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Calculation of prediction error variances using sparse matrix methods

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Introduction

Genetic evaluation of beef cattle based on Best Linear Unbiased Prediction (BLUP) (HENDERSON 1973) has been introduced recently in Britain (BRYAN et al. 1992a). Traits are evaluated using an animal model which includes maternal genetic effects for birth weight and 200 day weight. Estimates of accuracies can be calculated from (the diagonal elements of) the inverse of the coefficient matrix of the mixed model equations. In general, calculation of the inverse is considered to be too demanding computationally because of the large number of equations. Methods to calculate approximate accuracies are available which are appropriate for direct genetic effects for single trait sire models (e. g. VAN RADEN and FREEMAN 1985; GREENHALGH et al. 1986; ROBINSON and JONES 1987), single trait animal models (e. g. MISZTAL and WIGGANS 1988; MEYER 1989; BIOCHARD and LEE 1992) or multiple trait animal models (TIER et al. 1991). In these approximations the diagonal element is adjusted for connections to a few other effects decided by the known structure of the data, for example, MEYER (1989) makes adjustments for connections to parents, progeny and fixed effects for each animal effect. There has been little investigation of these approximate methods for models which include maternal effects.

The exact inverse of a mixed model coefficient matrix can be found using sparse matrix methodology (TIER and SMITH 1989; MISZTAL 1990). We develop this paper using partitioned matrix theory and sparse matrix methods, an algorithm which provides a major reduction in the number of calculations when only diagonals of the inverse are required. Either the exact inverse or an approximate inverse can result depending on the size of a threshold, whereby adjustments less than the threshold are ignored. A similar algorithm for calculating exact elements of inverses has been given by MISZTAL and PEREZ-ENCISO (1993) based on a result of TAKAHASHI et al. (1975) and properties of triangular matrices. MISZTAL and PEREZ-ENCISO show that the algorithm requires only three times the computing time as calculating the determinant of the system of equations, but also requires two to three times the memory. Our formulation shows that the calculations can be carried out using practically no extra memory. Originally, this method was investigated to provide an exact inverse as a benchmark for comparison with approximations resulting from extension of the approximate methods used for direct genetic effects. However, it has been found that the algorithm is sufficiently efficient that it is now used routinely within the genetic evaluation system for beef cattle in Britain.

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Methods

Model

A univariate animal model is considered with direct and maternal effects of the form

$$y = Xb + Z_a a + Z_m m + Z_c c + e \quad (1)$$

with $E(y) = Xb$ and

$$\mathrm{Var}\begin{pmatrix} a \\ m \\ c \\ e \end{pmatrix} = \begin{pmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & R \end{pmatrix}$$

where b represents fixed effects and a, m, c and e are vectors of random effects representing direct and maternal genetic effects, permanent environmental effects of dams and residual effects respectively. The incidence matrices X, Z_a, Z_m and Z_c link effects to the observations, y, and normally $Z_m = Z_c$. The mixed model equations are of the form $Cx = d$ with

$$C = \begin{bmatrix} X'R^{-1}X & X'R^{-1}Z_a & X'R^{-1}Z_m & X'R^{-1}Z_c \\ Z_a'R^{-1}X & Z_a'R^{-1}Z_a + A^{-1}\alpha_{aa} & Z_a'R^{-1}Z_m + A^{-1}\alpha_{am} & Z_a'R^{-1}Z_c \\ Z_m'R^{-1}X & Z_m'R^{-1}Z_a + A^{-1}\alpha_{ma} & Z_m'R^{-1}Z_m + A^{-1}\alpha_{mm} & Z_m'R^{-1}Z_c \\ Z_m'R^{-1}X & Z_c'R^{-1}Z_a & Z_c'R^{-1}Z_m & Z_c'R^{-1}Z_c + I\gamma_c \end{bmatrix}$$

$$x = \begin{bmatrix} b \\ a \\ m \\ c \end{bmatrix} \text{ and } d = \begin{bmatrix} X'R^{-1}y \\ Z_a'R^{-1}y \\ Z_m'R^{-1}y \\ Z_c'R^{-1}y \end{bmatrix}$$

with

$$\begin{pmatrix} \alpha_{aa} & \alpha_{am} \\ \alpha_{ma} & \alpha_{mm} \end{pmatrix} = \begin{pmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{ma} & \sigma_m^2 \end{pmatrix}^{-1}$$

and $\gamma_c = 1/\sigma^2_c$, $R = I\sigma^2$

The prediction error variances and covariances are the elements of C^{-1}. In practice results are often presented in terms of reliabilities for random effect i, r_i^2, which are the squared accuracies of predicted effects derived from prediction error variances, PEV_i, using $PEV_i = G_i(1-r_i^2)$ where G_i is the variance of the effect (e. g. σ_a^2 for direct genetic effects). The matrix C contains a large proportion of zero elements, therefore methods are investigated that take account of the sparseness of C.

Calculation of variances

Three methods of calculating inverses using sparse matrix methods have been described recently in the animal breeding literature (TIER and SMITH 1989; MISZTAL 1990; MISZTAL and PEREZ-ENCISO 1993).

These techniques can be explained using Gaussian elimination recursively on the set of equations $Cx = d$ using

$$\begin{pmatrix} C_n & c_n \\ c_n' & c_{n+1} \end{pmatrix} = C^*_{n+1}, \begin{pmatrix} x_n \\ x_{n+1} \end{pmatrix} = x^*_{n+1}, \begin{pmatrix} d_n \\ d_{n+1} \end{pmatrix} = d^*_{n+1} \quad (2)$$

where n + 1 is the number of rows in the symmetric matrix C^*_{n+1} and in the vectors x^*_{n+1} and d^*_{n+1}, and n is the number of rows in C_n, c_n, x_n and d_n. Note that c_{n+1}, x_{n+1} and d_{n+1} are scalars

and c'_n, κ'_n and d'_n are row vectors. This is a convenient way of denoting partitions of $(n + 1) \times (n + 1)$ matrices and $(n + 1)$ vectors. Initially $C^*_N = C$, $x^*_N = x$ and $d^*_N = d$ where N is the total number of effects to be estimated and predicted. The number of equations to be solved can be reduced by one by elimination of x_{n+1} resulting in

$$(C_n - r_n c_n') x_n = d_n - r_n d_{n+1} \tag{3}$$

where $r_n = c_n (c_{n+1})^{-1}$ is the regression of x_n on x_{n+1}. Initially n = N–1 and after elimination of x_{n+1} then

$$C^*_n = C_n - r_n c_n' d^*_n = d_n - r_n d_{n+1} \tag{4}$$

can be defined. Successive use of equations (2) and (4) with n = N–1, N–2, etc. defines c_{n+1} to be the variance for variable n + 1 after correction for the last N-n-1 variables and similarly C_n to be the covariance between the first n variables after correction for the last N-n-1 variables. Use of n = N-1, ... 1 in turn results in one equation in one unknown

$$C^*_1 x_1 = d^*_1$$

hence x_1 can be found and, in turn, x_2, ... ,x_N by using $x_{n+1} = d_{n+1}(c_{n+1})^{-1} - r_n' x_n$ (5)

The computational cost of (4) can be reduced if account is taken of the zero elements in c_n.

As $C\,C^{-1} = I$ the i-th column of C^{-1} can also be found as the solution of the equations $Cz_i = f_i$ where f_i is the column of the identity matrix. One disadvantage of this procedure when only variances are required, is that all elements of the i-th column are calculated, and there are redundant calculations if C is symmetric. MISZTAL (1990) discusses this technique in detail but it is not clear if he takes advantage of the sparseness in the columns of f_i.

TIER and SMITH (1989) also discuss sparse matrix methods and point out that solving a set of equations $Cx = d$ can be thought of using operations (2) and (4) on a partitioned matrix $C^* = \begin{pmatrix} B & D \\ D' & C \end{pmatrix}$ and if B, C and D are mxm matrices and B = O and D = I then after m operations of (2) and (4) then the matrix B will contain $-C^{-1}$. If only selected elements of B are required then the calculations in (4) can be reduced by only performing the calculations for the required elements. In both these techniques effectively dummy right hand sides are used: in the first, solutions are used to give C^{-1}, in the second, effectively sums of squares and products after 'fitting' a model are used to give C^{-1}.

An alternative algorithm was recently described by MISZTAL and PEREZ-ENCISO (1993) to allow the calculation of only selected elements in the inverse of C^{-1} based on work of TAKAHASHI et al. (1973). Their description is in terms of triangular matrices but an alternative recursive development of the algorithm in terms of partitioned matrices is of interest.

The inverse of C^*_{n+1} in (2) can be written as

$$\begin{pmatrix} \left(C_n - c_n (c_{n+1})^{-1} c_n'\right)^{-1} & -\left(C_n - c_n (c_{n+1})^{-1} c_n'\right)^{-1} c_n' (c_{n+1})^{-1} \\ -(c_{n+1})^{-1} c_n \left(C_n - c_n (c_{n+1})^{-1} c_n\right)^{-1} & (c_{n+1})^{-1} + (c_{n+1})^{-1} c_n \left(C_n - c_n (c_{n+1})^{-1} c_n\right)^{-1} c_n' (c_{n+1})^{-1} \end{pmatrix}$$

or

$$\begin{pmatrix} C_n^{*-1} & -C_n^{*-1} r_n \\ -r_n' C_n^{*-1} & (c_{n+1})^{-1} + r_n' C_n^{*-1} r_n \end{pmatrix}$$

so that

$$C^{**}_{n+1} = \begin{pmatrix} C^{**}_n & c^{**}_n \\ c^{**\prime}_n & c^{**}_{n+1} \end{pmatrix} \tag{6}$$

denotes the inverse of C^*_{n+1}, then $C^{**}_n = C^{*-1}_n$ and the covariance between x_n and x_{n+1} is given by $c^{**}_n = -C^{**}_n r_n$ (7)

and the variance of x_{n+1} given by $c^{**}_{n+1} = 1/c_{n+1} - c^{**}_n{}' r_n$ (8)

or $c^{**}_{n+1} = 1/c_{n+1} - r'_n C^{**}_n r_n$ (9)

MISZTAL and PEREZ-ENCISO (1993) have given similar formulae by decomposing C into U'DU, with their D corresponding to the diagonal elements c_n and U is upper triangular containing the column vectors r_n. Their equation (3) is equivalent to (7) and (8) if we note they eliminate effects in the reverse order.

From (9) the variance term, c^{**}_{n+1} can be thought of as a variance term of x_{n+1}, $1/c_{n+1}$, adjusted for $x_i (i>n+1)$ and an adjustment $r'_n C^{**}_n r_n$ for correction for terms $x_i (i<n+1)$. The recursion starts with C^{**}_1 as C^{*-1}_1 and (6) – (8) used with n = 1, ..., m–1 in turn.

If C is sparse and only variances are of interest then it is not necessary to calculate all the elements of C^{-1}. For example from (8) the covariance between x_i and x_{n+1} only needs calculating, to from c^{**}_{n+1}, if the regression of x_i on x_{n+1} is non-zero. TAKAHASHI et al. (1973) show that, if only variances are required, the only covariances required are those covariances corresponding to the 'sparsity pattern' of C. This sparsity pattern of C is related to the non-zero elements in the adjusted covariance matrices C_n (and C^*_n) (n = 1,. . .,N), and contains elements (i,j) if at any time during the construction of adjusted covariance matrices C^*_n the (i,j)th element is non-zero. This results partly from observing that the covariance required to evaluate (9) and so (8) and form C^{**}_{n+1} are precisely for those elements which are changed in forming C^*_n from C_n and so are non-zero elements of at least one of C^*_n and C_n. This sparsity pattern can potentially be larger than the pattern used by MISZTAL and PEREZ-ENCISO (1993) who suggest using the zero elements of U, essentially only considering the element of vectors r_n, to judge the sparsity. A numerical example below illustrates this difference but our analysis suggests this is a very minor problem.

TIER and SMITH (1989) give an algorithm to find C^*_n, and their algorithm can be easily modified to include in their list of elements the sparsity pattern. In their algorithm, in order to form C^*_n using (9), each initially non-zero or adjusted element of c_n is compared to a working zero. The calculation (4) only operates on the effectively non-zero elements. If all calculated elements were used then C^*_n corresponding to the sparsity pattern would be generated.

For ease of exposition, the development has been given in terms of C_n, C^*_n and C^{**}_n in practice the methods can be programmed so that C^*_n and C^{**}_n overwrite C^* using only minor extensions of the procedures described by TIER and SMITH (1989).

In contrast to (6)–(8) which calculate covariances by columns, c^{**}_n, the MISZTAL and PEREZ-ENCISO (1993) scheme calculates covariances by rows, this requiring two to three times as much space as our implementation.

Numerical Example

We consider a small numerical example to illustrate the formulae and the concept of the sparsity pattern of C. We use

$$C = C^*_5 = \begin{pmatrix} 2 & 1 & 1 & 0 & 0 \\ 1 & 3 & 0 & 1 & 1 \\ 1 & 0 & 3 & 0 & 1 \\ 0 & 1 & 0 & 1 & 1 \\ 0 & 1 & 1 & 1 & 2 \end{pmatrix}$$

Using (2)

$c'_4 = (0\ 1\ 1\ 1)$ and $c_5 = 2$

and hence $r'_4 = (0\ 0.5\ 0.5\ 0.5)$

Using (4) and (2) gives

$c'_3 = (0\ \ 0.5\ -0.5)$ and $c_4 = 0.5$

$r'_3 = (0\ 1\ 0)$

Continuing gives

$c'_2 = (1\ 0)$ and $c_3 = 2$

$r'_2 = (0.5\ 0)$

$r'_1 = (0.5)$, $c_2 = 2$ and $c_1 = 1$

Hence the matrix of regression coefficients U can be constructed as

$$U = \begin{pmatrix} 1 & 0.5 & 0.5 & 1 & 0 \\ 0 & 1 & [0] & 1 & 0.5 \\ 0 & 0 & 1 & -1 & 0.5 \\ 0 & 0 & 0 & 1 & 0.5 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

In the example all the elements except (1,5) are in the sparcity pattern of C. The element (2,3) altough zero in C_3^* and U was –0.5 in C_4^* and hence needs calculating in (6)–(8). In this case $c_1^{**} = c_1^{*-1} = (1)$.

Using (7) with n = 1

$c_1^{**\prime} = -r'_1 c_1^{**} = (-0.5)$

and $c_2^{**\prime} = 1/c_2 - c_1^{**\prime}\, r_1 = (0.5 + 0.25) = 0.75$

continuing gives

$c_2^{**\prime} = (-0.5\ 0.25)$, $c_3^{**} = 0.75$

$c_3^{**\prime} = (0\ -0.5\ 0.5)$, $c_4^{**} = 3$

$c_4^{**\prime} = (< >\ 0.25\ -0.75\ -1.5)$, $c_5^{**} = 1.75$

In this example the only covariance not requiring calculating in the formation of the variances was the (1,5) element indicated by $< >$.

Analysis

The performance of this algorithm depends on the proportion of elements of c_n that are in the sparsity pattern. If the effectively non-zero regression coefficients are equal to the number of elements in the sparsity pattern then it would be expected that the number of multiplications in (7) and (8) is approximately twice as many as those in (4) (Misztal and Perez-Enciso 1993). Misztal (1990) gives comparative times for the operations in (4) where the variances are formed by his method. If the Misztal and Perez-Enciso (1993) method takes three times as long as the operations in (4) then it should be 10–20 times faster from Misztal's example.

A symmetric banded matrix of width 2d + 1 with $C_{ij} = 0$ if $j<i + d$ is perhaps the simplest matrix to use to compare the methods. The Misztal (1990) scheme needs of the order of dm^2 multiplications to from both C^{-1} and the diagonals of C^{-1} taking account of the symmetry of C and sparsity of the right hand siddes. In contrast the Smith and Tier (1989) algorithm scheme requires of the order of $(m^3/6)$ multiplications to form C^{-1} but order of $(m^2(d + 1)/2)$ multiplications to form the diagonals of C^{-1}. In contrast the Misztal and Perez-Enciso (1993) scheme uses the order of (dm^2) multiplications to form C^{-1} but only of order $3(d^2m)/2$ multiplications to form the diagonal of C^{-1}. Hence if only the variances of x were required this partitioned algorithm being proportional to a lower power of m would be seen to be a major improvement.

Approximation

One problem with these methods is that a large number of elements may be required to form C_n^* exactly. The order of effects in the equations can have a drastic effect on the performance of the algorithm (BOLDMAN and VAN VLECK 1991). In the application to British beef cattle the effects are ordered with fixed effects and sires ordered first according to size and number of progeny and then the rest of the effects are ordered within female parentage. This means that a major part of the equations has a block diagonal structure. One approximation used to reduce 'infill' was to only initiate adjustment for an initially zero element if the magnitude of the adjustment was greater than a tolerance of 10^{-J} where J ist a prespecified number with $J \rightarrow \infty$ indicating that all adjustments are accumulated. JUGA (1992) has found that a value of 3 useful in giving adequate approximations to likelihoods in individual animal models. In addition covariances were only calculated and used in (8) if the regression coefficient was effectively non-zero.

Example

The algorithm was used in an analysis of data recorded and published by the Meat and Livestock Commission on South Devon cattle (BOND et al. 1992).

For 200 day weight there are 26 702 animals in the pedigree, 11 439 males and 15 262 females with 10 710 and 9,791 recorded males and females respectively. There were fixed effects of contemporary groups. Equations are ordered as described in the previous section. Parameter values were, in terms of the phenotypic variance, σ_p^2, $\sigma_a^2/\sigma_p^2 = 0.28$, $\sigma_m^2 = 0.07$, $\sigma_{am}/\sqrt{\sigma_a^2\sigma_m^2} = -0.32$, $\sigma_e^2/\sigma_p^2 = 0.08$. In forming C_i^*, regression coefficients r_n were calculated and written to disk for groups of 50 female families and after every 200 equations when sires and fixed effects were being eliminated because, after adjustment for x_{n+1} the r_n were not required in the formation of C_i^*. To form the prediction error variances the processes were repeated in reverse, reading in the required regression coeffcients and overwriting covariances not required further. For instance to calculate variances for fixed effects and sires, the regression coefficients on dams are not required. Similarly for the ith group of dam families only covariances for fixed and sire effects and regression coefficients for only that group are required. This was a primitive (but successful) attempt to reduce paging. The optimality of the technique depends on the configuration of the cumputer and the population structure.

Table 1 summarizes the performance of the algorithm on a Sun Sparcstation 2 workstation wit 64MB memory, for different values of the J threshold. This table shows that the total time varied between 2 and 3 times the time to form C_1^*. As J increases more elements

Table 1. **Comparison of algorithms to calculate diagonals of C^{-1} with different threshold (10^{-J}) in terms of number of elements used, number of adjustments ignored, time to form C_1 and total**

J	Maximum number of elements ($x10^3$)	Adjustments ignored ($x10^3$)	Time to form C_1 (secs)	Total time (secs)
∞	2,940	0	11,982	28,321
12	2,137	72,759	7,821	18,377
5	709	58,542	2,004	4,610
4	538	48,878	1,341	3,055
3	286	35,605	593	1,295
2	166	7,527	204	428
1.3	121	1,845	134	279
1	94	1,262	110	242

Table 2. Comparison of estimates of reliabilities for different thresholds with J = ∞

	Correlations			Maximum Difference		
J	Direct reliability	Maternal reliability	Permanent reliability	Direct	Maternal	Permanent
5	1.0000	1.0000	1.0000	0.0183	0.0102	0.0006
4	1.0000	1.0000	1.0000	0.0254	0.0183	0.0018
3	0.9999	1.0000	1.0000	0.0257	0.0224	0.0027
2	0.9999	0.9998	1.0000	0.0277	0.0471	0.0021
1.3	0.9985	0.9989	0.9999	0.0576	0.0461	0.0127
1	0.9934	0.9974	0.9996	0.1739	0.0791	0.0266

are stored and more adjustments are ignored and the time increases dramatically. Table 2 compares correlations between estimates of reliabilities based on different thresholds for J. The value J = 2 would seem to be perfectly adequate for practical purposes for these parameter values.

Discussion

Calculation and analysis suggest that the MISZTAL and PEREZ-ENCISO (1993) method is to be preferred. Both the TIER and SMITH (1989) and the MISZTAL (1990) schemes essentially calculate non-zero elements in adjusted right hand sides of equations (the element in D in the TIER and SMITH scheme). TIER and SMITH (1989) calculate variances from weighted sums of squares of elements of D and MISZTAL (1990) from back solution of the set of equations. The former will normally take less calculation than the latter. In the numerical example above to calculate the variances for 1,500 effects associated with sires took over 30 000 seconds using the TIER and SMITH scheme, suggesting that the calculation of all variances would be 15–25 times as long as the partitioned method. MISZTAL (1989) gives comparative times involved in his method. If the operations involved in (4) are a third of the time in the partitioned method, then for his examples the partitioned method should be 15–25 times faster. Using a threshold of 2 gave acceptable prediction error variances and reduced the computing time by a factor of over fifty.

This work was initiated to provide an exact inverse as a benchmark for comparison with approximations resulting from extension of the approximate methods used for direct genetic effects to maternal genetic effects. However, as a by-product it has generated a flexible class of approximations, and several common approximations to prediction error variance can be considered as specific examples within this framework. For example, the reciprocal of the diagonals of animals after absorbing fixed effects, a simple and common way of approximating prediction error variances particularly under a sire model (e. g. approximation 1 of ROBINSON and JONES 1987) corresponds to using a very high threshold (J) for adjustments between sires after correction for fixed effects. Better approximations can be made, if say for the i-th animal the off-diagonals between it and its parents, progeny and fixed effects are used (e. g. MEYER 1989). In this case J is usually ∞, but $-\infty$ for the specified adjustments. Other iterative procedures (e. g. MISZTAL and WIGGANS 1988) do not fit into this frameworks as naturally, but certainly J = ∞ is used for some of their adjustments and iteration between a form of (4) and (8) is used.

The method is now used routinely to provide estimates of accuracies for predicted breeding values in the British genetic evaluation system for beef cattle. Breeding values are predicted using a multiple trait animal model (BRYAN et al. 1992) but accuracies are calculated using a single trait models for each trait separately. An approximate multiple trait accuracy for each animal is calculated by combination of the single trait accuracies, but this

will be the subject of a separate note. In principle, the procedure can be used for a multiple trait coefficient matrix but in most national genetic evaluations the number of equations is prohibitive at present. The computer time results for the method can be severely influenced by the order of the equations on which operations are performed. The order has been chosen so that equations expected to have the least number of off-diagonal elements are eliminated first based on numbers of descendants for sires and using female family structure for dams. This ordering is based on information routinely calculated for summarisation of the results of the genetic evaluation, and is therefore achieved at no extra cost.

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Summary

The use of exact and approximate algorithms to calculate prediction error variances using sparse matrix methods are demonstrated for an individual animal effect including maternal effects. One exact algorithm is substantially faster than two others. An approximation of the best exact method gave an acceptable level of reliabilities and reduced the computation by a factor of approximately fifty compared with the exact computation and is routine in national beef evaluation in Britain.

References

BIOCHARD, P.; LEE, A. J., 1992: Approximate accuracy of genetic evaluation under a single trait animal model. J. Dairy Sci. **76:** 868–887.

BOLDMAN, K. G.; VAN VLECK, L. D., 1991: Derivate free restricted maximum likelihood estimation in animal models with a sparse matrix solver. J. Dairy Sci. **7:** 7337.

BOND, D. G.; BRYAN, J. G. E.; GUY, D. R.; WEIGLEB, B.; CRUMP, R. E.; SIMM, G.; FINDLAY, R. H.; NICHOLSON, D.; THOMPSON, R., 1992: South Devon National Sire and Dam Summary. Milton Keynes: Meat and Livestock Commission.

BRYAN, J. E.; WRAY, N. R.; CRUMP, R.; THOMPSON, R.; BOND, D., 1992: Development and application of multi trait BLUP analysis to the UK beef industry. Proceedings, Bristol Cattle Breeders Club, Cambridge, **47:** 32–40.

ERISMAN, A. M.; TINNEY, W. F., 1975: On computing certain elements of the inverse of a sparse matrix. Communications ACM, **18:** 177–179.

GREENHALGH, S. A.; QUAAS, R. L.; VAN VLECK, L. D., 1986: Approximating Prediction Error Variances for Multiple Trait Sire Evaluations. J. Dairy Sci. **3:** 2877–2883.

JUGA, J., 1992: Estimation of variances and covariances of milk traits by REML with an individual animal model. Acta Agric. Scand., Seit A, Animal Sci. **42,** 198–204.

MEYER, K., 1989: Approximate Accuracy of Genetic Evaluation under an Animal Model. Livestock Production Science, **21:** 87–100.

MISZTAL, I. C., 1990: Restricted Maximum Likelihood Estimation of Variance Components in Animal Model Using Sparse Matrix Inversion and a Supercomputer. J. Dairy Sci. **73:** 163–172.

MISZTAL, I.; PEREZ-ENCISO, M., 1993: Sparse Matrix Inversion for Restricted Maximum Likelihood Estimation of Variance Components by Expectation Maximization. J. Dairy Sci. **76:** 1479–1483.

MISZTAL, I.; WIGGANS, G. R., 1988: Approximation of Prediction Error Variance in Large-Scale Animal Models. J. Dairy Sci. **71** (Sup. 2): 27–32.

TAKAHASHI,K.; FAGAN, J.; CHEN, M. S., 1973: Formation of sparse impedance matrix and its application to short circuit study. Proc. 8th Int. PICA Conf. Minneapolis.

TIER, B.; SMITH, S. P., 1989: Use of sparse matrix absorption in animal breeding. Genet. Sel. Evol. **21:** 457–469.

TIER, B.; SCHNEEBERGER, M.; HAMMOND, K.; FUCHS, W. C., 1991: Determining the accuracy of estimated breeding values in multiple trait animal models. Proc. 9th Conf. AAABG, Armidale, 239–241.

VAN RADEN, D. M.; FREEMAN, A. E., 1985: Rapid Method to Obtain Bounds on Accuracies and Prediction Error Variances in Mixed Models. J. Dairy Sci. **68:** 2123–2122.

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