Direct and maternal genetic relationships between calving ease, gestation length, milk production, fertility, type, and lifespan of Holstein-Friesian primiparous cows

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ABSTRACT

As the emphasis in cattle breeding is shifting from traits that increase income toward traits that reduce costs, national breeding indices are expanding to include functional traits such as calving ease (CE). However, one issue is the lack of knowledge of genetic relationships between CE and other dairy traits. The same can be said about gestation length (GL), a potential novel selection trait with considerable heritabilities and possible genetic relationships with the calving process. This study aimed to estimate the genetic relationships between CE, GL, and other dairy traits of interest using a national data set of 31,053 primiparous cow performance records, as well as to separate direct and maternal genetic effects. Chosen dairy traits included fertility (calving interval, days to first service, non-return rate after 56 d, number of inseminations per conception), milk production (milk yield at d 110 in milk, accumulated 305-d milk yield, accumulated 305-d fat yield, accumulated 305-d protein yield), type (udder depth, chest width, rump width, rump angle, mammary composition, stature, body depth), and lifespan traits (functional days of productive life). To allow the separation of direct and maternal genetic effects, a random sire of the calf effect was included in the multi-trait linear trivariate sire models fitted using ASReml. Significant results showed that easily born individuals were genetically prone to high milk yield and reduced fertility in first lactation. Difficult calving primiparous cows were likely associated with being high-producing, wide and deep animals, with a reduced ability to subsequently conceive. Individuals that were born relatively early were associated with good genetic merit for milk production. Finally, individuals carrying their offspring longer were genetically associated with being wide and large animals that were themselves born relatively

early. The study shows that it is feasible and valuable to separate direct and maternal effects when estimating genetic correlations between calving and other dairy traits. Furthermore, gestation length is best used as an indicator trait for lowly heritable calving traits, rather than as a novel selection trait. As estimated direct and maternal genetic correlations differ, we can conclude that genetic relationships between CE, GL, and traits of interest are present, but caution is required if these traits are implemented in national breeding indices.

Key words: calving ease, gestation length, genetic correlation, milk production

INTRODUCTION

Worldwide, awareness is growing that, to maintain or improve economic efficiency, an emphasis on the genetic merit for functional traits is needed when selection decisions are made (Amer, 2012; Boichard and Brochard, 2012). Furthermore, the negative genetic relationships that are observed between production and functional traits have made it essential for functional traits to be included in national breeding indices to stop undesirable genetic trends on correlated traits.

Calvings are crucial events on a dairy cattle farm with complications leading to potential loss or impaired performance of the cow and calf and compromised animal welfare (Dematawewa and Berger, 1995; Lombard et al., 2007; Eaglen et al., 2011; Barrier et al., 2012). Under some assumptions, additional labor and veterinary costs cost the UK dairy cattle industry approximately £110 for a calving of moderate difficulty and £400 for one that is severe (McGuirk et al., 2007). With current incidences in the United Kingdom of 24 and 4% for moderately and severely difficult first calvings, respectively, calving ease (CE) is an economically important functional trait (Eaglen et al., 2011). Hence, if genetic selection could aid in reducing the number of difficult calvings, it would be of great benefit to the dairy cattle industry.

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Although the observed genetic variance for CE is low, genetic progress can be made. Consequently, CE is increasingly being introduced as a selection trait; the first CE proofs in the United Kingdom were officially released in 2010 (Wall et al., 2010). A genetic evaluation of CE automatically raises the question of the relationship of CE with existing selection traits. The phenotypic relationships of CE and selection traits such as milk production and fertility are frequently reported and signify the importance of this trait (e.g., Eaglen et al., 2011). However, genetic evaluations require knowledge of the underlying genetic relationships to avoid making genetic progress in CE while jeopardizing gains in other traits, and vice versa. Such published information is noticeably lacking. The estimation of genetic correlations in case of a maternal trait such as CE is complicated by a genetic maternal component. Statistical models must allow the estimation of multiple genetic (co)variances per trait rather than a single additive genetic variance (Willham, 1963). Estimation of only a direct or a maternal correlation is likely to result in bias (Willham, 1980; Meyer, 1992). A variety of approaches has been taken to avoid this problem (Ali et al., 1984; Dadati et al., 1985; Muir et al., 2004). However, to our knowledge, only 2 studies have attempted to estimate genetic correlations by actually separating direct and maternal effects and allowing for the appropriate covariance structure. First, Cue et al. (1990) presented genetic direct and maternal correlations of CE with type traits in a model in which sires were assumed to be unrelated, which is likely to have affected the capability of the model to separate all variance components. Second, López de Maturana (2007) separated direct and maternal effects with pedigree included to estimate the genetic relationships between CE, milk yield, and fertility.

Besides CE, stillbirth and gestation length (GL) have been evaluated for associations with the calving event. In the United Kingdom, stillbirth has little detectable genetic variation, whereas GL has been shown to be moderately heritable in both its direct and maternal components, which allows for potential genetic selection (Norman et al., 2011; Eaglen et al., 2012). Gestation length might affect the dairy cattle industry by affecting calving interval (CI) and milk yield (Hageman et al., 1991; Norman et al., 2011) but reports of genetic correlations between GL and traits of economic importance to dairy production are scarce. Moreover, to our knowledge, the separate direct and maternal genetic relationships of GL with other traits of interest have not yet been studied.

In summary, reliable information is lacking on what may be expected when CE or GL is emphasized in selection indices, beyond the improvement of the trait itself.

This study has the objective, therefore, of estimating the genetic correlations between CE, GL, and established dairy traits, such as fertility, milk production, and type and lifespan traits, using models that allow the full separation of direct and maternal effects.

MATERIALS AND METHODS

Direct and Maternal Effects

This study follows Willham (1963), which models the phenotype (P_i) for a maternally affected trait as

$$P_i = A_{D,i} + E_{D,i} + A_{M,j} + E_{M,j} \quad [1]$$

where the maternal effect is property of dam j , which is expressed in the phenotype of offspring i . Thus, in the life of individual i , the direct additive effect ($A_{D,i}$) is expressed at the start of life, whereas, when i is female, the maternal additive effect ($A_{M,i}$) is expressed whenever i calves. The environmental effects on P_i are represented in Equation [1] by the direct environmental effect ($E_{D,i}$), which is property of offspring i , and the maternal environmental effect ($E_{M,j}$), which is property of dam j .

Therefore, when referring to the direct breeding effect of CE (*CEd*) or GL (*GLd*), one is addressing the ease of birth or the length of gestation before *being born*, respectively. When the maternal effect of CE or GL is mentioned (*CEm* or *GLm*), this refers to CE or GL before *calving*, respectively.

Data Description

This study was restricted to first-parity CE records that were collected from 1995 to 2009 by 2 milk recording organizations in the United Kingdom. Data editing is described in detail by Eaglen et al. (2012) but major edits included a restriction on single-birth calvings and age of dam (18 to 48 mo) and a correction on the standard deviation of CE score within the herd-year contemporary group.

Gestation length was calculated from the last recorded insemination and calving date and was restricted to between 265 and 295 d. Calving ease was scored on a categorical scale that differed between the 2 data sources (a 4-point scale vs. a 5-point scale). The scales were therefore harmonized as explained in Eaglen et al. (2011). Subsequently, to account for their categorical nature, the scores were transformed to values on the underlying normal distribution (liability scale), as described in Eaglen et al. (2012). The frequency distribution of CE scores in the data set can be found in Table 1.

Table 1. Frequencies and definitions of calving ease (CE) categories

CE score	Frequency (%)	Definition
1	73.13	Easy, nonassisted
2	23.05	Moderate, assisted by farmer
3	3.17	Difficult, assisted by farmer
4	0.65	Very difficult, assisted by veterinarian

The edited calving trait data set, consisting of 33,051 records, was subsequently matched to the data containing phenotypes of all chosen dairy traits (fertility, production, type, and lifespan traits), which were recorded in the lactation following the recorded calving and extracted from national databases. Although not all animals matched between data sets, we found no relationship between a “match” and calving ease score. In other words, no indication was found of the culling or nonrecording of animals having experienced a severely difficult calving. Mean CE scores before and after merging of data sets did not differ.

Chosen dairy traits included fertility (calving interval, **CI**; days to first service, **DFS**; nonreturn rate after 56 d, **NR56**; number of inseminations per conception, **NINS**), milk production (milk yield at 110 DIM, **MY-110**; accumulated 305-d milk yield, **MY-305**; accumulated 305-d fat yield, **FY-305**; accumulated 305-d protein yield, **PY-305**), type (udder depth, **UD**; chest width, **CW**; rump width, **RW**; rump angle, **RA**; mammary composition, **MAMC**; stature, **STAT**; body depth, **BD**), and lifespan traits (functional days of productive life, **DPL**). With DPL, we refer to the number of days from first calving to culling, which is accounted for by the level of production and thus for voluntary culling due to low production. The trait therefore represents the ability to delay involuntary culling due to functional traits such as poor fertility (Forabosco et al., 2009).

Hence, a merged data set was created based on a range of cow identification variables (e.g., identification, herd, breed, and calving date). Validity checks were performed on the matched data set to ensure that all data were linked to the correct calving event and pedigree information was accurate. Incorrect records were removed and CI was restricted to be between 300 and 600 d, in line with data edits for fertility traits in the United Kingdom (Wall et al., 2005). The type traits included in this study were objectively scored by a classifier at inspection. The time between the inspection and the calving dates was restricted to be between 0 and 8 mo. Six of the 7 type traits were objectively scored on a categorical scale of 9, where 1 and 9 are applied to the extremes of the trait, as explained by Brotherstone et al. (1990). Scores at the extreme end of the scale represent the following type: CW: 1 = narrow,

9 = wide; RW: 1 = narrow, 9 = wide; RA: 1 = high pin bones, 9 = low pin bones; BD: 1 = shallow, 9 = deep; STAT: 1 = small, 9 = tall; UD: 1 = below hock, 9 = above hock. Mammary composition is a composite type trait that covers the strength and quality of the fore and rear attachment, strength of central ligament, teat quality, and udder texture; MAMC was scored on a scale that ranged from <64 (poor) to 100 (excellent). All scores were then adjusted for classifier by scaling by the classifier mean and standard deviation to achieve equal means with variances for all classifiers, as described by Brotherstone (1994).

The final edited data set contained 31,053 primiparous cow performance records, originating from 1,757 herds and representing 1,951 (service) sires and 2,719 maternal grandsires. For all records, 5 generations of pedigree records were available. In this data set, 100% of the records contained phenotypes for the calving and milk production traits and 80% for fertility traits. Type and lifespan data were present in 19 and 46% of the records, respectively. For the latter, only animals with an actual date of death received an actual DPL record. Thus, future DPL was not predicted for living animals. Hence, we conducted no preselection of data to ensure all animals were recorded for all traits. Descriptive statistics of all traits are given in Table 2.

Statistical Analyses

Reports on genetic correlations between CE, GL, and other traits are scarce. However, reports on genetic correlations between milk production and a variety of traits are extensive. Therefore, to facilitate better interpretation of results and make the discussion of results more viable, MY-305 was fitted as a correlated trait in every analysis. Total days of lactation ranged from 200 to 963 d, with a mean of 320 d. Trivariate linear mixed models were fitted using REML, by ASReml (Gilmour et al., 2009), after optional fixed effects and potential interaction effects were tested on their significance in SAS version 9.1 (SAS Institute, 2006). Eaglen et al. (2012) demonstrated that the sire-maternal grandsire model is the most appropriate model for the estimation of genetic parameters for calving traits. Therefore, it was chosen to fit a sire-maternal grandsire model.

Table 2. Descriptive statistics of all traits

Trait	Statistic			Phenotypic variance (σ_p^2)
	Minimum	Maximum	Mean	
Calving ease (CE)	1	4	1.3 (0.6)	0.4 (0.01)
Gestation length (GL; d)	265	295	281 (5.0)	25 (0.6)
Fertility				
Calving interval (CI; d)	300	600	404 (59)	3,286 (35)
Days to first service (DFS; d)	20	200	88 (32)	840 (9)
No. of inseminations to conception (NINS)	1	10	1.9 (1.3)	1.58 (0.02)
Nonreturn at d 56 after first insemination (NR56)	0	1	0.7 (0.5)	0.21 (0.00)
Production				
Actual milk yield at d 110 in milk (MY-110; kg)	5	55	27 (6)	25 (0.3)
Accumulated actual 305-d milk yield (MY-305; kg) ¹	2,754	12,349	7,523 (1,578)	1,440 (174)
Accumulated actual 305-d fat yield (FY-305; kg)	71	599	293 (64)	2,150 (24)
Accumulated actual 305-d protein yield (PY-305; kg)	65	418	242 (49)	1,275 (15)
Type				
Udder depth (UD)	0.4	10.4	5.9 (1.3)	1.4 (0.02)
Mammary composition (MAMC)	67.8	92.0	80.0 (5.0)	21.5 (0.40)
Rump width (RW)	0.4	9.8	5.5 (1.4)	1.6 (0.03)
Rump angle (RA)	0.4	10.5	4.3 (1.3)	1.5 (0.03)
Chest width (CW)	−0.8	9.9	5.2 (1.5)	1.8 (0.03)
Stature (STAT)	0.2	10.9	6.1 (1.4)	1.3 (0.02)
Body depth (BD)	0.4	10.0	5.8 (1.3)	1.4 (0.02)
Lifespan				
Days of productive life (DPL; d)	201	4,261	1,146 (662)	35 (0.5)

¹Variance is reported to the power of 10^{−3}.

Phenotypes were recorded on the cow; hence the sire of the cow was fitted to account for the additive direct effect of all but CE and GL. Every calving is affected by both the cow and the calf. Therefore, for CE and GL in the extended sire model, the sire of the calf accounted for the additive direct effect, whereas the sire of the cow accounted for the maternal genetic effect. The general linear statistical model fitted was

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \mathbf{y}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{1_sire.calf} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} \mathbf{a}_{1_sire.calf} \\ 0 \\ 0 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{1_sire.cow} & 0 & 0 \\ 0 & \mathbf{Z}_{2_sire.cow} & 0 \\ 0 & 0 & \mathbf{Z}_{3_sire.cow} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{1_sire.cow} \\ \mathbf{a}_{2_sire.cow} \\ \mathbf{a}_{3_sire.cow} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix}, \tag{2}$$

where $\mathbf{y}_i$ is a vector representing the observations for trait 1, trait 2, and trait 3 (trait 1 is consistently either CE or GL, trait 2 is a trait of interest, and trait 3 is consistently MY-305); $\mathbf{X}$, $\mathbf{Z}_{i_sire.calf}$, and $\mathbf{Z}_{i_sire.cow}$ are known incidence matrices for nongenetic and sire effects, respectively; $\mathbf{b}$ is a vector of nongenetic effects, $\mathbf{a}_{1_sire.calf}$ is a vector of the random additive direct effects of the sire of the calf, $\mathbf{a}_{i_sire.cow}$ is a vector of the random additive effects of the sire of the cow, which are direct effects for nonmaternal traits and maternal

effects for CE and GL, $\mathbf{a}_{1_sire.calf}$ and $\mathbf{a}_{i_sire.cow}$ were assumed to follow a multivariate normal (MVN) distribution, with $MVN(0, \mathbf{G} = \mathbf{G}_0 \otimes \mathbf{A})$, where $\mathbf{G}_0$ is a 4×4 direct-maternal variance-covariance matrix,

$$\text{Var} \begin{bmatrix} \mathbf{a}_{1_sire.calf} \\ \mathbf{a}_{1_sire.cow} \\ \mathbf{a}_{2_sire.cow} \\ \mathbf{a}_{3_sire.cow} \end{bmatrix} = \begin{bmatrix} \sigma_{a1_sire.calf}^2 & \sigma_{a1_sire.calf,sire.cow} & \sigma_{a1,2_sire.cow} & \sigma_{a1_sire.calf,3_sire.cow} \\ \sigma_{a1_sire.calf,sire.cow} & \sigma_{a1_sire.cow}^2 & \sigma_{a1,2_sire.cow} & \sigma_{a1,3_sire.cow} \\ \sigma_{a1,2_sire.cow} & \sigma_{a1,2_sire.cow} & \sigma_{a2_sire.cow}^2 & \sigma_{a2,3_sire.cow} \\ \sigma_{a1_sire.calf,3_sire.cow} & \sigma_{a1,3_sire.cow} & \sigma_{a2,3_sire.cow} & \sigma_{a3_sire.cow}^2 \end{bmatrix} \otimes \mathbf{A}, \tag{3}$$

$\otimes$ is the Kronecker product of matrices, $\mathbf{A}$ is the relationship matrix; and $\mathbf{e}$ is a vector of the residuals, assumed to be $MVN(0, \mathbf{R}\sigma_e^2)$, where $\mathbf{R}$ denotes the residual 3×3 variance covariance matrix and σ_e^2 is the residual variance. So, for every bull, 4 breeding values are estimated: a direct breeding value for CE or GL ($a_{1_sire.calf}$), a maternal breeding value for CE or GL ($a_{1_sire.cow}$), a direct breeding value for trait i ($a_{2_sire.cow}$) and a direct breeding value for MY-305 ($a_{3_sire.cow}$). Generally, for calving, fertility, and production traits, the nongenetic effects fitted in the model included sex of the calf, herd, the main effects of year and month of calving and their

interaction effect (year of calving $\times$ month of calving), a linear covariate of age of the dam (months), and a random effect of herd-year. Additional fixed effects fitted for the type traits included the main effects and interaction effect of year and month of inspection, the stage of lactation at inspection, the age at inspection (months) as a covariate, and a quadratic effect of age at inspection. For lifespan traits, an additional quadratic effect of age at calving (months) was included in the model.

As equations [2] and [3] indicate, the co(variances) estimated by an extended sire model are sire variances. These are then algebraically converted into direct and maternal variance components. The mathematical equations for this conversion are given in the Appendix. Significance of the estimated co(variances) was generally tested by a confidence interval of $1.96 \times$ standard error (P -value = 0.05). However, critical values (e.g., estimates with P -values close to 0.05) were tested for significance by a likelihood ratio test with the critical value of 2.79 (Stram and Lee, 1994). The trivariate analyses between calving traits, MY-305, and NR56 had difficulty in converging; MY-305 was therefore replaced by MY-110 in this specific analysis to allow convergence.

Studies on GL have reported potential nonlinear relationships of GL with other traits (Hansen et al., 2004; Norman et al., 2011). In case of a nonlinear relationship, correlation estimates obtained by a linear multi-trait model may be obscured. In this study, relationships between traits were tested on nonlinearity by plotting PTA obtained from univariate models against each other. In addition, genetic correlations with GL were double checked by reanalysis of all trivariate models fitting GL on a folded scale; that is, $295 = 265$, $294 = 267$, $293 = 266$, and so on, as in Wall et al. (2005).

RESULTS

Genetic Correlations with Calving Ease

In what follows, note that CE was scored on a scale that increases with difficulty. Hence, a higher CE score represents a more difficult calving.

Fertility Traits. Estimated genetic correlations between CE and fertility traits, presented in Table 3, showed that *CEm* was favorably associated with NINS (0.83 ± 0.20) and CI (0.67 ± 0.22) but not significantly associated with DFS. This implies that, genetically, a difficult first calving cannot be associated with a delay in time to breeding but rather with the inability to conceive. The *CEd* was found to be correlated with NR56 (0.67 ± 0.27), suggesting that a more difficult birth is genetically associated with a lower probability

of returning to estrus within 56 d after first insemination, in first lactation (Figure 1).

Production Traits. A moderate positive genetic correlation was detected between *CEm* and milk production in first lactation (0.34 ± 0.15 ; Table 3), suggesting that individuals with high genetic merit for milk production are genetically prone to a more difficult first calving. In addition, *CEm* was shown to be significantly correlated with FY-305 (0.39 ± 0.13). The positive relationship with FY-305 implies that individuals genetically prone to more difficult first calvings are also genetically prone to a higher fat content in the milk produced in the subsequent lactation. Ease of birth (*CEd*) was also genetically correlated with milk production. A significant negative genetic correlation was estimated between *CEd* and MY-110 (-0.45 ± 0.13) and between *CEd* and MY-305 (-0.44 ± 0.12), suggesting that, genetically, individuals with genetic merit for a relatively low milk yield in first lactation are genetically predisposed to be born with more difficulty. Similarly, *CEd* was genetically negatively associated with FY-305 (-0.60 ± 0.13) and PY-305 (-0.46 ± 0.13). Hence, more difficult births are genetically associated with lower fat and protein contents in the milk produced in first lactation as adult primiparous cows (Figure 1).

Type Traits. Table 3 demonstrates that *CEm* is genetically related to 2 out of 7 type traits. A significant genetic correlation was found with CW (0.55 ± 0.20) and BD (0.47 ± 0.18). The positive sign indicates that more difficult calvings are genetically associated with wider chests and deeper bodies. No significant genetic correlations were detected between *CEd* and type; thus, we cannot conclude from the results of this study that difficult births out of primiparous dams are related to the type traits recorded in first lactation.

Lifespan Trait. No significant genetic correlations were for CE with DPL; thus, we cannot conclude that either ease of birth or ease of calving is genetically related to the length of productive life (Table 3).

Genetic Correlations with Gestation Length

For all traits, potential nonlinearity with GL was tested by repetition of each model with a “folded” phenotypic value of GL, as defined by Wall et al. (2005); that is, $295 = 265$, $294 = 267$, $293 = 266$, and so on. A significant difference in the estimated correlations between the analyses using the normal scale and the analyses using the folded scale would indicate a nonlinear relationship between GL and the other dairy traits. However, no proof of nonlinearity was found in the relationships between GL and all other traits. Use of the linear multi-trait model was thereby validated.

Figure 1. Diagrammatic presentation of the genetic relationships between a difficult calving or a long gestation with milk production, fertility, and type in first-lactation cows. *CEd* and *CEm* = direct and maternal effects of calving ease; *GLd* and *GLm* = direct and maternal effects of gestation length.

Table 3. Genetic parameters following the trivariate analyses of calving ease (CE), 305-d milk yield (MY-305), and traits in primiparous cows

Trait ¹	h^2	Additive genetic variance (σ_A^2)	Genetic correlation with CE (direct, <i>CEd</i> , or maternal, <i>CEm</i>)		Genetic correlation with MY-305 ²
			r_{CEd}	r_{CEm}	r_d
Calving					
CE – direct	0.10 (0.02)*	0.02 (0.01)	1.00 (0.00)	–0.38 (0.18)*	–0.42 (0.16)*
CE – maternal	0.04 (0.02)*	0.01 (0.00)	–0.38 (0.18)*	1.00 (0.00)	0.27 (0.18)
Fertility					
CI	0.03 (0.01)*	111 (39)	–0.51 (0.24)	0.67 (0.22)*	0.60 (0.14)*
DFS	0.06 (0.02)*	50 (13)	–0.34 (0.21)	0.20 (0.24)	0.37 (0.10)*
NINS	0.02 (0.01)*	0.04 (0.01)	–0.24 (0.26)	0.83 (0.20)*	0.30 (0.15)*
NR56 ²	0.01 (0.01)	0.003 (0.01)	0.67 (0.27)*	–0.54 (0.31)	–0.13 (0.21) ²
Production					
MY-110	0.33 (0.03)*	7.9 (0.8)	–0.45 (0.13)*	0.27 (0.16)	0.99 (0.00)*
MY-305 ³	0.49 (0.04)*	0.7 (0.1)	–0.44 (0.12)*	0.34 (0.15)*	1.00 (0.00)*
FY-305	0.35 (0.03)*	764 (78)	–0.60 (0.11)*	0.39 (0.13)*	0.74 (0.03)*
PY-305	0.43 (0.04)*	550 (51)	–0.46 (0.13)*	0.38 (0.19)	0.92 (0.01)*
Type					
UD	0.24 (0.05)*	0.33 (0.07)	–0.13 (0.18)	–0.20 (0.20)	–0.47 (0.09)*
MAMC	0.26 (0.05)*	5.8 (1.13)	–0.21 (0.17)	0.15 (0.19)	0.40 (0.09)*
RW	0.33 (0.05)*	0.54 (0.10)	–0.07 (0.17)	0.29 (0.18)	0.17 (0.10)
RA	0.39 (0.06)*	0.60 (0.10)	0.01 (0.20)	0.22 (0.17)	0.09 (0.09)
CW	0.20 (0.04)*	0.37 (0.09)	–0.10 (0.18)	0.55 (0.20)*	–0.02 (0.11)
STAT	0.41 (0.06)*	0.56 (0.09)	0.03 (0.15)	–0.02 (0.17)	0.24 (0.09)*
BD	0.32 (0.05)*	0.44 (0.07)	–0.06 (0.16)	0.47 (0.18)*	0.22 (0.09)*
Lifespan					
DPL ³	0.11 (0.02)*	3.74 (0.84)	–0.34 (0.20)	0.38 (0.21)	–0.46 (0.10)*

¹Traits are as defined in Table 2.

²The analysis of NR56 was conducted with the correlated trait of MY-110, not 305, to allow convergence.

³Variances are reported to the power of 10^{-4} .

* $P < 0.05$.

Fertility Traits. The majority of correlations between GL and fertility traits (Table 4) were not significant; thus, on the basis of our results, we cannot conclude that the length of gestation (either before being born or before giving birth) genetically relates to subsequent fertility in first lactation. The significant genetic correlation between *GLm* and NINS (-0.47 ± 0.23), however, suggested that relatively long gestation periods before giving birth were genetically correlated to fewer services to conception.

Production Traits. Table 4 shows that *GLm* (length of gestation before giving birth) was not genetically related to milk production in first lactation, whereas *GLd* (length of gestation before being born) was. Significant negative correlations between *GLd* and MY-110 (-0.22 ± 0.10) and between *GLd* and MY-305 (-0.19 ± 0.09) suggested that calves that are in utero relatively long before they are born would have lower milk yields in their first lactation as adult primiparous cows. This is consistent with the equivalent correlation of *CEd* with milk production. Gestation length before being born was also found to correlate genetically with PY-305 (-0.22 ± 0.10) but not with FY-305.

Type Traits. Gestation length before giving birth showed a genetic correlation with type. Table 4 pres-

ents the significant correlations of *GLm* with RW (0.52 ± 0.15) and STAT (0.48 ± 0.15), which suggest that longer gestation periods before giving birth are genetically related to wider rumps and increased stature. We found no significant genetic correlations between *GLd* and type. Hence, from the results of this study, we cannot conclude that time of gestation before being born was genetically related to the type traits scored in first lactation.

Lifespan Trait. No significant genetic correlations were detected between GL and DPL; thus, we cannot conclude that the gestation length before birth or calving is genetically related to the length of productive life.

DISCUSSION

This study described has (1) provided new understanding on the genetic relationship of calving events with milk production, fertility, type, and lifespan traits; (2) allowed us to better characterize individuals and their potential problems, as presented in Figure 1; and (3) provided validation of previously established genetic relationships among milk production, fertility, and type traits. In what follows, we chose not to elaborate on

Table 4. Genetic parameters following the trivariate analyses of gestation length (GL), 305-d milk yield (MY-305), and traits in primiparous cows

Trait ¹	h^2	Additive direct genetic variance (σ_{Ad}^2)	Genetic correlation with GL (direct, <i>GLd</i> , or maternal, <i>GLm</i>)		Genetic correlation with MY-305 ²
			r_{GLd}	r_{GLm}	
Calving					
GL – direct	0.49 (0.05)*	12.1 (1.5)	–0.30 (0.13)*	1.00 (0.00)	–0.19 (0.09)*
GL – maternal	0.09 (0.03)*	2.1 (0.6)	1.00 (0.00)	–0.30 (0.13)*	0.04 (0.14)
Fertility					
CI	0.02 (0.01)*	76 (31)	0.19 (0.20)	–0.29 (0.26)	0.69 (0.14)*
DFS	0.07 (0.02)*	58 (14)	–0.06 (0.15)	–0.16 (0.21)	0.42 (0.10)*
NINS	0.02 (0.01)*	0.03 (0.01)	0.33 (0.20)	–0.47 (0.23)*	0.29 (0.17)
NR56 ²	0.01 (0.01)	0.001 (0.00)	0.18 (0.37)	0.30 (0.54)	–0.22 (0.34) ²
Production					
MY-110	0.32 (0.03)*	6.8 (0.7)	–0.22 (0.10)*	0.03 (0.15)	0.99 (0.00)*
MY-305 ³	0.50 (0.04)*	0.7 (0.1)	–0.19 (0.09)*	0.04 (0.14)	1.00 (0.00)*
FY-305	0.36 (0.03)*	788 (74)	–0.13 (0.10)	–0.10 (0.15)	0.72 (0.03)*
PY-305	0.46 (0.04)*	595 (50)	–0.22 (0.10)*	–0.01 (0.15)	0.92 (0.01)*
Type					
UD	0.18 (0.04)*	0.25 (0.05)	–0.07 (0.14)	0.31 (0.18)	–0.45 (0.09)*
MAMC	0.23 (0.04)*	4.92 (0.95)	–0.14 (0.13)	0.19 (0.18)	0.41 (0.09)*
RW	0.28 (0.05)*	0.45 (0.08)	0.09 (0.13)	0.52 (0.15)*	0.21 (0.09)*
RA	0.40 (0.06)*	0.60 (0.09)	0.09 (0.12)	–0.18 (0.16)	0.10 (0.09)
CW	0.20 (0.04)*	0.35 (0.07)	–0.09 (0.14)	0.35 (0.18)	–0.03 (0.11)
STAT	0.41 (0.05)*	0.53 (0.08)	–0.11 (0.12)	0.48 (0.14)*	0.20 (0.08)*
BD	0.32 (0.05)*	0.44 (0.07)	–0.10 (0.12)	0.28 (0.16)	0.25 (0.09)*
Lifespan					
DPL ⁴	0.11 (0.02)*	3.70 (0.86)	0.09 (0.15)	–0.23 (0.20)	–0.45 (0.11)*

¹Traits are as defined in Table 2.

²The analysis of NR56 was conducted with the correlated trait of MY-110, not MY-305, to allow convergence.

³Variances are reported to the power of 10^{-4} .

* $P < 0.05$.

the genetic correlations across the calving traits per se, as this was discussed extensively by Eaglen et al. (2012) and the estimates agree well between studies. Note that the pooled genetic correlation between *GLd* and *GLm* in this study was estimated to be negative and significant.

Heritabilities

The majority of heritabilities presented in Tables 3 and 4 were in line with previously reported estimates in the literature. Estimated heritabilities for fertility traits were low, ranging from 0.01 for NR56 (nonsignificant) to ± 0.06 for DFS, which is in line with Wall et al. (2005). Milk production traits showed estimated heritability of 0.33 for MY-110, ± 0.49 for MY-305, 0.35 for FY-305, and 0.43 for PY-305, and thereby conform to Berry et al. (2004). The heritabilities of type traits demonstrated that type traits were moderately heritable. Estimated heritabilities ranged from ± 0.18 for UD to 0.41 for STAT and all were in line with Brotherstone et al. (1990) and Cue et al. (1990). The heritability of DPL was estimated at 0.11 ± 0.02 , which is on the higher end of the range reported for lifespan in the literature: 0.025 to 0.166 (Forabosco et al., 2009). Yet, trait definitions tended to differ. Heritabilities of calving traits were low to moderate (López de Maturana et al., 2007b; Eaglen et al., 2012), with the maternal heritability being considerably lower than the direct heritability for both CE and GL.

Genetic Correlations with Calving Ease

A difficult calving, as a maternal trait, is associated with a high milk yield, wide and deep conformation score, and relatively poor fertility (Figure 1). The type and fertility descriptions match the literature descriptions of a high-producing cow (Berry et al., 2004), which gives confidence in the conducted analysis. The relatively high standard error on the estimated correlation between *CEm* and 305-MY may support the recent evidence of the relatively weak phenotypic association between a cow's ease of calving and her subsequent milk production reported previously (Berry et al., 2007; Eaglen et al., 2011). Considering the phenotypic association found by Eaglen et al. (2011) between *CEm* and milk yield in the first 90 d of lactation, one might have expected a genetic correlation between *CEm* and MY-110. This genetic correlation was not, however, detected, suggesting that the association detected by Eaglen et al. (2011) was primarily environmental. The moderate positive genetic correlation found between *CEm* and 305-MY contradicted the low negative estimate reported by López de Maturana et al. (2007c).

The data used by López de Maturana et al. (2007c), however, contained data on 8 lactations, whereas this study focuses on first-lactation CE only.

In the literature, narrow rumps and a low rump angle (e.g., high pin bones) are generally considered unfavorable for calving ease (Philipsson et al., 1976; Wall et al., 2005). In the current study, we did not detect significant genetic correlations between RW, RA, and CE. Our results therefore suggest that the reported phenotypic associations were primarily environmental, thereby contradicting findings by Dadati et al. (1985) and Thompson et al. (1980). Results of the current study are, however, supported by Naazie et al. (1991), who reported a very weak genetic relationship between pelvic dimensions and calving difficulty. The lack of consensus on these specific genetic correlations was also shown by Ali et al. (1984), who contradicted consensus by reporting a positive genetic correlation between hip width and CE (wider hips, more calving difficulty). The differences in statistical models used in these different studies may have contributed to the various outcomes of estimation. For example, direct and maternal effects might not have been "decomposed" properly or sires were assumed to be unrelated (Ali et al., 1984; Dadati et al., 1985; Cue et al., 1990).

This study showed that individuals born with difficulty are associated with poor genetic merit for milk production (Figure 1, CE as a direct trait). It thereby provides a genetic underpinning to the evidence of a phenotypic relationship between the ease of birth of a female calf and her subsequent milk production as an adult cow, as established by Eaglen et al. (2011) and by Heinrichs and Heinrichs (2011). In contrast to our results, however, López de Maturana et al. (2007c) report a weak negative genetic correlation between *CEd* and milk production (-0.13), although their standard error is of such magnitude (0.18) that a positive correlation cannot be ruled out. A conjecture arising from the results on relationships with fertility is that the unfavorable negative correlations established between *CEd* and fertility were mediated through the positive correlation of *CEd* with milk production. Hence, good direct calving ease is genetically associated with high milk yield, which in turn is negatively correlated with fertility.

The positive genetic correlation between *CEd* and NR56 found here demonstrates how misinterpretation can occur if there is no proper decomposition of the direct and maternal genetic effects. For example, Muir et al. (2004) estimate the genetic correlation between CE (direct and maternal combined) and NR56 to be positive. This is then interpreted as reflecting the correlation of NR56 with CE as a maternal trait, which in the current study is shown to be negative (Table 3).

The positive correlation found by Muir et al. (2004) can be explained by their model, because the total genetic correlation (r_g) of CE with NR56 is seen to be

$$r_g = \frac{(\sigma_{A_{CEd, NR56}} + \sigma_{A_{CEm, NR56}})}{\sqrt{\sigma_{TBV_{CE}}^2} \times \sqrt{\sigma_{A_{NR56}}^2}}, \quad [4]$$

where $\sigma_{TBV_{CE}}^2 = \sigma_{Ad}^2 + 2\sigma_{Adm}^2 + \sigma_{Am}^2$, TBV = total breeding value and A is the additive genetic effect (Eaglen et al., 2012). This results in a positive estimate (0.37 ± 0.25). Hence, the genetic correlation reported by Muir et al. (2004) consists in part of the correlation between *CEd* and NR56, (which in this study is negative), because the fitted model in Muir et al. (2004) does not allow for the separation of direct and maternal effects.

Genetic Correlations with Gestation Length

Although the genetic variances of GL were considerable, our results suggest that the trait is perhaps best used in multi-trait models to improve predictive ability (Eaglen et al., 2012) rather than in direct selection for the trait itself. The genetic relationships established for *GLd* and *GLm* seem to be limited to milk production and type, whereas phenotypic associations are found more often (e.g., CI, days open, milk yield, DPL; Norman et al., 2009, 2011).

The direct genetic correlations with GL indicate that early-born individuals are likely to have good merit for milk production, whereas the maternal correlations suggest that long-carrying animals are large with wide rumps. The lack of a significant genetic correlation between *GLm* and milk production contrasts with previous phenotypic evidence of long gestation periods being related to high milk yield (Norman et al., 2011). A greater consensus exists over the negative relationship of *GLd* with milk production. Norman et al. (2009) reports a decrease in length of productive life as PTA for *GLd* increase, although their methodology varied greatly from that used in this study.

The better knowledge of phenotypic and genetic relationships from this study widens the discussion on how selection on GL could benefit the dairy cattle industry. The economic importance of GL lies mainly in its association with CI and its potential relationship with milk production (Norman et al., 2011). The relationship with CI, however, is shown to be principally environmental, whereas the genetic relationship with milk production traits is shown to be complex. Furthermore, the phenotypic relationships reported by Norman et al. (2011) for a range of functional traits (e.g., calving ease, stillbirth, fertility) showed optimum performance

at intermediate GL (e.g., a very short or long gestation is unfavorable). Therefore, selecting on direct GL to achieve benefits in milk production appears irrational, because any gains in either lengthening or shortening GL would likely be counteracted by detrimental effects in other important functional traits. As GL has shown to improve the predictive ability of models estimating genetic parameters for lowly heritable calving traits such as CE (Eaglen et al., 2012), the trait perhaps has more value as an indicator trait rather than as a novel selection trait itself.

General Discussion

This study serves to fill a fundamental gap in knowledge about the genetic interrelationships with CE and GL. It allows the effect of future breeding objectives to be reliably predicted and demonstrates the value of estimating both direct and maternal relationships for these predictions. The estimation of maternal genetic parameters is complex, however, and the results of any statistical model incorporating a maternal effect require careful consideration (Willham, 1980). In this study, Tables 3 and 4 show the general tendency of the direct and maternal relationships to be opposite in sign; similar trends were shown by Cue et al. (1990). This was a consistent trend across a variety of dairy traits in the current study; thus, it cannot be ruled out that this phenomenon is an artifact of the fitted model. However, the fact that most of the genetic parameters yielded by this model were in line with estimates in literature (Brotherstone et al., 1990; Cue et al., 1990; Berry et al., 2004; Wall et al., 2005; López de Maturana et al., 2007a), which were obtained by a variety of statistical models, speaks strongly for its robust validity.

It has also been demonstrated in the current study that not all previously observed associations of selection traits with CE and GL have a direct genetic basis. For example, no significant genetic correlation was detected between DPL and CE and GL, despite the many reports of complications during first calving considerably increasing the culling risk of individuals (Beaudeau et al., 2000; López de Maturana et al., 2007b). Furthermore, despite a report of a phenotypic association between GL and milk production (Norman et al., 2011), we found no evidence of a genetic correlation between *GLm* and subsequent milk production. It is possible, however, that the genetic correlation of GL as a direct trait with milk production contributed to the association found by Norman et al. (2011). An important aspect of this study is therefore the partitioning of genetic relationships into the direct and maternal genetic covariance components to allow for a more detailed evaluation of what is, or is not, underlying the

phenotypic observations. This is not only crucial for the inclusion of calving traits in national breeding goals but is also essential for our understanding of how calving performance will be affected by future selection.

CONCLUSIONS

Both CE and GL in first-parity UK Holstein-Friesian dairy cattle were genetically related to other important traits in dairy cattle breeding, an important consideration if CE and GL are to be implemented into national breeding goals. As yet, however, results suggest that GL may be of better value to the dairy cattle industry as an indicator trait rather than as a novel selection trait of economic value. The separation of direct and maternal genetic effects in the estimation of genetic correlations between calving traits and other traits leads to a more precise evaluation of genetic interrelationships underlying observed phenotypic associations. This is essential for understanding the role of genetic selection in the current state of calving performance in first-parity UK dairy cattle and appropriately applying genetic selection to calving traits in the future. Easily born individuals are genetically prone to high milk yield and reduced fertility in first lactation. Difficult-calving primiparous cows are likely associated with being high-producing, wide and deep animals with a reduced ability to subsequently conceive. Individuals that are born relatively early are associated with good genetic merit for milk production. Finally, individuals carrying their young longer are genetically associated with being wide and large animals that were born relatively early themselves.

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APPENDIX

Sire (Co)variances to Direct and Maternal (Co)variances

Within Traits. Conversion from estimated sire (co)-variances to direct and maternal (co)variances for non-maternal traits:

Direct:

$$sire.cow = \frac{1}{2} Ad,$$

$$Ad = 2 \times sire.cow,$$

$$\sigma_{Ad}^2 = 4 \times \sigma_{sire.cow}^2.$$

Conversion from estimated sire (co)variances to direct and maternal (co)variances for calving (maternal) traits:

From sire variance to direct variance, where Ad is the additive direct genetic effect:

$$sire.calf = \frac{1}{2} Ad,$$

$$Ad = 2 \times sire.calf,$$

$$\sigma_{Ad}^2 = 4 \times \sigma_{sire.calf}^2.$$

From sire of cow (maternal grandsire) variance to maternal variance, where Am is the additive maternal genetic effect:

$$sire.cow = \frac{1}{2} Am + \frac{1}{4} Ad,$$

$$Am = 2 \times sire.cow - sire.calf,$$

$$\sigma_{Am}^2 = 4 \times \sigma_{sire.cow}^2 + \sigma_{sire.calf}^2 - 4 \times \sigma_{sire.calf, sire.cow}.$$

From the covariance between sire of calf (sire) and sire of cow (maternal grandsire, mgs) to the genetic direct-maternal covariance:

$$\text{cov}(Ad, Am) = \text{cov}(2sire, 2mgs - sire),$$

$$\sigma_{Adm} = 4 \times \sigma_{sire.calf, sire.cow} - 2 \times \sigma_{sire.calf}^2.$$

Between Traits. For example, trait 1 = calving ease, trait 2: calving interval.

From the covariance between the sire variance of trait 1 and the sire variance of trait 2 to the covariance between the direct effects of both traits, following a bivariate analysis between maternal and nonmaternal trait:

$$\begin{aligned} \text{cov}(Ad_1, Ad_2) &= \text{cov}(2 \times 1_sire.calf, 2 \times 2_sire.cow) \\ &= 4 \times \sigma_{a1_sire.calf, 2_sire.cow}. \end{aligned}$$

From the covariance between the sire of cow variance of trait 1 and the sire variance of trait 2 to the covariance between the maternal effect of trait 1 and the direct effect of trait 2, following a bivariate analysis between a maternal and nonmaternal trait:

$$\begin{aligned} \text{cov}(Am_1, Ad_2) &= \text{cov}(2 \times 1_sire.cow - 1_sire.calf, 2 \times 2_sire.cow) \\ &= 4 \times \sigma_{a1.2_sire.cow} - 2 \times \sigma_{a1_sire.calf, 2_sire.cow}. \end{aligned}$$