

Iterative Solution of Random Regression Models by Sequential Estimation of Regressions and Effects on Regressions

N. Gengler,^{*1,2} A. Tijani,² and G.R. Wiggans³

**Passage des Déportés 2, B-5030 Gembloux, Belgium*

phone + 32 81 62 22 06, fax + 32 81 62 21 15

e-mail: gengler.n@fsagx.ac.be

¹*National Fund for Scientific Research, B-1000 Brussels, Belgium*

²*Animal Science Unit, Gembloux Agricultural University, B-5030 Gembloux, Belgium*

³*Animal Improvement Programs Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705-2350, USA*

Abstract

An alternative algorithm for solving random regression test-day models was developed to allow use of those models for extremely large data sets such as the U.S. database for dairy records. The algorithm also facilitates integration of data from 305-day records when no test-day records are available and simplifies development of an index for lactation performance that includes genetic differences in lactation curve (persistence) and genetic effects of parity (maturity rate). Equations are solved in two iterative steps: 1) estimation or update of regression coefficients based on test-day yields for a given lactation and 2) estimation of fixed and random effects on those coefficients. Solutions were shown to be theoretically equivalent to regular solutions for this class of random regression model. In a test computation with 57,034 first-lactation test-day milk yields from 7173 Holstein cows, correlations between solutions from the two solution methods were all >0.98 after only two iterations on the two steps. In addition to the relative simplicity of the proposed method, it allows several other techniques to be applied in the second step: 1) a canonical transformation to simplify computations (uncorrelated regressions) by making use of recent advances in solving algorithms that allow missing values; 2) a transformation to limit the number of regressions and create variates with biological meanings such as total yield, persistence, and maturity rate; 3) more complicated (co)variance structures than those usually considered in random regression models (e.g., additional random effects such as interaction of herd and sire); and 4) accommodation of additional traits for cows without test-day records.

1. Introduction

Random regression models (e.g., Schaeffer and Dekkers, 1994) that have been proposed for analysis of test-day yields (Jamrozik *et al.*, 1997) are computationally demanding, and until now few algorithms existed that could be used to simplify the computations. A (co)variance function can be defined as a continuous function that represents the variance and (co)variance of traits measured at different points on a trajectory (Kirkpatrick *et al.*, 1990; Kirkpatrick *et al.*, 1994; Meyer and Hill, 1997). Recently, the equivalence

between random regression and (co)variance function models was shown (Meyer and Hill, 1997, van der Werf *et al.*, 1998). Therefore, (co)variance function coefficients can be computed directly as (co)variance components of the equivalent random regression model. The equivalence between random regression and (co)variance function models also can be used to simplify computations of random regression models (van der Werf *et al.*, 1998). The objective of this study was to develop an alternative algorithm to solve a random regression test-day model for use with extremely large data sets, such as the U.S. national database of dairy records. Additional objectives were to facilitate the

integration of data from 305-day records when no test-day records were available and to simplify the development of an index for lactation performance that includes genetic differences in lactation curve (persistence), and genetic effects of parity (maturity rate).

2. Equivalence Between Random Regression And Infinite-Dimensional Models

Consider the following model to represent a special class of random regression models:

$$\begin{aligned} \mathbf{y} &= \mathbf{X}\mathbf{b} + \mathbf{Q}\mathbf{r} + \mathbf{e} \\ &= \mathbf{X}\mathbf{b} + \mathbf{Q}(\mathbf{W}\mathbf{c} + \mathbf{Z}\mathbf{a} + \mathbf{p}) + \mathbf{e} \end{aligned}$$

where \mathbf{y} is the vector of observations (e.g., traits within animal), \mathbf{b} is a vector of time-dependent fixed effects (e.g., herd test-day), \mathbf{X} is an incidence matrix linking \mathbf{y} and \mathbf{b} , \mathbf{r} is a vector of time-independent random effects (e.g., phenotypic cow effects with several

effects per animal representing regression coefficients), \mathbf{Q} is a covariate matrix linking \mathbf{y} and \mathbf{r} and transforming time-dependent \mathbf{y} to time independent \mathbf{r} , \mathbf{c} is a vector of time-independent fixed effects (e.g., age-season of calving), \mathbf{W} is an incidence matrix linking \mathbf{r} and \mathbf{c} , \mathbf{a} is a vector of random additive genetic effects, \mathbf{Z} is an incidence matrix linking \mathbf{r} and \mathbf{a} , \mathbf{p} is a vector of random nongenetic cow effects, and \mathbf{e} is a vector of residual effects (e.g., measurement errors).

The means and covariance structures of \mathbf{y} , \mathbf{r} , \mathbf{a} , \mathbf{p} , and \mathbf{e} can be summarized as

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{r} \\ \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{X}\mathbf{b} + \mathbf{Q}\mathbf{W}\mathbf{c} \\ \mathbf{W}\mathbf{c} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and}$$

$$\text{Var} \begin{bmatrix} \mathbf{y} \\ \mathbf{r} \\ \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{Q}\mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}'\mathbf{Q}' + \mathbf{Q}(\mathbf{I} \otimes \mathbf{K}_P)\mathbf{Q}' + \mathbf{R} & \mathbf{Q}\mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}' + \mathbf{Q}(\mathbf{I} \otimes \mathbf{K}_P) & \mathbf{Q}\mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G) & \mathbf{Q}(\mathbf{I} \otimes \mathbf{K}_P) & \mathbf{R} \\ \mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}'\mathbf{Q}' + (\mathbf{I} \otimes \mathbf{K}_P)\mathbf{Q}' & \mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}' + \mathbf{I} \otimes \mathbf{K}_P & \mathbf{Z}(\mathbf{A} \otimes \mathbf{K}_G) & \mathbf{I} \otimes \mathbf{K}_P & \mathbf{0} \\ (\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}'\mathbf{Q}' & (\mathbf{A} \otimes \mathbf{K}_G)\mathbf{Z}' & \mathbf{A} \otimes \mathbf{K}_G & \mathbf{0} & \mathbf{0} \\ (\mathbf{I} \otimes \mathbf{K}_P)\mathbf{Q}' & \mathbf{I} \otimes \mathbf{K}_P & \mathbf{0} & \mathbf{I} \otimes \mathbf{K}_P & \mathbf{0} \\ \mathbf{R} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix}$$

where \mathbf{K}_G and \mathbf{K}_P are coefficients of the genetic and environmental covariance functions, respectively, and \otimes is the Kronecker product function.

The random regression model also can be written to represent an infinite-dimensional model in which $\mathbf{t} = \mathbf{Q}\mathbf{r}$:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{t} + \mathbf{e}$$

For every animal i with records,

$$\mathbf{y}_i = \mathbf{X}_i\mathbf{b} + \mathbf{t}_i + \mathbf{e}$$

where \mathbf{t}_i represents a vector of cow-specific effects that are observed for cow i .

The variance of \mathbf{t}_i then can be subdivided into genetic \mathbf{G}_i and environmental \mathbf{P}_i parts and modeled using covariance functions:

$$\begin{aligned} \text{Var}(\mathbf{t}_i) &= \mathbf{G}_i + \mathbf{P}_i \\ &= \mathbf{Q}_i\mathbf{K}_G\mathbf{Q}_i' + \mathbf{Q}_i\mathbf{K}_P\mathbf{Q}_i' \end{aligned}$$

The regression covariate matrix \mathbf{Q} is defined in general and can have different structures. The easiest way to understand this structure is through an example, e.g., the

analysis of milk, fat, and protein yields on first-lactation test days. Then,

$$\mathbf{Q} = \begin{bmatrix} \mathbf{Q}_1 & \dots & \mathbf{0} & \dots \\ \dots & \dots & \dots & \dots \\ \mathbf{0} & \dots & \mathbf{Q}_i & \dots \\ \dots & \dots & \dots & \dots \end{bmatrix}$$

where the milk, fat, and protein test-day yields are ordered as observations within trait within animal so that \mathbf{Q} can be split into \mathbf{Q}_i blocks with a different block for each of i animals. Each block is calculated as

$$\mathbf{Q}_i = \begin{bmatrix} \phi_{m_i} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \phi_{f_i} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \phi_{p_i} \end{bmatrix}$$

where ϕ is defined as the matrix of regression variables associated with test-day yields for milk (m), fat (f), or protein (p) for animal i . The ϕ matrices for milk, fat, and protein can be different, e.g., no protein recorded or more observations for milk than for component traits.

3. Alternative Solution Algorithm

Solution of a random regression model normally is done through mixed model equations:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} & \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{c}} \\ \hat{\mathbf{a}} \\ \hat{\mathbf{p}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}.$$

Because those equations are large and dense, their solution is difficult for large populations. However, the mixed model equations can be subdivided into two sets of equations that can be solved sequentially. The first set of equations estimates \mathbf{b} and \mathbf{p} ; the second estimates \mathbf{c} and \mathbf{a} .

3.1 Estimation of \mathbf{b} and \mathbf{p}

At iteration $k+1$, the new estimate for \mathbf{b} is obtained using current estimates for \mathbf{c} , \mathbf{a} and \mathbf{p} :

$$\hat{\mathbf{b}}^{(k+1)} = (\mathbf{X}'\mathbf{R}^{-1}\mathbf{X})^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)} + \hat{\mathbf{p}}^{(k)})]$$

which is derived from the mixed model equations. Solutions can be computed directly herd by herd if fixed effects in \mathbf{b} are defined

specific to herd (e.g., herd test date) because block inversion is possible (the order is equal to the herd-specific effects in \mathbf{b}).

The new estimate for \mathbf{p} is obtained using current estimates for \mathbf{b} , \mathbf{c} , and \mathbf{a} :

$$\hat{\mathbf{p}}^{(k+1)} = (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1} \mathbf{Q}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})]$$

which also is derived from the mixed model equations. An advantage of this approach is that solutions can be computed animal by animal because \mathbf{R} is block diagonal for every animal. Therefore, direct inversion can be used in the computations (the order of the inverted block is equal to the number of regressions per animal).

The vector \mathbf{r} is then updated using current estimates for \mathbf{c} , \mathbf{a} , and \mathbf{p} :

$$\hat{\mathbf{r}}^{(k+1)} = \mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)} + \hat{\mathbf{p}}^{(k+1)}$$

3.2 Estimation of \mathbf{c} and \mathbf{a}

Solutions for \mathbf{c} and \mathbf{a} in iteration round $k+1$ are obtained from equations that are similar to regular multivariate mixed model equations:

$$\begin{bmatrix} \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} & \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} \\ \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} & \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{c}}^{(k+1)} \\ \hat{\mathbf{a}}^{(k+1)} \end{bmatrix} = \begin{bmatrix} \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\hat{\mathbf{r}}^{(k+1)} \\ \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\hat{\mathbf{r}}^{(k+1)} \end{bmatrix}.$$

Several solution techniques are possible because the secondary-model is not completely specified:

- canonical transformation to simplify computation (uncorrelated regression) by

making use of solution algorithms that allow missing values (Ducrocq and Besbes, 1993) as well as other generalized uses of this transformation described by Ducrocq and Chapuis (1997),

- transformation to limit the number of regressions (Wiggans and Goddard, 1997), which could create variates with biological meaning (such as total yield, persistency, and maturity rate) that could facilitate the development of an index for lactation performance,
- more complicated (co)variance structure than those usually considered in random regression models (e.g., additional random effects such as interaction of herd and sire), and
- additional traits (such as 305-day yield for cows without test-day records).

3.3 Proof

To show that the solutions for \mathbf{b} , \mathbf{c} , and \mathbf{a} from the alternative solution algorithm are equivalent to those from the mixed model equations, first absorb \mathbf{p} into the mixed model equations:

$$\begin{bmatrix} \mathbf{X}'\mathbf{M}\mathbf{X} & \mathbf{X}'\mathbf{M}\mathbf{Q}\mathbf{W} & \mathbf{X}'\mathbf{M}\mathbf{Q}\mathbf{Z} \\ \mathbf{X}'\mathbf{M}\mathbf{Q}\mathbf{X} & \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} & \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} \\ \mathbf{Z}'\mathbf{M}\mathbf{Q}' & \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} & \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{c}} \\ \hat{\mathbf{a}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{M}\mathbf{y} \\ \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{y} \\ \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{y} \end{bmatrix}$$

where \mathbf{M} is the absorption matrix:

$$\begin{aligned} \mathbf{M} &= \mathbf{R}^{-1} - \mathbf{R}^{-1}\mathbf{Q}(\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1}\mathbf{Q}'\mathbf{R}^{-1} \\ &= [\mathbf{R} + \mathbf{Q}(\mathbf{I} \otimes \mathbf{K}_p)\mathbf{Q}']^{-1} \end{aligned}$$

The back solution for \mathbf{p} gives

$$\begin{aligned} \hat{\mathbf{p}} &= (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1}\mathbf{Q}'\mathbf{R}^{-1}[\mathbf{y} - \\ &\quad \mathbf{X}\hat{\mathbf{b}} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}} + \mathbf{Z}\hat{\mathbf{a}})] \\ &= (\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Q}'\mathbf{M}[\mathbf{y} - \mathbf{X}\hat{\mathbf{b}} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}} + \mathbf{Z}\hat{\mathbf{a}})] \end{aligned}$$

Next iterate on the mixed model equations with \mathbf{p} absorbed using two blocks:

$$\begin{aligned} \hat{\mathbf{b}}^{(k+1)} &= \\ &= (\mathbf{X}'\mathbf{M}\mathbf{X})^{-1}\mathbf{X}'\mathbf{M}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \end{aligned}$$

Both formulas are equivalent to estimating \mathbf{b} and \mathbf{p} in the alternative solution algorithm at $k+1$ rounds of iteration, and

$$\begin{bmatrix} \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} & \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} \\ \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} & \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{c}}^{(k+1)} \\ \hat{\mathbf{a}}^{(k+1)} \end{bmatrix} = \begin{bmatrix} \mathbf{W}'\mathbf{Q}'\mathbf{M}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) \\ \mathbf{Z}'\mathbf{Q}'\mathbf{M}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) \end{bmatrix}.$$

Now the different blocks of the coefficient matrix can be rewritten as

$$\begin{aligned} \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} &= \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} + [\mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} - \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W}] \\ &= \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} - \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})\mathbf{W} \end{aligned}$$

$$\begin{aligned} \mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} &= \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} + [\mathbf{W}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} - \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z}] \\ &= \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} - \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})\mathbf{Z} \end{aligned}$$

$$\begin{aligned} \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} &= \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} + [\mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{W} - \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W}] \\ &= \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} - \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})\mathbf{W} \end{aligned}$$

$$\begin{aligned} \mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} &= \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} + [\mathbf{Z}'\mathbf{Q}'\mathbf{M}\mathbf{Q}\mathbf{Z} - \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z}] \\ &= \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} - \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})\mathbf{Z} \end{aligned}$$

After introducing those blocks, moving them to the right-hand side, and using the estimates of \mathbf{b} at iteration $k+1$ and of \mathbf{c} and \mathbf{a} at iteration k ,

$$\begin{bmatrix} \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} & \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} \\ \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{W} & \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{c}}^{(k+1)} \\ \hat{\mathbf{a}}^{(k+1)} \end{bmatrix} = \begin{bmatrix} \mathbf{W}'\mathbf{Q}'\mathbf{M}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) + \mathbf{W}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)}) \\ \mathbf{Z}'\mathbf{Q}'\mathbf{M}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) + \mathbf{Z}'(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)}) \end{bmatrix}.$$

Then

$$\begin{aligned} &\mathbf{Q}'\mathbf{M}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) + \\ &(\mathbf{I} \otimes \mathbf{K}_p^{-1} - \mathbf{Q}'\mathbf{M}\mathbf{Q})(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)}) \\ &= (\mathbf{I} \otimes \mathbf{K}_p^{-1})\mathbf{r}^{(k+1)} \end{aligned}$$

which is the same equation as that obtained by including the alternative solution algorithm equation to update \mathbf{b} in the algorithm update of \mathbf{r} . Therefore, solutions for \mathbf{c} and \mathbf{a} obtained from the algorithm are equivalent to those from the mixed model equations.

3.4 Similarity to Method of van der Werf *et al.* (1998)

With cursory inspection, the alternative solution algorithm does not appear to resemble the equations of van der Werf *et al.* (1998). Their derivation was based on a totally different approach using a transformation of \mathbf{y} , whereas the alternative solution equations were developed by subdividing a class of random regression models into two models. However, the alternative solution algorithm can be shown to be a generalization of the van der Werf *et al.* (1998) equations by restructuring the same equation that was used to demonstrate the

equivalence between the solutions from the algorithm and the mixed model equations:

$$\begin{aligned}\hat{\mathbf{r}}^{(k+1)} &= \mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)} + (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1} \mathbf{Q}'\mathbf{R}^{-1}[(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \\ &= (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1} \mathbf{Q}'\mathbf{R}^{-1}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) + \\ &\quad [\mathbf{I} - (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1} \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}](\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)}).\end{aligned}$$

That generalization of the expression of van der Werf *et al.* (1998) includes time-dependent fixed effects, a general definition of \mathbf{R} and \mathbf{Q} , and no limitations on the covariance structures.

Indirectly, the derivation of the alternative solution algorithm also is a proof of the equations of van der Werf *et al.* (1998).

4. Possible Practical Uses

4.1 Expectation-Maximization Algorithm

Similar to the approach proposed by van der Werf *et al.* (1998), an expectation-maximization algorithm can be used to update \mathbf{r} . During

iteration, a part of \mathbf{r} would be estimated once and another part updated based on current estimates of \mathbf{b} , \mathbf{c} , and \mathbf{a} :

$$\begin{aligned}\hat{\mathbf{r}}^{(k+1)} &= \mathbf{Q}^* (\mathbf{y} - \mathbf{X}\hat{\mathbf{b}}^{(k+1)}) + (\mathbf{I} - \mathbf{Q}^* \mathbf{Q})(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)}) \\ &= \mathbf{Q}^* \mathbf{y} - \mathbf{Q}^* \mathbf{X}\hat{\mathbf{b}}^{(k+1)} + (\mathbf{I} - \mathbf{Q}^* \mathbf{Q})(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})\end{aligned}$$

where $\mathbf{Q}^* = (\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1})^{-1} \mathbf{Q}'\mathbf{R}^{-1}$. In contrast to van der Werf *et al.* (1998), who voluntarily avoided time-dependent fixed

effects, the need also to update \mathbf{b} leads to a second method that is based on a two-step approach.

4.2 Sequential Solution

The equations from the alternative solution algorithm for estimating \mathbf{b} , \mathbf{p} , \mathbf{r} , \mathbf{c} , and \mathbf{a} can be directly used to develop a sequential solution scheme. For most practical situations, solutions from a former evaluation are available and can be used as starting values. If genetic evaluations are calculated every 3 or 6 months, the relative number of additional records compared with the total number of records would be at most 5 to 10%. For most animals, values for \mathbf{a} and \mathbf{p} are available, and pedigree

values could replace estimates for \mathbf{a} for new animals. Therefore, the following scheme would be possible based on the equations in the alternative solution algorithm:

1. generate \mathbf{b} with starting values from a previous genetic evaluation.
2. update \mathbf{r} . The solutions for \mathbf{b} and for \mathbf{r} updated using \mathbf{b} can also be obtained together through the following mixed model equations:

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_p^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}}^{(k+1)} \\ \hat{\mathbf{p}}^{(k+1)} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \\ \mathbf{Q}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \end{bmatrix}.$$

3. solve for \mathbf{c} and \mathbf{a} in the alternative solution algorithm equation by using starting values from the last genetic evaluation.
4. update \mathbf{b} using the new estimates for \mathbf{c} and \mathbf{a} .
5. solve for \mathbf{p} using the new estimates for \mathbf{b} , \mathbf{c} , and \mathbf{a} , and update \mathbf{r} using the alternative solution algorithm equation.
6. update \mathbf{c} and \mathbf{a} using the solutions from the previous round of current genetic evaluation as starting values.
7. Repeat from 4. until desired convergence is reached.

This scheme obviously is approximate and similar to the method proposed by Wiggans and Goddard (1997). Such an approach also would be appropriate for advanced milk recording plans and continuous genetic evaluations. The estimations of \mathbf{b} and \mathbf{r} could be updated each time that data from a new test day are added for a given herd, thus allowing their use for management purposes. The estimation of \mathbf{c} and \mathbf{a} could then be updated for the whole population on a scheduled basis (e.g., weekly, monthly, quarterly).

5. Example Computations

5.1 Material and Methods

Data (Table 1) were from a subset of the data used by Gengler et al. (1999). A total of 57,034 first-lactation test-day records that were recorded between 7 and 305 days in milk were obtained for 7173 Holstein cows that calved from 1990 through 1996 in large herds in Pennsylvania. Pedigree information was available from the Animal Improvement Programs Laboratory database.

A model similar to the model of Gengler *et al.* (1999) was used except that fixed regression on third-order modified Legendre's polynomials (constant, linear, and quadratic) were added. The three regressions were $I_0 = 1$, $I_1 = 3^{0.5}x$, and $I_2 = (5/4)^{0.5}(3x^2 - 1)$, where $x = -1 + 2[(\text{DIM} - 1)/(305 - 1)]$ and DIM = days in milk.

The model used was

$$\mathbf{y} = \mathbf{H}\mathbf{h} + \mathbf{S}\mathbf{s} + \mathbf{Q}(\mathbf{W}\mathbf{c} + \mathbf{Z}\mathbf{a} + \mathbf{p}) + \mathbf{e}$$

where \mathbf{y} is the vector of test-day records for milk, fat, or protein yield; \mathbf{h} is the vector of effects for class of herd test day and milking frequency; \mathbf{s} is the vector of effects for class of age, season, and lactation stage; \mathbf{c} is the vector of fixed regression coefficients (three); \mathbf{a} is the vector of genetic random regression coefficients (three per animal); \mathbf{p} is the vector of permanent environmental random regression coefficients (three per cow with records); \mathbf{e} is the vector of residual effects; \mathbf{H} , \mathbf{S} , \mathbf{W} , \mathbf{Z} are incidence matrices; and \mathbf{Q} is the covariate matrix for the regressions with three columns per animal. Assumed (co)variance structures were

$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{K}_G & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_c \otimes \mathbf{K}_p & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix}$$

with $\mathbf{R} = \mathbf{I}_n \sigma_e^2$, where \mathbf{K}_G is the covariance matrix of the genetic random regressions, (the coefficients of the genetic covariance function), \mathbf{K}_p is the covariance matrix of the permanent environmental random regressions (the coefficients of the permanent environmental covariance function), \mathbf{A} is the additive genetic relationship matrix among animals, \mathbf{I}_c is the

Table 1. Numbers of cows with records, test-day records, animals included in the relationship matrix (\mathbf{A}^{-1}), and equations used in the random regression model.

Category	Number
Cows	7173
Test-day records	57,034
Animals in \mathbf{A}^{-1}	15,378
Equations	69,355

identity matrix of dimension c (number of cows or lactations), \mathbf{I}_n is the identity matrix of dimension n (number of test-day yields) and σ_e^2 , is the residual variance. For this example, classes for age, season, and lactation stage were defined so that small classes would be avoided, but such classes should be smaller for actual calculation of genetic evaluations. Calving ages were 20 to 24, 25 to 26, 27 to 28, and 29 to 35 months.

$$\begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{H}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} \\ & \mathbf{S}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{Q} \\ & & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{W} & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} & \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} \\ & \text{Symmetric} & & \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} + \mathbf{A}^{-1} \otimes \mathbf{K}_G^{-1} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q}\mathbf{Z} \\ & & & & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_P^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{h}} \\ \mathbf{s} \\ \mathbf{c} \\ \mathbf{a} \\ \hat{\mathbf{p}} \end{bmatrix} = \begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{W}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}.$$

5.2 Two-Step Sequential Solution

1. Based on the alternative solution algorithm equations for \mathbf{b} and \mathbf{p} modified to two fixed effects, Step 1 consists in solving

$$\begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes \mathbf{K}_P^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{h}}^{(k+1)} \\ \hat{\mathbf{s}}^{(k+1)} \\ \hat{\mathbf{p}}^{(k+1)} \end{bmatrix} = \begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \\ \mathbf{S}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \\ \mathbf{Q}'\mathbf{R}^{-1}[\mathbf{y} - \mathbf{Q}(\mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)})] \end{bmatrix}$$

and updating \mathbf{r} by computing: $\hat{\mathbf{r}}^{(k+1)} = \mathbf{W}\hat{\mathbf{c}}^{(k)} + \mathbf{Z}\hat{\mathbf{a}}^{(k)} + \hat{\mathbf{p}}^{(k+1)}$. The BLUPF90 program (Misztal, 1997) was used to set up and solve the equations. Because in the initial estimation of \mathbf{r} , no information was available for \mathbf{c} and \mathbf{a} , Step 1 was modified to:

Starting with January, six 2-month calving seasons were defined. Twenty-two lactation stages based on days in milk were defined: 7 to 13, 14 to 20, 21 to 27, 28 to 34, 35 to 41, 42 to 48, 49 to 55, 56 to 62, 63 to 76, 77 to 90, 91 to 104, 105 to 118, 119 to 132, 133 to 146, 147 to 167, 168 to 188, 189 to 209, 210 to 230, 231 to 251, 252 to 272, 273 to 293, and 294 to 305.

(Co)variance components were those obtained previously by Gengler *et al.* (1999) through REMLF90 (Misztal, 1998). All computations were done on a Digital Equipment Corporation (Marlboro, MA) Personal Workstation 433 with 512 megabytes of random access memory.

5.1 Solution with Random Regression Model

The following mixed model equations were constructed, stored in sparse matrix form, and solved by Gauss-Seidel iteration using the BLUPF90 program (Misztal, 1997):

$$\begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{H}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{S}'\mathbf{R}^{-1}\mathbf{Q} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{H} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{S} & \mathbf{Q}'\mathbf{R}^{-1}\mathbf{Q} + \mathbf{I} \otimes (\mathbf{K}_G + \mathbf{K}_P)^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{h}}^{(1)} \\ \hat{\mathbf{s}}^{(1)} \\ \hat{\mathbf{r}}^{(1)} \end{bmatrix} = \begin{bmatrix} \mathbf{H}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{S}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Q}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

which is equivalent to estimation of \mathbf{r} with a regular random regression model under the assumption that all cows are unrelated.

- Based on the alternative solution algorithm equation, Step 2 estimates \mathbf{c} and \mathbf{a} using the regular multitrait program MTJAAM (Gengler, 1998) with canonical transformation.

6. Results and Discussion

Table 2 shows the correlations between additive genetic solutions for the three regressions. After the first round of iteration under the assumption that animals were unrelated, the correlations were already all >0.95 . After an additional round of iteration, the correlations were all >0.98 , and four rounds of iteration yielded correlations that were all near 1.

Table 2. Correlations between solutions for additive genetic regression coefficients obtained by random regression and through indirect solution.

Iteration	Regressions		
	1	2	3
1	0.965	0.975	0.957
2	0.983	0.991	0.983
3	0.992	0.996	0.991
4	0.996	0.998	0.995

¹Initial computation was based on assumption that animals were unrelated to estimate \mathbf{r} .

7. Conclusions

Despite the similarity of the alternative solution algorithm and the method of van der

Werf *et al.* (1998), the derivations were based on different approaches: The alternative solution algorithm was developed by representing a phenotypic random regression model through a multitrait submodel on the phenotypic regressions, which was proved to be equivalent to a class of random regression models. However, \mathbf{R} in the alternative algorithm can describe much more complicated residual structures than can the diagonal matrix of van der Werf *et al.* (1998).

Test computations showed that even with incomplete sequential solution, correlations with solutions from the regular random regression model were all > 0.98 after only two iterations on the two steps. Therefore, the proposed method based on sequential estimation of regressions and effects on those regressions allows, in addition to its relative simplicity, several other techniques to be applied in the second step: 1) canonical transformation to simplify computations (uncorrelated regressions) by making use of solution algorithms that allow missing values; 2) transformation to limit the number of regressions and to create variates with biological meaning (e.g., total yield, persistency, and maturity rate) that could facilitate the development of an index for lactation performance; 3) more complicated (co)variance structures than those usually considered in random regression models (e.g., additional random effects such as interaction of herd and sire); and 4) accommodation of additional traits (e.g., 305-day yield for cows without test-day records).

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