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Including Records of Daughters of Selected Bulls in Estimation of Sire Component of Variance

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ABSTRACT

Methods to account for selection in estimation of variance components are computationally difficult and require inclusion of records on which selection was based. The last criterion often cannot be met. Within a time records of daughters in the small sample set for a bull should be relatively free of effects of selection. If only such records are used, many herd-year-season subclasses, however, contain only one record, so that those records are eliminated when herd-year-season effects are absorbed. Including records of daughters of few but heavily used and selected bulls would provide more comparisons within herd-year-seasons, but treating effects of such sires as random and unselected would bias estimates of variance components. Effects for proved sires can be treated as fixed and for sampling sires as random for estimation of sire and residual variances. For example, Method 3 estimates for an operational model including fixed herd-year-season effects ($\mathbf{h}$), fixed effects of proved sires ($\mathbf{s}_1$), and random effects of sampling sires ($\mathbf{s}_2$) are:

$$\hat{\sigma}_e^2 = [\mathbf{y}'\mathbf{y} - R(\mathbf{h},\mathbf{s}_1,\mathbf{s}_2)]/(N - c)$$

and:

$$\hat{\sigma}_s^2 = [R(\mathbf{s}_2|\mathbf{h},\mathbf{s}_1) - (r - 1)\hat{\sigma}_e^2]/\mathrm{tr}(\mathbf{Z}'\mathbf{W}\mathbf{Z})$$

where $\mathbf{y}'\mathbf{y}$ is total sum of squares, R( ) indicates a least squares reduction in sum of squares, N is number of records, c is rank of full coefficient matrix, r is rank, and $\mathrm{tr}(\mathbf{Z}'\mathbf{W}\mathbf{Z})$ is trace of coefficient matrix after absorption of effects of herd-year-seasons and proved sires.

INTRODUCTION

Reliable estimates of components of variance are required for best linear unbiased prediction. For genetic evaluation of sires, sire and residual components of variance should be those from the population before selection (3). Reports of an association between production and variation (7, 13, 14) and the problem of identifying genetically superior cows in herds with different variances (1, 10, 11) led to an attempt (9) to estimate sire and residual components of variance for first lactations started in each of several years under the impression that production increased over time.

The usual data set in any year for milk production in a population of cows resulting from artificial insemination (AI) includes records of at least two kinds: 1) records from a small number of daughters from the sampling period of their sires and 2) records from a large number of daughters of proved bulls. Thus, records on which selection decisions were made for bulls with large numbers of daughters would not be included in an analysis for that year. Robertson (12) warned against including records of daughters of proved bulls in estimation of variation among sires.

An alternative data set would include in each year only records of daughters resulting from the sampling period of their sires. Because relatively few records would be available, many herd-year-seasons of freshening would contain only daughters of a single sire. The result would be that some bulls would not contribute to the sire component of variance and that degrees of freedom for the residual component would be small.

Another alternative, and the subject of this note, is to include for each year records of daughters of bulls from their sampling period

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and of daughters of bulls resulting from services after the sampling period (i.e., daughters of proved bulls). Effects of sires on records of sampling daughters would be random, and effects of proved sires on their daughter records would be treated operationally as fixed to circumvent problems that expectation of effects of proved sires may not be zero and that variance of effects of proved sires may be reduced because of selection. This procedure would increase degrees of freedom for estimation of the residual component of variance and would allow estimation of a herd-year-season effect when the only other data in the herd-year-season is from a single daughter of a sampling sire—thus allowing the record to be used in estimating variance from sampling sires.

MATERIALS AND METHODS

Let the operational model be:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 \\ X_2 \end{bmatrix} (h) + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} s_1 \\ s_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

with:

$$E \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 h + Z_1 s_1 \\ X_2 h \end{bmatrix}$$

and:

$$V \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} I_1 \sigma_e^2 & 0 \\ 0 & Z_2 Z_2' \sigma_s^2 + I_2 \sigma_e^2 \end{bmatrix}$$

where:

- y_1 is the vector of records of daughters of proved bulls,
- y_2 is the vector of records of daughters of sampling bulls,
- e_1 and e_2 are corresponding vectors of random residual effects,
- h is a vector of herd-year-season of freshening effects (or other fixed effects),
- s_1 is a vector of effects of proved bulls that operationally will be considered fixed because $E(s_1) \neq 0$ (the computational procedure will eliminate the effects of s_1 in estimating the variance among sampling sires whether s_1 is considered fixed or a selected set of random effects),
- s_2 is a vector of random effects of sampling bulls,
- X_1 and X_2 are matrices relating elements of h to records in y_1 and y_2,
- Z_1 and Z_2 are matrices relating elements in s_1 and s_2 to records in y_1 and y_2,
- I_1 and I_2 are identity matrices of order the number of records in y_1 and y_2,
- σ_e^2 is the variance of elements of e_1 and e_2, and
- σ_s^2 is the variance of elements of s_2.

If, for example, Method 3 of Henderson (2) is used, the basic least squares equations are:

$$\begin{bmatrix} X_1'X_1 + X_2'X_2 & X_1'Z_1 & X_1'Z_2 \\ Z_1'X_1 & Z_1'Z_1 & 0 \\ Z_2'X_2 & 0 & Z_2'Z_2 \end{bmatrix} \begin{bmatrix} \hat{h} \\ \hat{s}_1 \\ \hat{s}_2 \end{bmatrix} = \begin{bmatrix} X_1'y_1 + X_2'y_2 \\ Z_1'y_1 \\ Z_2'y_2 \end{bmatrix}$$

If a restricted maximum likelihood (REML) procedure (see, e.g., 5) based on mixed model equations (3) is used, the initial equations are the least squares equations except that the last block ($Z_2'Z_2$) becomes $Z_2'Z_2 + I_R\lambda$ where λ is the initial guess of the ratio σ_e^2/σ_s^2 and I_R has order the number of sires in s_2.

For this model, reductions and expected values of reductions for estimating σ_s^2 and σ_e^2 are the obvious ones as in the appendix for Method 3.

For both Method 3 and each round of REML, the estimate of σ_e^2 is obtained from the difference:

$$y'y - R(h, s_1, s_2)$$

divided by:

$$N - \text{rank}(X_1, X_2, Z_1, Z_2)$$

TABLE 1. Number of records, proved and sampling bulls, and herd-year-seasons included in analyses of first lactation milk records of artificially sired daughters of Holstein bulls initiated in 1976 in the northeastern United States. Adapted from (9).[1]

Number	Includes proved and sampling bulls	Includes only sampling bulls
Records	39,331	5,102
Bulls		
Proved	73	
Sampling	370	353
Herd-year-seasons	9,242	2,867

[1] Both analyses began with the same number of sampling bulls: when only one bull has daughters in a herd-year-season those records effectively are not used in computing the reduction in sums of squares for sires after eliminating herd and proved sire effects.

for Method 3 and by:

$$N - \text{rank}(\mathbf{X}_1,\mathbf{X}_2,\mathbf{Z}_1)$$

for REML where N is the number of records in $\mathbf{y}_1$ and $\mathbf{y}_2$.

The estimate of σ_s^2 is obtained for Method 3 from $R(s_2|\mathbf{h},s_1)$ by subtracting $k_e\hat{\sigma}_e^2$ and then dividing by k_s where k_e is the coefficient of σ_e^2 and k_s is the coefficient of σ_s^2 in $E[R(s_2|\mathbf{h},s_1)]$:

$$\hat{\sigma}_s^2 = [R(s_2|\mathbf{h},s_1) - k_e\hat{\sigma}_e^2]/k_s$$

where as expected:

$$k_e = \text{rank}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$$

and:

$$k_s = \text{tr}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$$

with $\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2$ the coefficient matrix after absorption of herd-year-season and proved sire equations (see Appendix).

The solution for σ_s^2 with each round of iteration for REML is:

$$\hat{\sigma}_s^2 = [\hat{s}_2'\hat{s}_2 + \text{tr}(C_{22})\hat{\sigma}_e^2]/\text{tr}(I_R)$$

where:

$\hat{s}_2$ is the vector of solutions from the mixed model equations using the estimate of the ratio σ_e^2/σ_s^2 obtained in the previous round,

$\text{tr}(C_{22})$ is the trace of the lower block of the inverse of the coefficient matrix for the mixed model equations corresponding to the vector s_2, and

$\text{tr}(I_R)$ is the number of s_2 sires.

For Method 3, the necessary reductions in sum of squares can be obtained in several ways [e.g., (4) with the choice of reductions dependent on the structure and magnitude of the data]. The coefficient matrix after absorption of $\mathbf{h}$ and s_1 is used in the Appendix to show the expected value of $R(s_2|\mathbf{h},s_1)$.

EXAMPLE

Mirande (9) estimated sire and residual components of variance for each year of first freshening (1960 through 1982) from first lactation records of artificially sired daughters of Holstein bulls used in the northeastern United States. The three analyses used 1) the model described in the previous section, 2) only records of sampling daughters, and 3) records of daughters of both sampling and proved sires with all sires treated as random.

Table 1 demonstrates with the model treating proved sires as fixed that more random sires contributed to the sire component of variance and that many more degrees of freedom were associated with estimating the residual component of variance: 29,647 vs. 1,883. A more precise estimate of the residual component of variance also would contribute to reduction of sampling variance of the sire component of variance.

Table 2 demonstrates the well-known fallacy that proved sires are a random sample of sires. The large number of daughters of proved sires (average of about 500 vs. 14 for sampling sires) and reduced variation among selected proved sires combine to reduce the sire component of variance. Consequently, the estimate of the ratio, σ_e^2/σ_s^2, needed for mixed model equations (3) nearly doubles. Results for logarithm of milk yield follow the same pattern.

CONCLUSIONS

For appropriate situations, e.g., when records on which selection decisions were made

TABLE 2. Scaled estimates of sire, $\hat{\sigma}_s^2$, and residual, $\hat{\sigma}_e^2$, components of variance and the ratio, $\hat{\sigma}_e^2/\hat{\sigma}_s^2$, for milk yield and logarithm of milk yield. Adapted from (9).

Data	Sires treated as	Milk yield $\hat{\sigma}_s^2$	Milk yield $\hat{\sigma}_e^2$	Milk yield Ratio	Log (milk yield) $\hat{\sigma}_s^2$	Log (milk yield) $\hat{\sigma}_e^2$	Log (milk yield) Ratio
All	Random	244	6,562	27	101	3,036	30
All	Random and fixed	509	6,562	13	243	3,036	12
Sampling	Random	466	6,947	15	210	3,588	17

cannot be included, including records of daughters of selected bulls will increase the accuracy of estimating sire and residual components of variance by providing more degrees of freedom for both components. Computing costs often will be increased only slightly over using only sampling daughters, as most of computing time is required to obtain solutions after equations are constructed. The example shows the error of treating effects of all bulls as random when data are obtained for a limited time (12). After this project was begun (15), two references to a similar approach were discovered. Meyer (8) included records of daughters of six reference sires in a maximum likelihood analysis of multiple lactations. Hill et al. (6) did a similar analysis to examine the effect of heterogeneous variances on sire evaluation.

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APPENDIX

The least squares equations to serve as a basis for Method 3 or REML are:

$$\begin{bmatrix} X_1'X_1 + X_2'X_2 & X_1'Z_1 & X_2'Z_2 \\ Z_1'X_1 & Z_1'Z_1 & 0 \\ Z_2'X_2 & 0 & Z_2'Z_2 \end{bmatrix} \begin{bmatrix} \hat{h} \\ \hat{s}_1 \\ \hat{s}_2 \end{bmatrix} = \begin{bmatrix} X_1'y_1 + X_2'y_2 \\ Z_1'y_1 \\ Z_2'y_2 \end{bmatrix}$$

Note $X_1'X_1 + X_2'X_2$ is diagonal with elements the number of records in each herd-year-season and $Z_1'Z_1$ and $Z_2'Z_2$ are diagonal with elements the number of daughters of proved and sampling sires.

The purpose of this section is to show that the expectation of estimate of σ_s^2 does not contain elements of s_1 and to find the expectation of $R(s_2|h,s_1)$.

As a step in obtaining expectations, the equations, after the $\hat{h}$ equations are absorbed, can be represented as:

$$\begin{bmatrix} Z_1'M_{11}Z_1 & Z_1'M_{12}Z_2 \\ Z_2'M_{12}'Z_1 & Z_2'M_{22}Z_2 \end{bmatrix} \begin{bmatrix} \hat{s}_1 \\ \hat{s}_2 \end{bmatrix} = \begin{bmatrix} Z_1'M_{11}y_1 + Z_1'M_{12}y_2 \\ Z_2'M_{12}'y_1 + Z_2'M_{22}y_2 \end{bmatrix}$$

where for $D = X_1'X_1 + X_2'X_2$, $M_{11} = I_1 - X_1D^{-1}X_1'$, $M_{12} = -X_1D^{-1}X_2'$, and $M_{22} = I_2 - X_2D^{-1}X_2'$.

These equations can be solved iteratively to obtain solutions for $\hat{s}_1$ and $\hat{s}_2$. Then:

$$R(s_1,s_2|h) = \begin{bmatrix} \hat{s}_1 \\ \hat{s}_2 \end{bmatrix}' \begin{bmatrix} Z_1'M_{11}y_1 + Z_1'M_{12}y_2 \\ Z_2'M_{12}'y_1 + Z_2'M_{22}y_2 \end{bmatrix}$$

and:

$$R(h,s_1,s_2) = R(h) + R(s_1,s_2|h)$$

so that:

$$\hat{\sigma}_e^2 = [y_1'y_1 + y_2'y_2 - R(s_1,s_2|h) - R(h)] / [N - \mathrm{rank}(X_1,X_2,Z_1,Z_2)]$$

Absorption of proved sire equations would allow calculation of $R(s_2|h,s_1)$, but because the solutions for $\hat{s}_2$ will be the same as for $\hat{s}_1$ and $\hat{s}_2$ jointly, only the right-hand sides are needed for calculating the reduction. The coefficient matrix will be needed for calculation of k_e and k_s.

The expectation of $R(s_2|h,s_1)$ can be obtained from the equations after h and s_1 are absorbed.

Let:

$$W = M_{22} - M_{12}'Z_1(Z_1'M_{11}Z_1)^{-1}Z_1'M_{12}$$

and:

$$Q = M_{12}' - M_{12}'Z_1(Z_1'M_{11}Z_1)^{-1}Z_1'M_{11}.$$

Then the equations become:

$$(Z_2'WZ_2)\hat{s}_2 = Z_2'Wy_2 + Z_2'Qy_1$$

so that algebraically:

$$R(s_2|h,s_1) = \hat{s}_2'(Z_2'Wy_2 + Z_2'Qy_1)$$

The expectation of $R(s_2|h,s_1)$, as expected, does not contain any h or s_1 terms. The coefficient of σ_s^2 is:

$$k_s = \mathrm{tr}(Z_2'WZ_2),$$

and the coefficient of σ_e^2 is:

$$k_e = \mathrm{rank}(Z_2'WZ_2).$$

The $\mathrm{rank}(Z_2'WZ_2)$ usually is the number of sampling sires minus one. With confounding, an approximation is the number of nonzero diagonal elements of $Z_2'WZ_2$ minus one.

Then:

$$\hat{\sigma}_s^2 = [R(s_2|h,s_1) - \mathrm{rank}(Z_2'WZ_2)\hat{\sigma}_e^2] / \mathrm{tr}(Z_2'WZ_2).$$

Neither $\mathbf{W}$ nor $\mathbf{Q}$ are needed to obtain the estimate of σ_s^2. A proof, however, that $k_e = \text{rank}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$ is to show $\mathbf{QQ}' + \mathbf{WW} = \mathbf{W}$.

Algebraically:

$$R(s_2|\mathbf{h},s_1) = \hat{s}_2'[\mathbf{Z}_2'\mathbf{Q}\mathbf{y}_1 + \mathbf{Z}_2'\mathbf{W}\mathbf{y}_2]$$

where:

$$\hat{s}_2 = (\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^- \ (\mathbf{Z}_2'\mathbf{Q}\mathbf{y}_1 + \mathbf{Z}_2'\mathbf{W}\mathbf{y}_2)$$

In terms of the observation vectors, $\mathbf{y}_1$ and $\mathbf{y}_2$, the reduction is:

$$\begin{aligned}R(s_2|\mathbf{h},s_1) &= (\mathbf{y}_1'\mathbf{Q}' + \mathbf{y}_2'\mathbf{W})\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^-\mathbf{Z}_2' \\ &\quad \times (\mathbf{Q}\mathbf{y}_1 + \mathbf{W}\mathbf{y}_2) \\ &= \mathbf{y}_1'\mathbf{Q}'\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^-\mathbf{Z}_2'\mathbf{Q}\mathbf{y}_1 \\ &\quad + \mathbf{y}_2'\mathbf{W}\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^-\mathbf{Z}_2'\mathbf{W}\mathbf{y}_2 \\ &\quad + \mathbf{y}_1'\mathbf{Q}'\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^-\mathbf{Z}_2'\mathbf{W}\mathbf{y}_2 \\ &\quad + \mathbf{y}_2'\mathbf{W}\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^-\mathbf{Z}_2'\mathbf{Q}\mathbf{y}_1\end{aligned}$$

The models for $\mathbf{y}_1$ and $\mathbf{y}_2$ can be substituted and expectations taken separately for $\mathbf{h}$, s_1, s_2, and $\mathbf{e}$ terms. Product terms between $\mathbf{h}$ and s_1 and between $\mathbf{h}$ or s_1 and s_2 or $(\mathbf{e}_1, \mathbf{e}_2)$ will drop out because, as will be shown, $\mathbf{QZ}_1\mathbf{h} + \mathbf{WX}_2\mathbf{h} = \mathbf{0}$ and $\mathbf{QZ}_1 = \mathbf{0}$. Product terms between s_2 and $(\mathbf{e}_1, \mathbf{e}_2)$ and between $\mathbf{e}_1$ and $\mathbf{e}_2$ will drop out because they are uncorrelated.

$E[R(s_2|\mathbf{h},s_1)]$: Let $f(\mathbf{h})$ represent the expected value in terms of $\mathbf{h}$:

$$\begin{aligned}f(\mathbf{h}) = E[&\mathbf{h}'\mathbf{X}_1'\mathbf{Q}' + \mathbf{h}'\mathbf{X}_2'\mathbf{W})\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^- \\ &\mathbf{Z}_2'(\mathbf{QX}_1\mathbf{h} + \mathbf{WX}_2\mathbf{h})]\end{aligned}$$

This is expected to be zero because the $\mathbf{h}$ equations were eliminated by absorption. If $(\mathbf{QX}_1 + \mathbf{WX}_2)\mathbf{h} = \mathbf{0}$, then $f(\mathbf{h}) = \mathbf{0}$. A proof that $\mathbf{QX}_1 + \mathbf{WX}_2 = \mathbf{0}$ can be obtained in terms of $\mathbf{M}_{11}$, $\mathbf{M}_{12}$, $\mathbf{M}_{22}$, and $\mathbf{D} = \mathbf{X}_1'\mathbf{X}_1 + \mathbf{X}_2'\mathbf{X}_2$. By substitution for $\mathbf{Q}$ and $\mathbf{W}$:

$$\begin{aligned}\mathbf{QX}_1 + \mathbf{WX}_2 &= (-\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{X}_1 \\ &\quad + (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1(\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1} \\ &\quad \times \mathbf{Z}_1'(\mathbf{I}_1 - \mathbf{X}_1\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{X}_1 \\ &\quad + \mathbf{X}_2 - (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_2')\mathbf{X}_2 \\ &\quad - (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1(\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1} \\ &\quad \times \mathbf{Z}_1'(\mathbf{X}_1\mathbf{D}^{-1}\mathbf{X}_2')\mathbf{X}_2\end{aligned}$$

If terms with $\mathbf{D}^{-1}$ are collected and as $\mathbf{X}_1'\mathbf{X}_1 + \mathbf{X}_2'\mathbf{X}_2 = \mathbf{D}$, then

$$\begin{aligned}\mathbf{QX}_1 + \mathbf{WX}_2 &= \mathbf{X}_2 - \mathbf{X}_2\mathbf{D}^{-1} \\ &\quad \times (\mathbf{X}_1'\mathbf{X}_1 + \mathbf{X}_2'\mathbf{X}_2) \\ &\quad + (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1(\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1} \\ &\quad \times \mathbf{Z}_1'\mathbf{X}_1 - (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1 \\ &\quad \times (\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1}\mathbf{Z}_1'\mathbf{X}_1\mathbf{D}^{-1} \\ &\quad \times (\mathbf{X}_1'\mathbf{X}_1 + \mathbf{X}_2'\mathbf{X}_2) \\ &= \mathbf{X}_2 - \mathbf{X}_2\mathbf{I} \\ &\quad + (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1(\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1} \\ &\quad \times \mathbf{Z}_1'\mathbf{X}_1 - (\mathbf{X}_2\mathbf{D}^{-1}\mathbf{X}_1')\mathbf{Z}_1 \\ &\quad \times (\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1}\mathbf{Z}_1'\mathbf{X}_1 \\ &= 0\end{aligned}$$

Expectations of products involving $\mathbf{h}$ will be zero.

Let $f(s_1,s_2)$ represent the expected value in terms of s_1 and s_2:

$$\begin{aligned}f(s_1,s_2) = E[&(s_1'\mathbf{Z}_1'\mathbf{Q}' + s_2'\mathbf{Z}_2'\mathbf{W})\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^- \\ &\mathbf{Z}_2'(\mathbf{QZ}_1s_1 + \mathbf{WZ}_2s_2)]\end{aligned}$$

If $\mathbf{QZ}_1 = \mathbf{0}$ then, as expected, terms in s_1 do not exist in the expectation whether s_1 is fixed or random.

$$\begin{aligned}\mathbf{QZ}_1 &= \mathbf{M}_{12}'\mathbf{Z}_1 - \mathbf{M}_{12}'\mathbf{Z}_1(\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)^{-1}\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1 \\ &= \mathbf{M}_{12}'\mathbf{Z}_1 - \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{I} \\ &= \mathbf{0}\end{aligned}$$

Let $f(s_2)$ represent the expected value in terms of s_2:

$$\begin{aligned}f(s_2) &= E[s_2'(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^- \\ &\qquad (\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)s_2] \\ &= E[s_2'(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)s_2]\end{aligned}$$

by the properties of a generalized inverse, and thus:

$$f(s_2) = \sigma_s^2 \ \text{tr}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$$

if the sampling sires are unrelated. If the sires are related as described by the numerator relationship matrix $\mathbf{A}$, then:

$$f(s_2) = \sigma_s^2 (\mathbf{A}:\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$$

where $\mathbf{A}:\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2$ signifies the sum of products of corresponding terms in $\mathbf{A}$ and $\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2$.

Let $f(e_1,e_2)$ represent the expected value in terms of $\mathbf{e}_1$ and $\mathbf{e}_2$:

$$f(e_1,e_2) = E[(\mathbf{e}_1'\mathbf{Q}' + \mathbf{e}_2'\mathbf{W})\mathbf{Z}_2 \times (\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}\mathbf{Z}_2'(\mathbf{Q}\mathbf{e}_1 + \mathbf{W}\mathbf{e}_2)]$$

Of the four terms from the expansion, two have zero expectations because their expectations are products of $\mathbf{e}_1$ and $\mathbf{e}_2$. The other two can be represented as:

$$\begin{aligned} f(e_1,e_2) &= E[\mathbf{e}_1'\mathbf{Q}'\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}\mathbf{Z}_2'\mathbf{Q}\mathbf{e}_1] \\ &+ E[\mathbf{e}_2'\mathbf{W}\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}\mathbf{Z}_2'\mathbf{W}\mathbf{e}_2] \\ &= \sigma_e^2\ \{\mathrm{tr}[\mathbf{Q}'\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}\mathbf{Z}_2'\mathbf{Q}] \\ &+ \mathrm{tr}[\mathbf{W}\mathbf{Z}_2(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}\mathbf{Z}_2'\mathbf{W}]\ \} \end{aligned}$$

By use of the rotation rule for traces:

$$f(e_1,e_2) = \sigma_e^2\ \{\mathrm{tr}[\mathbf{Z}_2'(\mathbf{Q}\mathbf{Q}' + \mathbf{W}\mathbf{W})\mathbf{Z}_2 \times (\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}]\ \}$$

If $\mathbf{Q}\mathbf{Q}' + \mathbf{W}\mathbf{W} = \mathbf{W}$ then:

$$f(e_1,e_2) = \sigma_e^2\ \{\mathrm{tr}[(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)^{-}]\ \}$$

Then from the properties of generalized inverses:

$$f(e_1,e_2) = \sigma_e^2\ \mathrm{rank}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2).$$

The rank of $\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2$ usually will be the number of sampling sires minus one.

Proof that $\mathbf{Q}\mathbf{Q}' + \mathbf{W}\mathbf{W} = \mathbf{W}$

Let $\mathbf{U} = \mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1$. Then $\mathbf{W}\mathbf{W} + \mathbf{Q}\mathbf{Q}' =$

$$\mathbf{M}_{22}\mathbf{M}_{22} \quad [1]$$

$$- \mathbf{M}_{22}\mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} \quad [2]$$

$$- \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}\mathbf{M}_{22} \quad [3]$$

$$+ \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}\mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} \quad [4]$$

$$+ \mathbf{M}_{12}'\mathbf{M}_{12} \quad [5]$$

$$- \mathbf{M}_{12}'\mathbf{M}_{11}\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} \quad [6]$$

$$- \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{M}_{12} \quad [7]$$

$$+ \mathbf{M}_{12}'\mathbf{Z}'\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{M}_{11}\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} \quad [8]$$

Because $\mathbf{M}$ is idempotent:

$$\begin{bmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{12}' & \mathbf{M}_{22} \end{bmatrix} \begin{bmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{12}' & \mathbf{M}_{22} \end{bmatrix} = \begin{bmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} \\ \mathbf{M}_{12}' & \mathbf{M}_{22} \end{bmatrix}$$

so that:

$$\mathbf{M}_{11}\mathbf{M}_{11} + \mathbf{M}_{12}\mathbf{M}_{12}' = \mathbf{M}_{11}$$

$$\mathbf{M}_{11}\mathbf{M}_{12} + \mathbf{M}_{12}\mathbf{M}_{22} = \mathbf{M}_{12}$$

$$\mathbf{M}_{12}'\mathbf{M}_{11} + \mathbf{M}_{22}\mathbf{M}_{12}' = \mathbf{M}_{12}'$$

$$\mathbf{M}_{12}'\mathbf{M}_{12} + \mathbf{M}_{22}\mathbf{M}_{22} = \mathbf{M}_{22}$$

Thus:

$$[1] + [5] = \mathbf{M}_{22}$$

$$[3] + [7] = -\mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}$$

$$[2] + [6] = -\mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}$$

$$[4] + [8] = \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1\mathbf{M}_{11}\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}.$$

Because $\mathbf{U} = (\mathbf{Z}_1'\mathbf{M}_{11}\mathbf{Z}_1)$, [4] + [8] becomes:

$$\mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{U}\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} = \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12}$$

and:

$$\mathbf{W}\mathbf{W} + \mathbf{Q}\mathbf{Q}' = \mathbf{M}_{22} - \mathbf{M}_{12}'\mathbf{Z}_1\mathbf{U}^{-1}\mathbf{Z}_1'\mathbf{M}_{12} = \mathbf{W}.$$

Therefore, $f(e_1,e_2) = \sigma_e^2\ \mathrm{rank}(\mathbf{Z}_2'\mathbf{W}\mathbf{Z}_2)$.