Use of (Co)Variance Functions to Describe (Co)Variances for Test Day Yield

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ABSTRACT

(Co)variance functions for milk, fat, and protein yields during first lactation were developed from (co)variance components for four lactation stages of 75 d each that had been previously estimated using test day data from 17,190 Holstein cows from 37 herds in Pennsylvania and Wisconsin. The (co)variance functions were evaluated at 18, 43, 68, 93, 118, 143, 168, 193, 218, 243, 268, and 293 d in milk. Residuals were subdivided into time-dependent (permanent) and temporary environmental effects for estimation of (co)variance functions. Mean relative variance (portion of total variance) for time-dependent environmental effects was 0.50 for milk yield and 0.51 for fat and protein yields. Heritability estimates generally were lower at the start and end of lactation and were highest for milk yield; mean heritability estimates were 0.20 for milk, 0.16 for fat, and 0.17 for protein yields. Phenotypic and genetic correlations were higher between milk and protein yields than between milk and fat yields. Within yield traits, genetic correlations declined from $\geq$ 0.93 for adjacent lactation stages to 0.52 for milk, 0.58 for fat, and 0.60 for protein between initial and final lactation stages. Within lactation stage, mean genetic correlations were 0.40 between milk and fat yields, 0.78 between milk and protein yields, and 0.55 between fat and protein yields; corresponding mean phenotypic correlations were 0.65, 0.92, and 0.67. The (co)variance function methodology allowed interpolation and extension of (co)variance components over the entire lactation.
(**Key words:** (co)variance function, test day model, variance component estimation)

INTRODUCTION

The use of test day yields instead of 305-d lactation yields recently has become the focus of much research on evaluation systems for dairy genetics. Recent studies (1, 2, 3, 4, 7, 10, 11, 12,

13, 15, 16, 18, 19) have discussed the advantages that test day models have over lactation models, especially because environmental effects can be accounted for more accurately, and greater variability in milk recording plans can be accommodated.

Wiggans and Goddard (19) proposed a multitrait analysis of test day yields. However, this approach requires a large number of genetic parameters to be estimated, especially when test day records for milk, fat, and protein are considered as different traits within a lactation. Fortunately, canonical transformation can be used to simplify multitrait analysis. This procedure can be thought of as a linear transformation of the original measures to new variables that are genetically and phenotypically uncorrelated. Variance components can be estimated using those uncorrelated variables even when more than two variables are random (9).

Gengler et al. (1) used a multitrait analysis with canonical transformation to obtain (co)variance components for milk, fat, and protein test day yields for first lactations of US Holsteins. However, because canonical transformation requires that all values be present, their analysis was restricted to four lactation stages of 75 d each to minimize the number of missing values.

A full multitrait model assumes that each test day yield within a lactation is a distinct trait. That assumption results in a highly overparameterized analysis because of the high correlations among test days. In this case, the (co)variance functions proposed by Kirkpatrick et al. (5, 6) can be used to describe the full parameter space with a reduced number of parameters and to calculate (co)variances between any two traits. Generally, 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. This approach is equivalent to a regular multitrait (co)variance matrix of infinite dimension in which different traits are defined as points on the given trajectory (8). (Co)variance functions are particularly useful for situations modeling spatial or temporal data, and a trajectory can be linked to phenomena that are space, age, or time dependent, such as growth or lactation. (Co)variance structures at any point along a continuous (time) scale can be predicted with (co)variance functions, and greater flexibility is possible in using measurements at any point along the trajectory. If observations are sparse, information from all other measurements is used. The aim of this study was to show the use of (co)variance functions to interpolate and to extend the estimated (co)variance components obtained by Gengler et al. (1) to all DIM within first lactation.

MATERIALS AND METHODS

Data

Data were (co)variance estimates for milk, fat, and protein yields from the study of Gengler et al. (1), which used test day data from first lactation records of 17,190 cows that calved from 1990 through 1996 in 37 large herds in Wisconsin and Pennsylvania. To estimate those (co)variances, Gengler et al. (1) defined four lactation stages of 75 d each starting with d 6; test days nearest the center of each lactation stage (d 43, 118, 193, and 268) were retained. The model of Gengler et al. (1) was solved iteratively in two steps: 1) adjustment of test day yields for effects of herd, test date, and milking frequency and effects of lactation stage within class of age and season of calving and 2) estimation of (co)variance components with a model that accounted for effects of herd, year, and calving season; calving age; and breeding value.

(Co)variance Functions

The use of (co)variance functions allows a complete description of the (co)variance structure of milk, fat, and protein yields during first lactation. To illustrate the use of (co)variance functions, the 4 lactation stages of 75 d each of Gengler et al. (1) were replaced by 12 lactation stages of 25 d each that started at d 6. Twelve stages were chosen to minimize the likelihood of more than one test in the same lactation stage for records from monthly record keeping plans that would be used for genetic evaluations calculated with a test day model. The model to describe the (co) variance function was based on those used by Kirkpatrick et al. (5, 6), Meyer and Hill (8), and Veerkamp and Goddard (18).

Let Σ denote the (co)variance matrix for observations of three yield traits (milk, fat, and protein) in four lactation stages, and let Φ be defined as the matrix of Legendre polynomial functions evaluated for a yield trait during a lactation stage. Matrix Φ can be represented as $\Phi = \mathbf{I}_3 \otimes \Phi_t$ where $\otimes$ = Kronecker (direct) product, $\mathbf{I}_3$ = identity matrix of dimension 3 (the number of yield traits), and Φ_t = matrix of Legendre polynomial functions evaluated for the defined lactation stages (8). When a full-order fit is assumed, $\Sigma = \Phi \mathbf{K} \Phi'$, where **K** = matrix of (co)variance function coefficients, which can be estimated as $\Phi^{-1}\Sigma(\Phi')^{-1}$. For reduced fit, a new approach was used with $\mathbf{K} = (\Phi'\Phi)^{-1}\Phi'\Sigma\Phi(\Phi'\Phi)^{-1}$, where $(\Phi'\Phi)^{-1}\Phi'$ = generalized least squares inverse of Φ.

The method is straightforward for the genetic (co)variance matrix **G** with $\mathbf{K}_G = \Phi^{-1}\mathbf{G}(\Phi')^{-1}$ but is less clear for the residual (co)variance matrix **R**, because **R** contains combinations of two types of (co)variances. First, records are affected by nongenetic influences that affect successive observations. The resulting (co)variance structure would be similar to the genetic (co)variance matrix; (co)variances would decrease as the interval between test days increased. Second, records are affected by a random measurement error (8). This error can be considered to be a temporary environmental effect. If one yield trait (e.g., milk) is analyzed, the (co)variance structure of the random measurement error can be assumed to be a diagonal matrix. If correlated yields are analyzed, this structure becomes more complicated with linked random measurement errors for milk, fat, and protein.

The following decomposition of **R** was used: $\mathbf{R} = \mathbf{R}^* + (\mathbf{E} \otimes \mathbf{I}_4)$, where $\mathbf{I}_4$ = identity matrix of dimension 4 (the number of lactation stages); $\mathbf{E} = 3 \times 3$ matrix of temporary environmental (co) variances among milk, fat, and protein yields; and **R*** = part of **R** that remains after extracting temporary environmental (co)variances. This model can be considered approximate because temporary environmental (co)variances were considered constant across test days. The use of constant (co)variances for temporary environmental effects is consistent with the usual assumption of constant residual (co)variances for single trait models. Conversely, the assumption of constant (co)variances for measurement error is more logical because measurement errors should not be time dependent; i.e., variance of measurement error is constant even if the relative importance of measurement errors varies with the associated total variance. Therefore, **R*** is a time-dependent (permanent) environmental (co)variance matrix, and **E** is a time-independent (temporary) environmental (co)variance matrix.

A reduced (co)variance function is fit to $\mathbf{R}^* : \mathbf{K}_{R^*} = (\Phi_R'\Phi_R)^{-1}\Phi_R'\mathbf{R}^*\Phi_R(\Phi_R'\Phi_R)^{-1}$ Fitting a full-order (co)variance function for **G**, reducing order (12 - 3 = 9) of the (co)variance function for **R***, and estimating **E** results in a model equivalent to full fit (8). A reduced-fit model also was necessary for **R***, because a full fit on **R** yielded unlikely negative residual (co)variances in some preliminary analyses.

Kirkpatrick et al. (5) proposed a method to separate **R*** and **E** based on fitting a (co)variance function on the (co)variances only and estimating the variances without the measurement error. However, this approach was difficult to use because the structure of **R** - **R*** is not a simple diagonal matrix. Therefore, the following strategy was implemented.

Reduced genetic and environmental (co)variances with increased days between tests have been reported (7, 10, 13). However, this proportionality cannot be assumed for (co)variances of **G** and **R**, because **R** contains both time-dependent and time-independent (time-independent) environmental (co)variances. A preliminary study using the (co)variances estimated by Gengler et al. (1) showed that the correlation between all the elements of **G** and **R** was 0.75, and the correlation between the noncritical elements of **G** and **R** was 0.93. Therefore, **G** and **R*** were considered to have decreasing (co)variances with increasing time between test days, and similar rates of decrease were assumed to simplify computations.

Initial estimation of **R*** was based on the regression of elements of **R** on **G** with replacement of elements that contain measurement error with their estimates. Estimation of **E** as the part of **R** that was not contained in **R*** was based on the geometric mean of the elements of **R** - **R*** that correspond to a given measurement error (co)variance; **E** was checked for positive definiteness and adjusted. Then **R*** was updated as $\mathbf{R}^* = \mathbf{R} - (\mathbf{E} \otimes \mathbf{I}_4)$ with new elements used for **E**, checked for positive definiteness, and adjusted; **E** then was recomputed, and the iteration was continued until **R*** and **E** were positive definite so that the best possible fit of **R*** and best estimation of **E** could be achieved.

The matrix $\mathbf{G}_E$ with extended (and interpolated) genetic (co)variances was estimated as $\mathbf{G}_E = \Phi_{G_E}\mathbf{K}_G\Phi_{G_E}'$, where Φ_{G_E} = matrix of Legendre polynomial functions to estimate extended genetic (co)variances for milk, fat, and protein yields in the 12 lactation stages, and $\mathbf{K}_G$ = matrix of coefficients of the genetic (co)variance function. The residual (co)variance matrix $\mathbf{R}_E$ was estimated as $\mathbf{R}^*_E + (\mathbf{E} \otimes \mathbf{I}_{12}) = \Phi_{R_E}\mathbf{K}_R\Phi_{R_E}' + (\mathbf{E} \otimes \mathbf{I}_{12})$, where Φ_{R_E} = matrix of reduced Legendre polynomial functions to estimate extended residual (co)variances for milk, fat, and protein yields in the 12 lactation stages, and $\mathbf{K}_R$ = matrix of coefficients of the reduced residual (co)variance function.

RESULTS AND DISCUSSION

The initial and extended variances are in Table 1. Mean relative variance (a portion of the total variance) for time-dependent environmental effects were 0.50 for milk yield and 0.51 for fat and protein yields. Genetic variances for all yield traits tended to increase with lactation stage except for small decreases from first to third lactation stage for milk and fat yields and from first to fourth lactation stage for protein yield. In contrast, time-dependent environmental variances were

higher at the start and end of lactation, which indicates a greater influence by permanent environment during those stages of lactation.

TABLE 1. Estimates of genetic (g), time-dependent environmental (t), and temporary environmental (e) variances for milk, fat, and protein yields in 4 initial and 12 interpolated and extended lactation stages.

Yield trait	Midpoint of lactation stage	Initial variance[1]			Extended variance		
		g	t	e	g	t	e
	(DIM)						
Milk, $kg^2 \times 100$	18	. . .	. . .	. . .	461	1688	779
	43	397	1343	779	397	1330	779
	68	. . .	. . .	. . .	393	1158	779
	93	. . .	. . .	. . .	415	1098	779
	118	444	1128	779	444	1095	779
	143	. . .	. . .	. . .	472	1112	779
	168	. . .	. . .	. . .	497	1129	779
	193	518	1116	779	518	1144	779
	218	. . .	. . .	. . .	538	1175	779
	243	. . .	. . .	. . .	561	1256	779
	268	597	1446	779	597	1440	779
	293	. . .	. . .	. . .	663	1796	779
Fat, g^2	18	. . .	. . .	. . .	6111	43,718	14,409
	43	5333	28,813	14,409	5333	27,789	14,409
	68	. . .	. . .	. . .	5722	20,342	14,409
	93	. . .	. . .	. . .	6228	17,967	14,409
	118	6498	22,815	14,409	6498	18,039	14,409
	143	. . .	. . .	. . .	6550	18,724	14,409
	168	. . .	. . .	. . .	6537	18,969	14,409
	193	6595	19,355	14,409	6595	18,513	14,409
	218	. . .	. . .	. . .	6790	17,879	14,409
	243	. . .	. . .	. . .	7145	18,377	14,409
	268	7759	22,321	14,409	7759	22,107	14,409
	293	. . .	. . .	. . .	9018	31,951	14,409
Protein, g^2	18	. . .	. . .	. . .	3807	14,045	7236
	43	3093	10,406	7236	3093	10,270	7236
	68	. . .	. . .	. . .	2818	8875	7236

93	. . .	. . .	. . .	2815	8832	7236
118	2987	10,189	7236	2987	9376	7236
143	. . .	. . .	. . .	3274	10,002	7236
168	. . .	. . .	. . .	3631	10,467	7236
193	4020	11,248	7236	4020	10,788	7236
218	. . .	. . .	. . .	4393	11,244	7236
243	. . .	. . .	. . .	4722	12,374	7236
268	5009	15,098	7236	5009	14,980	7236
293	. . .	. . .	. . .	5320	20,124	7236

[1]Results from iterative analysis of Gengler et al. (1); g = genetic variance, and t + e = residual variance.

To illustrate the progression of those variances over first lactation, the relative variances for extended genetic, time-dependent, and temporary environmental effects are shown for milk yield (Figure 1), fat yield (Figure 2), and protein yield (Figure 3). For milk (Figure 1) and protein (Figure 3), initial and extended variances at corresponding DIM were similar for all three effects. For fat (Figure 2), relative genetic variance was slightly greater in the middle of the lactation. The behavior of the curve for relative genetic variance of fat yield results from the simultaneous fitting of all three yield traits.

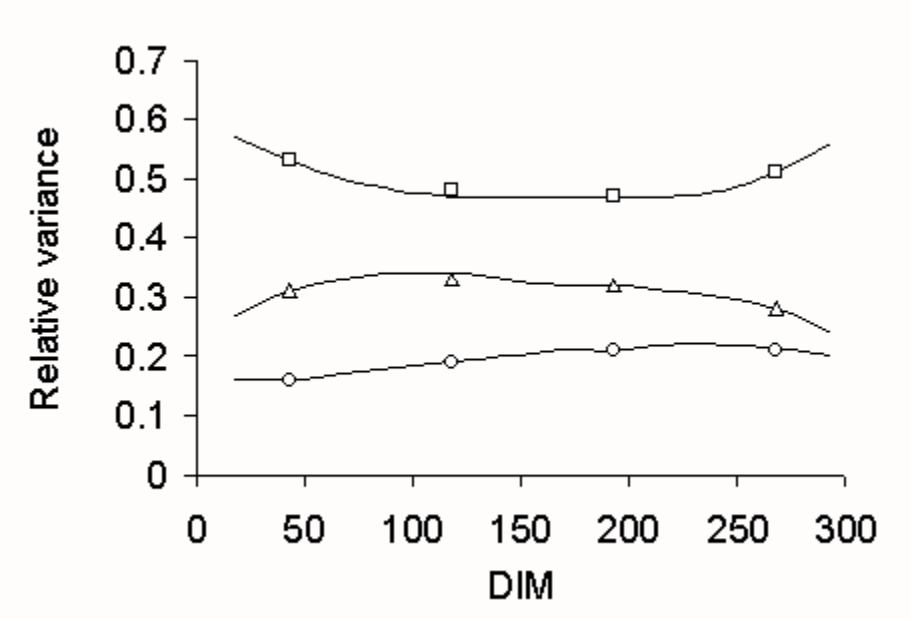

Figure 1. Evolution of extended (and interpolated) genetic (○), time-dependent (□), and temporary environmental (△) variances for milk yield expressed as a relative fraction of phenotypic (total) variance; initial estimates are designated by markers.

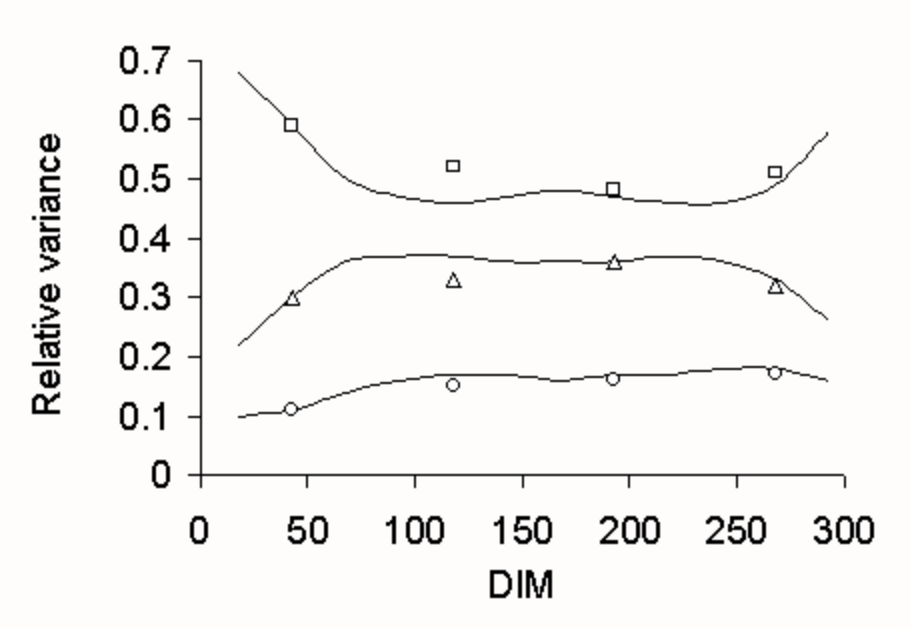

Figure 2. Evolution of extended (and interpolated) genetic (○), time-dependent (□), and temporary environmental (△) variances for fat yield expressed as a relative fraction of phenotypic (total) variance; initial estimates are designated by markers.

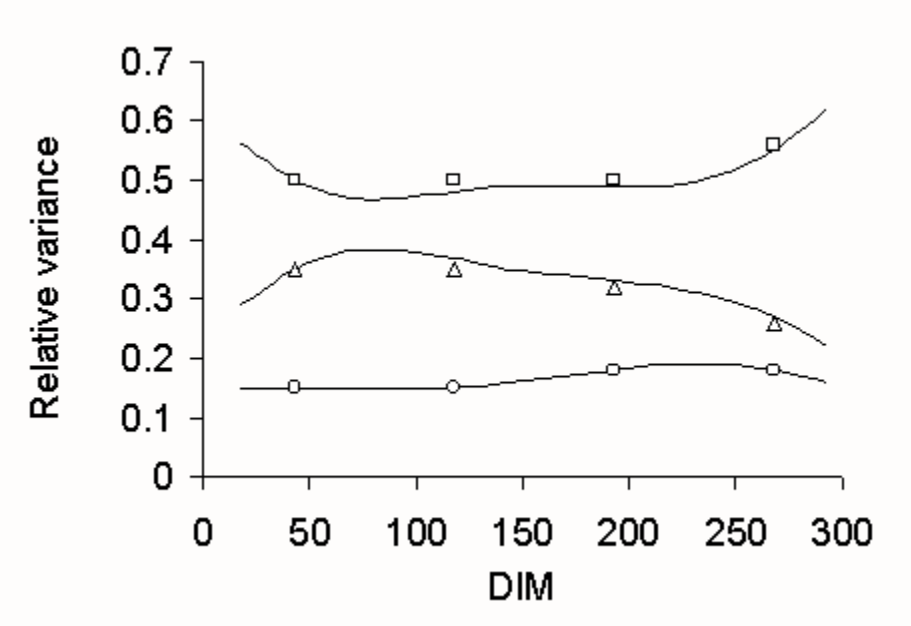

Figure 3. Evolution of extended (and interpolated) genetic (○), time-dependent (□), and temporary environmental (△) variances for protein yield expressed as a relative fraction of phenotypic (total) variance; initial estimates are designated by markers.

Estimates of correlations between time-independent (temporary) environmental variances were 0.78 for milk and fat yields, 0.98 between milk and protein yields, and 0.68 between fat and

protein yields. Gengler et al. (1) found that phenotypic and genetic correlations were highest between milk and protein yields and lowest between milk and fat yields.

Heritability estimates for the 12 lactation stages are in Table 2. All estimates were between 0.10 and 0.22. Heritability estimates usually were higher for milk yield (mean of 0.20) than for fat and protein yields (means of 0.16 and 0.17, respectively). Heritability estimates in midlactation were higher than at the beginning or end of lactation as is also shown in Figures 1 to 3. Gengler et al. (1) found that heritabilities generally increased with lactation stage and were highest for milk yield; their mean heritability estimates from the iterative analysis that provided the initial (co) variance estimates for this study were 0.20 for milk yield, 0.15 for fat yield, and 0.16 for protein yield. Estimated heritability for fat yield was increased by fitting the (co)variance function.

TABLE 2. Heritabilities (on diagonal and bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for milk, fat, and protein yields estimated using (co) variance functions for 12 lactation stages.

Yield trait	Midpoint of lactation stage	18 DIM	43 DIM	68 DIM	93 DIM	118 DIM	143 DIM	168 DIM	193 DIM	218 DIM	243 DIM	268 DIM	293 DIM
	(DIM)	Milk yield											
Milk	18	**0.16**	0.97	0.89	0.82	0.76	0.72	0.70	0.68	0.66	0.63	0.59	0.52
	43	0.69	**0.16**	0.98	0.94	0.90	0.87	0.85	0.83	0.81	0.79	0.75	0.69
	68	0.63	0.66	**0.17**	0.99	0.97	0.95	0.93	0.92	0.90	0.88	0.84	0.79
	93	0.56	0.62	0.65	**0.18**	0.99	0.99	0.97	0.96	0.95	0.93	0.89	0.84
	118	0.49	0.57	0.63	0.65	**0.19**	1.00	0.99	0.98	0.97	0.95	0.92	0.87
	143	0.44	0.53	0.60	0.64	0.66	**0.20**	1.00	0.99	0.98	0.97	0.94	0.89
	168	0.40	0.50	0.57	0.62	0.65	0.67	**0.21**	1.00	0.99	0.98	0.95	0.91
	193	0.37	0.47	0.54	0.60	0.63	0.66	0.67	**0.21**	1.00	0.99	0.97	0.93
	218	0.35	0.44	0.52	0.57	0.61	0.64	0.66	0.68	**0.22**	1.00	0.98	0.95
	243	0.34	0.42	0.48	0.53	0.57	0.60	0.63	0.66	0.68	**0.22**	0.99	0.97
	268	0.32	0.39	0.44	0.48	0.51	0.55	0.58	0.62	0.66	0.70	**0.21**	0.99
	293	0.31	0.35	0.38	0.41	0.44	0.48	0.52	0.57	0.62	0.68	0.73	**0.21**
Fat	18	0.60	0.40	0.37	0.34	0.30	0.28	0.25	0.23	0.22	0.20	0.19	0.17
	43	0.41	0.65	0.39	0.37	0.34	0.32	0.30	0.28	0.26	0.24	0.22	0.19
	68	0.37	0.39	0.65	0.37	0.36	0.34	0.32	0.31	0.29	0.27	0.25	0.21
	93	0.32	0.35	0.36	0.64	0.36	0.35	0.34	0.32	0.31	0.29	0.26	0.23
	118	0.28	0.31	0.33	0.34	0.62	0.34	0.34	0.33	0.32	0.30	0.28	0.25
	143	0.24	0.28	0.31	0.33	0.34	0.61	0.34	0.34	0.34	0.32	0.30	0.27
	168	0.22	0.26	0.29	0.32	0.33	0.34	0.62	0.35	0.35	0.35	0.33	0.30

	193	0.21	0.25	0.29	0.31	0.33	0.35	0.36	0.64	0.38	0.38	0.36	0.34
	218	0.20	0.25	0.28	0.31	0.34	0.36	0.37	0.39	0.67	0.41	0.41	0.39
	243	0.21	0.25	0.28	0.31	0.34	0.36	0.38	0.41	0.43	0.70	0.45	0.45
	268	0.21	0.25	0.28	0.30	0.33	0.35	0.38	0.41	0.44	0.46	0.72	0.49
	293	0.21	0.24	0.26	0.28	0.30	0.32	0.35	0.38	0.42	0.46	0.49	0.70
Protein	18	0.89	0.57	0.51	0.44	0.38	0.33	0.30	0.27	0.25	0.24	0.23	0.22
	43	0.59	0.91	0.55	0.51	0.46	0.42	0.39	0.36	0.34	0.32	0.29	0.26
	68	0.55	0.57	0.92	0.55	0.52	0.49	0.47	0.44	0.41	0.38	0.34	0.29
	93	0.49	0.53	0.56	0.91	0.55	0.54	0.52	0.50	0.47	0.43	0.38	0.32
	118	0.43	0.50	0.54	0.56	0.91	0.56	0.55	0.54	0.51	0.48	0.42	0.35
	143	0.39	0.46	0.52	0.55	0.57	0.91	0.58	0.57	0.55	0.51	0.46	0.39
	168	0.36	0.44	0.50	0.54	0.57	0.58	0.91	0.59	0.58	0.55	0.50	0.44
	193	0.34	0.42	0.48	0.53	0.56	0.58	0.59	0.92	0.60	0.59	0.55	0.50
	218	0.33	0.40	0.46	0.50	0.54	0.56	0.59	0.61	0.93	0.62	0.60	0.56
	243	0.33	0.38	0.43	0.47	0.50	0.53	0.57	0.59	0.62	0.93	0.64	0.62
	268	0.31	0.36	0.39	0.42	0.45	0.48	0.52	0.56	0.60	0.64	0.93	0.67
	293	0.30	0.32	0.34	0.36	0.38	0.41	0.46	0.50	0.56	0.62	0.67	0.93
		Fat yield											
Milk	18	0.61	0.53	0.42	0.34	0.30	0.28	0.28	0.29	0.31	0.33	0.35	0.35
	43	0.55	0.49	0.40	0.34	0.30	0.29	0.29	0.30	0.32	0.35	0.38	0.40
	68	0.47	0.43	0.37	0.32	0.29	0.28	0.28	0.30	0.32	0.35	0.39	0.42
	93	0.40	0.38	0.33	0.29	0.27	0.26	0.27	0.29	0.31	0.35	0.39	0.43
	118	0.36	0.35	0.31	0.27	0.26	0.25	0.26	0.28	0.31	0.35	0.39	0.43
	143	0.33	0.32	0.29	0.26	0.25	0.25	0.26	0.29	0.32	0.36	0.40	0.44
	168	0.32	0.31	0.28	0.26	0.25	0.25	0.27	0.29	0.33	0.37	0.42	0.45
	193	0.31	0.31	0.28	0.26	0.25	0.26	0.28	0.31	0.34	0.39	0.44	0.48
	218	0.31	0.30	0.28	0.26	0.26	0.27	0.29	0.32	0.36	0.41	0.46	0.50
	243	0.30	0.30	0.28	0.26	0.26	0.28	0.30	0.34	0.38	0.44	0.49	0.54
	268	0.28	0.29	0.28	0.27	0.27	0.29	0.32	0.35	0.40	0.46	0.52	0.57
	293	0.24	0.27	0.27	0.27	0.27	0.29	0.32	0.36	0.41	0.47	0.54	0.60
Fat	18	**0.10**	0.93	0.81	0.73	0.70	0.70	0.72	0.73	0.74	0.72	0.67	0.58
	43	0.71	**0.11**	0.97	0.93	0.91	0.90	0.90	0.89	0.88	0.85	0.82	0.76
	68	0.59	0.64	**0.14**	0.99	0.98	0.97	0.96	0.94	0.91	0.88	0.86	0.83
	93	0.45	0.55	0.61	**0.16**	1.00	0.99	0.97	0.95	0.92	0.89	0.88	0.86
	118	0.33	0.46	0.56	0.61	**0.17**	1.00	0.98	0.96	0.94	0.91	0.90	0.88
	143	0.25	0.39	0.51	0.59	0.62	**0.17**	1.00	0.98	0.96	0.94	0.92	0.90
	168	0.19	0.34	0.47	0.56	0.61	0.63	**0.16**	0.99	0.98	0.97	0.95	0.92
	193	0.17	0.31	0.43	0.52	0.58	0.61	0.63	**0.17**	1.00	0.99	0.97	0.93
	218	0.17	0.29	0.40	0.48	0.54	0.57	0.60	0.62	**0.17**	1.00	0.98	0.94

	243	0.20	0.29	0.37	0.43	0.47	0.51	0.55	0.58	0.62	**0.18**	0.99	0.96
	268	0.24	0.29	0.33	0.36	0.39	0.42	0.46	0.51	0.57	0.63	**0.18**	0.99
	293	0.28	0.29	0.29	0.28	0.28	0.30	0.34	0.40	0.48	0.59	0.68	**0.16**
Protein	18	0.62	0.42	0.36	0.30	0.24	0.20	0.17	0.16	0.16	0.17	0.19	0.19
	43	0.43	0.64	0.39	0.34	0.30	0.26	0.24	0.23	0.22	0.22	0.22	0.21
	68	0.39	0.41	0.65	0.37	0.34	0.31	0.29	0.28	0.28	0.27	0.25	0.23
	93	0.35	0.38	0.39	0.63	0.36	0.35	0.34	0.33	0.32	0.31	0.29	0.24
	118	0.32	0.35	0.37	0.38	0.62	0.37	0.36	0.36	0.36	0.35	0.32	0.27
	143	0.29	0.33	0.36	0.37	0.38	0.62	0.39	0.39	0.39	0.38	0.35	0.30
	168	0.27	0.31	0.35	0.37	0.38	0.39	0.64	0.41	0.42	0.42	0.39	0.34
	193	0.26	0.30	0.34	0.36	0.37	0.39	0.41	0.67	0.45	0.46	0.44	0.39
	218	0.25	0.29	0.32	0.34	0.36	0.38	0.41	0.44	0.70	0.49	0.48	0.45
	243	0.25	0.28	0.30	0.32	0.34	0.36	0.39	0.43	0.48	0.74	0.53	0.50
	268	0.24	0.26	0.27	0.29	0.30	0.33	0.36	0.41	0.47	0.52	0.75	0.55
	293	0.22	0.23	0.23	0.24	0.25	0.28	0.32	0.37	0.44	0.50	0.56	0.74
							Protein yield						
Milk	18	0.85	0.81	0.77	0.74	0.71	0.70	0.69	0.69	0.68	0.67	0.65	0.61
	43	0.78	0.79	0.78	0.76	0.75	0.74	0.74	0.74	0.74	0.74	0.72	0.69
	68	0.69	0.73	0.74	0.75	0.75	0.75	0.76	0.76	0.76	0.76	0.76	0.74
	93	0.61	0.66	0.70	0.72	0.74	0.75	0.75	0.76	0.76	0.77	0.77	0.76
	118	0.55	0.61	0.67	0.70	0.73	0.74	0.75	0.76	0.76	0.77	0.78	0.77
	143	0.51	0.58	0.64	0.69	0.72	0.74	0.75	0.76	0.77	0.78	0.79	0.79
	168	0.48	0.56	0.63	0.68	0.71	0.74	0.75	0.77	0.78	0.79	0.80	0.81
	193	0.46	0.55	0.62	0.68	0.71	0.74	0.76	0.77	0.79	0.80	0.82	0.83
	218	0.44	0.54	0.61	0.67	0.71	0.74	0.76	0.78	0.79	0.81	0.83	0.85
	243	0.42	0.52	0.60	0.66	0.70	0.73	0.75	0.77	0.79	0.82	0.84	0.87
	268	0.39	0.49	0.57	0.63	0.68	0.70	0.73	0.75	0.77	0.80	0.84	0.87
	293	0.34	0.44	0.53	0.59	0.63	0.66	0.68	0.70	0.73	0.77	0.81	0.86
Fat	18	0.74	0.74	0.73	0.73	0.73	0.74	0.74	0.74	0.74	0.72	0.68	0.61
	43	0.64	0.63	0.62	0.62	0.62	0.62	0.63	0.64	0.64	0.63	0.61	0.56
	68	0.51	0.50	0.50	0.49	0.49	0.50	0.51	0.52	0.52	0.53	0.52	0.49
	93	0.42	0.42	0.41	0.41	0.42	0.43	0.44	0.45	0.46	0.47	0.47	0.45
	118	0.37	0.37	0.37	0.38	0.39	0.40	0.42	0.43	0.45	0.46	0.46	0.45
	143	0.35	0.36	0.37	0.38	0.39	0.41	0.43	0.45	0.46	0.48	0.49	0.48
	168	0.35	0.36	0.38	0.40	0.42	0.44	0.46	0.48	0.50	0.52	0.53	0.53
	193	0.35	0.38	0.40	0.43	0.45	0.48	0.50	0.53	0.55	0.57	0.58	0.58
	218	0.36	0.39	0.42	0.45	0.48	0.51	0.54	0.56	0.59	0.61	0.63	0.63
	243	0.36	0.39	0.43	0.46	0.49	0.53	0.56	0.58	0.61	0.64	0.66	0.67

	268	0.35	0.38	0.42	0.45	0.48	0.52	0.55	0.58	0.61	0.64	0.67	0.69
	293	0.31	0.35	0.38	0.41	0.44	0.47	0.50	0.53	0.56	0.60	0.65	0.68
Protein	18	**0.15**	0.98	0.95	0.89	0.85	0.81	0.77	0.75	0.72	0.69	0.65	0.60
	43	0.66	**0.15**	0.99	0.96	0.92	0.89	0.86	0.83	0.81	0.78	0.75	0.70
	68	0.57	0.61	**0.15**	0.99	0.97	0.95	0.92	0.90	0.88	0.85	0.82	0.78
	93	0.48	0.56	0.60	**0.15**	0.99	0.98	0.96	0.95	0.93	0.91	0.88	0.84
	118	0.40	0.50	0.57	0.61	**0.15**	1.00	0.99	0.97	0.96	0.94	0.92	0.87
	143	0.34	0.45	0.54	0.60	0.63	**0.16**	1.00	0.99	0.98	0.97	0.94	0.90
	168	0.30	0.42	0.51	0.58	0.62	0.65	**0.17**	1.00	0.99	0.98	0.96	0.92
	193	0.28	0.39	0.49	0.56	0.61	0.64	0.66	**0.18**	1.00	0.99	0.97	0.94
	218	0.27	0.37	0.46	0.52	0.57	0.61	0.64	0.67	**0.19**	1.00	0.99	0.95
	243	0.27	0.35	0.42	0.47	0.52	0.56	0.60	0.64	0.68	**0.19**	1.00	0.97
	268	0.28	0.32	0.37	0.41	0.45	0.49	0.54	0.59	0.65	0.70	**0.18**	0.99
	293	0.28	0.29	0.31	0.32	0.35	0.39	0.45	0.51	0.59	0.67	0.74	**0.16**

Heritability estimates in Table 2 agree in general with those reported by Meyer et al. (7), Pander et al. (10), Pösö et al. (11), and Swalve (15). Jamrozik et al. (3) found clearly higher heritability estimates, but those higher estimates were due at least partially to inappropriate specification of the permanent environmental effect (14). The (co)variance functions used in this study were able to interpolate correctly between known lactation stages and to provide reasonable parameter estimates at the ends of the lactation curve.

Genetic and phenotypic correlations for the 12 lactation stages also are in Table 2. All correlations were positive and ranged from 0.16 to 1.00; correlations from the iterative analysis that provided the initial (co)variance estimates also were all positive and ranged from 0.21 to 0.97 (1).

Within a yield trait, genetic correlations declined from $\geq$ 0.93 for adjacent lactation stages to 0.52 for milk, 0.58 for fat, and 0.60 for protein between initial and final lactation stages. Phenotypic correlations for milk yield declined from $\geq$ 0.65 for adjacent lactation stages to 0.31 between initial and final lactation stages. For fat and protein yields, phenotypic correlations were highest ($\geq$ 0.60) between adjacent lactation stages and lowest (0.17 for fat and 0.27 for protein) between the beginning of lactation and 180 to 255 DIM. Gengler et al. (1) reported that genetic correlations within a yield trait declined from $\geq$ 0.90 for adjacent lactation stages to 0.75 for milk and protein and to 0.82 for fat between initial and final lactation stages; corresponding decreases for phenotypic correlations were from $\geq$ 0.56 to 0.38 for milk, from $\geq$ 0.38 to 0.27 for fat, and from $\geq$ 0.47 to 0.32 for protein.

Genetic correlations were lowest between milk and fat yields (0.24 to 0.61), intermediate between fat and protein yields (0.31 to 0.74), and highest between milk and protein yields (0.34 to 0.87). Within lactation stage, genetic correlations averaged 0.40 between milk and fat, 0.55 between fat and protein, and 0.78 between milk and protein. Mean phenotypic correlations within lactation stage were 0.65 between milk and fat, 0.67 between fat and protein yields, and 0.92 between milk and protein yields. Gengler et al. (1) reported mean genetic correlations of

0.40 between milk and fat, 0.56 between fat and protein, and 0.78 between milk and protein within lactation stage; corresponding mean phenotypic correlations were 0.64, 0.66, and 0.91.

Genetic and phenotypic correlations in Table 2 correspond to those reported by most researchers (7, 10, 13). However, Vargas et al. (17) reported slightly lower genetic correlations and notably higher phenotypic correlations than those in Table 2, which could have been caused by differences in populations, data, statistical models, or computational methods.

The (co)variance functions provided plausible interpolated and extended estimates. For example, the estimated genetic correlation between 18 and 93 DIM was 0.82 for milk yield, and Kettunen et al. (4) reported a genetic correlation of 0.83 between 25 and 85 DIM. Few unexpected patterns were observed with the exception of lower genetic correlations between yield traits within lactation stages during the middle of lactation than at the ends of the lactation curve. However, this pattern was present in the results of the iterative analysis of Gengler et al. (1) that provided the initial (co)variance estimates and, therefore, is not a consequence of the (co)variance function methodology.

CONCLUSIONS

The estimation of (co)variance components is crucial for the development of genetic evaluation systems based on test day yields. Genetic and residual (co)variance matrices for milk, fat, and protein yields in 12 lactation stages of 25-d each were constructed from estimates from 4 lactation stages of 75 d each using (co)variance functions and a decomposition of residuals into time-dependent and temporary environmental effects. Correlations between temporary environmental variances were lower for milk and fat yields than for milk and protein yields but higher than for protein and fat yields. Heritability estimates for yield traits ranged from 0.10 to 0.22. All genetic and phenotypic correlations were positive and ranged from 0.16 to 1.00. Genetic variances increased with increased DIM, which suggests that selection on the last part of lactation would be effective; however, genetic correlations between the start and end of lactation were positive and moderately high for all yield traits (0.52 for milk, 0.58 for fat, and 0.60 for protein). Genetic correlations between the same yield trait at different lactation stages were higher than the corresponding phenotypic correlations. Genetic correlations were comparable with those estimated iteratively by Gengler et al. (1) for lactation stages with corresponding midpoints.

The proposed (co)variance polynomial functions provide a valid method for increasing the density of (co)variance estimates over a lactation. However, testing of functions other than polynomials is warranted.

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