Validation of Genomic and Genetic Evaluations in 305d Production Traits of Nordic Holstein Cattle

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Abstract

As genomic selection has been used already for several years, it has become evident that the validation of genomic evaluations relying on traditional animal models is becoming unsuitable. The GEBV validation test recommended by Interbull is cross-validation based on the forward prediction. It was designed at the time when the multi-step genomic evaluation was the standard method. The aim of this study was to take a closer look on accuracy and stability of (G)EBVs. Validations for GEBVs were done using yield deviations (YD) or daughter yield deviations (DYD) calculated with single-step GBLUP instead of EBV model. Moreover, we studied the stability of (G)EBV estimations in consecutive evaluations. We used Nordic Holstein 305 days production data containing ca. 7.3 million cows with 15.6 million observations. Genotypes were available for 30056 animals which had either records or offspring in the full 305d data. The test setup consisted of four data sets: the full data, called $data_0$, included calvings up to March 2016. Three reduced data sets were $data_{-1}$, $data_{-2}$, and $data_{-3}$, from which one year of calvings was deleted at a time. This allowed studying the accuracy of predictions by production years, and also the stability of (G)EBV estimates across lactations. The bull validation was a regression of DYD_{EBV} on PA_{data-3} or, for $GEBV_{data-3}$, regression of DYD_{GEBV} on $GEBV_{data-3}$. The results suggested that after use of genomic selection the DYD from EBV model become biased and that GEBVs validated using DYDs from the BLUP model might receive too low reliability. The validation reliability for protein GEBV (r^2) was 0.34 using DYD from EBV model and 0.36 using DYD from ssGBLUP. Similarly, when making cow validations, it might be advisable to use YDs calculated from ssGBLUP for the validation. The r^2 in GEBV validations using YD from ssGBLUP were on average 5 % units higher compared to validations using YDs from the EBV model.

Key words: validation, genomic selection, genomic evaluation, Holstein

Introduction

Since Meuwissen *et al.* (2001) introduced the concept of genome-wide marker-assisted selection (GWMAS), also known as genomic selection, many alternative methods have been developed to put genomic selection into practice. Currently, genomic selection has been in wide use already several years.

The official Interbull validation test of EBV and GEBV is a cross-validation test that uses two data sets; full and truncated, and daughter yield deviations (DYD) or deregressed proofs (DRP) from the full data are regressed to EBV or GEBV (Mäntysaari *et al.*, 2010) from the truncated set.

The validation test was designed at the time when the multi-step genomic evaluation was the standard method. Now it has become clear that GEBV validation test is generally poorly suited for testing genomic animal model, the single-step GBLUP (ssGBLUP). Validation bulls are by definition young, and should not have daughters. However, genotyped daughters might be an essential part of the genomic reference population.

In most of the modern breeding programs, young bulls are heavily selected using GEBVs. This reduces the correlation between the estimated and the true breeding value, and thereafter the bull based validation reliability R^2 starts to decrease. In case the cow genotyping

are more random, the validation reliability estimated using cow GEBVs and cow yield deviations (YD) should better reflect the true accuracy of genomic evaluations. Moreover, after years of genomic selection, the EBV model accuracy starts to deteriorate and we cannot trust the DYDs used in the validation. Because of that, estimates of the regression coefficient b_1 and validation R^2 are lower than before. One solution would be to start using DYD from the ssGBLUP.

The aim of this study was to take a closer look at reliability and stability of (G)EBVs. We also tested the usability of genotyped cows for the validation. Moreover, we wanted to study the stability of (G)EBV estimations in consecutive evaluations.

Materials and Methods

Data

We compiled Nordic Holstein 305 days production data from the test day data used in the official Nordic TD evaluations. The full data included calvings up to March 2016. It included ca. 7.3 million cows with 15.6 million observations. For the study, three reduced data sets were created by removing one year of calvings at the time. Finally, we had four data sets: the full data called $data_0$, and three reduced data sets, $data_{-1}$ including calvings up to March 2015, $data_{-2}$ including calvings up to March 2014, and $data_{-3}$ including calvings up to March 2013. For the validation, we calculated YDs and DYDs both from the animal and ssGBLUP models.

The marker data included genotypes for 30056 Nordic Holstein animals which had either own 305 days records or offspring in the full 305d data. The standard **G**-matrix, including 10% of the polygenic variance (Christensen and Lund, 2010) was built for the genomic model. The genomic relationship matrix used the estimated base population allele frequencies, calculated as described by McPeek *et al.* (2004).

The unified relationship matrix **H** used in ssGBLUP defines the relationships among genotyped and non-genotyped animals. Usually, when the model includes genetic groups, only pedigree-based relationship matrix is augmented to include phantom parent groups (PPG). However, contributions to PPG due to genomic relationships can be similarly accounted (Mistzal *et al.*, 2013). Therefore, QT transformation was conducted to take into account PPG also due to the genomic information (Matilainen *et al.*, 2016).

Analysis

The evaluation model was a simple multi-trait (three lactations) model for protein only. The variance components for the model were derived from the variance components of the official TD model. The model was

$$y_{ijklm} = age_i + sea*yr_j + hy_k + add_l + e_{ijklm}$$

where y_{ijklm} is the 305 d protein record; age_i is the fixed effect of the calving age; $sea*yr_j$ is the fixed effect of the calving-year-season interaction; hy_k is the fixed effect of the herd-calving year interaction; and is the random additive genetic animal effect, and e_{hijklm} is the random residual effect. The number of test day records/10 was used as a weight in the model. Both the traditional animal model EBVs and the genomic animal model GEBVs were calculated using the same model. In addition, inbreeding coefficients were accounted in the computation of A^{-1} in all models. For all the results presented, the validated trait was a combined 305d protein yield with weights 0.5 for the first lactation (G)EBV, 0.3 for the second lactation (G)EBV and 0.2 for the third lactation (G)EBV.

Alternative validation procedures were tested for the bulls and cows. The bull validation was a regression of DYD from the full data ($data_0$) EBV model (DYD_{EBV}) on PA_{data-3} or for $GEBV_{data-3}$ from the reduced data with three years of data reduction, or alternatively regression of DYD from the ssGBLUP (DYD_{GEBV}) on $GEBV_{data-3}$. For the cows, it was possible to do the validations yearly. Validation was done by regression of YD_{EBV} or YD_{GEBV} derived from the data set in which the validation cow received her first lactation record on her PA or GEBV from earlier data, without own records. The validation R^2 was obtained by dividing the

regression model coefficient of determination by the reliability of YD in describing the combined protein yield breeding value.

The stability of evaluations was tested with a simple linear model. The difference between consecutive evaluations was explained by calving-year, parity, sire type (young or proven) and all their interactions. The aim was to test if the changes were bigger in daughters of young genomic tested bulls than in daughters of old proven bulls.

Results & Discussion

The genetic trends for bulls having at least 50 daughters in the full 305d data are shown in Figure 1. The genetic improvement due to genomic selection should not be observable before 2010, but presumably in conventional evaluation the bulls born 2008 already have started to suffer from the genomically selected younger bulls. In the year 2011, the difference between EBV and GEBV was 40% of the sire standard deviation. In cows, the difference between EBV and GEBV in genetic trend is small and starts to be visible after the year 2012 (Figure 2).

The model validation results for the bulls are in Table 1, and for the genotyped cows in Table 2. The tables present regression coefficients (b_1) and validation reliabilities (R^2). For the bulls, validation reliabilities from the validation using animal model DYD were 0.14 for PA and 0.36 for GEBV. When ssGBLUP DYD were used in the validation, the validation reliability increased to 0.39. Similarly, in cows, the results of the GEBV validation increased when the validation was based on a regression of YD from the ssGBLUP. In general, the validation results for the genotyped cows were considerably higher than for the bulls, the R^2 was on average 0.59 for cows. Also, the regression coefficient b_1 was close to one, while for the bulls, the b_1 was clearly less than one. Assuming that the problems in the validation test generally lead into underestimation of b_1 as well as R^2, it seems advisable to validate GEBVs by using DYD or YD from the ssGBLUP model, instead of a current official method. Also, moving from bull validation to cow validation would lessen the pre-selection problem. In the Denmark/Finland/Sweden breeding program for Red Dairy Cattle, the genomic reference population is increased by systematically genotyping cows. Although in Holstein the genotyped cows are, to some extent, a selected group of animals, they still seem to give higher R^2 than the bulls. This might be because the bulls are selected for AI by GEBVs, while cows are selected for genotyping by their PA. One more positive point in the cow validation is the possibility to do yearly validation tests by removing only one year of observations.

When the stability of evaluations was studied, all factors tested were significant because of a large number of observations. However, we did not find any clear patterns on the solutions, and there were no differences between animal model or ssGBLUP. Thus, measured as stability between consecutive evaluations, both methods were equally good.

Table 1. Bull validation (Bulls=723) results. Regression coefficients (b_1) and validation reliabilities (R^2) from the parent average (PA) and GEBV. DYD_{EBV} calculated from animal model DYD_{GEBV} calculated from the ssGBLUP model.

	PA		GEBV	
	b_1	R^2	b_1	R^2
DYD_{EBV}	0.67	0.14	0.75	0.36
DYD_{GEBV}			0.77	0.39

Table 2. Yearly cow validation results. Regression coefficients (b_1) and validation reliabilities (R^2) from the parent average (PA) and GEBV. YD_{EBV} calculated from animal model YD_{GEBV} calculated from the ssGBLUP model. The year is PA evaluation year.

Year	PA		GEBV	
YD_{EBV}	b_1	R^2	b_1	R^2
2012	1.35	0.38	1.14	0.59
2013	1.12	0.29	1.12	0.56
2014	1.25	0.29	1.15	0.56
YD_{GEBV}				
2012			1.16	0.62
2013			1.14	0.58
2014			1.18	0.59

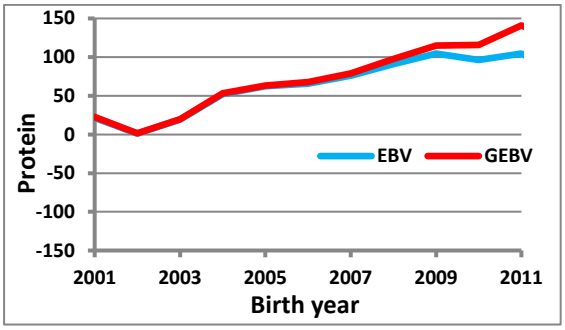

Figure 1. Genetic trends for genotyped bulls with at least 50 daughters by birth year. The trend for protein (G)EBV.

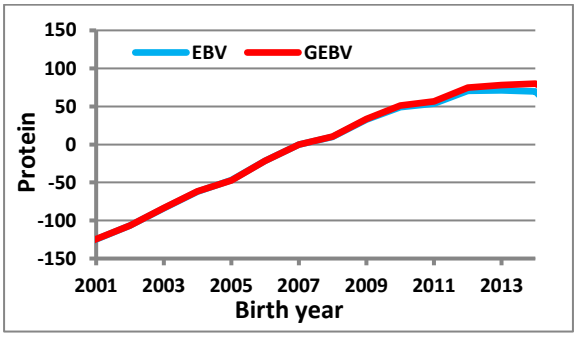

Figure 2. Genetic trends for cows with first lactation record by birth year. The trend for protein (G)EBV.

Conclusions

Use of DYDs from the animal model run will give lower validation reliability (0.36) than using DYD from ssGBLUP (0.39). The same trend was observed in the cow validations. Overall, the bull validations gave considerably lower regression coefficients and validation reliabilities than the cow validations. Thus, it would be beneficial to use cow validations instead of bull validations. Or meanwhile, use DYDs from the ssGBLUP in the GEBV validation.

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