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Evaluation of gestation length in Czech Holstein cattle

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Abstract: An objective of our study was to evaluate gestation length and its genetic variability in the Czech Holstein population. Data set consisted of 770 865 records of gestation length in 375 574 Holstein cows and covered the period from 2012 to 2018. Mean gestation length was 277 ± 4.9 days, and it was 1.4 days longer in male calves compared to females, and 1.1 days longer in cows compared to heifers. Animal repeatability model with maternal effect was employed for variance component estimation. The direct genetic effect explained the highest proportion of variability, and it corresponded with moderate direct heritability (0.48), while maternal heritability was much lower (0.06). We estimated conventional and genomic breeding values with the genomic matrix based on 39 145 single nucleotide polymorphisms in 13 844 animals. Genomic breeding values were weakly (< 0.25) but significantly correlated with breeding values for type, production and fitness traits. Pearson correlations between breeding values indicated a negative association of direct gestation length with milk production, longevity and fertility of bulls, and a positive association of maternal gestation length with most of the type traits related to the body composition. Genetic trends for male and female parts of the population showed a tendency to the shortening of gestation, which should be of concern, as short gestation could be reflected in a negative indirect response in other correlated traits, such as the incidence of stillbirth, the health status of cows after calving, culling, or conception rate.

Keywords: genetic trend; genomic evaluation; heritability; pregnancy

Gestation length (GL) is a physiological trait important for foetal and mammary gland development and successful transition of a cow (Davis 2017; Vieira-Neto et al. 2017). Intermediate GL is optimal for calving ease, stillbirth, culling, and length of productive life (Norman et al. 2011). It is associated with better health, production and reproduction traits, while shorter and longer intervals could lead to higher morbidity, culling, incidence of stillbirth, retained placenta, metritis, lower milk production and lower pregnancy after the first service (Eaglen et al. 2013; Vieira-Neto et al. 2017). The selection for shorter or longer gestation is not generally recommended (Hansen et al. 2004; Eaglen et al. 2013), though the selection for shortening GL is a common practice in pasture-based production systems. For example, Haile-Mariam and Pryce (2019) showed that GL could be modified by up to 3.5 days by selective mating of bulls with short GL estimated breeding value (EBV), which could contribute to a reduction of calving induction. Although GL is not a part of breeding programmes in many countries, with its moderate heritability, GL information could lead to higher accuracy of genetic evaluation of calving ease and perinatal survival of calves (Hansen et al. 2004; Jamrozik et al. 2005; Johanson et al. 2011; Eaglen et al. 2013) and

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should be included in the evaluation of calving performance.

Many environmental and genetic factors affect GL. Sex of the calf belongs to the most important when male calves are carried 1 to 2 days longer than female calves (Tomasek et al. 2017; Haile-Mariam and Pryce 2019). Another known factor is the age or the parity of the dam when heifers have up to 1.6 days shorter gestation than cows (Norman et al. 2009; Tomasek et al. 2017; Haile-Mariam and Pryce 2019). Shorter gestation is associated with spring and summer months of calving, higher temperature and humidity in the calving season (Hansen et al. 2004; Vieira-Neto et al. 2017). Tao and Dahl (2013) also reported shorter GL and lower birth weight due to heat stress, which compromised placental development, and led to foetal hypoxia, malnutrition and growth retardation. Significant differences in GL were reported between dairy cattle breeds (Norman et al. 2009; Wright and VanRaden 2017; Nienartowicz-Zdrojewska et al. 2018).

Genetic factors include direct genetic effect which is the property of the calf, and it is expressed at birth, and maternal genetic effect which is the property of the dam, and it is expressed whenever she calves (Eaglen et al. 2013). Direct heritability of GL varied from 0.27 to 0.50, while maternal heritability was usually considerably lower, from 0.02 to 0.13 (Hansen et al. 2004; Jamrozik et al. 2005; Norman et al. 2009; Haile-Mariam and Pryce 2019).

As gestation length is related to many economically important traits, there is a growing interest to include it as an indicator trait in the selection of Czech Holstein cattle. The objective of our study was to describe the variability of gestation length in the Czech population of Holstein cattle, to design a model for its genetic evaluation and to estimate heritabilities and breeding values for this trait.

MATERIAL AND METHODS

The reproduction data were obtained from the Czech Moravian Breeders' Association. Records covered the period from January 2012 to December 2018. Data were edited to include only the calvings of Holstein cows (H100 genes ≥ 75%) after artificial insemination (AI) with H100 bulls. Each cow had to have the record of her first (heifer) GL. Parities later than the second were merged into one class, as they did not differ significantly in GL. Gestation length was calculated as a difference between the date of calving and the date of the last preceding artificial insemination (AI). Records with GL < 260 and GL > 296 (the interval was defined as mean GL ± 3 SD), calves without identification number and twin births (2.8%) were excluded from evaluation. Each sire had to have at least 10 offspring, each class of herd-year-season (HYS) of calving effect had to have at least five records. The edited dataset consisted of 770 865 records of GL in 373 574 Holstein cows.

Gestation length in heifers and cows was treated as one trait, thus a single-trait animal model with maternal effect was employed for variance component estimation:

$$Y_{ijklmno} = \mu + sex_i + PAR_j + YS_k + HYS_l + PE_m + MAT_n + A_n + e_{ijklmno} \quad (1)$$

where:

$Y_{ijklmno}$ – gestation length;
μ – population mean;
sex_i – fixed effect of sex of calf (two levels: male, female);
PAR_j – fixed effect of parity of cow (two levels: 1 ≥ 2);
YS_k – fixed year-season of calving effect (15 levels);
HYS_l – random effect of herd-year-season of calving (9 245 levels: herd – 813 levels; season of calving – two levels: April–September, October–March; year of calving – six levels: 2012–2018);
PE_m – random maternal permanent environmental effect (373 574 levels);
MAT_n – random maternal genetic effect;
A_n – random direct additive genetic effect (1 370 085 animals in the pedigree);
$e_{ijklmno}$ – random residual error.

The model in matrix notation is:

$$y = Xb + Z_1h + Z_2a + Z_3m + Z_4pe + e \quad (2)$$

where:

y – the vector of phenotypic observation (gestation length);
X and Z – incidence matrices of fixed and random effects;
b – the vector of fixed effects (parity of cow, sex of calf, year-season of calving);
h – the vector of HYS effects;

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a – the vector of direct additive genetic effects;
m – the vector of maternal genetic effects;
pe – the vector of maternal permanent environmental effects;
e – the vector of residuals.

We assumed that random effects were normally distributed as $[h' \; a' \; m' \; pe' \; e']' \sim \mathrm{N}[0, \mathrm{V}]$ with:

$$\mathrm{V} = \textstyle\sum_{i=1}^{4} \mathrm{V}_i \qquad (3)$$

where:
V – the random covariance matrix;
V_1 – I ⊗ S (I is the identity matrix, S is the covariance matrix for HYS effects, ⊗ is the Kronecker product of matrices);
V_2 – A ⊗ G (A is the additive relationship matrix, G is the genetic covariance matrix for direct and maternal genetic effects);
V_3 – I ⊗ P (P is the covariance matrix for maternal PE effect);
V_4 – I ⊗ E (E is the residual covariance matrix).

The direct additive genetic variance (σ^2_{A}), the maternal genetic variance (σ^2_{M}), the herd-year-season variance (σ^2_{HYS}), the permanent environment variance (σ^2_{PE}) and the covariance between direct genetic and maternal effects ($\sigma_{\mathrm{A,M}}$) were derived directly from the animal model variance-covariance matrices.

Breeding values were estimated using pedigree (estimated breeding values, EBV) or pedigree and genomic (genomic breeding values, GEBV) information. A total of 13 884 animals (9 465 females, 4 419 males) were genotyped using the Illumina BovineSNP50 Bead Chip (Illumina, San Diego, CA, USA). After elementary quality control (SNPs with call rate < 0.90, SNPs with minor allele frequency MAF < 0.05, monomorphic SNPs, animals with call rate < 0.90, parent-offsrping Mendelian conflict) 39 145 SNPs were revealed. Genomic information was incorporated into the model equation by extending the additive relationship matrix A to matrix H (Legarra et al. 2009), which defines relationships between genotyped and non-genotyped animals so that:

$$\mathrm{H} = \mathrm{A} + \begin{vmatrix} 0 & 0 \\ 0 & \mathrm{G} - \mathrm{A}_{22} \end{vmatrix} \qquad (4)$$

where:
H – the modified genetic relationship matrix;
A – the additive relationship matrix;
G – the genomic relationship matrix.

Genomic breeding values were then calculated using a single-step approach – ssGBLUP (Aguilar et al. 2010; Christensen and Lund 2010). The sparse Cholesky (FSPAK) solver as implemented in BLUPF90 family of programs was employed for breeding value estimation that also calculated the standard errors for each breeding value. The reliabilities of breeding values were calculated as:

$$r^2_{\mathrm{(G)EBV}} = 1 - (SE^2/\sigma^2_{\mathrm{A}}) \qquad (5)$$

where:
$r^2_{\mathrm{(G)EBV}}$ – reliability of genomic breeding value;
SE – the standard error of estimated breeding value;
σ^2_{A} – the direct genetic variance.

Genetic trends were expressed as mean GL-GEBV of sires and females according to birth year. Pearson correlation coefficients between GL-GEBV of sires estimated with the reliability higher than 0.6 and officially published genomic breeding values [(G) EBV] were computed to approximate the associations between them. We used (G)EBV for 23 type traits (20 single traits and three total scores for body composition, udder and feet and legs, GEBV), six milk production traits (milk, fat and protein yield, fat and protein percentage, somatic cell count, GEBV), longevity trait (length of production life, GEBV) and six fertility traits (bull's own fertility tested on heifers, on cows and combined; calving ease – direct, maternal, direct in primiparous, EBV).

We used SAS/STAT® v9.4 software (SAS Institute Inc., Cary, NC, USA) for data editing and basic statistical evaluations. Variance components and breeding values were estimated with the BLUPF90 family of programs – REMLF90 for variance component estimation, BLUPF90 for EBV and GEBV estimation (Misztal et al. 2018).

RESULTS AND DISCUSSION

Fixed effects

The gestation length was calculated as the difference between the date of calving and the date of the last preceding insemination. The quality of GL data is, therefore, dependent on the quality of reproduction recording. As pointed out by Jamrozik et al. (2005), in herds with the lower management level the less complete recording of breeding data could result in overestimation of GL. The reproduction data recording and processing are defined by law in the Czech Republic, and each insemination, including re-insemination, has to be recorded to the central register. With the average herd size reaching 310 cows, 90% of breeders use early pregnancy diagnostics, including the sonography [Motycka Jiri, CEO (Holstein Cattle Breeders' Association, Hradistko, Czech Republic). Conversation with: Eva Kasna (Institute of Animal Science, Prague, Czech Republic). 2020 Aug 3]. Description of data used for evaluation is in Table 1. Mean GL was 277.6 ± 4.9 days with the mode of 278 days, which was comparable with the study of Norman et al. (2009) in US Holstein, who reported GL 278 days in heifers and 279 days in cows, and slightly less than those reported by Jamrozik et al. (2005) in Canadian Holstein (280 days) or by Haile-Mariam and Pryce (2019) in Australian Holstein (280.3 in heifers and 281.9 in cows).

All evaluated fixed effects were statistically significant ($P < 0.000\,1$). Sex of the calf explained 3% of total GL variability. GL was 1.4 days longer when male calves were born. Parity of the cow explained 2% of total variability and GL was 1.1 days shorter in heifers. Jamrozik et al. (2005) suggested evaluating GL in heifers and GL in cows as two different traits, as the correlation between them is lower than one. However, the estimates of genetic correlation were mostly > 0.95 in various studies (Norman et al. 2009; Haile-Mariam and Pryce 2019), so we decided to evaluate GL in heifers and cows as one trait.

Effects of calving year and season fitted as fixed explained 1% of the total variability. Gestations were 0.9 days shorter in summer (April–September) than in the winter season. Most authors explained this seasonal effect on gestation shortening by high temperature and humidity in summer (Hansen et al. 2004; Tao and Dahl 2013; Vieira-Neto et al. 2017). Tomasek et al. (2017) mentioned the possible effect of photoperiod during conception, when higher nocturnal melatonin secretion in decreasing daylight in autumn stimulates the development of the conceptus and also stimulates the production of progesterone with its beneficial effect on the conceptus growth, which leads to shorter gestations in late spring and summer months. The opposite tendency was documented by Nienartowicz-Zdrojewska et al. (2018) in Polish native cattle breeds, where winter gestations were 0.4 days shorter compared to gestations of cows calved in summer. We joined the effects of season and year of calving with the effect of herd, which itself explained 6% of the total variability. The resulting HYS effect was fitted as random mainly due to a large number of its levels. Herd-year-season as a random effect explained 5% of total phenotypic variance.

Table 1. Basic description of data used for gestation length evaluation

	n	%	Mean	SD
All	770 865	100.0	277.6	4.9
Parity of cow = 1	372 170	48.3	277.0	4.8
Parity of cow ≥ 2	398 695	51.7	278.1	4.9
Female calves	383 336	49.7	276.9	4.8
Male calves	387 529	50.3	278.3	4.9
Summer season (April–September)	386 903	50.2	277.1	4.9
Winter season (October–March)	383 962	49.8	278.0	4.8

n = number of animals; SD = standard deviation

Random effects

The estimates of variance components are shown in Table 2. Estimated total phenotypic variance (22.97), given as the sum of all variance components, corresponded well with sample phenotypic variance in Table 1 (24.01). Phenotypic variance reported for Holstein cattle in other studies ranged from 25.9 (Hansen et al. 2004) to 39.9 (Jamrozik

Table 2. Estimates of variance components of gestation length

Effect	Variance ± SE
Direct additive genetic σ^2_A	10.98 ± 0.263
Maternal genetic σ^2_M	1.41 ± 0.070
Direct – maternal genetic correlation $r_{A,M}$	0.05 ± 0.029
Permanent environment σ^2_{PE}	0.65 ± 0.041
Herd-year-season of calving σ^2_{HYS}	1.13 ± 0.070
Residual variance σ^2_E	8.79 ± 0.133
Total phenotypic variance σ^2_P	22.97
Ratios of variances	
Direct/total (direct heritability h^2_D)	0.48
Maternal/total (maternal heritability h^2_M)	0.06
Permanent environment/total	0.03
Herd-year-season/total	0.05
Residual/total	0.38

SE = standard error

et al. 2005) depending on the structure of evaluated data (shorter or longer GL interval, unknown sex of calves or including of twins). The direct genetic effect explained the highest proportion of variability and resulted in moderate direct heritability (0.48). Direct heritability estimates in other studies were mostly higher than 0.40 (Hansen et al. 2004; Norman et al. 2009; Johanson et al. 2011; Eaglen et al. 2013) except Jamrozik et al. (2005) and Haile-Mariam and Pryce (2019), who explained the lower estimates by methodology, considered components, as well as the quality and quantity of the data. As summarized by Hansen et al. (2004), maternal genetic effects had little influence on GL, as the onset of parturition is initiated by the calf. Most of the studies reported maternal heritability lower than 0.10 (Jamrozik et al. 2005; Johanson et al. 2011; Eaglen et al. 2013). Haile-Mariam and Pryce (2019) supposed that maternal effect could be omitted for practical reasons, as its reliability and usefulness were low, and the correlation of direct GL-EBV from the models with or without maternal component was higher than 0.96. On the contrary, Eaglen et al. (2013) supposed that the partitioning of the genetic relationship into direct and maternal components is crucial to understand how the trait would be affected by future selection. As reported by other authors (Hansen et al. 2004; Johanson et al. 2011), not taking into account the maternal effect could lead to overestimation of sire effect and biased estimate. In our opinion, considering the direct, maternal and permanent environment is necessary for a better understanding of the effect of offspring, sire and dam on gestation and its successful outcome. However, the permanent environmental effect is not reported in many studies, although its ignoring could inflate the maternal heritability. Our estimate of permanent effect was in line with those of Jamrozik et al. (2005) and Johanson et al. (2011).

Genetic correlation between direct and maternal effects was close to zero in our study, which was also reported by Hansen et al. (2004) and Johanson et al. (2011). Eaglen et al. (2013) found a stronger negative association between both components (–0.30 ± 0.13) and pointed out to the general tendency of the direct and maternal relationship to be opposite in sign across a variety of dairy traits. Also, Haile-Mariam and Pryce (2019) reported moderate negative genetic correlations estimated by sire-maternal grandsire model (–0.45 ± 0.11) and animal model (–0.36 ± 0.12).

Estimated breeding values

Average EBV and GEBV and their reliabilities are in Table 3. The genetic standard deviation for direct GL (SD = 2.35 days) corresponded with the results of other authors who reported SD values ranging from 1.41 (PTA of service sires, Norman et al. 2009) to 3.30 days (Hansen et al. 2004). The extreme values of direct GL-GEBV (–13.82 and +9.66 days in our study) were comparable with the range (–12.45 and +11.67 days) reported by Haile-Mariam and Pryce (2019). Lower variability was found in maternal GL-GEBV, as was expected based on heritability estimates. Standard deviations for maternal EBV ranged from 0.59 to 0.69 days, which indicated a comparable variability as was reported by Haile-Mariam and Pryce (2019). The correlation between conventional and genomic evaluation was close to one, although EBV were lower than GEBV. All means were negative, which indicated a general tendency to the shortening of GL in the Holstein population. This trend is well illustrated in Figure 1, where the reduction for direct genetic effect is evident in both male and female parts of the population, while the maternal effect is more or less stable. The shortening of gestation is probably the indirect response to long-term genetic selection for milk and protein yield and other economically important traits (longevity, fertility) that are negatively correlated with GL. The declining genetic

Table 3. Mean conventional (EBV) and genomic (GEBV) breeding values for direct (D) and maternal (M) genetic effect on gestation length in Czech Holstein cattle

	n	Mean ± SD	Reliability ± SD
EBV_D – all	1 370 095	–1.71 ± 2.353	0.46 ± 0.203
EBV_D – m	397 287	–2.37 ± 2.533	0.59 ± 0.065
EBV_D – f	972 808	–1.44 ± 2.219	0.40 ± 0.213
$GEBV_D$ – all	1 384 804	–1.04 ± 2.316	0.44 ± 0.195
$GEBV_D$ – m	399 637	–1.61 ± 2.539	0.58 ± 0.066
$GEBV_D$ – f	985 167	–0.82 ± 2.179	0.39 ± 0.204
EBV_M – all	1 370 095	–0.24 ± 0.600	0.24 ± 0.110
EBV_M – m	397 287	–0.31 ± 0.624	0.27 ± 0.073
EBV_M – f	972 808	–0.22 ± 0.588	0.23 ± 0.120
$GEBV_M$ – all	1 384 804	–0.79 ± 0.685	0.22 ± 0.097
$GEBV_M$ – m	399 637	–0.92 ± 0.662	0.24 ± 0.065
$GEBV_M$ – f	985 167	–0.73 ± 0.685	0.21 ± 0.106

f = females; m = males; *n* = number of animals; SD = standard deviation

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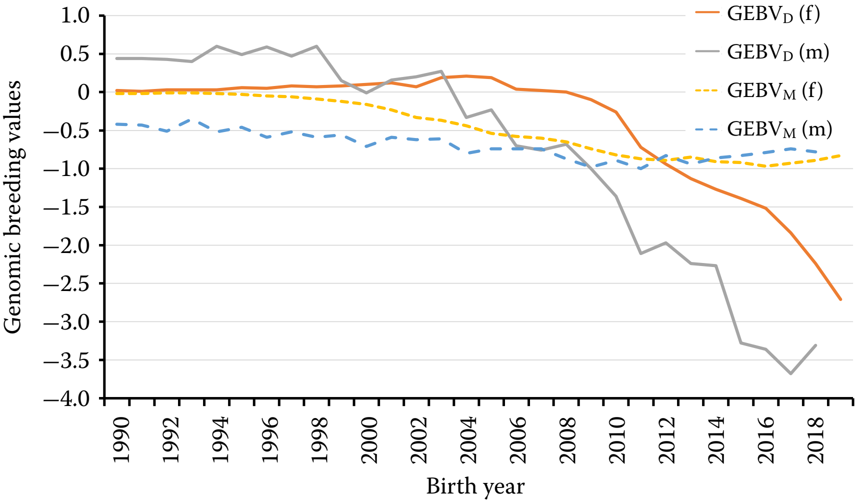

Figure 1. Genetic trends of gestation length in Czech Holstein for direct (D) and maternal (M) genetic effects of sires (m) and domestic females (f)
GEBV = genomic breeding values

trend was also observed in US Holstein (Wright and VanRaden 2017), where it was related to the selection for improving calving ease, fertility, yield and productive life, and in Australian Holstein bulls (Haile-Mariam and Pryce 2019), where the reduction coincided with the introduction of the genetic evaluation of fertility.

Mean reliabilities of EBV and GEBV were similar for all animals. Generally, the reliability of conventional breeding values is a function of pedigree, phenotype and genotype contributions, and additional information should lead to its increase (Misztal et al. 2013). Genomic information increased the reliabilities in genotyped females (+0.13) and males (+0.12) for direct genetic effect, and in genotyped females (+0.08) and males (+0.04) for maternal genetic effect (Figure 2) in our study. The genomic matrix included genotypes of 5 470 animals that did not have their own record of gestation length and were not included in the conventional estimation, as they were not direct ancestors of animals with phenotype. Their GEBV were predicted with mean reliabilities of 0.50 ± 0.140 for direct effect in males, 0.61 ± 0.069 for direct effect in females, 0.20 ± 0.089 for maternal genetic effect in males and 0.23 ± 0.061 for maternal genetic effect in females.

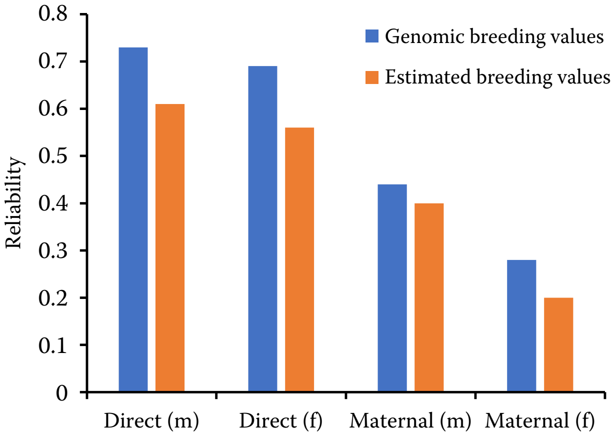

Figure 2. Mean reliabilities of conventional and genomic breeding values for direct and maternal genetic effects in genotyped males (m) and females (f)

The accuracy of predictions from single-step GBLUP is dependent on the compatibility of genomic and pedigree relationship matrix (G and A) and the weighting placed on the difference between them (Aguilar et al. 2010). Song et al. (2019) also mentioned the inappropriate weighting in H matrix construction as the source of higher bias. The same authors reported another two reasons, why the improvement of predictive ability with ssGBLUP was lower than expected. These include (1) the genotyped reference population was not large enough to provide more information compared to the pedigree; (2) traits with moderate to high heritability can obtain sufficient accuracy by the traditional BLUP method. Our results showed that the reliability of GEBV was on average higher than EBV reliability in animals without their own GL record, but animals with the phenotype tend to have the GEBV reliabilities lower by 0.01–0.02 compared to EBV. It might indicate some problem with the compatibility or with the structure of the genotyped animals.

Pearson correlations of breeding values

Figures 3 and 4 show significant Pearson correlations between GL-GEBV (direct and maternal) and official (G)EBV for production and fitness traits.

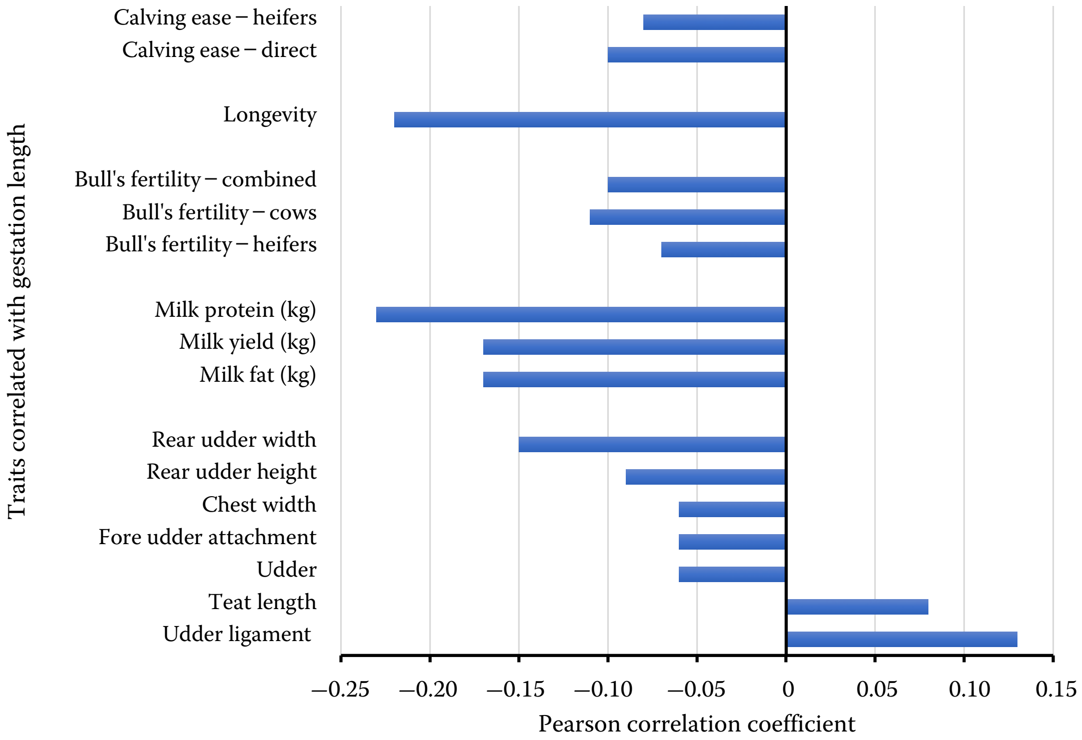

Figure 3. Significant correlations between direct genomic breeding values for gestation length and breeding values for routinely evaluated traits

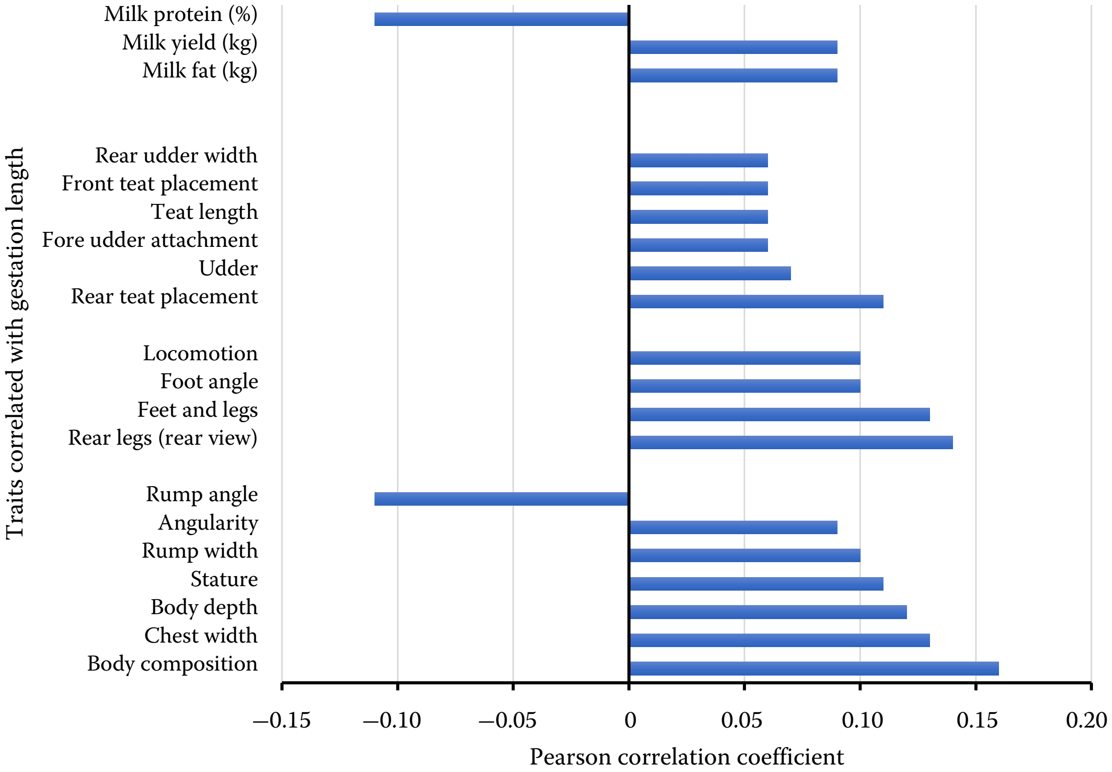

Figure 4. Significant correlations between maternal genomic breeding values for gestation length and breeding values for routinely evaluated traits

Correlations between breeding values could serve as the indicators of existing genetic associations, but their relevance depends on the reliabilities of EBV, which were lower for maternal GL. We found low but statistically significant correlations between direct GL-GEBV and (G)EBV for most other traits, which indicated that the cows born after shorter gestations would have a genetic predisposition to wider and higher rear udder attachment, stronger fore udder attachment, shorter teats, weaker udder ligament and better total udder score than the cows born from longer gestation. The bulls from shorter gestation would have a genetic predisposition to better fertility, while the cows would have a lower rate of calving difficulties (higher EBV for calving ease are favourable because they indicate the lower frequency of calving difficulties), higher milk, fat and protein yield, better fertility and longer production life. A negative genetic correlation between GL and milk yield in Holstein cattle was previously reported by Eaglen et al. (2013) and by Fang et al. (2019). They additionally showed that GL was significantly positively correlated with calving ability (stillbirth and calving ease) and body conformation traits (stature, body depth), whereas it was negatively correlated with conception and pregnancy rates, rump angle, net merit and productive life. Vieira-Neto et al. (2017) found that the cows with short gestations had the highest incidence of stillbirth, retained placenta, metritis, morbidity during 90 days in milk, culling in the first 300 days in milk and removing from the herd during 300 days in milk.

Maternal GL was mainly correlated with the body composition score, when tall cows with the wide chest, deep body and angular ribs would have a genetic predisposition to longer gestations. They would also have higher feet and leg score (parallel legs when viewed from the rear, steep foot angle), locomotion score and udder score (inside of quarter rear and fore teats, long teats, strong fore udder attachment, and wide rear udder). Negative correlations in Figure 4 indicate that the cows with long gestation would have lower protein percentage and high pins. Similarly, Wall et al. (2005) reported an unfavourable genetic correlation between calving interval and rump angle suggesting that the cows with high pin bones would have a genetic predisposition to longer calving interval. As Wall et al. (2005) did not observe any significant genetic or phenotypic correlation between high pin bones and days to first service or non-return rate, this predisposition to longer calving interval might be mainly related to the predisposition to longer gestation. Eaglen et al. (2013) found significant positive genetic correlations of maternal GL with the stature and the rump width, and a negative correlation with calving ease and services to conception, but all other associations were estimated with high standard errors and thus not different from zero.

As direct GL is genetically associated with many economically important traits, and its change may affect the profitability of cattle breeding, we could recommend integrating this trait into the genetic evaluation of Holstein cattle.

CONCLUSION

Evaluation of gestation length in Czech Holstein cattle showed moderate direct heritability and large genetic variability of this trait. Direct genomic breeding values for GL were negatively correlated with routinely estimated breeding values for most type, production and fertility traits, including milk yield, longevity and calving ease. Maternal genomic breeding values for GL were positively correlated with most type traits associated with body composition and udder support system and negatively correlated with rump angle and milk protein percentage. Comparison of mean GEBV according to the birth year of animals revealed a trend of the shortening of GL, which is caused by the selection for correlated traits, such as long-term selection for milk and protein yield, fertility and longevity. This trend is not favourable, as shorter gestation might lead to a negative indirect response in correlated traits and thus it should be handled with caution.

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Conflict of interest

The authors declare no conflict of interest.

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