates increased when variance components were estimated using sire models compared with estimates using interaction models. This overestimation increased with interaction level simulated in the data and as the data were more unbalanced. Estimates of sire variance were as much as 2.7 times larger than that expected, and heritability estimates were as much as 2.8 times larger than that expected.

(**Key words**: sire relationships, variance components, interaction of herd and sire)

Abbreviation key: G × E = interaction of genotype and environment, H × S = interaction of herd and sire, MIVQUE = minimum variance quadratic unbiased estimator, and MME = mixed model equations.

INTRODUCTION

Genetic effects are assumed to behave consistently across treatments, herd levels, or other environmental factors in most animal breeding models. When this assumption is violated, an interaction of genotype and environment (G × E) exists, and appropriate analysis is more complex. Studies of the correlation of breeding values estimated from multiple environments (i.e., herds, regions, or countries) (1, 11, 16, 19, 24) have found little evidence of G × E for milk yield in dairy cattle. Variance for interaction of herd and sire (H × S), usually estimated using Henderson's (5) method 1 or method 3, ranged from .2 to 10% of total variance (9, 10, 13, 23). For British Friesians, Meyer (12) used REML to estimate environmental correlations, which ranged from 2.1 to 4.2% of the total phenotypic variance, and concluded that environmental correlation was important for sire evaluations based on observations from only a few herds.

The effect of individual herds has become a concern for animal breeding because of the potential for preferential treatment of animals in a small number of herds affecting sire evaluations. If G × E is included in a statistical model, the influence of observations from any single environment on genetic prediction is limited, and the range of predictors is reduced (14). Although the influence of a single environment is limited by the addition of G × E to an evaluation, this addition should not greatly affect animals represented in many environments, such as AI sires. Despite noting that true H × S was not likely to be a concern, Norman (15) recommended inclusion of H × S in the form of an environmental correlation to limit the effect of preferential treatment.

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Foulley and Henderson (4) modified the multiple-trait model suggested by Quaas and Pollak (17) to allow for the use of known relationships to predict H × S effects and, more importantly, to estimate H × S variance components. Inclusion of these relationships is computationally more difficult. However, H × S effects for related sires may be correlated because the interaction might be a function of the genetic component shared by relatives.

The purpose of this study was to examine the effects of ignoring H × S and ignoring sire relationships on estimation of variance components when interaction was present in the data. Simulation was used to examine the effects of interaction, relationship, and data structure on biases in estimates of variance components.

MATERIALS AND METHODS

Simulation

A total of 1000 replicates of each combination of three data structures, five relationship matrices, and three interaction levels were generated using simulation.

Data Structures. The term data structure is used to describe a distribution of observations with respect to sires and herds that is repeatedly used to simulate data with a variety of underlying parameters (i.e., a data structure defines the incidence of the data but not the actual observations). For this study, three data structures were used, each of which had 20 sires with daughters in 50 herds. The data structures differed in the fraction of herd-sire subclasses filled. Data structure 1 represented nearly balanced data; all sires had daughters in all herds, and the number of daughters was nearly constant. For the second data structure, 25% of herd-sire subclasses were filled, corresponding to moderately unbalanced data. For the last data structure, only 10% of the herd-sire subclasses were filled, as an example of severely unbalance data. The expected number of observations totaled 2000 for all three structures. Simulation parameters and observed values are presented in Table 1.

TABLE 1. Simulation parameters and observed values for generating data structures, including proportion of filled subclasses (P), mean daughters per filled subclass (M), and the total number of observations (n).

Data structure		P	M	n
1	Simulated[1]	1.00	2.00	2000
	Observed[2]	1.00	2.02	2015
2	Simulated	.25	8.00	2000
	Observed	.26	7.64	1994
3	Simulated	.10	20.00	2000
	Observed	.12	20.70	2401

[1] Parameters used to generate data structure.

[2] Observed from data generated.

Connected data, as described by Searle (21), was ensured by the use of an algorithm described by Fernando et al. (3) because disconnected data may influence estimation of variance components (20). If the data were disconnected, a new data structure was generated and tested to ensure connected data. This procedure was repeated until a completely connected data structure was generated.

Sire Relationships. Five sire relationship matrices were used to simulate records for daughters of bulls. The first three relationship structures were for differently sized half-sib sire groups. Let $\mathbf{H}_n$ be defined as $\frac{3}{4}\mathbf{I}_n + \frac{1}{4}\mathbf{J}_n$, where $\mathbf{I}_n$ is an n × n identity matrix, and $\mathbf{J}_n$ is an n × n matrix with all elements equal to 1. The first relationship matrix was for 10 pairs of half-sib sires; then $\mathbf{A}_1 = \mathbf{I}_{10} \otimes \mathbf{H}_2$, where ⊗ denotes the direct or Kronecker product [see Searle (22) for discussion of the direct product operator]. The second set of relationships was for four sets of five half-sib sire groups, or $\mathbf{A}_2 = \mathbf{I}_4 \otimes \mathbf{H}_5$. The last structured relationship matrix was for 20 half-sib sires, i.e., $\mathbf{A}_3 = \mathbf{H}_{20}$.

The last two relationship matrices were generated from data representative of the current population of AI sires in the US. The inverse of Wright's numerator relationship matrix for 334 sires was obtained from the data used for the national calving ease evaluation. This matrix was inverted to obtain the numerator relationship matrix. The fourth relationship structure was generated by random selection of 20 sires from 100 young sires in the list of 334. None of the 100 sires had sons or grandsons in the data, so those sires were representative of the degree of relatedness among young sires that were progeny tested by AI organizations. The fifth relationship matrix was created by randomly choosing 20 sires from all of the 334 sires in the data.

Because Wright's numerator relationship matrix is positive definite (7), it can be factored using a Cholesky decomposition so that

$$\mathbf{A}_i = \mathbf{L}_i\mathbf{L}_i', \; i = 1, 2, \ldots, 5, \qquad [1]$$

where $\mathbf{L}_i$ is a lower triangular matrix. Each relationship matrix was decomposed using the Cholesky decomposition algorithm described by Burden et al. (2).

Interaction Levels. Data were simulated using three levels of interaction variance: 5, 15, and 25% of the total variance. Sire and total variance were constant for all data sets; however, residual variance decreased as interaction variance increased. Sire variance accounted for 6.25% of the total variance, resulting in a constant heritability equal to .25 for all of the data sets.

Data Simulation. The model used to simulate the data was

$$\begin{aligned} \mathbf{y} &= \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}, \\ \mathbf{u}' &= [\mathbf{u}_1'|\mathbf{u}_2'], \text{ and} \\ \mathbf{Z} &= [\mathbf{Z}_1|\mathbf{Z}_2], \end{aligned} \qquad [2]$$

where $\mathbf{y}$ is a vector of observations, $\mathbf{b}$ is a vector of fixed herd effects, $\mathbf{u}_1$ is a vector of random sire effects, $\mathbf{u}_2$ is a vector of random interaction effects, and $\mathbf{e}$ is a vector of random residual effects. The matrices $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are appropriately dimensioned incidence matrices.

If numerator relationship matrix i is denoted as $\mathbf{A}_i$, then let $\overline{\mathbf{A}}_i = \mathbf{I}_h \otimes \mathbf{A}_i$. Then $\overline{\mathbf{A}}_i$ is the covariance of H × S effects within herd resulting from relationships among sires. These simplifying assumptions were used for expected values and variance structure for the random variables: let $\mathbf{V} = \mathbf{V}_0\sigma_0^2 + \mathbf{V}_1\sigma_1^2 + \mathbf{V}_2\sigma_2^2$, where σ_0^2, σ_1^2, and σ_2^2 are the residual, sire, and interaction components of variance, respectively, and $\mathbf{V}_i = \mathbf{Z}_i\mathbf{G}_i\mathbf{Z}_i'$, with $\mathbf{Z}_0 = \mathbf{I}_n$, $\mathbf{G}_0 = \mathbf{I}_n$, $\mathbf{G}_1 = \mathbf{A}$, $\mathbf{G}_2 = \overline{\mathbf{A}}$. Then $\mathbf{V}_0 = \mathbf{I}_n$, $\mathbf{V}_1 = \mathbf{Z}_1\mathbf{A}\mathbf{Z}_1'$, and $\mathbf{V}_2 = \mathbf{Z}_2\overline{\mathbf{A}}\mathbf{Z}_2'$.

$$E\begin{bmatrix} \mathbf{y} \\ \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$V\begin{bmatrix} \mathbf{y} \\ \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{e} \end{bmatrix} =$$

$$\begin{bmatrix} \mathbf{V} & \mathbf{Z}_1\mathbf{A}\sigma_1^2 & \mathbf{Z}_2\overline{\mathbf{A}}\sigma_2^2 & \mathbf{I}\sigma_0^2 \\ \mathbf{A}\mathbf{Z}_1'\sigma_1^2 & \mathbf{A}\sigma_1^2 & 0 & 0 \\ \overline{\mathbf{A}}\mathbf{Z}_2'\sigma_2^2 & 0 & \overline{\mathbf{A}}\sigma_2^2 & 0 \\ \mathbf{I}\sigma_0^2 & 0 & 0 & \mathbf{I}\sigma_0^2 \end{bmatrix}.$$

Herd effects were simulated using a random number generator with a normal distribution supplied by Meyer (1989, unpublished data). Herd variance was 36% of the total variance of the random effects. Herd effects were independently and identically distributed and were uncorrelated with other effects in the model.

Sire effects were simulated by generating a vector of independent standard normal deviates, $\mathbf{r}$, and computing the vector of sire effects as $\mathbf{u}_1 = \mathbf{L}_i\mathbf{r}\sigma_1$, where $\mathbf{L}_i$ is the decomposition matrix described in Equation [1]. Then $V(\mathbf{u}_1) = \mathbf{L}_iV(\mathbf{r})\mathbf{L}_i' = \mathbf{L}_i\mathbf{I}\mathbf{L}_i'\sigma_1^2 = \mathbf{A}_i\sigma_1^2$. The H × S was simulated using a similar procedure so that $V(\mathbf{u}_2) = \overline{\mathbf{A}}\sigma_2^2$. The right-hand sides of the mixed model equations and the sum of squared observations, $\mathbf{y}'\mathbf{y}$, were calculated as the data were simulated.

Variance Component Estimation

Minimum variance quadratic unbiased estimation (MIVQUE) was used to estimate variance components because 1) MIVQUE does not require iteration, and the expectations of the quadratic forms are identical for replicates of the same data structure, model, and prior estimate of the variance components; 2) MIVQUE provides the minimum variance estimate of variance components when the true model and variance components are used (both are known in this study because the data were simulated); and 3) MIVQUE is unbiased when the correct model is used, so bias that is due to an incorrect model may be estimated by comparison of the unbiased estimates with those obtained using the incorrect model.

Variance components were estimated for five models described in Table 2. The two simplest models (models 1 and 2) consider only sire and residual variance, whereas the remaining models include interaction variance. Models 1 and 2 are referred to as sire models, and models 3, 4, and 5 are designated as interaction models. Within the sire and interaction model types, the models differed by the way that sire relationships were included when variance components for sire and interaction were estimated.

When sire models were used to analyze the data, the residual variance was redefined as the sum of the residual and interaction components used for the simulation.

The mixed model equations (MME) for interaction models were

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z_1} & \mathbf{X'Z_2} \\ \mathbf{Z_1'X} & \mathbf{Z_1'Z_1} + \mathbf{G_1^{-1}}\tilde{\alpha}_1 & \mathbf{Z_1'Z_2} \\ \mathbf{Z_2'X} & \mathbf{Z_2'Z_1} & \mathbf{Z_2'Z_2} + \mathbf{G_2^{-1}}\tilde{\alpha}_2 \end{bmatrix} \begin{bmatrix} \tilde{\mathbf{b}} \\ \tilde{\mathbf{u}}_1 \\ \tilde{\mathbf{u}}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z_1'y} \\ \mathbf{Z_2'y} \end{bmatrix},$$

and, for sire models, they were

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z_1} \\ \mathbf{Z_1'X} & \mathbf{Z_1'Z_1} + \mathbf{G_1^{-1}}\tilde{\alpha}_1 \end{bmatrix} \begin{bmatrix} \tilde{\mathbf{b}} \\ \tilde{\mathbf{u}}_1 \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z_1'y} \end{bmatrix},$$

where $\tilde{\alpha}_i = \tilde{\gamma}_0^2/\tilde{\gamma}_i^2$, and $\tilde{\gamma}_i^2$ is the prior estimate of σ_i^2. Because the residual variance differed for sire and interaction models, the variance ratios were also different. The MME can be written as $\tilde{\mathbf{C}}\tilde{\mathbf{s}} = \mathbf{W'y}$, where

$$\mathbf{W} = [\mathbf{X}|\mathbf{Z}_1|\mathbf{Z}_2] \text{ and}$$
$$\tilde{\mathbf{s}}' = [\tilde{\mathbf{b}}' \; \tilde{\mathbf{u}}_1' \; \tilde{\mathbf{u}}_2'].$$

TABLE 2. Models used to calculate estimates of variance components, considering variance structure of sire effects [Var(u$_1$)] and interaction effects [Var(u$_2$)].

Model	Var(u$_1$)[1]	Var(u$_2$)[2]
	Sire models	
1	$\mathbf{I}\sigma_1^2$	. . .
2	$\mathbf{A}\sigma_1^2$	. . .
	Interaction models	
3	$\mathbf{I}\sigma_1^2$	$\mathbf{I}\sigma_2^2$
4	$\mathbf{A}\sigma_1^2$	$\mathbf{I}\sigma_2^2$
5	$\mathbf{A}\sigma_1^2$	$(\mathbf{I} \otimes \mathbf{A})\sigma_2^2$

[1] I is an identity matrix, A is the numerator relationship matrix among sires, σ_1^2 is the sire variance.

[2] ⊗ is the direct or Kronecker product, σ_2^2 is the interaction variance.

Then

$$\tilde{\mathbf{s}} = \tilde{\mathbf{C}}^{-1}\mathbf{W'y}.$$

The tilde (~) will be used to indicate a value (scalar, vector, or matrix) that is a function of the prior estimates of the variance components (i.e., for variables for which the value may change if the priors change).

The inverse of the coefficient matrix, $\tilde{\mathbf{C}}^{-1}$, existed because herds were the only fixed effects considered in the model; i.e., $\tilde{\mathbf{C}}$ was full rank because the mean was included in herd effects.

The MIVQUE quadratics suggested by Rao (18) were used. Rao (18) defined a class of symmetric matrices **B** such that $\mathbf{BX} = \mathbf{0}$ and $\mathrm{tr}(\mathbf{BV}_i) = p_i$, $i = 0, 1, 2, \ldots, k$, where tr( ) indicates the trace operation. If $\boldsymbol{\sigma}' = (\sigma_0^2 \; \sigma_1^2 \cdots \sigma_k^2)$, then $\mathbf{y'By}$ is a class of unbiased translation invariant estimates of $\mathbf{p}'\boldsymbol{\sigma}$, where

$$\mathbf{p}' = (p_1 \; p_2 \; \ldots \; p_k).$$

The minimum variance estimator of $\mathbf{p}'\boldsymbol{\sigma}$ from that class is $\mathbf{y}'\tilde{\mathbf{B}}\mathbf{y}$, where

$$\tilde{\mathbf{B}} = \sum_{i=0}^{k} \lambda_i \tilde{\mathbf{P}}_\mathbf{V} \mathbf{V}_i \tilde{\mathbf{P}}_\mathbf{V},$$

$$\tilde{\mathbf{P}}_V = \tilde{\mathbf{V}}^{-1} - \tilde{\mathbf{V}}^{-1}\mathbf{X}\,(\mathbf{X}'\tilde{\mathbf{V}}^{-1}\mathbf{X})^{-}\,\mathbf{X}'\tilde{\mathbf{V}}^{-1},$$

and

$$\tilde{\mathbf{V}} = \sum_{i=0}^{k} \mathbf{V}_i\tilde{\gamma}_i.$$

The MIVQUE of $\mathbf{p}'\boldsymbol{\sigma}$ is $\tilde{\lambda}'\tilde{\mathbf{q}}$, where $\tilde{\lambda}$ is a solution to $\tilde{\mathbf{S}}\tilde{\lambda} = \mathbf{p}$, and $\tilde{\mathbf{S}}$ is a k + 1 by k + 1 matrix for which element i,j is $\mathrm{tr}(\tilde{\mathbf{P}}_V\mathbf{V}_i\tilde{\mathbf{P}}_V\mathbf{V}_j)$. More simply, $\tilde{\mathbf{S}}$ is the matrix of the expectations of the quadratic forms

$$\begin{aligned}\tilde{\mathbf{q}}' &= (\tilde{q}_0\ \tilde{q}_1\ \tilde{q}_2\ \ldots\ \tilde{q}_k), \text{ where}\\ \tilde{q}_i &= \mathbf{y}'\tilde{\mathbf{P}}_V\mathbf{V}_i\tilde{\mathbf{P}}_V\mathbf{y}.\end{aligned} \qquad [3]$$

Then, $\tilde{\mathbf{S}}\tilde{\boldsymbol{\sigma}} = \tilde{\mathbf{q}}$, equating the quadratics to their expectations. Finally, $\tilde{\boldsymbol{\sigma}} = \tilde{\mathbf{S}}^{-1}\tilde{\mathbf{q}}$.

A simpler form of the Rao (18) quadratic forms was computed as described by Schaeffer (1979, unpublished data). The quadratics were reorganized to use the solutions from the MME. Expanding Equation [3],

$$\begin{aligned}\tilde{q}_i &= \mathbf{y}'[(\tilde{\mathbf{V}}^{-1} - \tilde{\mathbf{V}}^{-1}\mathbf{X}(\mathbf{X}'\tilde{\mathbf{V}}^{-1}\mathbf{X})^{-}\mathbf{X}'\tilde{\mathbf{V}}^{-1})\\ &\quad \mathbf{V}_i(\tilde{\mathbf{V}}^{-1} - \tilde{\mathbf{V}}^{-1}\mathbf{X}(\mathbf{X}'\tilde{\mathbf{V}}^{-1}\mathbf{X})^{-}\mathbf{X}'\tilde{\mathbf{V}}^{-1})]\mathbf{y}\\ &= (\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}})'\tilde{\mathbf{V}}^{-1}\mathbf{V}_i\tilde{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}}),\end{aligned}$$

where

$$\tilde{\mathbf{b}} = (\mathbf{X}'\tilde{\mathbf{V}}^{-1}\mathbf{X})^{-}\ \mathbf{X}'\tilde{\mathbf{V}}^{-1}\mathbf{y}.$$

Then

$$\begin{aligned}\tilde{q}_i &= (\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}})'\tilde{\mathbf{V}}^{-1}\mathbf{Z}_i\mathbf{G}_i\mathbf{Z}_i'\tilde{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}})\\ &= (\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}})'\tilde{\mathbf{V}}^{-1}\mathbf{Z}_i\mathbf{G}_i\gamma_i(\gamma_i^{-1}\mathbf{G}_i^{-1}\gamma_i^{-1})\\ &\quad \gamma_i\mathbf{G}_i\mathbf{Z}_i'\tilde{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}}),\end{aligned}$$

and, because

$$\begin{aligned}\tilde{\mathbf{u}}_i &= \tilde{\gamma}_i\mathbf{G}_i\mathbf{Z}_i\tilde{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}})\ (6),\\ \tilde{Q}_i &= \tilde{\mathbf{u}}_i'\mathbf{G}_i^{-1}\tilde{\mathbf{u}}_i\tilde{\gamma}_i^{-2}\\ &= \tilde{\mathbf{u}}_i'\tilde{\mathbf{u}}_i\tilde{\gamma}_i^{-2} \text{ if } \mathbf{G}_i = \mathbf{I}.\end{aligned}$$

If we define $\tilde{\mathbf{u}}_0 = \tilde{\mathbf{e}}$, the estimated residual effects, then the calculation of $\tilde{q}_0 = \tilde{\mathbf{e}}'\tilde{\mathbf{e}}$ would require the estimated residual for each observation. However, using results from the MME,

$$\begin{aligned}\tilde{\mathbf{e}}'\tilde{\mathbf{e}} &= (\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}} - \mathbf{Z}\tilde{\mathbf{u}})'\ (\mathbf{y} - \mathbf{X}\tilde{\mathbf{b}} - \mathbf{Z}\tilde{\mathbf{u}})\\ &= \mathbf{y}'\mathbf{y} - \tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y} - \sum_{i=1}^{2} \tilde{\mathbf{u}}_i'\mathbf{V}_i^{-1}\tilde{\mathbf{u}}_i\tilde{\gamma}_i,\end{aligned}$$

but $\tilde{\boldsymbol{\sigma}} = \tilde{\mathbf{S}}^{-1}\tilde{\mathbf{q}}$, a linear combination of the MIVQUE quadratics defined by $\mathbf{H}$, such that $\mathbf{H}^{-1}$ exists, is also MIVQUE; i.e., solving $\mathbf{H}\tilde{\mathbf{S}}\tilde{\boldsymbol{\sigma}} = \mathbf{H}\tilde{\mathbf{q}}$ implies that

$$\tilde{\boldsymbol{\sigma}} = (\mathbf{H}\tilde{\mathbf{S}})^{-1}\mathbf{H}\tilde{\mathbf{q}} = \tilde{\mathbf{S}}^{-1}\mathbf{H}^{-1}\mathbf{H}\tilde{\mathbf{q}} = \tilde{\mathbf{S}}^{-1}\tilde{\mathbf{q}}\ (8).$$

Thus, to simplify calculations, two changes were made. First, $\tilde{q}_i$ for i = 1,2 were scaled such that $\tilde{q}_i^* = \tilde{q}_i\gamma_i$, and, second, $\tilde{q}_0^* = \mathbf{y}'\mathbf{y} - \tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y}$ were used in place of $\tilde{q}_0 = \tilde{\mathbf{e}}'\tilde{\mathbf{e}}$.

To calculate the expectations of the quadratic forms, it is useful to partition the matrix $[\mathbf{Z}_0|\mathbf{Z}_1|\mathbf{Z}_2]'\mathbf{W}$ and the inverse of the augmented equations (Schaeffer, 1979, unpublished data). Let

$$\mathbf{M} = \begin{bmatrix}\mathbf{M}_0\\ \mathbf{M}_1\\ \mathbf{M}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X} & \mathbf{Z}_1 & \mathbf{Z}_2\\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 & \mathbf{Z}_1'\mathbf{Z}_2\\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 & \mathbf{Z}_2'\mathbf{Z}_2\end{bmatrix},$$

and

$$\tilde{\mathbf{C}}^{-1} = \begin{bmatrix}\tilde{\mathbf{C}}^0\\ \tilde{\mathbf{C}}^1\\ \tilde{\mathbf{C}}^2\end{bmatrix},$$

such that

$$\begin{bmatrix}\tilde{\mathbf{b}}\\ \tilde{\mathbf{u}}_1\\ \tilde{\mathbf{u}}_2\end{bmatrix} = \begin{bmatrix}\tilde{\mathbf{C}}^0\mathbf{W}'\mathbf{y}\\ \tilde{\mathbf{C}}^1\mathbf{W}'\mathbf{y}\\ \tilde{\mathbf{C}}^2\mathbf{W}'\mathbf{y}\end{bmatrix}.$$

Then the expectation of $\tilde{q}_i^*$ for i = 1, 2,

$$\begin{aligned}&E(\tilde{\mathbf{u}}_i'\mathbf{G}_i^{-1}\tilde{\mathbf{u}}_i)\\ &\quad = E(\mathbf{y}'\mathbf{W}\tilde{\mathbf{C}}^{i\prime}\mathbf{G}_i^{-1}\tilde{\mathbf{C}}^{i}\mathbf{W}'\mathbf{y})\\ &\quad = \mathrm{tr}(\mathbf{W}\tilde{\mathbf{C}}^{i\prime}\mathbf{G}_i^{-1}\tilde{\mathbf{C}}^{i}\mathbf{W}'\mathbf{V})\end{aligned}$$

$$= \sum_{j=0}^{k} \mathrm{tr}(\mathbf{W}\tilde{\mathbf{C}}^{i\prime}\mathbf{G}_i^{-1}\tilde{\mathbf{C}}^{i}\mathbf{W}'\mathbf{Z}_j\mathbf{G}_j\mathbf{Z}_j')\sigma_j^2$$

$$= \sum_{j=0}^{k} \mathrm{tr}(\tilde{\mathbf{C}}^{i\prime}\mathbf{G}_i^{-1}\tilde{\mathbf{C}}^{i}\mathbf{W}'\mathbf{Z}_j\mathbf{G}_j\mathbf{Z}_j'\mathbf{W})\sigma_j^2$$

$$= \sum_{j=0}^{k} \mathrm{tr}(\tilde{\mathbf{C}}^{i\prime}\mathbf{G}_i^{-1}\tilde{\mathbf{C}}^{i}\mathbf{M}_j'\mathbf{G}_j\mathbf{M}_j)\sigma_j^2.$$

The expectation of $\tilde{q}_0^*$ is

$$E(\mathbf{y}'\mathbf{y} - \tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y}) = E(\mathbf{y}'\mathbf{y}) - E(\tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y}). \quad [4]$$

Taking the first half of the expectation of the quadratic form in Equation [4],

$$E(\mathbf{y}'\mathbf{y}) = \sum_{i=0}^{k} \mathrm{tr}(\mathbf{G}_i\mathbf{Z}_i'\mathbf{Z}_i)\sigma_i^2 + \mathbf{b}'\mathbf{X}'\mathbf{X}\mathbf{b}.$$

This expectation simplifies to $E(\mathbf{y}'\mathbf{y}) = \sum_{i=0}^{k} n\sigma_i^2 + \mathbf{b}'\mathbf{X}'\mathbf{X}\mathbf{b}$ if the diagonal elements of $\mathbf{G}_i$ are all 1, because the trace of a product of two matrices is the sum of the products of the diagonal elements if one or both of the matrices are diagonal (8). All diagonal elements of $\mathbf{G}_i$ are 1, if, as in this study, no sires are inbred. The second half of the expectation of the quadratic form of $\tilde{q}_0^*$ is

$$\begin{aligned} E(\tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y}) &= E(\mathbf{y}'\mathbf{W}\tilde{\mathbf{C}}^{-1}\mathbf{W}'\mathbf{y}) \\ &= E(\sum_{i=0}^{k} \mathrm{tr}(\tilde{\mathbf{C}}^{-1}\mathbf{M}_i'\mathbf{G}_i\mathbf{M}_i)\sigma_i^2 \\ &\quad + \mathbf{b}'\mathbf{X}'\mathbf{X}\mathbf{b}. \end{aligned}$$

Combining these expectations,

$$E(\mathbf{y}'\mathbf{y} - \tilde{\mathbf{s}}'\mathbf{W}'\mathbf{y}) = \sum_{i=0}^{k} (n - \mathrm{tr}(\tilde{\mathbf{C}}^{-1}\mathbf{M}_i'\mathbf{G}_i\mathbf{M}_i))\sigma_i^2.$$

Finally, the variance components were estimated by equating the expectations to the quadratics.

RESULTS AND DISCUSSION

Estimates of sire, interaction, and residual variance, and heritability averaged over 1000 replicates for each combination of relationship matrix, data structure, interaction level, and model type are presented in Table 3. All estimates were calculated using the true values of the variance components for the prior estimates in the MIVQUE estimators.

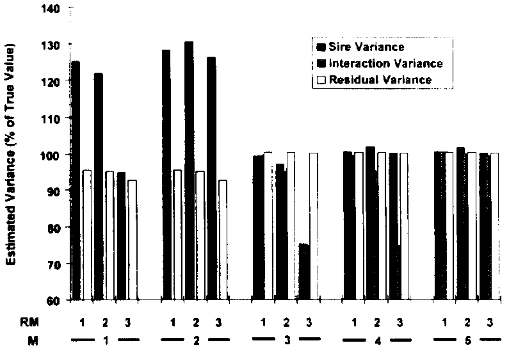

Figure 1. Average estimates of sire, interaction, and residual variance as a percentage of the true values for data with three structured relationship matrices (RM 1 = 10 pairs of half-sib sires, 2 = 4 sets of 5 half-sib sire groups, and 3 = 20 half-sib sires), 25% herd-sire subclasses filled, and interaction simulated at 15% of the total variance for five models (M) for estimation of variance components.

Sire Relationships

Estimates of sire and interaction variance decreased when relationships were ignored, in agreement with previous reports (4, 25). The reduction in variance was evident from comparisons of estimates for models 3 and 5 (sire and interaction variance) or models 1 and 2 (sire variance) for a specific data structure, interaction level, and relationship matrix. Figure 1 presents a characteristic example of the differences in estimates of variance components compared with true values for the three structured relationship matrices and five estimation models; interaction was simulated at 15% of the total variance, and 25% herd-sire subclasses were filled. The ratio of estimates of sire or interaction variance when relationships were ignored to those when relationships were considered [i.e., ratio of estimates from model 1 vs. 2 (sire variance) or model 3 vs. 5 (sire and interaction variance)] ranged from .97 to .99, .91 to .95, and .70 to .76, respectively, for relationship matrices 1 (10 pairs of half-sibs), 2 (4 sets of 5 half-sibs), and 3 (20 half-

TABLE 3. Average[1] minimum variance quadratic unbiased estimates[2] of sire, interaction, and residual variance components and heritability for each combination of the three structured relationship matrices[3] (RM), data structure[4] (DS), and interaction level[5] (IL) in the data for all models (M).

		RM1					RM2					RM3				
DS	IL	M1	M2	M3	M4	M5	M1	M2	M3	M4	M5	M1	M2	M3	M4	M5
— (%) —		Sire variance														
100	5	.0619	.0627	.0613	.0621	.0621	.0609	.0647	.0602	.0639	.0640	.0479	.0639	.0474	.0633	.0633
100	15	.0635	.0642	.0616	.0623	.0624	.0614	.0646	.0595	.0625	.0628	.0487	.0650	.0473	.0631	.0631
100	25	.0649	.0658	.0617	.0624	.0627	.0623	.0654	.0593	.0618	.0623	.0501	.0668	.0477	.0636	.0636
25	5	.0661	.0671	.0608	.0615	.0615	.0645	.0688	.0595	.0629	.0630	.0508	.0676	.0468	.0624	.0624
25	15	.0783	.0802	.0621	.0629	.0629	.0762	.0816	.0608	.0637	.0637	.0592	.0789	.0470	.0627	.0627
25	25	.0892	.0916	.0623	.0631	.0632	.0862	.0931	.0602	.0632	.0635	.0662	.0881	.0439	.0612	.0612
10	5	.0815	.0830	.0617	.0625	.0624	.0798	.0852	.0605	.0634	.0636	.0627	.0830	.0474	.0631	.0632
10	15	.1213	.1242	.0621	.0630	.0629	.1151	.1253	.0590	.0621	.0622	.0917	.1203	.0458	.0611	.0611
10	25	.1601	.1641	.0624	.0635	.0632	.1531	.1678	.0585	.0617	.0615	.1198	.1567	.0465	.0620	.0620
		Interaction variance														
100	5			.0492	.0492	.0498			.0483	.0483	.0508			.0376	.0376	.0501
100	15			.1489	.1489	.1510			.1438	.1438	.1523			.1123	.1122	.1497
100	25			.2486	.2485	.2519			.2396	.2396	.2530			.1894	.1894	.2526
25	5			.0491	.0491	.0496			.0471	.0472	.0497			.0370	.0369	.0493
25	15			.1493	.1494	.1510			.1428	.1428	.1503			.1120	.1120	.1493
25	25			.2508	.2509	.2536			.2378	.2378	.2502			.1867	.1867	.2488
10	5			.0497	.0497	.0506			.0476	.0476	.0501			.0380	.0380	.0507
10	15			.1488	.1486	.1509			.1422	.1421	.1501			.1140	.1140	.1521
10	25			.2559	.2454	.2493			.2378	.2373	.2505			.1840	.1840	.2453
		Residual variance														
100	5	.9384	.9384	.8913	.8913	.8914	.9369	.9369	.8907	.8907	.8909	.9258	.9258	.8898	.8898	.8898
100	15	.9337	.9337	.7913	.7913	.7913	.9271	.9271	.7896	.7896	.7891	.8990	.8990	.7917	.7917	.7917
100	25	.9280	.9280	.6904	.6904	.6903	.9182	.9182	.6891	.6891	.6890	.8706	.8706	.6895	.6895	.6895
25	5	.9245	.9245	.8898	.8898	.8898	.9246	.9246	.8913	.8913	.8912	.9168	.9168	.8907	.8907	.8907
25	15	.8965	.8966	.7911	.7911	.7911	.8927	.8927	.7917	.7917	.7918	.8690	.8690	.7899	.7899	.7899
25	25	.8678	.8679	.6902	.6902	.6902	.8574	.8574	.6893	.6893	.6894	.8216	.8216	.6899	.6899	.6899
10	5	.9098	.9099	.8920	.8920	.8920	.9070	.9070	.8900	.8900	.8900	.9063	.9063	.8927	.8927	.8927
10	15	.8432	.8433	.7901	.7901	.7901	.8421	.8423	.7908	.7908	.7908	.8303	.8305	.7895	.7895	.7894
10	25	.7779	.7781	.6903	.6903	.6903	.7745	.7749	.6897	.6897	.6897	.7563	.7566	.6904	.6904	.6904
		Heritability														
100	5	.246	.249	.243	.246	.246	.242	.256	.239	.253	.253	.196	.256	.193	.253	.250
100	15	.253	.256	.244	.247	.247	.246	.259	.238	.249	.248	.204	.267	.198	.259	.249
100	25	.259	.263	.245	.247	.248	.252	.264	.238	.248	.246	.216	.282	.205	.268	.251
25	5	.264	.268	.241	.244	.244	.259	.275	.237	.249	.249	.208	.272	.191	.250	.247
25	15	.318	.326	.245	.248	.248	.311	.331	.241	.252	.250	.253	.329	.197	.257	.248
25	25	.369	.378	.245	.249	.248	.361	.387	.241	.257	.250	.296	.383	.197	.258	.242
10	5	.325	.331	.243	.246	.245	.320	.339	.239	.250	.250	.257	.332	.192	.251	.248
10	15	.497	.507	.244	.248	.247	.474	.511	.233	.245	.243	.393	.499	.191	.249	.240
10	25	.671	.685	.245	.249	.247	.649	.699	.231	.243	.240	.539	.675	.199	.257	.243

[1] Average of 1000 replicates.

[2] True values: for sire variance, .0625; for interaction variance, .05, .15, and .25; for interaction simulated at 5, 15, and 25% of the total variance, respectively; for residual variance for interaction models, .8875, .7875, and .6875, for interaction simulated at 5, 15, and 25% of the total variance, respectively, and .9375 for all sire models; and for heritability, .25.

[3] Relationship matrices, 1 = 10 pairs of half-sib sires; 2 = 4 sets of 5 half-sib sire groups; 3 = 20 half-sib sires.

[4] Data structure, percentage of filled herd-sire subclasses.

[5] Interaction level simulated, measured as a percentage of the total variance.

sibs). Clearly, the reduction in variance is a function of the relationship matrix across interaction levels and data structures. Residual variance was unaffected by relationship considerations in the estimation model.

Following changes in sire variance, heritability estimates decreased when relationships were ignored when estimating sire variance and interaction was treated similarly (i.e., models 1 vs. 2 and models 3 vs. 4) (Table 3). However, when relationships were ignored only for interaction (model 4), heritability increased slightly because of the reduction in total estimated variance, and this bias increased with levels of interaction and relationship (Table 3).

Model Type

Interaction Models. The main differences observed in interaction models were due to differences in true variances. As true interaction variance increased in the data, the true residual variance decreased. As expected, the estimates for interaction and residual variance followed the same pattern. No differences existed because of data structures, relationship matrices, or interaction levels on the interaction models other than reduction in estimates that was due to ignoring relationships on sire and interaction variance previously discussed (Figures 1, 2, and 3).

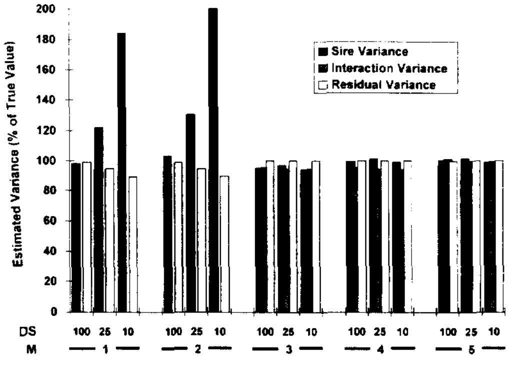

Figure 2. Average estimate of sire, interaction, and residual variance as a percentage of the true values for data with three proportions of herd-sire subclasses filled [data structures (DS)], the relationship matrix for four sets of five half-sib sire groups, and interaction simulated at 15% of the total variance for five models (M) for estimation of variance components.

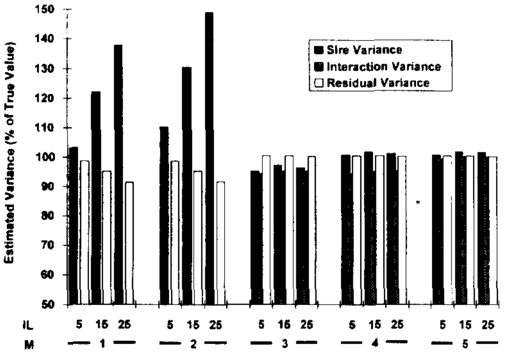

Figure 3. Average estimates of sire, interaction, and residual variance as a percentage of the true values for data with three simulated interaction levels (IL), the relationship matrix for four sets of five half-sib sire groups, and 25% herd-sire subclasses filled for five models (M) for estimation of variance components.

Sire Models. Estimates of sire variance increased when interaction was removed from the estimation model. This bias increased as the data were more unbalanced (Figure 2). When the data were nearly balanced (100% herd-sire subclasses filled), the sire variances estimated using sire models were similar to the corresponding estimates obtained with the interaction models. The increase in sire variance as data were less balanced may be due to confounding of prediction of sire breeding values and underlying H × S effects. If a sire is represented in few environments, the H × S effects in those herds may effect the predicted breeding value of that sire more severely than a sire represented in many herds. Estimates of sire variance also increased as the interaction level simulated in the data increased (Figure 3).

When sire and interaction models that estimated variance components using similar assumptions for sire relationships were compared (i.e., model 1 vs. 3 and 2 vs. 5), the sire variance estimated from the sire models was larger than that estimated from the interaction model. These differences were measured as a fraction of the estimate of interaction variance from the true model (model 5) for the same data. The proportions presented in Table 4 were similar for each combination of data structure and relationship matrix across interaction levels. The similarity of the ratios within a given combination of data structure and relationship matrix suggests that the in-

TABLE 4. Ratios[1] of differences[2] (RD) of average minimum variance quadratic unbiased estimates of sire variance when interaction was removed from the variance component model measured as a proportion of the interaction variance estimated using model 5 for combinations of the three structured relationships[3] (RM), data structures[4] (DS), and interaction levels[5] (IL).

		RM1		RM2		RM3	
DS	IL	RD1	RD2	RD1	RD2	RD1	RD2
(%)							
100	5	.012	.012	.012	.012	.010	.013
100	15	.012	.012	.012	.012	.010	.013
100	25	.013	.012	.012	.012	.009	.013
100	$\overline{\text{X}}$[6]	.012	.012	.012	.012	.009	.013
25	5	.107	.112	.102	.118	.080	.107
25	15	.107	.114	.103	.119	.082	.108
25	25	.106	.112	.104	.118	.090	.108
25	$\overline{\text{X}}$	.107	.113	.103	.119	.084	.108
10	5	.391	.408	.385	.431	.303	.391
10	15	.392	.406	.374	.421	.301	.389
10	25	.392	.405	.378	.424	.299	.386
10	$\overline{\text{X}}$	.392	.406	.379	.425	.301	.389

[1] Ratios of averages of 1000 replicates.

[2] Ratio of differences, 1 = differences for models with relationships ignored (models 1 and 3) [i.e., (model 1 sire − model 3 sire)/model 5 interaction], 2 = differences for models with relationships considered (models 2 and 5) [i.e., (model 2 sire − model 5 sire)/model 5 interaction].

[3] Relationship matrices, 1 = 10 pairs of half-sib sires, 2 = 4 sets of 5 half-sib sire groups, 3 = 20 half-sib sires.

[4] Data structure, percentage of filled herd-sire subclasses.

[5] Interaction level simulated, measured as a percentage of the total variance.

[6] Mean of the ratios for three interaction levels for a data structure.

crease in sire variance for each combination was proportional to the interaction level present in the data. The proportions were compared by calculating ratios of the mean proportions for the data structures. The ratios ranged from .10 to .12, .028 to .033, and .27 to .28, respectively, for 100 to 25, 100 to 10, and 25 to 10% herd-sire subclasses filled. These ratios were similar for all relationship matrices, suggesting that the increases in sire variance were a consistent function of the data structure.

The true value of residual variance in the sire models included the residual and interaction variances from the interaction model. In nearly all instances, the residual variance was underestimated. The degree of underestimation of residual variance increased as sires were more related (Figure 1), as the data were more unbalanced (Figure 2), and as interaction increased (Figure 3).

Similar to the comparison of changes in estimates of sire variance, differences in residual variance estimates that were due to removal of H × S from the estimation model were calculated for models using similar assumptions for sire relationships (i.e., models 1 vs. 3 and 2 vs. 5), and these differences were measured as a proportion of the interaction variance estimate from the true model (model 5) for the same data. The proportions presented in Table 5 were similar for each combination of data structure and relationship matrix across interaction levels. This pattern was similar to that for the differences in sire variance. The similarity of the proportions for combinations of data structure and relationship matrix suggests that the increase in residual variance for each combination was proportional to the interaction level present in the data. Similar to the comparison made for changes in sire variances, the changes in residual variance as a fraction of the interaction variance were compared across data structures by calculating ratios of mean proportions for the data structures. The ratios ranged from 1.3 to 1.4, 2.6 to 2.7, and 1.9 to 2.0, respectively, for 100 to 25, 100 to 10, and 25 to 10% filled herd-sire subclasses. The narrow range of ratios suggests

TABLE 5. Ratios[1] of differences[2] (RD) of average minimum variance quadratic unbiased estimates of residual variance components when interaction was removed from the variance component model measured as a proportion of the interaction variance estimated using model 5 for combinations of the three structured relationships[3] (RM), data structures[4] (DS), and interaction levels[5] (IL).

		RM1		RM2		RM3	
DS	IL	RD1	RD2	RD1	RD2	RD1	RD2
(%)							
100	5	.945	.943	.910	.906	.717	.717
100	15	.943	.943	.903	.906	.717	.717
100	25	.944	.944	.905	.906	.717	.717
100	$\overline{X}$[6]	.944	.944	.906	.906	.717	.717
25	5	.699	.700	.671	.672	.530	.530
25	15	.698	.698	.672	.672	.530	.530
25	25	.700	.701	.672	.672	.529	.529
25	$\overline{X}$	.699	.699	.671	.672	.530	.530
10	5	.352	.353	.338	.340	.268	.269
10	15	.352	.352	.341	.343	.269	.270
10	25	.351	.352	.339	.340	.269	.270
10	$\overline{X}$	.352	.353	.339	.341	.268	.269

[1] Ratios of averages of 1000 replicates.

[2] Ratio of differences, 1 = differences for models with relationships ignored (models 1 and 3) [i.e., (model 1 residual − model 3 residual)/model 5 interaction], 2 = differences for models with relationships considered (models 2 and 5) [i.e., (model 2 residual − model 5 residual)/model 5 interaction].

[3] Relationship matrices, 1 = 10 pairs of half-sib sires, 2 = 4 sets of 5 half-sib sire groups, 3 = 20 half-sib sires.

[4] Data structure, percentage of filled herd-sire subclasses.

[5] Interaction level simulated, measured as a percentage of the total variance.

[6] Mean of the ratios for three interaction levels for a data structure.

that the proportionate increase in residual variance when adjusted for the interaction level in the data was a consistent function of the data structure.

Heritability estimates using sire models ranged from slightly underestimated to dramatically overestimated (Table 3). Heritability estimates decreased if relationships were ignored compared with those with relationships (i.e., model 1 vs. model 2), and this bias increased with higher levels of sire relatedness (Table 3). Heritability increased as the interaction level increased and as the data were more unbalanced (Table 3) regardless of whether relationships were included or ignored. Heritability estimates were more biased than sire variance because the biases in estimates of sire and residual variance components tended to be in opposite directions so that as estimates of sire variance increased, the estimate of total variance often decreased. As a result, the heritability often increased drastically when interaction was removed from the model.

Relationship Matrices from Calving Ease Data

Relationship matrix 4, that of young sires, had average nonzero off-diagonals of .10 and 15% nonzero off-diagonal elements. Relationship matrix 5, that for 20 sires without restrictions, had average nonzero off-diagonal elements of .16 and 13% nonzero off-diagonals elements. The most common nonzero off-diagonal element in relationship matrices 4 and 5 was .0625.

Table 6 contains average sire, interaction, and residual variance, and heritability estimates for the relationship structures 4 and 5. In general, the estimates of variance components for relationship matrices 4 and 5 were very similar to those from the structured relationship matrix 1, corresponding to 10 pairs of half-sib sire pairs (see Table 3 for comparison). The ratios of average estimates of sire and interaction variance ignoring sire relationships to estimates with sire relationships ranged from .97 to .99 for relationship matrices 4 and 5. The range of ratios was nearly identical to

TABLE 6. Average[1] minimum variance quadratic unbiased estimates[2] of sire, interaction, and residual variance components and heritability for each combination of the two relationship matrices selected from the calving ease data[3] (RM), data structure[4] (DS), and interaction level[5] (IL) in the data for all models (M).

		RM4					RM5				
DS	IL	M1	M2	M3	M4	M5	M1	M2	M3	M4	M5
(%)		Sire variance									
100	5	.0635	.0645	.0629	.0638	.0639	.0612	.0626	.0606	.0620	.0620
100	15	.0642	.0650	.0624	.0631	.0632	.0639	.0655	.0621	.0635	.0637
100	25	.0646	.0655	.0615	.0623	.0625	.0652	.0664	.0620	.0631	.0633
25	5	.0672	.0684	.0619	.0628	.0628	.0664	.0682	.0612	.0626	.0627
25	15	.0770	.0786	.0609	.0618	.0619	.0766	.0789	.0608	.0622	.0622
25	25	.0903	.0925	.0636	.0646	.0646	.0893	.0924	.0625	.0640	.0640
10	5	.0819	.0833	.0622	.0630	.0631	.0805	.0829	.0612	.0622	.0622
10	15	.1203	.1228	.0616	.0623	.0624	.1217	.1269	.0632	.0640	.0639
10	25	.1632	.1670	.0623	.0630	.0632	.1585	.1658	.0600	.0608	.0605
		Interaction variance									
100	5			.0491	.0491	.0498			.0489	.0489	.0497
100	15			.1481	.1481	.1504			.1476	.1476	.1511
100	25			.2463	.2463	.2501			.2460	.2460	.2515
25	5			.0485	.0485	.0493			.0485	.0485	.0499
25	15			.1483	.1483	.1506			.1459	.1459	.1502
25	25			.2463	.2463	.2502			.2453	.2452	.2523
10	5			.0488	.0488	.0494			.0495	.0495	.0503
10	15			.1476	.1477	.1497			.1457	.1460	.1483
10	25			.2497	.2498	.2532			.2461	.2461	.2501
		Residual variance									
100	5	.9384	.9384	.8914	.8914	.8914	.9389	.9389	.8921	.8921	.8924
100	15	.9323	.9323	.7906	.7906	.7906	.9318	.9318	.7907	.7907	.7905
100	25	.9269	.9269	.6914	.6914	.6912	.9255	.9255	.6903	.6903	.6903
25	5	.9269	.9269	.8926	.8926	.8926	.9251	.9251	.8909	.8909	.8909
25	15	.8954	.8955	.7906	.7906	.7906	.8946	.8946	.7917	.7917	.7916
25	25	.8649	.8650	.6908	.6908	.6908	.8622	.8623	.6892	.6892	.6892
10	5	.9080	.9081	.8906	.8906	.8906	.9082	.9082	.8904	.8904	.8904
10	15	.8445	.8447	.7915	.7915	.7915	.8432	.8434	.7910	.7910	.7910
10	25	.7794	.7796	.6908	.6908	.6908	.7785	.7788	.6905	.6905	.6905
		Heritability									
100	5	.252	.256	.249	.253	.252	.243	.248	.240	.245	.245
100	15	.256	.259	.247	.250	.250	.255	.260	.246	.251	.251
100	25	.259	.262	.245	.248	.247	.261	.266	.246	.250	.250
25	5	.269	.272	.245	.248	.248	.266	.273	.242	.248	.248
25	15	.314	.320	.241	.245	.244	.312	.321	.241	.246	.245
25	25	.375	.382	.251	.255	.254	.371	.383	.248	.253	.251
10	5	.328	.333	.245	.248	.249	.322	.331	.241	.245	.245
10	15	.492	.500	.242	.244	.244	.499	.516	.249	.251	.251
10	25	.680	.693	.243	.245	.245	.664	.689	.236	.238	.237

[1] Average of 1000 replicates

[2] True values: for sire variance, .0625; for interaction variances, .05, .15, and .25, for interaction stimulated at 5, 15, and 25% of the total variance, respectively; for residual variance for interaction model, .8875, .7875, and .6875; for interaction simulated at 5, 15, and 25% of the total variance, respectively, and .9375 for all sire models, and for heritability, .25.

[3] Relationship matrices, 4 = 20 young sires from the calving ease data, 5 = 20 sires of any age for the same data set.

[4] Data structure, percentage of filled herd-sire subclasses.

[5] Interaction level simulated, measured as a percentage of the total variance.

that for relationship matrix 1. Considering or ignoring relationships for estimation of variance components had little effect on estimates of any of the variance components. Sire variance was overestimated using sire models, and this bias increased as interaction levels increased and the data were more unbalanced (Table 6). Heritability tended to be overestimated using sire models, whereas estimates from interaction models were much less biased (Table 6). As expected from results for the estimates of variance components only minor biases in heritability estimates were caused by ignoring sire relationships.

CONCLUSIONS

When relationships were ignored, sire and interaction variances tended to be underestimated, and the average bias was larger for populations with more closely related sires. Sire variance was overestimated for sire models, and the bias depended on the data structure and interaction level of the data. Residual variance was underestimated when variance components were estimated from sire models, resulting in heritability estimates sometimes being extremely biased.

Although interaction was underestimated when relationships were ignored, the degree of bias was relatively small for the relationship matrices considered to be representative of the AI population. This small bias suggests 1) that relationships may be ignored with little affect when sires are not closely related and 2) that interaction is not extremely high. However, even with relatively low levels of interaction, biases in sire variance and heritability estimates were substantial when interaction was removed from the model. These biases indicate that interaction should be included in the variance component model (with relationships ignored for H × S, if necessary) even if the data are only moderately unbalanced and H × S is expected to be present at relatively low levels.

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