Estimation of genetic parameters for test-day records of dairy traits in a seasonal calving system

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ABSTRACT

Variance components for test-day milk yield were estimated for primiparous animals in a seasonal calving system where 80% of calvings occur within a 5-mo period in the spring. The objective was to investigate if the variance components of milk production were affected by seasonality via month in milk and test month (TM). These effects were, therefore, fitted for both the permanent environment effect and additive genetic effect. Estimates of heritability (0.14–0.27) were found to be lowest during early and late lactation for all calving months. The peak in heritability (0.22–0.27) occurred later in lactation for animals that calved toward the end of the spring calving season. Genetic variance of test day milk yield for all calving months was found to be highest at the beginning of the lactation (2.23–3.36 kg²), with a plateau toward the middle of the lactation. Genetic variance was found to be highest (2.98–3.36 kg²) for animals calving early in the season. Genetic correlations between corresponding stages of lactation were strongest (0.99–1.00) between consecutive calving months. Genetic correlations were slightly weaker when intervals between calving months increased; however, they remained above 0.96 in all cases. Akaike's information criterion values from models both inclusive and exclusive of TM, suggest that the model exclusive of TM is the preferred model. Estimated breeding values of lactation milk yield from bulls with 20 or more daughters, predicted for a full 305-d lactation, were used to compare the model with the standard test-day model (i.e., exclusive of TM), based on DIM. Correlations were higher than 0.995 for milk yield (and higher than 0.930 for persistency) between models inclusive and exclusive of TM, suggesting that given the straightforward approach taken in the current study, an apparent benefit for including seasonality in the evaluation of test-day milk yield was not found; however, there may be benefits of including it in the estimation of persistency.

Key words: genetic parameter, seasonal calving, test-day model

INTRODUCTION

Genetic evaluation models for milk production traits have generally changed from full lactation models (Olori and De Jong, 1999) to test-day models first introduced by Schaeffer and Dekkers (1994). Lactation models generally use a single 305-d yield for evaluation that is predicted from the individual test-day records (Olori and Galesloot, 1999). This predicted 305-d yield assumes a standard shape of a lactation curve and that variation between the animals is only caused by differences in the mean between animals. The developed test-day models use all records along a lactation curve directly in the evaluation, and allow the mean and shape of the lactation curve to differ between animals by modeling the variance and covariance between test-day records. This allows differences in genetic parameters along the lactation curve. The current national evaluation model for milk yield in Ireland is a lactation model, but investigations are underway toward the introduction of a test-day model.

Whereas most countries have a roughly consistent production pattern through the year, some countries such as Ireland and New Zealand have a major seasonal component to the calving season (Dillon et al., 1995). The reasons for this are many (Roche et al., 1996), including synchronizing calving with the initiation of grass growth. Grazed grass has been shown to be the cheapest, most efficient way of producing milk (Dillon, 2006) under Irish conditions. The trend toward seasonal calving is becoming more pronounced (Department of Agriculture, Food and the Marine, 2002, 2009) with 87.4% of dairy calvings occurring between January and June, and 65.3% of dairy calvings occurring in the months of February, March, and April.

Previous work (Veerkamp et al., 1994) has shown that under differing feed systems, the possibility exists for differences in both genetic and phenotypic variances, and correlations between feeding systems might not be unity due to genotype by environment

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interaction ($G \times E$; Cromie et al., 1998; Hammami et al., 2006). Genotype by environment interaction occurs when differences exist in the expression of genotypes in different environments. Because substantial differences will exist in the grass available, in both quantity and quality, for animals calving in January (early calvers), compared with animals calving in May (late calvers), it is reasonable to expect that the genetic (co)variance structure for test-day milk yield is not only affected by DIM but by season as well. This might have consequences for the implementation of a test-day model in Ireland, especially because the effect of seasonal calving is undoubtedly very much confounded with the effect of DIM. Accounting for this effect of seasonality is particularly relevant, as some bulls are used selectively later in the breeding season due, for example, to having a lower EBV for gestation length (i.e., shorter gestation length). With an effect of seasonal calving on genetic variation of yield or persistency of milk production, this could lead to bias in the estimation of EBV. Daughters of certain bulls might also be more, or less, affected by seasonality, and this might be important information for bull selection, depending on the farming system applied. The ability to identify such bulls, and combine this with information such as gestation length EBV would be of substantial interest to farmers in Ireland. The objective of this study was to investigate the seasonality effect on variance components of test-day milk production as affected by both stage of lactation and month of production, and to determine the scale of any differences that may exist.

MATERIALS AND METHODS

Data

Data were available from Irish Cattle Breeding Federation (ICBF, Cork, Ireland). For the purposes of estimating variances and covariances, data were chosen and edited to be representative of the Irish national dairy herd and also to only include herds and sires that had sufficient data to be useful. A total of 4,159,042 milk test-day records from 657,911 primiparous Holstein-Friesian cows, calving between 2003 and 2009 were available. The data were edited with the following requirements: known sire and dam, age at first calving between 20 and 39 mo, daily milk yield between 1.5 and 80 kg, protein and fat percentage both between 1.5 and 8.5%. Only animals with at least 4 milk tests and herds test with at least 4 eligible animals were included. Days in milk was required to be between 5 and 305. Each sire had to have at least 7 progeny with at least 20 test-day records, spread across at least 5 herds. After

editing, 2,139,653 usable records from 333,194 animals in 6,869 herds remained; 3,085 sires were represented in the edited data set. The average number of animals per herd per year was 11.9 and the average number of progeny per sire per year was 32.3.

To overcome computational problems, the size of this data set was reduced, a random sample of the herds was taken, and the edits were reapplied within that reduced set of herds. A total of 357,869 records from 56,734 animals in 1,034 herds remained and the animals were sired by 513 different sires. The number of test-day records per animal varied between 4 and 21, with the mean being 6.3 records per animal. The number of animals per herd per year varied between 4 and 107, with the mean being 13.4 animals per herd per year. The average number of progeny per sire per year was 28.4. Of the 513 sires 473, 511, 487, 408, and 250 had daughters in the data set calving in January, February, March, April, and May, respectively. The number of animals calving in January, February, March, April, and May were 8,501, 24,798, 12,806, 3,565, and 949, respectively. Ideally, the complete data set would have been used in the analysis; this was not possible due to limited computation resources. This subset of data was a representative sample, as can be seen from the figures for national data and subset taken above.

Analysis

The primary focus of this analysis was the investigation of the seasonality effect on variance components of test-day milk production. It is clear from Table 1 that seasonality is inherent in the Irish production system, with animals calving in springtime, resulting in a corresponding rise in number of records (from 6,588 in January to 38,549 in April). Similarly, after reaching peak milk production in April/May, production decreases through the remainder of the season (from 24.6 kg/d in April to 14.9 kg/d in October), with lactations ending in October/November. With the exception of the beginning and end of lactations (i.e., January and December), where little data are available, higher phenotypic variances coincide with higher production. To examine this seasonality effect, 2 random regression effects were included in an attempt to account for the seasonality effects and lactation stage effects simultaneously. The first term, test month (**TM**), represented the month of the year in which the test occurred (1 = January, 2 = February, and so on). The second term, month in milk (**MIM**), was the number of months between calving and the current test date (1 to 10), which modeled the stage of lactation. Variance components were estimated using ASReml software (Gilmour et al., 2006).

Table 1. Phenotypic variances, means, and number of records for test-day milk yield for each recording month

Month	No. of records	Test-day milk variance (kg ²)	Mean test-day milk yield (kg)
Jan.	6,588	42.7	23.4
Feb.	12,787	27.7	22.9
Mar.	29,812	26.1	23.4
Apr.	38,549	23.6	24.6
May	41,879	23.1	23.8
Jun.	41,151	20.3	21.4
Jul.	41,226	19.2	19.8
Aug.	39,915	17.6	18.0
Sep.	36,664	17.1	16.3
Oct.	38,394	21.2	14.9
Nov.	23,105	36.1	14.6
Dec.	7,799	55.4	18.6

Model

The general model used was

$$y = \mu + \text{fixed effects} + S_{\text{Sire}} + \frac{1}{2}S_{\text{mgs}} + PERM_{\text{animal}} + \varepsilon,$$

where y is test-day milk yield; μ is general mean; fixed effects were age at calving (20–22, 23–24, 25–26, 27–28, 29–30, 31–32, and 33–39 mo of age) and days carried in calf (**DCC**), which was calculated using the subsequent calving date for the animal and an assumed gestation length of 285 d; $PERM_{\text{animal}}$ is permanent environment effect; and ε is general residual. The DCC term was fitted as a polynomial of order 2. The polynomial term on DCC was fitted from 0 to 282; DCC 0 represented either animals early in lactation (i.e., not yet in calf) or animals that did not subsequently recalve. All animals had a chance to recalve, as data was only taken up to 2009. Days in milk was taken as the number of days between calving and occurrence of the milk test, and was fitted as a polynomial of order 8. Although order 8 is high, inclusion of higher-order terms remained significant up to this level. The contemporary group effect was fitted as the unique combination of herd and test date. There were 33,765 herd-test groups with a mean number of animals of 10.6 and a range of 4 to 97 animals.

The random sire effects (S) were fitted by overlaying the sire (S_{sire}) and 1/2 the maternal grandsire effects (S_{mgs}), resulting in 1 estimate per effect for a sire. The sire effects were modeled with second-order Legendre polynomials on both MIM and TM, resulting in a 5×5 (co)variance matrix, using the random regression model

$$S = \sum_{m=0}^2 a_m z_m + \sum_{n=1}^2 b_n z_n,$$

where z_m = the m th Legendre polynomial on MIM, a_m = the m th random regression coefficient for the additive genetic effect (MIM component), b_n = the n th Legendre polynomial on TM, and z_n = the n th random regression coefficient for the additive genetic effect (TM component). Note that the $m = 0$ index in refers to the intercept term, which was fitted with the MIM term.

In a similar manner, the random permanent environment term was modeled with second-order Legendre polynomials on both MIM and TM, resulting in a 5×5 (co)variance matrix:

$$PERM_{\text{animal}} = \sum_{m=0}^2 p_m z_m + \sum_{n=1}^2 q_n z_n,$$

where z_m = the m th Legendre polynomial on MIM, p_m = the m th random regression coefficient for the permanent environment effect of the particular animal (MIM component), z_n = the n th Legendre polynomial on TM, and q_n = the n th random regression coefficient for the permanent environment effect of the particular animal (TM component).

Covariance Structure

The covariance structure was defined as follows:

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{P} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \end{bmatrix},$$

where $\mathbf{a}$ is a vector of random regression coefficients for sire genetic effect, $\mathbf{p}$ is a vector of random regression coefficients for permanent environmental effects, $\mathbf{e}$ is a vector of residual effects, $\mathbf{G}$ is the 5×5 covariance matrix of the random regression coefficients for sire effects, $\mathbf{A}$ is the additive genetic relationship matrix between sires, $\mathbf{P}$ is the 5×5 covariance matrix of the PE regression coefficients, $\mathbf{I}$ is the identity matrix for each animal, $\mathbf{R}$ is a diagonal matrix containing the constant residual variance, and $\otimes$ is the Kronecker product function.

Transformation of Genetic Parameters to a MIM/TM Scale

The sire genetic variance matrix for MIM/TM was obtained in a similar manner to (Druet et al., 2003) as follows: first, the genetic (and permanent environmental) (co)variances for the effects of TM and MIM [i.e., the 22×22 (co)variance matrix ($\mathbf{M}$)] was calculated as

$$\mathbf{M} = \mathbf{\Lambda}\mathbf{G}\mathbf{\Lambda}',$$

where

$$\mathbf{\Lambda} = \begin{pmatrix} \mathbf{\Lambda}_{MIM} & 0 \\ 0 & \mathbf{\Lambda}_{TM} \end{pmatrix},$$

where $\mathbf{\Lambda}_{MIM}$ is a 10×3 matrix whose elements are the Legendre coefficients for MIM (including intercept) and $\mathbf{\Lambda}_{TM}$ is a 12×2 matrix whose elements are the Legendre coefficients for TM; $\mathbf{M}$ thus gives the details of how the genetic variance is partitioned into variance attributable to TM and MIM separately; $\mathbf{M}$ contains genetic (co)variances due to MIM, genetic (co)variances due to TM, and the covariance between TM and MIM.

Second, the genetic (co)variances were calculated for different combinations of MIM and TM. This matrix represents the (co)variance for an animal being in a particular MIM and a particular TM, and was calculated as

$$\mathbf{G}^* = \mathbf{\Phi}\mathbf{G}\mathbf{\Phi}',$$

where $\mathbf{G}^*$ is a 120 (12×10) by 120 sire genetic (co)variance matrix (i.e., each combination of 12 values of TM $\times$ 10 values of MIM is obtained separately) and $\mathbf{\Phi}$ is a 120×5 matrix with the values of the 3 coefficients of the second-order Legendre polynomial for each MIM and the 2 coefficients of the second-order Legendre polynomial for each TM. Similar calculations were used for the permanent environment effect; $\mathbf{G}^*$ thus gives the genetic (co)variance between each combination of MIM/TM. This is different from $\mathbf{M}$, where the variance was partitioned in portions attributable to TM and MIM.

Genetic Parameters and Breeding Values

The genetic parameters were calculated from the estimated variance components. As a sire/maternal grandsire model was used, the additive genetic variance was calculated as 4 times the sire genetic variance. The phenotypic variance was calculated as the sum of permanent environmental variance, residual variance, and the sire variance multiplied by 1.25. The multiplication by 1.25 was necessary, as the maternal grandsire was fitted in the model separately (de Haas et al., 2002). Heritability was calculated for each MIM/TM as additive genetic variance divided by phenotypic variance.

The EBV for milk yield for a complete lactation were calculated, based on a summing the EBV for each MIM between 1 and 10. The same data subset was

used as was used for parameter estimation. Only sires with data on at least 20 daughters were included in the estimation of EBV. The EBV were also obtained from a second model excluding TM (i.e., the standard test-day model solely considering stage of lactation). As lactation yield is the sum of all test-day yields, heritabilities for lactation yield can be calculated from test-day variance components (Liu et al., 2000b).

In addition, persistency was calculated for models both inclusive and exclusive of TM. Although many formulations of persistency exist (e.g., Cole and VanRaden, 2006; Strabel and Jamrozik, 2006a), one of the most commonly used definitions is given by Jamrozik et al. (1998), who defined persistency as the difference in production between d 280 and 60 of lactation. In this case, difference in milk production EBV between MIM 9 and 2 was taken as measure of persistency.

RESULTS

Heritability of test-day milk yield was found to be between 0.14 and 0.27 (Figure 1), with the peak of heritability toward the middle of the lactation. A larger range in heritability was seen for later-calving animals (i.e., January calvers had a range of 0.19–0.21, whereas May calvers has a range of 0.14–0.27). Overall, due to the effects of seasonality, differences (Figure 1) existed in the heritability for animals calving in different seasons. Partitioning the sire genetic variance into components due to TM and MIM separately (Table 2) shows that the sire genetic variances of test-day milk yield attributable to MIM (Table 2) ranged from 1.24 to 2.48 kg², with the extremes found at start and end of the lactation (i.e., the diagonal elements on the top left of Table 2). When describing the full genetic variance (that is, the combined effect of TM and MIM) for early-, mid-, and late-calving daughters of bulls (Table 3), it is clear that the genetic variance is more reduced the later an animal calved in the season (Table 3). For example, in mo 4 of lactation (MIM = 4), these genetic variances were 2.25, 2.11, and 2.10 for a January, March, and May calver respectively. Genetic covariances between MIM and TM (Table 2) ranged from –0.12 to 0.36, with positive covariances between animals producing early in the year (TM = 1, 2, and 3) and very much later in the year (TM = 11 and 12) and all MIM, whereas covariances between animals producing midseason (TM = 4–10) and all MIM are generally negative. The sire genetic variances were much smaller for TM, partly because the intercept was already accounted for in the variances of MIM. However, also the range in variances for TM was less than that found for MIM.

Figure 1. Heritability of test-day milk yield in Irish primiparous animals across month in milk and test month for each month of the spring calving season.

Strong genetic correlations (Table 2) were present between adjacent MIM and became weaker when the distance between the MIM increased, more so at the beginning of lactation. Genetic correlations, however, became more strongly negative (e.g., -0.76 between TM 3 and 8), again suggesting that genetic merit for animals producing in the summer months (6 to 8) is different from those producing in mo 1 to 3 and 10 to 11. The covariances are easier to interpret when presented for an animal calving in a particular month. Overall, the phenotypic variance (Figure 2) was roughly equal (at the same stage of lactation) across calving month, so for MIM = 1, phenotypic variance ranged between 14.2 and 17.6 kg², with larger values for early calvers.

For MIM = 4, the phenotypic variance ranged between 9.1 and 10.1 kg², again with larger values for earlier calvers.

The permanent environmental variances decreased rapidly initially in the lactation (Figure 3), with the rate of decrease becoming more gradual later in the lactation. For later-calving animals, the initial level of permanent environmental variance (i.e., at the start of the lactation) was lower, whereas the level later in the lactation was quite similar for all calving months. The biggest difference was between January and February calvers, with similar, lower differences between later adjacent calving months (Table 3). Correlations between permanent environmental effect in consecutive

Table 2. Partitioning of genetic parameters into portion attributable to month in milk (MIM) and test month (TM)¹

Item	MIM										TM											
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12
MIM																						
1	2.48	0.97	0.91	0.83	0.75	0.69	0.63	0.57	0.52	0.46	0.60	0.52	0.33	-0.05	-0.45	-0.64	-0.70	-0.65	-0.45	-0.11	0.17	0.34
2	2.32	2.28	0.98	0.94	0.88	0.83	0.78	0.73	0.68	0.6	0.55	0.47	0.30	-0.04	-0.40	-0.58	-0.63	-0.59	-0.41	-0.11	0.15	0.30
3	2.16	2.20	2.24	0.99	0.96	0.92	0.88	0.84	0.79	0.7	0.47	0.41	0.26	-0.03	-0.34	-0.50	-0.54	-0.51	-0.36	-0.10	0.12	0.26
4	1.96	2.12	2.20	2.24	0.99	0.97	0.95	0.91	0.86	0.77	0.40	0.35	0.23	-0.03	-0.29	-0.42	-0.46	-0.43	-0.31	-0.08	0.10	0.22
5	1.80	2.00	2.16	2.24	2.24	0.99	0.98	0.95	0.91	0.82	0.35	0.30	0.19	-0.02	-0.25	-0.36	-0.39	-0.37	-0.26	-0.07	0.09	0.18
6	1.60	1.84	2.04	2.16	2.20	2.16	1.00	0.98	0.94	0.86	0.30	0.26	0.17	-0.02	-0.22	-0.31	-0.34	-0.32	-0.23	-0.06	0.08	0.16
7	1.40	1.68	1.88	2.00	2.08	2.08	2.04	0.99	0.97	0.9	0.27	0.23	0.15	-0.02	-0.20	-0.28	-0.31	-0.29	-0.20	-0.05	0.07	0.15
8	1.20	1.48	1.68	1.84	1.92	1.92	1.88	1.80	0.99	0.94	0.25	0.21	0.13	-0.03	-0.19	-0.27	-0.29	-0.27	-0.19	-0.04	0.08	0.15
9	1.00	1.24	1.44	1.60	1.68	1.72	1.68	1.64	1.52	0.98	0.25	0.21	0.13	-0.04	-0.20	-0.27	-0.29	-0.27	-0.18	-0.03	0.09	0.15
10	0.80	1.00	1.16	1.28	1.36	1.40	1.44	1.40	1.36	1.24	0.25	0.21	0.12	-0.05	-0.22	-0.29	-0.31	-0.28	-0.18	-0.02	0.10	0.17
TM																						
1	0.36	0.32	0.28	0.24	0.20	0.16	0.16	0.12	0.12	0.12	0.16	0.98	0.85	0.43	-0.18	-0.6	-0.85	-0.99	-0.94	-0.63	-0.27	-0.02
2	0.20	0.20	0.16	0.12	0.12	0.08	0.08	0.08	0.08	0.04	0.08	0.08	0.94	0.61	0.03	-0.43	-0.73	-0.94	-0.99	-0.78	-0.46	-0.22
3	0.08	0.08	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.84	0.37	-0.09	-0.44	-0.76	-0.98	-0.95	-0.74	-0.54
4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.81	0.46	0.11	-0.29	-0.71	-0.97	-0.99	-0.91
5	-0.08	-0.08	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.89	0.67	0.33	-0.17	-0.65	-0.9	-0.98
6	-0.12	-0.12	-0.08	-0.08	-0.08	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.93	0.72	0.3	-0.24	-0.6	-0.79
7	-0.12	-0.12	-0.12	-0.08	-0.08	-0.08	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.92	0.62	0.13	-0.27	-0.51
8	-0.12	-0.12	-0.08	-0.08	-0.08	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.88	0.51	0.12	-0.14	
9	-0.08	-0.08	-0.08	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.58	0.36
10	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.00	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.92	0.79
11	0.08	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.00	0.00	0.04	0.04	0.97
12	0.16	0.16	0.12	0.12	0.08	0.08	0.08	0.08	0.08	0.08	0.00	0.00	-0.04	-0.04	-0.04	-0.04	-0.04	0.00	0.00	0.04	0.08	0.12

¹Sire genetic variances (along diagonal), sire genetic covariances (below the diagonal), and sire genetic correlations (above diagonal) attributable to MIM and TM.

Table 3. Additive sire genetic variances (along diagonal, bold), sire genetic correlations (below diagonal), animal permanent environmental correlations (above diagonal), and heritability (at bottom of table) of test-day milk yield in Irish primiparous animals for early (Jan.), mid (Mar.), and late (May) calvers in a seasonal calving system¹

Item			Jan. calvers (TM first row; MIM second row)								Mar. calvers (TM first row; MIM second row)								May calvers (TM first row; MIM second row)							
			1	2	3	4	5	6	7	8	3	4	5	6	7	8	9	10	5	6	7	8	9	10	11	12
	TM	MIM	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Jan. calvers	1	1	3.36	0.98	0.90	0.78	0.64	0.52	0.43	0.38																
	2	2	0.97	2.71	0.97	0.89	0.79	0.68	0.60	0.55																
	3	3	0.90	0.98	2.39	0.97	0.91	0.83	0.76	0.70																
	4	4	0.80	0.92	0.98	2.25	0.98	0.94	0.88	0.83																
	5	5	0.70	0.84	0.94	0.99	2.17	0.99	0.96	0.91																
	6	6	0.61	0.77	0.89	0.96	0.99	2.08	0.99	0.96																
	7	7	0.54	0.71	0.84	0.93	0.97	0.99	1.93	0.99																
	8	8	0.48	0.65	0.79	0.88	0.94	0.97	0.99	1.72																
Mar. calvers	3	1	1.00	0.98	0.92	0.82	0.73	0.64	0.57	0.51	2.70	0.97	0.90	0.78	0.67	0.57	0.51	0.49								
	4	2	0.96	1.00	0.98	0.94	0.87	0.80	0.74	0.69	0.97	2.28	0.97	0.90	0.81	0.73	0.68	0.64								
	5	3	0.87	0.96	1.00	0.99	0.96	0.91	0.87	0.82	0.89	0.98	2.13	0.98	0.93	0.87	0.82	0.77								
	6	4	0.77	0.89	0.97	1.00	0.99	0.97	0.94	0.90	0.80	0.92	0.98	2.11	0.98	0.95	0.91	0.86								
	7	5	0.68	0.82	0.93	0.98	1.00	0.99	0.98	0.95	0.71	0.85	0.95	0.99	2.11	0.99	0.97	0.92								
	8	6	0.60	0.76	0.88	0.95	0.99	1.00	0.99	0.98	0.63	0.80	0.91	0.97	0.99	2.07	0.99	0.96								
	9	7	0.55	0.71	0.84	0.92	0.97	0.99	1.00	0.99	0.58	0.75	0.87	0.94	0.98	0.99	1.97	0.98								
	10	8	0.52	0.68	0.80	0.89	0.94	0.97	0.99	0.99	0.54	0.71	0.83	0.90	0.95	0.98	0.99	1.80								
May calvers	5	1	0.99	0.98	0.92	0.84	0.74	0.66	0.58	0.53	1.00	0.98	0.90	0.81	0.72	0.65	0.60	0.56	2.35	0.98	0.90	0.79	0.68	0.57	0.48	0.42
	6	2	0.94	0.99	0.98	0.94	0.88	0.82	0.76	0.71	0.96	1.00	0.98	0.93	0.87	0.81	0.77	0.73	0.97	2.09	0.97	0.91	0.82	0.72	0.63	0.54
	7	3	0.85	0.95	0.99	0.99	0.96	0.92	0.88	0.83	0.88	0.97	1.00	0.99	0.95	0.92	0.88	0.84	0.90	0.98	2.04	0.98	0.92	0.85	0.77	0.66
	8	4	0.76	0.89	0.96	0.99	0.99	0.97	0.94	0.91	0.79	0.91	0.98	1.00	0.99	0.97	0.95	0.91	0.81	0.93	0.99	2.10	0.98	0.94	0.87	0.76
	9	5	0.68	0.83	0.93	0.98	0.99	0.99	0.97	0.95	0.71	0.86	0.95	0.99	1.00	0.99	0.98	0.95	0.73	0.87	0.96	0.99	2.16	0.99	0.94	0.84
	10	6	0.63	0.78	0.89	0.95	0.98	0.99	0.98	0.97	0.65	0.81	0.91	0.97	0.99	1.00	0.99	0.98	0.67	0.83	0.93	0.97	1.00	2.18	0.98	0.91
	11	7	0.59	0.74	0.86	0.93	0.96	0.98	0.98	0.98	0.62	0.77	0.88	0.94	0.97	0.99	0.99	0.99	0.63	0.79	0.89	0.95	0.98	0.99	2.13	0.97
	12	8	0.58	0.72	0.82	0.89	0.92	0.94	0.96	0.97	0.59	0.74	0.84	0.90	0.93	0.96	0.97	0.99	0.61	0.75	0.85	0.91	0.95	0.97	0.99	2.03
h^2			0.19	0.20	0.21	0.22	0.23	0.23	0.23	0.21	0.18	0.19	0.20	0.22	0.23	0.24	0.25	0.24	0.16	0.18	0.20	0.23	0.25	0.26	0.27	0.27

¹MIM = month in milk; TM = test month.

Figure 2. Phenotypic variance (σ_p^2) of test-day milk yield in Irish primiparous animals across month in milk and test month for each month of the spring calving season.

months within a lactation were higher than 0.97 in all cases. This correlation decreased as the distance between stage of lactation increased, with the correlation between first month in milk and eighth month in milk varying between 0.38 and 0.49. For the later calvers a sudden increase in the permanent environmental variance occurred when there was a shift from TM 12 to 1. For example, the last 3 mo of a May calver's lactation corresponded to TM 12, 1, and 2, respectively. The sudden increase was seen at the end of the lactation (Figure 3) for April/May calvers. A similar rise was not observed for the genetic variances (Figure 4).

As the primary focus of this study was on the influence of seasonality, genetic correlations between milk yield at the same stage of lactation but for different calving month were of interest. The strongest correlations were observed between adjacent calving months. The correlations between January calvers and March calvers were higher than 0.99 for all values of MIM. For more distant calving months (e.g., January calvers and May calvers), the correlations were still strong, with values greater than 0.98 for all MIM except for the last. Table 3 shows a more detailed picture of genetic parameters for early, mid, and late calvers (in a spring

Figure 3. Permanent environmental variance (σ^2_{pe}) of test-day milk yield in Irish primiparous animals across month in milk and test month for each month of the spring calving season.

seasonal calving system). Within any given calving month, the genetic correlation between adjacent MIM was greater than 0.97 for models inclusive/exclusive of TM (Table 3).

The log-likelihood of the model with TM and without TM effect was $-490,219$ and $-490,942$, respectively. Comparing the models by Akaike information criterion (Akaike, 1973) values (981,947 and 980,464, respectively) suggests that the model without TM is preferred (TM model estimated 31 parameters, whereas the model without TM estimated 13 parameters). When comparing EBV from sires with more than 20

daughters (Table 4) across both models, correlations were very strong for complete lactation milk yield EBV (>0.995 in all cases), suggesting little benefit in including seasonality into the variance components. However, for persistency, the breeding values differed more between the model without TM and the model with TM, especially because persistency between January and May calvers differed, as predicted by the model with TM. In addition, lactation yield heritabilities (for the TM model) were calculated as 0.33, 0.32, 0.32, 0.34, and 0.35 for January, February, March, April, and May calvers respectively; these compare with parameters for

Figure 4. Genetic variance (σ_a^2) of test-day milk yield in Irish primiparous animals across month in milk and test month for each month of the spring calving season.

305-d milk yield, in the current Irish national evaluation model, of 0.35 for heritability and 0.20 for the ratio between the permanent environment variance and phenotypic variance. Given the consistent nature of the heritability values estimated in this study across the calving season, this further suggests little benefit in including seasonality into the variance components.

DISCUSSION

The objective was to estimate (co)variance components for test-day milk yield and investigate whether

Table 4. Genetic correlations of 305-d milk yield (above diagonal) and of persistency (below diagonal) between model exclusive of test month (No TM) and model inclusive of TM effect, for sires with more than 20 progeny

	No TM	Jan.	Mar.	May
No TM		0.999	0.999	0.996
Jan.	0.988		0.999	0.998
Mar.	0.993	0.989		0.998
May	0.964	0.939	0.980	

the genetic (co)variance components were affected by seasonality. Previous research (Cromie et al., 1998) has found some evidence of $G \times E$ interaction for 305-d milk yield across high/low-concentrate herds in Ireland. Similarly, Nauta et al. (2006) found genetic correlations across production systems of less than unity. Given the considerable effect, in both quantity and quality, of grass available at different stages in the season, an effect of seasonality on the variances might be expected.

If (co)variance components are influenced by the seasonal production system, it would be important to take this into account in breeding value estimation. Although calving month or TM could be used in the model to account for the seasonality effect, TM was chosen, as there was a more uniform spread of data across TM, and the primary interest was in separating the effects of TM from that of MIM. Although 80% of animals in the data set calved in 3 mo of the spring, 8 different TM have to be combined to cover 80% of the data. It was envisaged that this spread of data across the chosen variable would better allow for partitioning the genetic variance into parts attributable to TM and MIM. In addition, the main practical reason for the seasonality effect is the supply of grass, which is also best accounted for by calendar month. The decision to use a subset of the data instead of the complete data set resulted in relatively small numbers of animals calving in May. It is possible that this has a bearing on results presented, especially for May calvers. The results also suggest a consistent pattern from January to May calving, with heritability being higher at the start of the lactation for earlier calvers, and heritability being lower toward the end of the lactation for earlier calvers. Initial attempts at using an animal model failed, the likely reason being the fact that MIM and TM are highly correlated (in a seasonal production system). For that reason, a sire/maternal grand sire model was used, allowing more records per animal and a better ability to disentangle MIM and TM effects.

The heritability estimates for test-day milk yield across the lactation (0.14–0.27) were similar to estimates from previous studies (Pool et al., 2000; Jakobsen et al., 2002; Druet et al., 2003). This range and the observed pattern in heritabilities (highest at the middle of lactation and lower at the extremities of lactation) are similar to those in the current study. Genetic variance appears to be higher at the beginning of lactation, especially so for early (January and February) calvers. Genetic variance was found to be low at the end of the lactation in comparison with previous studies (Liu et al., 2000a); however, this may be due to deficiency of data toward the end of the lactation, as the median lactation length in Ireland is 284 d. This is shorter

than most other nonseasonal dairy-producing countries (e.g., the average lactation length is 342 d in the Netherlands; van Arendonk and Liinamo, 2003), resulting in relatively less data available toward the end of the lactation in the Irish data. It is interesting that genetic correlations between milk yield at the beginning and end of a lactation (i.e., between MIM 1 or 2 and MIM 7 or 8) were weak, with values ranging between 0.48 and 0.79, suggesting that milk yield at the beginning and at the end of the lactation were somewhat different traits. The genetic correlations for MIM were stronger for values of MIM, which were closer and weaker for more distant values of MIM. Previous results, such as those of Liu et al. (2000a) and Druet et al. (2003), comparing early and late lactation, were similar to those in the current study.

Various approaches have been used to model seasonality. In most genetic evaluation models, seasonality is included in the model as a fixed effect of season of year or of test date (Olori et al., 1999; Haile-Mariam et al., 2003). These models assume that the genetic (co)variances are homogenous and genetic correlations are unity across the fixed effects levels. In the model used here, we have loosened this assumption by allowing the genetic variance to change according to season, and to allow the genetic correlation to be less than unity. To do so, the genetic variances were partitioned into variance attributable to MIM and TM. Genetic correlations between values of TM within 3 mo of each other were generally positive, whereas those more than 3 mo apart were generally negative. For example, the genetic correlation between TM 2 and TM 3 (i.e., milk test occurring in February and March, respectively) was 0.94, whereas the genetic correlation between TM 2 and TM 7 (i.e., milk test occurring in February and July, respectively) was -0.73 . This appears to suggest that the TM genetic component of milk production early in year is strongly negatively correlated with TM genetic component of milk production 5 to 6 mo later in the year, and strong evidence that $G \times E$ interaction exists. In practice, it is very difficult to interpret this as an actual biological entity, as it is based on partitioning the genetic variance into 2 components, of which this (TM) has the smaller effect. However, most of the genetic variance was attributable to the general sire effect (intercept) plus the components that vary for MIM (ranging from 2.50 kg² for MIM = 1 to 1.25 kg² for MIM = 10). The effect on the genetic variance of TM was relatively small (ranging from 0.16 kg² for TM = 1 to 0.12 kg² for TM = 12). Although some of this was due to the inclusion of the intercept with the MIM term, it suggests that the major part of the variance was explained by the stage of lactation (i.e.,

MIM) and that TM explained a much lesser part of the variance. Whereas it is usual in implementation of random regression test-day models to have heterogeneous residual variance (Pool and Meuwissen, 1999; Druet et al., 2003), in this model, we assumed a homogeneous residual term. This was estimated as 3.59 kg². Olori et al. (1999) found that homogeneous residual variance results in residual variances being underestimated and heritability estimates overestimated early in lactation. However, in this case, given the computation difficulties encountered and the fact that permanent environment variance was fitted as a random regression term across the lactation, a homogeneous residual variance was assumed.

The model used here fitted 2 curves for each sire: 1 expressing the breeding value for the lactation curve across TM and 1 estimating the breeding value for the lactation curve across MIM. An interesting expansion would be to allow a lactation curve for each sire to be estimated for each month of calving. We have attempted this by fitting an interaction term (TM $\times$ MIM) for each sire. This model, including an interaction term (TM $\times$ MIM) for each sire, gave convergence problems, probably because of the little variance that TM explained. Although such a parameterization might contain more effects to be estimated per sire, it is probably easier to disentangle by, for example, fitting a lactation curve by season of calving similar to that of Strabel and Jamrozik (2006b). This approach of fitting a separate lactation curve by season of calving was not attempted. With more data and computing resources this may be possible; however, it is difficult to speculate what such a model might reveal. With the small effect found of seasonality on genetic parameters, it was deemed less important to incorporate the higher parameterization required to incorporate any potential sire selection on gestation EBV.

Another disadvantage of the current parameterization of the model is the apparent discontinuity in genetic parameters for later-calving animals. This coincides with the end of a calendar year (e.g., for May-calving animals the end of the lactation is in the following calendar year). For each month, permanent environment variance increases between December to January and phenotypic variance also increases between December and January, whereas genetic variance decreases slightly between December and January, which overall leads to much lower heritability. This appeared to be independent of the coding of months as January = 1, February = 2, and so on; an alternative version with July = 1, August = 2, . . . , December = 6, January = 7, . . . , June = 12 produced a similar effect between June and July. This is likely to be due to the nature of the polynomials fitted, in that they oscillate at extremities of the range,

so attempting to create a continuous solution across years requires a more detailed model. Similar effects, especially at the end of lactation have been discussed by others previously (Strabel et al., 2005). This oscillating nature of polynomial curves might also affect the breeding values for persistency, especially when limited data are available at the end of the lactations (Pool and Meuwissen, 1999). One possibility would be to code subsequent years with consecutive values; however, for this data, that particular approach did not converge.

The main issue from a practical view is whether actually any difference exists in the predictive ability of a model including TM as well as stage of lactation, versus a model excluding TM, solely containing stage of lactation. Although very little difference was observed between models including/excluding seasonality, individual bulls did exhibit different solution curves for daughters calving in different months. From examining the correlations between lactation yield EBV in both types of models, and also from examining the overall lactation yield heritability, with the current model we concluded that genetic parameters across MIM (or DIM) are probably not dissimilar for Ireland than found in other countries and that accounting for the effect of seasonality on the genetic variances is probably not required based on the current analysis.

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