



Multiple-trait genomic evaluation of linear type traits using genomic and phenotypic data in US Holsteins

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ABSTRACT

Currently, the USDA uses a single-trait (ST) model with several intermediate steps to obtain genomic evaluations for US Holsteins. In this study, genomic evaluations for 18 linear type traits were obtained with a multiple-trait (MT) model using a unified single-step procedure. The phenotypic type data on up to 18 traits were available for 4,813,726 Holsteins, and single nucleotide polymorphism markers from the Illumina BovineSNP50 genotyping Beadchip (Illumina Inc., San Diego, CA) were available on 17,293 bulls. Genomic predictions were computed with several genomic relationship matrices (\mathbf{G}) that assumed different allele frequencies: equal, base, current, and current scaled. Computations were carried out with ST and MT models. Procedures were compared by coefficients of determination (R^2) and regression of 2004 prediction of bulls with no daughters in 2004 on daughter deviations of those bulls in 2009. Predictions for 2004 also included parent averages without the use of genomic information. The R^2 for parent averages ranged from 10 to 34% for ST models and from 12 to 35% for MT models. The average R^2 for all \mathbf{G} were 34 and 37% for ST and MT models, respectively. All of the regression coefficients were <1.0 , indicating that estimated breeding values in 2009 of 1,307 genotyped young bulls' parents tended to be biased. The average regression coefficients ranged from 0.74 to 0.79 and from 0.75 to 0.80 for ST and MT models, respectively. When the weight for the inverse of the numerator relationship matrix (\mathbf{A}^{-1}) for genotyped animals was reduced from 1 to 0.7, R^2 remained almost identical while the regression coefficients increased by 0.11–0.26 and 0.12–0.23 for ST and MT models, respectively. The ST models required about 5 s per iteration, whereas MT models required 3 (6) min per iteration for the regular (genomic) model. The MT single-step approach is feasible for 18 linear

type traits in US Holstein cattle. Accuracy for genomic evaluation increases when switching ST models to MT models. Inflation of genomic evaluations for young bulls could be reduced by choosing a small weight for the \mathbf{A}^{-1} for genotyped bulls.

Key words: genomic evaluation, linear type trait, US Holstein

INTRODUCTION

Genomic selection in US Holsteins has been conducted by the USDA-ARS Animal Improvement Programs Laboratory (Beltsville, MD) since 2008, using a multi-step procedure (MSP), where regular PTA are used to create genomic predictions (VanRaden, 2008). The MSP uses a single-trait (ST) model, and improved genomic relationships influence only the genotyped animals.

Misztal et al. (2009) proposed that genomic evaluations be performed in a single-step procedure (SSP) with complete phenotypic, pedigree, and genomic information. Aguilar et al. (2010) applied the SSP to obtain genomic EBV (GEBV) for final score of US Holsteins, where a pedigree-based relationship matrix (\mathbf{A}) in the evaluation procedure is replaced by a matrix (\mathbf{H}) that combines \mathbf{A} and a genomic relationship matrix (\mathbf{G}). They reported that accuracy and inflation of genomic evaluation varied with different \mathbf{G} , with the best \mathbf{G} derived using equal allele frequencies (GE). The inflation of genomic evaluation could be reduced or eliminated with small modifications to the \mathbf{H} matrix. Computing time of SSP with the ST model was close to that of a regular BLUP procedure with \mathbf{A} .

Performance of SSP has been evaluated in other species. Chen et al. (2011) used SSP to analyze 3 traits in 2 separately selected lines of chickens. The improvement in accuracy after adding the genomic information varied between the 2 lines, despite similar heritability for 3 traits. Variation in performance of the SSP in the 2 lines was attributed to the different selection goals. Forni et al. (2011) used SSP to analyze litter sizes in pigs. Predictions obtained with different \mathbf{G} were highly

Received February 9, 2011.

Accepted April 8, 2011.

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correlated; however, heritability estimates varied by type of \mathbf{G} , whereas heritability estimates were the same as with \mathbf{G} scaled similarly to \mathbf{A} .

Chen et al. (2011) investigated the effect of using different \mathbf{G} and their scaling in chickens. Accuracy with \mathbf{G} assuming current allele frequencies (\mathbf{GC}) was marginally higher than that assuming GE. However, predictions from both \mathbf{G} were biased. The bias could be eliminated by shifting \mathbf{G} so that averages of off-diagonals in \mathbf{G} and in \mathbf{A} for genotyped animals were equal within 0.001. The bias due to the incorrect offset of \mathbf{G} was greater when the training population had low accuracy, and increased with stronger selection (Vitezica et al., 2010).

A multiple-trait (MT) animal model is currently used for the regular national genetic evaluation of linear type traits in US Holsteins. As more selection decisions are being made utilizing genomic information, it becomes critical that all genomic information be included in a single national evaluation. Substantial bias in genomic evaluations caused by selection on genotyped animals was reported by simulation studies of Patry and Ducrocq (2009) and Liu et al. (2009). The objectives of this study were to evaluate the feasibility of an MT SSP using a large number of animals for 18 linear type traits in Holsteins for routine use, quantify the improvement in accuracy using an MT SSP compared with an ST SSP, and investigate how modifications to \mathbf{H} , which combines \mathbf{G} and \mathbf{A} , reduce the inflation of GEBV.

MATERIALS AND METHODS

Data

Genetic SNP markers from the Illumina BovineSNP50 genotyping Beadchip (Illumina Inc., San Diego, CA), consisting of 38,416 informative SNP, were available on 17,293 Holstein bulls. Those SNP markers were converted to 0, 1, or 2 for calculation of \mathbf{G} as described in Aguilar et al. (2010). Two data sets, a reduced file having data up to the year 2004 and a full file having data up to the year 2009, were used. Comparing early predictions from the reduced 2004 file with the more recent 2009 data allowed us to assess reductions in bias and accuracy. Pedigree information included 7,860,183 animals for cows with phenotypes and bulls with genotypes. The 2004 data set included 7,715,925 phenotypic records on 4,813,726 cows. The 2009 data set included 8,865,120 phenotypic records of 5,657,787 cows. Of the 17,293 genotyped bulls, 6,913 bulls had genotypes in 2004. Of the 6,913 bulls, 1,307 had no daughters with phenotypes in 2004 and at least 50 daughters with phenotypes in 2009.

Model

The MT animal model used in the genetic evaluation for 18 linear type traits is described in Tsuruta et al. (2005). In the genomic evaluation, the inverse of \mathbf{H} (\mathbf{H}^{-1}) replaced the inverse of \mathbf{A} (\mathbf{A}^{-1}). Aguilar et al. (2010) and Christensen and Lund (2010) describe the decomposition of \mathbf{H}^{-1} as follows:

$$\mathbf{H}^{-1} = \begin{bmatrix} \mathbf{A}^{11} & \mathbf{A}^{12} \\ \mathbf{A}^{21} & \mathbf{A}^{22} + \tau\mathbf{G}^{-1} - \omega\mathbf{A}_{22}^{-1} \end{bmatrix},$$

where \mathbf{A}_{22} is a pedigree-based numerator relationship matrix for 6,913 genotyped animals, and τ and ω are weight factors for \mathbf{G}^{-1} and \mathbf{A}_{22}^{-1} , respectively. Using phenotypes and \mathbf{A}^{-1} , EBV in 2004 and 2009 were calculated with traditional ST and MT models. Using phenotypes and \mathbf{H}^{-1} with pedigree and genomic relationships, GEBV in 2004 were calculated with ST SSP and MT SSP, varying the weight (ω) on \mathbf{A}_{22}^{-1} for genotyped animals. Changes in weights of \mathbf{G}^{-1} were not investigated ($\tau = 1$) as this parameter had a small effect on accuracy and inflation (Misztal et al., 2010). The \mathbf{G} used in our SSP genomic evaluations were centered on 4 different allele frequencies: $p = q = 0.5$ (GE), base population allele frequencies calculated with the method of Gengler et al. (2007) (GB), derived directly from the genomic information (GC), and current allele frequencies with \mathbf{G} scaled to match \mathbf{A} (GCS; Chen et al., 2011).

Computation

To assess the bias of GEBV, regression coefficients (δ) of daughter deviations (\mathbf{DD}), defined by VanRaden (2008), for traditional EBV in 2009 ($\mathbf{EBV09}$) on GEBV in 2004 were calculated for the 1,307 young bulls with no daughters in the 2004 and with at least 50 daughters in 2009. Coefficients of determination (R^2) of the regression models were also calculated for the same bulls to quantify the accuracy of GEBV. Traditional EBV in 2004 were used to calculate parent average (\mathbf{PA}). All EBV and GEBV were computed with the modified BLUP90IOD program (Tsuruta et al., 2001), which uses iteration on data with preconditioned conjugate gradient, on an Intel Xeon server with 2.93-GHz clock speed and 12 MB of cache memory. To improve the convergence rate, the preconditioned conjugate gradient algorithm used a block preconditioner (size = 18) for MT models (Tsuruta and Misztal, 2008). The squared ratio of the norms of residual and right-hand-side vectors for $\mathbf{Cx} = \mathbf{b}$ (where \mathbf{C} = coefficient matrix,

\mathbf{x} = solution vector, and \mathbf{b} = observation vector in a system of equations) was used as an indication of iterative convergence (i.e., $\|\mathbf{b} - \mathbf{C}\mathbf{x}\|^2 / \|\mathbf{b}\|^2$). Convergence criteria ranging from 10^{-11} to 10^{-16} and from 10^{-11} to 10^{-12} were used to stop the program for ST and MT models, respectively.

RESULTS AND DISCUSSION

Almost all of the older genotyped bulls (born before 2000) had classified daughters (Figure 1). The genomic evaluations of genotyped young bulls born after 2004 had limited to no daughter information. Thus, the group of bulls providing the basis of comparison for the performance of different models was born between 2001 and 2004. Some of these bulls would have been genotyped, evaluated, and then culled. Slightly fewer than half of the genotyped bulls in this period (2,619 bulls) had no daughters with phenotypic records in 2004, and of 2,619 bulls, 1,307 had at least 50 daughters with records in 2009 as mentioned before.

To assess the convergence rate, the R^2 (%) and the number of rounds to convergence under several convergence criteria are shown for strength as an example of 18 traits in Table 1. Among the ST models, satisfactory convergence was achieved at the criterion of 10^{-16} . At the 10^{-14} , 10^{-15} , and 10^{-16} levels, differences in R^2 with different \mathbf{G} were negligible. At a less conservative criterion of 10^{-11} , the R^2 were 7 to 10% lower than those at 10^{-14} , and R^2 seemed to be the highest with GE. No improvement was obtained using stricter con-

vergence criteria. Therefore, differences in GEBV with different \mathbf{G} in dairy traits; for example, as in Aguilar et al. (2010), may be due to insufficient convergence. The necessary value of the convergence criterion can be determined based upon examination of R^2 for PA, as patterns of convergence were similar for PA with different \mathbf{G} , with a slight exception for GC. All ST models required about 5 s per one round of iteration. The number of rounds varied from about 100 with the criterion of 10^{-11} to a range of about 240 to 700 with 10^{-14} .

When using a block preconditioner of the preconditioned conjugate gradient algorithm for MT models, the convergence pattern varied significantly. On the other hand, when using a scalar preconditioner, the convergence pattern was smooth, although a large number of iterations (>5 times more than those for MT models, depending on allele frequencies and convergence criteria) was required to reach convergence. Therefore, a scalar preconditioner was not used for MT models. For MT models with the convergence criterion 10^{-11} , differences in R^2 with different \mathbf{G} were smaller than for ST models. For the MT model with GB, reducing the criterion to 10^{-12} from 10^{-11} changed R^2 very slightly, with no change for PA. In this study, the criterion of 10^{-11} seemed to be satisfactory for MT with GB. The number of rounds at 10^{-11} was about 330 with any allele frequencies but increased to >2,000 at 10^{-12} for all MT models except with GB; the computer time per iteration was 3 min for PA (traditional models) and 6 min with \mathbf{G} . To improve the convergence rate for MT

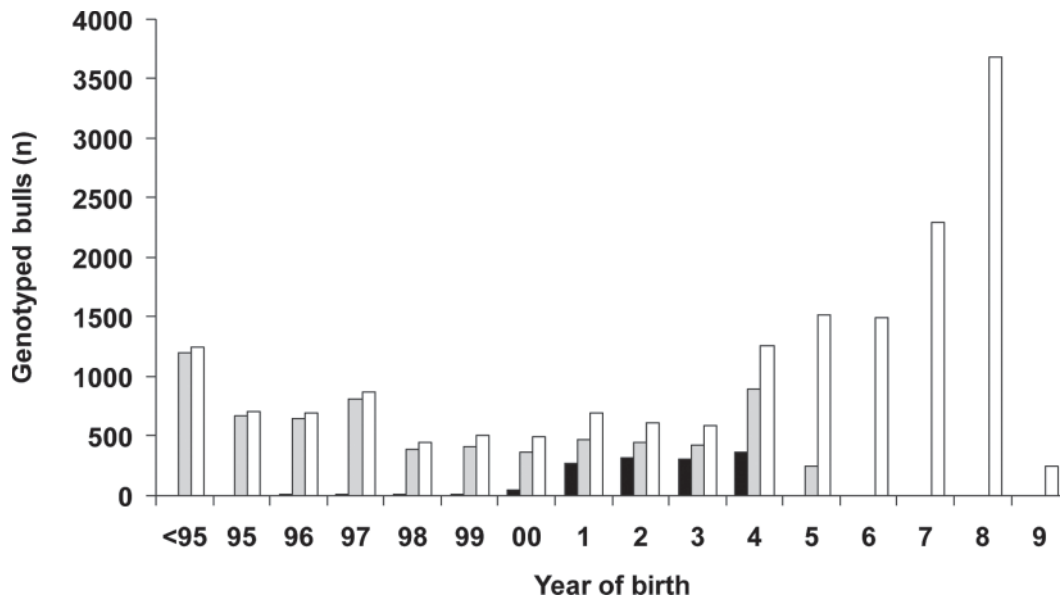


Figure 1. Distributions of genotyped bulls by year of birth: black bars = genotyped bulls with no daughter in 2004 and >50 daughters in 2009; gray bars = genotyped bulls with daughters in 2009; white bars = all genotyped bulls.

Table 1. Coefficients of determination (R^2 , %) of daughter deviations in 2009 on genomic evaluations of 1,307 genotyped young bulls in 2004 for strength and number of rounds for single-trait and multiple-trait models with equal, base, current, and scaled current allele frequencies (number of rounds in parentheses)

Convergence criterion	Single-trait model					Multiple-trait model				
	PA ¹	Equal	Base	Current	Scaled current	PA	Equal	Base	Current	Scaled current
10 ⁻¹¹	22.1 (98)	33.1 (107)	30.5 (98)	29.6 (97)	30.7 (98)	29.4 (324)	45.2 (338)	44.6 (329)	43.1 (346)	45.1 (332)
10 ⁻¹²	22.4 (151)	38.6 (145)	38.0 (145)	37.0 (143)	38.2 (144)	29.4 (565)	NA ²	44.8 (561)	NA	NA
10 ⁻¹³	24.9 (224)	40.5 (221)	40.0 (219)	39.6 (254)	40.2 (209)	NA	NA	NA	NA	NA
10 ⁻¹⁴	25.2 (278)	40.6 (529)	40.1 (238)	40.5 (696)	40.4 (541)	NA	NA	NA	NA	NA
10 ⁻¹⁵	25.2 (285)	40.6 (701)	40.1 (279)	40.5 (750)	40.5 (724)	NA	NA	NA	NA	NA
10 ⁻¹⁶	25.2 (700)	40.6 (756)	40.2 (554)	40.6 (790)	40.5 (788)	NA	NA	NA	NA	NA

¹Parent average from genetic evaluation in 2004.

²NA = not available.

models, the block preconditioner could be modified. Further study is needed to clarify the cause of the slow convergence and the possibility of converging the MT models with other allele frequencies.

The R^2 of DD regressions on GEBV for 1,307 genotyped bulls with no weight for A_{22}^{-1} are shown in Table 2. The R^2 for PA ranged from 10 to 34% for ST models and from 12 to 35% for MT models, with convergence criteria of 10^{-14} and 10^{-11} , respectively. The relatively lower R^2 obtained for the last 4 traits (teat length, rear legs rear view, feet and legs score, and rear teat placement) may be due to the recent start of recording for those traits (i.e., 71, 69, 43, and 6% of 7,715,925 records in the complete file, respectively). The R^2 for GEBV were about 16% higher on average than those for PA. For ST models, R^2 for GEBV were similar and averaged 34.6% with GE, 34.1% with GB, 34.2% with GC, and 34.6% with GCS. Aguilar et al. (2010) reported 4% difference in R^2 among different G for final score. However, by using a stricter convergence criterion (e.g., $<10^{-13}$), differences among those R^2 became negligible. Vitezica et al. (2010) and Chen et al. (2011) suggested using GCS as a general way to increase accuracies of GEBV. In those studies, GEBV of the training population had low accuracy, and therefore, incorrectly scaled G could reduce accuracy for the training population. In dairy, GEBV of the training population had relatively high accuracies and the original G was similar to A . As a result, the type of G had a small effect on GEBV of the training population. In general, the improvement of GEBV over EBV is dependent upon the trait and the population structure.

Ideally, δ values of DD from 2009 on PA and GEBV from 2004 should be 1.0. Table 3 shows the regression

coefficients for 1,307 genotyped bulls with at least 50 daughters when no weight for A_{22}^{-1} (i.e., $\omega = 1.0$) was used for ST and MT models with the same convergence criteria as in Table 3 (i.e., 10^{-14} and 10^{-11} , respectively). A δ value <1.0 denotes a higher GEBV than DD of EBV09, indicating that GEBV were overestimated or that EBV09 were underestimated. All of the δ values for PA were <1.0 , indicating that EBV09 of 1,307 genotyped young bulls' parents tended to be biased. The average δ ranged from 74 to 79 and from 75 to 80 for ST and MT models, respectively. In general, the δ values were similar for all models and traits. For ST and MT models with $\omega = 1.0$, the highest values of δ were obtained when using GE and the lowest with GC. Small differences between δ values using ST and MT models suggest that biases are not due to selection on correlated type traits. Similar δ values for all 4 options indicate that biases could be systematic in US Holsteins when using pedigree and genomic information without phenotypic data. Whereas some of the biases can be due to preferential treatment, some of the bias can be due to the structure of a dairy population that cannot be fully modeled. For example, such biases are present in the Israeli population where only young sires are used and there is no preferential treatment (J. Weller, Institute of Animal Science, Bet Dagan, Israel, personal communication, 2010). On average, the bias was smallest and R^2 highest with GE. Although the use of GE in broilers resulted in biases (Chen et al., 2011), in dairy the bias due to GE may be partially compensating the bias present in PA, which is systemic to the dairy population.

In a preliminary analysis, we tested various combinations of τ and ω ranging from 0.1 to 1.5 and found that

Table 2. Coefficients of determination (R^2 , %) of daughter deviations in 2009 on genomic evaluations in 2004 using single-trait and multiple-trait models with equal, base, current, and scaled current allele frequencies for genotyped bulls with at least 50 daughters

Trait	Single-trait model					Multiple-trait model				
	PA ¹	Equal	Base	Current	Scaled current	PA	Equal	Base	Current	Scaled current
Stature	34	55	55	54	55	35	55	55	54	55
Strength	25	41	40	41	41	29	45	45	43	45
Body depth	28	45	45	45	45	30	48	47	46	48
Dairy form	20	40	40	39	40	21	42	41	39	41
Rump angle	25	45	44	45	45	25	45	45	45	45
Thurl width	29	42	42	42	42	31	45	45	43	45
Rear legs side view	14	27	26	26	27	16	29	29	29	29
Foot angle	15	25	24	25	25	21	33	32	32	33
Fore udder attachment	14	34	33	34	34	17	40	39	36	40
Rear udder height	18	33	32	33	33	19	36	35	31	36
Rear udder width	16	30	29	29	30	18	33	33	29	33
Udder cleft	19	33	32	32	33	20	36	35	34	36
Udder depth	17	40	40	40	40	17	42	41	41	42
Front teat placement	16	37	36	36	36	17	39	38	36	38
Teat length	12	31	30	31	31	12	32	31	31	31
Rear legs rear view	10	18	19	18	19	13	23	23	22	23
Feet and legs score	10	19	19	18	19	12	23	22	21	23
Rear teat placement	13	28	27	27	28	16	37	36	35	36

¹Parent average from genetic evaluation in 2004.

ω values of 0.5 or 0.7 and $\tau = 1$ resulted in the least bias without affecting accuracy. This result indicates that contributions from $\mathbf{A}^{22} + \mathbf{G}^{-1} - \omega\mathbf{A}_{22}^{-1}$ (i.e., $\mathbf{A}^{22} - \omega\mathbf{A}_{22}^{-1}$ or \mathbf{G}^{-1}) are too small to estimate unbiased GEBV for young genotyped bulls. To reduce the inflation of GEBV for bulls with only genomic information, $\mathbf{A}^{22} - \omega\mathbf{A}_{22}^{-1}$ or \mathbf{G}^{-1} can be increased. Table 4 shows that all δ values with $\omega = 0.7$ for ST and MT models were higher and closer to 1.0 than those with $\omega = 1.0$. By

using $\omega = 0.7$ for \mathbf{A}_{22}^{-1} , \mathbf{H}^{-1} for genotyped animals, $\mathbf{A}^{22} + \mathbf{G}^{-1} - \omega\mathbf{A}_{22}^{-1}$, becomes larger than that with no weight ($\omega = 1.0$); therefore, absolute values of GEBV for genotyped will be smaller, resulting in a higher δ or less bias in GEBV. With $\omega = 0.7$, R^2 were the same for both ST and MT models, whereas the δ values were 0.11 to 0.26 higher for the ST models and 0.12 to 0.23 higher for the MT model with scaled \mathbf{G} . In a study involving final scores of US Holsteins (Misztal et al.,

Table 3. Regression ($\delta \times 100$) of daughter deviations in 2009 on genomic evaluation in 2004 using single-trait and multiple-trait models with equal, base, current, and scaled current allele frequencies for genotyped bulls with at least 50 daughters

Trait	Single-trait model					Multiple-trait model				
	PA ¹	Equal	Base	Current	Scaled current	PA	Equal	Base	Current	Scaled current
Stature	86	86	83	82	83	87	86	83	84	84
Strength	78	78	75	74	75	80	78	76	75	75
Body depth	78	77	75	73	76	78	78	75	74	75
Dairy form	78	83	79	76	80	78	86	82	78	83
Rump angle	86	94	89	90	91	85	93	91	90	90
Thurl width	88	85	82	82	83	87	86	83	81	83
Rear legs side view	82	77	72	72	73	81	79	76	76	76
Foot angle	75	73	68	68	69	75	72	69	70	69
Fore udder attachment	70	75	71	70	72	74	78	74	72	75
Rear udder height	71	74	67	68	71	69	74	70	66	71
Rear udder width	67	71	65	64	68	66	71	67	63	68
Udder cleft	84	85	79	80	82	83	87	82	79	84
Udder depth	81	84	81	80	81	78	85	82	82	83
Front teat placement	76	83	78	78	80	76	84	80	77	81
Teat length	75	82	77	77	78	74	83	79	78	79
Rear legs rear view	69	71	68	62	67	67	67	63	63	63
Feet and legs score	64	60	56	53	56	63	61	57	56	57
Rear teat placement	84	92	85	80	86	80	89	84	81	85

¹Parent average from genetic evaluation in 2004.

Table 4. Regression ($\delta \times 100$) of daughter deviations in 2009 on genomic evaluation in 2004 using single-trait and multiple-trait models with equal, base, current, and scaled current allele frequencies for genotyped bulls with at least 50 daughters with weight $\omega = 0.7$ for \mathbf{A}_{22}^{-1} for genotyped bulls

Trait	Single-trait model				Multiple-trait model			
	Equal	Base	Current	Scaled current	Equal	Base	Current	Scaled current
Stature	96	95	94	95	97	96	95	96
Strength	89	87	87	87	88	87	87	87
Body depth	86	86	86	87	88	87	87	87
Dairy form	96	96	96	97	101	98	93	100
Rump angle	103	103	103	103	104	103	102	103
Thurl width	96	96	96	96	97	95	93	96
Rear legs side view	88	88	88	89	91	90	92	91
Foot angle	84	84	84	85	84	83	85	85
Fore udder attachment	87	87	87	88	92	89	86	92
Rear udder height	84	84	84	85	86	83	77	85
Rear udder width	82	82	82	83	84	81	75	84
Udder cleft	97	97	97	98	100	98	95	99
Udder depth	98	98	98	98	100	98	98	98
Front teat placement	96	96	96	97	99	96	94	98
Teat length	96	96	96	96	99	96	97	97
Rear legs rear view	81	81	81	83	80	78	78	79
Feet and legs score	71	71	71	72	74	72	72	74
Rear teat placement	110	112	110	112	105	102	99	104

2010), the authors reported that smaller ω increased δ but reduced R^2 slightly. Assuming that bias of $\pm 15\%$ is acceptable, 15 out of 18 traits would fall into this category. In addition, the smaller weight for \mathbf{A}_{22}^{-1} did not affect GEBV for old genotyped bulls because \mathbf{G}^{-1} for those bulls was larger than \mathbf{A}_{22}^{-1} . A smaller weight (e.g., $\omega = 0.5$) could produce less-biased GEBV for traits that still have $\delta < 1.0$ with small or no reduction in R^2 but could underestimate GEBV for traits that have $\delta > 1.0$. Therefore, $\omega = 0.7$ or 0.5 should be used as a common weight factor for all 18 traits. To reduce bias, the source needs to be determined for any trait. In particular, the elimination of biases in GEBV requires knowledge about their sources with PA. If the sources are unknown, the most effective way to avoid accumulation of biases over multiple cycles of genomic selection may be the continued collection of phenotypes.

CONCLUSIONS

The multiple-trait single-step approach is feasible for 18 linear type traits in the national genetic evaluation of US Holstein cattle. The use of the multiple-trait model and genomic information leads to an increase in computational costs, whereas the single-trait model does not increase computational time. Accuracy for genomic evaluation increases when switching from single-trait models to multiple-trait models, but the increase depends on traits. Inflation of genomic evaluations for young bulls could be reduced without affecting accuracy by choosing a small weight to account for contributions

from the inverse of the numerator relationship matrix for genotyped bulls. Using 0.7 for the weight could be a common factor for all 18 linear type traits; however, further study should be conducted to reduce the bias of genomic evaluations for any traits.

ACKNOWLEDGMENTS

This study was partially funded by the Holstein Association USA Inc. (Brattleboro, VT) and by AFRI grants 2009-65205-05665 and 2010-65205-20366 from the USDA NIFA Animal Genome Program.

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