

A Multi-Parity Animal Model for Genetic Evaluation of Calving Traits Enhanced with Genomic Information

Z. Liu, E. Pasman, F. Reinhardt and R. Reents
vit, Heideweg 1, 27283 Verden, Germany

Abstract

A multi-parity animal model with correlated direct and maternal effects was developed for genetic evaluation of calving ease and stillbirth, replacing the previous single-trait model used in Germany. First three parities were treated as genetically distinct traits in this new calving model, direct and maternal genetic effects of both calving ease and stillbirth were estimated jointly. Genetic parameters of the new calving model were estimated using a large data set. Low heritability values were obtained for the calving traits, genetic correlations between parities ranged from 0.47 to 0.91 indicating genetic heterogeneity between parities. A genetic evaluation software system was developed for German Holstein, Red Dairy Cattle and Jersey breeds based on this multi-parity calving model. Genetic trends of the new model were validated using Interbull trend validation method III. Reasonably high genetic correlations were obtained between Germany and major dairy countries in a MACE test evaluation. SNP effects were estimated for German Holstein using EuroGenomics genotypes and the most recent MACE evaluation. In order to determine the optimal residual polygenic variance for each trait, five scenarios of residual polygenic variance, 0%, 1%, 5%, 10% and 20%, were investigated. With the optimal residual polygenic variances, the genomic evaluation model was validated. In April 2012, the multi-parity calving model was officially introduced in Germany for conventional genetic and genomic evaluations of the calving traits.

Key words: calving ease, stillbirth, genetic evaluation, genomic information, dairy cattle

Introduction

Calving difficulty can cause high cost and decrease profitability of milk production for farmers. Calving ease (CE) and stillbirth (SB) are the two commonly evaluated traits in national as well as international genetic evaluations (Ducrocq *et al.*, 2000; Philipsson and Steinbock 2003; Jakobsen *et al.*, 2003; Jamrozik *et al.*, 2005; Wiggans *et al.*, 2008; van Pelt and de Jung, 2011; Eaglen *et al.*, 2011). For genetic evaluation of CE or SB in Germany until 2011, all parities were treated as genetically the same trait using a single trait repeatability linear animal model with correlated direct and maternal effects (Averdunk *et al.*, 1995). Because calving difficulties or stillbirth in first calving heifers and later parity cows were genetically different

traits (Philipsson and Steinbock, 2003), the objectives of this study were to develop a multi-parity model for conventional genetic evaluation of the calving traits, and to estimate genomic breeding values for the new calving traits.

Materials and Methods

A multi-parity model for calving evaluation

For a joint genetic evaluation of calving ease and stillbirth, a linear animal model was developed:

$$y_{ijklmmt} = HY_{ilt} + RYS_{jlt} + YMA_{klt} + d_{mlt} + m_{nlt} + e \quad [1]$$

where $y_{ijklmmt}$ is Snell score of calving ease ($t=1$) or stillbirth ($t=2$), HY_{ilt} is the i -th fixed effect of herd-year of trait t in parity l , RYS_{jlt} is the j -th fixed effect of region-year-season of calving x calf sex of trait t in parity l , YMA_{klt} is the k -th fixed effect of year-month-age of calving x calf sex of trait t in parity l , d_{mlt} represents direct genetic effect of calf m of trait t in parity l , m_{nlt} represents maternal genetic effect of cow n of trait t in parity l , and e is the residual effect. The three fixed effects were fitted on herd level (HY_{ilt}), regional (RYS_{jlt}) and population (YMA_{klt}) levels. Direct and maternal genetic effects were considered to be correlated. There were a total of 12 EBV per animal: 2 traits x 3 parities x 2 effects. Prior to the estimation of the model effects, the original CE or SB scores were transformed to Snell scores within each level of the regional fixed effect RYS_{jlt} and parity.

Data material for calving evaluation

Recording procedure of calving ease was harmonized across regions in Germany in 2000, followed by a fine tuning in 2005. Therefore, only calving data recorded since 2000 were considered in the new calving evaluation. Calving ease was scored on a scale of 1 for unassisted/easy pull, 2 for normal pull, 3 for hard pull with or without veterinary aid, and 4 for caesarean. Stillbirth was defined as live (0) or dead (1) within 48 hours after birth. Calving ease were subjectively scored and stillbirth reported by farmers in Germany, these data were routinely collected via milk recording programme, partially as voluntary specification registered in the obligatory animal identification and registration system in national data base. Calving records from embryo transfer or multiple births were excluded from genetic evaluation. Age at

calving must be 20-24, 30-56, and 44-75 months for first three parities, respectively. Gestation length (GL) must be between 265 and 295 days. Unknown calves, always with sex and dam identified in Germany, were treated as a real animal in genetic evaluation as if they were included in the national pedigree data base. For April 2012 calving evaluation, 21,127,336 calving records from first three parities were evaluated. The number of cows and calves amounted to 26,926,132. There were 33,040,123 animals in pedigree connected to the calving data. Figure 1 shows phenotypic trends of both traits in German Holsteins.

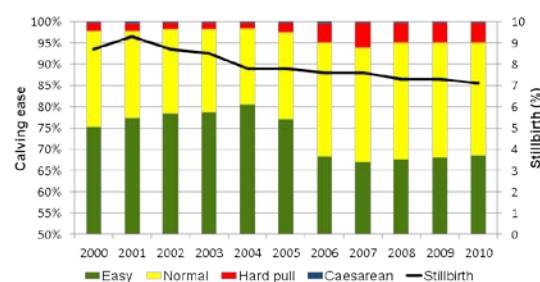


Figure 1. Phenotypic trends of calving ease and stillbirth in German Holsteins.

It can be seen in Figure 1 that the second harmonization in 2005 made the calving data more homogeneous across the last years. On a population level average percentage of easy calving was close to 70% and percentage of stillbirth 7%.

Estimation of genetic parameters

Instead the animal model [1], a sire-maternal grandsire model was used for estimating (co)variances of the new calving model in order to make the parameter estimation feasible for using a large data set. Calving data were extracted from April 2010 national evaluation which was based on the previous single trait model. To ensure a reasonably good data structure for the parameter estimation, at least 10 calving records were

required for each herd-year-parity class. Furthermore, bulls must have 100 calves or more across three parities and at least 60 daughters in first parity. A total of 1,996,597 calving records remained after the data selection, belonging to 25,003 herd-year classes. There were 3134 bulls remained after all the selection steps and the final pedigree contained 10,094 animals.

Gestation length was considered in the parameter estimation, in addition to the two traits CE and SB. The complete parameter estimation for 3 traits x 3 parities x 2 genetic effects had to be divided into sub-analyses including all the three different parities to avoid a bias by the selection on parity number. Parameter estimates were averaged across all the sub-analyses, followed by a bending step to make the final genetic and residual (co)variance matrices positive definite. The (co)variance estimates of the sire-maternal grandsire model were subsequently converted to the animal model for routine genetic evaluation.

Genetic evaluation system

A software system was developed for routine genetic evaluation of the calving traits using model [1]. Fortran 90 source programs were automated using Linux shell scripts. Mixed model equations of model [1] were solved using Gauss-Seidel algorithm and iteration on data technique (Schaeffer and Kennedy, 1986). As prior values of the model effects, solutions from the previous evaluation were used to reduce computing time. In addition to the regular convergence criteria (Liu *et al.*, 2004), correlations of direct and maternal effect estimates were calculated for additional monitoring the convergence of the iteration process. For all sires of calves or cows, effective daughter contribution (EDC) were calculated following the multi-trait EDC approach (Liu *et al.*, 2004) with an extra

adjustment for data contribution by cow and calf (Jakobsen *et al.*, 2003) because they share the same calving record. Reliabilities of EBV of all animals in the pedigree were approximated with a multi-trait EDC method (Liu *et al.*, 2004).

First parity proof was currently defined as official proof, which corresponded to 100% weight on first parity proof and zero weight on second or third parities. Direct or maternal effect estimates of CE and SB were equally weighted to form a direct or maternal calving index, respectively. The maternal calving index was subsequently considered in the calculation of German total merit index with a current weight of 3%. Calving EBV and indices were expressed on a relative breeding value scale with a mean of 100 and standard deviation of 12.

Genetic trend validation

In order to validate the new calving model a special test evaluation was conducted, following Interbull trend validation procedure, by truncating last four years data. Calving EBV from this truncated evaluation were compared to the complete one using all available data until December 2011. The purpose of this trend validation procedure was to check the consistency of genetic evaluations across time horizons or evaluation runs.

With the December 2011 evaluation results based on the new calving model, Germany participated in Interbull January 2012 MACE test run for Holstein, Red Dairy Cattle breeds. Genetic correlations were estimated between Germany and other countries by Interbull.

Genomic evaluation and validation

For the official, first-parity calving breeding values, single nucleotide polymorphism (SNP)

effects were estimated using a BLUP SNP model with a residual polygenic effect (Liu *et al.*, 2011a). As dependent variable, deregressed proofs (DRP) of Holstein bulls from January 2012 Interbull MACE test evaluation were analysed with EDC as weighting factor. Additionally, national EBV of sires of calves or cows, with 10 EDC or more, were deregressed (Liu *et al.*, 2011) for genomic analyse. Since international evaluation contains more information than the national ones, DRP of MACE proofs were chosen when DRP of both national and international evaluations were available for a bull. Direct genomic values were combined with conventional EBV or male pedigree index to obtain genomic evaluation (GEBV).

For validating the genomic model, the genomic reference population was divided into a smaller reference and validation set by birth years of the genotyped bulls (Mäntysaari *et al.*, 2010). Because no historical MACE EBV from four years ago were available for the genomic validation of the new calving model, calving evaluation results from the Interbull January 2012 test run were used instead.

Results and Discussion

Estimates of genetic parameters

The parameter estimation was conducted with VCE 6 (Groeneveld *et al.*, 2008) on 64-bit Linux servers. Due to the large amount of calving data, the parameter estimates had small standard errors: all heritability or genetic correlation estimates with standard error less than 0.001.

Table 1 shows estimates of heritabilities and genetic correlations. Overall, the heritability estimates were low, and first parity had the highest ones among the parities. For first parity, maternal stillbirth had the highest heritability of 5.4% and direct stillbirth the

lowest heritability of 2.7%. These heritability estimates were lower than those obtained from a threshold model (Wiggans *et al.*, 2008). Genetic correlations between parities were moderate to high, ranging from highest correlation for direct effects of CE 0.91 to lowest for maternal effect of SB 0.47. Similar levels of genetic correlation between parities were also found by Philipsson and Steinbock (2003). These between-parity genetic correlation estimates, significantly < 1, justified the new multi-parity calving model. Direct genetic effects were slightly higher correlated between both traits than the maternal genetic effects. The correlation between direct and maternal effects was slightly negative, except for third parity of SB. The slightly positive correlation in later parity was also reported in the Dutch study (Van Pelt and De Jung, 2011).

Residual correlation estimates are given in Table 2. Between parities the residual correlations were nearly 0 for either CE or SB. Within the same parity, both traits were moderately positively correlated with residual correlations about 0.25. In comparison to genetic correlation estimates, the two traits were much lower residually correlated than genetically for either direct or maternal effects.

Gestation length as predictor trait

Heritability estimates of direct genetic effects of GL were 0.39, 0.39 and 0.36 for the three parities respectively, similar to the estimates by Jamrozik *et al.* (2005). Also maternal effects of GL had higher heritability estimates than CE or SB (results not shown here). Genetic correlations between parities for direct effects of GL were 0.99, suggesting a single repeatability model would suffice for modelling the direct genetic effects. Maternal genetic effects of GL had very high correlations between parities as well, ranging from 0.91 to 0.99. Much lower genetic

correlations of GL with CE or SB were found than those between CE and SB within parity, especially for maternal genetic effect. Residual correlation of GL with CE or SB was almost null, being much lower than that between CE and SB. Based on the parameter estimates, we found GL not a useful early predictor for CE or SB. Additionally, we noticed that the relationship of GL with CE or SB was non-linear. Therefore, we decided to exclude GL from calving evaluation.

Genetic evaluation results

Figure 2 and Figure 3 show trends in direct and maternal genetic effect EBV in Black and White Holstein AI bulls respectively, based on the December 2011 national evaluation. Those bulls were required to have a minimal reliability of 0.35 and at least 50 daughters or progeny. The number of bulls selected for the two figures was 12,451 and 14,412 for direct and maternal genetic effects, respectively. It can be seen in both figures that there were practically no clear genetic trends or slightly positive trends in German Holstein breed for the official, first parity traits (CE_1p, SB_1p). The direct (RZK_dir) or maternal calving index (RZK_mat) showed no trends either. However, the later parity direct stillbirth (SB_23p) showed a biologically favourable trend in the specified 10 years. Similar genetic trends were also seen in Holstein cows or calves.

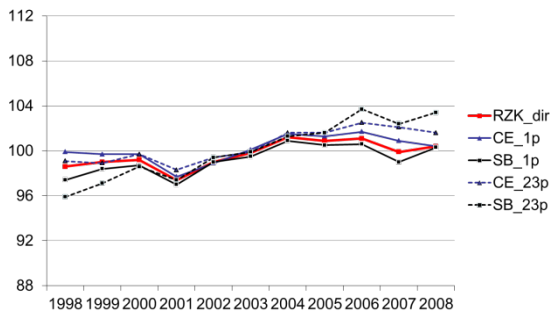


Figure 2. Trends in direct genetic effect EBV in Holstein bulls.

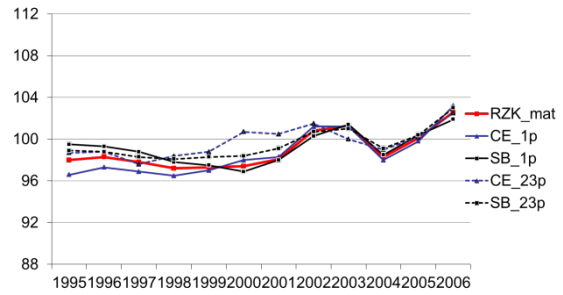


Figure 3. Trends in maternal genetic effect EBV in Holstein bulls.

Genetic trend validation results

Of a total of 20,486,871 calving records in December 2011 evaluation, 6,802,841 records in the last four years were deleted to simulate a genetic evaluation four years ago. The number of cows or calves was reduced from 26,203,131 to 18,413,893. According to the Interbull trend validation procedure, estimates of the trends in EBV, by comparing the current to that of four-years ago, must not exceed 2% of genetic standard deviations. The trend estimate, expressed in genetic standard deviations, was -0.004% for direct effect of calving ease, -0.283% for maternal effects of calving ease, 0.004% for direct effect of stillbirth, and -0.898% for maternal effect of stillbirth, respectively. These trend estimates suggest that the new multi-parity calving model gave unbiased prediction of genetic merits of the calving traits.

Genetic correlations with other countries were estimated in Interbull MACE test run January 2012 for the four calving traits: direct and maternal genetic effects of calving ease and stillbirth in first parity. For German Holsteins, average country correlation was 0.81 for direct calving ease, 0.72 for maternal calving ease, 0.63 for direct stillbirth and 0.76 for maternal stillbirth, respectively. Germany had much higher genetic correlations with major countries, such as Canada, France, The Netherlands or Nordic countries, than with

smaller countries. The high country correlations for German Holsteins, e.g. 0.96 for maternal stillbirth with Nordic countries, were partially a result of using multi-parity calving models in the countries.

Genetic trends in MACE proofs were similar to those in national proofs for German domestic bulls. Also no clear trends could be seen in foreign bulls. However, Holstein bulls from Nordic countries seemed to clearly have a biologically favourable genetic trend in all the calving traits, which may be contributed by the Nordic total merit index with a high weight on calving traits.

SNP effect estimation

MACE proofs of all Holstein bulls were deregressed using Interbull pedigree file and national EDC following the procedure by Liu *et al.* (2011). Depending on the number of populations in each of the four calving traits in MACE January 2012 test evaluation, the number of Holstein bulls with deregressed MACE proofs ranged from 62,155 for maternal stillbirth to 87,887 for direct calving ease. Holstein bulls with MACE and German national DRP were merged to genotyped animal list to form genomic reference population, which contained from 18,943 Holstein bulls for direct stillbirth to 22,660 for direct calving ease. SNP effects were estimated based on the reference populations with a genomic model (Liu *et al.*, 2011a). Additionally, SNP effects were estimated for a smaller reference population of Holstein bulls with national DRP. For instance, for direct calving ease the number of reference bulls was 9907 for using national evaluation, 22,660 for using combined MACE and national evaluations, and 18,534 for the genomic validation study. In order to determine the optimal residual polygenic variance for each of the four calving traits, five scenarios were considered with 0%, 1%, 5%, 10% and 20%

residual polygenic variance. Table 3 shows the SNP effect estimates of direct calving ease using the three different reference populations for the scenario of 0% residual polygenic variance. As the size of the reference population increased, variance of SNP effect estimates became bigger and so was the largest SNP effect. The two reference populations with MACE EBV shared the most common bulls and thus had the highest correlation of SNP effect estimates. Because the reference population with national EBV represented a sub-sample of the third, complete reference population and not of the second one, its SNP correlation was higher with the third reference population than with the second one.

Genomic validation

For the genomic validation, youngest reference bulls were treated as validation animals. Because bulls received EBV of direct genetic effects earlier than maternal genetic effects, the validation population, and consequently also the reference population, for direct genetic effects were younger. All Holstein bulls with progeny information born in 2006 and later were defined as validation bulls for direct effects of both calving traits, whereas bulls born since 2005 were included in the validation population of maternal genetic effects. For direct genetic effects, validation bulls must have at least 20 progeny in the official, first parity, in addition to a minimum of 20 EDC (Mäntysaari *et al.*, 2010). The largest reference population for the genomic validation study composed of 18,534 Holstein bulls for direct effect of calving ease, and the largest validation population contained 1725 Holstein bulls for maternal stillbirth. In order to find the optimal value of residual polygenic variance for each of the four traits, SNP effects were estimated for the following scenarios of 0%, 1%, 5%, 10% and 20% residual polygenic variance. Based on estimated regression coefficient of DRP on GEBV of the validation

bulls (Mäntysaari *et al.*, 2010), the optimal residual polygenic variance was 20% of genetic variance for all the calving traits, except 10% for maternal stillbirth. Realised genomic reliabilities ranged from 0.49 to 0.59, with lowest for direct stillbirth and highest for direct calving ease and maternal stillbirth. Explanations for the higher realised genomic reliabilities for maternal stillbirth are that it had the highest heritability, 5.4%, among the four calving traits, and rather high country correlations. Direct calving ease had the highest correlations with the other countries and its reference population contained the most bulls among the four calving traits. The reason for the least satisfactory genomic validation result for direct stillbirth was fourfold: its heritability being lowest, country correlations much lower than the other traits, its reference population containing the least number of reference bulls, and four of 12 countries in the MACE evaluation for direct stillbirth supplying a replacement trait instead of direct stillbirth itself.

In comparison to the previous calving model, a significant increase in genomic reliability, about 10%, was obtained for the new multi-parity calving model. This can be attributed to the more homogeneous calving data and differentiated modelling of parities and the use of international MACE evaluation for SNP effect estimation.

Conclusions

A multi-parity animal model was developed for routine genetic evaluation of calving ease and stillbirth for German Holstein, Red Dairy Cattle and Jersey breeds. First parity calving was treated as a genetically different trait than the later parities. Genetic parameters of the new multi-parity calving model were estimated based on a large data set. Estimates of genetic correlations between parities ranged from 0.47 to 0.91, justifying the multi-parity calving

model. The multi-parity model for conventional evaluation was validated with Interbull trend validation method III. Reasonably high genetic correlations were obtained between Germany and major countries. The optimal residual polygenic variance was determined with a genomic validation study for each of the four calving traits. The genomic evaluation for the calving traits was validated according to Interbull GEBV test. Since April 2012, the new multi-parity calving model has been used for conventional calving evaluation in Germany and the genomic evaluation based on MACE information has been introduced for German Holsteins. A joint conventional and genomic evaluation for the calving traits will be developed using a single step SNP model.

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Table 1. Estimates of heritabilities (on the diagonal) and genetic correlations (above diagonal) of the multi-parity calving model.

		Direct effects of calving ease in parity			Direct effects of stillbirth in parity			Maternal effects of calving ease in parity			Maternal effects of stillbirth in parity		
		1	2	3	1	2	3	1	2	3	1	2	3
Direct effects of calving ease	Parity 1	.048	0.89	0.87	0.74	0.82	0.68	-0.05	-0.17	0.03	0.01	-0.29	0.17
	Parity 2		.026	0.91	0.64	0.83	0.73	-0.06	-0.14	0.08	-0.02	-0.08	0.00
	Parity 3			.017	0.58	0.77	0.82	-0.08	-0.28	-0.07	0.04	-0.22	0.04
Direct effects of stillbirth	Parity 1				.027	0.80	0.73	-0.03	-0.09	0.10	-0.02	-0.27	-0.01
	Parity 2					.008	0.81	0.06	-0.12	0.09	0.07	-0.10	0.09
	Parity 3						.006	-0.08	-0.16	0.03	0.08	-0.09	0.11
Maternal effects of calving ease	Parity 1							.039	0.76	0.64	0.71	0.62	0.61
	Parity 2								.010	0.91	0.34	0.60	0.66
	Parity 3									.012	0.28	0.41	0.58
Maternal effects of stillbirth	Parity 1										.054	0.63	0.56
	Parity 2											.006	0.47
	Parity 3												.005

Table 2. Estimates of residual correlations of the multi-parity calving model.

		Calving ease of parity			Stillbirth of parity		
		First	Second	Third	First	Second	Third
Calving ease of parity	First	1	0.03	0.01	0.26	-0.01	-0.01
	Second		1	0.03	-0.01	0.25	-0.01
	Third			1	-0.01	-0.01	0.24
Stillbirth of parity	First				1	0.02	0.01
	Second					1	0.02
	Third						1

Table 3. SNP effect estimates for direct genetic effect of calving ease.

Reference population	Number of Holstein bulls	Std dev of SNP effect estimates	Largest SNP effect estimate [§]	Correlation of SNP effect estimates with scenario	
				2. MACE, older bulls	3. MACE, all bulls
1. National EBV	9,907	1	3.59	0.74	0.79
2. MACE EBV, older bulls for validation	18,534	1.29	6.07		0.96
3. MACE EBV, all bulls	22,660	1.35	6.40		

[§] SNP effect estimate was expressed in standard deviation of SNP markers.