Inbreeding versus Crossbreeding: the Potential Bias of Breeding Values in Dutch Dairy Cattle

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ABSTRACT

Inbreeding and crossbreeding oppositely affect the performance of livestock; inbreeding negatively- and crossbreeding positively affects all traits. This study examined if it is appropriate that breeding value estimations (EBVs) in Dutch dairy cattle only take into account the effects of crossbreeding (heterosis). Performance and EBVs for milk yield, fat, and protein; somatic cell count; and fertility of 219 purebred Holstein Friesian cows and 191 crossbred cows were compared. The outcomes suggest a bias in the EBVs for milk yield, and fat; and fertility, that may very well be caused by inbreeding depression.

Keywords

Dairy cattle, EBVs, inbreeding depression, heterosis.

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INTRODUCTION

Years of intense selection on a few traits, combined with reproduction techniques such as artificial insemination and genomic selection, have resulted in the loss of over 80% of the genetic diversity within the world’s most popular dairy cattle breed: Holstein Friesian (HF) (Yue, et al., 2015). This loss of most of the breed’s genetic diversity, over time resulted in increasing inbreeding rates in the breed. Currently, inbreeding rates in the Dutch HF population have become irreversible, and are increasing with 1.8% per generation (Doekes, et al., 2018). Thus, inbreeding rates are increasing almost twice as fast as the maximum of 1.0% per generation, as advised by world health organization FAO (Villanueva, 2011).

To prevent the effects of inbreeding depression, which negatively affect all traits, crossbreeding strategies may be applied. Crossbreeding does not only prevent the negative effects of inbreeding, additionally it causes the opposite effect of inbreeding depression: heterosis. Non-production traits such as fertility and longevity are most susceptible to the effects of heterosis or inbreeding depression (Buckley, et al., 2014). Both inbreeding depression and heterosis are non-heritable. For inbreeding depression that is for as long as their effects are reversible. At the point at which inbreeding of the next generation has become inevitable, the effects of inbreeding depression can no longer be prevented within-breed (Leroy, 2014).

Estimated breeding values (EBVs) aim to represent solely the heritable, additive genetic part of an animal’s potential for a trait. Therefore, EBVs of crossbred dairy cattle in the Netherlands are corrected for heterosis effects. However, EBV calculations for purebred HFs do not take into account the negative effects of inbreeding depression. This study examined if this is appropriate, especially considering the rapidly and irreversibly increasing inbreeding rates in the breed.

LITERATURE REVIEW

As was stated in the introduction, inbreeding depression and heterosis have opposite effects on animal performance. Their effects on the performance of dairy cattle are further explained in the following paragraphs.

Inbreeding depression

Inbreeding depression results in the reduction of the mean value of a trait, and has been documented in all livestock species (Leroy, 2014). The effects of inbreeding depression on the performance of Holstein Friesian dairy cattle have been studied numerous times. The table below describes the average effect of inbreeding depression per 1% inbreeding (F), as found by multiple studies.

Trait	Inbreeding depression (per 1% F)
Milk yield (kg/lactation)	-50
Milk fat (g/day)	-2
Milk protein (g/day)	-1.5
Somatic cell count (cells/ml)	+1500
Calving interval (days)	+0.5

Table 1: Average effects of inbreeding depression on milk yield, fat, protein, somatic cell count and calving interval, per 1% inbreeding (Bezdicek, et al., 2007; Bjelland, et al., 2013; Dezetter, et al., 2015; VanRaden, 2017).

The mean inbreeding coefficient in the current Dutch HF population is 4.6%, so in order to calculate the effects of inbreeding on the average Dutch HF cow, the effects in the above table should be multiplied by 4.6.

Heterosis

Similar to inbreeding depression, the effects of heterosis on crossbred dairy cattle have been studied several times throughout the last 15 years. Table 2 below describes the average heterosis effects that were found in those studies.

Trait	Heterosis effects (100% heterosis)
Milk yield (kg/lactation)	+2% up to +5%
Milk fat (g/day)	+2% up to +5%
Milk protein (g/day)	+2% up to +5%
Somatic cell count (cells/ml)	-5% up to -10%
Calving interval (days)	-5% up to -10%

Table 2: Average heterosis effects on milk yield, fat, protein, somatic cell count and calving interval, as found by (Hansen, et al., 2013; Freyer, et al., 2008; Jönsson, 2015; Dezetter, et al., 2015).

Estimated breeding values (EBVs)

EBVs for dairy cattle in the Netherlands are calculated by studbook CRV, using a Best Linear Unbiased Prediction (BLUP) model. Some EBVs are presented in absolute values (e.g. kilograms), others in a relative value that is based on the population mean. The population mean on which those EBV values are based, is adapted to the actual reference population every 5 years (CRV, 2014).

Heterosis corrections in breeding value estimations

Heterosis effects are, as stated before, corrected for in the breeding value estimations of crossbred dairy cows in the Netherlands. Table 3 displays the heterosis corrections as applied in EBV calculations of crossbred dairy cattle that exploit 100% heterosis. Crossbred animals which are (partially) backcrossed to one of their parental breeds, exploit partial heterosis and partial recombination loss.

Trait	Heterosis corrections
Milk yield (kg/lactation)	-217 (lactation 1) up to -271 (≥ lactation 5)
Milk fat (kg/lactation)	-10.8 (lactation 1) up to -12.6 (≥ lactation 5)
Milk protein (kg/lactation)	-7.9 (lactation 1) up to -9.8 (≥ lactation 5)
Somatic cell count	Not corrected
Calving interval (days)	+2.8

Table 3: Heterosis corrections (100% heterosis) as applied by studbook CRV in EBV calculations of Dutch crossbred dairy cows. Lactations are based on 305 productive days.

METHODOLOGY

Research design

The aim of the study was to determine if it is appropriate that heterosis is accounted for in the estimation of breeding values for crossbred dairy cattle in the Netherlands, and inbreeding depression in Holstein Friesians is not. The study consisted of an analytic observational study with a cohort study design. To determine possible effects of inbreeding depression on performance of HF cows, differences between genetic potential (EBV) and actual performance were compared between purebred HF and crossbred ProCROSS cows. ProCROSS is a rotational 3-way-cross strategy, that involves the breeds Holstein Friesian, Montbéliarde and Viking Red (Vitorino, et al., 2017). The traits examined in this study were milk yield, fat, and protein; somatic cell count; and fertility (calving interval).

If the model that is used in breeding value estimations is correct and unbiased, the difference between EBV and actual performance should be approximately equal for purebred and crossbred cows from the same population. However, if inbreeding depression withholds the Holstein Friesians from achieving their full genetic potential, their actual performance will be lower than expected and EBVs will be overestimated.

Data collection

In order to achieve approximately equal bias of farm-management factors, data were collected from 3 farms that had a mixed herd consisting of both HF and ProCROSS cows. Culling criteria were equal for both breeds, culling rates approximately equal. The analysis of production traits (milk yield, fat, protein, somatic cell count) included 206 HF and 154 ProCROSS cows, with a total of 810 lactations. The fertility analysis, in which heifers were excluded (lack of calving interval), included 174 HF and 140 ProCROSS cows with a total of 585 calving intervals.

Data processing

Statistical software program SPSS was used to analyse the data. Parametric tests, which are able to analyse longitudinal and unbalanced data, were the preferred method to test for breed-differences in performance and EBVs. Normality assumptions were tested using Kolmogorov-Smirnov tests. Normality of EBVs was tested per trait, normality of performance records was tested per trait and lactation.

For the analysis of breed-differences in performance records, either a parametric Linear Mixed Model or a non-parametric Mann-Whitney U test was used; depending on acceptance or decline of normality assumptions. When the Linear Mixed Model was used, the best model-fit was determined by the -2-log-likelihood, as presented by SPSS in smaller is better form. For the analysis of potential breed-differences in EBVs, either a parametric Univariate General Linear Model or a non-parametric Mann-Whitney U-test was used.

Both the Linear Mixed Model and the Univariate General Linear Model in this study were modelled as:

$$Y = \beta_0 + X\beta + \varepsilon \qquad with\ \varepsilon \sim R$$

Y = vector of responses; cow number
B0 = intercept
X = fixed-effects design matrix
β = vector of fixed effects parameters; breed + lactation number
ε = residual errors
R = covariance structure
Assumed is that ε is distributed as R
Confidence interval = 95%

RESULTS & DISCUSSION

Heterosis corrections

The heterosis corrections as applied by studbook CRV in breeding value estimations of crossbred cows (see table 3), are in line with heterosis effects as stated in literature for milk yield, milk fat, and milk protein (see table 2). However, this is not the case for somatic cell count. Both literature and studbook CRV state heterosis effects for SCC, by the studbook formulated as an expected heterosis effect of -0.7% up to -1.0% increased SCC per lactation (CRV, 2017). However, the same studbook does not correct for SCC in EBV calculations of crossbred cattle, their motives to do so remained unknown.

Another striking difference between literature findings and corrections applied by CRV, was found for fertility. The applied correction for 100% heterosis is +2.8 days calving interval. With a mean of 408 days in the reference population, this corresponds to an expected heterosis effect of 0.7% on calving interval. This is not in line with literature, in which an average heterosis effect of 5% up to 10% on fertility traits is stated.

Milk yield

The HF cows produced 10,887 kg/305 days and the ProCROSS cows produced 10,428 kg/305 days (after corrections). The breed-difference is 459 kg in favour of the Holstein Friesians, but was not found significant (P=0.589). The mean EBV for milk yield was 441 kg for the HF cows, and 226 kg for the ProCROSS cows. The breed-difference of 215 kg was found significant (P=0.020).

The (corrected) milk yield over 305 days lactation and consecutive EBVs of both breed groups per lactation are displayed in figure 1. No significant breed*lactation interaction was found (P=0.800).

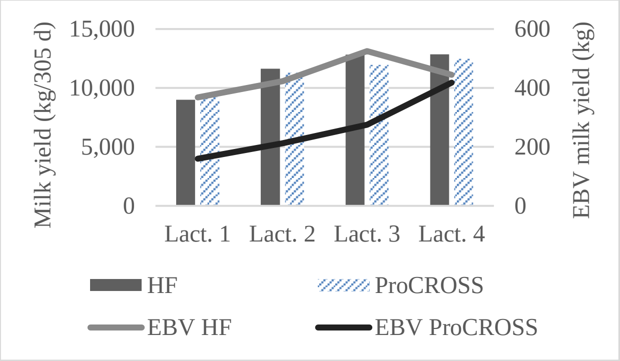

Figure 1: Milk yield (corrected) and EBVs for both breed groups, per lactation.

The fact that there is no significant breed-difference in actual (corrected) performance, whilst the HF cows do have a significantly higher EBV, suggests a bias. This bias might very well be caused by inbreeding depression taking it's toll on the yield of the HF cows.

Milk fat

Mean milk fat percentage over 305 days lactation for the HF cows was 4.06%, the corrected mean for the ProCROSS cows was 4.16%. With a breed-difference of 0.1%, the ProCROSS cows had a significantly higher milk fat percentage over 305 days lactation (P=0.033). Mean EBV for fat percentage was -0.057% for the HF cows and 0.019% for the ProCROSS cows. The breed-difference of 0.076% in favour of the ProCROSS cows was not found significant (P=0.155).

The (corrected) fat percentages and EBVs of both breed groups per lactation, are displayed in figure 2. No significant breed*lactation interaction was found (P=0.140).

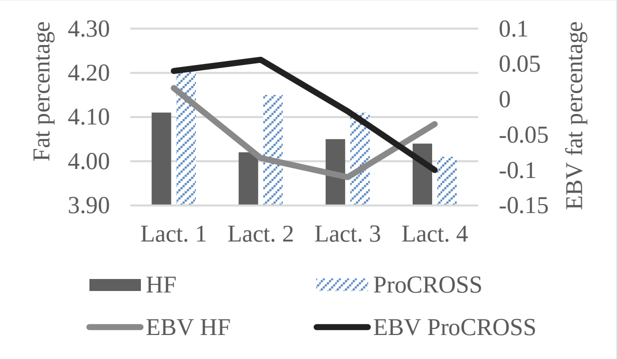

Figure 2: Milk fat percentages (corrected) and fat percentage EBVs for both breed groups, per lactation.

The lack of a significant breed-difference in EBVs, whilst the ProCROSS cows do have a significantly higher (corrected) fat percentage, points towards another bias. It could very well be that the EBVs of the HF cows are overestimated due to inbreeding depression withholding them from reaching their full genetic potential.

Milk protein

The HF cows had a mean protein percentage of 3.53% over 305 days lactation, for the ProCROSS cows the corrected mean was 3.47% protein over 305 days lactation. The breed-difference of 0.06% in favour of the Holstein Friesians was found significant (P=0.012). Mean EBV for protein percentage was 0.01% in the HF cows, and -0.0008% in the ProCROSS cows. The breed-difference of 0.0018% – in favour of HF – was significant (P=0.034).

Figure 3 shows the (corrected) milk protein percentages and their EBVs for of both breed groups, per lactation.

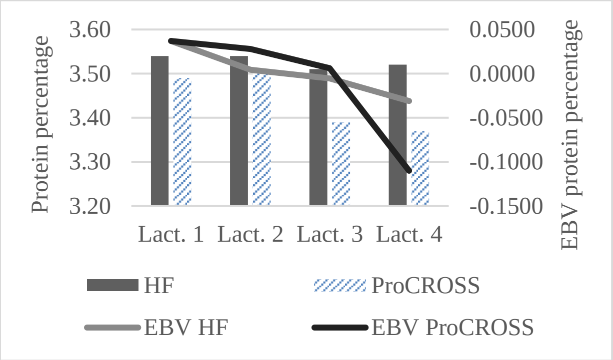

Figure 3: Milk protein percentages (corrected) and protein percentage EBVs for both breed groups, per lactation.

A significant breed*lactation interaction was found for lactation 4 (P=0.028). Further analysis found that the breed-difference for protein percentages was significant in lactation 4 (P=0.005). There is no evidence of a potential bias from inbreeding depression on milk protein percentages.

Somatic cell count (SCC)

The number of increased somatic cell counts or subclinical mastitis cases (≥250.000 cells/ml milk) measured per lactation were used as performance parameter. The mean number of increased counts per lactation was 1.26 for the HF cows, and 1.17 for the ProCROSS cows. The breed-difference of 0.09 increased somatic cell count measures per lactation was not found significant (P=0.758). EBVs for SCC are presented in points, in which 100 points is the population mean. In this study, the mean EBV was 102.4 points in the HF cows, and was 102.6, in the ProCROSS cows. The breed-difference of 0.2 points was not found significant (P=0.458).

The mean number of increased somatic cell counts per lactation, and EBVs for SCC are displayed per breed and lactation in the following figure. No significant breed*lactation interaction was found.

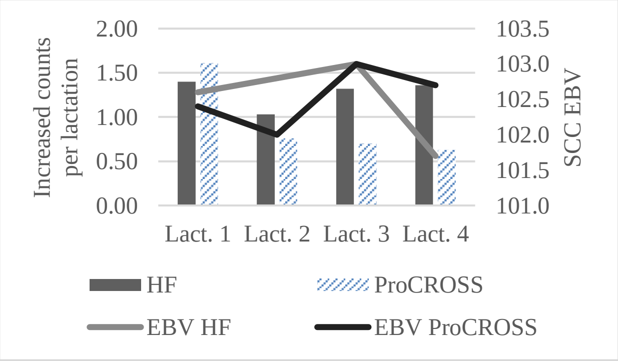

Figure 4: Number of increased SCC/lactation and SCC EBVs per breed and lactation.

Fertility – calving interval

The (corrected) mean calving interval was 406 days for the HF cows in this study, and 380 days for the ProCROSS cows. The breed-difference of 26 days was highly significant (P=0.000). Except for lactation 3, for which the breed-difference was not significant (P=0.317). EBVs for fertility are presented in the same points system as those for SCC. The mean for the HF cows was 100 points, for the ProCROSS cows this was 102 points. The breed-difference of 2 points was found highly significant (P=0.000).

Figure 5 displays the calving intervals and fertility EBVs for both breeds, per lactation.

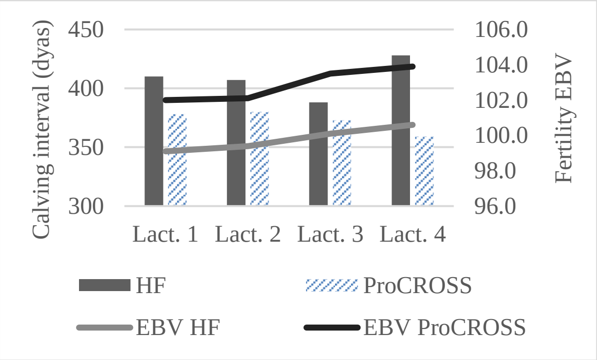

Figure 5: Mean calving interval and fertility EBV per breed and lactation.

Although the ProCROSS cows had a significantly shorter calving interval (after corrections) as well as a significantly higher EBV, the difference in EBVs suggests a breed-difference of about 5 days calving interval. The actual (corrected) difference was 26 days. However, due to the large difference between expected heterosis effects as stated in literature and as corrected by CRV, a possible influence of inbreeding depression could not be determined.

CONCLUSION

The bases of EBV calculations are adapted to the performance of the reference population for all traits every five years. By which EBVs are in part automatically corrected for the effects of inbreeding depression in the reference population. Still, this study found differences between the breed groups for milk yield, fat percentages, and fertility that may very well be caused by inbreeding depression. A biased model leads to biased EBVs, which might result in wrong impressions when comparing purebred and crossbred cattle on their genetic potential for a trait.

Altogether, this study was too small to draw confident conclusions about the total population, the outcomes strongly indicate a bias in the model used in EBV calculations. This bias could very well be caused by the ignorance of inbreeding depression effects in EBV calculations of purebred Holstein Friesians. In order to draw more confident conclusions, it is recommended to perform further research into this subject. A large-scale and independent study into the effects of inbreeding depression on the performance of dairy cattle is recommended to distinguish and remove any biases from the model used in EBV calculations. Additionally, based on the large difference between literature and studbook for some traits, it is recommended to studbook CRV to perform further research on the applied heterosis corrections in EBV calculations of crossbred cows in the Netherlands.

ROLE OF THE STUDENT

This study was designed, planned and carried out by undergraduate student Jikke Snelder. The topic and research questions were composed by Jikke Snelder, together with commissioner Koole&Liebregts. Throughout the study, Jikke Snelder was coached and supervised by Marcel van Oijen. The gathering, processing and analysis of results, formulation of the conclusion and recommendations, as well as writing of the report and paper, were done by the student.

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