

Indirect Estimation of (Co)Variance Functions for Test-Day Yields During First and Second Lactations in the United States

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ABSTRACT

(Co)variance components for milk, fat, and protein yields during first and second lactations were estimated from test-day data from 23,029 Holstein cows from 37 herds in Pennsylvania and Wisconsin using a multitrait test-day model. Canonical transformation was used with an expectation-maximization algorithm. To allow description of (co)variances within and across yield traits and parities, four lactation stages of 75 d were defined for each parity, and the test day nearest the center of each interval was used. Prior to analysis, data were adjusted for lactation curves within lactation stages using all records from all available cows. Data from cows with missing values were excluded to allow a canonical transformation to be used for estimation of (co)variance matrices. Data from 9110 cows were available for canonical analysis of lactations with test days in all lactation stages. (Co)variance functions were used to describe (co)variance structure within and across yield trait and parity. (Co)variance components of biological functions (305-d yield, persistency defined as difference between yields on d 280 and 60, and maturity rate defined as difference between second- and first-lactation yields) were developed from (co)variance functions. Heritabilities ranged from 0.09 to 0.22 for test-day yields, from 0.21 to 0.23 for 305-d yields, from 0.03 to 0.11 for persistencies, and from 0.05 to 0.07 for maturity rates. Phenotypic correlations between first- and second-lactation persistencies were low, but genetic correlations were high. Genetic correlations with maturity rate ranged from 0.11 to 0.61 for 305-d yields and persistencies.

(Key words: genetic parameters, (co)variance functions, test-day model, genetic evaluation)

INTRODUCTION

Direct use of test-day information (e.g., [Everett et al., 1994](#); [Jamrozik et al., 1996](#); [Jamrozik et al., 1997](#); [Ptak and Schaeffer, 1993](#); [Swalve, 1995a](#); [Swalve, 1995b](#); [Wiggans and Goddard, 1997](#)) by fitting a model to test-day data provides more accurate accounting of environmental effects and allows improved prediction of genetic values for total yields than using a model based on lactation yields. In addition, new traits such as persistency of lactation yield and genetic differences in maturity rate can be evaluated. Efforts to reduce the cost of milk recording have resulted in fewer test-day records and a loss of information that is available for computation of 305-d yields. Direct use of test-day data can accommodate the less frequent measurement that has resulted from as well as allow better monitoring of management systems ([Everett et al., 1994](#)). Although genetic parameters across 305-d yields for different parities are well known, additional research is needed to determine the (co)variance structures among test days within and across lactations.

Two methods are currently used for the estimation of (co)variance components of test-day yields. The first method is based on the analysis of test-day data with a model that estimates random regression coefficients of the lactation curve for each animal (e.g., [Jamrozik et al., 1996](#)). This method was used recently by several authors ([Gengler et al., 1999b](#); [Jamrozik and Schaeffer, 1997](#); [Pösö et al., 1996](#)) for estimation of (co)variance components and theoretically should be the best approach. The estimated (co)variances across random regressions provide the needed (co)variance structure of test-day yields. The second method is to apply a multitrait analysis in which different test-day yields are treated as different traits (e.g., [Gengler et al., 1999c](#)). Multitrait (co)variance components obtained from this method do not allow a direct continuous description of the (co)variance structure. Fortunately, recent work on (co)variance functions ([Kirkpatrick et al., 1994](#)) has enabled the development of continuous descriptions of the (co)variance structure a posteriori.

Results obtained by the two methods are not equivalent. Several possible explanations exist for the differing solutions: fixed effects are not estimated the same way; multivariate models use fixed stages to restrict the number of traits; and the random regression approach is highly influenced by the nature of the regressions. In particular, the correct description of the beginning and of the end of the lactation (e.g., [Gengler et al., 1999b](#); [Jamrozik and Schaeffer, 1997](#)) can be problematic. Similar problems are expected when estimating (co)variance components across lactations. The objective of this study was to extend the simplified, but robust, multitrait approach that was described by Gengler et al. ([1999c](#)) and Tijani et al. ([1999](#)) to estimate (co)variances for milk, fat, and protein yields across and within first and second parities simultaneously.

MATERIALS AND METHODS

Data

The data and procedures used by Gengler et al. ([1999b](#)) were extended to include yields from second lactations. First- and second-lactation records were obtained for 23,029 Holstein cows that calved from 1990 through 1996 in 37 large herds in Pennsylvania (mean of 287 cows per herd) and Wisconsin (mean of 261 cows per herd). Complete data were required to estimate the full set of genetic parameters. Therefore, first- and second-lactation records were used for the estimation of variance components from only the 9110 cows with test-day data in all lactation stages for both parities. Four lactation stages of 75 d each were defined starting with d 6 for each

lactation. The test day that was nearest to the center of the lactation stage (d 43, 118, 193, or 268) was retained. Only four lactation stages were defined to increase the likelihood of observations in all stages. The 24 traits analyzed included milk, fat, and protein yields recorded during the four lactation stages of first and second parities.

Pedigree information was included for animals born during 1980 or later. Pedigree data for animals born prior to 1980 were not included because of concern that the inclusion of this data in the analysis would slow convergence during iteration. Eight groups were defined for animals with unknown parents based on birth year of the animal: 1980 and earlier, 1981 through 1982, ..., 1991 through 1992, and 1993 and later.

Model

Because a test day could occur on any day within a 75-d stage, a model that adjusted for the shape of the lactation curve was necessary. The model was based on Gengler et al. (1999c) but adapted to allow bilactational analysis:

$$y_{ijklmn} = \text{HTF}_j + \text{AS}_k + \text{AS}_k(b_1)\text{DIM}^{0.5} + \text{AS}_k(b_2)\log(\text{DIM}) + \text{HYS1}_{il} + \text{C1}_{im} + \text{HYS2}_{il} + \text{C2}_{im} + a_{in} + e_{ijklmn},$$

where y_{ijklmn} = test-day record for milk, fat, or protein yield of cow n during lactation stage i for class j of herd, test day, and milking frequency (HTF) defined across parities and lactation stages, class k of calving age and season (AS) across lactation stages within parity; class l of herd, year, and calving season (HYS), and class m for calving age (C) in months within lactation stage; b = regression coefficient; a = animal effect (breeding value); and e = residual effect. Milking frequency for HTF classes was two or three times daily, and HTF classes were required to have at least three records. For HYS, the number of effects had to be doubled and separated according to parity (i.e., HYS1 and HYS2, C1 and C2) because the multitrait step that uses canonical transformation requires the same model. Classes for AS were 20 to 23, 24 to 25, 26 to 27, 28 to 31, and 32 to 35 mo for first parity and 31 to 35, 36 to 38, 39 to 43, and 44 to 56 for second parity. Starting with January, six 2-mo calving seasons were defined for AS and HYS. Because of the impact of calving age and season on yield and persistency (e.g., Gengler, 1996), AS was included in the model along with regressions on a function of DIM that was nested within AS. Defining HYS within trait and lactation stage (in contrast to HTF, which is defined across lactation stage) allowed the consideration of different effects of environment by lactation stage. Inclusion of C within trait and lactation stage accounted for differences by age in persistency that were not accounted for by nesting regressions within AS.

(Co)Variance Components

Canonical transformation requires that the same model apply to all traits. However, traits from different lactation stages necessarily occur on different test days. Therefore, data were analyzed with the computational strategy in [Table 1](#).

Table 1. Computational strategy for estimation of (co)variance components from test-day data for milk, fat, and protein yields from first and second lactations.

Iteration round	Computation	Definition
1	1	Perform Step 1 ¹ using original test-day data.
2 through 4	2	Estimate (co)variance components using test-day data that were adjusted with the most recent solutions from Step 1.
	3	Perform Step 2 ² using most recent (co)variance components from Computation 2 and test-day data that were adjusted with the most recent solutions from Step 1.
	4	Perform Step 1 using test-day data that were adjusted with the most recent solutions from Step 2.
	5	Repeat Computations 2 through 4 until mean relative differences between animal solutions are <1%.
	6	Repeat Computation 2.

¹Step 1: Estimation of effects for herd, test day, and milking frequency and for calving age and season within parity; estimation of regression coefficients for DIM^{0.5} and log(DIM).

²Step 2: Estimation of effects for herd, year, and calving season; calving age; and animal (breeding value).

The solution procedure was similar to that proposed by Wiggans and Goddard (1997). Step 1 estimated effects that were not specific to lactation stage (HTF, AS, and shape of lactation curve) with the following fixed submodel:

$$y_{ijklmn}^{[1]} = \text{HTF}_j + \text{AS}_k + \text{AS}_k(b_1)\text{DIM}^{0.5} + \text{AS}_k(b_2)\log(\text{DIM}) + e_{ijklmn}^{[1]},$$

where $y_{ijklmn}^{[1]}$ = test-day yield adjusted for all effects not included in Step 1; i.e., $y_{ijklmn}^{[1]} = y_{ijklmn} - (\text{HYS1}_{il} + \text{C1}_{im} + \text{HYS2}_{il} + \text{C2}_{im} + a_{in})$. Data from all 23,029 cows were used with the general linear models procedure of SAS (1994).

Step 2 estimated effects that were specific to parity and lactation stage (HYS, C, and a) using canonical transformation with an expectation-maximization algorithm for missing values (Ducrocq and Besbes, 1993). Only the data from the 9110 cows with complete data was used in this step. Test day yields used were adjusted for effects in Step 1: $y_{ijklmn}^{[2]} = y_{ijklmn} - [\text{HTF}_j + \text{AS}_k$

+ $AS_k(b_1)DIM^{0.5} + AS_k(b_2)\log(DIM)$]. Therefore, this submodel was a multitrait animal model:

$$y_{ijklmn}^{[2]} = HYS1_{il} + C1_{im} + HYS2_{il} + C2_{im} + a_{in} + e_{ijklmn}^{[2]}$$

Steps 1 and 2 were solved iteratively as shown in [Table 1](#). Required (co)variance components for solving Step 2 were obtained from the previous round of iteration. (Co)variance components were estimated using canonical transformation with an expectation-maximization REML algorithm ([Misztal et al., 1992](#); [Misztal et al., 1995](#)). This method was preferred over a bivariate analysis to assure that (co)variance matrices were positive definite even with high correlations among yields from close test days.

(Co)Variance Functions

(Co)variance functions were fitted to the estimated genetic and residual (co)variance matrices to allow a complete description of the (co)variance structure of test-day yields. The procedure of [Tijani et al. \(1999\)](#) for fitting reduced (co)variance functions was adapted for milk, fat, and protein test-day yields from different stages of first and second lactations that were considered to be 24 different traits ([Meyer and Hill, 1997](#)):

$$\mathbf{K} = (\Phi'\Phi)^{-1}\Phi'\Sigma\Phi(\Phi'\Phi)^{-1},$$

where \mathbf{K} = matrix of (co)variance function coefficients, Φ = matrix of Legendre polynomial functions evaluated for a yield trait (milk, fat, or protein) during a lactation stage of first or second parity, and Σ = (co)variance matrix for test-day yields (24 x 24); the generalized least squares inverse of Φ is $(\Phi'\Phi)^{-1}\Phi'$.

For the genetic (co)variance matrix (\mathbf{G}), the matrix of (co)variance function coefficients (\mathbf{K}_G) was

$$\mathbf{K}_G = (\Phi'\Phi)^{-1}\Phi'\mathbf{G}\Phi(\Phi'\Phi)^{-1}.$$

The order for genetic (co)variance functions was reduced to constant, linear, and quadratic Legendre polynomials:

$$\begin{aligned} I_0 &= (1/2)^{0.5}, \\ I_1 &= (3/2)^{0.5}x, \text{ and} \\ I_2 &= (5/8)^{0.5}(3x^2 - 1), \end{aligned}$$

where $x = -1 + 2[(DIM - 1)/(305 - 1)]$. Eigenvalues of genetic and residual correlation matrices were computed to determine if the proposed reduction of parameters for the genetic (co)variance matrix would provide adequate fit.

The residual (co)variance matrix (\mathbf{R}) was decomposed to account for two types of (co)variances: permanent (\mathbf{R}^*) and temporary (\mathbf{E}) environmental effects (Tijani et al., 1999). For \mathbf{R}^* , the matrix of (co)variance function coefficients $\mathbf{K}_{\mathbf{R}^*}$ was

$$\mathbf{K}_{\mathbf{R}^*} = (\Phi'\Phi)^{-1}\Phi'\mathbf{R}^*\Phi(\Phi'\Phi)^{-1}.$$

Initial estimation of \mathbf{R}^* was based on regression of elements of \mathbf{R} on \mathbf{G} with replacement of elements that contain measurement error with their estimates. Estimation of \mathbf{E} was based on the geometric mean of $\mathbf{R} - \mathbf{R}^*$ that corresponded to a given measurement error (co)variance. Then \mathbf{R}^* was updated as $\mathbf{R}^* = \mathbf{R} - (\mathbf{E} \otimes \mathbf{I})$, where \mathbf{I} = identity matrix. Iteration was continued until \mathbf{R}^* and \mathbf{E} were both positive definite to ensure the best possible fit of \mathbf{R}^* and the best estimation of \mathbf{E} .

Lactation Yield, Persistency, and Maturity Rate

(Co)variance functions allow easy definition of functions of yields at different test days. Those functions have more understandable biological meaning than random regressions and (co)variance function coefficients. Three types of biological variates were defined as functions of test-day yields. Lactation (305-d) milk, fat, and protein yields were defined across first and second parities as 305 times the mean of test-day yields between d 1 and 305. To allow comparison with existing persistency evaluations from Canada (Canadian Dairy Network, 1999; Jamrozik et al., 1997), persistency was defined as yield at d 280 minus yield at d 60. Because persistency is a different trait for different parities (Swalve and Gengler, 1998), first- and second-parity persistencies were defined for milk, fat, and protein yields. Maturity rate was defined as 305-d lactation yield from second parity minus 305-d lactation yield from first parity.

(Co)variance functions enable generation of genetic and phenotypic (co)variances among all 12 biological variates through a summing matrix \mathbf{S} of test-day effects. Therefore, genetic (\mathbf{G}_B) and phenotypic (\mathbf{P}_B) (co)variance matrices for those variates could be defined as $\mathbf{G}_B = \mathbf{S}\mathbf{K}_G\mathbf{S}'$ and $\mathbf{P}_B = \mathbf{S}(\mathbf{K}_G + \mathbf{K}_{\mathbf{R}^*})\mathbf{S}' + \mathbf{D}$, where \mathbf{D} represents temporary environment (co)variances that were computed from elements in \mathbf{E} associated with the biological functions. Heritabilities and genetic and phenotypic correlations among the biological variates also were calculated.

RESULTS AND DISCUSSION

Descriptive Statistics

Table 2 shows the number of cows with test-day yields for each lactation stage of each parity. Means and standard deviations for test-day yields are in Table 2 for all cows and in Table 3 for the 9110 cows with no missing observations. Means were slightly higher and standard deviations were slightly lower when only animals without missing observations were considered.

Table 2. Numbers of cows and means and standard deviations for milk, fat, and protein test-day yields for four lactation stages for first and second parities.

Parity	Lactation stage ¹	Cows	Milk		Fat		Protein	
			(no.)	(kg)	(kg)	(g)	(g)	(g)
			Mean	SD	Mean	SD	Mean	SD
1	1	23,029	29.3	6.8	1056	283	862	193
	2	20,631	30.0	6.4	1027	256	927	189
	3	18,848	28.0	6.5	1002	251	902	200
	4	17,214	24.7	6.7	937	256	828	211
2	1	13,536	39.0	8.9	1372	395	1149	252
	2	11,799	35.7	8.1	1211	339	1102	220
	3	10,401	30.4	8.1	1089	325	983	248
	4	9110	24.1	8.3	911	326	819	267

¹Lactation stages: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day nearest to d 268 between 231 and 305 d.

Table 3. Means and standard deviations for DIM and milk, fat, and protein test-day yields for four lactation stages for first and second parities for 9110 cows with test days in all lactation stages.

Parity	Lactation stage ¹	DIM		Milk		Fat		Protein	
		(d)	(d)	(kg)	(kg)	(g)	(g)	(g)	(g)
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	1	42.5	12.2	30.4	6.1	1084	264	889	171
	2	116.7	11.6	30.5	5.9	1041	246	942	173
	3	191.6	11.5	28.2	6.1	1008	236	907	184
	4	266.5	11.6	24.7	6.4	940	243	826	196
2	1	42.2	12.2	40.2	8.1	1404	380	1182	231
	2	116.8	11.7	36.5	7.6	1234	328	1125	220
	3	191.7	12.0	31.0	7.6	1107	315	1000	233
	4	265.7	12.9	24.1	8.3	911	326	820	267

¹Lactation stage: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day nearest to d 268 between 231 and 305 d.

Means and standard deviations for DIM are also reported in [Table 3](#). For similar first-parity data,

Gengler et al. (1999b) reported peak milk yields around 65 d. Therefore, the test-day record for the first lactation stage (nearest to d 43) is most likely from before peak yield, and the test-day record for the second stage (nearest to d 118) is most likely after peak yield. Gengler et al. (1999b) reported no clear peak for fat yield and a peak after d 100 for protein yield. For protein, component yield means in Table 3 supported those findings. The test-day record for the second stage is around peak yield. For second parity, peak yields were larger and occurred earlier during lactation than for first parity. A comparison of Tables 2 and 3 shows that cows with test days in all lactation stages had slightly higher mean yields and slightly lower variances.

(Co)Variance Components

Heritability estimates for yield traits during first lactation (Table 4) generally increased slightly during mid-lactation and then decreased; first-parity estimates were similar to those reported by Gengler et al. (1999c). For second parity (Table 5), heritability estimates increased across lactation stages, which differed slightly from the trend found for first parity. Estimates of heritability were rather low compared with estimates in most other studies (e.g., Jamrozik and Schaeffer, 1997; Pösö et al., 1996; Rekaya et al., 1995); however, estimates by Veerkamp and Goddard (1998) were similar. Gengler et al. (1999b) used similar first-parity data and found heritability estimates to be around 20% higher if a direct random regression approach was used. Theoretical work by van der Werf et al. (1998) indicated that random regression and (co) variance function models are equivalent. The most likely reason for the lower heritability estimates found in this study is the long lactation stages, which assumed that yield on every test day within the 75-d period was the same trait.

Table 4. Heritabilities (on diagonal and bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for test-day yields of milk, fat, and protein during first lactation.

Yield trait	Lactation stage ¹	Lactation stage											
		Milk				Fat				Protein			
		1	2	3	4	1	2	3	4	1	2	3	4
Milk	1	0.13	0.84	0.80	0.69	0.33	0.08	0.15	0.29	0.69	0.68	0.62	0.62
	2	0.56	0.18	0.96	0.85	0.21	0.24	0.26	0.34	0.48	0.69	0.66	0.68
	3	0.48	0.63	0.21	0.90	0.26	0.25	0.30	0.37	0.45	0.68	0.72	0.76
	4	0.38	0.52	0.61	0.18	0.16	0.21	0.26	0.46	0.29	0.48	0.52	0.75
Fat	1	0.63	0.33	0.27	0.21	0.11	0.75	0.81	0.74	0.57	0.59	0.65	0.58
	2	0.26	0.57	0.30	0.25	0.36	0.12	0.95	0.87	0.13	0.33	0.40	0.42
	3	0.25	0.33	0.60	0.33	0.34	0.46	0.16	0.74	0.57	0.59	0.65	0.58
	4	0.22	0.31	0.38	0.70	0.28	0.38	0.48	0.16	0.16	0.34	0.41	0.61
Protein	1	0.90	0.45	0.37	0.28	0.64	0.25	0.23	0.20	0.13	0.87	0.77	0.61
	2	0.48	0.89	0.51	0.42	0.33	0.59	0.34	0.31	0.48	0.14	0.95	0.80

3	0.41	0.53	0.90	0.51	0.30	0.32	0.63	0.39	0.40	0.55	0.18	0.88
4	0.34	0.46	0.53	0.92	0.26	0.29	0.37	0.74	0.32	0.45	0.55	0.13

¹Lactation stages: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day nearest to d 268 between 231 and 305 d.

Table 5. Heritabilities (on diagonal and bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for test-day yields of milk, fat, and protein during second lactation.

Yield trait	Lactation stage ¹	Lactation stage											
		Milk				Fat				Protein			
		1	2	3	4	1	2	3	4	1	2	3	4
Milk	1	0.09	0.83	0.73	0.61	0.21	0.16	0.28	0.42	0.72	0.66	0.67	0.54
	2	0.53	0.14	0.86	0.60	-0.01	0.13	0.15	0.23	0.49	0.69	0.67	0.46
	3	0.43	0.59	0.16	0.89	-0.07	0.14	0.39	0.55	0.41	0.55	0.78	0.76
	4	0.29	0.44	0.61	0.22	0.03	0.20	0.55	0.80	0.43	0.43	0.76	0.92
Fat	1	0.56	0.25	0.21	0.14	0.14	0.78	0.63	0.46	0.42	0.28	0.22	0.20
	2	0.24	0.54	0.31	0.27	0.34	0.13	0.82	0.57	0.27	0.29	0.33	0.33
	3	0.24	0.34	0.67	0.42	0.29	0.43	0.15	0.88	0.33	0.28	0.55	0.69
	4	0.19	0.29	0.45	0.81	0.22	0.35	0.49	0.22	0.45	0.33	0.65	0.88
Protein	1	0.89	0.43	0.35	0.24	0.56	0.24	0.24	0.19	0.12	0.86	0.77	0.60
	2	0.45	0.90	0.50	0.37	0.26	0.56	0.35	0.29	0.47	0.15	0.87	0.58
	3	0.38	0.52	0.93	0.56	0.24	0.33	0.70	0.47	0.38	0.54	0.15	0.88
	4	0.27	0.40	0.57	0.96	0.17	0.29	0.45	0.84	0.26	0.40	0.59	0.21

¹Lactation stages: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day nearest to d 268 between 231 and 305 d.

Genetic and phenotypic correlations for milk, fat, and protein test-day yields are in [Table 4](#) for first parity and in [Table 5](#) for second parity. Phenotypic correlations were similar for both parities, with a slight tendency for those for second parity to be lower; as expected, phenotypic correlations were high between test-day yields during the same lactation stages. Except for genetic correlations between milk and fat test-day yields for second parity, all genetic correlations were as expected. The low, even slightly negative, correlations between fat test-day yield during lactation stage 1 and milk test-day yield in later lactation stages for second parity were unexpected. Gengler et al. (1999c) found similar heritabilities and genetic and phenotypic correlations from a data set that included the data in this study for first parity but with a slightly

different model. In a different study that used a random regression model with similar first-lactation data, Gengler et al. (1999b) generally found lower genetic correlations for lactation stage 1 within each trait.

Genetic correlations between first- and second-lactation stages are in Table 6 for milk, fat, and protein test-day yields; corresponding phenotypic correlations are in Table 7. Genetic correlations were moderately to highly positive except for fat test-day yield. Within yield trait, genetic correlations among the same lactation stages for different parities generally were high (around 0.70). Phenotypic correlations were all positive and low to moderate. Phenotypic correlations between parities for the same lactation stage were similar to corresponding correlations for adjoining lactation stages within yield trait combinations. Those results support the hypothesis that residual (co)variances across parities are 0. Similar patterns for milk yield were reported by Rekaya et al. (1995); however, they also found that phenotypic correlations tended to be lower than genetic correlations between parities. In this study, genetic correlations between corresponding lactations stages were lower between parities (Table 6) than within parity (Tables 4 and 5), especially for fat yield. Although Rekaya et al. (1995) did not make a similar comparison in their study, they did report higher genetic correlations between parities for test days at the middle or end of lactation. For phenotypic correlations, results of this study were more similar to those of Rekaya et al. (1995).

Table 6. Genetic correlations between first- and second-lactation stages for test-day yields of milk, fat, and protein.

Yield trait	First-lactation stage	Second-lactation stage ¹											
		Milk				Fat				Protein			
		1	2	3	4	1	2	3	4	1	2	3	4
Milk	1	0.79	0.71	0.55	0.42	0.07	-0.01	0.05	0.19	0.44	0.48	0.41	0.32
	2	0.77	0.75	0.65	0.48	0.03	-0.09	0.00	0.17	0.38	0.36	0.38	0.31
	3	0.76	0.77	0.73	0.57	0.03	-0.04	0.04	0.24	0.40	0.41	0.46	0.40
	4	0.68	0.73	0.81	0.77	0.00	0.03	0.22	0.45	0.31	0.32	0.49	0.56
Fat	1	0.35	0.06	0.03	0.16	0.84	0.55	0.51	0.50	0.60	0.46	0.38	0.35
	2	0.26	-0.02	0.07	0.20	0.79	0.67	0.67	0.57	0.34	0.09	0.19	0.30
	3	0.35	0.06	0.03	0.16	0.84	0.55	0.51	0.50	0.60	0.46	0.38	0.35
	4	0.43	0.19	0.34	0.51	0.73	0.68	0.83	0.83	0.39	0.24	0.43	0.59
Protein	1	0.57	0.40	0.21	0.19	0.30	0.06	0.00	0.14	0.78	0.69	0.48	0.31
	2	0.68	0.48	0.38	0.35	0.29	0.00	0.07	0.26	0.81	0.67	0.59	0.45
	3	0.71	0.53	0.47	0.42	0.34	0.10	0.17	0.32	0.84	0.74	0.69	0.52
	4	0.72	0.61	0.69	0.72	0.30	0.23	0.42	0.61	0.77	0.71	0.82	0.78

¹Lactation stages: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day

nearest to d 268 between 231 and 305 d.

Table 7. Phenotypic correlations between first- and second-lactation stages for test-day yields of milk, fat, and protein.

Yield trait	First-lactation stage	Second-lactation stage ¹											
		Milk				Fat				Protein			
		1	2	3	4	1	2	3	4	1	2	3	4
Milk	1	0.29	0.28	0.24	0.19	0.09	0.08	0.11	0.10	0.24	0.23	0.20	0.16
	2	0.32	0.36	0.34	0.27	0.10	0.11	0.15	0.15	0.27	0.28	0.28	0.22
	3	0.30	0.38	0.37	0.30	0.09	0.12	0.17	0.16	0.25	0.30	0.30	0.25
	4	0.27	0.33	0.37	0.35	0.08	0.13	0.19	0.22	0.24	0.26	0.30	0.30
Fat	1	0.14	0.13	0.13	0.13	0.19	0.18	0.20	0.20	0.17	0.17	0.17	0.16
	2	0.13	0.15	0.15	0.14	0.23	0.26	0.27	0.23	0.16	0.17	0.18	0.17
	3	0.15	0.16	0.18	0.17	0.26	0.29	0.31	0.27	0.17	0.19	0.22	0.20
	4	0.15	0.17	0.22	0.24	0.20	0.26	0.32	0.32	0.18	0.20	0.25	0.27
Protein	1	0.24	0.22	0.18	0.14	0.12	0.09	0.10	0.10	0.28	0.26	0.22	0.16
	2	0.28	0.29	0.27	0.21	0.14	0.13	0.17	0.15	0.31	0.33	0.30	0.23
	3	0.27	0.31	0.31	0.25	0.14	0.15	0.19	0.18	0.30	0.35	0.34	0.27
	4	0.26	0.29	0.32	0.31	0.14	0.17	0.23	0.25	0.29	0.32	0.35	0.32

¹Lactation stages: 1 = test day nearest to d 43 between 6 and 80 d, 2 = test day nearest to d 118 between 81 and 155 d, 3 = test day nearest to d 193 between 156 and 230 d, and 4 = test day nearest to d 268 between 231 and 305 d.

Eigenvalues of Correlation Matrices

For the genetic correlation matrix among yields from the two parities, the 4 largest of the 24 eigenvalues explained 90% of total variance, which could be expected from the literature (e.g., [Wiggans and Goddard, 1997](#)) because most variation among test-day yields can be assumed to be related to few eigenvalues; the first 18 eigenvalues explained over 99% of genetic variance. For the residual correlation matrix, the 4 largest eigenvalues explained only 64% of total variance, but the first 18 eigenvalues also explained over 99%. Those results confirm that the proposed use of 18 (co)variance function parameters to model the (co)variance structures, and therefore reduce its rank, is justified.

(Co)Variance Functions

Because coefficients for (co)variance functions are cumbersome and difficult to interpret, they are provided only in the Appendix. [Tables A1](#), [A2](#), and [A3](#) show coefficients for genetic (co)

variance functions for first and second parities and between parities, respectively; corresponding correlations between Legendre polynomials are in [Tables A1, A2, and A4](#). [Tables A5, A6, and A7](#) show corresponding coefficients for permanent environmental (co)variance functions; correlations between Legendre polynomials are in [Tables A5, A6, and A8](#). Measurement error variances are in [Table A9](#).

[Figures 1 and 2](#) show heritabilities for different test-day yields computed from (co)variance functions for milk, fat, and protein during first and second lactations, respectively. Heritabilities for first parity were lower at the beginning and end of lactation as expected ([Tijani et al., 1999](#)). For second parity, heritabilities surprisingly increased during the last half of lactation, which has also been reported by [Strabel and Misztal \(1999\)](#). [Swalve and Gengler \(1998\)](#) reported similar differences between first and later parities for persistency.

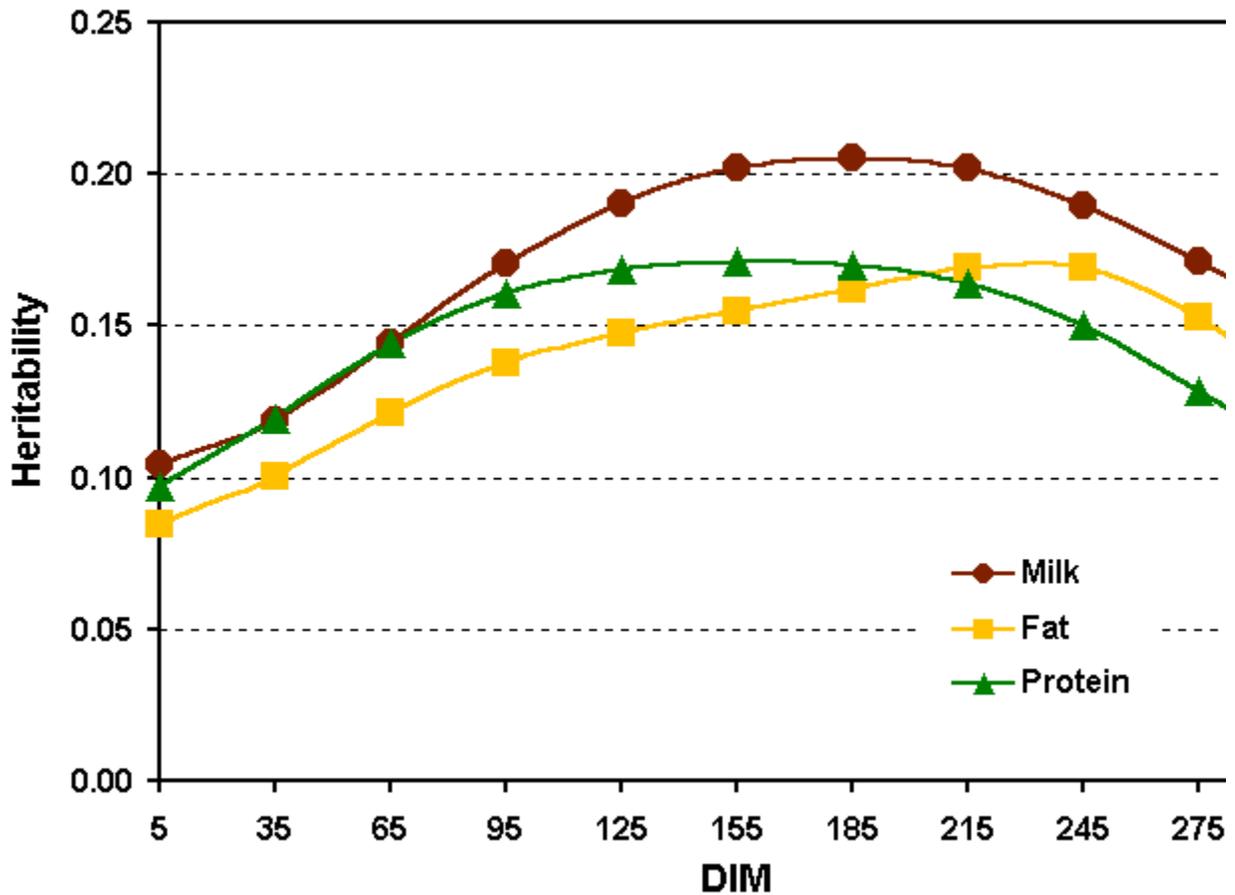


Figure 1. Heritabilities of test-day yields computed from (co)variance functions for yield tr during first lactation.

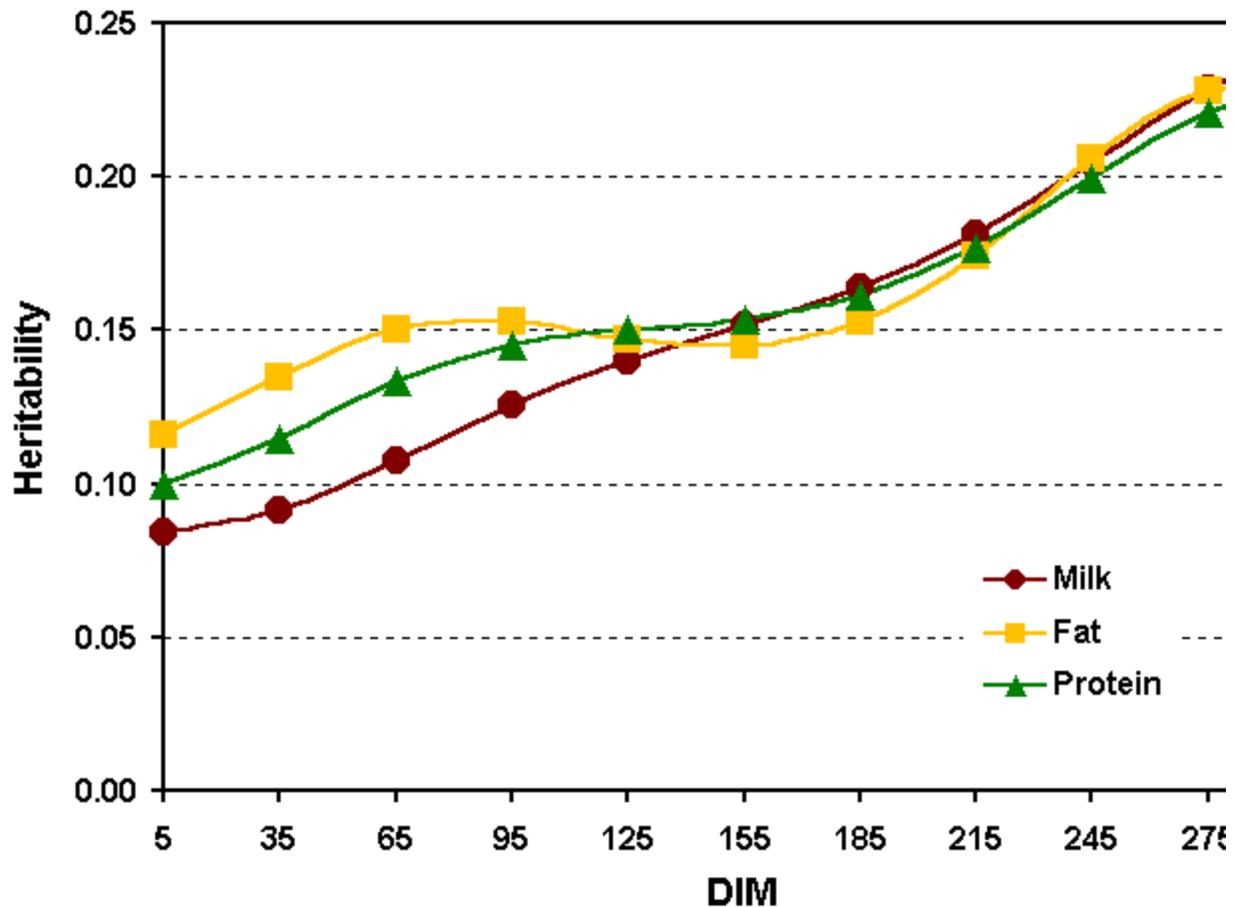


Figure 2. Heritabilities of test-day yields computed from (co)variance functions for yield traits during second lactation.

Figures 3, 4, and 5 show the distribution of genetic correlations between different test-day yields computed from (co)variance functions for milk, fat, and protein, respectively. Results for first parity are above the diagonal; results for second parity are below. For all yield traits, the area that represented correlations of ≥ 0.85 was larger for first than for second parity. The shape of that area also was similar among yield traits: correlations between test-day yields were higher during midlactation. Areas that represented correlations of < 0.55 generally were small for all yield traits and both parities, but area shapes were not consistent. The largest area for correlations of < 0.55 was for fat yield during second lactation (Figure 4) and included test days at the beginning and end of lactation.

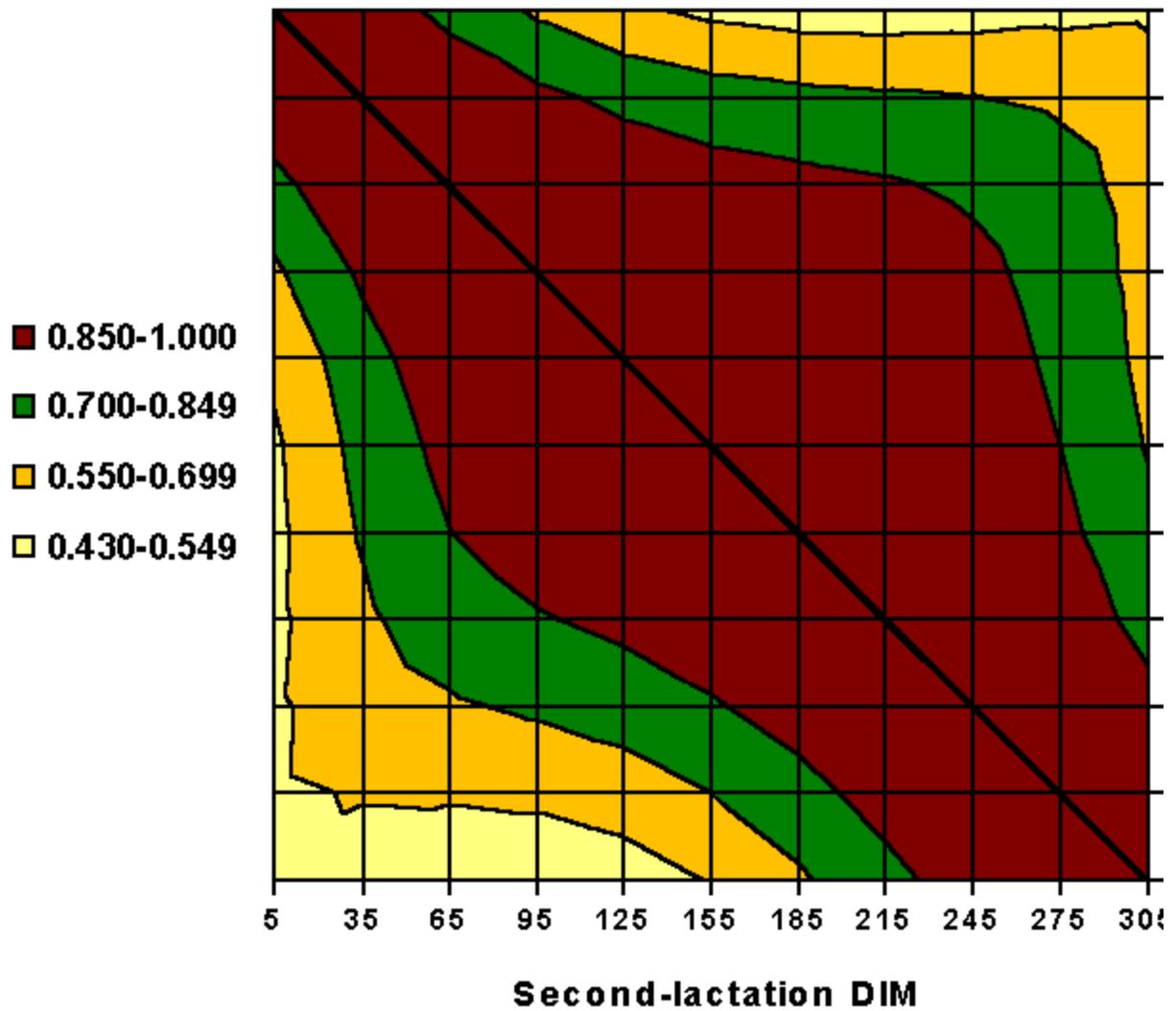


Figure 3. Genetic correlations between test-day yields computed from (co)variance function of milk during first (above diagonal) and second (below diagonal) lactations.

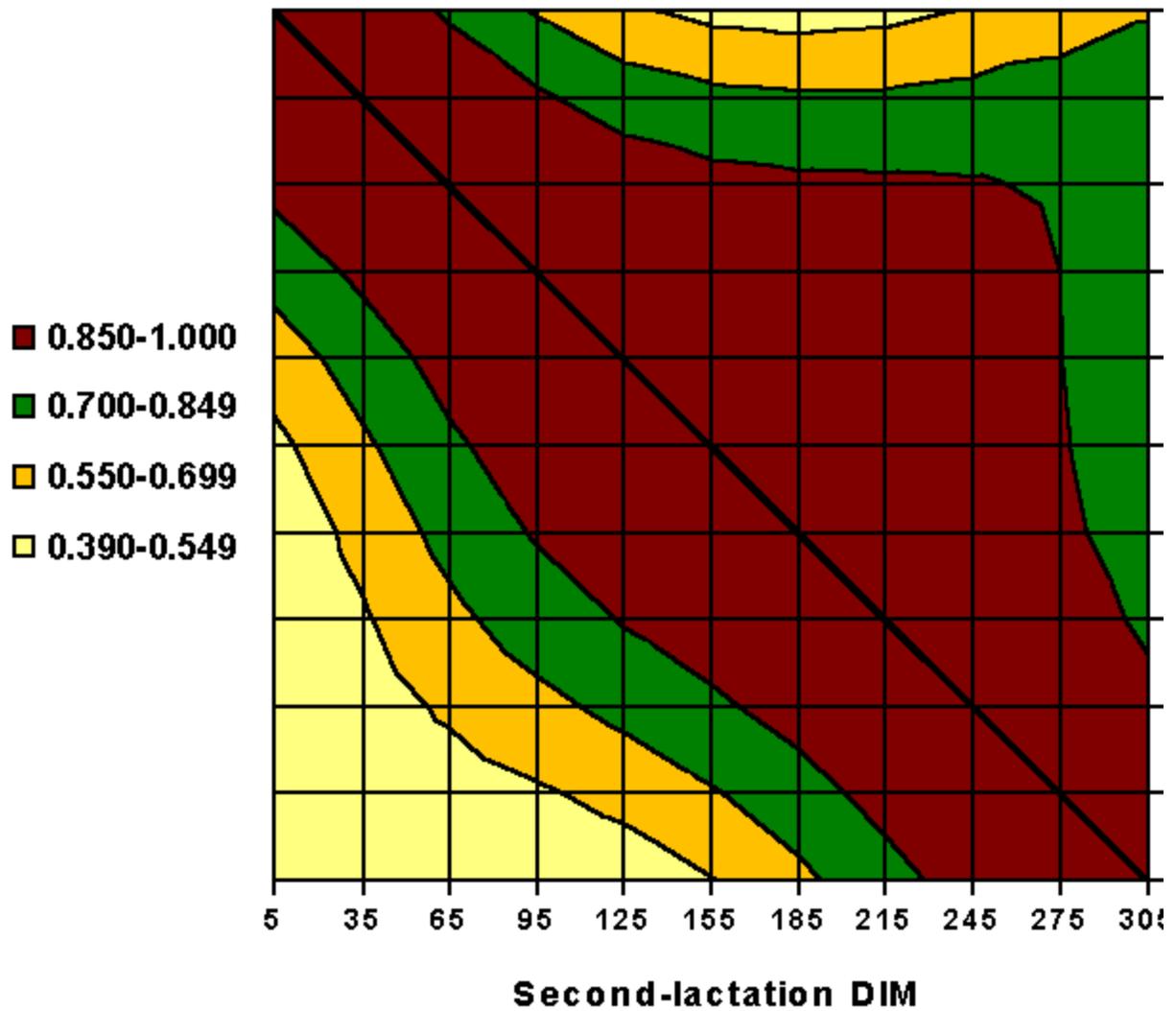


Figure 4. Genetic correlations between test-day yields computed from (co)variance function of fat during first (above diagonal) and second (below diagonal) lactations.

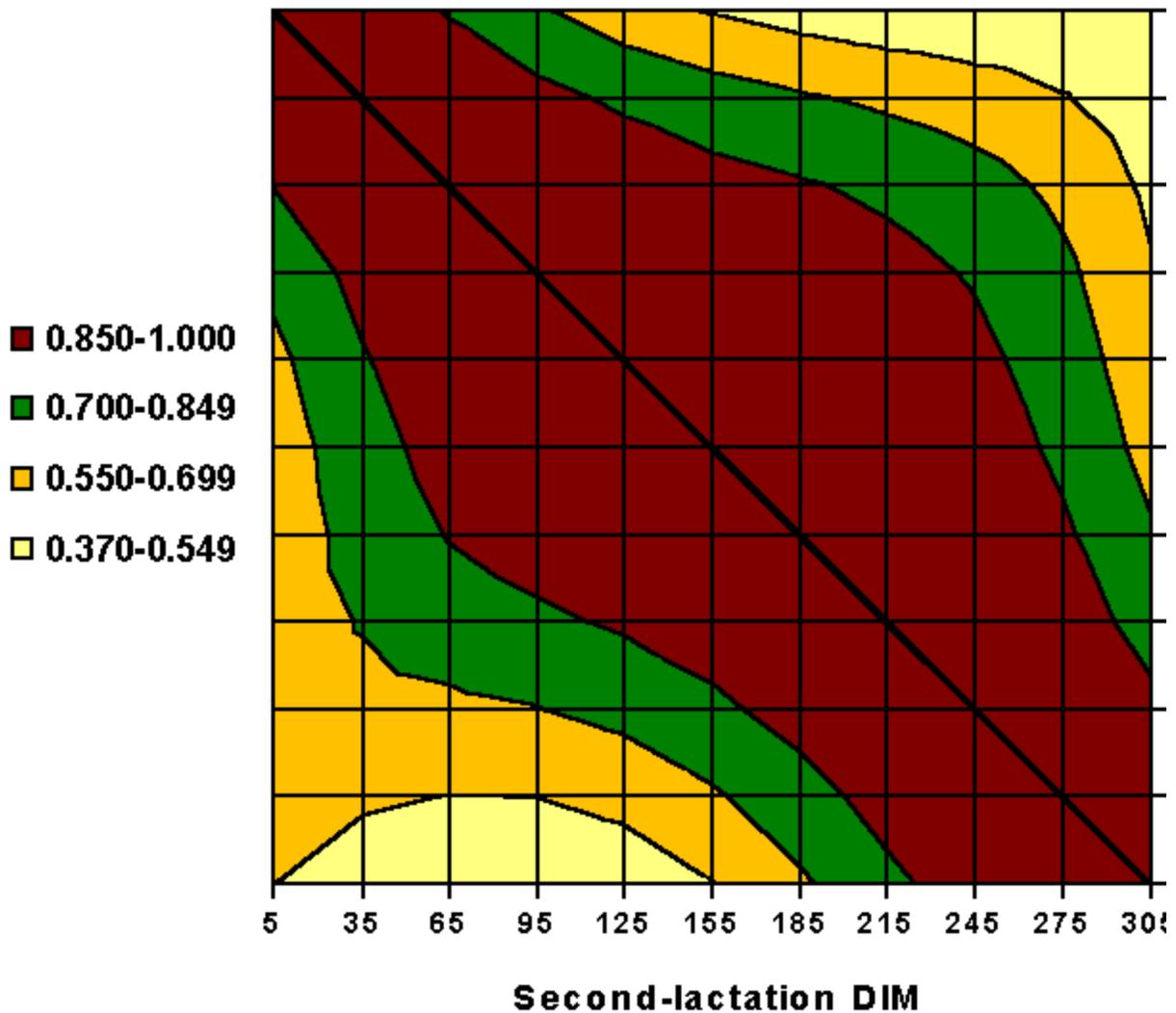


Figure 5. Genetic correlations between test-day yields computed from (co)variance function of protein during first (above diagonal) and second (below diagonal) lactations.

Figures 6, 7, and 8 show the distribution of genetic correlations between first- and second-lactation test-day yields for milk, fat, and protein, respectively. Area shapes for correlations of ≥ 0.75 were similar for milk, fat, and protein. However, areas for correlations of < 0.45 were larger for milk and protein than for fat, which indicates that milk and protein yields are more similar to each other genetically than to fat yield.

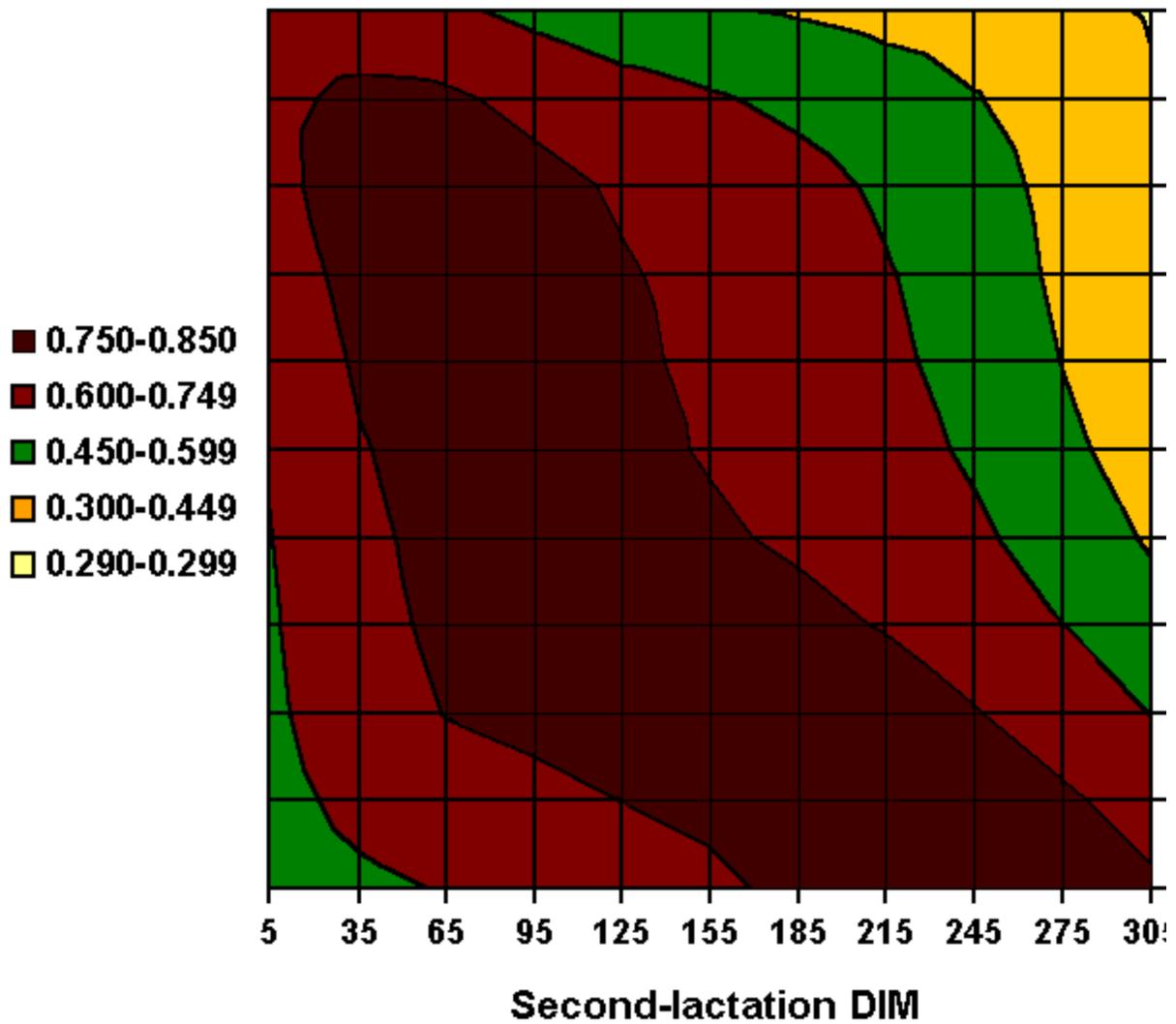


Figure 6. Genetic correlations between first- and second-lactation test-day yields computed from (co)variance functions for milk.

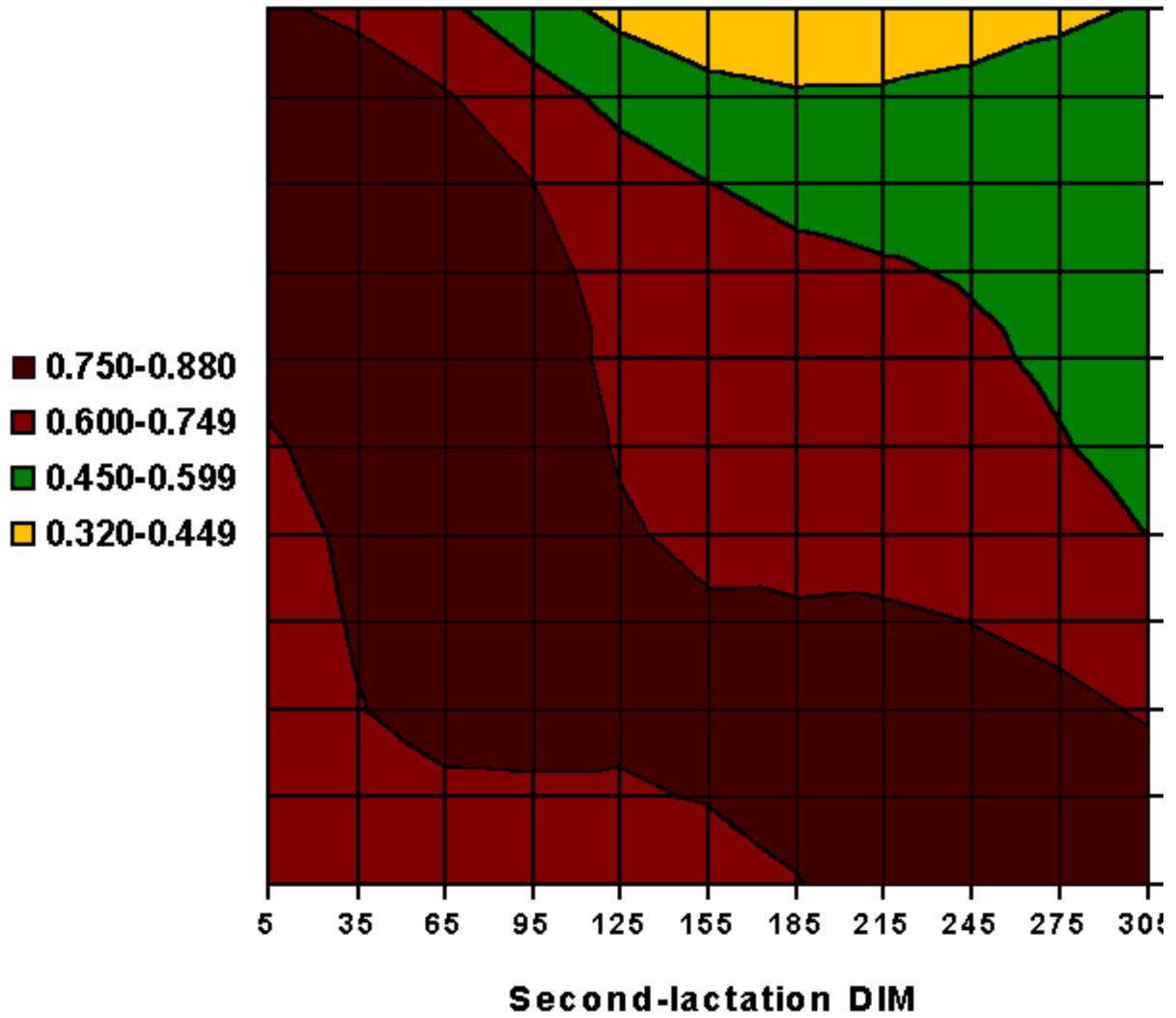


Figure 7. Genetic correlations between first- and second-lactation test-day yields computed from (co)variance functions for fat.

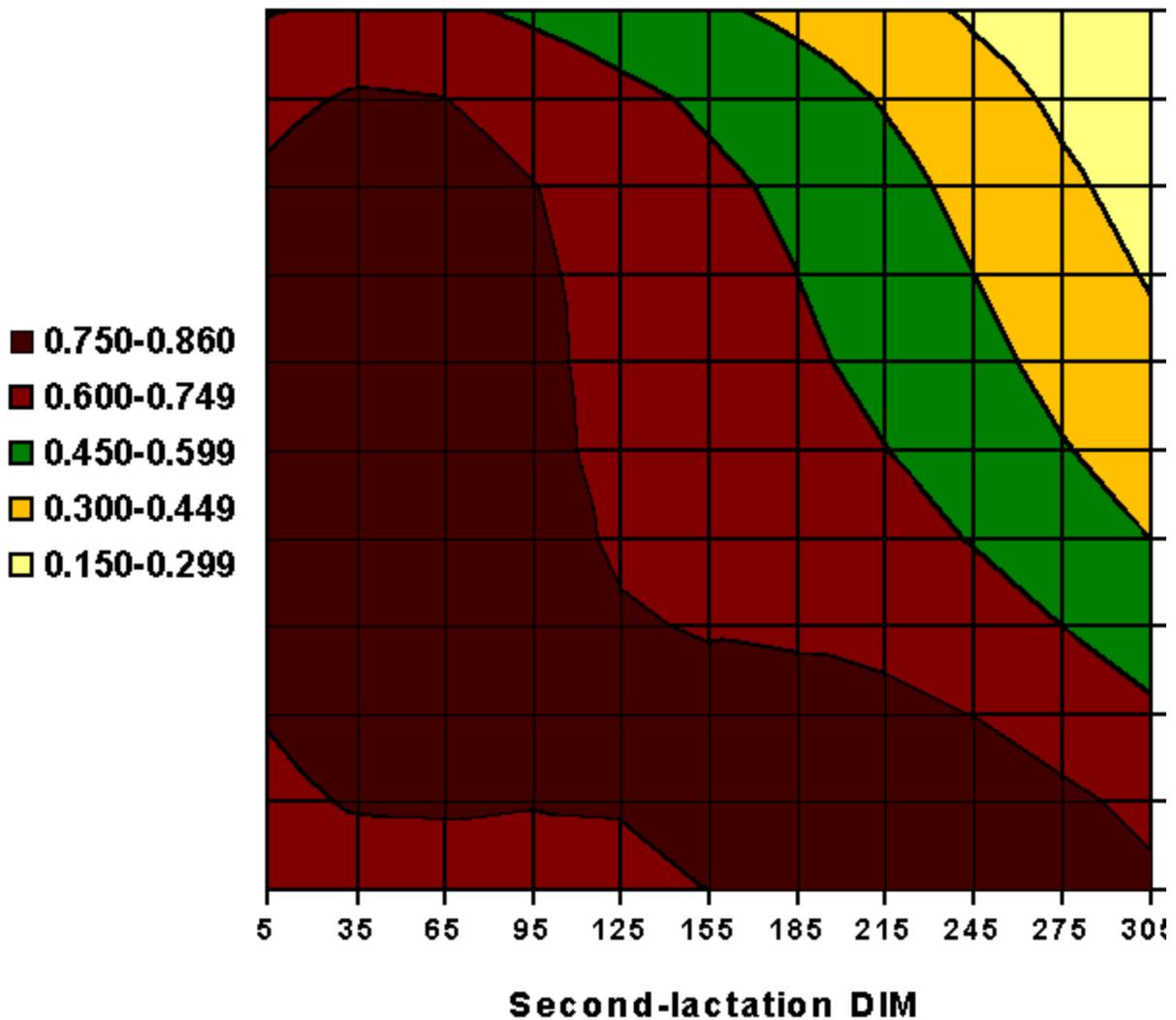


Figure 8. Genetic correlations between first- and second-lactation test-day yields computed from (co)variance functions for protein.

305-d Yield, Persistency, and Maturity Rate

Heritabilities for 305-d yields, persistencies, and maturity rates are in [Table 8](#). Heritabilities for 305-d yield (mean of 305-d yields during first and second lactations) were 0.21 for milk and protein and 0.23 for fat; those estimates were lower than those reported recently for US Holsteins ([Van Tassell et al., 1997](#)). Heritabilities for persistency, which was defined separately for first and second parities, were low (0.03 for fat and 0.05 for milk and protein) during first lactation and 0.11 for all traits during second lactation. For maturity rate, which was defined as the difference between first- and second-lactation 305-d yields, heritabilities were low (0.05 for fat, 0.06 for milk, and 0.07 for protein).

Table 8. Heritabilities (bold on diagonal), genetic correlations (above diagonal), and phenotypic

correlations (below diagonal) for 305-d yields, persistencies, and maturity rates for milk, fat, and protein yields during first and second lactations.

Yield function trait	Persistency ²											
	305-d Yield ¹			First lactation			Second lactation			Maturity rate ³		
	Milk	Fat	Protein	Milk	Fat	Protein	Milk	Fat	Protein	Milk	Fat	Protein
305-d Yield												
Milk	0.21	0.30	0.72	0.27	0.50	0.41	0.32	0.50	0.40	0.32	0.11	0.31
Fat	0.66	0.23	0.51	0.20	0.35	0.38	0.35	0.13	0.39	0.29	0.58	0.39
Protein	0.91	0.70	0.21	0.06	0.15	0.23	0.29	0.39	0.28	0.42	0.23	0.47
Persistency												
First lactation												
Milk	0.27	0.24	0.26	0.05	0.60	0.81	0.77	0.53	0.68	0.41	0.36	0.44
Fat	0.23	0.26	0.20	0.73	0.03	0.73	0.63	0.68	0.77	0.45	0.51	0.53
Protein	0.31	0.26	0.31	0.94	0.67	0.05	0.65	0.54	0.70	0.44	0.35	0.55
Second lactation												
Milk	0.30	0.36	0.31	0.10	0.06	0.09	0.11	0.84	0.95	0.55	0.49	0.59
Fat	0.33	0.27	0.31	0.07	0.06	0.07	0.77	0.11	0.85	0.54	0.23	0.56
Protein	0.35	0.37	0.35	0.09	0.06	0.09	0.95	0.73	0.11	0.56	0.53	0.61
Maturity rate												
Milk	0.53	0.47	0.53	0.40	0.30	0.36	0.44	0.41	0.48	0.06	0.72	0.96
Fat	0.42	0.60	0.40	0.33	0.40	0.26	0.43	0.36	0.43	0.80	0.05	0.77
Protein	0.52	0.46	0.56	0.39	0.26	0.39	0.47	0.40	0.51	0.96	0.75	0.07

¹Mean of 305-d yields during first and second lactations.

²Difference between test-day yields at d 280 and 60.

³Difference between 305-d yields during second and first lactations.

Genetic and phenotypic correlations among all yield function traits (Table 8) were positive. Genetic correlations between yield traits were remarkably low (0.30 to 0.72) for 305-d yield; phenotypic correlations were higher (0.66 to 0.91). Genetic correlations of persistency and maturity rate with 305-d yields were moderate (0.06 to 0.58); corresponding phenotypic correlations were similar (0.20 to 0.60). Persistency, as defined by the Canadian Dairy Network, was not a phenotypically independent trait from 305-d yield. A major concern recently has been extremely low correlations between persistency of first and later lactations as reported by Swalve and Gengler (1998). Phenotypic correlations between first and second-lactation persistency in Table 8 also were low (0.06 to 0.10), but genetic correlations were much higher (0.54 to 0.77).

CONCLUSIONS

A major obstacle in test-day model development and implementation is the estimation of useful and correct genetic parameters that are needed for genetic evaluation. This already arduous task in multitrait, multilactation models is even more difficult because of the data structure in test-day models. This study used an indirect approach to produce parameters that should be considered preliminary because of expected advances in methodology and because of the limited amount of data on which the parameters are based. A recent study ([Strabel and Misztal, 1999](#)) that used random regression and a two-trait model was limited to around 11,000 cows, but the method in the current study could include information from six traits from a similar number of cows.

Some similarities were found with results from an earlier study that used the same methodology but only first-lactation records from the same cows ([Tijani et al., 1999](#)). That study also found heritability estimates at the lower boundary of expected values and rather low correlation of fat yields across lactations. However, that study and most others did not analyze the three biological functions (305-d yield, persistency, and maturity rate).

A weakness of the proposed methodology is the need to adjust test-day yield within lactation stage prior to analysis. Alternative strategies, such as Gibbs sampling (e.g., [Jamrozik and Schaeffer, 1997](#)), should be considered for future studies. Recent advances also have been reported on other possible solution algorithms for test-day models (e.g., [Gengler et al., 1999a](#)). Future research should determine if alternative (co)variance estimation strategies could be based on those or similar approaches.

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APPENDIX

Table A1. Genetic (co)variance function coefficients (on and above diagonal) and correlations

among Legendre polynomials (below diagonal) for milk, fat, and protein yields during first lactation.

Yield trait	Legendre polynomial ¹	Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk, kg ² × 100	I ₀	668	55	-65	772	176	154	1272	221	-101
	I ₁	0.25	64	-11	118	129	-54	-7	159	4
	I ₂	0.38	0.21	43	-92	3	94	-147	-38	95
Fat, g ²	I ₀	0.30	0.15	0.14	9718	700	-311	3514	960	-390
	I ₁	0.25	0.59	0.02	0.26	753	-239	-353	458	104
	I ₂	0.22	0.25	0.54	0.12	0.33	703	520	-126	181
Protein, g ²	I ₀	0.70	0.01	0.32	0.51	0.18	0.28	4977	241	-512
	I ₁	0.34	0.79	0.23	0.38	0.66	0.19	0.14	640	-61
	I ₂	0.23	0.03	0.85	0.23	0.22	0.40	0.43	0.14	289

¹I₀ = (1/2)^{0.5}, I₁ = (3/2)^{0.5}x, and I₂ = (5/8)^{0.5}(3x² - 1), where x = -1 + 2[(DIM - 1)/(305 - 1)].

Table A2. Genetic (co)variance function coefficients (on and above diagonal) and correlations among Legendre polynomials (below diagonal) for milk, fat, and protein yields during second lactation.

Yield trait	Legendre polynomial ¹	Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk, kg ² × 100	I ₀	1005	218	34	1642	1277	335	2426	786	195
	I ₁	0.47	212	59	684	851	77	563	613	253
	I ₂	0.11	0.41	100	688	311	273	293	176	283
Fat, g ²	I ₀	0.37	0.33	0.49	19,692	1223	1342	7613	2684	1830
	I ₁	0.56	0.81	0.43	0.12	5174	262	3026	2770	1223

	I_2	0.24	0.12	0.61	0.21	0.08	2003	1478	89	697
Protein, g ²	I_0	0.78	0.39	0.30	0.55	0.43	0.34	9588	1925	626
	I_1	0.55	0.93	0.39	0.42	0.85	0.04	0.43	2045	734
	I_2	0.20	0.56	0.92	0.42	0.55	0.51	0.21	0.53	949

¹ $I_0 = (1/2)^{0.5}$, $I_1 = (3/2)^{0.5}x$, and $I_2 = (5/8)^{0.5}(3x^2 - 1)$, where $x = -1 + 2[(DIM - 1)/(305 - 1)]$.

Table A3. Genetic (co)variance function coefficients for milk, fat, and protein yields for first with second lactations.

First-lactation yield trait	Legendre polynomial ¹	Second-lactation yield trait								
		Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I_0	I_1	I_2	I_0	I_1	I_2	I_0	I_1	I_2
Milk, kg ² × 100	I_0	650	56	-3	474	464	392	1212	260	84
	I_1	102	82	9	204	258	39	145	204	90
	I_2	-27	27	23	195	125	-43	2	83	40
Fat, g ²	I_0	904	156	493	11,927	-333	1892	4503	829	1266
	I_1	394	226	64	1631	1211	-165	427	855	403
	I_2	171	40	27	-165	304	404	694	134	-83
Protein, g ²	I_0	1343	12	156	3093	300	1739	5372	80	270
	I_1	406	217	45	1311	921	75	966	738	237
	I_2	-25	87	13	325	323	-262	-185	234	48

¹ $I_0 = (1/2)^{0.5}$, $I_1 = (3/2)^{0.5}x$, and $I_2 = (5/8)^{0.5}(3x^2 - 1)$, where $x = -1 + 2[(DIM - 1)/(305 - 1)]$.

Table A4. Genetic correlations among Legendre polynomials for milk, fat, and protein yields for first with second lactations.

First-lactation	Legendre	Second-lactation yield trait		
		Milk	Fat	Protein

yield trait	polynomial ¹	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk	I ₀	0.79	0.15	0.01	0.13	0.25	0.34	0.48	0.22	0.11
	I ₁	0.40	0.70	0.11	0.18	0.45	0.11	0.19	0.56	0.37
	I ₂	0.13	0.28	0.35	0.21	0.27	0.15	0.00	0.28	0.20
Fat	I ₀	0.29	0.11	0.50	0.86	0.05	0.43	0.47	0.19	0.42
	I ₁	0.45	0.57	0.23	0.42	0.61	0.13	0.16	0.69	0.48
	I ₂	0.20	0.10	0.10	0.04	0.16	0.34	0.27	0.11	0.10
Protein	I ₀	0.60	0.01	0.22	0.31	0.06	0.55	0.78	0.03	0.12
	I ₁	0.51	0.59	0.18	0.37	0.51	0.07	0.39	0.65	0.30
	I ₂	0.05	0.35	0.08	0.14	0.26	0.34	0.11	0.30	0.09

¹I₀ = (1/2)^{0.5}, I₁ = (3/2)^{0.5}x, and I₂ = (5/8)^{0.5}(3x² - 1), where x = -1 + 2[(DIM - 1)/(305 - 1)].

Table A5. Permanent environmental (co)variance function coefficients (on and above diagonal) and correlations among Legendre polynomials (below diagonal) for milk, fat, and protein yields during first lactation.

Yield trait	Legendre polynomial ¹	Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk, kg ² × 100	I ₀	1924	-34	-6	5281	-157	324	5287	245	-72
	I ₁	-0.04	427	-44	-6	1166	-57	15	1210	-94
	I ₂	-0.01	-0.15	194	-4	-53	366	15	-90	606
Fat, g ²	I ₀	0.72	0.00	0.00	28,160	-1920	230	15,844	1114	57
	I ₁	-0.04	0.56	-0.04	-0.11	10,117	-2132	212	4080	-239
	I ₂	0.08	-0.03	0.28	0.01	-0.23	8563	995	-77	2271
Protein, g ²	I ₀	0.96	0.01	0.01	0.75	0.02	0.09	15,812	861	-87
	I ₁	0.09	0.90	-0.10	0.10	0.62	-0.01	0.10	4255	-364
	I ₂	-0.03	-0.09	0.83	0.01	-0.05	0.47	-0.01	-0.11	2728

$${}^1I_0 = (1/2)^{0.5}, I_1 = (3/2)^{0.5}x, \text{ and } I_2 = (5/8)^{0.5}(3x^2 - 1), \text{ where } x = -1 + 2[(\text{DIM} - 1)/(305 - 1)].$$

Table A6. Permanent environmental (co)variance function coefficients (on and above diagonal) and correlations among Legendre polynomials (below diagonal) for milk, fat, and protein yields during second lactation.

Yield trait	Legendre polynomial ¹	Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk, kg ² × 100	I ₀	3465	28	30	9824	437	295	9524	979	168
	I ₁	0.01	1113	-78	941	2869	-196	481	3194	-17
	I ₂	0.02	-0.11	482	30	-171	900	19	-129	1419
Fat, g ²	I ₀	0.71	0.12	0.01	54,604	-4532	2049	29,608	5523	573
	I ₁	0.05	0.55	-0.05	-0.12	24,321	-7535	2575	9460	88
	I ₂	0.04	-0.04	0.29	0.06	-0.34	19,948	489	-8	4014
Protein, g ²	I ₀	0.95	0.08	0.01	0.75	0.10	0.02	28,773	3205	544
	I ₁	0.16	0.92	-0.06	0.23	0.58	0.00	0.18	10,907	-267
	I ₂	0.04	-0.01	0.87	0.03	0.01	0.38	0.04	-0.03	5569

$${}^1I_0 = (1/2)^{0.5}, I_1 = (3/2)^{0.5}x, \text{ and } I_2 = (5/8)^{0.5}(3x^2 - 1), \text{ where } x = -1 + 2[(\text{DIM} - 1)/(305 - 1)].$$

Table A7. Permanent environmental (co)variance function coefficients for milk, fat, and protein yields for first with second lactations.

First-lactation yield trait	Legendre polynomial ¹	Second-lactation yield trait								
		Milk, kg ² × 100			Fat, g ²			Protein, g ²		
		I ₀	I ₁	I ₂	I ₀	I ₁	I ₂	I ₀	I ₁	I ₂
Milk, kg ² × 100	I ₀	1201	-50	-45	2975	176	-340	3420	-37	-61
	I ₁	87	95	-30	361	261	-149	315	243	-64

	I_2	-74	-5	51	-210	4	147	-164	-39	125
Fat, g ²	I_0	3210	306	-243	16,298	1200	2012	10,375	1255	-485
	I_1	69	190	-78	1148	576	-539	759	413	-330
	I_2	108	120	152	-1317	1187	156	258	354	523
Protein, g ²	I_0	3318	-90	-178	9193	536	1151	10,103	13	-364
	I_1	392	238	-68	1685	683	-322	1343	738	-177
	I_2	-164	-13	150	-444	-7	467	-398	-75	452

¹ $I_0 = (1/2)^{0.5}$, $I_1 = (3/2)^{0.5}x$, and $I_2 = (5/8)^{0.5}(3x^2 - 1)$, where $x = -1 + 2[(DIM - 1)/(305 - 1)]$.

Table A8. Permanent environmental correlations among Legendre polynomials for milk, fat, and protein yields for first with second lactations.

First-lactation yield trait	Legendre polynomial ¹	Second-lactation yield trait								
		Milk			Fat			Protein		
		I_0	I_1	I_2	I_0	I_1	I_2	I_0	I_1	I_2
Milk	I_0	0.47	0.03	0.05	0.29	0.03	0.05	0.46	0.01	0.02
	I_1	0.07	0.14	0.07	0.07	0.08	0.05	0.09	0.11	0.04
	I_2	0.09	0.01	0.17	0.06	0.00	0.07	0.07	0.03	0.12
Fat	I_0	0.32	0.05	0.07	0.42	0.05	0.08	0.36	0.07	0.04
	I_1	0.01	0.06	0.04	0.05	0.04	0.04	0.04	0.04	0.04
	I_2	0.02	0.04	0.07	0.06	0.08	0.01	0.02	0.04	0.08
Protein	I_0	0.45	0.02	0.06	0.31	0.03	0.06	0.47	0.00	0.04
	I_1	0.10	0.11	0.05	0.11	0.07	0.03	0.12	0.11	0.04
	I_2	0.05	0.01	0.13	0.04	0.00	0.06	0.04	0.01	0.12

${}^1I_0 = (1/2)^{0.5}$, $I_1 = (3/2)^{0.5}x$, and $I_2 = (5/8)^{0.5}(3x^2 - 1)$, where $x = -1 + 2[(DIM - 1)/(305 - 1)]$.

Table A9. Measurement error variances (diagonal), (co)variances (above diagonal), and correlations (below diagonal) for milk, fat, and protein yields during first and second lactations.

Yield trait	First-lactation yield trait			Second-lactation yield trait		
	Milk, $\text{kg}^2 \times 100$	Fat, g^2	Protein, g^2	Milk, $\text{kg}^2 \times 100$	Fat, g^2	Protein, g^2
Milk, $\text{kg}^2 \times 100$	630	2247	1840	968	3941	2798
Fat, g^2	0.82	11,804	5620	0.91	19,251	10,369
Protein, g^2	0.97	0.68	5747	0.97	0.80	8669