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B.J. DeGroot
University of Nebraska - Lincoln

Jeffrey F. Keown
University of Nebraska - Lincoln, jkeown1@unl.edu

L. Dale Van Vleck
University of Nebraska - Lincoln, dvan-vleck1@unl.edu

Stephen D. Kachman
University of Nebraska, skachman1@unl.edu

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Estimates of genetic parameters for Holstein cows for test-day yield traits with a random regression cubic spline model

B.J. DeGroot[1], J.F. Keown[1], L.D. Van Vleck[2] and S.D. Kachman[1]

[1]Department of Animal Science, University of Nebraska, Lincoln, NE, USA
[2]Roman L. Hruska U.S. Meat Animal Research Center, ARS-USDA, Lincoln, NE, USA
Corresponding author: J.F. Keown
E-mail: jkeown1@unl.edu

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ABSTRACT. Genetic parameters were estimated with restricted maximum likelihood for individual test-day milk, fat, and protein yields and somatic cell scores with a random regression cubic spline model. Test-day records of Holstein cows that calved from 1994 through early 1999 were obtained from Dairy Records Management Systems in Raleigh, North Carolina, for the analysis. Estimates of heritability for individual test-days and estimates of genetic and phenotypic correlations between test-days were obtained from estimates of variances and covariances from the cubic spline analysis. Estimates were calculated of genetic parameters for the averages of the test days within each of the ten 30-day test intervals. The model included herd test-day, age at first calving, and bovine somatropin treatment as fixed factors. Cubic splines were fitted for the overall lactation curve and for random additive genetic and permanent environmental effects, with five predetermined knots or

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four intervals between days 0, 50, 135, 220, and 305. Estimates of heritability for lactation one ranged from 0.10 to 0.15, 0.06 to 0.10, 0.09 to 0.15, and 0.02 to 0.06 for test-day one to test-day 10 for milk, fat, and protein yields and somatic cell scores, respectively. Estimates of heritability were greater in lactations two and three. Estimates of heritability increased over the course of the lactation. Estimates of genetic and phenotypic correlations were smaller for test-days further apart.

Key words: Random regression, Genetic parameters, Cubic spline

INTRODUCTION

There has been an increased interest in changing the type of data used for genetic evaluation of dairy cattle. Traditional models use data from test-day records combined into 305-day mature equivalent lactation records. The test-day model would use test-day records collected at various times during the lactation. The test-day model could provide some advantages compared to traditional models. These advantages would include: 1) an increased accuracy of genetic evaluations for yields, 2) direct and more precise adjustments for temporary environmental effects on test-days, 3) end-of lactation yields would not need to be extended for culled cows or for cows with records in-progress (Jensen, 2001), and 4) models could include the shape of the lactation curve for individual cows (Schaeffer and Dekkers, 1994). Test-day models tend to be more complex with more equations and parameters to be estimated, which is the main disadvantage compared to more traditional models (Jensen, 2001).

Various test-day models have been described in reviews by Swalve (2000), Misztal et al. (2000), Schaeffer et al. (2000), and Jensen (2001). These models have included a multiple-trait model with reduced rank, a repeatability model, a random regression model, and a covariance function model (Ptak and Schaeffer, 1993; Schaeffer and Dekkers, 1994; Wiggans and Goddard, 1997; Meyer and Hill, 1997). With the multiple-trait model, each test-day is modeled as a separate trait. Wiggans and Goddard (1997) suggested that the many test-day traits could be reduced to a few traits with a canonical transformation. With the repeatability model, test-day records within a lactation are considered to be repeated measures with fixed regression on days in milk, as defined by Ali and Schaeffer (1987). This model was later modified by Ptak and Schaeffer (1993) to adjust for test-day means at different stages of lactation.

Schaeffer and Dekkers (1994) and Jamrozik and Schaeffer (1997) extended the fixed regression model to a random regression model that was proposed by Henderson Jr. (1982). With such models, the shape of the lactation curve is modeled as a function of fixed effects. The random genetic and permanent environmental effects associated with an individual cow are modeled as deviations from the fixed lactation curve. Other authors developed functions that model lactation curves based on the natural shape of the lactation (e.g., Wilmink, 1987). Kirkpatrick et al. (1990, 1994) illustrated a method of estimating a matrix of coefficients for covariance functions with Legendre polynomials. Meyer and Hill (1997) demonstrated that models with a covariance function are equivalent to models with covariances among traits defined as a function of time or age.

White et al. (1999) described the use of smoothing cubic splines to model the lactation curve using test-day records. This random regression model consisted of fitting a series of cubic polynomials that are continuous and centered through knots or intervals along the lactation curve. White et al. (1999) explained that the spline function provided more flexibility to produce a "good" fit compared with polynomial functions. Another advantage of the spline models is the number of parameters that need to be estimated. The spline models need only four (co)variance parameters to be estimated (White et al., 1990), whereas the polynomial models require 0.5q(q+1) (co)variance parameters to be estimated, where q is the order of the polynomial (White et al., 1990).

We estimated genetic parameters for test-day milk, fat, and protein yields and somatic cell scores (SCS) for lactations one, two and three of Holstein cows, with a random regression, cubic spline model.

MATERIAL AND METHODS

Data

Test-day yields of Holstein cows that calved from 1994 through early 1999 were obtained from Dairy Records Management Systems of Raleigh, North Carolina. Each cow was required to have 2X per day milking, 305-day mature equivalent lactation yields, with at least eight test-day records. Lactation records were eliminated if days in milk was less than 200 days or greater than 350 days, if sire or dam identification was missing, lactation was initiated by abortion, or calving data were missing. Each test-day record was coded whether the cow was or was not treated with bovine somatotropin (bST). Only herds in which at least half of the cows received bST treatment were included in the analysis. Cows were considered bST-treated if the bST treatment started no later than test-day three and if bST treatment was coded for at least five consecutive test-days (coded 1 in analyses). Untreated cows were required not to have any bST treatment codes during the lactation (coded 0 in the analysis). Table 1 contains the number of test-day observations after edits that were used in the analysis for each trait and lactation combination. Fewer test-day records for fat and protein yields and SCS were available because some herds recorded only milk yield.

Table 1. Summary of the milk yield data.

	Lactation 1	Lactation 2	Lactation 3
Lactation records	17,168	12,432	7886
Number of test-day records	144,139	104,266	67,618
Test-day records per cow (mean)	8.40	8.39	8.57

MODEL AND METHODOLOGY

A single-trait, random regression, cubic spline model was used to fit fixed lactation curves and deviations for each animal for both random genetic and permanent environmental components. The cubic spline model consists of a series of piecewise cubic

polynomials that are defined for a set of pre-assigned interval along the lactation curve. The model is constrained so that the cubic spline function and its first two derivatives are continuous at the knots (breakpoints along the lactation curve), which determine the intervals (White et al., 1999).

Verbyla et al. (1999) and White et al. (1999) demonstrated how to incorporate the cubic spline function into the standard mixed model when the knots are assigned before the analysis. The model can be written as a random regression animal model:

$$y = X\beta + Z_s s + W_a a_1 + Z_a a_s + W_{pe} pe_1 + Z_{pe} pe_s + e$$

where **y** is a vector of test-day yields or test-day SCS. The vector β contains fixed effects, including fixed regression coefficients, and **X** is the incidence matrix for the fixed effects, which includes the bST code (0,1), herd test-day, covariate for age at the beginning of lactation, and a covariate for days in milk for each test-day record. The random effects are: **s**, a vector of overall spline parameters with length q-2; $\mathbf{a}_1$, a vector of genetic intercept (a_i) and slope (a_{sl}) breeding value parameters for each animal of length 2m with m equal to the number of animals; $\mathbf{a}_s$, a vector of spline breeding value parameters for the cubic spline function for each animal with length (q-2) · m; $\mathbf{pe}_1$, a vector of permanent environmental intercept (pe_i) and slope (pe_{sl}) parameters with length 2p with p equal to the number of levels of factors; $\mathbf{pe}_s$, a vector of permanent environmental parameters for the spline function with length (q-2)p, and **e**, a vector of residual effects. The matrices $\mathbf{W}_a$ and $\mathbf{W}_{pe}$ are the incidence matrices of the linear coefficients for animal genetic and permanent environmental effects, and $\mathbf{Z}_s$, $\mathbf{Z}_a$, and $\mathbf{Z}_{pe}$ are the incidence matrices of the spline coefficients for overall spline, animal genetic, and permanent environmental parameters of the spline function based on the number of predetermined knots. The distributions of the random effects are defined as:

$$s \sim N(0, D\sigma^2_s),\ a_S \sim N(0, A \otimes D\sigma^2_{as}),\ pe_S \sim N(0, I \otimes D\sigma^2_{pes})$$

$$a_1 \sim N(0, A \otimes \Phi_a),\ pe_1 \sim N(0, I \otimes \Phi_{pe}),\ e \sim N(0, I\sigma^2), \text{ with}$$

$$\Phi_a = \begin{pmatrix} \sigma^2_{a_i} & \sigma_{a_i a_{sl}} \\ \sigma_{a_i a_{sl}} & \sigma^2_{a_{sl}} \end{pmatrix} \text{ and } \Phi_{pe} = \begin{pmatrix} \sigma^2_{pe_i} & \sigma_{pe_i pe_{sl}} \\ \sigma_{pe_i pe_{sl}} & \sigma^2_{pe_{sl}} \end{pmatrix}$$

where **D** is an identity matrix of dimensions (q-2) x (q-2), **I** are the identity matrices of appropriate order, and **A** is the animal numerator relationship matrix.

The analysis was done using ASREML to estimate (co)variance components (Gilmour et al., 1997). The predetermined knots were at days 0, 50, 135, 220, and 305. Convergence was presumed when the REML log-likelihood changed less than 0.002 from the previous iteration and the individual variance parameter estimates changed less than 1%. The analysis was restarted after the first convergence until the log-likelihood value was considered converged.

RESULTS AND DISCUSSION

Test-day milk yield

Estimates of genetic, permanent environmental, and phenotypic variances for test-day milk yields for the first three lactations are in Table 2, as calculated for the midpoints of the test-day intervals. Table 3 contains the estimates of heritabilities for the first three lactations. Test-day milk yields had estimates of heritability that ranged from 0.10 to 0.15, 0.10 to 0.18, and 0.09 to 0.17 for lactations one, two, and three, respectively. Estimates of heritability increased steadily from test one to test 10. Estimates in later lactations were greater than for lactation one. The estimates of heritability were less than estimates reported by White et al. (1999), who used a random regression cubic spline model, Tijani et al. (1999), who used a random regression model using Legendre polynomials covariance functions, and were much smaller than estimates by Jamrozik and Schaeffer (1997), who used a random regression model with functions of ratios of days and the natural logarithm of days in milk. The estimates were similar to estimates reported by Gengler et al. (2001), using a random regression model with Legendre polynomials as the covariance function for lactation one. Estimates were less compared to later lactations.

Table 2. Estimates of genetic variance (σ^2_a), permanent environmental variance (σ^2_{pe}), and phenotypic variance (σ^2_p) for test-day milk yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1			Lactation 2			Lactation 3		
		σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p
1	18	3.43	20.58	36.01	5.53	35.49	57.14	6.16	42.50	66.99
2	46	3.01	17.68	32.70	4.33	29.96	50.41	5.54	34.86	58.72
3	76	2.98	17.16	32.14	4.42	28.02	48.56	5.25	32.62	56.20
4	106	3.20	18.04	33.24	5.28	28.37	49.77	5.29	33.54	57.16
5	136	3.57	19.45	35.03	6.46	29.74	52.32	5.60	35.58	59.51
6	167	3.96	20.37	36.33	7.44	30.62	54.18	6.13	36.25	60.71
7	196	4.31	20.64	36.95	8.11	30.82	55.05	6.83	35.34	60.50
8	227	4.74	20.70	37.44	8.74	30.96	55.52	7.81	33.69	59.82
9	256	5.18	20.64	37.82	9.31	31.14	56.57	8.94	31.69	58.96
10	288	5.91	21.72	39.63	10.59	33.29	60.00	10.52	32.07	60.92

For the three lactations, the overall genetic variance decreased from test one to test three and then gradually increased over the course of the lactation. The permanent environmental variances were variable during the early stages of lactations and were relatively constant during the mid and later stages of lactations. The estimates of genetic correlations ranged from 0.34 to 0.98 for lactation one and were similar for later lactations. The estimates of genetic and phenotypic correlations were high between test-day milk yields

Table 3. Estimates of heritability (h^2) for test-day milk yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1	Lactation 2	Lactation 3
1	18	0.095	0.097	0.092
2	46	0.092	0.086	0.094
3	76	0.093	0.091	0.093
4	106	0.096	0.106	0.093
5	136	0.102	0.123	0.094
6	167	0.109	0.137	0.101
7	196	0.117	0.147	0.113
8	227	0.126	0.157	0.130
9	256	0.137	0.165	0.152
10	288	0.149	0.177	0.173

on test-days close together compared with yields for test-days that were more days apart. Estimates are similar to those reported in previous studies (Tijani et al., 1999; White et al., 1999; Gengler et al., 2001).

Test-day fat and protein yields

Estimates of genetic, permanent environmental, and phenotypic variances for the first three lactations are in Tables 4 and 5 for test-day fat and protein yields, respectively. Tables 6

Table 4. Estimates of genetic variance (σ^2_a), permanent environmental variance (σ^2_{pe}), and phenotypic variance (σ^2_p) for test-day fat yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1			Lactation 2			Lactation 3		
		σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p
1	18	0.005	0.040	0.080	0.006	0.069	0.124	0.009	0.080	0.146
2	46	0.005	0.032	0.072	0.005	0.055	0.109	0.007	0.065	0.129
3	76	0.005	0.030	0.070	0.006	0.050	0.105	0.007	0.058	0.122
4	106	0.006	0.030	0.071	0.007	0.050	0.106	0.008	0.055	0.120
5	136	0.007	0.032	0.074	0.009	0.052	0.109	0.010	0.055	0.121
6	167	0.007	0.033	0.075	0.010	0.051	0.110	0.011	0.053	0.120
7	196	0.007	0.032	0.074	0.012	0.048	0.109	0.012	0.049	0.118
8	227	0.007	0.030	0.072	0.013	0.045	0.107	0.013	0.045	0.115
9	256	0.007	0.028	0.070	0.015	0.040	0.104	0.014	0.040	0.111
10	288	0.007	0.028	0.071	0.017	0.040	0.106	0.016	0.040	0.113

and 7 contain estimates of heritabilities for test-day fat and protein yields, respectively. Test-day fat yields had estimates of heritability that ranged from 0.06 to 0.10, 0.05 to 0.16, and 0.06 to 0.15 for lactations one, two, and three, respectively. Test-day protein yields had estimates of heritability that ranged from 0.09 to 0.15, 0.08 to 0.16, and 0.07 to 0.15 for lactations one, two, and three, respectively. Estimates of heritability for test-day fat and protein yields increased steadily over the course of the lactations. The estimates of heritability for test-day fat and protein yields were less than estimates reported by Tijani et al. (1999) and Gengler et al. (2001), who used a random regression model with Legendre polynomials as covariance functions and were much less than estimates by Jamrozik and Schaeffer (1997), using a random regression model with functions of ratios of days and natural logarithm of days in milk.

Table 5. Estimates of genetic variance (σ^2_a), permanent environmental variance (σ^2_{pe}), and phenotypic variance (σ^2_p) for test-day protein yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1			Lactation 2			Lactation 3		
		σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p
1	18	0.003	0.016	0.032	0.004	0.028	0.049	0.004	0.031	0.055
2	46	0.002	0.013	0.029	0.003	0.023	0.043	0.004	0.025	0.049
3	76	0.002	0.013	0.028	0.003	0.022	0.042	0.004	0.023	0.047
4	106	0.003	0.014	0.040	0.004	0.023	0.044	0.004	0.025	0.049
5	136	0.003	0.015	0.031	0.005	0.025	0.047	0.005	0.027	0.052
6	167	0.003	0.016	0.033	0.006	0.026	0.049	0.005	0.029	0.054
7	196	0.004	0.017	0.034	0.006	0.027	0.050	0.006	0.029	0.055
8	227	0.004	0.017	0.034	0.007	0.028	0.052	0.007	0.029	0.056
9	256	0.005	0.017	0.035	0.008	0.028	0.053	0.008	0.028	0.056
10	288	0.005	0.018	0.037	0.009	0.031	0.057	0.009	0.030	0.059

Table 6. Estimates of heritability (h^2) for test-day fat yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1	Lactation 2	Lactation 3
1	18	0.062	0.048	0.060
2	46	0.063	0.049	0.055
3	76	0.071	0.056	0.058
4	106	0.080	0.067	0.068
5	136	0.088	0.080	0.080
6	167	0.094	0.094	0.092
7	196	0.098	0.108	0.102
8	227	0.101	0.125	0.115
9	256	0.102	0.144	0.127
10	288	0.104	0.164	0.144

Table 7. Estimates of heritability (h^2) for test-day protein yield (kg) for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1	Lactation 2	Lactation 3
1	18	0.085	0.077	0.070
2	46	0.085	0.066	0.075
3	76	0.084	0.070	0.080
4	106	0.084	0.083	0.084
5	136	0.087	0.099	0.089
6	167	0.093	0.112	0.097
7	196	0.103	0.124	0.108
8	227	0.116	0.136	0.122
9	256	0.131	0.146	0.137
10	288	0.146	0.160	0.151

Estimates of overall genetic variances for test-day fat and protein yields increased from the early to mid stages of lactation and remained constant from mid to later stages of lactation. Estimates of overall permanent environmental variances decreased slightly over the lactation. The estimates of overall genetic variance were nearly constant during the early part of the lactation and increased during the mid and later stages of lactation. Estimates of permanent environmental variances were variable during the early stages of lactation and remained constant during the mid and later stages of lactation. The estimates of genetic correlations ranged from 0.49 to 0.97 and 0.36 to 0.99 for lactation one test-day fat and protein yields, respectively. The estimates of genetic correlations were similar for the later lactations. Estimates of correlations were high between test-day fat and protein yields on test-days close together compared with yields on test-days that were more days apart. These estimates are similar to those reported in previous studies (Tijani et al., 1999; Gengler et al., 2001).

Somatic cell scores

Estimates of genetic, permanent environmental, and phenotypic variances for test-day SCS for the first three lactations are in Table 8. Table 9 contains the estimates of heritabilities for the first three lactations. Test-day SCS had estimates of heritability that ranged from 0.02 to 0.06, 0.04 to 0.04, and 0.03 to 0.06 for lactations one, two, and three, respectively. The estimates of heritability were less than estimates reported by Haile-Mariam et al. (2001) for a random regression model with a second-order polynomial.

The estimates of overall permanent environmental variance decreased and then increased during the early stage of lactation and were relatively constant during the mid and later stages of lactation. The estimates of genetic correlations ranged from 0.83 to 0.99 for lactation one and were similar for the later lactations. Estimates of genetic correlations among test-day SCS were high between test-day SCS on test-days close together compared with scores on test-days that were farther apart. These estimates are similar to those reported by Haile-Mariam et al. (2001).

Table 8. Estimates of genetic variance (σ^2_a), permanent environmental variance (σ^2_{pe}), and phenotypic variance (σ^2_p) for test-day somatic cell scores for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1			Lactation 2			Lactation 3		
		σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p	σ^2_a	σ^2_{pe}	σ^2_p
1	18	0.073	1.434	3.097	0.137	1.790	3.485	0.105	1.612	3.291
2	46	0.081	1.234	2.903	0.108	1.521	3.186	0.094	1.377	3.046
3	76	0.097	1.233	2.920	0.108	1.493	3.159	0.103	1.363	3.040
4	106	0.117	1.341	3.049	0.125	1.594	3.276	0.121	1.468	3.162
5	136	0.138	1.484	3.213	0.146	1.724	3.428	0.142	1.604	3.320
6	167	0.157	1.570	3.317	0.160	1.766	3.483	0.159	1.669	3.401
7	196	0.172	1.591	3.353	0.163	1.710	3.431	0.168	1.650	3.382
8	227	0.187	1.579	3.356	0.162	1.594	3.314	0.175	1.586	3.334
9	256	0.199	1.544	3.333	0.158	1.442	3.157	0.179	1.493	3.245
10	288	0.215	1.584	3.389	0.166	1.372	3.096	0.191	1.483	3.248

Table 9. Estimates of heritability (h^2) for test-day somatic cell scores for 10 representative days in milk (DIM) for lactations one, two, and three.

Test	DIM	Lactation 1	Lactation 2	Lactation 3
1	18	0.024	0.039	0.032
2	46	0.028	0.034	0.031
3	76	0.033	0.034	0.034
4	106	0.038	0.038	0.038
5	136	0.043	0.043	0.043
6	167	0.047	0.046	0.047
7	196	0.051	0.048	0.049
8	227	0.056	0.049	0.052
9	256	0.060	0.050	0.055
10	288	0.064	0.054	0.059

CONCLUSIONS

The cubic spline model provided flexibility for estimating genetic parameters from test-day yields and SCS. The flexibility of the model extends to estimating genetic and permanent environmental (co)variances (White et al., 1999). Estimates of heritability increased as days in milk increased for all lactations for test-day yields and SCS. Estimates of heritability were less than previous estimates reported with other types of random regression models. The smaller estimates could be due to the type of data set used in the analysis. This data set contained more grade cows than registered cows. Estimates of genetic parameters are usually lower for grade cows compared to registered cows, which may be caused by a greater chance of misidentification of sires and dams for grade cows.

Estimates of genetic and permanent environmental variances for test-day yields and SCS were higher for lactations two and three than for lactation one. Lactation two had estimates of variances due to genetic and permanent environmental effects in the spline function that were more variable than estimates for lactations one and three. Estimates of genetic and phenotypic correlations decreased with an increase in days between when the yields were measured.

The cubic spline model may be a suitable method of estimating genetic parameters over the course of the lactation. In our study, the estimates of genetic parameters with the cubic spline model were comparable to estimates found with other methods. The major advantage of this method is the smaller number of variance components that need to be estimated, when compared with polynomial and multiple trait methods. Further research would need to be done to determine the proper number and placement of the knots for days in milk and comparison of computational time needed to set up and solve equations for other methods used to estimate genetic parameters.

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