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Relationships Among Sires in Estimating Genetic Variance

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ABSTRACT

A method to account for relationships among sires in estimating covariance among paternal half-sibs and heritability is described. The reduction in sum of squares from fitting sire effects after eliminating all other effects in the model is divided by the sum of products of elements of the matrix of coefficients after absorption and elements of the matrix of relationships among sires rather than by the trace of the matrix of coefficients. The method requires computation of relationships that for many sires may be difficult.

INTRODUCTION

Possibly the most used method of estimating genetic variance and heritability is from the component of variance of sires, which is equivalent to the covariance among paternal half-sibs. The usual assumption that sire effects are uncorrelated implies sires are unrelated; otherwise a covariance among effects would be expected. The assumption probably is a carry-over from models for estimation of variances from other random effects for which the assumption is necessary for computing reasons. The assumption may not be necessary when correlations among sire effects are due only to additive (Wright's numerator) relationships among sires.

The ease with which relationships among the sires can be considered is best illustrated with Henderson's method 3 or other procedures that eliminate all effects except sire and residual effects in the quadratic to estimate the sire component of variance. A stimulus for examining the effect of relationships on estimating the sire component of variance is that a similar

model is used with best linear unbiased prediction procedures to predict realized sire effects with the exception that sires are considered related in prediction but unrelated in estimating variance of sires. For prediction the inverse of the relationship matrix is needed. Henderson's (2) discovery of a rapid method of determining the inverse directly without calculation of the relationship matrix allowed relationships to be considered efficiently in sire evaluation (1).

THE MODEL

Consider the linear mixed model $\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}s + \mathbf{e}$, where \mathbf{y} is an $(N \times 1)$ vector of observations, β is a vector of fixed effects (for estimating the sire component of variance by Henderson's method 3, β can contain all other random effects except those of sires), s is an $(S \times 1)$ vector of sire effects, \mathbf{e} is an $(N \times 1)$ vector of residuals, and \mathbf{X} and \mathbf{Z} are incidence matrices defined by which elements of β and s are included in each observation. The $E(\mathbf{y}) = \mathbf{X}\beta$, where random elements of β can have zero expectation. If random elements are in β , then the assumption $E(\beta s') = \mathbf{0}$ is needed.

When sires are related,

$$V \begin{bmatrix} s \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}_S \sigma_s^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_N \sigma_e^2 \end{bmatrix}.$$

This is the model often used for sire evaluation where \mathbf{A}_S is the $S \times S$ matrix of additive relationships among sires. The usual assumption in estimating variance components is that $\mathbf{A}_S = \mathbf{I}_S$, i.e., sires are unrelated.

ESTIMATION CONSIDERING RELATIONSHIPS

The procedure will be illustrated with Henderson's method 3 where the reduction chosen to equate to its expected value is $R(s|\beta)$ in which β can contain all other random effects.

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Method 3 is based on the ordinary least squares equations:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

The σ_e^2 can be estimated from any unbiased procedure, but from solutions to the ordinary least squares equations, one estimate is:

$$\hat{\sigma}_e^2 = [y'y - R(\beta, s)] / [N - \text{rank}(XZ)],$$

where $R(\beta, s) = \hat{\beta}'X'y + \hat{s}'Z'y$. There are several alternative computing procedures to obtain $R(\beta, s)$ of which some may be more efficient than others (6). The reduction for estimating σ_s^2 , $R(s|\beta)$, also may be computed in several ways. The easiest way, however, to obtain the expectation of $R(s|\beta)$ is from equations resulting after β equations are absorbed. This procedure would yield estimates of s and then $R(s|\beta)$ directly as usually is described. After absorption

$$Z'MZ\hat{s} = Z'My, \text{ where}$$

$M = I - X(X'X)^{-1}X'$ is idempotent and symmetric. Then $\hat{s} = (Z'MZ)^{-1}Z'My$ and $R(s|\beta) = \hat{s}'Z'My$.

The expectation of $R(s|\beta)$ does not contain any terms from β or products of terms from s and e .

When e 's are independent, the coefficient of σ_e^2 in $E[R(s|\beta)]$ is the rank of $Z'MZ$. The coefficient of σ_s^2 in $E[R(s|\beta)]$ can be found by substitution of Zs for y in $R(s|\beta)$. The expectation is:

$$E[s'Z'MZ(Z'MZ)^{-1}Z'MZs] = E[s'Z'MZs].$$

Elements of $Z'MZ$ are coefficients of $E(s_i s_j)$, for $i, j = 1, S$, where s_i is the i th element of s . If, as usual, s_i represents $g_i/2$, where g_i is the additive genetic merit of sire i , then:

$$E(s_i s_j) = .25E(g_i g_j) = .25a_{ij}\sigma_g^2,$$

where a_{ij} is the additive relationship between sires i and j and σ_g^2 is the additive genetic variance. The sire component of variance is the

same as the paternal half-sib covariance, $\sigma_s^2 = .25\sigma_g^2$. Thus,

$$E(s_i s_j) = a_{ij}\sigma_s^2.$$

Therefore, the coefficient of σ_s^2 in $E[R(s|\beta)]$ is the sum of products of elements of $Z'MZ$ and A , which will be denoted as $W:A$, where $W = Z'MZ$; i.e., $k = \sum\sum w_{ij}a_{ij}$.

If sires are unrelated as usually assumed, $a_{ij} = 1$ and $a_{ij} = 0$ for $i \neq j$ so that $k = \sum\sum w_{ii} = \text{tr}(Z'MZ)$ as is usually given (6). Thus, if the rank of $Z'MZ$ is $S-1$, then σ_s^2 is estimated as:

$$\hat{\sigma}_s^2 = [R(s|\beta) - (S-1)\hat{\sigma}_e^2] / k$$

The only difference from the usual procedure is that relationships among sires are considered in calculating k .

In many cases, a direct inverse solution for s may not be possible. The inverse of $Z'MZ$, however, is not required in the expectation of $R(s|\beta)$ so that an iterative solution for \hat{s} may be used to obtain $R(s|\beta)$.

EXAMPLE

Hudson and Van Vleck (5) estimated sire components for several traits from records of five breeds of dairy cattle. Their model included fixed herd-year-season effects, fixed genetic group effects and random effects of sires within groups. Sires were considered unrelated. Milk production records were from only the first or test group of daughters to minimize effects of selection. The $Z'MZ$ matrices from that study were available for use in computing $k = W:A$.

Results are in Table 1. The only differences in the two sets of estimates are the denominators in estimation of σ_s^2 from $R(s|\beta)$, i.e., $\text{tr}(Z'MZ)$ vs $Z'MZ:A$. As in Table 1, the denominator terms for $Z'MZ:A$ are 2 to 5% smaller than $\text{tr}(Z'MZ)$. Thus, estimates of sire components are increased by 2 to 5% when A is considered. The increase would be the same for all traits having the same X and Z and sires involved. The estimate of heritability does not increase in quite the same proportion as $\hat{\sigma}_s^2$, because the estimate of total variance also increases.

Because diagonal terms of A are usually 1

TABLE 1. Increase in heritabilities for milk yield from considering relationships among sires.

Breed	No. of sires		k		Fraction $a_{ij} > 0$	% Increase in $\hat{\sigma}^2_s$	Heritability with	
	In calculating relationships	With daughters	Σw_{ii}	$\Sigma \Sigma w_{ij} a_{ij}$			Σw_{ii}	$\Sigma \Sigma w_{ij} a_{ij}$
Ayrshire	192	94	1623.8	1586.0	.085	2.4	.419	.428
Guernsey	493	239	1755.1	1718.8	.062	2.1	.191	.195
Holstein	4094	2532	60137.0	59067.0	.218	1.8	.312	.317
Jersey	611	306	2567.0	2510.4	.098	2.3	.343	.351
Brown Swiss	204	89	406.3	384.8	.218	5.6	.261	.275

and did average nearly 1, why should Σw_{ii} be greater than

$$\Sigma w_{ii} a_{ii} + \Sigma \Sigma_{i \neq j} w_{ij} a_{ij}?$$

The answer is $Z'MZ$ has the well-known properties that each row sums to zero and diagonals, w_{ii} , are positive. Thus,

$$w_{ii} = -\Sigma_{i \neq j} w_{ij}$$

and because a_{ij} will be zero or positive then $\Sigma w_{ij} \geq \Sigma \Sigma w_{ij} a_{ij}$. The fractions of nonzero, off-diagonal elements in A also are shown by breed in Table 1. Examination of heritabilities suggests that the increase is of no practical importance for these populations. Larger and more frequent relationships among sires would be more important.

Hinkelmann (3, 4) described modifications to expected mean squares from considering relationships for two-way random models when dams are nested in sires and when dams and sires are crossclassified. He suggested (4) that in special cases ignoring inbreeding and relationships may lead to overestimation of heritability, which is contrary to results in the previous two paragraphs.

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