Information from later lactations improves accuracy of genomic predictions of fertility-related disorders in Norwegian Red

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ABSTRACT

Our aim was to investigate whether including information from later lactations improves accuracy of genomic breeding values for 4 fertility-related disorders: cystic ovaries, retained placenta, metritis, and silent heat. Data consisted of health records from 6,015,245 lactations from 2,480,976 Norwegian Red cows, recorded from 1979 to 2012. These were daughters of 3,675 artificial insemination bulls. The mean frequency of these disorders for cows in lactation 1 to 5 ranged from 0.6 to 2.4% for cystic ovaries, 1.0 to 1.5% for metritis, 1.9 to 4.1% for retained placenta, and 2.4 to 3.8% for silent heat. Genomic information was available for all sires, and the 312 youngest bulls were used for validation. After standard editing of a 25K/54K single nucleotide polymorphism data set that was imputed both ways, a total of 48,249 single nucleotide polymorphism loci were available for genomic predictions. Genomic breeding values were predicted using univariate genomic BLUP for the first lactation only and for the first 5 lactations and multivariate genomic BLUP with 5 lactations for each disorder was also used for genomic predictions. Correlations between estimated breeding values for the 4 traits in 5 lactations with predicted genomic breeding values were compared. Accuracy ranged from 0.47 and 0.51 for cystic ovaries, 0.50 to 0.74 for retained placenta, 0.21 to 0.47 for metritis, and 0.22 to 0.60 for silent heat. Including later lactations in a multitrait genomic BLUP improved accuracy of genomic estimated breeding values for cystic ovaries, retained placenta, and silent heat, whereas for metritis no obvious advantage in accuracy was found.

Key words: fertility-related disorders, genomic prediction, dairy cattle

INTRODUCTION

In a progeny testing scheme, only first lactation information from the daughters is available when the bulls get their first official proofs. The frequency of fertility-related disorders such as cystic ovaries (**CO**), retained placenta (**RP**), and metritis (**MET**), however, often increases as the cow gets older (Haugaard and Heringstad, 2013). This implies that potentially valuable information is not yet available at the time when the elite sires are selected. With the introduction of genomic selection, information from later lactations may more easily be used, as the reference population includes older bulls with information from daughters of all ages.

Some of the factors affecting the accuracy of genomic predictions are the size of the reference population, heritability of the trait, quality and number of available phenotypes, population structure and effective population size, as well as the density of the genomic markers (Hayes et al., 2009). Functional traits, such as fertility and health, have low heritability and show lower accuracy in genomic predictions compared with production traits (Luan et al., 2009; Zhou et al., 2014). Few populations record direct health traits, though several countries have recently started recording health traits as well as production traits in contract herds (Gernand et al., 2012) or in the main population (e.g., Koeck et al., 2012; Egger-Danner et al., 2012). In the Scandinavian countries, disease records have been collected for more than 30 yr, and direct health traits (e.g., mastitis) are included in routine genetic evaluations. Fertility-related disorders have so far not been included in the routine genetic evaluations in Norway, except RP, which is included in other diseases, a trait with 2% relative weight in the current total merit index for Norwegian Red. Fertility-related disorders is a disease category that has increased somewhat in frequency in recent years. The number of cows treated for any fertility-related disorder per cow-year (incidence rate) increased from 6.6% in 2008 to 8.5% in 2013 (Norwegian Cattle Health Services, 2014), and inclusion in the breeding scheme may therefore become desired.

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The main aim of the current study was to examine whether including information from later lactations would increase accuracy of genomic predictions for fertility related disorders in Norwegian Red. Accuracy of genomic predictions based on data from first lactation only versus using lactations 1 to 5 was compared. More than 30 yr of health recordings of the 4 most common fertility-related disorders, CO, RP, MET, and silent heat (SH), were used.

MATERIALS AND METHODS

Data

Records on calving and health (veterinary treatments of disease) from 2,480,976 cows calving from January 1979 through December 2012 and sired by Norwegian Red AI bulls were extracted from the Norwegian Dairy Herd Recording System. Information on CO, RP, MET, and SH from the first 5 lactations were used. The 4 disorders were chosen as these are the most frequent fertility-related disorders in Norway. Cows without first lactation records in the data set were omitted, and the cows had to be 20 to 36 mo old at first calving and have reasonable calving intervals (280–500 d) thereafter. The traits were defined as binary (0 = healthy, 1 = affected) for each disorder in each lactation. For RP, the veterinary treatment had to occur within the first 5 d after calving, whereas for the other disorders all health records within a lactation were used. The overall mean frequency of each disorder in each lactation is presented in Table 1. The mean frequency varied from 0.6 (CO in first lactation) to 4.1% (RP in fifth lactation). Only daughters of bulls with at least 150 first-lactation daughters were included in the data set. There were a total of 26,858 animals in the pedigree file, which consisted of the 3,675 bulls with daughters in the data set and their dams and sires traced back as far as possible, back to the 1950s.

Genomic information was available for all 3,675 sires, where 2,165 were genotyped with the 25K SNP chip

from Affymetrix (Affymetrix Inc., Santa Clara, CA) and 1,967 were genotyped with the 55K SNP chip from Illumina (Illumina Inc., San Diego, CA). A total of 457 of the sires were genotyped with both. An imputed 25K/54K SNP data set (imputed both ways, imputation procedure described in Solberg et al., 2011) after standard editing had 48,249 SNP loci used for genomic predictions.

Daughter Yield Deviations

Daughter yield deviations (DYD) of the reference population were used as the response variable for the genomic predictions. These were estimated using a subset containing only records from lactations starting before January 1, 2008. The 3,363 bulls with at least 150 first-lactation daughters in this subset of data were included in the reference population, whereas the youngest 312 bulls that by January 1, 2008, did not have 150 first-lactation daughters was defined as the validation set. The mean number of first lactation daughters per sire in the reference population and validation set was 675 (minimum = 150; maximum = 10,197) and 227 daughters (minimum = 150; maximum = 2,742), respectively.

Each of the 4 fertility-related disorders was analyzed separately using linear sire models to predict parameters for calculation of DYD using the subset and to predict EBV using the full data set for comparison with genomic EBV (GEBV) from the genomic predictions. For MET and SH, the 5 lactations were analyzed as genetically correlated traits in multivariate models. Cystic ovaries were analyzed treating the 5 lactations as repeated records in a univariate repeatability model. A repeatability model was also used for RP in lactation 2 to 5, whereas RP in the first lactation was analyzed as a correlated trait in a bivariate model. The choice of models was based on Haugaard and Heringstad (2013). For CO, the systematic effects were year-season of calving (132 levels, seasons defined as January–March, April–June, July–September, and October–December) and age at calving in months (76 single-month classes).

Table 1. Number of records and mean frequency of cystic ovaries (CO), retained placenta (RP), metritis (MET), and silent heat (SH) in lactation 1 to 5 in the full data set

Lactation number	No. of records	Frequency, ¹ %			
		CO	RP	MET	SH
1	2,480,976	0.6	1.9	1.5	3.8
2	1,645,094	1.4	2.5	1.0	2.9
3	1,021,604	2.0	3.1	1.1	2.8
4	576,709	2.3	3.6	1.2	2.6
5	290,862	2.4	4.1	1.2	2.4
Overall	6,015,245				

¹Frequency of at least 1 veterinary treatment.

For MET, the systematic effects were year-season of calving and twinning, recorded as 1 (single calf) or 2 (2 or more calves). For RP, the systematic effects were year-season of calving, twinning, and calving interval in the previous lactation, divided into 6 categories: (1) ≤ 325 d, (2) 325–340 d, (3) 341–355 d, (4) 356–370 d, (5) 371–400 d, and (6) >400 d. For SH, the systematic effects were year-season of calving and calving interval in the previous lactation. Herd and sire were treated as random effects in all models. Single-trait analyses of the first lactation for each disorder were also performed. Solutions from the linear models of the reduced data sets were then used to calculate DYD to be used as response variable in the genomic predictions described below, where DYD is the average performance of the bulls daughters subtracted for all systematic and nongenetic random effects. All linear analyses were done using the DMU4-program in DMU (Madsen and Jensen, 2010). Heritability for all traits used in the analyses is presented in Table 2.

Accuracy of Genomic Predictions

Direct GEBV were predicted in 3 different ways:

- (1) single-trait genomic BLUP (**GBLUP**) using DYD from first lactation only as response variable (**GEBV-1**),

- (2) single-trait GBLUP using DYD from each of the 5 lactations separately as response variable (**GEBV-S**), and
- (3) multitrait GBLUP using DYD from the 5 lactations simultaneously as response variable; for MET, the 5-variant GBLUP analyses did not converge, so only the first 4 lactations was used in a 4-variant GBLUP (**GEBV-M**).

These analyses were performed using DMUAI in DMU (Madsen and Jensen, 2010). In matrix notation, the model can be written as $y = 1\mu + Zg + e$, where y is the response variable DYD, 1 is a vector of ones, μ is the overall mean, g is a vector of genomic breeding values, Z is the incidence matrix of g , and e is residuals. It was assumed that $\text{var}(g) = G_0 \otimes G$ and $\text{var}(e) = R \otimes D$, where G is the genomic relationship matrix, D is a diagonal matrix containing weighting factors for the residuals, and G_0 and R are the corresponding scalar (GEBV-1 and GEBV-S) or 5×5 (GEBV-M) matrices containing the genetic and residual (co)variance.

The genomic relationship matrix was calculated using the program Gmatrix (Su and Madsen, 2012), constructed by method 1 of VanRaden (2008). Accuracy of genomic predictions was calculated as the correlation between GEBV for the 312 sires in the validation set and their EBV obtained from the full data set. In the GEBV-S and GEBV-M approach, EBV for each lactation was correlated with GEBV of the same lactation, whereas in the GEBV-1 approach, EBV for all 5 lactations was correlated with the GEBV from the first lactation. The correlations were based only on those bulls in the validation set with daughters in the respective lactation, meaning that the validation set for lactations 4 and 5 were smaller (265 and 169 bulls, respectively) than for lactations 1, 2, and 3 (312 bulls). Regression analyses were used to validate whether GEBV over- or underpredicted the genetic merit for the fertility-related disorder in each case.

RESULTS AND DISCUSSION

Accuracy

Accuracy of genomic predictions ranged from 0.22 to 0.54 for GEBV-1, 0.21 to 0.74 in GEBV-S, and 0.24 to 0.74 in GEBV-M (Table 3). These accuracies were in the upper range of those previously reported for functional traits in Norwegian Red. Luan et al. (2009) and M. Svendsen (Geno Breeding and A.I. Association Ås, Norway; personal communication) found accuracies for various production and health traits in Norwegian Red in the range 0.15 to 0.41 and 0.16 to 0.77, respectively. In both of those studies, health and fertility

Table 2. Heritability of fertility-related disorders used for prediction of EBV

Trait ¹	Heritability ²
CO1–5	0.009
RP1	0.008
RP2–5	0.010
MET1	0.002
MET2	0.001
MET3	0.001
MET4	0.001
MET5	0.002
SH1	0.005
SH2	0.002
SH3	0.002
SH4	0.002
SH5	0.002

¹CO = cystic ovaries, analyzed with the 5 lactations as repeated records in a univariate repeatability model. RP = retained placenta, analyzed in lactation 2 to 5 as repeated records in a repeatability model, together with RP in the first lactation as a correlated trait in a bivariate model. MET = metritis and SH = silent heat, analyzed with 5 lactations as genetically correlated traits in multivariate models.

² $h^2 = (4 \times \sigma_{sire}^2) / (\sigma_{sire}^2 + \sigma_{herd}^2 + \sigma_{residual}^2)$, where σ_{sire}^2 , σ_{herd}^2 , and $\sigma_{residual}^2$ are the sire variance, herd variance, and residual variance, respectively. Estimated variance components were larger than their SE, and SE for σ_{sire}^2 was < 0.00001 for all traits.

traits showed lower accuracies than production traits, and the highest accuracies among functional traits were 0.46 for mastitis (Svendsen, personal communication) and 0.43 for calving ease (Luan et al., 2009). Compared with the present study, Luan et al. (2009) analyzed fewer bulls (500) with fewer SNP (25K). These are factors that affect the results of the genomic predictions, and can explain the differences in the results. Ødegård et al. (2014) presented accuracies of GEBV for claw health in Norwegian Red ranging from 0.29 to 0.32, which were lower than accuracies in the present study. As claw health is a novel trait in Norwegian Red, with records available since 2004 (disease records from claw trimming), the limited size of the reference population and low reliability of the response variable may be a reason for the lower accuracies of Ødegård et al. (2014) compared with the present study.

The accuracy of CO was 0.47 and 0.51 for GEBV-1 and GEBV-S, respectively (Table 3), indicating that using information from only the first lactation gave slightly lower accuracy than using information from all 5 lactations. High genetic correlations, above 0.90,

between CO in the 5 first lactations (Haugaaard and Heringstad, 2013) indicate that the disorder is genetically the same across lactations. Therefore, it seems reasonable that using information from 1 lactation to predict others is a possibility.

For RP, the differences between GEBV-1 and GEBV-S were larger than for CO (Table 3). For first lactation RP, the accuracy was the same in both scenarios (0.50), whereas for second to fifth lactation RP the accuracy was lower in GEBV-1 than in GEBV-S (0.51 vs. 0.74). The highest accuracies were acquired from using the GEBV-M approach with 0.55 and 0.74 for first and second to fifth lactation, respectively. In all 3 approaches, the accuracy for RP was lower in first lactation than in second to fifth lactation.

For MET, the lowest accuracy was obtained from the GEBV-M approach, and accuracies decreased with increasing lactation number from 0.47 in the first lactation to 0.21 in the fifth lactation (Table 3). The accuracies from the GEBV-S approach were similar but slightly higher than for the GEBV-M approach, whereas the overall highest accuracies were obtained with the GEBV-1 approach, ranging from 0.39 to 0.47. Among the 4 fertility-related disorders, MET had the lowest mean frequency and the same level across lactations (Table 1). Estimates of variance components and EBV for MET were therefore less accurate, especially in the later lactations where information was sparse (Haugaaard and Heringstad, 2013). However, the genetic correlations between MET in first lactation and MET in later lactations were moderate (0.51–0.67; Haugaaard and Heringstad, 2013). Therefore, it was not expected that first lactation was as good a predictor of later lactations as of that lactations itself (GEBV-1 vs. GEBV-S/GEBV-M; Table 3).

For SH, the accuracy was approximately the same in all 3 approaches for first lactation (Table 3), but whereas the accuracies decreased with increasing parity for the GEBV-1 and GEBV-S approaches, the accuracies increased slightly with increasing parity for the GEBV-M approach. Silent heat had the highest mean frequency among the 4 disorders (Table 1), but decreased with increasing parity.

In general, accuracy of genomic predictions increased when using information from all lactations, and the highest accuracies were obtained by using the GEBV-M approach for most of the fertility-related disorders. The exception was MET, where the highest accuracy was obtained by using the first lactation to predict all lactations (GEBV-1). For SH, the GEBV-M approach gave higher accuracies but varied between lactations, which was better than the GEBV-1 and GEBV-S approach. Among the fertility-related disorders, the highest accuracy was obtained for RP. This may be due to

Table 3. Correlation (SE^1) between EBV for cystic ovaries (CO), retained placenta (RP), metritis (MET), and silent heat (SH) in lactations 1 to 5, with genomic predictions based on first lactations only (GEBV-1) or 5 lactations (GEBV-S and GEBV-M)

Trait ²	Genomic predictions		
	GEBV-1 ³	GEBV-S ⁴	GEBV-M ⁵
CO1–5	0.47 (0.05)	0.51 (0.05)	—
RP1	0.50 (0.05)	0.50 (0.05)	0.55 (0.05)
RP2–5	0.51 (0.05)	0.74 (0.04)	0.74 (0.04)
MET1	0.47 (0.05)	0.47 (0.05)	0.45 (0.05)
MET2	0.41 (0.05)	0.46 (0.05)	0.39 (0.05)
MET3	0.43 (0.05)	0.23 (0.06)	0.30 (0.05)
MET4	0.39 (0.05)	0.28 (0.05)	0.24 (0.06)
MET5	0.46 (0.05)	0.21 (0.06)	—
SH1	0.54 (0.05)	0.54 (0.05)	0.54 (0.05)
SH2	0.40 (0.05)	0.50 (0.05)	0.57 (0.05)
SH3	0.34 (0.05)	0.51 (0.05)	0.58 (0.05)
SH4	0.22 (0.06)	0.57 (0.05)	0.60 (0.05)
SH5	0.35 (0.05)	0.22 (0.06)	0.60 (0.05)

¹SE was calculated as $\sqrt{(1-r^2)/(n-2)}$, where n is the number of individuals.

²CO = cystic ovaries, analyzed with the 5 lactations as repeated records in a univariate repeatability model. RP = retained placenta, analyzed in lactation 2 to 5 as repeated records in a repeatability model, together with RP in the first lactation as a correlated trait in a bivariate model. MET = metritis and SH = silent heat, analyzed with 5 lactations as genetically correlated traits in multivariate models.

³EBV for the 5 lactations of a disorder correlated with the genomic EBV (GEBV) of the first lactation of the same disorder, GEBV estimated from a single-trait genomic BLUP.

⁴EBV correlated with GEBV of the same lactation for the same disorder, GEBV estimated from a single-trait genomic BLUP.

⁵EBV correlated with GEBV of the same lactation for the same disorder, GEBV estimated from a multitrait genomic BLUP.

the structure of the model (repeatability model), but also because this is the disorder that has few false negatives as it is easy to discover and demands veterinary attention. Both MET and SH are more troublesome disorders that can be difficult to discover and, therefore, have more false negatives. Regarding SH, cows may be culled instead of being treated or the disorder may go unnoticed and therefore untreated; likewise, many false negatives may occur.

Regression analyses were used to validate whether GEBV over- or underpredicted the genetic merit. The regression coefficients with their standard errors are given in Table 3. Regression coefficients (β) larger than 1 indicate that genetic merit is underpredicted by GEBV, whereas β -values lower than 1 indicate overprediction. Table 3 shows large variation between traits and approaches, with β -values ranging from 0.18 to 2.63. Indications of serious underprediction (β -values >2) were found for MET2 and MET4 when using single-trait GBLUP (GEBV-S; Table 4). Using GEBV based on first lactation to predict later lactations (GEBV-1) tended to overpredict genetic merit (β -values <1) for MET and SH. Traits analyzed by a repeatability model, CO and RP2–5, tended to underpredict genetic merit. The exception was CO in the GEBV-S approach, for which β -value, in addition to the regression coefficients for SH1 and RP1 in all 3 approaches, was closest to 1.

Assumptions and Limitations

The present study used a relatively small validation set, containing approximately 10% of the total number of genotyped bulls. The validation bulls were the youngest, and some of them did not have daughters in the latest lactations, which reduced the validation set further. It would be possible to include more bulls in the validation set, but then the reference population would be reduced.

In the present study the youngest bulls were defined as the validation set and the oldest bulls were in the reference population. This is how genomic selection would appear in practice. For the reference population, all data after a cut-off date was removed, pretending they had not yet happened. In this scheme no sires would be predicted by their sons, as would happen in a full cross validation study.

Another issue is the precision of EBV for the fourth and fifth lactation in the validation set. As some of the bulls did not have fifth lactation daughters, the validation set was smaller for these traits. Also, the number of daughters per bull was lower in the later lactations. Consequently, the precision of the bulls EBV is less accurate than in the first lactation. The accuracy in the fourth and fifth lactation is therefore based on a

smaller validation set with less precise EBV. A solution could be to set a limit on a minimum of 150 daughters, for example, in the fifth lactation in the validation set, but this would decrease the validation set drastically.

An important question is which EBV and GEBV to compare. In the present study, EBV for each lactation and disorder was correlated with the GEBV of the same lactation or with GEBV for the first lactation. The latter is a measure of how well first-lactation GEBV predict the later lactations. Another approach could be to use GEBV from the 5 first lactations (together or separately) to predict the first and perhaps the second lactation of the disorder. Which method to choose depends on the aim of the scheme; to reduce susceptibility to fertility-related disorders in the first and second lactations, or to breed for a cow with reduced susceptibility to fertility-related disorders over many lactations.

Implementation

Health data, including veterinary treatment of fertility-related disorders, from more than 30 yr are available. Haugaard and Heringstad (2013) estimated heritabilities on the underlying scale of CO, MET, RP, and SH between 0.03 and 0.14. The present study

Table 4. Predicted β -values (SE) from regression analyses of EBV and genomic EBV (GEBV)

Trait ¹	GEBV-1 ²	GEBV-S ³	GEBV-M ⁴
CO1–5	1.70 (0.18)	0.91 (0.09)	—
RP1	0.87 (0.09)	0.87 (0.09)	0.83 (0.07)
RP2–5	1.81 (0.17)	1.50 (0.08)	1.43 (0.07)
MET1	0.53 (0.06)	0.52 (0.06)	0.56 (0.06)
MET2	0.27 (0.03)	2.63 (0.28)	0.36 (0.05)
MET3	0.38 (0.04)	0.41 (0.10)	0.32 (0.06)
MET4	0.36 (0.05)	2.66 (0.52)	0.24 (0.06)
MET5	0.68 (0.08)	0.69 (0.18)	—
SH1	0.91 (0.08)	0.91 (0.08)	0.88 (0.08)
SH2	0.41 (0.05)	0.87 (0.09)	0.71 (0.06)
SH3	0.32 (0.05)	0.74 (0.07)	0.66 (0.05)
SH4	0.18 (0.05)	0.84 (0.07)	0.58 (0.04)
SH5	0.23 (0.04)	0.99 (0.25)	0.56 (0.04)

¹CO = cystic ovaries, which were analyzed with the 5 lactations as repeated records in a univariate repeatability model. RP = retained placenta, analyzed in lactation 2 to 5 as repeated records in a repeatability model, together with RP in the first lactation as a correlated trait in a bivariate model. MET = metritis and SH = silent heat, analyzed with 5 lactations as genetically correlated traits in multivariate models.

² β -value from regression between EBV for the 5 lactations of a disorder and GEBV of the first lactation of the same disorder, GEBV estimated from a single-trait genomic BLUP.

³ β -value (SE) from regression between EBV and GEBV of the same lactation for the same disorder, GEBV estimated from a single-trait genomic BLUP.

⁴ β -value from regression between EBV and GEBV of the same lactation for the same disorder, GEBV estimated from a multitrait genomic BLUP.

shows accuracies of GEBV in the upper range of what has previously been reported for traits with similar heritabilities for Norwegian Red. Reliability of GEBV for these fertility-related disorders are expected to be higher than the reliability of parent average EBV (at the time of birth of the bull calf) and lower than the reliability of EBV after progeny testing. Genetic evaluation of these fertility-related disorders can therefore be implemented in the breeding scheme for Norwegian Red with at least as precise evaluations as other health traits.

CONCLUSIONS

Accuracy of genomic predictions for fertility-related disorders was in the upper range of those previously reported for functional traits in Norwegian Red. Including later lactations improved accuracy of GEBV for CO, RP, and SH, whereas no obvious advantage in terms of accuracy was found for MET.

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