Genetic parameters across lactation for feed intake, fat- and protein-corrected milk, and liveweight in first-parity Holstein cattle

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ABSTRACT

Breeding values for dry matter intake (DMI) are important to optimize dairy cattle breeding goals for feed efficiency. However, generally, only small data sets are available for feed intake, due to the cost and difficulty of measuring DMI, which makes understanding the genetic associations between traits across lactation difficult, let alone the possibility for selection of breeding animals. However, estimating national breeding values through cheaper and more easily measured correlated traits, such as milk yield and liveweight (LW), could be a first step to predict DMI. Combining DMI data across historical nutritional experiments might help to expand the data sets. Therefore, the objective was to estimate genetic parameters for DMI, fat- and protein-corrected milk (FPCM) yield, and LW across the entire first lactation using a relatively large data set combining experimental data across the Netherlands. A total of 30,483 weekly records for DMI, 49,977 for FPCM yield, and 31,956 for LW were available from 2,283 Dutch Holstein-Friesian first-parity cows between 1990 and 2011. Heritabilities, covariance components, and genetic correlations were estimated using a multivariate random regression model. The model included an effect for year-season of calving, and polynomials for age of cow at calving and days in milk (DIM). The random effects were experimental treatment, year-month of measurement, and the additive genetic, permanent environmental, and residual term. Additive genetic and permanent environmental effects were modeled using a third-order orthogonal polynomial. Estimated heritabilities ranged from 0.21 to 0.40 for DMI, from 0.20 to 0.43 for FPCM yield, and from 0.25 to 0.48 for LW across DIM. Genetic correlations between DMI

at different DIM were relatively low during early and late lactation, compared with mid lactation. The genetic correlations between DMI and FPCM yield varied across DIM. This correlation was negative (up to -0.5) between FPCM yield in early lactation and DMI across the entire lactation, but highly positive (above 0.8) when both traits were in mid lactation. The correlation between DMI and LW was 0.6 during early lactation, but decreased to 0.4 during mid lactation. The highest correlations between FPCM yield and LW (0.3–0.5) were estimated during mid lactation. However, the genetic correlations between DMI and either FPCM yield or LW were not symmetric across DIM, and differed depending on which trait was measured first. The results of our study are useful to understand the genetic relationship of DMI, FPCM yield, and LW on specific days across lactation.

Key words: feed intake, milk yield, liveweight, genetic correlation, random regression

INTRODUCTION

Feed costs represent above 50% of the total costs of dairy production (EC, 2011), so reducing costs by improving dairy cow feed efficiency is a way to increase profitability (Veerkamp, 1998; de Haas et al., 2012; Veerkamp et al., 2012). However, feed efficiency is a complex trait, with many definitions (Korver, 1988) of which some also include nutrition, health, and reproduction factors (Berry and Crowley, 2013). The most classic definition is the ratio between kilograms of milk produced and kilograms of DMI (Veerkamp and Emmans, 1995). This trait shows that to be able to define feed efficiency in dairy cattle breeding goals, accurate estimates of genetic parameters for DMI are needed. However, DMI is not recorded in commercial herds and, therefore, in most studies, the number of DMI records is small and estimates of genetic parameters have large sampling errors. In addition, in most of those studies,

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DMI was only recorded until 150 or 180 DIM, and not through the entire lactation (Veerkamp, 1998; Berry and Crowley, 2013).

The difficulty of recording hinders direct selection for feed intake, as no records are available on daughters of progeny-tested bulls. This difficulty might be overcome with the introduction of genomic selection (Pryce et al., 2012), but still the number of available records in the genomic reference population has to be >10,000 to obtain accurate breeding values (Calus et al., 2013). Additionally, indirect selection through moderate to highly correlated traits, which can be more easily measured, might be viable (Pszczola et al., 2013). Milk yield traits and liveweight (**LW**) could be useful predictors of DMI, because they would allow proper accounting for the amount of feed required for production and maintenance, respectively, and consequently allow an approximation of net feed efficiency (Kennedy et al., 1993; Veerkamp, 1998). These traits are relatively easy and cheap to measure on a large scale, especially when LW is predicted using linear type traits (Veerkamp and Brotherstone, 1997; Parke et al., 1999; Banos et al., 2012; Liinamo et al., 2012). However, estimates of genetic parameters are required to evaluate the benefit of using LW and milk yield in addition to genomic prediction.

Dry matter intake is influenced by several biological processes that change during the course of lactation and, therefore, DMI could have a different genetic background at different lactation stages (Koenen and Veerkamp, 1998). In fact, estimated heritabilities of DMI change during lactation (Koenen and Veerkamp, 1998; Berry et al., 2007; Buttchereit et al., 2011), and low genetic correlations were estimated between DMI recorded in early and late lactation (Koenen and Veerkamp, 1998; Liinamo et al., 2012). Similarly, LW and milk yield may not be genetically the same trait across lactation, and genetic correlations between them may also change across lactation. Therefore, the objective of the current study was to estimate genetic parameters for DMI, fat- and protein-corrected milk (**FPCM**) yield, and LW across the entire first lactation. By combining data from historical nutritional experiments in the Netherlands, a unique large data set was created, which makes this probably the largest study of its kind currently available.

MATERIALS AND METHODS

Data Collection

A total of 307,007 daily records on DMI, FPCM yield, or LW were available from 2,977 Holstein-Friesian cows that calved between 1990 and 2011. These cows par-

ticipated in nutritional experiments conducted on several farms in the Netherlands [e.g., Aver Heino (Heino, the Netherlands), Bosma Zathe (Ureterp, the Netherlands), Cranendonck, (Soerendonk, the Netherlands), 't Gen (Lelystad, the Netherlands), Minderhoudhoeve, (Swifterbant, the Netherlands), Waiboerhoeve Dairy Unit 2, 3 (Lelystad, the Netherlands), Zegveld farm (Zegveld, the Netherlands), Hoorn (Lelystad, the Netherlands), and New Wairboerhoeve (Lelystad, the Netherlands)]. A description of the methodology of most experiments has been summarized previously (Veerkamp et al., 2000; Beerda et al., 2007; Zom et al., 2012; van Kneegsel et al., 2014), and an overview is given in Table 1. All cows were kept indoors in conventional cubicle housings, were offered complete mixed diets *ad libitum*, and were milked twice per day, except half of the cows at Bosma Zathe ($n = 50$) that were milked 3 times per day.

Traits

Dry matter intake was, depending on the experiment, recorded 1, 2, 3, or 5 times per week (Beerda et al., 2007; Zom et al., 2012). Feed intake was recorded using computer-controlled access gates (Calan feeding system) at the experimental farms Bosma Zathe, Zegveld, Aver Heino, and Waiboerhoeve Dairy Unit 3. Offered feed was recorded automatically, but feed refusals were weighed manually. Data from these historical nutritional experiments were combined from 4 separate data sets, and an overview is shown in Table 1. In the nutritional experiments described by Zom et al. (2012), fresh forage mixtures were offered once or twice daily and the refusals were weighed and removed daily. To ensure *ad libitum* intake of forage (mixtures), the quantities offered were such that the feed refusals were at least 10% of the amount offered. At the other experimental farms, automated feed intake units were used, where feed was provided via a roughage intake control system (Insentec BV, Marknesse, the Netherlands), which allowed monitoring the daily TMR per individual. The roughage intake control system consists of a feeding gate that controls access via neck collars. The visit time is registered as well as the amount of feed that a cow ate during the visit.

Weighing platforms were used to automatically monitor LW 3 times per week or daily, depending on the experiment. To represent milk yield and its components, FPCM yield was calculated, where the milk yield is corrected for its fat and protein content to a standard of 4.0% fat and 3.3% protein (FAO, 2010). Fat and protein contents in milk were measured weekly, and they were used to calculate FPCM yield according to the following formula (FAO, 2010):

Table 1. Description of available phenotypic records of DMI, fat- and protein-corrected milk (FPCM) yield, and liveweight (LW) for 4 data sets of first-parity Holstein-Friesian cows

Item	Data set			
	1	2	3	4
No. of experimental treatments	4	1	39	51
No. of sites	1	1	9	2
No. of cows				
DMI	99	682	367	149
FPCM yield	99	714	647	825
LW	99	701	367	194
Total	99	714	647	826
No. of weekly records				
DMI	1,462	19,365	8,233	1,423
FPCM yield	2,167	25,130	14,015	8,665
LW	1,456	20,183	8,318	1,999
Total	2,220	25,576	14,131	9,517
DMI recording period (DIM)	104	294	324	324
Years interval	2003–2005	1990–1998	1990–2001	1995–2011
Publication	Beerda et al. (2007)	Veerkamp et al. (2000)	Zom et al. (2012)	Unpublished

$$\text{FPCM (kg)} = [0.337 \times \text{raw milk (kg)}] + [11.6 \times \text{fat content (kg)}] + [5.999 \times \text{protein content (kg)}].$$

Data Editing

The raw data consisted of 307,007 records from 2,977 animals. All records from animals without information on pedigree, parity number, calving date, or date of measurement were removed, and only DMI records in the first 324 DIM (46 wk) were retained. These edits resulted in a data set with 299,338 records from 2,651 animals from parity 1 to 14. Weekly means of daily DMI and LW records were calculated, so that the phenotypes were consistent for each experimental treatment. This resulted in a data set with 195,810 records from 2,651 cows.

Finally, only first-lactation records were kept and cows with less than 75% Holstein-Friesian genes were deleted. This resulted in a data set consisting of 30,483 records for DMI on 1,297 animals, 49,977 records for FPCM yield on 2,285 animals, and 31,956 records for LW on 1,361 animals. Descriptive information of phenotypic records of DMI, FPCM yield, and LW for the 4 data sets is shown in Table 1. The total number of experimental treatments was 95, but varied from 1 to 51 through the 4 data sets, and the total number of cows ranged between 99 and 826 per data set. The total number of weekly records per data set ranged from 2,220 to 25,576. The number of cows with FPCM yield records was twice the number of cows with DMI records in data set 3, and 3 times as much as those in data set 4. This is because in those experiments the period of interest for DMI recording was late first lactation and early second lactation, whereas milk production was measured during the entire lactation (van Kneegsel et

al., 2014). The pedigree was traced back for 18 generations and included 10,226 animals.

Statistical Analysis

A trivariate analysis of DMI, FPCM yield, and LW was performed to estimate the variance and covariance components between these 3 traits for each day of lactation, with a test-day random regression model using ASReml software (Gilmour et al., 2009). The model included random effects for experimental treatment, year-month of measurement, and the additive genetic, permanent environmental, and residual term. The fixed effects in the model were year by season of calving (with 4 classes: January–March, April–June, July–September, and October–December), age of cow at calving (**ACC**; in days), and DIM. Age of cow at calving and DIM were modeled with third- and fourth-order Legendre orthogonal polynomials, respectively. Additive genetic and permanent environmental covariance functions were modeled using third-order Legendre orthogonal polynomials. This implies that the covariance structure depends on a set of orthogonal polynomials, as a function of the lactation stage (van der Werf et al., 1998).

The model used was as follows:

$$y_{ijklmno} = \mu + \text{YSC}_i + \sum_{j=0}^3 C_j \beta_j + \sum_{k=0}^4 D_k \Phi_k + \sum_{kl=0}^3 a_{kl} \Phi_{kl} + \sum_{kl=0}^3 p e_{kl} \Phi_{kl} + \text{EXP}_m + \text{YM}_n + e_{ijklmno},$$

where $y_{ijklmno}$ is the phenotype for DMI, FPCM yield, and LW; μ is the mean; YSC_i is the fixed effect of year-season of calving ($i = 1$ to 83); C_j is the fixed

regression coefficient for ACC; β_j is the term of the third-order Legendre polynomial for ACC; D_k is the fixed regression coefficient of DIM; Φ_k is the term of the fourth-order Legendre polynomial for DIM; a_{kl} is the k th regression coefficient of the Legendre polynomial for the additive genetic effect of the l th cow; pe_{kl} is the k th regression coefficient of the Legendre polynomial for the permanent environmental effect of the l th cow; Φ_{kl} is the term of the third-order Legendre polynomial for a and pe , where the time variable was DIM; EXP_m is the random effect of the m th experimental treatment ($n = 94$); YM_n is the random effect of the year-month of measurement ($n = 257$); and $e_{ijklmno}$ is the residual error. Residual errors were assumed to have heterogeneous variances and were divided into 4 classes according to the distribution of DIM records (1 = 1 to 48 DIM, 2 = 49 to 97 DIM, 3 = 98 to 160 DIM, and 4 = 161 to 324 DIM). Residual covariances between traits at the same DIM were estimated, but residual covariances within the same trait at different DIM were assumed to be zero as well as the residual covariances between traits at different DIM. Estimated (co)variance components of the random regression were used together with the Legendre polynomials to calculate heritabilities, genetic and permanent environmental covariances, and correlations for each DIM using the methodology of Fischer et al. (2004):

$$\mathbf{G} = \mathbf{\Phi K \Phi'};$$

$$\mathbf{PE} = \mathbf{\Phi K PE \Phi'},$$

where $\mathbf{G}$ is the genetic variance-covariance matrix across traits and DIM; $\mathbf{\Phi}$ is the matrix of order $t \times n$, which contains 4 orthogonal polynomial coefficients from DIM, FPCM yield, and LW through 324 DIM, where $t = 12$ (3×4) and $n = 972$ (3×324); and $\mathbf{K}$ is the matrix of order $n \times n$, which contains the estimated covariance function describing the genetic variance components for the random regression coefficients. Likewise, $\mathbf{PE}$ is the permanent environmental variance-covariance matrix and $\mathbf{KPE}$ is the matrix of order $n \times n$, which contains the covariance function for the permanent environmental variance components. At the same time, experimental treatment, year-month, and residual components of (co)variances were used to calculate the phenotypic variance-covariance matrix ($\mathbf{P}$). Standard errors of (co)variances, correlations, heritabilities, and permanent environmental ratio were approximated by an automated procedure in the R software programming language (<http://www.r-project.org/>) to produce the input files (pin) required by ASReml to calculate them.

Additionally, genetic and permanent environmental variances for the entire lactation were calculated by

summing Φ through 324 d, and multiplying this by $\mathbf{K}$ (Liu et al., 2000). Experimental treatment, year-month, and residual matrices were also formed, using the sum of those variances, to calculate total lactation phenotypic variances, heritability and permanent environmental ratio (c^2).

To have a better overview of what is happening with the genetic correlations when the distance in days increases independently of the time when they were recorded during lactation, average genetic correlations within a trait were calculated. This helped to show if DMI, FPCM yield, and LW were in fact different traits at different DIM. Therefore, average genetic correlations within DMI, FPCM yield, and LW were calculated taking all correlations when the difference in recording was 10, 20, . . . , 300 d and calculating the average of those correlations. It is important to mention that the number of correlations is larger when the difference in recording is shorter (i.e., the average genetic correlation when the difference was 10 d was calculated from 314 different genetic correlations, whereas the average genetic correlation when the difference was 200 d was calculated from 124 different genetic correlations).

RESULTS

The number of records for DMI, FPCM yield, and LW were constant for the first 100 DIM, with more weekly records available for FPCM yield than for DMI and LW (Figure 1). After 100 DIM, the number of records decreased until the end of lactation (324 d), mainly because the experimental treatments in data set 1 and 2 had a target of recording DMI for at least the first 100 DIM, and did not necessarily contain measurements throughout the entire lactation. Descriptive

Figure 1. Frequency distribution of the number of records for DMI, fat- and protein-corrected milk (FPCM) yield, and liveweight (LW) per DIM.

Table 2. Descriptive statistics [mean value with SD, minimum (min), and maximum (max) values] of DMI, fat- and protein-corrected milk (FPCM) yield, and liveweight (LW) for 4 data sets of first-parity Holstein-Friesian cows

Item	Data set				
	1	2	3	4	All ¹
DMI (kg/d)					
Mean	15.7	19.9	18.7	16.7	19.2
SD	3.2	3.2	2.7	3.4	3.3
Min	5.4	1.0	6.9	7.5	1.0
Max	24.6	33.4	35.8	27.8	35.8
FPCM yield (kg/d)					
Mean	24.8	28.2	26.2	29.1	27.7
SD	5.7	5.2	5.2	5.2	5.4
Min	3.4	2.0	8.4	2.0	2.0
Max	41.7	53.9	45.1	53.3	53.9
LW (kg)					
Mean	521.6	549.6	568.2	571.2	554.5
SD	41.9	53.8	59.1	52.9	55.9
Min	412.5	387.0	420.0	450.0	387.0
Max	655.2	793.0	963.0	751.5	963.0

¹All databases.

statistics of DMI, FPCM yield, and LW for the 4 data sets are shown in Table 2. The averages varied between data sets, from 15.7 to 19.9 kg of DMI per day, 24.8 to 29.1 kg of FPCM yield per day, and 521.6 to 571.2 kg of LW. Data set 1 had a lower DMI, FPCM yield, and LW than the other data sets, but a similar standard deviation. The lower average FPCM yield and DMI in data set 1 was because one of experimental treatments included cows with a low genetic merit for milk yield, with half of them having a low energy density diet (Beerda et al., 2007).

Entire-Lactation Parameters and Experimental Effects

The estimated heritabilities of the entire lactation were 0.46 for DMI and FPCM yield, and 0.38 for LW (Table 3). The estimated c^2 of the entire lactation were 0.23 for DMI, 0.41 for FPCM yield, and 0.60 for LW. The estimated entire-lactation genetic correlation between DMI and FPCM yield was 0.86, whereas the corresponding phenotypic correlation was 0.62. The

estimated entire-lactation genetic correlation between DMI and LW was 0.45, and 0.06 between FPCM yield and LW. The corresponding phenotypic correlations were 0.33 and -0.01 , respectively (Table 3).

Estimated variance components for the effects of experimental treatment and year-month showed that experimental treatment was more important than year-month (after adjusting for the other fixed effects in the model) for DMI and FPCM yield, but not for LW (Table 3). The ratios of experimental treatment variance over the entire-lactation phenotypic variance were 0.19 for DMI, 0.10 for FPCM yield, and 0.00 for LW; and the ratios of year-month variance over the entire-lactation phenotypic variance were 0.12 for DMI, 0.04 for FPCM yield, and 0.01 for LW. These ratios were smaller than the estimated heritability and c^2 , indicating that the contribution of those variances to the phenotypic variance was small. Experimental treatments that had a positive effect on DMI also had a positive effect on LW, as reflected by the high positive correlation (0.81) between DMI and LW for experimental treatment. However, the estimated correlation between DMI and

Table 3. Entire-lactation heritability (h^2), permanent environmental ratio (c^2), experimental treatment variance ratio ($\sigma_{\text{exp}}^2/\sigma_p^2$), year-month variance ratio ($\sigma_{\text{ym}}^2/\sigma_p^2$), genetic (below) and phenotypic correlations (above), and experimental treatment (below) and year-month (above) correlations between DMI, fat- and protein-corrected milk (FPCM) yield, and liveweight (LW)

Trait	Ratio				Genetic and phenotypic correlation			Experimental treatment and year-month correlation		
	h^2	c^2	$\sigma_{\text{exp}}^2/\sigma_p^2$	$\sigma_{\text{ym}}^2/\sigma_p^2$	DMI	FPCM yield	LW	DMI	FPCM yield	LW
DMI	0.46	0.23	0.19	0.12		0.62	0.33		0.23	0.00
FPCM yield	0.46	0.41	0.10	0.04	0.86		-0.01	0.20		0.14
LW	0.38	0.60	0.00	0.01	0.45	0.06		0.81	0.25	

LW for year-month was zero. The correlations between DMI and FPCM yield for experimental treatment and year-month were 0.20 and 0.23, respectively, and the corresponding correlations between FPCM yield and LW were 0.25 and 0.14, respectively (Table 3).

Estimated residual variances for DMI, FPCM yield, and LW were smallest between 49 and 97 DIM for all 3 traits, highest for DMI and LW after 161 DIM, and highest for FPCM yield between 1 and 48 DIM (results not shown). Moderate residual correlations were estimated between DMI and FPCM yield (ranging between 0.24 and 0.37), which was consistent between all periods. The estimated residual correlations between DMI and LW ranged from 0.08 to 0.20, and the residual correlations between FPCM yield and LW ranged from 0.01 to 0.11.

Estimated Heritabilities Within Lactation

Estimated daily heritabilities of DMI ranged from 0.21 to 0.40 across lactation (Figure 2), which is lower than the entire-lactation heritability. Heritability of DMI was lowest (0.21) in early lactation (31 DIM), with a subsequent increase to 0.40 at 138 DIM, followed by a decrease in late lactation (to 0.34 at 223 DIM). Overall, the estimated daily heritabilities were highest between 80 and 205 DIM.

Estimated daily heritabilities for FPCM yield showed a similar pattern as the heritability for DMI, showing the lowest value of 0.22 in early lactation at 26 DIM, followed by an increase, and reaching its maximum heritability of 0.43 at 165 DIM (Figure 2). Estimated daily heritabilities for LW presented a different trend (sigmoid curve) with the highest values at early lactation (0.48 at 49 DIM), followed by a decrease to 0.25 until 215 DIM (Figure 2).

Estimated daily c^2 were highest for LW and lowest for DMI (Figure 3). Daily c^2 for DMI decreased from 0.38 to 0.16 in the first 111 DIM, followed by an increase to 0.60 until the end of lactation, whereas daily c^2 for LW showed the lowest point at 35 DIM (0.43) and the highest point at 220 DIM (0.69). Together, the heritability and c^2 determine the repeatability of feed intake records during lactation.

Genetic Correlations Within Traits Across Lactation

Genetic correlations within DMI, FPCM yield, and LW across lactation are shown in Figure 4a–c. For DMI, genetic correlations between DMI on different DIM were positive for the majority of the lactation, and were highest during mid lactation [>0.80 (SE = 0.07)]. Genetic correlations were slightly negative (a minimum of -0.2) between DMI recorded in early lac-

Figure 2. Estimated daily heritabilities from 1 to 324 DIM for (1) DMI (SE of median = 0.05; SE of third quartile = 0.05), (2) fat- and protein-corrected milk (FPCM) yield (SE of median = 0.04; SE of third quartile = 0.04), and (3) liveweight (LW; SE of median = 0.07; SE of third quartile = 0.07).

tation (before 50 DIM) and DMI recorded in the rest of the lactation. Genetic correlations between FPCM yields at different DIM showed the same trend as DMI, showing positive correlations throughout the majority of the lactation (above 0.80), with an average standard error of 0.02. The only negative correlations were estimated between FPCM yield recorded in early lactation and FPCM yield recorded in very late lactation (i.e., before 50 DIM and after 300 DIM).

To get an overview of the strength of the correlations between the same trait measured at increasing days apart, the average of genetic correlations within DMI,

Figure 3. Estimated daily permanent environmental ratio from 1 to 324 DIM for (1) DMI (SE of median = 0.04; SE of third quartile = 0.05), (2) fat- and protein-corrected milk (FPCM) yield (SE of median = 0.04; SE of third quartile = 0.04), and (3) liveweight (LW; SE of median = 0.04; SE of third quartile = 0.04).

FPCM yield, and LW was calculated when the difference between 2 recordings was 10, 20, . . . , 310 DIM (Figure 5). The average genetic correlation decreased faster for DMI than for FPCM yield and LW. For DMI, the average genetic correlation between all records of DMI taken 10 d apart was 0.99, and this average correlation decreased to 0.67, 0.44, and 0.27 when the records were taken 100, 200, and 300 d apart, respectively. For FPCM yield, the average genetic correlation decreased from 0.99 to 0.86, 0.77, and 0.19, respectively. For LW, the average genetic correlation decreased from 0.99 to 0.90, 0.84, and 0.69, respectively.

Genetic Correlations Between Traits at the Same DIM

Genetic correlations between DMI and FPCM yield at the same DIM (Figure 6) were negative before 38 DIM (-0.55) and positive from 60 DIM until the end of lactation (>0.7), presenting the highest correlation at 195 DIM (0.91). Genetic correlations between DMI and LW were positive across lactation, ranging between 0.29 and 0.56, reaching a maximum value at 34 DIM and a minimum at 153 DIM. Genetic correlations between FPCM yield and LW were slightly negative (until -0.06) in early lactation and at the end of the lactation.

Genetic Correlations Between Traits Across Lactation

Pairwise genetic correlations between DMI, FPCM yield, and LW at different DIM are shown in Figure 7a–c. Genetic correlations between DMI and FPCM yield were positive (>0.8) when both traits were recorded during mid lactation (between 110 and 230 DIM for DMI, and between 140 and 260 DIM for FPCM yield). Negative genetic correlations (up to -0.5) were estimated between FPCM yield recorded during the first 50 DIM, and DMI recorded in the entire lactation.

Positive genetic correlations (>0.6) were estimated when DMI and LW were both recorded during early (<100 DIM), or when LW was recorded in late lactation (from 260 to 300 DIM), and DMI was recorded in mid lactation. The lowest genetic correlations (~ 0.2) were estimated when both traits were recorded during mid lactation. Negative correlations (up to -0.2) were estimated when LW was recorded in mid lactation and DMI in early or late lactation.

The highest genetic correlations between FPCM yield and LW (0.3 to 0.5) were estimated when LW was recorded between 50 and 230 DIM, and FPCM yield was recorded between 110 and 250 DIM.

To get an overview of the strength of the correlations between different traits measured at increasing days

apart, the average of genetic correlations between DMI, FPCM yield, and LW was calculated when the difference between 2 recordings was 50, 100, . . . , 250 DIM. It turned out that this calculated average of estimated genetic correlations between DMI and FPCM yield differed, depending on which trait was measured first (results not shown). The calculated average of the genetic correlations between DMI and FPCM yield was much higher when DMI was measured first (i.e., 0.76 and 0.60 when records were taken 50 or 250 d apart, respectively), than when FPCM yield was measured first (0.70 to 0.18, respectively). The calculated averaged of the estimated genetic correlations between DMI and LW did not vary much when the distance increased (from 0.28 to 0.38 for 50 to 250 d apart). When LW was measured before DMI, the calculated average was always 0.40, independent of the distance between 2 recordings.

DISCUSSION

Genetics of DMI and LW During Lactation

Heritability. Estimated heritabilities for DMI and LW have been reported widely, but most studies included either only records until 150 or 180 DIM (Veerkamp and Brotherstone, 1997; Koenen and Veerkamp, 1998; Hüttmann et al., 2009; Buttchereit et al., 2011; Spurlock et al., 2012), or used smaller data sets with 320 up to 970 cows (Karacaören et al., 2006; Berry et al., 2007; Vallimont et al., 2010). Estimated daily heritabilities of DMI in this study were between 0.21 to 0.40, and were within the range (0.12 to 0.54) published in previous studies (Veerkamp and Brotherstone, 1997; Koenen and Veerkamp, 1998; Veerkamp and Thompson, 1999; Karacaören et al., 2006; Berry et al., 2007; Vallimont et al., 2010; Spurlock et al., 2012; Tetens et al., 2014). Estimated entire-lactation heritabilities were slightly higher than estimated daily heritabilities, which is due to the fact that the genetic covariances are higher than permanent environmental and residual covariances.

Although the estimated daily heritabilities were within the range of previous studies, the trajectory of the heritability during lactation in our study was different compared with several other studies (Karacaören et al., 2006; Berry et al., 2007; Spurlock et al., 2012; Tetens et al., 2014). In the current study, highest daily heritabilities were estimated during mid lactation, which is similar to the findings of Spurlock et al. (2012) when they also analyzed only the data of primiparous cows. However, when they analyzed the data of both primiparous and multiparous cows, the highest daily heritabilities (above 0.25) were estimated during early lactation (between 15 and 30 DIM). Tetens et al. (2014), however, estimated highest daily heritabilities (~ 0.40) in early (10 DIM) and mid lactation (180 DIM), show-

Figure 4. Estimated genetic correlations within same trait recorded from 1 to 324 DIM for (a) DMI (SE of median = 0.07; SE of third quartile = 0.11), (b) fat- and protein-corrected milk (FPCM) yield (SE of median = 0.02; SE of third quartile = 0.06), and (c) liveweight (LW; SE of median = 0.04; SE of third quartile = 0.06). Color version available in the online PDF.

ing a curve which is opposite to the one reported in the current study. Karacaören et al. (2006) presented a sigmoid curve for the entire lactation (until 305 DIM), with the highest estimated daily heritabilities (~ 0.3) between 77 and 96 DIM and at the end of lactation (305 DIM), and with a standard error of 0.20 during the entire lactation. Overall, all studies showed that the heritability of DMI differed across lactation, but the curves for the daily heritability of DMI were different in shape across studies. One explanation for these different curves might be that different recording practices or different feeding systems affected the residual variance, but the most likely explanation is that the limited data hindered accurate estimates of daily heritabilities of DMI in the entire lactation.

Estimated daily heritabilities for LW in the current study (0.25 to 0.48) were within the range of estimated daily heritabilities published in previous studies (0.22 to 0.74; Koenen and Veerkamp, 1998; Karacaören et al., 2006; Hüttmann et al., 2009; Spurlock et al., 2012). The recording periods of those studies differed from the recording period of the current study. Therefore, at first sight, it might seem that some studies have published higher estimated daily heritabilities [e.g., from 0.43 to 0.56 (Koenen and Veerkamp, 1998) or from 0.57 to 0.74 (Spurlock et al., 2012)], but their included recording periods correspond with the period where the highest daily heritabilities were estimated in the current study. In the current study, the lactation curve of estimated daily heritabilities for LW presented a sigmoidal curve (i.e., highest at early lactation and lowest at approximately 200 DIM), which was different from the one presented by Karacaören et al. (2006), with a shape of a decreasing line from early lactation to late lactation.

Genetic Correlations Within DMI and LW Across Lactation. Genetic correlations within traits across lactation are important when judging how these traits differ through early, mid, and late lactation. Several studies have shown that DMI is a different trait in early and mid lactation (Koenen and Veerkamp, 1998; Karacaören et al., 2006; Hüttmann et al., 2009; Linamo et al., 2012). Generally, the genetic correlations between DMI recorded in early and in mid lactation were negative when records were taken far (~ 150 d) apart, and positive when records were taken less far (< 50 d) apart. All studies agreed that genetic correlations within DMI across lactation decreased faster than the genetic correlations within FPCM yield and LW across lactation (Figure 5). In some cases, the genetic correlation between DMI recorded at separate lactation stages even became negative (Koenen and Veerkamp, 1998; Karacaören et al., 2006), whereas in other cases, the correlation decreased slower and stayed positive

Figure 5. Calculated average of estimated genetic correlations within DMI, fat- and protein-corrected milk (FPCM) yield, and live-weight (LW) when the difference between 2 recordings is 10, 20, . . . , 310 DIM.

across the entire lactation (Hüttmann et al., 2009; Liinamo et al., 2012).

Genetic correlations between LW recorded at separate DIM are consistently positive in the entire lactation (Koenen and Veerkamp, 1998; Veerkamp and Thompson, 1999; Liinamo et al., 2012). Most of these studies reported genetic correlations above 0.76 through lactation, which is similar to the genetic correlations estimated in the current study (i.e., above 0.60 for most of the lactation). This performance was similar in milk yield, where genetic correlations within lactation did not decrease below 0.70 during most of the lactation in the current study, and not below 0.73 according to Hüttmann et al. (2009) and not below 0.62 according to Veerkamp and Thompson (1999).

Overall, compared with FPCM yield and LW, DMI showed more variation in estimated daily heritabilities and in genetic correlations within DMI across lactation, and also showed more negative correlations during early and late lactation. These results suggest that the genetics of DMI is more variable during lactation than, for example, that of milk yield and LW, which is important to take into account when measuring during DMI in a breeding program.

Correlations Between DMI, FPCM Yield, and LW During Lactation

To our knowledge, not many studies have presented genetic correlations between DMI, FPCM yield, and LW throughout the entire lactation. However, several studies have presented correlations between DMI and milk yield over a fixed period (Veerkamp and Brotherstone, 1997; Veerkamp and Thompson, 1999; Karacaören et al., 2006; Hüttmann et al., 2009; Vallimont et

Figure 6. Pairwise genetic correlations when 2 traits are measured on the same day from 1 to 324 d DIM between (1) DMI and fat- and protein-corrected milk yield (DMI-FPCM; SE of median = 0.06; SE of third quartile = 0.09), (2) DMI and liveweight (DMI-LW; SE of median = 0.11; SE of third quartile = 0.10), and (3) fat- and protein-corrected milk and liveweight (FPCM-LW; SE of median = 0.12; SE of 3rd quartile = 0.13).

al., 2010), and also between DMI and LW (Veerkamp and Brotherstone, 1997; Veerkamp and Thompson, 1999; Karacaören et al., 2006; Hüttmann et al., 2009; Vallimont et al., 2010; Liinamo et al., 2012; Spurlock et al. 2012).

When weekly FPCM yield information throughout the entire lactation (1–46 wk) was used in a selection index to predict DMI in the entire lactation, the accuracy of selection was 0.66. If this was done for LW, an accuracy of 0.36 was calculated. However, if FPCM yield and LW were used together to predict DMI, an accuracy of up to 0.73 was calculated. This high accuracy based on phenotypic data justifies the estimation of genetic parameters for these traits, with the aim to construct a national selection index.

In the current study, negative (up to -0.54) genetic correlations were estimated between DMI recorded in the entire lactation and FPCM yield recorded during first 50 DIM. However, for the majority of lactation, positive genetic correlations between DMI and FPCM yield were estimated in the current study (above 0.70 and up to 0.92). These values above 0.70 were higher than the correlations reported by Vallimont et al. (2010; 0.52), Veerkamp and Brotherstone (1997; 0.34), and van Elzakker and van Arendonk (1993; 0.46). Due to the high positive genetic correlations (above 0.7) between DMI and FPCM yield during most of the lactation estimated in the current study, selection for milk yield is also expected to increase DMI. The estimated genetic correlations of >0.7 indicate that $>49\%$ of the genetic variation in DMI can be explained by milk yield.

Figure 7. Pairwise genetic correlations when 2 traits are measured on different days between 1 to 324 DIM between (a) DMI and fat- and protein-corrected milk yield (DMI-FPCM; SE of median = 0.07; SE of third quartile = 0.10), (b) DMI and liveweight (DMI-LW; SE of median = 0.12; SE of third quartile = 0.13), and (c) fat- and protein-corrected milk and liveweight (FPCM-LW; SE of median = 0.12; SE of third quartile = 0.14). Color version available in the online PDF.

The low genetic correlations between FPCM yield recorded in early lactation (first 50 DIM) and DMI recorded during the entire lactation can be explained by a larger increase in milk production than in feed intake during early lactation, according to Tamminga et al. (1997). That means that after calving, both DMI and milk yield increase, but at different rates (Grummer, 2007). Milk yield will first increase sharply and then DMI will slowly increase. As a result, in the first 5 to 7 wk postcalving, a cow will get part of her energy from the mobilization of body tissue, rather than from her diet (Grummer, 2007). It has been shown that some of the genes involved in high-producing cows are also related to a larger capacity to mobilize muscle protein and fat reserves (Veerkamp et al., 2003; Friggens et al., 2013). As a consequence, selecting for high-producing cows is also a selection for higher capacity of tissue mobilization (Wathes et al., 2007).

In addition, the asymmetry in the genetic correlations between DMI and FPCM yield across lactation (Figure 7a) indicates that the genetic correlation is also affected by which of the 2 traits was measured first. For example, when DMI was measured first, the average genetic correlation was above 0.7 when recording was up to 220 d apart, but when FPCM yield was measured first, the corresponding genetic correlation was approximately 0.27.

Genetic correlations between DMI and LW have been previously reported (Veerkamp and Thompson, 1999; Karacaören et al., 2006; Hüttmann et al., 2009; Spurlock et al., 2012). In the current study, at same DIM, low to moderate genetic correlations were estimated between DMI and LW. Hüttmann et al. (2009) estimated a genetic correlation of 0.03 when both DMI and LW were recorded between 31 to 60 DIM, and a correlation of 0.42 when both traits were recorded between 121 to 180 DIM. Karacaören et al. (2006) estimated mainly negative genetic correlations between DMI and LW (−0.89 to 0.29) across lactation. However, the highest positive correlations estimated in the current study (above 0.6) between DMI and LW are in line with those reported by Veerkamp and Thompson (1999) and by Spurlock et al. (2012). The low correlations (−0.2 to 0.2) between LW recorded in mid lactation and DMI recorded in either early or late lactation indicate that the amount of feed that a cow eats during early lactation is not necessary according to her weight at mid lactation. The cow experiences a negative energy balance during the first 5 to 7 wk postcalving, with consequent fat and protein mobilization from the body reserves to be used for milk production (Tamminga et al., 1997). Therefore, even when a cow consumes a considerable amount of feed, she can still be losing weight due to the tissue mobilization. The body mobilization can vary consider-

ably from one individual to another (i.e., from 15 to 60 kg; Tamminga et al., 1997). A trait that reflects the body mobilization is BCS, which reflects the adiposity of the cow and can be used as an indicator of the energy status and fat mobilization (Roche et al., 2009). The genetic correlations between DMI and LW can, therefore, be a result of the relationship of DMI with body energy, where body energy supplies the energy for milk production (FPCM) instead of DMI. The heritability of BCS is, however, somewhat lower than the heritability of LW (0.26; Battagin et al., 2012).

Vallimont et al. (2010) showed that a decrease in LW during the first weeks of lactation (3–6 wk) is followed by a decrease in BCS in subsequent weeks (9–12 wk). Therefore, LW seems to show the changes more instantly than BCS.

The genetic correlations between DMI and LW are asymmetric, indicating that the genetic correlations between DMI and LW depend on which trait was measured first. Veerkamp and Thompson (1999) also reported some asymmetry for DMI and LW, and they concluded that the correlation between DMI and LW appeared to be less affected by lactation stage than the correlation between LW and DMI.

Genetic correlations between FPCM yield and LW presented in this study (–0.4 to 0.6) were similar to those reported by Karacaören et al. (2006) between milk yield and LW (–0.60 to 0.54). However, Hüttmann et al. (2009) presented negative correlations of –0.41 to –0.04 between milk yield and LW until 180 DIM. The slightly negative correlation estimated in the current study between LW in early lactation and FPCM yield during the entire lactation indicates that a heavier cow in early lactation does not necessarily produce more milk than a lighter cow. This can be explained by the body tissue mobilization of high-producing cows during some parts of lactation, affecting their LW in this way (Veerkamp and Brotherstone, 1997). Moderate genetic correlations between LW and FPCM yield are estimated during mid lactation, indicating that the milk production of a cow during mid lactation is proportional to her weight in mid lactation. The wide range of the genetic correlations between DMI, FPCM yield, and LW across the entire lactation showed how the genetics of these traits differ per lactation stage, and this study provides important information about the genetic relationships within and between traits that should be taken into account when constructing a national selection index.

CONCLUSIONS

The heritabilities, genetic variances, and genetic correlations of DMI, FPCM yield, and LW changed across the different stages of lactation, mainly differing during

early and late lactation compared with mid lactation. These parameters suggest that the genetics of DMI varies across lactation. The average genetic correlation decreased faster for DMI than for FPCM yield and LW when 2 recordings of the same trait were taken more days apart. For the majority of the lactation, DMI and FPCM yield do not genetically correlate differently when recorded on the same day; only in early lactation were different genetic correlations estimated. Dry matter intake and LW, however, do genetically correlate differently during lactation; the highest genetic correlations were estimated when both traits were recorded in either early or late lactation, and lowest when both traits were recorded in mid lactation. When DMI and LW were not recorded on the same day, the lowest genetic correlations were estimated when LW was recorded in mid lactation and DMI was recorded in either early or late lactation. However, the genetic correlations between DMI and FPCM yield or LW were not symmetric in time, indicating that the genetic correlation depends both on the temporal distance between 2 recordings, and on which trait was measured first. The results of our study are useful to understand the genetic relationship between DMI, FPCM yield, and LW on specific days across lactation, and should be taken into account when constructing a national selection index.

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