

Estimation of inbreeding effect on conception in Czech Holstein

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Abstract: The influence of calculated inbreeding coefficients on the conception of heifers and cows was analysed by a two-trait binary model for conceived/not conceived after each insemination on 677 234 Czech Holstein cows and heifers with 3 248 299 insemination records as the covariable in a statistical model. The data between 1996 and 2014 were analysed. Various effects and their statistical influence on traits were tested by a generalized linear model. Consequently, genetic parameters were estimated by the Gibbs sampling method and used in predicting breeding values using the best linear unbiased prediction by animal model (BLUP-AM). The mean for the conception rate of cows averaged over lactations was 33.7% and for heifers it reached 53.8%. Average inbreeding coefficient increased from 1% in 1996 to almost 5% by 2013 and was in the range of 0–45%. The rate of inbreeding per generation was 0.20%. Although the effect of inbreeding was statistically significant ($P = 0.05$) for both traits, the proportion of variability explained by the models was relatively low. Estimated genetic parameters were low for both traits. Coefficient of heritability was 2.00% and 1.30% for cows and heifers, respectively, whereas coefficients of repeatability reached 6.09% and 7.08% for cows and heifers, respectively. The random effect of the permanent environment (PE) reached higher values than the additive genetic variance (G) and explained 5.67% and 4.09% of variability for cows and heifers, respectively. A negative impact of inbreeding on heifer and cow conception was observed, whereby every 10% increase in inbreeding coefficient resulted in a conception decline by 2.23%. Calculated Spearman's rank correlation coefficient between estimated breeding values considering and not considering the effect of inbreeding was close to one. Presented results indicate that inbreeding has a negligible influence on the breeding values of conception. The results also indicate that it is not necessary to include inbreeding coefficient in the routine breeding value evaluation of conception rate of heifers and cows. On the other hand, monitoring of inbreeding is necessary to avoid an increase of its rate.

Keywords: BLUP; breeding value; dairy cattle; Gibbs sampling; inbreeding depression

The artificial insemination era jointly with global market and together with efficient and more accrued estimation of breeding values, not only in dairy cattle populations, makes high pressure on using small groups of excellent breeding animals, especially breeding bulls. The breeding objectives, focused only on an increase of milk yield and improvement of milk solid components (Brade 2016) in breeding programs, also have a consid-

erable influence on it. These intensive breeding programs with high selection intensity on animals could cause increasing inbreeding coefficients (F) due to mating the related individuals and consequently a decrease in genetic variability of the population. Inbreeding reduces the number of heterozygous assemblies, increases the homozygosity of the entire genome, and boosts the probability of genetic defects (Thornhill 1993). The

frequent mating of related individuals could result in inbreeding depression as a measurable impact of *F* on traits. The inbreeding depression could negatively impress on all economically important production and reproductive traits (Sorensen et al. 2005; Zhang et al. 2015). Even though some authors concluded that *F* had a negligible impact on large populations, its effect is more evident in smaller local populations (du Toit et al. 2012).

As Bjelland et al. (2013) concluded, the negative impact of inbreeding depression on production traits (Thompson et al. 2000) as well as on reproduction or survivability trait (Mc Parland et al. 2007) has been well documented. For example, in Spanish dairy cattle Gonzales-Recio et al. (2007) revealed that the pregnancy rate decreased by 1.68% in cows with the *F* value between 6.25% and 12.5%. These authors also found that inbreeding depression had a greater effect in cows with *F* higher than 25%. Also Sorensen et al. (2005) stated that it is necessary to monitor inbreeding in dairy cattle which increases with selection intensity, when in the Holstein population in Denmark it rose from 0.74 to 1.03 within ten years and in the Danish Red breed even from 0.32 to 1.07.

Biotechnological manipulation of sperm and ovum (Kurykin et al. 2016) as well as of freezing techniques for semen and embryos (Dolezalova et al. 2016) are being tested to improve fertility.

The negative impact of *F* on maternal ability or on early embryo vitality was also reported. For example, Dezetter et al. (2015) found a relationship between declining fertility and inbreeding, egg and embryo quality (Luttgenau et al. 2016), and the onset of the luteal phase after egg release (Tenghe et al. 2016) could also be affected. Inbreeding could also influence fitness, mastitis and metritis according to Pinedo et al. (2016). Nevertheless, fertility traits are relatively lowly heritable (Jakubec et al. 2010) and therefore it is more difficult to select individuals so that the reproductive capacity of cows could thereby be improved (Weller and Ron 1992), it is also important to measure the influence of *F* on them. This claim is supported by some authors' opinion that the influence of inbreeding depression on lowly heritable traits is usually undervalued; even the decreasing reproductive measures due to selection for milk yield are currently the most common reason for removing cows from herds (Muller et al. 2017). Rokouei et al. (2010) detected a deleterious

effect of inbreeding on milk yield (ranging from –18 to –27 kg of milk per 1% increase in inbreeding) whereas an impact on reproductive traits was negligible (except for calving interval and age at first calving).

The aims of the present study were to analyse inbreeding in the Czech Holstein population and to estimate inbreeding depression for conception rates of heifers and cows by using two-trait animal models. Assumptions were that inbreeding has a negative impact on analysed fertility traits and the inbreeding coefficient should be included in the routine system of breeding value estimation for the Czech Holstein population performed in the Czech Republic.

MATERIAL AND METHODS

The input data covered information about conception and pedigrees collected by the Holstein Cattle Breeders Association of the Czech Republic and provided by Plemdat Ltd responsible for routine processing of breeding data.

Data obtained for all inseminations of heifers and cows born between 1996 and 2014 were analysed. Only purebred Holstein females were used. Each insemination was considered as an alternative binary trait of conceiving (conceived/not conceived) of heifers or cows. Females with calving interval longer than 500 days were omitted from analyses. Total number of herds in the evaluated data was 858. The herds that did not satisfy the minimum number of observations (10 per one herd) were also omitted. In total, 3 248 299 observations (2 399 143 from cows and 849 156 from heifers) for 677 234 cows and heifers were used in this study after data editing. The mean value for the number of observations per herd was 989 and 2796 for heifers and cows. On average, after data editing there were 1.67 and 4.93 conceptions for each heifer and cow, respectively.

The appropriate pedigree file contained all animals with data, their parents and all other available related animals. In total, the pedigree file included 1 235 982 individuals and was used for the calculation of all necessary genetic variability parameters. The quality and integrity of pedigree information were evaluated by maximum generations traced back, average equivalent complete generations, percentage of known ancestors and by

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the pedigree completeness index (PCI). Maximum generations traced back were assumed as the number of generations between an animal and its earliest ancestor. Average equivalent complete generations (i.e. number of generations in a comparable complete pedigree) were computed according to Maignel et al. (1996) using the formula:

$$ceg = \frac{1}{N} \sum_{j=1}^N \sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}}$$

where:

N = number of animals in a reference population

n_j = total number of ancestors of animal j in the population under study

g_{ij} = number of generations between animal j and its ancestor i

The percentage of known ancestors was the relative expression of all known ancestors per generation. The pedigree completeness index was computed following the MacCluer et al. (1983) algorithm. This procedure summarised the proportion of known ancestors in each ascending generation. It quantifies the change in detecting inbreeding in the pedigree (Sorensen et al. 2005). The following equations were used:

$$I_d = \frac{4 I_{d-pat} I_{d-mat}}{I_{d-pat} + I_{d-mat}}$$

$$I_{dk} = \frac{1}{d} \sum_{i=1}^d a_i \quad k = pat, mat$$

where:

k = maternal or sire line of an individual

a_i = proportion of known ancestors in generation i

d = number of generations found

The values can vary between 0 and 1. If all ancestors are known, $I_d = 1$, if one of the parents is unknown, $I_d = 0$.

The software packages POPREP (Groeneveld et al. 2009) and PEDIG (Boichard 2002) were used for the calculation of the above-mentioned parameters. The inbreeding coefficients were calculated for all individuals using a procedure described by Colleau (2002) incorporated into the CFC software package (Sargolzaei et al. 2006).

First, the General Linear Model (GLM) procedure of SAS statistical package (Version 9.4, 2013) was applied to the data for studying the influence of factors affecting the investigated traits. Several statistical models were tested separately for cows

and heifers while including fixed effects in different combinations. Fixed effects in statistical models of evaluation were as follows: age at insemination in days, interval from calving to first insemination (insemination interval, only for cows), inbreeding coefficient and lactation number (only for cows). Additional information was included in order to create the following peer groups: (1) Herd, year and season of birth (HYS_b). The four seasons were defined here as spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). (2) Herd, year and season of insemination (HYS_i). The season was defined here by each calendar month. (3) Insemination technician and year of insemination (TY_i). (4) Sire and year of insemination (SY). In addition to these fixed effects, there were two random effects: genetic animal effect (G), and permanent environment of the female (PE). The effects of age at insemination, interval from calving to first insemination, and inbreeding coefficient were assumed as quadratic regression. After iterative rounds to remove groups with small numbers of observations, there were 28 172 HYS_b groups, 70 545 HYS_i groups, 4884 SY groups, and 2083 TY_i groups. There were 4.8 records per each female on average.

In addition, two-trait models were used for the estimation of genetic parameters and components of variances and covariances by the Gibbs sampling method as it is incorporated into the GibbsF90 software (Misztal et al. 2002). In this study, Gibbs sampling counted 800 000 iterations. The average components of variance were taken from the last 130 000 iterations and were used as final covariance matrices.

The statistical model of BLUP evaluation in matrix notation can be written as follows:

$$Y = Xb + Za + Wu + e$$

where:

Y = vector of observations of traits (conception in cows and in heifers)

X, Z, W = known incidence matrices for the fixed effects, the random additive genetic animal effect, and the random permanent environmental effect of female

b = vector of fixed effects

a = vector of random additive genetic animal effects

u = vector of random permanent environmental effects of female

e = vector of residuals

Then, the BLUP-AM using the BlupF90 software (Misztal et al. 2014) was used to assess how the inclusion of the effect of inbreeding coefficient influenced the breeding value. The convergence criterion for the BLUP-AM was set at 10^{-17} . The calculation was run for comparison with or without inbreeding coefficients. Spearman's rank correlation coefficient was used for the quantification of relationships between different types of breeding values and was calculated by the CORR procedure as it is implemented in the SAS statistical package (Version 9.4, 2013).

RESULTS

The data included females from the first to the 12th lactation, and the average was within the range of the third lactation. The oldest cow conceived for the last time at 5444 days. The mean insemination (conception) success rate was 33.7% for cows (averaged over lactations) and 53.8% for heifers. The average interval from calving to first insemination was 132 days.

To calculate inbreeding coefficients, 1 235 982 animals were included in the CFC program. Of these, 976 900 animals had known inbreeding coefficients. Among bulls, 23 094 sires had 1 203 688 known progenies. Among cows, 839 639 dams had 1 140 223 known progenies. The data included 25 423 founders with 32 435 progenies. Overall, 70 336 animals had unknown dams and 6871 animals had unknown sires. Both parents were known for 1 113 352 animals. There were 19 405 full-sib groups. Table 1 shows that most individuals (65.93%) had inbreeding coefficients between 0% and 5%, there was one cow with the inbreeding coefficient of 43.92%. Only 0.39% (4780 animals) had inbreeding coefficients exceeding 10%. The average inbreeding coefficient in 1996 was 1.3% and by 2013 it was almost 5%. This rising trend is illustrated in Figure 1.

Table 1. Distribution of animals based on inbreeding coefficient

Inbreeding coefficient	Animals <i>n</i>	Total	(%)
0.10 < F ≤ 0.45	4 780	4 780	0.39
0.05 < F ≤ 0.10	157 228	162 008	12.72
0.00 < F ≤ 0.05	814 892	976 900	65.93
0.00 ~ non-inbred	259 082	1 235 982	20.96

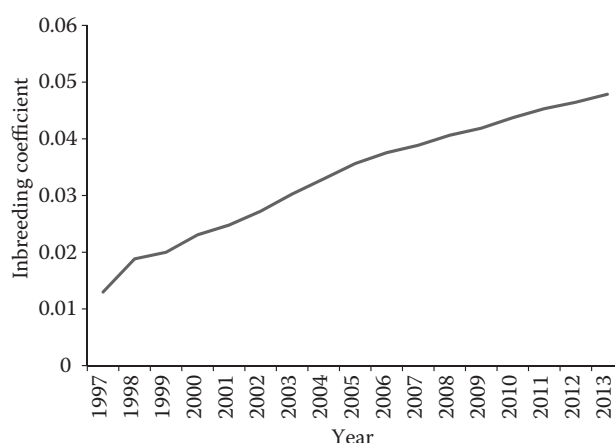


Figure 1. The increasing trend of average inbreeding coefficient per year

The accuracy and reliability of calculated inbreeding coefficients and subsequently the derived parameters depend to a large extent on the quality of the pedigree to be evaluated. The trend of the pedigree completeness index for the last six generations since 1985 is presented in Figure 2. In 1987, over 90% of all animals in the first generation had known ancestors, with slightly decreasing percentage in the next generations. The maximum number of generations of ancestors was 26 whereas the equivalent number of known generations reached 5.56 years.

Average equivalent complete generations (i.e. the number of generations in a comparable complete pedigree) were 10.28. Another important parameter of the population dynamics is expressed by the number of contributing founders to genetic variability of the breed. Within the evaluated population, 14 980 animals reported 100% of the total genetic variability. 75% of the genetic variability of the population was explained by 304 animals and half of the genetic variability was explained by 60 animals.

Table 2. Estimated proportions of variance for all random effects

Variance component	Cows (%)	Heifers (%)	R^2 between cows and heifers
Residual variance	93.92	92.92	0.76
Variance of permanent environment of animal	4.09	5.70	0.24
Genetic variance (heritability)	1.99	1.30	0.56
Repeatability	6.08	7.01	0.32

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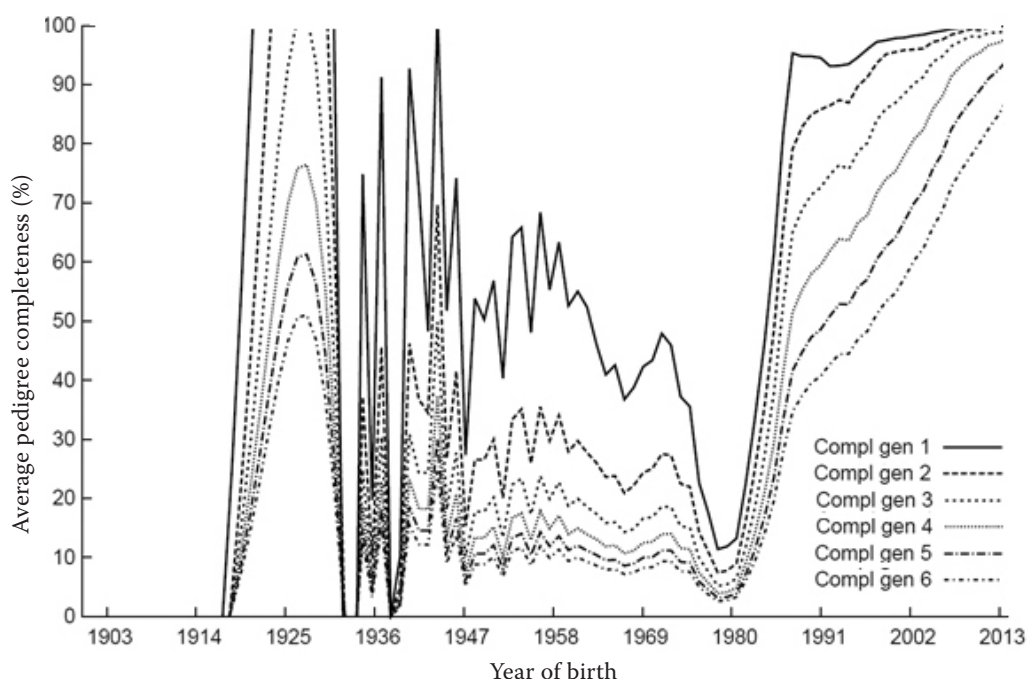


Figure 2. Trend of the pedigree completeness index since 1985 for the last six generations

The best model in GLM included effects of herd-year-season of birth, herd-year-season of insemination, insemination technician-year of insemination, age at insemination, insemination interval, sire-year of insemination, lactation number, and inbreeding coefficient explained 34% of the variance in conception for cows and 22% of the variance in conception for heifers. Even though the best model included all fixed effects, the two herd-year-season effects (HYS_b , HYS_i) were the most important. These two effects explained 33% of the variance in pregnancy for cows and 20% of the variance in pregnancy for heifers. Adding the effect of inbreeding increased the explanation of variability in conception by a maximum of 0.01%. All fixed effects were statistically significant, with P -values < 0.00001.

From outputs from Gibbs sampling, Table 2 shows that heritability for cows was $h^2 = 1.99\%$ with repeatability of 6.08% and for heifers $h^2 = 1.30\%$ with repeatability of 7.00%. PE was more important than G because it explained 4.09% of the variability for cows and 5.70% for heifers. Residual, genetic, and phenotype correlations between cows and heifers were intermediate. The correlations for PE between cows and heifers and their repeatability were low.

Although the input data were alternative traits – they had only two values (yes/no), the results of the effects were continuous variables showing nearly normal distributions. Table 3 presents standard

deviations for the original input data (ID) and then standard deviations for effects estimated by BLUP-AM. The largest standard deviations were for the two herd-year-season effects and the lowest variabilities were for PE and breeding value. PE and estimated breeding values (EBV) for heifers were less variable than were those for cows. This may be due to the lower values of genetic parameters and lower number of records on heifers than on cows.

Table 3. Standard deviations of original data, effects included in the best linear unbiased prediction by animal model (BLUP-AM) and predicted breeding values (in %)

Effect	n^4	Cows (%)	Heifers (%)
Original input data ¹	3 248 299	47.28	49.86
Herd-year-season of birth ²	28 172	12.31	30.24
Herd-year-season of insemination ²	70 545	13.55	31.03
Technician-year of insemination ²	2 083	9.12	18.11
Lactation number ²	12	5.46	–
Sire-year ²	4 884	6.18	14.95
Permanent environment ²	677 234	3.06	2.91
Estimated breeding value ³	1 223 658	4.98	2.40

¹standard deviation of data before estimation of genetic parameters, ²standard deviation of effects included in BLUP-AM, ³standard deviation of predicted breeding values,

⁴number of observations/levels of fixed effects

Table 4. Basic statistical characteristics of predicted breeding values for conception of cows and heifers (in %)

Cows	Mean	Median	Standard deviation	Minimum	Maximum
Cows without inbreeding	–7.23	–8.06	5.68	–35.21	12.05
Cows with inbreeding	–6.87	–7.32	4.98	–34.12	11.05
Heifers without inbreeding	–2.75	–2.60	2.82	–24.44	10.15
Heifers with inbreeding	–2.38	–1.98	2.40	–23.30	11.07

Using the BLUP calculation with the effect of inbreeding, two additional effects were included: linear and quadratic of regression terms. The average predicted breeding value was by 3.6 units higher when inbreeding was included than the average estimated breeding value without inclusion of inbreeding coefficient, as shown in Table 4. Because of a lower standard deviation, the variability of “inbred” breeding values was smaller.

In comparison with cows, heifers had higher average predicted breeding values with lower variances (Table 4). Like in cows, heifers also showed lower predicted breeding values with higher variability when inbreeding was not included in the model equation (Table 4). The correlation between inbreeding and non-inbreeding breeding values was 0.99 (the value was the same when computed only with individuals with higher inbreeding). Therefore, the inclusion of inbreeding in the model did not affect the prediction of breeding value. Even though no influence of inbreeding on breeding value was identified, the influence of inbreeding on conception was found (see Figure 3, produced from BLUP).

DISCUSSION

Overall, the quality of the pedigree of the reference population is at a good level and it can be assumed

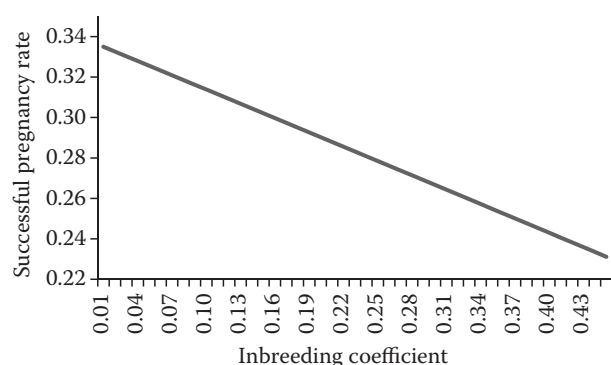


Figure 3. Evaluated negative influence of inbreeding on conception of cows

that the inbreeding coefficients are calculated with sufficient precision. The influence of the inbreeding level on conception and on breeding value prediction was derived from the following researches: inbreeding has been shown to have negative effects on the interval from calving to first insemination, days open (Bezdicsek et al. 2007), calving interval (Rokouei et al. 2010), conception rate (Dezetter et al. 2015), as well as embryo quality, development and viability (Hinrichs et al. 2015). In addition to its occurrence in cattle, inbreeding is extremely prevalent also in horses (Szwaczkowski et al. 2016; Vostra-Vydrova et al. 2016) and inbreeding depression is known to occur in bird populations (Cecchi et al. 2016). In our study the negative influence of inbreeding on conception was confirmed (Figure 3), but the prediction of EBV was not affected. One of the reasons could be that EBV also includes the values of the relatives which might not be influenced by inbreeding depression. Results could also be influenced by the statistical model. For example, in the official national evaluation for the Czech Republic the quantity of milk in the first 100 days of lactation is included in the model. The effect of lactation (lactation number) was included in our model which partly cumulated the age of the animal with the quantity of milk and physiological stress of animals.

A certain shortcoming that could affect the results was the limited number of known generations of ancestors although all available data were used to calculate inbreeding coefficients. Inbreeding coefficients were calculated also for individuals without taking into account the possibility of unknown inbred ancestors, as described by VanRaden (1992); it is possible that the coefficients of individual animals are not very accurate.

Despite an insignificant change in the prediction of breeding values, the negative influence of inbreeding on the reproductive capacity of females was demonstrated. The level of inbreeding depression was comparable with the standard deviation of breeding values.

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The heritabilities for milk yield and conception explained by these model equations were low, relative to heritabilities used in routine evaluation (39.00% for milk yield, 4.40% for cow conception and 3.90% for heifer conception).

It would be appropriate in future studies either to include the inbreeding effect directly in the equation of the accredited animal breeding model or to determine the inbreeding coefficient for unknown individuals according to VanRaden (1992). An ideal approach would be to evaluate both inbreeding calculations (using 0 and average inbreeding coefficients for unknown ancestors) because in older generations with poorly known records the average values of inbreeding coefficients could be significantly distorted and overestimated. In addition to traditional calculations, it would also be useful to use genomic results when single nucleotide polymorphism (SNP) chips are available, as it is possible to estimate homozygous DNA segments with unambiguous precision using chips (Aliloo et al. 2017) and quantitative trait locus (QTL) sections were shown to positively affect reproductive characteristics in cows (Muller et al. 2017).

The influence of the negative energy balance could also be included in the breeding value prediction (Brade 2016). Furthermore, it would be appropriate to take into account the quality of eggs and embryos (Hinrichs et al. 2015) and the onset of the luteal phase after egg release (Tenghe et al. 2016).

CONCLUSION

The inbreeding coefficient need not necessarily be included in the calculations used in predicting breeding value for the conception of the Czech Holstein population because the estimated breeding values are the same regardless of the inbreeding inclusion. Inbreeding does not influence the prediction because the estimated breeding value considers information also from the relatives. However, the inbreeding coefficient should be taken into account in the mating plan, because inbreeding negatively affects not only reproductive traits, which was documented here, but also productive traits such as milk yield or percentage of milk components. In addition to including traditional records, it is appropriate to link phenotypic indicators with genomic information on heterosis and recombination and to take these into account

when estimating breeding values for conception in dairy cattle. In addition to the influence of inbreeding on conception, a significant influence of PE was also proved. Because the effect of cow's PE is more important than G, PE should be included in the model equation for dairy cattle conception. We can better focus on the improvement of the environment but it is also necessary to improve the genetic trend which is currently negative.

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