

Effect of Including Inbreeding, Heterosis and Recombination Loss in Prediction of Breeding Values for Fertility Traits

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Introduction

Inbreeding results from the mating of related individuals and is becoming increasingly important in domestic livestock populations. Inbreeding depression is the reduction of the mean phenotypic value, particularly for traits connected with reproduction or fitness (Miglior *et al.*, 1992). Inbreeding depression has been shown to decrease milk production by approximately 9-26 kg of milk per lactation for each 1% of inbreeding (Thompson *et al.*, 2000a&b). Research from the US estimated an economic loss in relative net income of approximately £8 per 1% increase in inbreeding over the lifetime of a cow (Smith *et al.*, 1998). Very little data exists for non-production related traits such as fertility, but it is expected that inbreeding depression could be substantially greater for these types of traits than for production traits.

There has been a large influx of North American Holstein genes into the UK dairy population resulting in a steep increase in the proportion of Holstein in the UK population (Figure 1). There is, however, a population of Friesians and crossing and upgrading occurs between Friesian and Holstein populations. This can result in the favourable effect of heterosis, whereby crossbred progeny have a performance advantage over the mid-parent mean for that trait (Shull, 1914) and useful heterosis is where the crossbred outperforms both purebred parents. Of the heterosis in the F₁ population, a proportion is lost due to the recombination between parental line genes (Dickerson, 1969) and is a measure of the epistatic interaction of genes.

The purpose of this study was to examine the impact of inbreeding, heterosis, recombination loss and proportion of Holstein on dairy cow fertility. Covariates with a significant effect were then included in the BLUP estimation model to examine the impact of inbreeding,

heterosis and/or recombination loss on the estimation of fertility breeding values for UK sires.

Materials and Methods

Animal, sire and dam records for nearly 8.5 million pedigree animals born since 1900 were extracted from the Holstein UK database. After edits and updates, the pedigree file contained 7,359,582 animals. Inbreeding coefficients were calculated using the algorithm of Meuwissen and Luo (1992). This method is based on the decomposition of the additive genetic relationship matrix as described by Henderson (1969), and is especially useful in large population sizes.

Animal records containing inbreeding coefficients were then matched to the most recent UK fertility index BLUP evaluations file (described in Wall *et al.*, 2003). Just over 50% (900,000) of the cow records used in the fertility evaluations could be matched to the HUK pedigree file. Percent Holstein was calculated for all animals in this dataset, based on the average percent Holstein of the parents. Additional assumptions on percent Holstein based on the breed code of a sire or dam were also applied. Heterosis (het) and recombination loss (rec) were calculated for all cows as follows:

$$\text{het} = P_S(1-P_D) + P_D(1-P_S)$$

$$\text{rec} = P_D(1-P_D) + P_S(1-P_S)$$

where P_S and P_D are the proportion of Holstein in the sire and dam respectively.

Stringent editing rules were applied to this dataset to result in a manageable dataset, which was necessary due to the computational demands of the analysis. All cow records were for animals born since 1997, and were full

pedigree. Sire progeny groups contained at least 40 offspring and herd-year-season groups were of minimum size 10, resulting in 276,893 first lactation records with a mean inbreeding coefficient of 1.7% (s.d. 2.0%), recombination loss of 14.7% (10%), heterosis of 30.4% (26%) and % Holstein of 83.0% (17%).

Inbreeding, heterosis, recombination loss and percent Holstein were fitted as covariates in the models for all traits (milk kgs at day 110, MILK; body condition score on a 1-9 scale, BCS; calving interval, CI; days in milk until first service, DFS; non-return rate after 56 days, NR56, and number of inseminations resulting in a calf, INS). The reduced BLUP estimation dataset was analysed using an exact solver in PEST. Due to the size of the dataset, bivariate sire maternal-grandsire analyses were carried out for each of the five traits (CS, CI, NR56, DFS and INS) with MILK. This yielded solutions for each of the covariates and their standard errors. A two-way t-test was performed for each covariate, apart from inbreeding as it was assumed that inbreeding would only have an unfavourable effect on each of the traits and therefore only a one-way t-test was performed.

A covariate was added to the model for a trait (described in Wall *et al.*, 2003) if it was found to have a significant effect after the above analyses. BLUP analyses were run with and without fitting these additional effects in the model. The effect of their inclusion was estimated by the rank correlation between the two BLUP analyses.

Results

Figure 1 shows the average inbreeding (F) and percent Holstein by year of birth since 1965. The first notable increase in inbreeding occurred around 1967. Based on linear regression, inbreeding increased slowly at a rate of about 0.03% per year from 1968 until 1991. However, since 1991 inbreeding has accelerated rapidly and is currently increasing by 0.17% per year, a rate similar to the US Holstein population. Currently, the average level of inbreeding is 2.6% for females and 3.1% for males. More than 90% of males and females born in 2000 are inbred to some degree (Table 1). The majority of these animals have inbreeding coefficients less than 6.25% but more than 5% of males born in

2000 have inbreeding coefficients between 6.25 and 12.5%. This represents a doubling of the number of males that are inbred at this level since 1990.

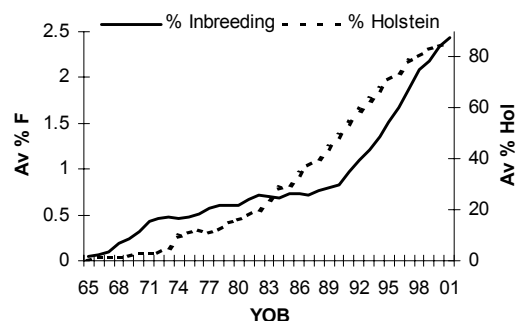


Figure 1. Trend in inbreeding and percent Holstein since 1965.

Table 1. Proportion of males and females and inbreeding level for animals born in 2000.

Inbreeding %	Males	Females
0	10.4	7.6
0 < F ≤ 6.25	83.9	87.9
6.25 < F ≤ 12.5	5.2	3.9
12.5 < F ≤ 25	0.5	0.5
> 25	0.02	0.1

Table 2 shows the estimates of the inbreeding, heterosis, recombination loss and percent Holstein covariates from the bivariate analyses of MILK with each of the other traits. The solution for inbreeding was significant for all traits. Percent Holstein was significant for CI, BCS, MILK and INS, heterosis and recombination loss was significant for MILK and DFS. Inbreeding had a negative effect on all traits. The difference between a non-inbred animal and the offspring of a grandsire-granddaughter mating ($F = 6.25\%$) was; 2.3 days increase in CI, 0.17 units decrease in BCS, 0.25 kg decrease in MILK, 1.125 days increase in DFS, 0.025 increase in INS. Miglior *et al.* (1995) found that 1% inbreeding caused a 0.4% decrease in the phenotypic mean of total lactation yield whereas this analysis found a 0.16% decrease of yield at day 110. Fioretti *et al.* (2002) found a negative effect on reproductive traits for each percent increase in inbreeding in Piedmontese cattle. However different traits were analysed and therefore a direct comparison is not possible. The difference between a Friesian and a 100% Holstein animal

was: 9.9 day increase in CI, 1.94 units decrease in BCS (1-9 scale), 3.5 kg increase in MILK and 0.15 insemination increase in INS.

Table 2. Solutions for the non-additive genetic covariates from the bivariate analyses.

	F	het	rec	ph
CI	36.89	-2.34	-2.34	9.90
(days)	±6.85***	±1.26	±1.26	±2.39***
BCS	-2.68	-0.10	-0.01	-1.94
(1-9)	±0.27***	±0.12	±0.08	±0.23***
MILK	-4.02	0.57	-1.45	3.46
(kg)	±0.45	±0.13***	±0.11***	±0.25***
DFS	17.91	-1.63	-2.15	3.44
(days)	±3.22***	±0.64*	±0.81**	±1.21
NR56	-0.10	-0.01	-0.01	-0.03
(0/1)	±0.06**	±0.01	±0.01	±0.02
INS	0.45	-0.02	-0.02	0.15
(count)	±0.14***	±0.02	±0.03	±0.05**

***, **, * significant at the 0.1, 1 and 5% level respectively.

Inbreeding was added to the model for each trait and recombination loss and heterosis was included in the models for MILK and DFS. Percent Holstein was significant for the majority of traits, however this effect is accounted for by fitting genetic groups in the sire maternal-grandsire model and would result in a confounding of these effects if both were used.

Including inbreeding in the model, on average, causes a very slight and unfavourable change in the index and its components (e.g., the average value for CI increases). The mean value for fertility index decreases as the mean value for CI increases and NR56 decreases. The standard deviation of each trait is slightly larger with the inclusion of the non-additive genetic effects in the model. However, there is little change in overall rank of animals by fitting these additional effects in the model. The rank correlations between the PTAs and the fertility index (with and without the additional non-additive effects in the model) was over 0.99.

Discussion

Inbreeding levels in the UK Holstein population have been increasing steadily over the last decade or so. Currently, this trend shows little sign of changing. At the current levels of inbreeding, losses in production due to

inbreeding depression are likely to be offset by genetic gain. Nevertheless, inbreeding can reduce performance in traits not currently considered in selection indices in the UK, such as fertility traits.

Inbreeding had a significant negative effect when it was fitted in the models for the majority of the traits and could be considered for inclusion in the evaluation system. However, the rank correlation between the PTAs using models with and without the significant inbreeding effects was high. On closer examination it could be seen that there was a slight re-ranking of bulls and changes in the PTAs. Proportion Holstein was significant for several of the traits but its effect is accounted for by fitting genetic groups in the sire maternal-grandsire model.

This analysis fitted inbreeding as a linear covariate. However, it is quite possible that inbreeding does not have a linear relationship to some or all of the traits of interest. To examine if this is the case each cow was assigned to one of 13 inbreeding classes (0, 1-10, 10-15, 15+) and inbreeding was added to the model of each trait as a fixed effect in a bivariate analysis of each trait with MILK. The solutions for each of the inbreeding classes would show the true effect of inbreeding on each trait and indicate if higher classes of inbreeding had a more severe depression on each of the traits.

Figure 2 shows the effect of inbreeding on MILK and CI which is generally more severe at the extreme levels of inbreeding (10%+). However the solutions for CI above 6% were not significantly different from zero. Figure 2 shows that low levels of inbreeding (up to 3%) has a positive effect on milk yield around day 110 (MILK). A similar trend is seen in the American Holsteins for test day milk after day 70 (Thompson *et al.*, 2000b).

Inbreeding had a similar (and significant) effect on DFS as it had on CI, with highly inbred animals (15%+) having 4.5 additional days to 1st service compared to non-inbred animals. The solutions for the effect of inbreeding on INS and NR56 were generally non-significant. Figure 3 shows the effect of inbreeding on BCS and MILK and shows that the effect of inbreeding on BCS is not as severe at the higher inbreeding classes as seen in other traits. However, even animals in low inbreeding classes have a

depressed condition score compared to non-inbred animals (0.5 of a BCS).

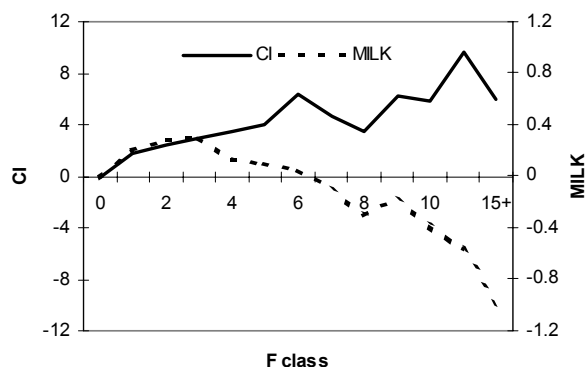


Figure 2. Effect of inbreeding on kgs of milk on day 110 (MILK) and calving interval (CI).

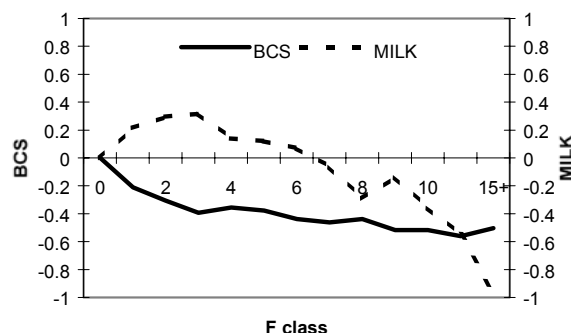


Figure 3. Effect of inbreeding on kgs of milk on day 110 (MILK) and condition score (BCS).

Conclusions

Non-additive effects of inbreeding, heterosis, recombination loss and percent Holstein were shown to have a significant effect on some or all of the traits used in the estimation of the UK fertility index. On closer examination it was shown that the effect of inbreeding was more severe at higher levels of inbreeding than lower levels. In fact, there was a slight positive advantage of a low level of inbreeding on milk yield close to day 110. It is the recommendation of this study that, at current levels of inbreeding, there is little need to include these non-additive effects in the models for estimation of fertility PTAs. However, if the proportion of animals in higher inbreeding classes continue to rise the effect of inbreeding depression could be severe and this recommendation should be reviewed regularly.

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