Strategies for Estimating the Parameters Needed for Different Test-Day Models

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ABSTRACT

Currently, most analyses of parameters in test-day models involve two types of models: random regression, where various functions describe variability of (co)variances with regard to days in milk, and multiple traits, where observations in adjacent days in milk are treated as one trait. The methodologies used for estimation of parameters included Bayesian via Gibbs sampling, and REML in the form of derivative-free, expectation-maximization, or average-information algorithms. The first method is simpler and uses less memory but may need many rounds to produce posterior samples. In REML, however, the stopping point is well established. Because of computing limitations, the largest estimations of parameters were on fewer than 20,000 animals. The magnitude and pattern of heritabilities varied widely, which could be caused by simplifications in the model, over-parameterization, small sample size, and unrepresentative samples. Patterns of heritability differ among random regression and multiple-trait models. Accurate parameters for large multi-trait random regression models may be difficult to obtain at the present time. Parameters that are sufficiently accurate in practice may be obtained outside the complete prediction model by a constructive approach, where parameters averaged over the lactation would be combined with several typical curves for (co)variances for days in milk. Obtained parameters could be used for any model, and could also aid in comparison of models.

Key words: genetic parameters, test-day models, dairy cattle

Abbreviation key: AI = average information, CT = canonical transformation, DF = derivative free, EM = expectation maximization, HTD = herd test day, MCMC = Markov-chain Monte Carlo; PE = permanent environmental, RRM = random regression model; TDM = test-day model.

INTRODUCTION

A current trend is to change the data used for genetic evaluation from combined 305 d to test days. While models used for the 305-d records were relatively simple and required just a few parameters, models used for analyses of test days are much more complex and may require hundreds of parameters. Estimation in models with a large number of parameters is computationally expensive, and requires a compromise in size of data, type of data, or methodology. If estimated parameters are biased or have high sampling variance, gains expected from the use of test-day data may not be realized.

The most general test-day model (TDM) for random effects is a daily multiple-trait model; each test-day record is treated as a separate trait. Because such a model is overparameterized and computationally unfeasible, various simplified models have been proposed. Although more complex models should, in general, be more accurate, in practice the difference can be small, while computational demands could be drastically higher. The goal of parameter estimation in test-day models is not to obtain “true” estimates because, as such, they do not exist, but to achieve an acceptable compromise between model complexity and accuracy of estimation. Various TDM can be compared on the basis of likelihood (20) or mean square error of prediction.
The goal of research is to review methods currently used to estimate parameters in TDM, to propose a new methodology, and to present a methodology for comparing various TDM.

305-D MODELS AND TDM

In 305-d models, the unit of information is 305-d yield. A popular 305-d model is a repeatability model as used by USDA for production traits (44). It is a single-trait model with three random effects: animal additive, permanent environmental, and herd x sire interaction. Three parameters per trait are sufficient for this model, although they are augmented to allow for heterogeneous intraherd and regional variance (45). Parameters for the three production traits are very similar. Thus, just a few parameters are sufficient for milk, fat, and protein yields.

In TDM, the unit of information is one test-day yield. (Co)variances of test-day records vary with DIM. Several hypothetical shapes of additive variance as a function of DIM are shown in Figure 1. Also, the correlation between test-day records at different DIM, say DIM1 and DIM2, can vary. Such correlations can be represented as a two-dimensional function. Sections of such a function as hypothetical correlation curves between DIM of \{30, 90, 270\} and an arbitrary DIM are shown in Figure 2.

In the most complete but overparameterized TDM, each daily observation would be treated as a separate trait. For three parities, each with a length of 305 d, a total of 915 traits would be present. If three milk components per parity are treated as correlated traits, a total of 2745 traits would be defined. Such a model would require millions of parameters and is of theoretical importance only because of excessive computations.

Also, because contemporary groups in the form of test-day DIM would mostly have only one animal, resulting in a large loss of data, these groups would have to be redefined. Therefore, in practice, simplified models need to be used.

The assumptions of flat (co)variances with regard to DIM leads to the repeatability TDM (29). Two random effects in this model for one trait and single parity would be animal and permanent environment, although herd test day (HTD) also could be random (27, 28). Multiple parities can be added by assuming very high correlations among parities and having several permanent environmental effects, one for each parity and one across parities; or as correlated traits as in model used for national evaluations in Germany (30).

The assumption of functional variances and covariances leads to a random regression TDM (34). In such a model, all covariances vary with DIM; shape is specified by the function used in random regressions. For example, quadratic random regressions would result in fourth-order shapes for (co)variances for DIM and quadratic shapes for (co)variances between two different DIM. An important issue in random regression models (RRM) is assigning functional variances to all effects in the model, including the residual. Assumption of constant variance to any random effect could lead to bias in heritability estimates.

Another set of simplified TDM would be reduced dimensionality models. In block multiple-trait models, which are generally called TDM multiple-trait models, traits for blocks of adjacent DIM would be assumed identical (14, 32, 39, 40). For example, all observations for DIM of 1 to 30 would be redefined as first trait, those for 31 to 60 as second, etc. [model used for comparison by Rekaya et al. 1999 (32)]. In a principal components
Table 1. Number of variance parameters in different test-day models for three types of data.

<table>
<thead>
<tr>
<th>Type of model</th>
<th>Single parity and 1 trait</th>
<th>3 parities and 1 trait</th>
<th>3 parities and 3 traits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Repeatability</td>
<td>2</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>Quadratic random regression</td>
<td>15</td>
<td>99</td>
<td>810</td>
</tr>
<tr>
<td>Reduced dimensionality-monthly</td>
<td>90</td>
<td>930</td>
<td>8190</td>
</tr>
<tr>
<td>Reduced dimensionality-principal components</td>
<td>?</td>
<td>?</td>
<td>?(42)</td>
</tr>
</tbody>
</table>

1Assumes single-trait model with one permanent environment effect per parity.

approach (45), it is assumed that most eigenvalues of (co)variance matrices in the general TDM are very close to 0, and therefore a transformation of data is possible that would result in much lower dimensionality models. Such models are not useful for parameter estimation because a canonical-transformation (CT) algorithm with missing data is not available.

Table 1 shows the number of parameters necessary for several simplified models and several types of data. The number of parameters increases drastically from a few in the 305-d model to a few thousand for some simplified models. The only difference between repeatability and RRM is in shapes added in the latter. A RRM allows for different shape of each variance and covariance among traits and parities, resulting in the increase in the number of parameters by a factor of \((r + 1)(r + 2)/2\), where \(r\) is the order of regression. This increase is 6 times for quadratic regressions and 10 for cubic over the number of parameters for the repeatability model. If shapes of many variances and covariances are similar or even nearly identical, the RRM can possibly be simplified, and its number of parameters could be greatly reduced (45).

### ESTIMATION OF PARAMETERS

#### General Procedures

Parameters of the general TDM (with one trait per each day of lactation) cannot be estimated directly and, therefore, parameters are estimated for simplified models. Two procedures are usually used for estimation. The first procedure is estimation by the same model that is to be used for predictions of breeding values (11, 30). Estimation is by a general-model method that supports different models per trait and missing traits. All limitations of the model of estimation will be present in the estimates. In the second procedure, a block multi-trait procedure is used, usually with blocks of about 30 d, which would result in 10 traits with one milk component to 30 traits with three milk components (32, 43). Parameters of this procedure are used to gain information on shapes of (co)variances with respect to DIM and for eventual conversion to covariance functions (16) and RRM. Estimation is either by a general-model method or by CT, as discussed later. Because of computational limitations of general-model procedures, parameters of a large model would be obtained by combining results of many two- to three-trait analyses. Because the complete (co)variance matrices are nearly singular, they are likely to be estimated as non-positive-definite and may require adjustments to become positive-definite. If estimation is by CT, the data need to be edited so that only complete records are analyzed and contemporary groups are the same for all traits. With CT, all traits can be analyzed simultaneously, much larger data sizes are possible, and estimates are positive definite. Greater accuracy in CT via the possibility of using more data is offset by bias caused by data editing, ignoring differences within classes of DIM, and having the same contemporary groups for all traits.

#### Methods for Parameter Estimation

Parameters in TDM are obtained by three methodologies: general-model REML, general-model Markov-chain Monte Carlo (MCMC) via Gibbs sampling, and CT REML. Currently, most analyses with REML use derivative as opposed to derivative-free (DF) maximization because of greater numerical stability and lower cost when the number of parameters is high. The expectation-maximization (EM) algorithm (19) using first derivatives only as used in DMURR by E. A. Mäntysaari or REMLF90 (22) is very stable, but the convergence rate is slow, and 100 to 300 rounds may be necessary for satisfactory convergence. The average information (AI) REML (6, 12, 21) uses second derivatives. It may converge in fewer than 10 rounds, but in instances when the AI matrix is not positive definite, the convergence requires heuristics and may not occur or be much slower. Computationally, the derivative REML is restricted memory- and time-wise by sparse matrix factorization and inversion. With FSPAK (26) or FSPAK90 (25), the limits are about 300,000 equations with 512 Mbytes of memory, with variations due to models. The computing time increases approximately quadratically with respect to number of animals and cubically with respect to number of traits and order of random regressions. MCMC methods (13), popularly called Gibbs sampling, require only storage of the mixed model equations and, consequently, have memory requirements proportional to the number of animals. Computing time per
round increases approximately linearly for the number of animals. Increase for number of traits and the order of random regressions is quadratic for scalar sampling and becomes cubic for block sampling with large blocks. Block sampling results in much faster mixing and, therefore, a smaller number of rounds for burn-in to obtain sufficiently accurate posterior means. The necessary number of rounds is not as easily determined as in REML and could be 100,000 or higher, resulting in long running times.

Canonical transformation REML (20) is an extension of single-trait REML to multiple traits at low cost. Supported models are restricted to same model per trait, no missing trait, and one random effect, although an approximation allows for several random effects (18, 23). The main advantage of CT REML is cost, because computations increase linearly with the number of traits and memory increases very little. Also, the CT REML procedure contains mechanisms to compute estimates reliably from highly correlated traits. While general REML is limited in practice to about six traits, CT REML could handle over 30 traits with much larger data sets.

Results of Analyses

Results of many studies on TDM have been summarized by Swalve (38). Recent studies include analyses with one-trait fourth-order random regression and three-trait repeatability model using MCMC by Rekaya et al. (32), and with two-trait quadratic RRM by Strabel and Misztal (36).

The largest analysis so far in terms of number of estimated parameters was a 12-trait model (4 dairy traits × 3 parities) using a RRM with Wilmink function by MCMC using block Gibbs sampling (10); computations with about 3700 animals with records took weeks. The same analysis was recently extended to fourth-order random regressions in an analysis that took 3.5 mo of computing. The same order of random regression with larger data but in single-trait only was reported in a study by Rekaya et al. (32), who used data on approximately 14,000 animals with records. The same study also reported an analysis with a three-trait repeatability model; the RRM model was not used for multiple-trait analysis probably because of excessive computations. The largest analysis with REML was by Strabel and Misztal (36), who analyzed a two-trait quadratic RRM with data on approximately 12,000 animals. The calculations with the accelerated EM REML algorithm took about 2 wk.

Parameters obtained in various models and with various data sets show great variability in both average values and shapes. The average daily heritability of the
shapes of variances between first and third lactation, second and third, shape of heritability at third lactation, and shape of covariances among milk components.

Shapes of heritability are most likely as heterogeneous as variances. Gengler at al. (5) found different shapes of heritabilities for milk, fat, and protein in data sets from different states. While accounting for heterogeneous within-herd variance is straightforward in repeatability models (17), accounting for different shapes of variances may be limited to only a few classes (41).

Large variability of estimates in various studies including shapes could be due to several factors, including too simplified models, small amount of data and resulting large sampling errors, unrepresentative data samples, and artifacts of random regressions where extremes greatly influence the estimates. A complete TDM should account for variations in DIM for all the effects. While current studies account for variations for the PE effect, in most studies the residual variance is either fixed or estimated in a few discrete steps. Variations in the residual with a polynomial shape can be accounted for by inserting extra effects in the model corresponding to linear and higher terms, with a large increase in the number of equations (7), by changes to mixed model equation following the ideas of Foulley et al. (3, 4) and Foulley (2), or by changepoint techniques (31).

If random regressions are used, an important consideration is the order and type of regressions. Regressions with three terms, either polynomial quadratic, quadratic with Legendre polynomials, or by Wilmink’s function, are commonly used but may not be able to model the random variations accurately, for example if the real shape is similar to the phenotypic shape. With three terms, few data points at the beginning and at the end of lactation together with insufficient flexibility of three order regressions can result in best fit in the middle of the lactation, which would lead to poor fit in the extremes. Higher order regressions are likely to model the shape of variances better (9, 27, 40), but with a large increase in the number of parameters and poor extrapolating properties. Splines are one alternative to polynomials (42). They are probably easier to fit than high-order polynomials, partly because there are fewer variance components, and, partly because the curves are local, i.e., a parameter for a curve has only an effect between three knots. One problem with splines is the computational cost, which probably led to the use of the sire model by White et al. (42).

Variance of various effects in test-day data are relatively flat with DIM but correlations among effects for two different DIM vary. With random regressions, if complex fit is attempted for the correlations, artifacts...
may appear for variances with DIM. A regular pattern of correlations between DIM can be modeled by autoregressive models, thus reducing the artifacts. Carvalheira et al. (1) modeled the PE effect by a first-order autoregressive process. In a more general model, additive effect could also be modeled by such a process.

Because of the large number of parameters estimated, studies in TDM use relatively small data sets. Also, data sets are usually selected from larger herds with more complete recording, and sometimes records of animals with incomplete test-day records are removed. Although the small size results in large sampling variances, data selection could cause bias, and estimates may not be representative of the complete data set. Even small errors in parameters of polynomials can have a relatively large effect on their shape. Approximate sampling errors can be obtained from AI REML and standard errors of the posterior could be obtained from MCMC procedures. However, insufficient length of Gibbs chain could result in an underestimation of standard errors.

**Dilemmas**

The current procedures may not be able to accurately estimate parameters for multi-trait TDM with variability because DIM is not fully accounted for. The parameters can be estimated more accurately by methodological improvements, making computations more reliable and less expensive, or by creating the parameters from partial models, which will be described later as the constructive approach.

**Methodological Improvements**

Most of the parameters in the RRM are used for describing shapes of variances and covariances with respect to DIM. Variance for each trait and each covariance among the traits is allowed two shapes: one single-dimensional to describe variation due to DIM, and one two-dimensional describing correlations between two DIM. For random regression of order r, this results in the r(r + 1)/2 increase in the number of parameters. In fact, shapes for many variances may be nearly identical. Estimation of parameters describing almost identical shapes would result in negligible improvement in predicted breeding values, but could also lead to numerical problems due to nearly singular matrices. At best, RRM would have a dimensionality-reduction feature, similar to that found in CT REML and as studied by Meyer (21) and Van Der Werf et al. (40). Consider a random regression term from a RRM:

\[ \sum_{i=1}^{n} \alpha_i a_{ij} = \alpha_a a_j, \text{ var}(a_j) = G_0 \]

where \( \alpha_i \) is the covariable i and \( a_{ij} \) is the animal effect j corresponding to the covariable i. The variance of the animal effect for the animal j is \( G_0 \). Find eigenvectors \( V \) and eigenvalues \( D \) of \( G_0 \), and reparameterize the random regression terms:

\[ G_0 = VD\bar{V}, \quad \alpha* = V\alpha, \quad a* = V' a_j, \quad \text{var}(a_j) = D \]

so that the variance of the \( a* \) effect is diagonal. Then, covariates corresponding to very small eigenvalues can be eliminated. Such a diagonalization and covariate-elimination process could be repeated during estimation until convergence, and would result in nearly orthogonal although complicated terms for random regressions.

In derivative REML, the majority of computations are in sparse matrix factorization and inversion. FSPAK (26), which is a popular choice for such computations, is a scalar package. If the factorization and inversion are by dense blocks, memory requirements can be almost halved and computing speed increased by a factor of 10 (Ian Duff, 1999, personal communication).

**CONSTRUCTIVE APPROACH**

Moderate deviations of parameters from their optimum values, say 20%, have negligible effect on accuracy of breeding values. Single-trait sire models are known for robustness against incorrect parameters (35). Schaeffer (33) found a very small increase in prediction error variances when differences between true and estimated covariances were below 0.3. Additionally, because of compromises the “true” parameters do not exist in TDM, and attempts to estimate parameters in complex models with large data sets may divert attention from issues found important in other models that have not been studied in TDM. Such issues include ways to model heterogeneous variances, age adjustments as a function of DIM, and properties of estimates of unknown parent groups with random regressions.

The optimal strategy for estimation of parameters in TDM may be to obtain estimates that result in “reasonable” estimates of heritabilities and genetic correlations, and have “reasonable” shapes. Such parameters for any TDM can be assembled by the following procedure, which may be called the constructive approach:

1. Obtain variance-covariance matrices for additive, PE, and residual effects for all combinations of traits and parities, averaged over DIM:
where i (j) denotes a parity × trait combination.

2. Create a set of standarized shape functions that model a) changes of variances as a function of DIM:

\[ G_0 = \{ g_{0ij} \}, \quad R_0 = \{ r_{0ij} \} \]

\[ f_i(dim), i = 1, n_f, h(dim,dim) = 1 \]

and b) correlations between two different DIM.

\[ h_i(dim1,dim2), i = 1, n_h, h(dim, dim) = 1 \]

where \( n_f \) and \( n_h \) are numbers of one- and two-dimensional functions, respectively; \( n_f \) and \( n_h \) may be smaller than the number of trait × parity combinations because each of the functions may be used for several combinations.

3. Assign two functions to each variance component: one one-dimensional and one two-dimensional.

4. Create a function that calculates (co)variances for any combination of traits and DIM. If \( f_k \) is assigned to trait i and \( f_k \) is assigned to trait j, and if \( h_l \) is assigned to the combinations of traits i and j for the effect associated with \( G_0 \), this function can be constructed as:

\[ g^{(i,j,dim1,dim2)} = g_{0ij} \sqrt{f_k(dim1) f_l(dim2) h_{1(dim1, dim2)}} \]

5. Use the above function to create (co)variance matrices for any TDM, for example in a way similar to methods used to construct covariance functions (16).

Let \( G' \) be a (co)variance matrix for one effect in a RRM, and let \( q_{ik} \) be vector of covariates for trait × parity i and DIM k. Then, \( G' \) can be estimated by least squares by minimizing

\[ \sum_{i} \sum_{j} \sum_{k=1}^{305} \sum_{l=1}^{305} [g^{(i,j,k,l)} - q_{ik} G' q_{il}]^2 \]

A weight function could result in better fit for parts of lactation that need to be estimated more precisely.

Matrices in step 1 can be obtained via a repeatability TDM and partially by using the literature and common sense. Parameters describing the first part of the first lactation are likely to be the most critical because they influence evaluations of an animal with little information. Similarly, parameters corresponding to later lactations are less critical. Shapes can be obtained by running simpler, single- or two-trait analyses. A library of shapes with known properties can be developed and used as needed.

**Numerical Example**

Let

\[ G_0 = \begin{bmatrix} 1 & 2 \\ 2 & 5 \end{bmatrix} \]

Assume that all variances are modeled by function \( f_1 \) with value of \( \alpha \) at DIM = 1, value of 0.6\( \alpha \) for DIM = 50, value of 0.5\( \alpha \) for DIM = 200, value of 0.8\( \alpha \) for DIM = 250, and value of 0.6\( \alpha \) for DIM = 305; other values were obtained by linear interpolation and \( \alpha = 1.57 \) was a normalizing constant. Assume the first-order autoregressive structure of all correlations as modeled by \( h_1 \):

\[ h_1(dim1, dim2) = \rho^{dim1 - dim2} \]

where \( \rho \) is chosen so that \( h_1(1,305) = 0.4 \). Specific values of the computed (co)variances for some points were:

\[ g^{(1,1,1,1)} = 1.57, g^{(1,1,1,301)} = 0.50, g^{(1,1,301,301)} = 0.97 \]

Assume random regression with covariates of the form

\[ \text{dim1/305}^i \]

for each trait, where \( i \) is the order of regression. For the quadratic regressions, i.e., three random regression coefficients, \( G' \) is (2×3) × (3×2) matrix, and is estimated as:

\[
G' =
\begin{bmatrix}
1.485 & -2.405 & 1.481 & 2.970 & -4.810 & 2.962 \\
2.970 & -4.810 & 2.962 & 7.245 & -12.025 & 7.405 \\
-4.810 & 18.967 & -14.997 & -12.025 & 47.420 & -37.495 \\
\end{bmatrix}
\]

For fourth-order regressions, the part of \( G' \) due to the first trait only is:

\[
G' =
\begin{bmatrix}
1.654 & -4.204 & 6.232 & -3.154 & -0.106 \\
-4.204 & 28.115 & -56.598 & 32.362 & 0.299 \\
6.232 & -56.598 & 136.304 & -85.194 & -0.954 \\
-3.154 & 32.362 & -85.194 & 56.259 & 0.666 \\
-0.106 & 0.299 & -0.954 & 0.666 & 0.343
\end{bmatrix}
\]
If there is only one set of functions $f$ and $h$, and if $G'_{1}$ is the block of $G'$ due to trait 1, the complete $G'$ can be created by:

$$ G' = G'_{1} \otimes G_{0} / g_{011} $$

Figure 6 presents variances as functions of DIM as assumed and as estimated by quadratic and fourth-order random regressions. Both regressions modeled the shape of variances quite well, although they lacked the ability to model more complex variations of variances around $\text{DIM} = 250$. Both regressions resulted in inflated variances at large DIM. Figure 7 presents correlations between the first and given DIM. For the autoregressive shape of correlations, the quadratic random regression inflated correlations at close DIM and reduced correlations at distant DIM. The fourth-order regression modeled the correlations more accurately.

**Advantages of the Constructive Approach**

The constructive method offers a few advantages. First, parameters averaged over the lactation and simple shapes are relatively easy to obtain, e.g., from a repeatability TDM or even from the literature. Second, all parameters can easily be verified as “reasonable,” including all (co)variances and shapes. Third, the parameters obtained from the constructive method can be used to create parameters for any simplified model, including the principal component model. In particular, parameters created for higher-order regressions can be analyzed for possible reparameterization of regressions for reduced dimensionality, as discussed previously. Fourth, parameters for extended lactations with DIM $> 305$ can be obtained reasonably accurately even in the absence of large data for these DIM. Also, the parameters could be useful for other analyses, such as creation of parameters for hybrid models combining 305-d and test-day data, and for comparison of models.

**TDM and Data Structure**

The constructive approach could also be used in research on the effects of data structure on parameter estimates at a cost being a small fraction of that necessary for a similar analysis with real data. For instance, to visualize the quality of estimates with data restricted from extreme DIM, as studied experimentally by Pool and Meuwissen (27), the parameters of random regressions were estimated using variances with DIM restricted to the range of 30 to 250. The variances shown in Figure 8 were relatively stable at low DIM but were overestimated over 2.5 times for quadratic and over 4.5 times for fourth-order regression at high DIM. The correlations, as shown in Figure 9, had not changed much for the quadratic but were approaching 0.0 for the extreme DIM in the fourth-order regressions.

**Model Comparison**

Given general parameters obtained by the constructive methods, the next problem is selection of a parsimo-
nious model. Comparison of several models assuming that parameters obtained by the constructive approach are correct can be done as follows:

1. for every animal generate DIM for all hypothetical observations,
2. generate variance components corresponding to generated DIM and desired traits,
3. generate random values using generated variance components,
4. create records, using general procedures,
5. eliminate some test days to simulate missing data particular to a desired structure,
6. estimate parameters for models under comparison,
7. predict breeding values using all models,
8. compare breeding values with those used in data generation.

A particular shape of fixed effect due to DIM needs to be assumed in point 4.

CONCLUSIONS

Current parameter estimation in TDM is from simplified models. Estimates obtained from these models show large variation from analysis to analysis that are due to idiosyncrasies of models and small size of data used. More reliable estimates can be obtained by making the estimation methodology more efficient, or by abandoning the attempt to estimate all parameters in one model. The constructive approach, where parameters are created from parameters averaged over lactation and (co)variance curves, allows parameters to be obtained with predictable properties for any TDM, and also allows for model comparison.

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