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Genetic parameters of calving ease trait in Korean Holstein cattle using an animal-maternal model and a sire-maternal grandsire model

Mahboob Alam[a], Jae-Gu Lee[a,*], Chang-Gwon Dang[a], Mina Park[a], Jaebeom Cha[a], Ha-Seung Seong[a], Sang-Min Lee[a], Eun-Ho Kim[a], Dong Kyu Lee[a], Hyuk-Kee Chang[a]

[a]*Animal Breeding and Genetics Division, National Institute of Animal Science, Cheonan 31000, Republic of Korea*

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ABSTRACT

This study estimated the genetic parameters of calving ease (CE) in Korean Holstein using linear animal-maternal (AMAT) and linear sire-maternal grandsire (SMGS) models. Calves born from the first three parities of cows (P1, P2, P3) between 2000 and 2024 were analyzed in two parity-level data subsets. The first subset comprised 133,998 (P1), 185,988 (P2), and 122,297 (P3) records. The second subset had at least seven records per herd-year subclass, with 104,469, 104,095, and 46,280 records for P1, P2, and P3, respectively. CE was defined as a calf trait, and the scores ranged between 1 and 4. Higher scores indicated greater difficulty at birth. Parity-level (co)variances were obtained for each dataset using the BLUPF90+ software package. Heritability (h^2) values for direct effects ranged between 0.002 and 0.008. Maternal h^2 values from the AMAT and SMGS models were between 0.002 and 0.353 and between 0.004 and 0.008, respectively. Genetic correlations between direct and maternal effects varied widely in the AMAT model but were relatively narrow in the SMGS model. The correlation of estimated breeding value (EBV) of sire between datasets and sire EBV reliabilities was more stable for SMGS than AMAT. We conclude that the AMAT model would be suitable for routine evaluations due to extensive population coverage, whereas SMGS would be better for robust genetic parameter estimations. To leverage the strengths of both models, we suggest using the genetic (co)variance components estimated from the SMGS model within the framework of the AMAT model for the national evaluation of CE in Korean Holstein cattle.

1. Introduction

The calving ease (CE) trait of Korean Holstein cattle has gained interest in recent years due to its adverse effects on farm profits. Numerous reports on dairy cattle point to the adverse effects of CE (Dematawewa & Berger, 1997; Carnier et al., 2000; Mee, 2004), ranging from high production costs to the loss of animals and many other long-term animal health and fertility problem concerns. Aside from the stress experienced by the calf and dam during a difficult birth, the dam's subsequent fertility and production performance can be substantially impacted (Buckley et al., 2003). The CE trait is generally considered a combined interaction between direct and maternal genetic effects (Philipsson, 1976; Meijering, 1984). The direct component is expressed as the genetic ability of a calf to be born easily and is primarily influenced by its body size. The maternal component indicates how easily a female calf can give birth when she becomes a dam and is mainly influenced by the pelvic size of the mature cow. Due to the biological aspects of these two components and their antagonistic relationships (Thompson et al., 1981; Meijering, 1986), each of the genetic effects demands consideration in CE improvement programs. Earlier reports on their relationships suggest that even though female calves are likely to be born easily due to their small size, they are also likely to encounter undesired CE as dams because of their reduced pelvic sizes, which is a negative impact of the small body size at birth.

Despite the appeal of improving CE and evidence of genetic variances (Varona et al., 1999; Carnier et al., 2000), genetic evaluations become challenging due to the choice of statistical evaluation models for this categorical trait. Earlier reports on CE applied different approaches to choosing evaluation models. Many earlier studies applied linear models (Eriksson et al., 2004; Jamrozik et al., 2005) and threshold models (Varona et al., 1999; Ramirez-Valverde et al., 2001). Threshold models are often considered more suitable for CE due to their categorical nature (Gianola, 1982). In contrast, linear models are easy to implement, although they violate some critical statistical assumptions for a quantitative trait. Some linear model-based studies performed logistic transformations of their observations through Snell scoring (Snell, 1964; Tong et al., 1977; Mujibi & Crews, 2009) before analysis to improve the underlying distribution of the data. However, arguments supporting the linear model fit have some practical scenarios, such as, in a population with relatively small contemporary or sire group sizes, where such a model could perform better (Phocas & Laloe, 2003). Our initial observation of the Korean Holstein population also suggests that the data fit the latter scenario more closely. However, developing a statistical model of CE, especially with a target for

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***Corresponding author:**
E-mail address: jindog2929@korea.kr (J-G. Lee)

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national-level implementation, may require more effort and will differ from that of other cattle populations. Eaglen et al. (2012) emphasized that a statistical model for a maternally affected trait such as CE should reflect a meticulous balance between the model's predictive ability and computational feasibility. On the other hand, CE in dairy cattle is often evaluated as a calf trait rather than a dam trait, offering significant advantages for genetic evaluation. This approach allows both male and female calves from the current generation to contribute through traits such as birth weight and body size. Additionally, it facilitates direct estimation of the service sire's genetic influence on CE, which is crucial for selecting dairy bulls. In contrast, assessing CE as a dam trait restricts evaluations to female animals, focusing primarily on maternal characteristics like pelvic size.

CE is one of the least investigated traits in the Korean Holstein population, and only a few reports have been published on its genetic merit (Lee, 2002; Alam et al., 2017). Also, a comparative analysis of linear animal-maternal (AMAT) and linear sire-maternal grandsire (SMGS) models for CE evaluation has not been performed on Korean Holsteins. Therefore, this study aimed to investigate CE genetic parameters through multiple genetic evaluation models and assess their performance in the Korean Holstein population.

2. Materials and methods

2.1 Animals, calving ease phenotype, and pedigree data

This study was performed on field-based CE records from parity 1 to parity 3 calf birth events of Korean Holstein heifers and cows between December 2000 and February 2024. CE was treated as a progeny (calf) trait. CE scores ranged between 1 and 4 according to the increased level of assistance rendered to a dam during the birth event. A CE of 1 indicated a non-assisted calving event, a CE of 2 indicated a slightly assisted calving event (by one person); a CE of 3 indicated a moderately assisted calving event (by two or more persons), and a CE of 4 indicated a difficult calving event requiring veterinary assistance.

Before data screening, all calves with missing identification numbers but valid parental information were assigned pseudo-identification numbers for inclusion in the analysis. Then, we applied several data filters to the raw datasets to obtain the final datasets. This screening process removed calves without valid parental information. Information on multiple births (twins and triplets) was also discarded. Farms that provided only normal CE scores were removed from the dataset to avoid recording bias. The gestational length related to a calf was restrained to between 260 and 310 days. We also excluded calves' records from parity 2 and parity 3 progeny datasets if their dam's calving interval in that parity was longer than 1100 days. Dam's age at calving was also constrained to within 20–42 months, 30–54 months, and 42–66 months for the parity 1, 2, and 3 datasets, respectively. After editing, our first calf dataset in each parity category was obtained and called the whole dataset (DATA_T). A total of 133,998 (parity 1, P1), 185,988 (parity 2, P2), and 122,297 (parity 3, P3) calf records remained in all parity-level DATA_T subsets for final analysis. For model validation, a second dataset was extracted from each DATA_T by applying a minimum of seven calf record restrictions per birth herd-year subclass, also referred to as DATA_7 in the following sections. The number of records remaining across the three DATA_7 datasets were 104,469 (P1), 104,095 (P2), and 46,280 (P3). Each dataset for analysis consisted of information on the sex of the calf (SEX), birth herd, birth year, birth season, and its dam's calving age information. Four birth seasons (i.e., summer, June to August; autumn, September to November; winter, December to February; and spring, March to May) were considered. Detailed information on the final datasets is shown in Table 1.

For genetic analysis, unique and appropriate pedigrees were constructed for each of the six datasets and utilized in the evaluation model accordingly.They represented calves from three parities, with two datasets per parity (Table 1). All pedigree datasets related to animals with phenotypes in DATA_T and DATA_7 were prepared by tracing ancestors as far as 25 generations back. The Dairy Cattle Improvement Center (DCIC), Republic of Korea, provided the raw phenotype dataset and oversees dairy cattle record management. The Korea Animal Improvement Association (KAIA) supplied the raw animal pedigree dataset and holds a major responsibility for livestock pedigree management in Korea.

2.2 Statistical analysis

2.2.1 Analysis using the linear animal-maternal model

We estimated the (co)variance components and genetic parameters for the CE trait using a linear univariate animal-maternal (AMAT) model and the DATA_T and DATA_7 data subsets from specific parity-born calves. The random calf (or direct) and dam (or maternal) components were assumed to be correlated. A maternal permanent environment effect was ignored as each calf can have only one CE at birth. The effect of SEX was treated as a fixed variable in the model. The effect

Table 1.
Structure of calving ease datasets on calves in the first, second and third parity of Korean Holstein and their related pedigree.

Factor/term	Level	Parity 1		Parity 2		Parity 3	
		DATA_T	DATA_7	DATA_T	DATA_7	DATA_T	DATA_7
Phenotype data							
Total observation	-	133,998	104,469	185,988	104,095	122,297	46,280
Calf sex	Male	66,335	51,406	98,131	54,773	65,073	24,706
	Female	67,663	53,063	87,857	49,322	57,224	21,574
Birth herd (H)	-	1584	1244	2688	1745	2353	1186
Birth year (Y)	-	2000-2024	2002-2023	2001-2024	2001-2023	2000-2023	2001-2023
Birth season (S)	Spring	33,905	26,595	41,309	23,186	26,041	9782
	Summer	32,091	25,365	43,523	24,312	25,572	9660
	Autumn	32,922	26,070	52,566	29,922	36,694	14,465
	Winter	35,080	26,439	48,590	26,675	33,990	12,373
Number of sires	-	1887	1710	2089	1926	2004	1714
Number of dams	-	133,998	104,469	185,998	104,095	122,297	46,280
Number of birth herd-year (HY)	-	18,295	8339	35,772	10,329	30,646	5026
Number of birth year-season (YS)	-	93	75	94	92	95	92
Calving ease score	1	109,929	85,684	164,169	94,434	107,712	42,408
	2	23,520	18,382	20,745	9150	13,712	3652
	3	507	368	986	459	786	198
	4	42	35	88	52	87	22
Pedigree data							
PED_{AP}	-	352,799	287,951	467,210	297,406	325,542	151,715
PED_{SP}	-	2745	2559	3082	2836	3023	2653

DATA_T: Dataset with 1 or more calves per birth herd-year subclass; DATA_7: Dataset with 7 or more calves per birth herd-year subclass; PED_{AP}: Animal pedigree used for a linear animal-maternal model analysis; PED_{SP}: Sire pedigree used for a linear sire-maternal grandsire model analysis.

of the dam's age at calving (DAGE; in days) was considered a fixed covariate effect. The DAGE term was used to control the effect of different ages of dams on CE. Effects of birth herd-year (HY) and birth year-season (YS) were also fitted as fixed effects. The BLUPF90+ software package (Misztal et al., 2014) was used to estimate variance components through the average-information REML algorithm, genetic parameters, and standard errors (SEs). The linear AMAT model in the matrix notation was as follows:

$$y = \mathbf{X}b + Z_d d + Z_m m + e$$

where y is the vector related to CE; b is the fixed effects vector, i.e., SEX, DAGE, HY, and YS for individual parity-born calves; d is the random direct (calf) effect vector indicating the additive genetic effect; m is the random maternal (dam) effect vector; and e is the random residual effect vector. $\mathbf{X}$, $\mathbf{Z}_d$, and $\mathbf{Z}_m$ were design matrices relating effects to the CE phenotype. A covariance structure for random effects was assumed as follows:

$$\mathrm{var}\begin{bmatrix} d \\ m \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{dm} & 0 \\ \mathbf{A}\sigma_{md} & \mathbf{A}\sigma_m^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where σ_a^2 is the direct genetic variance, σ_m^2 is the maternal genetic variance, σ_e^2 is the residual variance, and σ_{am} is the covariance between the direct and maternal genetic effects. Therefore, the genetic covariance matrix ($\mathbf{G}_0$) between d and m was:

$$\mathbf{G}_0 = \begin{bmatrix} \sigma_d^2 & \sigma_{dm} \\ \sigma_{md} & \sigma_m^2 \end{bmatrix}$$

The total phenotypic variance (σ_p^2) (Willham, 1972; Eaglen & Bijma, 2009), different heritability estimates (direct- h_d^2, maternal- h_m^2), and direct-maternal genetic correlations (r_{dm}) were calculated using the above (co)variance components as follows:

$$\sigma_p^2 = \sigma_d^2 + \sigma_m^2 + \sigma_{dm} + \sigma_e^2,$$

$$h_d^2 = \frac{\sigma_d^2}{\sigma_p^2},$$

$$h_m^2 = \frac{\sigma_m^2}{\sigma_p^2},$$

$$\text{and } r_{dm} = \frac{\sigma_{dm}}{\sqrt{\sigma_d^2 \times \sigma_m^2}},$$

Approximated SE of the genetic parameters from the AMAT model were obtained from the (co)variance components using BLUPF90+ software, with a Monte Carlo method implemented for SE computation following Houle & Meyer (2015).

2.2.2 Analysis using the linear sire-maternal grandsire model

We also estimated (co)variances for the CE trait using a univariate SMGS model and the $DATA_T$ and $DATA_7$ datasets for each of the three individual parity-born calves. The SMGS model included fixed effects similar to the AMAT model. The sire and maternal grandsire (MGS) of the calf were used as random genetic effects in the SMGS model. The BLUPF90+ software package was used to estimate the sire and MGS (co)variance components of CE using the following linear mixed model:

$$y = \mathbf{X}b + Z_s s + Z_{mgs} mgs + e$$

where y is the vector related to CE; b is the fixed effects vector, i.e., SEX, DAGE, HY, and YS for individual parity-born calves; s is the random sire effect vector; mgs is the random maternal grandsire effect vector; and e is the random residual effect vector. $\mathbf{X}$, $\mathbf{Z}_s$, and $\mathbf{Z}_{mgs}$ are design matrices relating effects to the CE phenotype.

Sire (σ_s^2) and MGS (σ_{mgs}^2) variances and their covariance ($\sigma_{s,mgs}$) were converted to direct (σ_d^2) and maternal (σ_m^2) genetic variances and covariance (σ_{dm}) estimates using the following relationship:

$$\begin{bmatrix} \sigma_d^2 \\ \sigma_{dm} \\ \sigma_m^2 \end{bmatrix} = \begin{bmatrix} 4 & 0 & 0 \\ -2 & 4 & 0 \\ 1 & -4 & 4 \end{bmatrix} \begin{bmatrix} \sigma_s^2 \\ \sigma_{s,mgs} \\ \sigma_{mgs}^2 \end{bmatrix}$$

After calculating the phenotypic variance as $\sigma_p^2 = \sigma_s^2 + \sigma_{s,mgs} + \sigma_{mgs}^2 + \sigma_e^2$ using the SMGS model variance component estimates, all heritability, genetic correlation, and their SE estimates were obtained using the similar formula and steps described earlier for the AMAT model. The SEs of these parameters were also obtained using an approach similar to the AMAT model.

2.3 Model comparison

We evaluated the stability of the AMAT and SMGS models by determining the correlation of the EBV for common sires between $DATA_T$ and $DATA_7$. We also compared the expected reliability (R^2) of sire EBV to evaluate the predictive ability of the models. R^2 was calculated from the prediction error variance (PEV) of EBV as $R^2 = 1 - PEV\sigma_a^2$, where PEV estimate was derived from the inverse of the mixed model equation (MME) coefficient matrix using the BLUPF90+ software package. The direct and maternal (co)variance components obtained through SMGS model analysis were further used to predict sire EBV using animal relationships from complete pedigree data applied to the AMAT model. This additional analysis was referred to as AMAT* for all three parity analyses. The R^2 of sire EBVs from AMAT* (with $DATA_T$ and $DATA_7$) for each parity was then compared with R^2 values from the other two models.

3. Results

Table 2 presents the (co)variances and genetic parameter estimates for variances in the direct and maternal CE components for each parity analysis of the two datasets using the AMAT model. The direct heritability (h_d^2) estimates were relatively low (< 1%) within and between the parity data sets (0.002 ± 0.002 to 0.006 ± 0.002). However, the maternal heritability (h_m^2) estimates varied broadly across the parity levels, where h_m^2 from P2 and P3 were relatively higher (0.197 ± 0.015 to 0.354 ± 0.024). Within each parity, dataset differences showed some variability in h_m^2, especially for calves from higher parities. Also, compared to direct heritability, maternal heritability appeared larger in P2 and P3 calves. Genetic correlation estimates between direct and maternal effects (r_{dm}) in the AMAT model were highly variable and demonstrated noticeable inconsistencies. For P1 calves, the correlation estimates varied from a moderately negative ($DATA_7$: -0.39 ± 0.57) to a positive correlation range ($DATA_T$: 0.20 ± 1.79). For P3 calves, r_{dm} estimates varied largely in the two dataset analyses ($DATA_T$: -0.85 ± 0.85, $DATA_7$: -0.03 ± 0.65). However, P2 calf associations were moderately negative and similar, ranging between -0.34 and -0.46.

Table 3 presents the genetic parameter estimates of the SMGS model using the two different datasets. Like the AMAT model, direct heritability (h_d^2) estimates from the SMGS model were generally low for all datasets across the parity levels (0.004 to 0.008). Maternal heritability (h_m^2) estimates using this model also appeared very similar to the h_d^2 values, which were different from those in the AMAT model. The h_m^2 values estimated by the SMGS model from $DATA_T$ and $DATA_7$ were as small as the direct heritability estimates, and their differences were negligible across animals from all parity levels. The r_{dm} estimates were moderately antagonistic, ranging between -0.36 ± 0.00 and -0.60

Table 2.
Estimates of variance components, genetic parameters (with SE) using the linear animal-maternal model.

Dataset	Parity	σ^2_d	σ_{dm}	σ^2_m	σ^2_e	σ^2_p	h^2_d (SE)	h^2_m (SE)	r_{dm} (SE)
$DATA_T$	1	0.0003	0.0000	0.0001	0.0694	0.0699	0.004 (0.002)	0.002 (0.002)	0.20 (1.79)
	2	0.0004	-0.0011	0.0146	0.0561	0.0700	0.006 (0.002)	0.209 (0.012)	-0.46 (0.30)
	3	0.0002	-0.0016	0.0220	0.0544	0.0750	0.002 (0.002)	0.293 (0.016)	-0.85 (0.85)
$DATA_7$	1	0.0004	-0.0001	0.0003	0.0661	0.0667	0.006 (0.003)	0.004 (0.002)	-0.39 (0.57)
	2	0.0002	-0.0006	0.0124	0.0510	0.0631	0.004 (0.002)	0.197 (0.015)	-0.34 (0.42)
	3	0.0002	-0.0001	0.0216	0.0391	0.0608	0.004 (0.004)	0.354 (0.024)	-0.03 (0.65)

$DATA_T$: Dataset with 1 or more number of calves per herd-year class; $DATA_7$: Dataset with 7 or more calves per birth herd-year subclass; σ^2_d: Direct genetic variance; σ^2_m : Maternal genetic variance; σ^2_e: Residual variance; σ^2_p : Phenotypic variance; σ_{dm} : Variance between direct and maternal genetic variance; h^2_d : Direct heritability; h^2_m : Maternal heritability; r_{dm} : Genetic correlation between direct and maternal effects; SE: Standard error. Estimates of 0.0000 indicates values ≤ 0.00001.

Table 3.
Estimates of variance components, genetic parameters (with SE), using the linear sire-maternal grandsire model.

Dataset	Parity	σ^2_d	σ_{dm}	σ^2_m	σ^2_e	σ^2_p	h^2_d (SE)	h^2_m (SE)	r_{dm} (SE)
$DATA_T$	Parity 1	0.0005	-0.0002	0.0004	0.06924	0.0699	0.006 (0.000)	0.006 (0.000)	-0.36 (0.00)
	Parity 2	0.0005	-0.0002	0.0004	0.06648	0.0671	0.008 (0.000)	0.005 (0.000)	-0.50 (0.00)
	Parity 3	0.0003	-0.0002	0.0003	0.07041	0.0708	0.004 (0.000)	0.004 (0.000)	-0.60 (0.00)
$DATA_7$	Parity 1	0.0005	-0.0003	0.0005	0.06596	0.0667	0.008 (0.000)	0.007 (0.000)	-0.52 (0.00)
	Parity 2	0.0004	-0.0002	0.0004	0.05988	0.0605	0.007 (0.000)	0.007 (0.000)	-0.53 (0.00)
	Parity 3	0.0004	-0.0002	0.0005	0.05562	0.0563	0.006 (0.000)	0.008 (0.000)	-0.40 (0.00)

$DATA_T$: Dataset with 1 or more number of calves per herd-year class; $DATA_7$: Dataset with 7 or more calves per birth herd-year subclass; σ^2_d: Direct genetic variance; σ^2_m : Maternal genetic variance; σ^2_e : Residual variance; σ^2_p : Phenotypic variance; σ_{dm} : Variance between direct and maternal genetic variance; h^2_d : Direct heritability; h^2_m : Maternal heritability; r_{dm} : Genetic correlation between direct and maternal effects; SE: Standard error.

± 0.00 across the parities and datasets. These correlation estimates were relatively more consistent across datasets than those from AMAT model evaluations.

Table 4 provides Pearson's and Spearman rank correlations for common sires' EBVs between $DATA_T$ and $DATA_7$ from AMAT and SMGS analyses. The correlation of sires' direct EBV varied widely between 0.13 and 0.91 in the three parity records, whereas their range was medium to high (0.59 to 0.86) for the maternal EBV. Overall, the strength of the correlation between sire EBVs and the sire ranking in the datasets decreased gradually in higher-parity animals. The consistency of the direct and maternal EBVs calculated from $DATA_T$ and $DATA_7$ was also higher in the SMGS model than in the AMAT model. The sire direct EBV and sire rank were noticeably different using two datasets, as reflected by their low-rank correlation (15%).

Table 5 gives the sire reliability of EBV (R^2) for direct and maternal effects based on $DATA_T$ and $DATA_7$ using AMAT, SMGS, and AMAT*. The AMAT* model integrates direct and maternal variance components from the SMGS model. It uses the parameters estimated by the SMGS model as the final variance approximations for EBV estimation in the AMAT model. The sire reliabilities for the three parity animals varied considerably in the AMAT model analyses using $DATA_T$ (direct: 0.29–0.60, maternal: 0.17–0.86) and $DATA_7$ (direct: 0.14–0.28; maternal: 0.21–0.88). These estimates were more consistent for both $DATA_T$ (direct: 0.11–0.30, maternal: 0.14–0.30) and $DATA_7$ (direct: 0.21–0.33, maternal: 0.23–0.24) in the SMGS model. The R^2 estimate from AMAT* demonstrated similarities to R^2 values from the SMGS model. In P3, sire's direct reliability in AMAT analysis also varied noticeably over different data sizes (0.14 to 0.60) compared to SMGS (0.15 to 0.21) and AMAT* (0.14 to 0.19) analyses. Overall, AMAT model-based sire reliabilities showed higher variability between the two datasets than SMGS model-based estimates.

Table 4.
Pearson's correlation (with rank correlation) of common sires' genetic effects (direct and maternal EBV) between $DATA_T$ and $DATA_7$ according to AMAT and SMGS model from parity 1 to 3.

Model	Effect	Parity 1	Parity 2	Parity 3
AMAT	Direct EBV	0.87 (0.83)	0.85 (0.82)	0.13 (0.15)
	Maternal EBV	0.76 (0.74)	0.75 (0.71)	0.59 (0.51)
SMGS	Direct EBV	0.91 (0.87)	0.82 (0.81)	0.66 (0.64)
	Maternal EBV	0.88 (0.83)	0.80 (0.75)	0.68 (0.65)

$DATA_T$: Dataset with no restriction on number of calves per herd-year class, $DATA_7$: Dataset with at least 7 calves per herd-year class, AMAT: The linear animal-maternal model analysis, SMGS: The linear sire-maternal grandsire model analysis; EBV: Estimated breeding value.

Table 5.
Reliability estimates sires with 100 or more daughters for direct and maternal effects using $DATA_T$ and $DATA_7$ from different models.

Dataset	Parity	R^2-AMAT		R^2-SMGS		R^2-AMAT*	
		Direct EBV	Maternal EBV	Direct EBV	Maternal EBV	Direct EBV	Maternal EBV
$DATA_T$	P1	0.29	0.17	0.30	0.27	0.28	0.27
	P2	0.35	0.86	0.30	0.27	0.30	0.25
	P3	0.60	0.85	0.15	0.11	0.14	0.16
$DATA_7$	P1	0.28	0.21	0.33	0.24	0.30	0.29
	P2	0.30	0.27	0.29	0.23	0.26	0.27
	P3	0.14	0.88	0.21	0.23	0.19	0.25

$DATA_T$: Dataset with 1 or more number of calves per herd-year class, $DATA_7$: Dataset with 7 or more calves per birth herd-year subclass, R^2-AMAT: EBV reliability using variance components from the animal-maternal model, R^2-SMGS: EBV reliability using variance components from the sire-maternal grandsire model, R^2-AMAT*: EBV reliability using direct and maternal variance components from sire-maternal grandsire model in an AMAT model. AMAT: The linear animal-maternal model, SMGS: The linear sire-maternal grandsire model, EBV: Estimated breeding value.

4. Discussion

The knowledge of various sources of genetic effects, such as direct and maternal effects and their relationship, is the key to improving CE in any dairy cattle. This study demonstrated that heritability (h^2) estimates ranged from very small to low across parities. A previous study using a SMGS model in Korean Holstein and first parity animals (Alam et al., 2017) revealed direct h^2 (0.11) and maternal h^2 (0.05) estimates that were larger than any model estimates in this study. Such a difference could be attributed to the different models and datasets between the previous report and the present study. A study by Salimi et al. (2017) in Iranian Holstein cattle reported small direct h^2 (0.02) and maternal h^2 (0.002) estimates, which also provides support for the low h^2 values in this study. Another animal model study on Iranian Holsteins (Ghiasi et al., 2014) also suggested similar lower h^2 estimates (direct: 0.041, maternal: 0.012). Similar low heritability estimates for direct (0.03) and maternal CE (0.02), like in our estimation range, were reported by Eaglen et al. (2012). The estimates reported by Eaglen and Bijma (2009) in Dutch Holstein-Friesian partially agree with ours (direct h^2: ∼0.08 and maternal h^2: ∼0.04). Our estimates were also slightly lower than reports on beef breeds using the linear model (Phocas & Laloe, 2003; Mujibi & Crews, 2009). Differences among reports are mainly due to differences in fitted factors, model types, trait definitions, and breeds. Some studies (Luo et al., 1999; Jamrozik et al., 2005) showed that linear models yielded lower estimates than threshold models. Salimi et al. (2017) argued that an underestimation of their population's direct and maternal components could be caused by the large phenotypic variances (or residual variances) compared to genetic variances due to recording methods and herd management practices. The previous study in Korean Holstein using the SMGS model by Alam et al. (2017) fitted HYS as a random effect compared to the fixed effect of HY and YS in this study.

The genetic correlation estimates between direct and maternal effects varied across parities and models. Although these correlation estimates were mainly negative, the AMAT model estimate for P1 appeared positive with a high standard error, indicating the possibility of estimation error. In P3 calves, the inconsistency in correlation estimates regarding dataset differences was apparent. However, the SMGS model exhibited greater consistency across datasets and parities. Overall, moderately antagonistic relationships (-0.36 to -0.60) between genetic effects were identified using the SMGS model. Previous reports provided good overall support for our observed negative correlation estimates. Like this study, Alam et al. (2017) also studied first parity Korean Holstein calves and reported an r_{dm} estimate of -0.68 for service-sire CE, further supporting the findings in the present study. Comparable estimates (-0.41 to -0.43) were also reported by Salimi et al. (2017) and Ghiasi et al. (2014) in Iranian Holstein. Similarly, the animal model correlation estimates (-0.04 to -0.44) by Eaglen and Bijma (2009) coincided with the data in our study. More dairy cattle reports using SMGS models (Luo et al., 1999; Wiggans et al., 2003; Hickey et al., 2007) on r_{dm} also suggested a range of -0.08 to -0.47, consistent with the present report. While a study in Charolais cattle (Mujibi & Crews, 2009) extended support by a correlation estimate of -0.27, some disagreements in Holstein cattle reported a near absence of correlation (i.e., weakly negative to weakly positive) (Steinbock et al., 2003; Hansen et al., 2004). The variations across reports could be due to differences in breeds or populations, such as beef cattle, in which correlation estimates are often strongly negative (Robinson, 1996). A possible estimation bias is also likely for the genetic covariance between direct and maternal effects (Koch, 1972; Willham, 1980; Meyer, 1992). The present report found noticeable differences between AMAT and SMGS models for genetic parameter estimates. The inconsistency in AMAT model estimates could indicate problems in the present data structure, where dams and their daughters are somewhat confounded to herds. This is because dams and their female progenies rarely change herds in the Korean dairy production system. Using an SMGS model with such datasets could help to efficiently separate herd effects from genetic components and, therefore, reduce estimation bias originating from the confounding data structure.

The stability of sire EBV using AMAT and SMGS models was assessed by correlations between EBV obtained from parity-level $DATA_T$ and $DATA_7$ datasets. We found an overall higher stability of sire EBV using the SMGS model than the AMAT model. The AMAT model also performed poorly with P3 animals. Our results disagreed with the CE study findings of Ramirez-Valverde et al. (2001) in beef cattle, which showed higher stability with a linear animal model than a linear SMGS model. Sun et al. (2009) also compared animal models with various sire models in Danish Holstein and reported a relative superiority of their animal models over sire models for fertility traits. However, such differences in genetic models could be related to differences in traits for evaluation, data structure, and breeds of interest across studies. Our study showed that the present animal model analyses suffered from variance component estimations and varied across data subsets and parities.

We also compared the expected reliability of sire EBV between direct and maternal effects. Our comparison of EBV reliability for sires suggested that the SMGS model could provide direct EBV as reliably as the AMAT model. Even though the reliability of maternal EBV using the SMGS model was relatively smaller than that of the AMAT model for the full dataset ($DATA_T$), there was greater consistency across parity-level datasets in the SMGS model. More support for SMGS-based EBV reliability was found from a similar AMAT* model. In contrast, Sun et al. (2009) showed that their animal model provided higher reliability for fertility traits than sire models.

Generally, an animal model is expected to provide higher EBV accuracy (or reliability) as it allows all relatives to contribute to evaluating an animal. In contrast, sire models use less information on relatives. The confounded data structure in this study could limit an accurate estimation of animal EBV in the Korean Holstein population using an AMAT model. However, due to the advantages of animal models, AMAT could be a model choice for national routine evaluations as it would allow for the inclusion of contributions from all relatives related to the animal. An SMGS model, based on the stability of predictions in this study, could be appealing for genetic parameter estimations in Korean Holstein. Although, in theory, a simple sire model is considered inferior to an animal model due to its lack of consideration for all relatives and its estimation bias for EBV (Schaeffer, 1983; Sun et al., 2009) this model can significantly reduce computational demands. An SMGS model, which adequately incorporates genetic relationships among males and females, could reduce the bias associated with a simple sire model (Everett et al., 1979; Schaeffer, 1983). This study showed that AMAT model-based parameter estimates were less stable, which could be associated with the existing dataset limitations described earlier. However, the SMGS model could minimize some bias related to data structures, as suggested by the greater stability of its estimates.

The present study identified multiple challenges regarding estimating variance components and genetic parameters of CE by AMAT and SMGS models. While the SMGS model had superior overall performance, its limited scope regarding animal inclusion (i.e., dam and progeny) for genetic evaluation poses a significant challenge for large-scale national evaluations. Conversely, despite its slightly inferior genetic parameter estimates, the AMAT model offers a comprehensive inclusion of animals, which is crucial for a robust national evaluation. To leverage the strengths of both models in CE evaluation, we suggest using the genetic (co)variance components estimated from the SMGS model within the framework of the AMAT model. This approach would allow us to derive animal EBVs that benefit from the SMGS model's robust genetic parameter estimates while maintaining the population coverage of the AMAT model. This combined approach could offer a more accurate and comprehensive tool for the Korean national breeding program, effectively balancing the accuracy of EBV and practical applicability.

On the other hand, the SMGS model evaluation can still be valuable for the improvement of CE in Korean Holsteins. EBVs based on the SMGS model can assist in selecting service sires to improve calving ease in heifers, particularly in commercial herds. The SMGS model EBVs can assist breeding programs by focusing on superior maternal lines by identifying sires that can produce easy-calving calves and contribute to a future generation of dams with the desired CE. SMGS-EBVs can also be helpful for the cross-validation of AMAT-EBVs to improve the overall accuracy of EBVs by detecting any discrepancies between animal EBVs from both models. A greater alignment of AMAT-EBVs with those from the SMGS model can suggest the robustness of predictions of the national evaluation. Also, an effective comparison of AMAT and SMGS EBVs can allow breeders to identify the over-representation of sires' genetics in the population (i.e., similar sires appear at the top of ranking from both models) and help decide to reduce the overuse of a small sire group through selection of a wider range of sires with better performances.

5. Conclusion

In this study, we compared the genetic parameters of the direct and maternal genetic components of CE in P1–P3 Holstein calves using AMAT and SMGS models. Two datasets were used to compare the genetic parameter estimates: one included all calves, and the other included only herd-years with a minimum of seven calves within each parity. Variance components and genetic parameters showed notable influences of model and dataset differences. The direct heritability estimates were mainly very low across parities and datasets. The maternal heritability values varied from low to moderate across parity levels and datasets in the AMAT model, whereas low and consistent values were found in SMGS analyses. The genetic correlation between direct and maternal genetic effects varied largely (-0.85 to 0.20) across parities in the AMAT model using the complete dataset. Genetic correlation estimates were primarily moderate and negative using the SMGS model. The EBV of sires and their ranking were more stable in the SMGS model than in the AMAT model. P3 sire EBVs were the least stable in this study. The expected reliability of sires (with more than 100 calves) was more inconsistent in the AMAT model than in the SMGS model. Overall, SMGS model estimates were more consistent in terms of genetic parameters, reliability of sire EBV, and ranking of sires. We suggest that due to the relative advantage of AMAT, this model can be implemented for national routine evaluations of CE in Korea. In contrast, the SMGS model could be suitable for evaluating CE genetic parameters. This comparative study of linear AMAT and SMGS models was a first in the Korean Holstein population. Our findings are expected to assist future CE evaluation of Korean Holsteins.

CRediT authorship contribution statement

Mahboob Alam: Writing – original draft preparation, Conceptualization, Methodology, Software, Formal analysis, Visualization. **Jae-Gu Lee:** Writing – review and editing, Conceptualization, Methodology, Resources, Investigation, Data curation, Supervision, Project administration. **Chang-Gwon Dang:** Writing – review and editing, Conceptualization, Methodology, Resources, Investigation, Data curation. **Mina Park:** Writing – review and editing, Validation, Supervision, Project administration. **Jaebeom Cha:** Writing – review and editing, Validation. **Ha-Seung Seong:** Writing – review and editing, Validation. **Sang-Min Lee:** Writing – review and editing, Validation. **Eun-Ho Kim:** Writing – review and editing, Validation. **Lee Dong Kyu:** Writing – review ad editing, Validation. **Hyuk-Kee Chang:** Writing – review and editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors confirm that there was no use of artificial intelligence (AI)-assisted technology for assisting in the writing or editing of the manuscript and no images were manipulated using AI.

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References

Alam, M., Dang, C., Choi, T., Choy, Y., Lee, J., Cho, K., 2017. Genetic parameters of calving ease using sire-maternal grandsire model in Korean Holsteins. Asian-Australas J. Anim. Sci. 30, 1225-1233. https://doi.org/10.5713/ajas.16.0322

Buckley, F., O'Sullivan, K., Mee, J., Evans, R., Dillon, P., 2003. Relationships among milk yield, body condition, cow weight, and reproduction in spring-calved Holstein-Friesians. J. Dairy Sci. 86, 2308-2319. https://doi.org/10.3168/jds.S0022-0302(03)73823-5

Carnier, P., Albera, A., Dal Zotto, R., Groen, A., Bona, M., Bittante, G., 2000. Genetic parameters for direct and maternal calving ability over parities in Piedmontese cattle. J. Anim. Sci. 78, 2532-2539. https://doi.org/10.2527/2000.78102532x

Dematawewa, C., Berger, P., 1997. Effect of dystocia on yield, fertility, and cow losses and an economic evaluation of dystocia scores for Holsteins. J. Dairy. Sci. 80, 754-761. https://doi.org/10.3168/jds.s0022-0302(97)75995-2

Eaglen, S., Bijma, P., 2009. Genetic parameters of direct and maternal effects for calving ease in Dutch Holstein-Friesian cattle. J. Dairy. Sci. 92, 2229-2237. https://doi.org/10.3168/jds.2008-1654

Eaglen, S., Coffey, M., Woolliams, J., Wall, E., 2012. Evaluating alternate models to estimate genetic parameters of calving traits in United Kingdom Holstein-Friesian dairy cattle. Genet. Sel. Evol. 44, 23. https://doi.org/10.1186/1297-9686-44-23

Eriksson, S., Näisholm, A., Johansson, K., Philipsson, J., 2004. Genetic parameters for calving difficulty, stillbirth, and birth weight for Hereford and Charolais at first and later parities. J. Anim. Sci. 82, 375-383. https://doi.org/10.2527/2004.822375x

Everett, R.W., Quaas, R.L., McClintock, A.E., 1979. Daughters' maternal grandsires in sire evaluation. J. Dairy Sci. 62, 1304-1313. https://doi.org/10.3168/jds.s0022-0302(79)83416-5

Ghiasi, H., Khaldari, M., Taherkhani, R., 2014. Genetic parameters and calving ability index for direct and maternal calving difficulty and stillbirth in Iranian Holstein cows. Livestock Sci. 165, 22-26. https://doi.org/10.1016/j.livsci.2014.04.021

Gianola, D., 1982. Theory and analysis of threshold characters. J. Anim. Sci. 54, 1079-1096. https://doi.org/10.2527/jas1982.5451079x

Hansen, M., Lund, M.S., Pedersen, J., Christensen, L.G., 2004. Gestation length in Danish Holsteins has weak genetic associations with stillbirth, calving difficulty, and calf size. Livestock Production Science 91, 23-33. https://doi.org/10.1016/j.livprodsci.2004.06.007

Hickey, J., Keane, M., Kenny, D., Cromie, A., Amer, P., Veerkamp, R., 2007. Heterogeneity of genetic parameters for calving difficulty in Holstein heifers in Ireland. J. Dairy Sci. 90, 3900-3908. https://doi.org/10.3168/jds.2006-717

Houle, D., Meyer, K., 2015. Estimating sampling error of evolutionary statistics based on genetic covariance matrices using maximum likelihood. J. Evol. Biol. 28, 1542-1549. https://doi.org/10.1111/jeb.12674

Jamrozik, J., Fatehi, J., Kistemaker, G., Schaeffer, L., 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. J. Dairy Sci. 88, 2199-2208. https://doi.org/10.3168/jds.S0022-0302(05)72895-2

Koch, R., 1972. The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. J. Anim. Sci. 35, 1316-1323. https://doi.org/10.2527/jas1972.3561316x

Lee, D.H., 2002. Estimation of genetic parameters for calving ease by heifers and cows using multi-trait threshold animal models with Bayesian approach. Asian Australas. J. Anim. Sci 15, 1085-1090.

Luo, M.F., Boettcher, P.J., Dekkers, J.C.M., Schaeffer, L.R., 1999. Bayesian analysis for estimation of genetic parameters of calving ease and stillbirth for Canadian holsteins. J. Dairy Sci. 82, e1-1848. https://doi.org/10.3168/jds.s0022-0302(99)75416-0

Mee, J., 2004. Managing the dairy cow at calving time. Vet. Clin. North Am. Food Anim. Pract. 20, 521-546. https://doi.org/10.1016/j.cvfa.2004.06.001

Meijering, A., 1984. Dystocia and stillbirth in cattle — A review of causes, relations and implications. Livestock Production Sci. 11, 143-177. https://doi.org/10.1016/0301-6226(84)90057-5

Meijering, A., 1986. Dystocia in dairy cattle breeding with special attention to sire evaluation for categorical traits Ph.D. dissertation, Wageningen Agricultural University.

Meyer, K., 1992. Bias and sampling covariances of estimates of variance components due to maternal effects. Genet. Sel. Evol. 24, 487. https://doi.org/10.1186/1297-9686-24-6-487

Misztal, I., S. Tsuruta, D. Lourenco, Aguilar, I., Legarra, A., Vitezica, Z. 2014. Manual for BLUPF90 family of programs. Retrieved Apr 26, 2024, from https://nce.ads.uga.edu/wiki/lib/exe/fetch.%0Aphp?media=blupf90_all2.pdf.

Mujibi, F., Crews, D., 2009. Genetic parameters for calving ease, gestation length, and birth weight in Charolais cattle. J. Anim. Sci. 87, 2759-2766. https://doi.org/10.2527/jas.2008-1141

Philipsson, J., 1976. Studies on calving difficulty, stillbirth and associated factors in Swedish cattle breeds. Acta Agriculturae Scandinavica 26, 211-220. https://doi.org/10.1080/00015127609435090

Phocas, F., Laloë, D., 2003. Evaluation models and genetic parameters for calving difficulty in beef cattle. J. Anim. Sci. 81, 933-938. https://doi.org/10.2527/2003.814933x

Ramirez-Valverde, R., Misztal, I., Bertrand, J., 2001. Comparison of threshold vs linear and animal vs sire models for predicting direct and maternal genetic effects on calving difficulty in beef cattle. J. Anim. Sci. 79, 333-338. https://doi.org/10.2527/2001.792333x

Robinson, D.L., 1996. Models which might explain negative correlations between direct and maternal genetic effects. Livestock Production Sci. 45, 111-122. https://doi.org/10.1016/0301-6226(96)00002-4

Hossein Salimi, M., Hossein-Zadeh, N.G., Ahad Shadparvar, A., Reza Eghbal, A., 2017. Genetic evaluation of dystocia and its relationship with productive and reproductive traits in Holstein cows. Rev. Colomb Cienc Pecu 30, 126-137. https://doi.org/10.17533/udea.rccp.v30n2a04

Schaeffer, L., 1983. Effectiveness of model for cow evaluation intraherd. J. Dairy Sci. 66, 874-880. https://doi.org/10.3168/jds.S0022-0302(83)81870-0

Snell, E.J., 1964. A scaling procedure for ordered categorical data. Biometrics 20, 592. https://doi.org/10.2307/2528498

Steinbock, L., Näsholm, A., Berglund, B., Johansson, K., Philipsson, J., 2003. Genetic effects on stillbirth and calving difficulty in Swedish Holsteins at first and second calving. J. Dairy Sci. 86, 2228-2235. https://doi.org/10.3168/jds.S0022-0302(03)73813-2

Sun, C., Madsen, P., Nielsen, U., Zhang, Y., Lund, M., Su, G., 2009. Comparison between a sire model and an animal model for genetic evaluation of fertility traits in Danish Holstein population. J. Dairy Sci. 92, 4063-4071. https://doi.org/10.3168/jds.2008-1918

Thompson, J., Freeman, A., Berger, P., 1981. Age of dam and maternal effects for dystocia in Holsteins. J. Dairy Sci. 64, 1603-1609. https://doi.org/10.3168/jds.S0022-0302(81)82732-4

Tong, A.K.W., Wilton, J.W., Schaeffer, L.R., 1977. Application of a scoring procedure and transformations to dairy type classification and beef ease of calving categorical data. Can. J. Anim. Sci. 57, 1-5. https://doi.org/10.4141/cjas77-001

Varona, L., Misztal, I., Bertrand, J., 1999. Threshold-linear versus linear-linear analysis of birth weight and calving ease using an animal model: I. Variance component estimation. J. Anim. Sci. 77, 1994-2002. https://doi.org/10.2527/1999.7781994x

Wiggans, G., Misztal, I., Van Tassell, C., 2003. Calving ease (Co)variance components for a sire-maternal grandsire threshold model. J. Dairy Sci. 86, 1845-1848. https://doi.org/10.3168/jds.S0022-0302(03)73771-0

Willham, R., 1972. The role of maternal effects in animal breeding. 3. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35, 1288-1293. https://doi.org/10.2527/jas1972.3561288x

Willham, R.L., 1980. Problems in estimating maternal effects. Livestock Production Sci. 7, 405-418. https://doi.org/10.1016/0301-6226(80)90080-9