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Genetic background of calving ease in beef-on-dairy

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ABSTRACT

A common practice in dairy herds is to breed females not selected as replacement heifers to beef bulls. This increases the market value of the surplus calves sold for beef purposes. Some beef breed associations have built selection indices focusing mainly on carcass traits; however, calving ease (CE) is also an important trait, given that crossbreeding with beef bulls can change gestation patterns (e.g., gestation length) or calf conformation (e.g., weight and size), generating a negative effect on the health, and consequently on the production, of the cows. We used linear and threshold animal models to estimate genetic parameters and breeding values for direct and maternal additive effects for CE in beef-on-dairy crosses, considering only the first or the first 3 lactations. We analyzed 231K CE records in the first lactation and 1.2 million in the first 3 lactations from Holstein and Jersey cows inseminated with Angus, Charolais, or Simmental semen. Although CE was scored in 5 categories, we reduced this to a binary trait (1 = easy and 2, 3, 4, 5 = difficult). The average incidence of difficult calving (scores ≥2) was ~15%. Direct and maternal heritabilities for the linear (threshold) model were 0.01 ± 0.002 (0.01 ± 0.001) and 0.02 ± 0.002 (0.04 ± 0.004), respectively, using the first lactation, and equal to 0.01 ± 0.002 (0.01 ± 0.009) and 0.19 ± 0.002 (0.26 ± 0.006), respectively, considering the first 3 lactations. Maternal heritabilities were always greater than the direct ones. Maternal heritabilities were inflated when we considered more than one lactation, most likely because of a confounding with the maternal permanent environmental effect that could not be estimated. Linear and threshold models provided similar direct EBV rankings, with a correlation of at least 0.86 when considering all different breeds; for maternal effect, it was high for dairy breeds (>0.9) and close to zero in beef breeds. Validation metrics were better for the linear model with only first lactation records. Although with the small direct heritabilities, the results showed that direct genetic variability exists, and that it would be possible to select beef bulls based on their direct EBV for CE in beef-on-dairy systems. One of the challenges in beef-on-dairy analyses is the lack of pedigree depth on the sire side. When this is the case, we suggest using linear models considering only the first lactation to evaluate CE, given that EBV are highly correlated with those obtained by the threshold model but are less biased and converge almost 10 times faster, proving to be more efficient for routine genetic evaluations.

Key words: calving difficulty, crossbreed, linear and threshold models, variance components

INTRODUCTION

Beef-on-dairy is not a recent practice, but it has been intensified due to a combination of factors, such as exploring heterosis effect and complementarity, increasing the use of dairy-sire X-bearing sexed semen so that more females not selected as replacement heifers are crossed with beef bulls, resilience to volatile milk prices through the sale of surplus calves, and increasing availability of beef bulls with easy calving and short gestation (Berry, 2021). In the United States, beef-on-dairy herds represent 20.5% to 22.7% of beef production (DelCurto et al., 2017). Some studies have shown that dystocia rates increase in dairy cows mated to certain breeds of beef sires (Fouz et al., 2013; Eriksson et al., 2020). Thus, beef-on-dairy may not be profitable if such calves negatively affect the health and production of cows that carry beef-on-dairy calves.

The American Angus Association (St. Joseph, MO) has created an Angus-on-Dairy Index (Miller, 2021). This

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index is an economic weighting of EBV for important traits in beef-on-dairy crosses. It shows the expected performance of a future beef-on-dairy progeny of each Angus sire, on average, when compared with a progeny of other Angus sires, if the sires were randomly mated and the calves were exposed to the same environment. So far, indices have been developed for crosses of Angus with Holstein and Jersey cows considering traits of calving ease (**CE**), growth from birth through the feeding phase, feed intake, dressing percent, yield grade, quality grade, muscling, and height. All these traits have different weights in the indices for Holstein and Jersey, except for height, which is only considered for Holsteins, and CE, which has more weight in the Jersey index.

Calving ease is a categorical trait that indicates the ability of a cow to give birth without difficulty or the degree of assistance required during calving. Dairy cattle producers in the United States use the National Association of Animal Breeders CE scoring system, in which a CE score of 1 indicates no problem, 2 indicates slight problem, 3 indicates needed assistance, 4 indicates considerable force, and 5 indicates extreme difficulty (Berger, 1994). In contrast, beef cattle producers used to use the CE scoring according to Beef Improvement Federation Guidelines, where a CE score of 1 indicates no assistance, 2 is some assistance, 3 is mechanical assistance, 4 is a cesarean section, and scores equal to 5 used to be excluded because it indicates abnormal presentation and is not inherited (BIF, 2022). Generally, these scores are combined to form a binary trait indicating either easy or difficult calving. The method of combining these scores depends on the incidence rate. The International Committee for Animal Recording recommends that if a single CE class has a very low incidence (less than 1%), it should be merged with an adjacent class (ICAR, 2022). In the United States, beef cattle genetic evaluations define difficulty as a calving score of ≥2 (Patterson, 2005), whereas dairy cattle genetic evaluations consider scores of ≥4 as indicating difficulty (CDCB, 2022).

Calving ease can be affected by 2 additive genetic components: the direct effect, which is the calf's contribution, and the maternal effect, which is the dam's contribution. In theory, threshold models are preferred over linear models for genetic analysis of categorical traits with a discrete probability distribution (Gianola, 1982). However, it is possible to use linear models and obtain similar results in animal ranking in a faster and more computationally efficient way (Hidalgo et al., 2024). This explains why most of the routine genetic evaluations of categorical calving traits are based on linear models (Interbull, 2013), although such data violate the normality assumption. One notable exception to this trend is the US national genetic evaluation for CE, which uses a sire-maternal grandsire threshold model (Van Tassell et al., 2003). We aimed to estimate variance components and direct and maternal heritabilities for CE in beef-on-dairy crosses, comparing linear and threshold models. We used phenotypes collected in the first and first 3 lactations. In addition, we tested 2 ways of combining the CE categories to create a binary trait. The models were compared considering the computational time and the animal ranking correlation based on breeding values.

MATERIALS AND METHODS

Animal care and use committee approvals were unnecessary as data were obtained from pre-existing databases.

Dataset

Data from URUS Group LP (Madison, WI) were used in this study. The pedigree included 1.2 million Holstein, Jersey, Angus, Charolais, and Simmental animals, born from 1951 to 2021, and 1.3 million crossbreds born from 2014 to 2023. The pedigree only had 3 generations. All phenotyped animals had to have information about the sire and dam breeds to be considered beef-on-dairy. All dams of generation II had information about their sires (29,773 bulls) and unknown dams, but only 401 sires from generation II had pedigree information. A pedigree chart with the number of animals in each generation and breed is shown in Figure 1. The phenotypes were assigned to calves. There were about 230K CE records in the first lactation and almost 1.3 million total in the first 3 lactations from Holstein and Jersey cows inseminated with Angus, Charolais, or Simmental semen. Considering only singleton calves, in the first lactation, we had 142,175 male and 86,991 female calves; considering the first 3 lactations, we had 827,263 males and 440,658 females. In the first lactation, the heifers had an average of 24 ± 1.8 mo of age; for the first 3 lactations, the females had an average of 39 ± 9.4 mo. The incidence of unassisted calving in the first 3 lactations was equal to 87.4%, 88.6%, and 87.5%, respectively, and the incidence of all 5 categories in the first 3 lactations is presented in Table 1. To determine the CE categories (easy or difficult) in our work, we considered the score combinations most commonly used for pure breeds of beef and dairy cattle. For the dairy cows inseminated with beef cattle semen, we classified score 1 as easy and combined scores 2, 3, 4, and 5 as difficult.

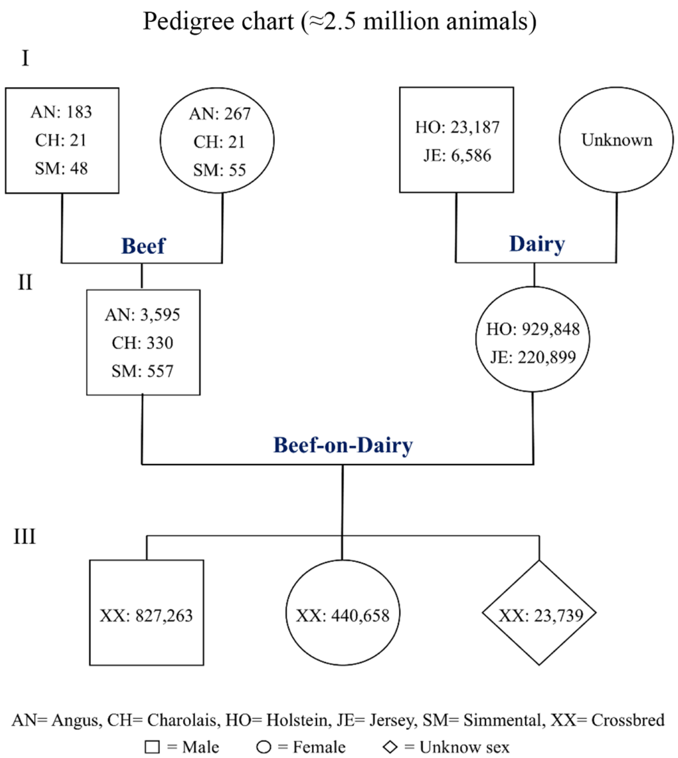

Figure 1. Pedigree chart with the number of animals in each generation and breed.

Variance Components and Breeding Value Estimation

Variance components were estimated using single-trait, linear, or threshold models, based on pedigree

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{h} + \mathbf{Z}_2\mathbf{a} + \mathbf{Z}_3\mathbf{m} + \mathbf{e},$$

in which **y** is a vector with CE scores; **b** is a vector of fixed effects of sex, dam-sire breed interaction, year-season, age of the cow (covariate), and lactation order when considering the first 3 lactations; **h**, **a**, **m**, and **e** are vectors for herd-year interaction, direct genetic, maternal genetic, and residual as random effects; and **X**, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{Z}_3$ are the respective incidence matrices.

The assumed covariance structures were

$$\mathbf{h} \sim N\left(\mathbf{0}, \mathbf{I}\sigma_h^2\right)$$

$$\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\end{bmatrix} \sim \mathrm{N}\left(\mathbf{0}, \begin{matrix}\mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{a,m}\\ \mathbf{A}\sigma_{m,a} & \mathbf{A}\sigma_m^2\end{matrix}\right)$$

$$\mathbf{e} \sim \mathrm{N}\left(\mathbf{0}, \mathbf{I}\sigma_e^2\right),$$

where **A** is the pedigree relationship matrix, **I** is an identity matrix of proper order, σ_h^2, σ_a^2, σ_m^2, $\sigma_{a,m}$, and σ_e^2 are the variances for the herd-year interaction, direct genetic, maternal genetic, covariance between direct and maternal, and residual. After initial investigation, we assumed the covariances between direct and maternal genetic effects equal to zero ($\mathbf{A}\sigma_{a,m} = \mathbf{A}\sigma_{m,a} = \mathbf{0}$).

In the threshold model, it was assumed that CE is the expression of an underlying continuous random variable, the liability (l_{ce_i}) of individual i. If l_{ce_i} exceeds an unknown fixed threshold (t), then $y_{ce_i} = 2$ (difficult calving), and $y_{ce_i} = 1$ (easy calving), otherwise. We assumed that liability was normally distributed with mean vector $\boldsymbol{\Theta}$ and unit variance

$$\mathbf{l}_{\mathrm{ce}} \sim \mathrm{N}(\mathbf{s}\boldsymbol{\Theta}, 1),$$

where $\boldsymbol{\Theta}' = (\mathbf{b}', \mathbf{h}', \mathbf{a}', \mathbf{m}')$ is a vector of fixed and random effects, and **s** is an incidence vector linking $\boldsymbol{\Theta}$ to the phenotypic records.

The conditional response of CE, given the liability and the threshold, was modeled with the following distribution:

Table 1. Number of observations and (incidence%) of calving ease scores in the first 3 lactations

Lac[1]	Calving ease score[2]					Total
	1	2	3	4	5	
1	202,528 (87%)	15,839 (7%)	10,518 (5%)	1,719 (.5%)	1,238 (.5%)	231,842
2	467,972 (88%)	34,819 (7%)	19,807 (4%)	3,046 (.5%)	2,591 (.5%)	528,235
3	465,347 (88%)	38,964 (7%)	21,182 (4%)	3,399 (.5%)	2,691 (.5%)	531,583
Total	1,135,847	89,622	51,507	8,164	6,520	1,291,660

[1]Lac is the lactation number.

[2]Calving ease score equal to 1 indicates no problem, 2 indicates slight problem, 3 indicates needed assistance, 4 indicates considerable force, and 5 indicates extreme difficulty.

$$p\left(\mathbf{y} \mid \mathbf{l}_{\mathrm{ce}},,,t\right)=\prod_{i=1}^{n}\begin{array}{l}\left[I\left(l_{cei}\leq t\right)I\left(y_{cei}=1\right)\right.\\ \left.+I(l_{cei}>t)I\left(y_{cei}=2\right)\right]\end{array},$$

where I is an indicator function that takes the value of 1 if the specified condition is true, otherwise, it takes the value of 2.

Variance components were estimated on the observed and liability scales using linear and threshold models, respectively, under a Bayesian approach using the Gibbs sampling methodology implemented in the GIBBSF90+ v3.23 software (Misztal et al., 2014; Lourenco et al., 2022). First, a Gibbs chain of 100K samples was generated. Then, after discarding the initial 20K samples, 1 in every 10 samples was stored to compute the means and SD of the posterior distributions. Estimated breeding values were obtained via the BLUP under the linear and threshold models described above. Computations were done using the BLUP90IOD3 v3.139 and CBLUP90IOD2 v3.39 software (Misztal et al., 2014) for linear and threshold models, respectively. Both programs implement the preconditioned conjugate gradient algorithm with iteration on data (Tsuruta et al., 2001) for optimal computing performance.

Model Comparison

For model comparison, we used the LR method. This method, derived from linear regression, compares genetic evaluations using partial and whole data based on differences in means, covariance, and correlation (Legarra and Reverter, 2018). Data after 2022 were used as a validation set, allowing us to estimate dispersion, bias, and correlation for EBV. Additionally, we assessed the accuracy of the partial dataset using the equation provided by Legarra and Reverter (2018). For the first lactation, the complete and partial datasets had 231,842 and 220,520 phenotypes, respectively. Considering the first 3 lactations, the complete and partial datasets had 1,291,660 and 1,223,583 phenotypes, respectively.

To investigate the concordance between EBV from linear and threshold models, we used Spearman rank correlation, considering purebred and crossbred animals, and bulls with reliabilities greater than or equal to 0.5. Computing time and the number of iterations to reach convergence were also evaluated as model feasibility indicators. Furthermore, we compared the proportion of easy calving progeny for the top 5% and bottom 5% bulls based on linear EBV and threshold EBV, considering 1 or 3 lactations.

RESULTS AND DISCUSSION

Table 2 presents the CE incidence for all crosses in the first and first 3 lactations and the number of records in each case. It is possible to see that there is a preference in the choice of animals to be crossed. Regarding breeds, there are ~4 times more Holstein than Jersey cows, and there is a preference for Angus and Simmental bulls. Crossbreeding with Charolais represents only 4% and 7% of the records for the first and first 3 lactations, respectively. This preference for Holstein, Angus, and Simmental seems to come from the fact that these dairy and beef breeds are known for their success in reducing calving difficulty and birth weight (Saad et al., 2020; Miller, 2021). Another factor that seems to be preferred, based on the number of records, is the parity of the cows. The number of records in the second and third parities is 2 times as high as the number of records in the first parity. Depending on the dam-sire breed combination, CE scores equal to 1, indicating "easy" births free from dystocia, were more frequent in the first 3 lactations than in the first lactation alone (Table 2).

In this study, ~88% and 7% of the scores were equal to 1 (no problem) and 2 (slight problem), respectively, independently of lactation order (Table 1), showing that calving difficulty is not frequent in these beef-on-dairy data. The high rate of easy calvings indicates low variability of the trait, which could result in low genetic variability and genetic parameters of small magnitude. In contrast, the low incidences of difficult calving are probably because beef breed associations focus on obtaining lighter calves at birth (Bourdon and Brinks, 1982; Togashi et al., 2024). Smaller, lighter calves are less likely to have birth issues. Basiel et al. (2024) investigated the effect of several beef bull breeds on dystocia when they were used to inseminate cows in US dairy herds. The authors initially considered dystocia as CE scores ≥4 and found an incidence of less than 1%. Due to the low incidence, the authors decided to consider dystocia scores ≥3, which increased the incidence to 3%. Although the change in coding increased the average probability of dystocia incidence by calf sire breed, the authors did not find significant differences among breeds in both scenarios. As in Basiel et al. (2024), our initial idea was to use different thresholds to define easy or difficult calving, as in the one proposed by CDCB (2022), in which easy = 1 to 3 and difficult = 4 and 5. However, due to the low incidence of difficult calvings when using this coding, we could not achieve model convergence. Therefore, we considered only the first coding (easy = score equal to 1, difficult = scores from 2 to 5) to estimate the variance components and breeding values.

Table 2. Incidence of calving ease score and number of observations (N_{CE}) per crossing considering the first and (first 3) lactations

Breed[1]		Calving ease incidence (%)[2]					N_{CE}[3]
Dam	Sire	1	2	3	4	5	Lac_1 (Lac_3)
HO	AN	88 (88)	6 (7)	5 (4)	0.5 (0.5)	0.5 (0.5)	161,572 (824,589)
	CH	73 (88)	10 (5)	12 (5)	3 (1)	2 (1)	3,421 (32,949)
	SM	88 (87)	7 (8)	4 (4)	1 (1)	0 (0)	24,479 (188,336)
JE	AN	91 (92)	5 (4)	3 (3)	1 (0.5)	0 (0.5)	20,394 (85,144)
	CH	90 (94)	5 (3)	3 (1)	1 (1)	1 (1)	6,665 (55,113)
	SM	78 (84)	16 (12)	5 (3)	0.5 (0.5)	0.5 (0.5)	15,311 (105,529)

[1]HO = Holstein; AN = Angus; CH = Charolais; SM = Simmental; JE = Jersey.

[2]Calving ease score equal to 1 indicates no problem, 2 indicates slight problem, 3 indicates needed assistance, 4 indicates considerable force, and 5 indicates extreme difficulty.

[3]Lac_1 = first lactation, Lac_3 = first 3 lactations.

Estimation of Variance Components and Genetic Parameters

Variance components and genetic parameters were different from zero, except for the covariance between direct and maternal effects, which was disregarded. Variance components estimated by threshold models are usually greater than those estimated by linear models, despite the proportion of genetic variance being close (Vanderick et al., 2014). Direct and maternal heritabilities from the linear (threshold) model were respectively equal to 0.014 ± 0.002 (0.002 ± 0.001) and 0.016 ± 0.002 (0.040 ± 0.004) for the first lactation and equal to 0.014 ± 0.002 (0.011 ± 0.009) and 0.186 ± 0.002 (0.256 ± 0.006) considering the first 3 lactations. The variance components and genetic parameters for the first and first 3 lactations can be seen in Table 3.

Herd-year interaction presented the highest variances in all models. This effect represents differences in phenotypes due to births occurring in different herds and years, so the high variances may be partly due to differences in subjective scoring of CE within each herd. Vanderick et al. (2014) found the same behavior using linear and threshold models for CE in Holsteins. In their work, the authors highlight the importance of considering herd-year as random to avoid statistical and convergence problems. We can have such problems when considering the contemporary group as a fixed effect in threshold models because they contain groups of small size or without variation in scores, that is, with an extreme category problem (Misztal et al., 1989; Lourenco et al., 2022).

The heritabilities of calving performance traits are generally low (ICAR, 2022). In our study, the direct genetic h^2 was low and identical in all scenarios ($h^2_a = 0.01$), except for the threshold model using 3 lactations, when it was equal to 0.03. In general, higher heritabilities are usually expected more with threshold models than linear models (Weller and Gianola, 1989; Vanderick et al., 2014). McGuirk et al. (1998) estimated genetic parameters for calving traits in beef × dairy crosses in the United Kingdom, considering 3 categories of CE on both observed and liability scales using a sire model. These authors found a sire h^2 of 0.09 and 0.16 for observed and liability scales, respectively. Although we have obtained results with smaller direct heritabilities and similar behavior regarding linear and threshold models, in which

Table 3. Posterior mean ± posterior SD of variance components and genetic parameters for calving ease in beef-on-dairy using linear (LIN) and threshold (THR) models considering only the first ($_1$) and first 3 ($_3$) lactations

Parameter[1]	LIN_1	THR_1	LIN_3	THR_3
σ^2_h	0.061 ± 0.002	1.683 ± 0.063	0.066 ± 0.001	3.902 ± 0.160
σ^2_a	0.002 ± 0.000	0.005 ± 0.004	0.002 ± 0.000	0.075 ± 0.069
σ^2_m	0.002 ± 0.000	0.113 ± 0.011	0.024 ± 0.000	1.712 ± 0.058
σ^2_e	0.062 ± 0.000	1.00 ± 0.004	0.038 ± 0.000	0.999 ± 0.002
h^2_a	0.014 ± 0.002	0.002 ± 0.001	0.014 ± 0.002	0.011 ± 0.009
h^2_m	0.016 ± 0.002	0.040 ± 0.004	0.186 ± 0.002	0.256 ± 0.006

[1]Where: σ^2 are the variance components for herd-year (h), direct genetic (a), maternal genetic (m), residual genetic (e) effects; h^2 are the heritabilities for direct (a) and maternal (m) effects.

the threshold model exhibited greater h^2, the results are not directly comparable, as the models and the categories for CE used differed. Due to the lack of studies evaluating genetic parameters in beef-on-dairy, we compared our results with previous studies that used purebred beef or dairy cattle breeds. Direct CE heritabilities previously published ranged between 0.02 and 0.29, in which dairy breeds usually present lower values than beef breeds (Ahlberg et al., 2016; ICAR, 2022). In Holsteins, heritabilities ranged from 0.03 to 0.12 (Weller and Gianola, 1989; Wiggans et al., 2003; López de Maturana, 2007; Eaglen et al., 2012). Jeyaruban et al. (2016) estimated genetic parameters for calving difficulty in 5 beef breeds in Australia and found direct heritabilities equal to 0.24, 0.22, and 0.17 for Angus, Charolais, and Simmental breeds, respectively. Eaglen et al. (2012) compared primiparous and multiparous Holstein cows and found that the percentage of easy calving increased by 11 percentage points for multiparous cows and that direct and maternal heritabilities were reduced by at least half in analyses using data from multiparous cows. In our case, the incidences did not differ when we considered the first 3 lactations, so there were no drastic changes in direct h^2 values.

Maternal heritabilities were greater than direct in all models. When considering only the first lactation, the slight difference observed comes from potential confounding between direct and maternal genetic effects. They were much larger when we considered the first 3 lactations than when we used only the first lactation. This may have been partly due to the lack of maternal permanent environmental effect in the model, as cows did not have enough data to ensure convergence for this effect. Therefore, the maternal permanent environmental effect seems to have been captured by the maternal effect, as Vanderick et al. (2014) found in their preliminary analyses of CE in Holstein. Maternal heritabilities were within the range found in the literature, which was between 0.02 and 0.20 (Wiggans et al., 2003; Eaglen et al., 2012; Jeyaruban et al., 2016; ICAR, 2022; American Angus Association, 2024). Maternal heritabilities from models considering 3 lactations were more similar to those found in beef breeds, such as Charolais and Angus, than those found in dairy breeds (Jeyaruban et al., 2016; American Angus Association, 2024). These estimates are not directly comparable because the authors consider purebreds and use different models, such as sire and maternal grandsire and multiple-trait models, and different effects, for example, some of them did not consider maternal or maternal permanent environment effects.

To investigate the maternal h^2 inflation, we randomly omitted data from cows with more than one scored calving. Using the same model, with the first 3 lactations and only one record per dam, considering 1.1 million CE records, we found that the maternal h^2 was equal to 0.03 ± 0.003 for the linear model and 0.02 ± 0.002 for the threshold model. The direct heritabilities remained the same as when using data with cows with repeated records, equal to 0.01 ± 0.001 and 0.02 ± 0.002 for the linear and threshold models, respectively. These results suggest that there were not enough records per cow to accurately estimate the maternal effect, especially the permanent environmental maternal effect. The latter, when included, could not be estimated, as the model did not converge. This is also one of the reasons why the maternal effect was overestimated in the model with 3 lactations.

We also tested the same model by considering the 2 different dairy breeds, Holstein and Jersey, separately. Most of the variance components and genetic parameters were different from zero. However, when we used threshold models under Gibbs sampling, the Gibbs chains showed very large fluctuation due to the limited and unbalanced number of phenotypes in each combination with beef breeds (Angus, Charolais, or Simmental). The number of observations in each breed combination is in Table 2. For the direct effect, we found heritabilities ranging from 0 to 0.08, and for the maternal effect, this ranged from 0.01 to 0.25 (Appendix Table A1).

The direct heritabilities in our study were low, which can indicate that the pedigree is shallow and disconnected. In the future, more information on relatives or the use of genomic information can help capture more genetic variation.

Model Comparison

Considering all animals in the pedigree, the EBV ranking correlations from the linear and threshold models for direct and maternal effects were 0.96 and 0.98, respectively, when we analyzed the first lactation and 0.91 and 0.97, respectively, when we analyzed the first 3 lactations. Because we are working with 5 different breeds, it is important to note that there may be differences in these correlations within some breeds. The Spearman ranking correlations between the EBV from the linear and threshold models for direct and maternal effects within each breed are presented in Table 4.

For the dairy breeds, Holstein and Jersey, distinguishing between the cows (female) and the cows' sires (male), we can see that the correlations were high, where for direct EBV, this ranged from 0.93 to 0.98, and for maternal EBV, it ranged from 0.94 to 0.98. When we look at the bulls of the beef breeds, Angus, Charolais, and Simmental, for the direct effect, the EBV ranking correlations were high and ranged from 0.91 to 0.95, but the EBV correlations for the maternal effect were very close to zero and even negative for Angus, considering the first lactation, and Charolais, considering the first 3 lactations. These distinct correlations, when compared with the dairy breeds, probably occurred because we have almost no female animals in these breeds. Only about 400 bulls have information on at least 1 known parent, with only 343 known dams (for the number within each breed, see Figure 1). Due to the lack of dam information in the beef pedigree and the fact that we do not have phenotyped beef females, the estimation of the maternal genetic value for this effect proved to be inconsistent between the 2 evaluations. Fortunately, in beef-on-dairy systems in the United States, the maternal EBV of beef bulls, which tells us about the ability of the daughter of that animal to have an easy calving, is useless because the calf resulting from the cross is the final product and will be harvested. For all breeds, the ranking correlations between direct EBV estimated in the 2 models, linear and threshold, were at least 0.87. These high correlation values between direct EBV suggest that selection decisions will not be substantially affected using linear instead of threshold models.

The intensity with which we use an animal for breeding is determined by the confidence we have in its EBV. This confidence is called reliability, which ranges from 0 to 1, and the closer to 1, the more likely it is that the EBV is close to the animal's true breeding value. Animals with high reliability are preferentially selected, and because of this, we also investigated the EBV rank correlation, estimated by the linear and threshold models, using only bulls with reliabilities greater than 0.5 in each breed (Table 5). As expected, with the filter applied to reliability, the number of animals decreased considerably, but the behavior did not change. The correlations for direct EBV remained close to 1 for all breeds, and for the beef breeds, the maternal correlations were very close to zero.

Alongside the rank correlations, we used the LR validation metrics to compare models. Within the metrics, bias and b_0 equal to or close to zero, and b_1 equal to or close to 1, are ideal. Where b_0 and b_1 are the parameters of the regression of EBV in the complete data on EBV in the partial data. When b_1 values are lower than 1, EBV from partial data are overdispersed, and values greater than 1 indicate that EBV from partial data are underdispersed. Correlation and accuracy values, where accuracy is the accuracy of the partial EBV, as described in Legarra and Reverter (2018), as close to 1 as possible, are desirable. Pearson correlation between the EBV obtained from total and partial data shows the consistency between the estimations, whereas the partial data accuracy shows the accuracy of the EBV from partial data as a function of the EBV from whole data (Legarra and Reverter, 2018). Table 6 shows the LR parameters for linear and threshold models considering only the first and first 3 lactations. The b_0 and bias values were considered ideal in all sce-

Table 4. Spearman rank correlations between EBV from threshold and linear models for the first (LAC_1) and first 3 (LAC_3) lactations, considering only purebred animals

Item	Female				Male				Male					
	Holstein		Jersey		Holstein		Jersey		Angus		Charolais		Simmental	
	LAC_1	LAC_3	LAC_1	LAC_3	LAC_1	LAC_3	LAC_1	LAC_3	LAC_1	LAC_3	LAC_1	LAC_3	LAC_1	LAC_3
Direct	0.97	0.97	0.97	0.96	0.98	0.95	0.98	0.93	0.95	0.92	0.94	0.92	0.93	0.91
Maternal	0.98	0.97	0.98	0.97	0.98	0.95	0.98	0.94	−0.02	0.15	0.07	−0.05	−0.11	0.08
$N_{ANIMALS}$	189,472	929,848	42,370	220,899	10,838	23,187	2,858	6,586	1,921	3,595	132	330	257	557

Table 5. Spearman rank correlations between EBV from threshold and linear models for the first (LAC_1) and first 3 (LAC_3) lactations, considering only purebred bulls with reliabilities ≥0.5

	Dairy bull				Beef bull					
	Holstein		Jersey		Angus		Charolais		Simmental	
Item	LAC_1	LAC_3	LAC_1	LAC_3	LAC1	LAC3	LAC1	LAC3	LAC1	LAC3
Direct	0.97	0.94	0.97	0.92	0.89	0.93	0.97	0.95	0.86	0.92
Maternal	0.97	0.96	0.97	0.96	0.24	0.28	0.09	−0.05	−0.08	−0.09
$N_{ANIMALS}$	222	793	33	181	63	1,043	4	103	20	141

narios. Both values were close to zero, indicating that there was no bias. As previously mentioned, the slope (b_1) shows the breeding values dispersion. The linear model using only the first lactation presented the least dispersion, with a slope close to 1. Nevertheless, the threshold model, also considering only the first lactation, was shown to be largely underestimated, with a slope 2 times as large as expected. This indicates that the EBV of the partial data in this scenario were much smaller than the EBV obtained when using the complete data. This is reasonable because we have many fewer phenotypes when considering only the first lactation, and the animals do not have a connected pedigree to be able to estimate these EBV. In addition, threshold models are generally more complex because they have more variables to be estimated (thresholds) than linear models. The high correlation in this model supports that all EBV in this scenario had the same behavior (underestimated). The models using the first 3 lactations were overdispersed but more stable.

Accuracies ranged from 0.14 to 0.35. Models using the first 3 lactations showed higher accuracies when compared with equivalent models using only the first lactation. Because they have more data over time and more data per animal, it is expected that excluding recent data will have less effect on the accuracy of breeding values than when having a small amount of data. The threshold model, considering only the first lactation, had the lowest accuracy, reinforcing the underestimation of EBV in the partial data of this model. In general, linear models perform better than threshold models and are less computationally expensive. Misztal et al. (1989) showed that threshold models require 3 to 5 times more computing time than linear models. The computational cost is a function of the number of iterations and the time per iteration. In addition to the number of iterations being greater when using the threshold model, the time per iteration when using the threshold model was at least 2.5 times greater than when using the linear model, reflecting the computational complexity of this nonlinear statistical method. As expected, linear models and models that included only the first lactation were faster. It took at least 9-fold less time when we used linear instead of threshold models, and models with only the first lactation took at least half the time of models using the first 3 lactations. Considering only the first lactation, the linear model took 5 min and the threshold 45 min to converge (75 and 4K iterations, respectively). When we added the phenotypes from the other 2 lactations, the linear model took 10 min, and the threshold took 270 min to converge (289 and 5K interactions, respectively).

The proportion of progeny with easy calvings for the top 5% and bottom 5% bulls based on EBV from linear and threshold models (Figure 2) shows that the linear model was better at distinguishing progeny from top and bottom bulls. Considering only the first lactation, the proportion of progeny with easy calvings in the top bull group was higher for the linear model (91%) compared with the threshold model (89%). In contrast, the proportion was lower for the bottom 5% bulls using the linear model (81%) compared with the threshold model (85%). When looking at the first 3 lactations, there was almost no difference between the 2 models for the top 5% bulls (90% in linear vs. 89% in threshold). However, the linear model still showed a lower proportion of easy calvings for the bottom 5% bulls (82%) compared with the threshold model (86%). Therefore, the linear model was better able to differentiate the progeny performance between top and bottom bulls, as the differences between the 2 groups were larger (about 10 percentage points compared with 4 percentage points in threshold models). The numerical differences in favor of 1 versus 3 lactations were negligible.

Table 6. Parameters for linear (LIN) and threshold (THR) models considering the first ($_1$) and the first 3 ($_3$) lactations using the LR method

Parameter[1]	LIN_1	THR_1	LIN_3	THR_3
b_0	−0.0001	0.0001	0.0002	0.0011
b_1	0.98	2.11	0.80	0.96
bias	0.0001	0.0009	−0.0005	−0.0017
corr	0.89	0.95	0.89	0.94
acc	0.31	0.14	0.35	0.17

[1]Where: b_0 and b_1 are the linear regression parameters, bias $= \widehat{\mathbf{u}}_p - \widehat{\mathbf{u}}_w$, corr = Pearson correlation, acc = accuracy.

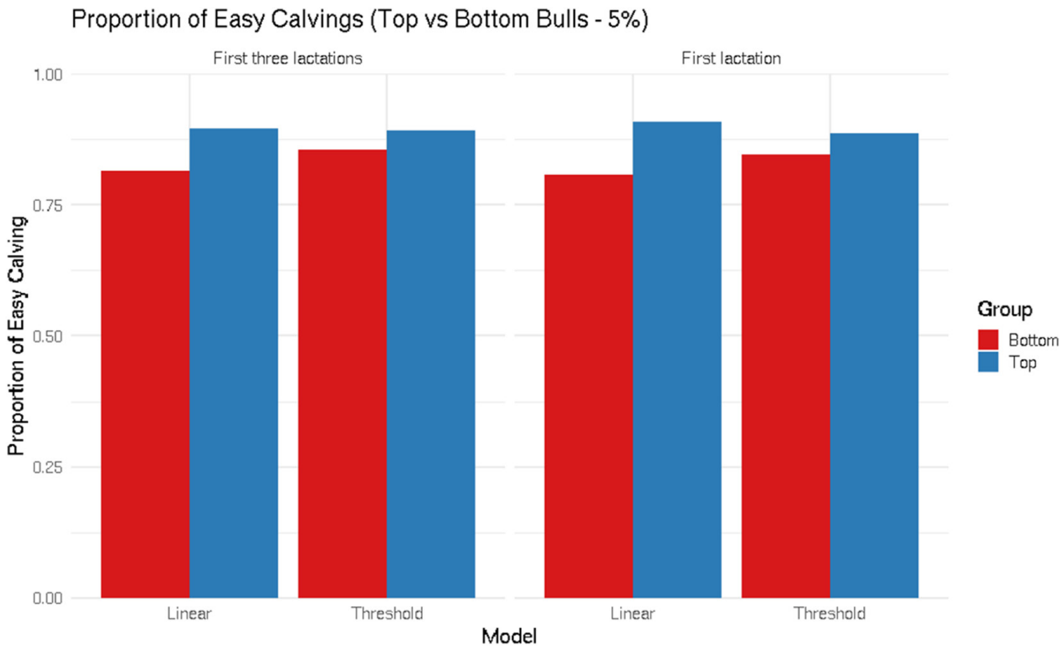

Figure 2. Proportion of easy calvings (calving ease score = 1) for the top 5% and bottom 5% of sires ranked by EBV obtained when using linear and threshold models. Results are shown for the first lactation (left panel) and the first 3 lactations combined (right panel).

Working with genetic parameters in a beef-on-dairy scenario is challenging, and the biggest challenge is in the structure of the dataset and pedigree. The phenotype must always be attributed to the calf, as it is the only link between the 2 breeds. If the phenotype is attributed to the cow, the beef bulls would be left without breeding value predictions. Additionally, accurate separation of direct and maternal effects requires CE records for the dams at birth, a large number of progenies with CE phenotypes per dam, and deep pedigree information. In beef-on-dairy, however, phenotypes are typically available only for a single progeny generation, as crossbred animals are not retained for breeding, although some collateral information may be available. Furthermore, the primary selection objective is to improve the performance of purebred parents. When cows are selected for CE based on their progeny performance (i.e., when progeny phenotypes are included in the evaluation), genetic progress can occur in both direct and maternal effects.

Regarding the pedigree, as the sire and dam are of different breeds, the pedigrees are disconnected and collected with different focuses. For dairy cattle, greater attention is given only to the sires of the cows, and for beef cattle, the bulls' pedigree used in this scenario is often full of gaps. Some bulls have a large number of phenotyped progeny, which increases their EBV reliability, but because most bulls have no known ancestry, this large amount of information does not help the reliability of the others. Moreover, we know that the h^2 for this trait is usually higher than that found here, especially for beef cattle. This leads us to believe that a better and more connected data structure, as well as a more complete and connected pedigree inside each breed, would help us find higher and more accurate heritabilities for this trait in the beef-on-dairy scenario. It would be valuable to have access to the pedigree records from the associations of the breeds involved.

CONCLUSIONS

We evaluated the computational aspects and the genetic background of CE in beef-on-dairy crosses. Overall, working with beef-on-dairy data is still challenging. The data structure and lack of pedigree depth and connection can make variance components estimation an ambitious task. Low incidences of extremely difficult calving (scores 4 and 5) make it hard to apply the definition of easy and difficult calving proposed by the dairy cattle industry (1 to 3 = easy; 4 to 5 = difficult). Adopting the definition used in beef cattle (1 = easy; 2 to 5 = difficult) is attainable. Although the direct heritabilities in our study were low, there is genetic variability for CE, and accounting for this trait when selecting beef bulls can help reduce the incidence of difficult calving in beef-on-dairy crosses. When the data structure is limited, we suggest using linear models considering only the first lactation, given that EBV are highly correlated with those obtained by the threshold model but are less biased and almost 10 times faster, proving to be more efficient for routine genetic evaluations. Furthermore, the linear model was better than the threshold model at distinguishing the proportion of progeny with easy calvings between the top 5% and bottom 5% bulls. Larger datasets with more repeated records should be investigated for the effect of the maternal permanent environment effect and better estimation of the additive genetic maternal effect. Replicating this study with larger, more connected beef and dairy datasets will help to validate our results.

NOTES

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Nonstandard abbreviations used: CE= calving ease; LR = derived from linear regression.

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APPENDIX

Table A1. Posterior mean ± posterior SD of variance components and genetic parameters for calving ease (CE) in beef-on-dairy and linear (LIN) and threshold (THR) models considering only the first ($_1$) and first 3 ($_3$) lactations for Holstein and Jersey breeds separately

Holstein[1]	LIN_1	THR_1	LIN_3	THR_3
σ_h^2	0.03 ± 0.001	1.29 ± 0.063	0.03 ± 0.000	1.57 ± 0.412
σ_a^2	0.00 ± 0.000	0.11 ± 0.018	0.00 ± 0.000	0.18 ± 0.050
σ_m^2	0.00 ± 0.000	0.07 ± 0.026	0.01 ± 0.000	0.46 ± 0.520
σ_e^2	0.03 ± 0.000	1.00 ± 0.005	0.02 ± 0.000	0.99 ± 0.002
h_a^2	0.02 ± 0.002	0.04 ± 0.007	0.01 ± 0.000	0.06 ± 0.027
h_m^2	0.01 ± 0.001	0.03 ± 0.010	0.20 ± 0.000	0.11 ± 0.116
Jersey[2]				
σ_h^2	0.01 ± 0.001	0.64 ± 0.089	0.02 ± 0.001	1.15 ± 0.142
σ_a^2	0.00 ± 0.000	0.16 ± 0.043	0.00 ± 0.000	0.19 ± 0.029
σ_m^2	0.00 ± 0.000	0.08 ± 0.030	0.00 ± 0.000	0.89 ± 0.112
σ_e^2	0.04 ± 0.000	1.00 ± 0.001	0.02 ± 0.000	1.00 ± 0.004
h_a^2	0.03 ± 0.004	0.08 ± 0.020	0.00 ± 0.001	0.05 ± 0.007
h_m^2	0.02 ± 0.005	0.04 ± 0.014	0.18 ± 0.006	0.25 ± 0.020

[1]Where: σ^2 are the variance components for herd-year (h), direct genetic (a), maternal genetic (m), and residual effects; h^2 are the heritabilities for direct (a) and maternal (m) effects.