Genetic Parameters of Calving Traits at First and Second Calving in Danish Holsteins

M. Hansen,[123] M. S. Lund,[1] J. Pedersen,[2] and L. G. Christensen[3]
[1] Danish Institute of Agricultural Sciences, Dept. of Animal Breeding and Genetics, Research Centre Foulum, P.O. Box 50, DK-8830 Tjele, Denmark
[2] Danish Cattle Federation, Udkærsvej 15, Skejby, 8200 Aarhus N, Denmark
[3] The Royal Veterinary and Agricultural University, Dept. of Animal Science and Animal Health, Grønnegårdsvej 2, DK-1870, Frederiksberg C, Denmark

ABSTRACT
The aim of this study was to estimate heritabilities and genetic correlations for stillbirth, calving difficulty, and calf size at second calving and to estimate genetic correlations between these calving traits at first and second calving. Data originated from Holstein cows calving from 1988 to 2002. Bivariate threshold models using Gibbs sampling were fitted for estimation of heritabilities and genetic correlations between the traits at second calving. For estimation of the genetic correlation between calving traits at first and second calving bivariate linear models using REML were fitted. The direct and maternal heritabilities at second calving were 0.05 and 0.005 for stillbirth, 0.08 and 0.04 for calving difficulty, and 0.16 and 0.05 for calf size. The genetic correlations between these traits at second calving were high (0.65 to 0.99) between the direct effects and moderate to high (0.44 to 0.92) between the maternal effects. The genetic correlation of each calving trait at first and at second calving ranged from 0.89 to 0.99 for the direct effects and from 0.74 to 0.88 for the maternal effects.

INTRODUCTION

Stillbirth and calving difficulty are relevant traits to include in the breeding scheme of dairy cattle (Groen et al., 1998). Breeding strategies for reducing stillbirth and calving difficulty have focused on first calving when these traits are most prevalent (Dekkers, 1994; Meijering, 1986). In Holsteins the incidence of stillbirth and calving difficulty has been shown to be around twice as high at first calving than at second calving (Meyer et al., 2001; Nielsen et al., 2002; Steinbock et al., 2003). In genetic evaluations of calving difficulty it is often assumed that calving difficulty is genetically the same trait at first and later calvings and that the genetic variance is the same (e.g. Ducrocq, 2000; Wiggans et al., 2003). However, The genetic correlations between the calving traits at first and at later calvings seem to be less than one (Harbers et al., 2000;Luo et al., 2002; Steinbock et al. 2003) and the genetic variances of calving difficulty at second calving have been shown to be significant lower than the genetic variances at first calving (Luo et al., 2002; Steinbock et al., 2003). For stillbirth an even larger difference between first and second calving has been found (Meyer et al., 2001; Steinbock et al., 2003).

The goal of this study was to estimate heritabilities and genetic correlations for stillbirth, calving difficulty, and calf size at second calving and to estimate genetic correlations between the traits at first and second calving. We hypothesized that: i) Heritabilities of stillbirth and calving difficulty are lower at second calving than at first calving. ii) Genetic correlations between stillbirth, calving difficulty, and calf size at second calving are moderate to high for both the direct and the maternal trait. iii) The genetic correlations between these calving traits at first and second calving are moderate to high for both direct and maternal effects.

MATERIALS AND METHODS

Data was collected on dairy farms in the south-western part of Denmark from 1985 to 2002. The farmers assessed stillbirth, calving difficulty, and calf size in named categories, which were transformed to numbers. Stillbirth was coded as: 0 = alive 24 hours after birth and 1 = dead at birth or within 24 hours after birth and. Calving difficulty was coded as: 1 = easy, 2 = easy with assistance, 3 = difficult but without veterinary assistance, and 4 = difficult with veterinary assistance. calf size was coded as: 1 = small, 2 = just below medium, 3 = just above medium, and 4 = large. Only records of Holstein calves with a known AI-bull as sire and as maternal grandsire were used. Records from around 184,000 first calvings and 108,000 second calvings were included. Stillbirth was observed for all records, but 14% to 21% had missing information of either calving difficulty or calf size (Table 1).

Table 1. Number of observations and proportion of observations in categories for stillbirth, calving difficulty, and calf size at first and second calving.

			Proportion of observations in category			
Trait	Calving	No.	1	2	3	4
Stillbirth	First	184,141	.101	.899	-	-
	Second	108,071	.050	.950	-	-
Calving difficulty	First	146,310	.457	.431	.082	.030
	Second	89,936	.693	.269	.027	.011
Calf size	First	152,741	.098	.438	.377	.088
	Second	93,310	.054	.317	.483	.146

Statistical Methods

The statistical analyses consisted of two parts: 1) Estimation of genetic parameters at second calving and 2) estimation of genetic correlations between traits at first and second calving. In the first part Bayesian analyses with Gibbs sampling were carried out with bivariate threshold models. In the second part AI-REML analyses were carried out.

Genetic parameters at second calving.

In the threshold model an unknown liability was assumed. The liabilities were modeled as:

$$\begin{bmatrix}\mathbf{U}_1\\ \mathbf{U}_2\end{bmatrix}=\begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}\mathbf{H}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{H}_2\end{bmatrix}\begin{bmatrix}\mathbf{cg}_1\\ \mathbf{cg}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{11} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{12}\end{bmatrix}\begin{bmatrix}\mathbf{s}_1\\ \mathbf{s}_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_{21} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_{22}\end{bmatrix}\begin{bmatrix}\mathbf{mgs}_1\\ \mathbf{mgs}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix},$$

where $\mathbf{U}_j$ was a vector containing the liabilities, $\mathbf{b}_j$, $\mathbf{cg}_j$, $\mathbf{s}_j$ and $\mathbf{mgs}_j$ were vectors containing non-genetic effects, contemporary group effects, sire effects, and maternal grandsire effects, and $\mathbf{X}_j$, $\mathbf{H}_j$, $\mathbf{Z}_{1j}$, and $\mathbf{Z}_{2j}$, were incidence matrices relating the effects to the observations for trait j. In both $\mathbf{b}_1$ and $\mathbf{b}_2$ were included cross-classified effects of: Sex of calf (male, female), month of calving (1,2,…,12), calving interval in months from first to second calving in three classes (+11;12-14;15+), and year of calving (1988,…,2002). The prior distributions of the effects were all normal. for the (co)variance components improper flat priors were adopted.

For stillbirth the threshold was fixed to zero and the residual variance was fixed to one. For calf size, the first and last threshold was set to zero and one and the threshold in between (*t)* was a priori assumed to be uniform distributed in the interval [0;1]. Calving difficulty category three and four were combined in this analysis, as the frequency in category four was very low (0.01). This meant that no threshold needed to be sampled for this trait. Then the first threshold was fixed to zero and the second threshold was fixed to one.

Marginal posterior distributions were obtained with Gibbs sampling using software described by Korsgaard et al. (2003). All location parameters were sampled jointly for achieving a fast movement in the parameter space. The length of the burn-in period was assessed by visual inspections of trace plots of dispersion parameters. To infer about the effective number of posterior samples all the posterior samples were divided into twenty consecutive batches. The effective sample size was then calculated as the within batch variance divided by the between batch variance (e.g. Sorensen and Gianola, 2002). The goal was to achieve at least 100 effective samples for all (co)variances and derived variables. To fulfill this 30,000 to 60,000 Gibbs sampling rounds were computed for each model.

Genetic correlations between first and second calving. To obtain genetic correlations between the traits at first and second calving bivariate linear models were fitted directly to the data using AI-REML (Jensen et al., 1997). Each analysis consisted of one trait at first calving and another trait at second calving. In total nine bivariate analyses were carried out to get all genetic correlations for stillbirth, calving difficulty, and calf size at first calving with stillbirth, calving difficulty, and calf size at second calving. The model included the same effects as the Bayesian model. The exception was in the sub-model for the trait at first calving, where an effect of calving age in months was included instead of the effect of calving interval. In these analyses **b** was treated as fixed effects and **cg**, **s**, and **mgs** were treated as random effects.

RESULTS

Basic Statistics

Stillbirth and calving difficulty were experienced twice or more as often at first calving than at second calving but calves were largest at second calving (Table 1). At first and second calving the stillbirth rate was 0.10 and 0.05, the frequency of calving difficulties (category three and four) was 0.11 and 0.04, and the frequency of calves scored large was 0.09 and 0.15.

Heritabilities

Both direct and maternal heritabilities of stillbirth and calving difficulty at second calving were low (Table 2). The marginal posterior means were 0.05, 0.08 and 0.16 for the direct heritabilities of stillbirth, calving difficulty, and calf size and 0.005, 0.04, and 0.05 for the maternal heritabilities of stillbirth, calving difficulty, and calf size.

From the linear model the estimated heritabilities of stillbirth and calving difficulty were around two and five times higher at first calving than at second calving, but for calf size the heritabilities were only slightly higher at first calving (Table 3).

Genetic Correlations Between Traits at Second Calving

The direct effects of stillbirth, calving difficulty, and calf size were highly correlated at first calving. The marginal posterior means of these correlations ranged from 0.65 between stillbirth and calf size to 0.99 between calving difficulty and calf size (Table 2). The marginal posterior means of maternal correlations ranged from 0.44 between stillbirth and calf size to 0.92 between stillbirth and calving difficulty. The marginal posterior means of correlations between direct and maternal effects were in general weak, ranging from –0.16 to 0.37.

Table 2. Marginal posterior means of heritabilities, and genetic correlations for calving traits at second calving from bivariate threshold models. Standard deviations of the marginal posterior distributions are given in subscripts.

			Genetic correlations				
			Direct		Maternal		
		h^2	Calving difficulty	Calf size	Stillbirth	Calving difficulty	Calf size
Direct	Stillbirth	$.050_{.010}$	$.77_{.08}$	$.65_{.09}$	$.25_{.15}$	$-.16_{.16}$	$-.12_{.15}$
	Calving difficulty	$.082_{.008}$		$.99_{.003}$	$.37_{.11}$	$-.01_{.12}$	$-.04_{.08}$
	Calf size	$.164_{.011}$			$.07_{.08}$	$-.15_{.08}$	$-.12_{.08}$
Maternal	Stillbirth	$.005_{0.01}$				$.92_{.02}$	$.44_{.10}$
	Calving difficulty	$.040_{.008}$					$.55_{.10}$
	Calf size	$.046_{.007}$					

A) Flat improper priors of dispersion parameters were used.

Table 3. Estimates of direct and maternal heritabilities (h_D^2 and h_M^2), contemporary group ratio (cg^2), and phenotypic variance (σ_P^2) from the linear model. Standard errors are given in subscripts.

Trait	Calving	h_D^2	h_M^2	cg^2	σ_P^2
Stillbirth	First	$.052_{.006}$	$.059_{.006}$	$.008_{.001}$	$.091_{.0003}$
	Second	$.011_{.002}$	$.004_{.002}$	$.006_{.001}$	$.047_{.0002}$
Calving difficulty	First	$.109_{.009}$	$.061_{.007}$	$.096_{.002}$	$.543_{.003}$
	Second	$.049_{.004}$	$.027_{005}$	$.105_{.003}$	$.345_{.002}$
Calf size	First	$.185_{.012}$	$.037_{.005}$	$.125_{.003}$	$.587_{.003}$
	Second	$.141_{009}$	$.035_{.005}$	$.112_{.003}$	$.571_{.003}$

Genetic Correlations Between Traits at First and Second Calving

The genetic correlations between the same calving trait expressed at first and second calving were all high (Table 4). The correlations between the same direct trait at first and at second calving ranged from 0.89 to 0.99. The correlations between the same maternal trait at first and at second calving ranged from 0.74 to 0.88. The correlations between all the direct traits at first and second calving were in general high. The lowest correlation was 0.62, which was found between stillbirth at first calving and calf size at second calving. Lower correlations were found between the maternal traits. The correlation between the maternal effects of calving difficulty at second calving and stillbirth at first calving was 0.34, but the correlation between stillbirth at second calving and calving difficulty at first calving was 0.77. The maternal effect of calf size at second calving had only weak associations with the maternal effects of stillbirth and calving difficulty at first calving. The genetic correlations between direct and maternal effects at different parities were very weak ranging from -0.23 to 0.20.

DISCUSSION

In agreement with the expectation, the heritabilities of stillbirth and calving difficulty at second calving was considerable lower than the heritabilities at first calving estimated by Hansen (200). These results are supported by the findings of Steinbock et al. (2003). The heritabilities of calf size at second calving were only slightly lower than the heritabilities of calf size estimated at first calving (Hansen, 2004).

Table 4. Estimated genetic correlations between calving traits at first and second calving from bivariate linear models. Standards errors are given in subscripts.

			Second calving					
			Direct			Maternal		
			Stillbirth	Calving difficulty	Calf size	Stillbirth	Calving difficulty	Calf size
First calving	Direct	Stillbirth	$.89_{.08}$	$.70_{.07}$	$.62_{.06}$	$.08_{.18}$	$.00_{.12}$	$-.02_{.11}$
		Calv. difficulty	$.81_{.09}$	$.99_{.02}$	$.91_{.03}$	$.20_{.19}$	$.02_{.09}$	$-.07_{.09}$
		Calf size	$.72_{.09}$	$.94_{.03}$	$.99_{.01}$	$.11_{.17}$	$-.15_{.09}$	$-.05_{.08}$
	Maternal	Stillbirth	$.07_{.11}$	$-.02_{.08}$	$.05_{.06}$	$.81_{.15}$	$.34_{.10}$	$-.11_{.10}$
		Calv. difficulty	$.01_{.12}$	$.00_{.08}$	$.04_{.07}$	$.77_{.21}$	$.74_{.07}$	$.24_{.10}$
		Calf size	$-.23_{.13}$	$-.04_{.08}$	$-.05_{.07}$	$.29_{.20}$	$.53_{.10}$	$.88_{.05}$

The genetic correlations between the calving traits at second calving were in agreement with genetic correlations between the traits at first calving (Hansen, 2004). Fore example, larger calves also gave more stillbirths and calving difficulties at second calving. This indicates that a disproportion between the calf size and the pelvic size also exists at second calving. However, this is less problematic as the genetic variance of stillbirth and calving difficulty is much smaller at second calving than at first calving.

The genetic correlations between the calving traits at first and at second calving was expected to be moderate to high, but they were found to be high, especially for the direct effects. This means that the traits at first and second calving may be considered as the same trait, where the size of the genetic effects is largest at first calving. This suggests that a model including all parities accounting for the heterogeneity of variance between parities might be acceptable. Kizelkaya et al. (2002) developed a framework for threshold models with heterogeneous variances using Markov Chain Monte Carlo methodologies. They applied a model with a different residual variance for each sub class resulting in different heritabilities in each subclass. However, a multi-trait model where traits at first calving traits at later calving traits are treated as separate traits seems to be preferred. Thereby, the genetic correlations between first and later calving traits, which were less than one, can be accounted for and the difference in variances between first and later calving traits is taken into account. Such a multi-trait approach is currently applied in the Danish genetic evaluation of calving traits but with the use of linear models (Danish Cattle Federation, 2003).

Calf size seemed to be a very promising indicator trait for improving the prediction of direct effects of stillbirth and calving difficulty at first calving. Direct effects of calf size both at first and second calving was highly correlated with the direct effect of stillbirth and calving difficulty. The direct heritability of calf size was much higher than the direct heritability of stillbirth and calving difficulty, especially at second calving. This is very important as most calving records for testing AI-bulls as sires are obtained at second or later calvings. Calf size is therefore an important trait to record for improving the identification of low risk sires. As the preferential mating of heifers with low risk sires is very important from an economical and animal welfare point of view (Dekkers, 1994) the costs of recording calf size (or birth weight) and implementing it in a genetic evaluation seems to be justified.

CONCLUSION

Stillbirth and calving difficulties express much less direct and maternal genetic variation at second calving than at first calving, but for calf size the genetic variances were similar at first and second calving. The genetic correlations between stillbirth, calving difficulty, and calf size at second calving were high for the direct effects and moderate to high for the maternal effects. The genetic correlations between the traits at first calving with the same trait at second calving were very high (0.89 to 0.99) for the direct effects and high for the maternal effects (0.74 to 0.88). This indicates that these calving traits might be modeled with a repeatability model, but the heterogeneity of genetic variances between parities should be taken into account. However, regarding stillbirth and calving difficulties at first and later calving as separate traits in a multi-trait threshold model seems to be preferred.

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