



Genetic correlations of days open with production traits and contents in milk of major fatty acids predicted by mid-infrared spectrometry

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ABSTRACT

The objective of this study was to estimate the genetic relationships between days open (DO) and both milk production traits and fatty acid (FA) content in milk predicted by mid-infrared spectrometry. The edited data set included 143,332 FA and production test-day records and 29,792 DO records from 29,792 cows in 1,170 herds. (Co)variances were estimated using a series of 2-trait models that included a random regression for milk production and FA traits. In contrast to the genetic correlations with fat content, those between DO and FA content in milk changed considerably over the lactation. The genetic correlations with DO for unsaturated FA, monounsaturated FA, long-chain FA, C18:0, and C18:1 *cis*-9 were positive in early lactation but negative after 100 d in milk. For the other FA, genetic correlations with DO were negative across the whole lactation. At 5 d in milk, the genetic correlation between DO and C18:1 *cis*-9 was 0.39, whereas the genetic correlations between DO and C6:0 to C16:0 FA ranged from -0.37 to -0.23 . These results substantiated the known relationship between fertility and energy balance status, explained by the release of long-chain FA in early lactation, from the mobilization of body fat reserves, and the consequent inhibition of de novo FA synthesis in the mammary gland. At 200 d in milk, the genetic correlations between DO and FA content ranged from -0.38 for C18:1 *cis*-9 to -0.03 for C6:0. This research indicates an opportunity to use FA content in milk as an indicator trait to supplement the prediction of genetic merit for fertility.

Key words: fatty acid, genetic correlation, days open, random regression

INTRODUCTION

Most dairy production systems have suffered a decline in cow fertility over the past 5 decades. Fertility is a multifactorial trait and its deterioration has been caused by a combination of genetic, environmental, and management factors (Walsh et al., 2011). However, improving dairy cow fertility through genetic selection has become increasingly important in recent years since it was established that declining fertility cannot be arrested solely by improved management (Veerkamp and Beerda, 2007). Most dairy cattle populations have, by now, routine genetic evaluation systems for female fertility (Interbull, 2011a) and such fertility traits are now almost always included in national breeding goals (Miglior et al., 2005). Furthermore, international genetic evaluations for female fertility are now available (Interbull, 2011b).

Direct selection for female fertility, however, might be complicated by the following factors: (1) the difficulty in collecting large quantities of relevant direct fertility records, especially for unfertile animals (e.g., no calving interval records for animals that are infertile), (2) the long period required to validate some phenotypes (e.g., calving interval) and its subsequent effect on generation interval and thus genetic gain, and (3) the generally low heritability of most traditional fertility phenotypes (from 0.01 to 0.05; Veerkamp and Beerda, 2007). These factors contribute to low accuracy of EBV, especially for cows and young bulls. Therefore, indicator traits could be very useful to supplement the prediction of genetic merit for fertility as long as these traits are easier to measure, recorded earlier in the cow's lactation, heritable, and genetically correlated with fertility. Several previous studies have documented a benefit of using correlated traits in genetic evaluations of fertility such as milk, fat, protein yields, type traits, or traits related to the extent and the duration of postpartum negative energy balance such as BW or BCS (Wall et al., 2003; de Jong, 2005). Moreover, energy balance status is expected to be associated with milk yield and milk composition. de Vries and Veerkamp (2000)

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suggested that a decrease in fat percentage in early lactation might serve as an indicator of energy balance. Also, milk FA profile is thought to be related to energy balance status of cows in early lactation (Stoop et al., 2009; Mc Parland et al., 2011). At initiation of lactation when cows are in negative energy balance, adipose FA are mobilized and incorporated in milk, causing an increase of C18 FA proportion in milk fat and a consequent inhibition of de novo synthesis of FA by the mammary gland (Palmquist et al., 1993; Barber et al., 1997). Moreover, previous studies have clearly shown that milk FA content is heritable (Soyeurt et al., 2007; Stoop et al., 2008). Therefore, FA contents in milk could be considered as potential indicator traits for fertility. Although the genetic relationship between fertility and traditional production traits (milk, fat, and protein) has been reported in several studies (Veerkamp et al., 2001; Windig et al., 2006), to our knowledge, the genetic relationship between fertility and milk FA profile has not been investigated.

The objective of this study was to investigate the genetic relationships between fertility, measured as the interval from calving to conception or days open (DO), and FA content in milk. The genetic correlations between fertility and both milk production traits and content in milk of 17 groups and individual FA predicted by mid-infrared spectrometry were estimated for first-parity Walloon Holstein cows using random regression test-day animal models for milk production and FA traits.

MATERIALS AND METHODS

Data Editing

Daily milk yield (kg), fat yield (kg), protein yield (kg), fat content (%), protein content (%), and DO records of first-parity Holstein cattle were extracted from the edited database used for the Walloon genetic evaluation in Belgium. This data set included cows with a known birth date and calving for the first time between 21 and 49 mo of age. Production records ranged between 5 and 365 DIM and only records where values were between 3 and 85 kg for milk yield, between 1 and 7% for protein content, and between 1.5 and 9% for fat content were used. These thresholds are used in the official genetic evaluation for production traits in the Walloon region of Belgium and are based on International Committee for Animal Recording (ICAR) guidelines (ICAR, 2012). Days open and pregnancy rate (which is derived from DO) are the only traits currently available in the Walloon fertility database used for genetic evaluation. Because AI data are scarce, DO is often estimated us-

ing the next calving date by subtracting 280 d from the calving interval. Days open <21 were deleted and DO >355 were set to 355.

Contents (g/dL of milk) of individual and groups of FA used in this study were predicted by applying, to the Walloon spectral database, the calibration equations developed by Soyeurt et al. (2011) using 517 samples selected in 3 countries (Belgium, Ireland, and United Kingdom) from various breeds, cows, and production systems (Table 1). Contents of FA in milk fat (g/100 g of fat) were not used for 2 reasons. First, Soyeurt et al. (2011) demonstrated that mid-infrared prediction of FA contents in milk fat was inferior to predictions of contents in milk. Second, by expressing FA content in milk, results could be directly compared with those obtained for fat and protein content. To provide an indication of the accuracy of mid-infrared spectroscopy at predicting milk FA content, the coefficient of determination of the cross-validation (R_{cv}^2) and the ratio of (standard error of) prediction to (standard) deviation (RPD) are provided in Table 1. For each equation, the RPD was calculated and defined as the ratio of the standard deviation of the data used to build the calibration equation (i.e., gas chromatographic data) to the standard error of the cross-validation (further details are provided in Soyeurt et al., 2011). Soyeurt et al. (2011) further indicated that equations with R_{cv}^2 greater than 75% could be used for animal breeding purposes. Williams (2007) suggested that the prediction can be considered as reliable if the RPD is higher than 3. Based on this criterion, predictions for 16 out of the 29 predicted groups and individual FA presented by Soyeurt et al. (2011) were included in the present study. An exception was the group of PUFA with an RPD close to 3 (2.6) because of the usefulness of including the major groups of FA in the analysis. Since January 2007, the Walloon spectral database has included most of the spectra generated during the analysis of milk samples collected through milk recording in the Walloon region. Milk recording is organized by the Walloon Breeding Association (Ciney, Belgium), and milk samples are analyzed using mid-infrared MilkoScan FT6000 spectrometer (Foss, Hillerød, Denmark) by the milk laboratory Comité du Lait (Battice, Belgium). The 7 FA groups used in this study were SFA, unsaturated (UFA), MUFA, PUFA, short-chain fatty acids (SCFA), including FA with 4 to 10 carbons, medium-chain fatty acids (MCFA), including FA with 12 to 16 carbons, and long-chain fatty acids (LCFA), including FA with 17 to 22 carbons. To eliminate potentially abnormal records, FA contents in milk below the 1st and above the 99th percentile were discarded.

Table 1. Mean and standard deviation of days open ($n = 29,792$) and production and FA traits ($n = 143,332$) in the data set used for genetic correlations estimation; lactation heritability estimates (h_{305d}^2), average daily heritability estimates (h_d^2), and lactation genetic correlations with days open (r_{305d}) are also presented¹

Trait	R_{cv}^2	RPD	Mean	SD	h_{305d}^2	h_d^2	r_{305d}
Days open	—	—	147	83	0.05	—	—
Milk (kg)	—	—	23.08	5.99	0.31	0.21	0.51
Fat (kg)	—	—	0.904	0.226	0.29	0.18	0.42
Protein (kg)	—	—	0.765	0.187	0.29	0.17	0.38
Fat (%)	—	—	3.964	0.544	0.68	0.40	-0.15
Protein (%)	—	—	3.343	0.324	0.67	0.44	-0.34
Fatty acids ² (g/dL of milk)							
SFA	1.00	15.7	2.793	0.461	0.68	0.43	-0.12
MUFA	0.99	8.9	1.129	0.206	0.58	0.21	-0.15
PUFA	0.85	2.6	0.167	0.032	0.69	0.31	-0.16
Unsaturated FA	0.99	9.6	1.310	0.226	0.60	0.23	-0.16
Short-chain FA	0.98	6.7	0.348	0.063	0.68	0.42	-0.10
Medium-chain FA	0.98	6.5	2.134	0.412	0.68	0.43	-0.13
Long-chain FA	0.98	6.5	1.625	0.307	0.56	0.20	-0.13
C4:0	0.94	4.1	0.106	0.018	0.63	0.34	-0.03
C6:0	0.97	5.7	0.074	0.013	0.67	0.42	-0.07
C8:0	0.97	6.1	0.046	0.009	0.68	0.43	-0.11
C10:0	0.96	5.1	0.109	0.027	0.68	0.42	-0.15
C12:0	0.96	5.2	0.132	0.035	0.69	0.43	-0.18
C14:0	0.97	5.4	0.467	0.087	0.68	0.43	-0.13
C16:0	0.95	4.6	1.236	0.269	0.67	0.41	-0.11
C17:0	0.89	3.1	0.030	0.004	0.70	0.39	-0.20
C18:0	0.90	3.2	0.407	0.093	0.59	0.23	-0.06
C18:1 <i>cis</i> -9	0.97	5.9	0.803	0.167	0.52	0.17	-0.13

¹Standard errors ranged from 0.01 to 0.04 for h_{305d}^2 , were 0.02 for h_d^2 , and ranged from 0.07 to 0.10 for r_{305d} .

²For fatty acids, the coefficient of determination of the cross-validation (R_{cv}^2) and the ratio of (standard error of) prediction to (standard) deviation (RPD; Soyeurt et al., 2011) are presented.

To estimate genetic correlations among DO and both milk production and milk FA content, cows from the edited data set were required to have a DO record and full information on production and FA content for at least 3 test-days. Descriptive statistics of the data set used for the estimation of genetic correlations are in Table 1. The final data set included 143,332 FA and production records and 29,792 DO records from 29,792 cows in 1,170 herds. The data set included cows that had calved between March 2006 and July 2010. Pedigree data were extracted from the database used for the official Walloon genetic evaluation and were limited to animals born after 1985. The pedigree file contained 91,032 animals.

Model

The model used in this study was based on models used for Walloon genetic evaluations for production and fertility (Croquet et al., 2006; Mayeres et al., 2006). A total of 22 two-trait (DO and each of the 22 production and FA traits) analyses were run using the following bivariate model:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_1 \\ \boldsymbol{\beta}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{H}_2 \\ \mathbf{0} \end{bmatrix} \mathbf{h}_2 + \begin{bmatrix} \mathbf{0} \\ \mathbf{W}_1 \end{bmatrix} \mathbf{w}_1 \\ + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix},$$

where \mathbf{y}_1 was a vector of records of production or FA traits; \mathbf{y}_2 was a vector of DO records; $\boldsymbol{\beta}_1$ was the vector of the following fixed effects for production and FA traits: (1) herd \times test-day, (2) gestation stage, (3) stage of lactation (classes of 5 DIM), and (4) stage of lactation (classes of 73 DIM) \times age at calving \times season of calving; $\boldsymbol{\beta}_2$ was the vector of the following fixed effects for DO: (1) herd, (2) year \times month of calving, and (3) age at calving \times season of calving; \mathbf{h}_2 was the vector of the herd \times year of calving random effect for DO; \mathbf{w}_1 was the vector of herd \times period of calving random regression coefficients for FA and production traits; \mathbf{p}_1 was the vector of within-lactation permanent environmental random regression coefficients for production traits and FA; \mathbf{p}_2 was the vector of nongenetic cow-specific (within-animal) environmental random effect

for DO; \mathbf{a}_1 was the vector of additive genetic random regression coefficients for FA and production traits; \mathbf{a}_2 was the vector of additive genetic random effect for DO; \mathbf{e}_1 and \mathbf{e}_2 were the vector of residuals for \mathbf{y}_1 and \mathbf{y}_2 , respectively; and \mathbf{X}_1 , \mathbf{X}_2 , \mathbf{H}_2 , \mathbf{W}_1 , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices assigning observations to effects.

Regression curves were modeled using modified Legendre polynomials of the second order. Random effects were assumed to be normally distributed, and residual variances were assumed to be independent and constant over the lactation. Genetic covariances were modeled among genetic effect for DO and genetic random regression effects for production traits or FA. No residual covariance was modeled between DO and other traits because they were obtained from different sources and not recorded simultaneously. Therefore, to avoid environmental covariances being considered as genetic covariances, within-animal environmental covariance among traits was modeled by the permanent environmental effect, as proposed by Negussie et al. (2008) and Bastin et al. (2010). This effect allowed for a cow-specific, nongenetic link between the traits of the 2 data sets.

(Co)variance components estimation was performed using Gibbs sampling (Misztal, 2010). Posterior means and posterior standard errors of (co)variance components were estimated using 90,000 samples after a burn-in of 10,000 samples.

Genetic Parameters

Daily heritability estimates (h_d^2) were defined for the production and FA traits as the ratio of the genetic variance to the sum of genetic, environmental, herd \times period of calving, and residual variances for each day between 1 and 305 DIM. Genetic, environmental, and herd \times period of calving daily variances for production and FA traits at DIM t were estimated as \mathbf{qKq}' , where \mathbf{K} was the elementary covariance matrix among the Legendre polynomial coefficient of the corresponding effect for the trait of interest, and \mathbf{q} was a line vector of Legendre polynomials coefficients computed for DIM t . Average daily heritabilities were defined as the average across the entire lactation. Lactation heritability or 305-d heritability (h_{305d}^2) was estimated in the same way as daily estimates using 305-d variances; genetic, environmental, and herd \times period of calving 305-d variances of production and FA traits were estimated by replacing \mathbf{q} by \mathbf{q}_{305d} , which was the vector of Legendre polynomial coefficients cumulated from 1 to 305 d. Residual 305-d variance was computed as $\mathbf{s}\sigma_e^2$, where \mathbf{s} was 305 and σ_e^2 was the estimated residual variance. Herita-

bility for DO was defined as the ratio of genetic variance to the sum of all random effect variances and was averaged across the 22 two-trait analyses.

To calculate daily genetic correlations between DO and production and FA traits, the daily genetic covariance at DIM t between DO and the production or FA trait of interest was obtained as \mathbf{qc}' , where \mathbf{c} was the additive genetic covariance line vector among both traits. Similarly, lactation genetic covariance (or 305-d genetic covariance) was obtained by replacing \mathbf{q} by \mathbf{q}_{305d} in the above formula.

Calculation of standard errors of parameters (heritability and genetic correlations) was based on formulas presented by Fischer et al. (2004) using posterior standard errors of the (co)variance components.

RESULTS AND DISCUSSION

Heritability estimates for the different traits are presented in Table 1. Heritability for DO was 0.05, with a standard error of 0.01, and was similar to estimates from the literature for fertility. Mayeres et al. (2006) reported heritability of 0.05 for pregnancy rate in Walloon data. In that study, pregnancy rate was expressed as a percentage and computed as $21/(\text{DO} - 45 + 11)$, where 45 represents the voluntary waiting period in the Walloon production system and 11 represents half of a normal estrus cycle. Veerkamp and Beerda (2007) reported a mean heritability for DO estimated across 17 studies of 0.024; VanRaden et al. (2004) estimated a heritability of 0.037 for DO in first-lactation Holstein cows in the United States, and Hou et al. (2009) reported a heritability of 0.066 for DO in first-parity Danish Holstein cows. Lactation heritability estimates for milk, fat, and protein yields were almost 0.10 lower than those used in Walloon genetic evaluations at, respectively, 0.41, 0.43, and 0.40 (Auvray and Gengler, 2002). Lactation heritabilities for FA ranged between 0.52 for C18:1 *cis*-9 and 0.70 for C17:0. The average daily heritability of FA ranged from 0.17 to 0.43 and was similar to previous estimates by Bastin et al. (2011). Standard errors of the heritability estimates were all <0.04 . The de novo synthesized FA (C4:0 to C14:0 and half of C16:0) had generally higher heritabilities than FA originating from the diet and from body fat mobilization (LCFA and PUFA), which is in line with previous studies (Bobe et al., 2008; Stoop et al., 2008).

Lactation genetic correlations between DO and production traits and FA contents in milk are presented in Table 1. Lactation genetic correlations between DO and FA content in milk were low and ranged between -0.20 and -0.03 ; standard errors of the estimates ranged from 0.07 to 0.10. Daily genetic correlations

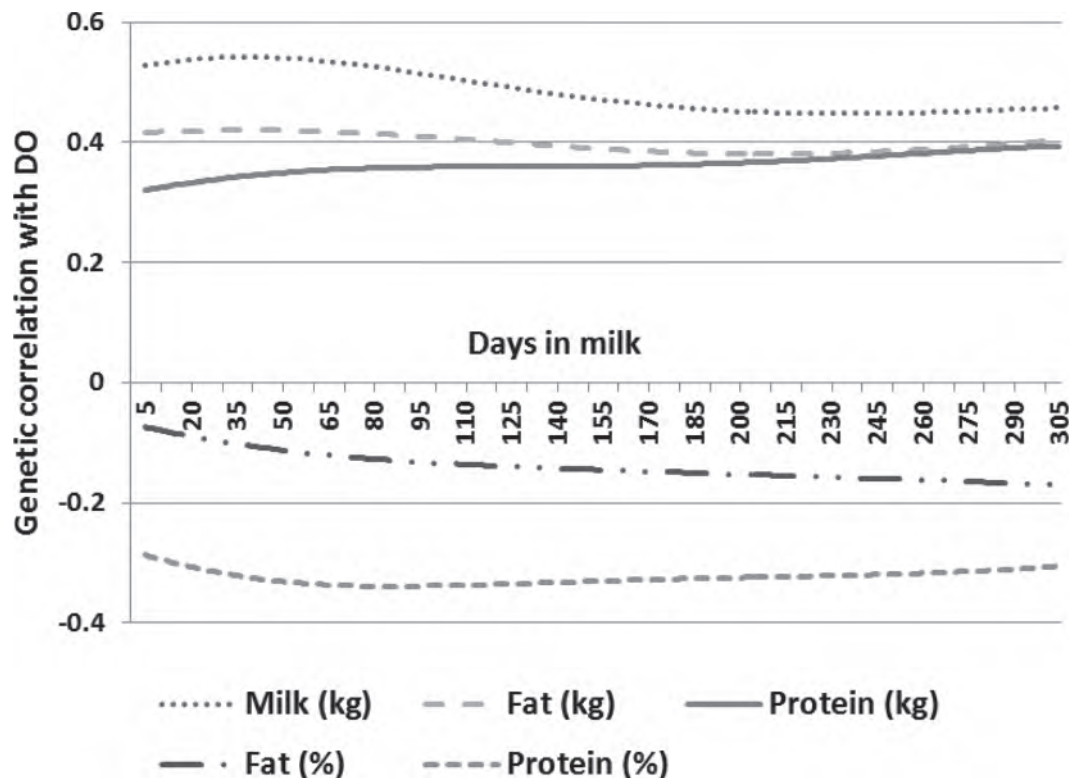


Figure 1. Daily genetic correlations between days open (DO) and milk, fat, and protein yields, and fat and protein contents in milk. Standard errors of estimates ranged from 0.07 to 0.12.

between DO and production traits and FA content in milk are presented in Figures 1, 2, and 3; standard errors of the estimates ranged from 0.07 to 0.13. Daily genetic correlations between DO and the yield traits were positive and did not change greatly over DIM (Figure 1). Genetic correlations ranged between 0.45 at 245 DIM and 0.54 at 35 DIM for milk yield, between 0.38 at 185 DIM and 0.42 at 50 DIM for fat yield, and between 0.32 at 5 DIM and 0.39 at 305 DIM for protein yield. Lactation correlations with DO were 0.51 for milk yield, 0.42 for fat yield, and 0.38 for protein yield. This is in agreement with previous studies reporting antagonistic genetic correlations between interval fertility traits and milk yield. Veerkamp et al. (2001) reported genetic correlations with interval between first and second calving of 0.67 for 305-d milk yield, 0.58 for 305-d fat yield, and 0.67 for 305-d protein yield. Windig et al. (2006) also reported positive genetic correlations between milk yield and days to first service varying over environments from 0.30 in small herds to 0.48 in herds with low average fertility. These correlations suggest that selection for higher yield alone, without any knowledge of other (functional) traits, would negatively affect fertility performances. However, a complex relationship exists between milk yield, health, and re-

productive performances; therefore, no clear evidence exists of a direct cause-effect association between yield and fertility (Weigel, 2006).

Although genetic correlations between fat content in milk and DO were negative and relatively stable across the lactation (correlations ranged from -0.17 at 305 DIM to -0.07 at 5 DIM; Figure 1), the genetic correlations between DO and some FA content in milk varied over the lactation. This suggests that changes in overall FA profile in milk over lactation were not simply explained by changes in overall fat percentage. For UFA, MUFA, LCFA, C18:0, and C18:1 *cis*-9, the genetic correlations with DO were positive in early lactation but negative after 100 DIM. For the other groups and individual FA, genetic correlations with DO were negative across the entire lactation (Figures 2 and 3).

The pattern of genetic correlations between fertility and FA content in milk is likely related to the cow's physiological state, especially in early lactation. At the initiation of lactation, cows are in negative energy balance (Berry et al., 2006), causing catabolism of adipose FA and leading to an increase in C18 FA in milk (Palmquist et al., 1993; Barber et al., 1997; Van Haelst et al., 2008). The FA composition of milk has therefore a much higher proportion of C18:0 and C18:1 *cis*-9

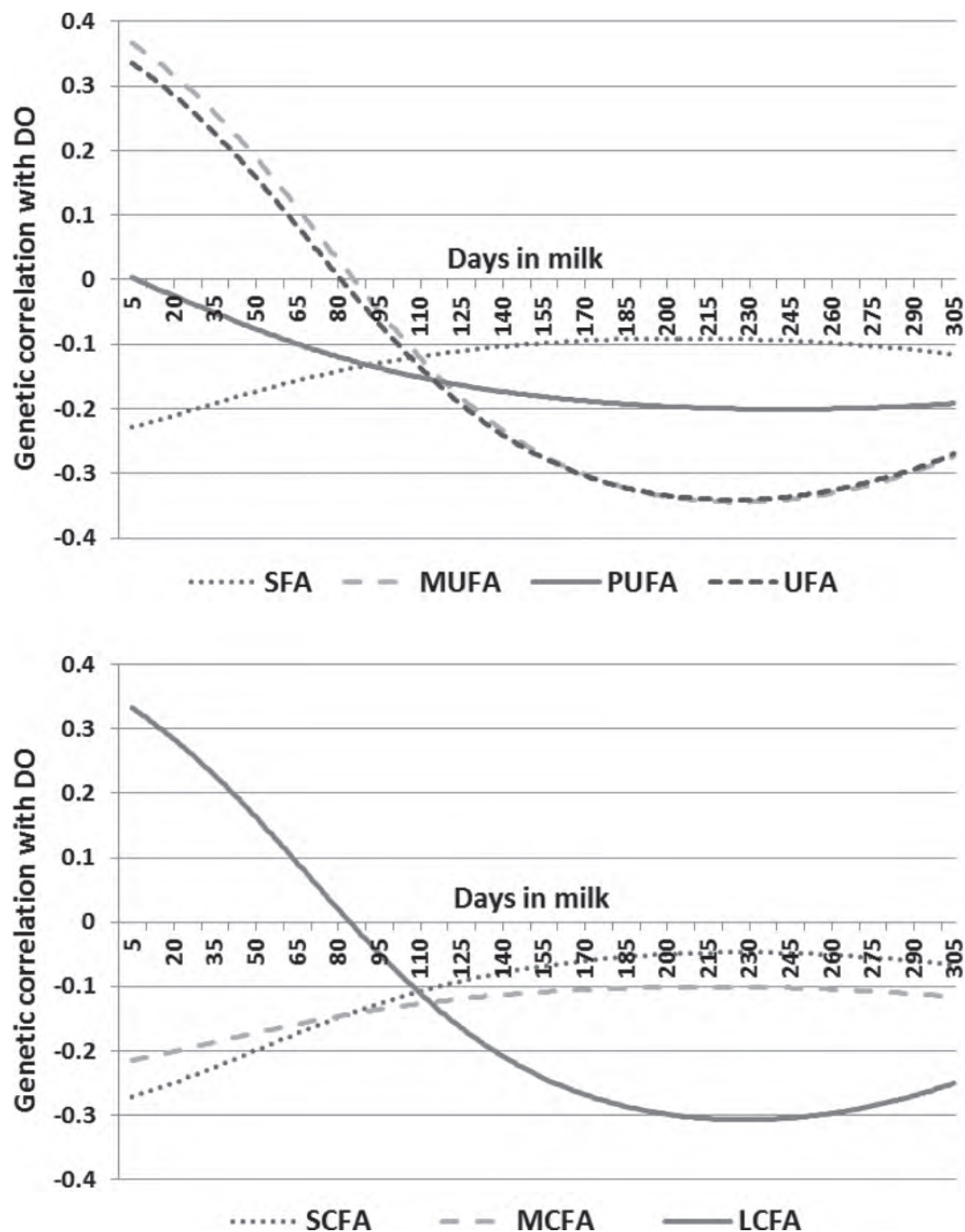


Figure 2. Daily genetic correlations between days open (DO) and groups of FA content in milk (g/dL of milk): SFA, MUFA, PUFA, unsaturated FA (UFA), short-chain FA (SCFA), medium-chain FA (MCFA), and long-chain FA (LCFA). Standard errors of estimates ranged from 0.07 to 0.13.

when lipolysis is high (i.e., when the cow is in negative energy balance). This is supported by Mc Parland et al. (2011), who presented correlations between LCFA content in milk and body energy status of -0.20 in cows fed a high concentrate diet and -0.24 in cows fed a low concentrate diet. Because negative energy balance is

known to be associated with reduced fertility (de Vries and Veerkamp, 2000), the expectation is that higher contents of C18:0 and C18:1 *cis-9* in milk could be associated with poorer fertility performance. The genetic correlation at 5 DIM was 0.40 between DO and C18:1 *cis-9*, indicating that higher content of C18:1 *cis-9* in

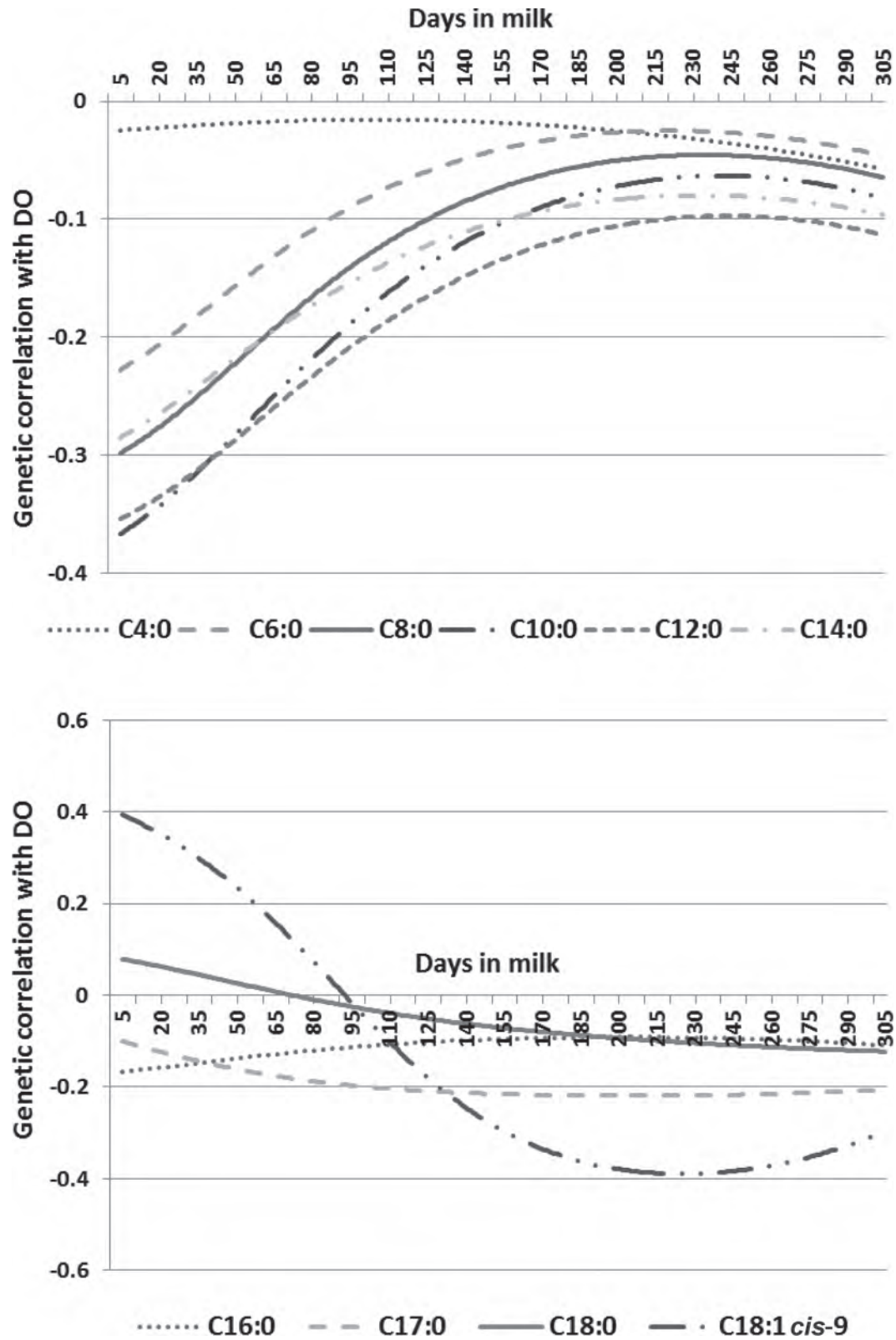


Figure 3. Daily genetic correlations between days open (DO) and individual FA content in milk (g/dL of milk): C4:0, C6:0, C8:0, C10:0, C12:0, C14:0, C16:0, C17:0, C18:0, and C18:1 *cis*-9. Standard errors of estimates ranged from 0.07 to 0.13.

milk was indeed related to greater DO. Because it is already available in the Walloon region and potentially in other countries in the near future from predictions derived from mid-infrared spectroscopy, the content of C18:1 *cis*-9 (or its changes) in early lactation could be an indicator of energy status that is more readily available than BCS. Body condition score is often only collected within type-recording schemes, leading to one record per lactation, or even just one record in the lifetime of the animal. Also, BCS is generally not systematically collected in early lactation. However, the inclusion of C18:1 *cis*-9 in breeding programs as a predictor of energy balance status should be considered with regard to its nutritional, technological, and sensory properties. Although lower contents of MUFA in early lactation would be more desirable from the point of view of energy balance status, higher contents of MUFA may be more desirable with regard to the human health aspects (Grummer, 1991). This last issue leads to the requirement for further considerations of both aspects in future comprehensive breeding schemes.

Concomitant with the release of adipose FA into milk in early lactation, the high uptake of LCFA inhibits *de novo* synthesis of FA by mammary gland tissue through the inhibition of acetyl-coenzyme A carboxylase. This inhibition intensifies with increasing chain lengths (Palmquist et al., 1993). Lower contents of C6:0 to C14:0 FA in milk could therefore also be associated with greater body fat mobilization and poorer fertility performance. This was substantiated by the negative genetic correlations observed in this study. Genetic correlations at 5 DIM between DO and C6:0 to C14:0 ranged between -0.37 (C10:0) and -0.23 (C6:0; Figure 3). Furthermore, the synthesis of C4:0 is not inhibited in early lactation because it originates in pathways independent of the inhibited acetyl coenzyme A carboxylase pathway (Palmquist et al., 1993). Therefore the genetic correlation between DO and content of C4:0 in milk was close to zero. Finally, the genetic correlation between C16:0 content in milk and DO was negative throughout lactation and ranged from -0.17 at 5 DIM to -0.10 at 305 DIM. Because C16:0 originates from both *de novo* synthesis and circulating blood lipids (Grummer, 1991), genetic correlations between DO and C16:0 are difficult to interpret biologically.

After 150 DIM, genetic correlations between DO and contents of FA in milk were all negative and ranged between -0.39 for C18:1 *cis*-9 at 230 DIM to -0.02 for C4:0 at 150 DIM. These correlations indicated that selection for higher contents in milk of C18:1 *cis*-9 in mid to late lactation is related to improved fertility.

Polyunsaturated FA content in milk was not strongly genetically associated with fertility, especially in early lactation (Figure 2); genetic correlations between DO

and PUFA ranged from -0.20 at 230 DIM to 0.00 at 5 DIM. Polyunsaturated FA are not synthesized by ruminants, and their concentration in milk is closely related to dietary intake of PUFA (Chilliard et al., 2000). Therefore, our results indicated that processes involved in the inclusion of PUFA in milk in early lactation are not likely to be genetically related to fertility in dairy cows.

Further research might consider the genetic relationship between fertility and FA volumes or FA contents in fat. Although the mid-infrared prediction of FA contents in fat presents much lower accuracy than the mid-infrared prediction of FA in milk (Soyeurt et al., 2011), this trait might reflect more clearly the equilibrium among FA originating from different metabolic origins. Moreover, even if correlations between fertility and volumes of FA were more dependent on milk yield, this trait could be useful to account for the “dilution” effect and to distinguish 2 cows that present the same content of FA in milk but that produce different quantities of milk and FA.

CONCLUSIONS

Results from this study confirmed the unfavorable genetic association between fertility and milk, fat, and protein yields. Genetic correlations between DO and FA content in milk substantiated the known unfavorable relationship between fertility and energy balance status and could be explained by the release of LCFA content in early lactation resulting from the mobilization of body fat reserves and the consequent inhibition of *de novo* FA synthesis in the mammary gland. In particular, the content of C18:1 *cis*-9 in early lactation seems to be a useful indicator of body fat mobilization and consequently of reproductive performance.

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REFERENCES

- Auvray, B., and N. Gengler. 2002. Feasibility of a Walloon test-day model and study of its potential as tool for selection and management. *Interbull Bull.* 29:123–127.
- Barber, M. C., R. A. Clegg, M. T. Travers, and R. G. Vernon. 1997. Lipid metabolism in the lactating mammary gland. *Biochim. Biophys. Acta* 1347:101–126.
- Bastin, C., N. Gengler, and H. Soyeurt. 2011. Phenotypic and genetic variability of production traits and milk fatty acid contents across days in milk for Walloon Holstein first-parity cows. *J. Dairy Sci.* 94:4152–4163.
- Bastin, C., S. Loker, N. Gengler, A. Sewalem, and F. Miglior. 2010. Genetic relationships between body condition score and reproduction traits in Canadian Holstein and Ayrshire first-parity cows. *J. Dairy Sci.* 93:2215–2228.
- Berry, D. P., R. F. Veerkamp, and P. Dillon. 2006. Phenotypic profiles for body weight, body condition score, energy intake, and energy balance across different parities and concentrate feeding levels. *Livest. Sci.* 104:1–12.
- Boebe, G., J. A. Minick Bormann, G. L. Lindberg, A. E. Freeman, and D. C. Beitz. 2008. Short communication: Estimates of genetic variation of milk fatty acids in US Holstein cows. *J. Dairy Sci.* 91:1209–1213.
- Chilliard, Y., A. Ferlay, R. M. Mansbridge, and M. Doreau. 2000. Ruminant milk fat plasticity: Nutritional control of saturated, polyunsaturated, *trans* and conjugated fatty acids. *Ann. Zootech.* 49:181–205.
- Croquet, C., P. Mayeres, A. Gillon, S. Vanderick, and N. Gengler. 2006. Inbreeding depression for global and partial economic indexes, production, type, and functional traits. *J. Dairy Sci.* 89:2257–2267.
- de Jong, G. 2005. Usage of predictors for fertility in the genetic evaluation, application in the Netherlands. *Interbull Bull.* 33:69–73.
- de Vries, M. J., and R. F. Veerkamp. 2000. Energy balance of dairy cattle in relation to milk production variables and fertility. *J. Dairy Sci.* 83:62–69.
- Fischer, T. M., A. R. Gilmour, and H. J. J. van der Werf. 2004. Computing approximate standard errors for genetic parameters derived from random regression models fitted by average information REML. *Genet. Sel. Evol.* 36:363–369.
- Grummer, R. R. 1991. Effect of feed on the composition of milk fat. *J. Dairy Sci.* 74:3244–3257.
- Hou, Y., P. Madsen, R. Labouriau, Y. Zhang, M. S. Lund, and G. Su. 2009. Genetic analysis of days from calving to first insemination and days open in Danish Holsteins using different models and censoring scenarios. *J. Dairy Sci.* 92:1229–1239.
- Interbull. 2011a. Description of national genetic evaluation systems for dairy cattle traits as applied in different Interbull member countries. Accessed Nov. 3, 2011. http://www-interbull.slu.se/national_ges_info2/framesida-ges.htm.
- Interbull. 2011b. Interbull routine genetic evaluation for female fertility traits—August 2011. Accessed Nov. 3, 2011. http://www-interbull.slu.se/Female_fert/framesida-fert.htm.
- ICAR. 2012. International Committee for Animal Recording: ICAR recording guidelines. Accessed Mar. 15, 2012. http://www.icar.org/pages/recording_guidelines.htm.
- Mayeres, P., S. Vanderick, C. Croquet, H. Soyeurt, H. Hammami, and N. Gengler. 2006. Genetic evaluation of female fertility for Walloon dairy and dual purpose cows using a parity random regression model: First results. *Interbull Bull.* 34:42–46.
- McParland, S., P. Schmidely, N. C. Friggens, G. Banos, H. Soyeurt, M. P. Coffey, E. Wall, R. F. Veerkamp, and D. P. Berry. 2011. Relationship between milk fatty acids and body energy status in Holstein dairy cows. *Agricultural Research Forum*, Tullamore, Ireland.
- Miglior, F., B. L. Muir, and B. J. Van Doormaal. 2005. Selection indices in Holstein cattle of various countries. *J. Dairy Sci.* 88:1255–1263.
- Misztal, I. 2010. BLUPF90 family of programs. University of Georgia. Accessed Mar. 25, 2010. <http://nce.ads.uga.edu/~ignacy/newprograms.html>.
- Negussie, E., I. Strandén, and E. A. Mäntysaari. 2008. Genetic association of clinical mastitis with test-day somatic cell score and milk yield during first lactation of Finnish Ayrshire cows. *J. Dairy Sci.* 91:1189–1197.
- Palmquist, D. L., A. D. Baulieu, and D. M. Barbano. 1993. Feed and animal factors influencing milk fat composition. *J. Dairy Sci.* 76:1753–1771.
- Soyeurt, H., F. Dehareng, N. Gengler, S. McParland, E. Wall, D. P. Berry, M. Coffey, and P. Dardenne. 2011. Mid-infrared prediction of bovine milk fatty acids across multiple breeds, production systems, and countries. *J. Dairy Sci.* 94:1657–1667.
- Soyeurt, H., A. Gillon, S. Vanderick, P. Mayeres, C. Bertozzi, and N. Gengler. 2007. Estimation of heritability and genetic correlations for the major fatty acids in bovine milk. *J. Dairy Sci.* 90:4435–4442.
- Stoop, W. M., H. Bovenhuis, J. M. L. Heck, and J. A. M. van Arendonk. 2009. Effect of lactation stage and energy status on milk fat composition of Holstein-Friesian cows. *J. Dairy Sci.* 92:1469–1478.
- Stoop, W. M., J. A. M. van Arendonk, J. M. L. Heck, H. J. F. van Valenberg, and H. Bovenhuis. 2008. Genetic parameters for major fatty acids and milk production traits of Dutch Holstein-Friesians. *J. Dairy Sci.* 91:385–394.
- Van Haelst, Y. N. T., A. Beeckman, A. T. M. Van Kneegsel, and V. Fievez. 2008. Short communication: Elevated concentrations of oleic acid and long-chain fatty acids in milk fat of multiparous subclinical ketotic cows. *J. Dairy Sci.* 91:4683–4686.
- VanRaden, P. M., A. H. Sanders, M. E. Tooker, R. H. Miller, H. D. Norman, M. T. Kuhn, and G. R. Wiggans. 2004. Development of a national genetic evaluation for cow fertility. *J. Dairy Sci.* 87:2285–2292.
- Veerkamp, R. F., and B. Beerda. 2007. Genetics and genomics to improve fertility in high producing dairy cows. *Theriogenology* 68(Suppl. 1):S266–S273.
- Veerkamp, R. F., E. P. C. Koenen, and G. De Jong. 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *J. Dairy Sci.* 84:2327–2335.
- Wall, E., S. Brotherstone, J. A. Woolliams, G. Banos, and M. P. Coffey. 2003. Genetic evaluation of fertility using direct and correlated traits. *J. Dairy Sci.* 86:4093–4102.
- Walsh, S. W., E. J. Williams, and A. C. O. Evans. 2011. A review of the causes of poor fertility in high milk producing dairy cows. *Anim. Reprod. Sci.* 123:127–138.
- Weigel, K. A. 2006. Prospects for improving reproductive performance through genetic selection. *Anim. Reprod. Sci.* 96:323–330.
- Williams, P. 2007. Near-infrared technology—Getting the best out of light. PDK Grain, Nanaimo, BC, Canada.
- Windig, J. J., M. P. L. Calus, B. Beerda, and R. F. Veerkamp. 2006. Genetic correlations between milk production and health and fertility depending on herd environment. *J. Dairy Sci.* 89:1765–1775.