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Estimation of Genetic (Co)Variances for Milk Yield in First Three Lactations Using an Animal Model and Restricted Maximum Likelihood

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ABSTRACT

Genetic relationships among lactation records are of interest because most selection of bulls is on first lactations. Selection also complicates estimation of genetic parameters. Techniques unbiased by selection should be used. Estimation of genetic and environmental (co)variances was done using restricted maximum likelihood with an expectation-maximization algorithm for an animal model. The algorithm involved solving mixed model equations by direct inversion of coefficient matrix that became feasible by neglecting relationships across herds. From data consisting of first to third lactation milk records of New York Holsteins, two computationally manageable subsets were selected of 15 herds each totaling 3070 and 2900 cows. Each cow had a recorded first lactation and a recorded second lactation if she had a recorded third record. Herds were chosen according to frequency of related animals and about 200 cows per herd. After 18 rounds of iteration, changes in estimates between successive rounds were constantly decreasing and small. Estimates averaged from both subsets gave heritabilities of $h_1^2 = .33$, $h_2^2 = .33$, $h_3^2 = .34$, genetic correlations of $r_{g12} = .86$, $r_{g13} = .85$, $r_{g23} = .87$, and phenotypic correlations of $r_{p12} = .57$, $r_{p13} = .52$, $r_{p23} = .65$.

INTRODUCTION

Development and realization of animal breeding plans require knowledge of the heri-

tabilities and phenotypic and genetic correlations of the traits considered. These parameters are needed to evaluate the breeding plan itself as well as to predict breeding values. In contrast to animal breeding plans for meat production, breeding plans for dairy cattle have to consider repetitive performance of the animal, i.e., the potential for more than one lactation per cow. Lifetime production is an important economic parameter when defining the breeding objective. The importance raises the question of whether the performance of a cow in subsequent lactations is repetitive enough genetically so that performance in first lactation can contribute useful information also about later lactations. A further question is how to combine records for evaluation purposes if information on more than one lactation is available. Often performance in later lactations is assumed to be genetically due to the same genes that influence performance in first lactation. The majority of procedures for prediction of breeding values in dairy cattle, therefore, either consider only first lactations or imply a genetic correlation of 1.0 between all lactations. With data usually available, the validity of this assumption is difficult to evaluate because selection has occurred based on knowledge of part of the data. In such cases, estimators of variances and covariances by methods such as Henderson's Method 3 are likely to be biased (11, 15, 16), and methods such as minimum variance quadratic unbiased estimation (MIVQUE), maximum likelihood (ML), and restricted maximum likelihood (REML) should be used (4). All three methods are computationally demanding for the multivariate case, especially for REML if no simplifying assumptions such as zero residual covariances (17) are made. Despite the computational difficulty, REML was chosen for the analysis presented in this paper because REML estimators, in contrast to ML estimators, are not biased by the estimation of fixed effects included in the model (2) and in contrast to

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MIVQUE are not greatly dependent on the use of appropriate prior values for variances and covariances (16).

The purpose of the study was to estimate the variances and covariances needed for multiple trait evaluation of production in different lactations and which also can be used to determine the urgency of using other than first lactation records for selection.

MATERIALS AND METHODS

Simulation studies by Meyer and Thompson (11) and Sorensen and Kennedy (16) have shown that ML estimators of variance components unbiased from selection can be achieved only if all available data are used. An animal model with complete relationship matrix makes use of all data. For multitrait analysis considering milk yield in first three lactations to be different traits, the following model was used:

$$y = Xb + Za + e \tag{1}$$

where y is a vector of observations of milk records in the first three lactations, b is a vector of fixed effects (herd-year-seasons), a is a vector of additive genetic values of individual animals for the three traits (lactation milk yields), e is a vector of residual effects, and X and Z are known incidence matrices for fixed and random effects.

Expectations and variances are defined as:

$$E \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \quad \text{Var} \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

The mixed model equations are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix} \tag{2}$$

Let n denote the number of animals and $t = 3$ the number of traits. With data ordered lactations within animals and missing lactations included as zero rows or columns, R is block diagonal having n blocks, R_k , or order t . Each block corresponds to the combination of traits recorded for a specific animal. If the

data are restricted to allow later lactations only if the preceding records are also available, t different R_k are possible. These are derived from R_0 , the $t \times t$ variance-covariance matrix of the residuals, by crossing out rows or columns associated with missing records. Instead of R_k^{-1} for animals with missing lactations, then R_k^- , the "zeroed" type of a g inverse of R_0 , is used (6) with the notation R^- instead of R^{-1} . $G^{-1} = A^{-1} * G_0^{-1}$ where $*$ denotes the direct product operation, A is the numerator relationship matrix, and G_0 is the $t \times t$ variance-covariance matrix among additive genetic effects.

The method applied was REML using the EM algorithm proposed by Henderson (4, 5). It consists of equating appropriate quadratics in \hat{a} and \hat{e} to their expectations where \hat{a} and \hat{e} are the vectors of solutions for random and residual effects from the mixed model equations with \hat{e} calculated as $\hat{e} = y - X\hat{b} - Z\hat{a}$. This is done iteratively, and at each round of iteration, the expectations are taken under the pretense that $G = \tilde{G}$ and $R = \tilde{R}$ where \tilde{G} and \tilde{R} are prior values of the additive genetic and residual variance-covariance matrices, respectively.

Equating the quadratics to their expectations under a general model gives the following equations.

$$\hat{a}'Q\hat{a} = \text{tr } Q(G - C_{22}) \tag{3}$$

where C_{22} denotes the submatrix of a g inverse of the mixed model coefficient matrix pertaining to the random effects, and:

$$\hat{e}'Q\hat{e} = \text{tr } Q(R - WCW') \tag{4}$$

where C is a g inverse of the mixed model coefficient matrix and $W = [X : Z]$.

For the model [1] given, Q in [3] and [4] can be specified by simplifying the equation for quadratics in \hat{a} and \hat{e} .

Quadratics in \hat{a} :

$$\text{tr } A^{-1}G = \hat{a}'_i A^{-1} \hat{a}_j + \text{tr } A^{-1}C_{ij} \tag{5}$$

Elements of [5] correspond to mixed model equations set up by ordering animals within traits. C_{ij} is the submatrix of C associated with traits i and j . Because $G = G_0 * A$, further simplification leads to:

$$\text{tr } A^{-1} A g_{ij} = \hat{a}'_i A^{-1} \hat{a}_j + \text{tr } A^{-1} C_{ij}$$

so that the ij^{th} element of G_0 , g_{ij} , is estimated by:

$$\hat{g}_{ij} = (\hat{a}'_i A^{-1} \hat{a}_j + \text{tr } A^{-1} C_{ij})/n \quad [6]$$

Computation of [6] can also be carried out under ordering of traits in animals as in [2] by picking the proper elements from \mathbf{a} and \mathbf{C} .

Quadratics in $\hat{\mathbf{e}}$:

$$\text{tr } \mathbf{Q}_{ij} \mathbf{R} = \hat{\mathbf{e}}' \mathbf{Q}_{ij} \hat{\mathbf{e}} + \text{tr } \mathbf{Q}_{ij} \mathbf{W} \mathbf{C} \mathbf{W}' \quad [7]$$

In contrast to [5], where \mathbf{Q}_{ij} was specified as A^{-1} for all i, j ($i, j = 1, \dots, 3$), \mathbf{Q} in [7] is different for each element, r_{ij} , of \mathbf{R}_0 , which is to be estimated. For $t = 3$, six different matrices \mathbf{Q}_{ij} ($j \geq i$) are necessary. All \mathbf{Q}_{ij} are defined as follows:

$$\mathbf{Q}_{ij} = \begin{bmatrix} \mathbf{B}_{1ij} & & & & & \\ & \mathbf{B}_{2ij} & & & & 0 \\ & & \ddots & & & \\ & & & \ddots & & \\ 0 & & & & & \mathbf{B}_{nij} \end{bmatrix}$$

The blocks along the diagonal of \mathbf{Q}_{ij} , \mathbf{B}_{kij} , are derived from the $t \times t$ blocks $\mathbf{R}_{\bar{k}}$ of \mathbf{R}^{-} . Let $\mathbf{R}_{\bar{k}} = [f_1 \ f_2 \ f_3]$, then $\mathbf{B}_{kii} = f_i f'_i$ and $\mathbf{B}_{kij} = f_i f'_j + (f_j f'_i)'$ for $i \neq j$. For the case of successive lactations there are three unique \mathbf{B}_{kij} for each of the six \mathbf{Q}_{ij} since there are three unique $\mathbf{R}_{\bar{k}}$. Of these 18 \mathbf{B}_{kij} , however, eight are null matrices so that for computation of [7], only 10 different \mathbf{B}_{kij} of order t have to be stored. In [7] the trace of a product of two block diagonal matrices of equal design involving \mathbf{R}_0 is equated to the sum of two scalars. If all $t(t+1)/2$ elements to be estimated are considered simultaneously, a solution is possible if [7] is expressed as:

$$\mathbf{T} \mathbf{r} = \mathbf{q}_1 + \mathbf{q}_2 \quad [8]$$

so that $\hat{\mathbf{r}} = \mathbf{T}^{-1} \mathbf{q}$ for $\mathbf{q} = \mathbf{q}_1 + \mathbf{q}_2$, where \mathbf{q}_1 and \mathbf{q}_2 are vectors containing the $t(t+1)/2 = 6$ scalars, $\hat{\mathbf{e}}' \mathbf{Q}_{ij} \hat{\mathbf{e}}$ and $\text{tr } \mathbf{Q}_{ij} \mathbf{W} \mathbf{C} \mathbf{W}'$. These can be accumulated animal by animal.

\mathbf{T} is symmetric of order $t(t+1)/2$ and can be set up directly after all animals are processed. For each r_{ij} , one row of \mathbf{T} is formed by multiplying all elements of the appropriate half-stored matrix \mathbf{B}_{kij} by the number of cows which show the specific combination of traits corresponding to the three unique \mathbf{B}_{kij} for all $i, j = 1, 2, 3$ ($j \geq i$). All elements $i \neq j$ in \mathbf{B}_{kij} are also multiplied by 2 and the products for the three combinations of traits are added together. The nonsingular, symmetric matrix \mathbf{T} results upon completion so that [8] can be solved.

The main computational problem in iterating on [6] and [7] is the need for the inverse of the coefficient matrix of [2]. The number of equations in [2] is equal to the number of levels for fixed effects plus the number of animals times the number of traits so that processing of a reasonably sized data set becomes impossible without making further simplifications. To simplify computations, canonical transformation of [2] in some cases results in unrelated residuals (12). The mixed model equations [2] then simplify to those for single trait analysis. This method, however, requires that all observations on traits recorded for a specific animal are assigned to the same classes of fixed and random effects. Under an animal model as given in [1], this is certainly true for the animal's additive genetic effects; all observations for a specific animal are assigned to this animal. For fixed effects the requirement is more difficult to fulfill. For the herd effect, it would be possible to restrict the data so that cows do not change herds. For year-seasons, however, obviously a later lactation is recorded for a different year-season as compared with the corresponding first lactation. However, under the assumption that calving intervals do not differ considerably from 365 d, assignment of all lactations recorded for a cow to a single herd-year-season would still be feasible. After screening the data available with respect to calving intervals, however, such an assumption was found to be invalid.

Other assumptions had to be made. If relationships across herds were ignored, it was possible to solve [2] herd by herd and to accumulate the quadratics in [6] and [7]. Now the order of each of the blocks of the coefficient matrix for which inverses were

needed was dependent mainly on herd size and the number of years included. For further reduction of the number of equations to be solved, no equations for base animals were set up. Base animals were those without records that created relationships among animals with records and would be mostly sires and dams without records. After directly obtaining A_+^{-1} with Henderson's rules, the inverse of the numerator relationship matrix including base animals without records, rows or columns for all base animals were absorbed into rows or columns for cows actually having records using rules for inversion of partitioned matrices as in (3). For:

$$A_+^{-1} = \begin{bmatrix} P_{11} & P_{12} \\ P_{12}' & P_{22} \end{bmatrix}$$

P_{22} is the submatrix of A_+^{-1} corresponding to relationships among cows actually having records, whereas P_{11} denotes the submatrix pertaining to relationships among base animals. A^{-1} , the inverse of the numerator relationship matrix of cows actually having records, is then found as:

$$A^{-1} = P_{22} - P_{12}' P_{11}^{-1} P_{12} \quad [9]$$

Although computation of [9] is costly in computing time, the reduction in computing time for the entire analysis is substantial because [9] has to be carried out only once for each herd.

The original data set consisted of mature equivalent lactation milk yields from 294,401 New York Holstein cows first freshening between 1977 and 1984 and passing usual edits. All cows were required to have a recorded first lactation; later lactations were accepted if preceding lactations were recorded. Processing of the entire data set was impossible due to the enormous computing time that would have been necessary. Therefore, a computationally manageable data set had to be selected. One requirement was a high frequency of related animals per herd. A second requirement was to balance the need for large herds against computing time for the inversion of the coefficient matrix for each herd. Increase of data per herd was expected to lead to improved likelihood functions, i.e., to avoid very flat likelihood functions.

The final data set was formed from two subsets. Each subset contained 15 herds. Herds were selected from the range of herd sizes of 170 to 230 for cows with first records. Frequency of related animals was monitored by inspection of the diagonal elements of A_+^{-1} , which was set up for 43 herds preselected arbitrarily by examination with the goals of a large number of daughter-dam pairs and a small number of sires per herd. A summary of the structure of the data is in Table 1.

Computing time was almost entirely dependent on the time for inversion of the herd blocks of the coefficient matrix. Time for inversion of one matrix of order 650 was 12 min central processing unit (CPU) time on an IBM 4341 computer so that for each data set approximately 3 h were needed for one round of iteration.

RESULTS AND DISCUSSION

For each replicate, 18 rounds of iteration were done. Starting values were found by trying out considerably different values in the following manner: two rounds of iteration used starting values far higher than what could be expected, and similarly two rounds used low values. Observed trends in these four rounds were combined into a final guess of starting values. However, it seemed that this way of finding starting values reduced only the magnitude of differences between estimates in the

TABLE 1. Structure of the data.

	Data set 1	Data set 2
Lactation 1		
No.	3070	2900
Mean, kg	9037	8552
Lactation 2		
No.	1943	1828
Mean, kg	9127	8769
Lactation 3		
No.	1080	1082
Mean, kg	8943	8682
Average cows per herd	205	194
Average equations per herd	655	620

TABLE 2. Starting values (round 0) and estimates¹ for residual (R_0) and additive genetic (G_0) variances and covariances for milk yield in first three lactations for 18 rounds of iteration (data set 1).

Round	R_0						G_0					
	r_{11}	r_{12}	r_{13}	r_{22}	r_{23}	r_{33}	g_{11}	g_{12}	g_{13}	g_{22}	g_{23}	g_{33}
0	.4560	.1970	.1520	.5510	.2820	.4940	.2500	.2390	.2210	.2880	.2490	.2770
1	.4750	.2132	.1667	.5663	.2838	.5063	.2544	.2431	.2248	.2921	.2525	.2805
2	.4846	.2226	.1756	.5746	.2865	.5129	.2560	.2444	.2260	.2935	.2534	.2815
3	.4897	.2280	.1810	.5794	.2891	.5169	.2562	.2445	.2260	.2935	.2531	.2814
4	.4926	.2313	.1844	.5824	.2914	.5195	.2559	.2438	.2254	.2930	.2522	.2808
5	.4843	.2335	.1867	.5844	.2933	.5214	.2552	.2429	.2245	.2921	.2511	.2799
6	.4956	.2351	.1884	.5859	.2949	.5229	.2544	.2419	.2235	.2911	.2498	.2788
7	.4965	.2363	.1896	.5871	.2963	.5241	.2536	.2408	.2225	.2900	.2485	.2778
8	.4973	.2374	.1907	.5881	.2975	.5251	.2527	.2397	.2214	.2889	.2471	.2767
9	.4980	.2383	.1917	.5890	.2986	.5261	.2519	.2386	.2203	.2879	.2458	.2757
10	.4987	.2392	.1925	.5898	.2997	.5269	.2511	.2375	.2193	.2868	.2445	.2747
11	.4993	.2401	.1933	.5906	.3007	.5277	.2503	.2364	.2183	.2858	.2433	.2737
12	.4999	.2409	.1941	.5913	.3016	.5284	.2495	.2354	.2173	.2848	.2420	.2727
13	.5005	.2416	.1948	.5920	.3026	.5291	.2487	.2344	.2164	.2839	.2408	.2717
14	.5011	.2424	.1955	.5927	.3034	.5298	.2480	.2334	.2154	.2830	.2397	.2708
15	.5016	.2431	.1962	.5933	.3043	.5305	.2473	.2325	.2145	.2821	.2385	.2699
16	.5021	.2438	.1969	.5939	.3052	.5311	.2466	.2316	.2137	.2812	.2374	.2690
17	.5026	.2445	.1975	.5945	.3060	.5317	.2460	.2307	.2128	.2804	.2363	.2682
18	.5031	.2452	.1982	.5951	.3068	.5323	.2454	.2298	.2120	.2796	.2352	.2674

¹ Estimates are standardized; multiply by 2,000,000 to convert to squared kilograms.

TABLE 3. Starting values and estimates¹ for residual (R_0) and additive genetic (G_0) variances and covariances for milk yield in first three lactations for 18 rounds of iteration (data set 2).

Round	R_0						G_0					
	r_{11}	r_{12}	r_{13}	r_{22}	r_{23}	r_{33}	g_{11}	g_{12}	g_{13}	g_{22}	g_{23}	g_{33}
0	.6861	.3124	.2376	.7441	.4172	.8601	.2733	.2443	.2655	.3057	.2878	.3358
1	.5934	.2748	.2295	.6374	.3619	.7017	.2608	.2317	.2520	.2923	.2738	.3208
2	.5588	.2531	.2151	.5954	.3337	.6443	.2550	.2257	.2455	.2858	.2668	.3135
3	.5444	.2410	.2044	.5762	.3179	.6189	.2527	.2229	.2426	.2828	.2635	.3099
4	.5377	.2340	.1972	.5666	.3087	.6061	.2520	.2219	.2415	.2816	.2620	.3083
5	.5343	.2300	.1925	.5613	.3031	.5989	.2521	.2217	.2412	.2813	.2615	.3078
6	.5323	.2276	.1894	.5583	.2995	.5947	.2527	.2220	.2414	.2815	.2615	.3078
7	.5309	.2259	.1873	.5564	.2973	.5919	.2535	.2224	.2419	.2819	.2616	.3080
8	.5299	.2248	.1859	.5551	.2957	.5900	.2543	.2230	.2424	.2825	.2620	.3083
9	.5289	.2239	.1846	.5541	.2946	.5888	.2552	.2237	.2430	.2830	.2624	.3088
10	.5280	.2231	.1837	.5533	.2938	.5878	.2561	.2243	.2436	.2837	.2628	.3092
11	.5272	.2224	.1831	.5526	.2933	.5871	.2571	.2250	.2443	.2844	.2633	.3097
12	.5264	.2218	.1824	.5520	.2927	.5864	.2580	.2258	.2450	.2850	.2638	.3101
13	.5256	.2212	.1818	.5514	.2923	.5860	.2590	.2265	.2456	.2857	.2643	.3107
14	.5249	.2207	.1813	.5509	.2918	.5856	.2599	.2271	.2462	.2862	.2646	.3111
15	.5242	.2201	.1807	.5503	.2915	.5851	.2608	.2277	.2469	.2869	.2651	.3115
16	.5234	.2197	.1803	.5497	.2912	.5848	.2617	.2284	.2474	.2876	.2655	.3119
17	.5227	.2191	.1798	.5493	.2909	.5844	.2626	.2290	.2480	.2881	.2658	.3124
18	.5221	.2186	.1794	.5488	.2905	.5841	.2634	.2296	.2485	.2887	.2663	.3127

¹ Estimates are standardized; multiply by 2,000,000 to convert to squared kilograms.

first two rounds and did not necessarily reduce the number of iterations needed.

Tables 2 and 3 show starting values and estimates of additive genetic and residual variances and covariances to round 18 for both data sets. All records were scaled by dividing by the overall standard deviation of first lactation milk yield to avoid round-off problems. In both data sets estimates for residual variances and covariances seemed to converge earlier than for additive genetic ones. This pattern is analogous to results of Rothschild and Henderson (14) who used an ML procedure for a sire model.

In data set 1, estimates for R_0 were constantly increasing with each round of iteration but were constantly decreasing in data set 2. In each data set, changes between estimates for R_0 in successive rounds were constantly decreasing. Estimates for G_0 were steadily decreasing after the third round of iteration in data set 1 and steadily increasing after round 7 in data set 2. Changes in estimates for G_0 between successive rounds were constantly decreasing after round 8 for data set 1 and after round 12 for data set 2. Monotonically decreasing changes between rounds were also found by Rothschild et al. (15) when applying an ML algorithm for 30 rounds of iteration for a data set simulated for a random effects model. As can be seen from Tables 2 and 3, convergence was not reached after 18 rounds of iteration. Changes, however, were very small.

Estimated parameters obtained from round 18 solutions are in Table 4. Similar trends can be seen in estimates from both data sets. In general, the estimates are somewhat in agreement with estimates by other authors for different Holstein populations. However, heritabilities are higher, especially for second and third lactations, than those commonly reported, which may be due to using an animal model that may be less affected by selection than sire models. Phenotypic correlations for both data sets are more similar than genetic correlations where the estimates show slightly different trends. As compared with given estimates (1, 7), the estimate $r_{g23} = .860$ appears to be slightly small for data set 1, and the estimate $r_{g12} = .833$ from data set 2 also seems to be somewhat small, whereas $r_{g13} = .866$ from the same data set may be too

TABLE 4. Estimated heritabilities (h^2) and genetic (r_g) and phenotypic (r_p) correlations for milk yield in first three lactations from two data sets.

Estimate	Data set 1	Data set 2	Averaged
h_1^2	.328	.335	.332
h_2^2	.320	.345	.333
h_3^2	.334	.349	.342
r_{g12}	.877	.833	.857
r_{g13}	.828	.866	.847
r_{g23}	.860	.886	.873
r_{p12}	.587	.553	.570
r_{p13}	.530	.510	.520
r_{p23}	.648	.642	.645

large. Pooling estimates across the data sets results in general agreement with the pattern found in the literature. When considering only studies that used ML procedures, estimates of genetic correlations are in good agreement with results by Tong et al. (17) and slightly smaller than in Rothschild and Henderson (14) and Meyer (8, 9, 10). Phenotypic correlations, and especially the estimate $r_{p23} = .645$, are somewhat larger than usually reported for repeatability, which may be due to using an animal model.

CONCLUSIONS

Estimation of genetic variances and covariances for first three lactations using REML for an animal model is computationally feasible. However, extensive computing time was required for the present analysis. Further research should concentrate on finding computing techniques that reduce the computing time needed so that larger data sets can be processed. One approach would be the derivation of a REML algorithm for a reduced animal model, which was presented by Quaas and Pollak (13) for genetic evaluation of animals. Another way to reduce computing time may be the use of supercomputers, which use vector mode to perform the extensive arithmetic needed in matrix inversion.

Estimated genetic parameters show a strong relationship between milk yield performance

in first three lactations. The estimates indicate that the expected response for lifetime production from selection and evaluation based on first lactations only or evaluation based on a constant repeatability therefore are justified especially when generation intervals (18) and present computing costs are considered.

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