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Comparison of single-trait to multi-trait national evaluations for yield, health, and fertility[1]

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ABSTRACT

Flexible software was designed to replace the current animal model programs used for national genetic evaluations. Model improvements included (1) multi-trait processing, (2) multiple fixed class and regression variables, (3) differing models for different traits, (4) random regressions, and (5) foreign data included using pseudo-records. Computational improvements included (6) parallel processing, (7) renumbering class variables to equation numbers within the program so that estimated effects are output with original identification numbers, and (8) reliability computed within the same program. When applied to 3 fertility traits of 27,971,895 cows and heifers, the new model used daughter pregnancy rate as a correlated trait to improve heifer and cow conception rate evaluations for older animals and in herd-years where records are missing, and also added information from crossbreds. When applied to 7 traits and 76,846,327 lactation records of 30,064,300 cows, gains in accuracy were small for yield and somatic cell score, moderate for daughter pregnancy rate, and larger for productive life for recent bulls compared with single-trait evaluations. For very old bulls, multi-trait gains were also large for protein because lactation records were available only for milk and fat. Multi-trait productive life was computed with exact rather than approximate methods; however, correlated information from conformation was excluded, reducing advantages of the new model over the previous software. Estimates of breed differences, inbreeding depression, and heterosis were similar to previous estimates; new estimates were obtained for conception rates. Predictions were compared by truncating 4 yr of data, and genetic trend validation was applied to all breed–trait combinations. The estimates of trend account for increases in inbreeding across time. Incorporation of foreign data gave correlations above 0.98 for new with previous evaluations of foreign Holstein bulls, but lower for other breeds. The 7-trait model required 35 GB of memory and 3 d to converge using 7 processors. The new software was implemented for fertility traits in 2013 and is scheduled for implementation with yield, somatic cell score, and productive life in 2014. Further revision of the models and software may be needed in the near future to account for genomic preselection.

Key words: animal model, genetic evaluation, correlated trait, best linear unbiased prediction

INTRODUCTION

Multi-trait models often include multiple genetic effects within the same trait or multiple traits within the same trait group. Examples of the former are direct and maternal calving effects (Pasman and Reinhardt, 2002) or separate lactation effects used in many countries to model yield, SCS, or fertility traits. Examples of the latter are multi-trait evaluations for type traits (Tsuruta et al., 2011), fertility traits (Liu et al., 2008), or yield and SCS (Schaeffer et al., 2000), because the same model and data pattern may apply to each trait within the group. In a few cases, correlated traits from another trait group are included, such as yield traits or BCS in fertility evaluations (Biffani et al., 2005; de Jong, 2005; Sun et al., 2010). In other cases, mainly for longevity, approximate multi-trait methods are used (VanRaden, 2001) to combine many traits across several trait groups.

Genetic evaluations of US milk, fat, and protein yields have been computed by a single-trait animal model since 1989 using programs originally designed to minimize memory with very large data sets (Wiggans et al., 1988). Much of the original code remained, but the programs were later revised to adjust for heterogeneous variance (Wiggans and VanRaden, 1991), inbreeding (VanRaden, 2005), heterosis, and breed differences (VanRaden et al., 2007). The programs were also revised to evaluate additional traits productive life (**PL**)

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and SCS in 1994 and daughter pregnancy rate (**DPR**) in 2003. These 6 traits (milk, fat, and protein yields, PL, SCS, and DPR) were evaluated by using multi-breed models including crossbred cows, whereas 2 other traits—heifer conception rate (**HCR**) and cow conception rate (**CCR**)—were evaluated by using single-breed models and BLUPF90 software (Misztal et al., 2002) beginning in 2010. Multi-trait processing, more uniform modeling across traits, the increasing numbers of traits, and simpler incorporation of genomic and foreign information required a complete revision of software.

Genetic evaluations for dairy cattle are computed from national data sets using software and models that often are developed separately within each country. Information is then exchanged using multi-trait across-country evaluation (**MACE**) for males and by conversion formulas applied to evaluations of foreign females. More direct use of foreign information is now needed in national genomic evaluations to estimate genetic marker effects, along with simultaneous equations to combine phenotypes, genotypes, and pedigrees to avoid biases from genomic preselection. Maintaining or improving the accuracy of selection may require new models or development of new genetic evaluation software (Aguilar et al., 2010; Mäntysaari and Strandén, 2010; Patry and Ducrocq, 2011; Stoop et al., 2013).

Foreign information has been directly included in some traditional national evaluations using pseudo-records for daughters of foreign bulls in the mixed model (Bonaiti and Boichard, 1995; Pedersen et al., 1999). Methods to include foreign information in single-step genomic evaluations with single-trait or multi-trait models were recently developed and tested (VanRaden, 2012; Přibyl et al., 2013). Nearly all countries include foreign information from MACE to improve reliability when estimating marker effects in multi-step genomic evaluations.

Goals of the current research were to (1) develop flexible methods of evaluation for very large data sets, (2) compare predictive ability of single-trait and exact multi-trait models within and across trait groups, (3) compare trait definitions and models for fertility, and (4) include information from foreign bulls in an all-breed model.

MATERIALS AND METHODS

Data

Traits examined in the first analysis were milk, fat, protein, PL, SCS, and DPR using 76,846,327 lactation records from the US national database as of December 2012. The 3 fertility traits HCR, CCR, and DPR were examined in a second, separate analysis using records as of August 2013. The national database includes records collected since 1960 for milk, fat, protein, PL, and DPR; since 1988 for SCS; and since 2003 for HCR and CCR. Trait DPR includes historical data from days open, calving intervals, and reasons for culling plus recent data from inseminations and pregnancy examinations. The trait PL includes completed lifetime records of dead cows and predicted longevity of live cows, and it benefits from multi-trait processing because other, more heritable traits are measured earlier. Fertility traits also benefit from multi-trait processing because many records are missing and genetic correlations among the fertility traits are high.

Lactation records for yield, SCS, and DPR were preadjusted to equalize genetic variance and were weighted for differing error variance such as from numbers of test days included per lactation using the same factors and weights previously applied to those traits in US evaluations. The previous conception rate evaluations were based on individual binary observations for HCR (Kuhn et al., 2006) and CCR and used models similar to that for sire conception rate (Kuhn and Hutchison, 2008; Kuhn et al., 2008). Effects of region-month of breeding, service number, and sex-selected or conventional semen were estimated from the previous official models and used in the new CCR and HCR models to preadjust the individual observations, which were then averaged to create 13,119,424 lactation records for CCR and 3,820,912 for HCR. Records derived from >1 observation were weighted by number of observations per lactation (n) using weights calculated as $n/[1 + (n - 1) \times \text{repeatability}]$.

A fourth cow fertility trait, days from calving to first insemination (**CFI**), was not evaluated directly but instead constructed as a linear function of DPR and CCR evaluations. Direct evaluation of CFI is difficult with US data because many herds use timed AI, causing the date of first insemination to be determined more by management than by biology. Based on previous covariance estimates (VanRaden et al., 2004), CFI PTA and reliabilities (REL) were constructed as follows:

$$\text{PTA CFI} = 1.2\ (\text{PTA CCR}) - 3.6\ (\text{PTA DPR}) \text{ and}$$

$$\text{REL CFI} = 0.37\ (\text{REL CCR}) + 0.63\ (\text{REL DPR}).$$

Trait CFI is exchanged in MACE but is not yet published in the United States.

The pedigree file included 63,021,784 animals of many breeds and crossbred combinations. For the most recent birth year (2009) with complete data, a total of 989,424 cows had usable first-lactation records for milk yield. The breed groups supplying the most records were 848,533 Holsteins (85.8%), 76,974 Jerseys

(7.8%), 32,893 first-generation crossbreds (3.3%), 19,815 later-generation crossbreds (2.0%), 6,263 Brown Swiss (0.6%), 2,334 Guernseys (0.2%), 1,907 Ayrshires (0.2%), and 705 Milking Shorthorns (0.1%). Previous evaluations had excluded old, young, or other animals without phenotypes and included only those ancestors needed to link the phenotyped animals within each trait group, whereas all animals in the pedigree were evaluated together in the new model. Unknown parents were grouped by birth year, breed, and, for Holsteins, separately for US and foreign animals. Unknown sires and dams of cows were grouped separately, but unknown parents of bulls were in a combined group. For HCR and CCR, the birth year groups before 2000 were combined because phenotypes were missing before that time.

Models, Parameters, and Computation

National genetic evaluations were computed by single-trait and multi-trait methods using an all-breed animal model and were compared with traditional evaluations from the previous software (VanRaden et al., 2007). Factors included in the new model were nearly the same as in the previous model, but management groups were redefined for some traits to make definitions more uniform and simpler to store across traits. The same management groups based on calving date that were defined for yield traits were applied to other traits where possible in the new software, whereas groups in the previous software were defined separately by trait and were based on birth date for longevity or insemination date for fertility.

The first analysis combined milk, fat, protein, PL, SCS, and DPR records. Trait PL was included twice, both with and without correlations to other traits, to provide multi-trait PL (combined longevity) published nationally and single-trait PL (direct longevity) required for exchange within Interbull evaluations. When foreign information was added, single-trait MACE PL was also included in both traits and was upgraded to multi-trait in the first case by the correlations with other traits in MACE, or remained single-trait in the second case where correlations were set to 0. For each trait, the all-breed model solved for 63,021,784 breeding values, 30,064,300 permanent environment effects, 7,631,724 herd management groups, 11,637,447 herd-by-sire interactions, 450 age-parity effects, 669 unknown-parent groups, and 2 regressions for inbreeding and heterosis.

The second analysis combined the 3 fertility traits HCR, CCR, and DPR. Traits HCR and CCR measure the percentage of inseminated heifers or cows that become pregnant at each service, whereas DPR measures the percentage of nonpregnant cows that become pregnant during each 21-d time interval. The second analysis used the same model, but solved for slightly fewer effects because DPR records were present for only about 85% of milk records.

Variance components, genetic standard deviations, genetic correlations, and phenotypic correlations for completed records used for all breeds in the multi-trait model for the first analysis are given in Table 1. Most genetic correlations were from sire model REML using the same methods as VanRaden et al. (2004), but some were PTA correlations using high-reliability bulls. Genetic SD were the latest estimates from MACE. The herd variance preadjustment also adjusts other breed data to have the same genetic SD as Holsteins. Heritability for yield records was reduced from 30% in the previous model to 20% for Holsteins to mimic the effect of cow adjustments (Wiggans et al., 2012) implemented to reduce bias when cows are included in the genomic reference population. Corresponding heritabilities for Jerseys and Brown Swiss were reduced from 35 to 23%. Reduced heritabilities had been examined previously using the previous software, but in this study were applied only in the new software. The error covariance matrix (**E**) was the phenotypic minus genetic covariance, and its inverse was then multiplied by square roots of the weights for each pair of traits measured within each lactation. Productive life continued to be modeled with just one lifetime record rather than separate lactation records, and age-parity effects were excluded from the PL model.

For the second analysis, genetic correlation estimates were 0.45 for HCR with CCR, 0.86 for CCR with DPR, and 0.36 for HCR with DPR. Error correlation estimates were 0.10 for HCR with CCR, 0.70 for CCR with DPR, and 0.10 for HCR with DPR. Conception rates were previously modeled using multiple binary success records per lactation (such as no, no, yes), whereas DPR is a continuous lactation measure derived from days open. For simpler multi-trait modeling, conception rate records are now preadjusted for environmental effects and are combined into lactation records before analysis. Estimated genetic SD were 3.9 for HCR, 5.6 for CCR, and 3.4 for DPR.

Computation used block inversion for the multi-trait model, a combination of first- and second-order Jacobi iteration, and parallel processing. Inverses of the error covariance matrix for each combination of missing traits are precomputed and stored before iteration, and class variables are renumbered to equation numbers. Within each iteration, solutions from the previous iteration are multiplied by coefficients of the mixed model equations in parallel by trait, using as many processors as traits. Block diagonal submatrices are then inverted and mul-

Table 1. Multi-trait variance components, genetic (above diagonal), and error (below diagonal) correlations, and heritabilities[1] (on diagonal) by trait

Trait[2]	Genetic SD	Permanent environment variance[1]	Herd-sire variance[1]	Trait: Milk yield	Fat yield	Protein yield	SCS	DPR	PL
Milk yield (kg)	656	28	7	20	0.45	0.81	0.20	−0.32	0.08
Fat yield (kg)	24	28	7	0.69	20	0.60	0.15	−0.33	0.08
Protein yield (kg)	17	28	7	0.90	0.75	20	0.12	−0.35	0.10
SCS ($\log_2$)	0.46	18	5	−0.10	−0.10	−0.10	12	−0.30	−0.38
DPR (%)	3.4	12	4	−0.10	−0.10	−0.10	−0.05	4	0.51
PL (mo)	5.0	0	5	0.15	0.14	0.17	−0.15	0.20	8

[1]Percentage of phenotypic variance.

[2]DPR = daughter pregnancy rate; PL = productive life.

tiplied in batches of 100,000 per processor, potentially using as many processors as desired. More traits could be included in the same multi-trait model to improve reliability and better account for traditional selection, but more parallel processors and memory would be required. The run time increases in proportion to number of records (not number of traits) for single-trait models but in proportion to numbers of records and traits for multi-trait models. Reliabilities were computed by iterative single-trait methods in parallel by trait and then upgraded to approximate multi-trait using methods and algorithm of VanRaden (2001).

Heterosis should increase and accumulate across time as relationships increase within breeds but not across breeds. The model including both heterosis and inbreeding should estimate heterosis in the base population (animals born before 1960). Current heterosis then equals the base heterosis minus the average current inbreeding coefficient times the inbreeding regression, because first generation crossbreds have no inbreeding whereas purebreds do. Base and current estimates of heterosis are both provided, whereas heterosis was previously estimated separately at a given point in time (VanRaden et al., 2007).

Effects of past inbreeding and heterosis were removed by preadjustment in the previous software, and future effects were included by postadjustment (VanRaden, 2005; VanRaden et al., 2007). In the new software, the inbreeding and heterosis regressions are not treated as known but are estimated within the model. The US genetic evaluation for dairy cattle remains the only one that accounts for inbreeding depression. The definition of heterosis could be expanded in the future as in some other national evaluations to estimate specific breed combinations and recombination losses.

Foreign information was included using one record weighted by daughter equivalents for each bull that had foreign daughters instead of one pseudo-record for each foreign daughter as in Bonaiti and Boichard (1995). Daughter equivalents estimate numbers of standard daughters that provide equivalent information (VanRaden and Wiggans, 1991) and are very similar to the effective daughter contributions (Fikse and Banos, 2001) exchanged in MACE. Let EBV_M, PA_M, and y_M be MACE evaluations, parent averages, and deregressed evaluations, respectively, and let REL_M be the reliability obtained from the difference of daughter equivalents in the reliabilities of EBV_M and PA_M for the bull. Although simultaneous matrix deregression of all bulls might be better as in Přibyl et al. (2013), y_M was estimated using the simpler one-bull-at-a-time method:

$$y_M = PA_M + (EBV_M - PA_M)/REL_M.$$

This formula was applied to bulls that had only foreign daughters. For bulls that had both domestic and foreign daughters, y_M contained only the foreign portion of information obtained by replacing PA_M in the formula above with domestic EBV (EBV_D) and obtaining REL_M from the MACE minus domestic daughter equivalents. For bulls with few foreign daughters or many domestic daughters such that EBV_M differs little from EBV_D, the y_M will be close to EBV_D and the blended EBV will also differ little from EBV_D:

$$y_M = EBV_D + (EBV_M - EBV_D)/REL_M.$$

Mixed-model equations for single-trait models converted the daughter equivalents in REL_M to record equivalents and added those to the bull's diagonal and multiplied by y_M on the right hand side as in Přibyl et al. (2013). This method was also adapted to multi-trait models by defining vector $\mathbf{y}$ to include y_M for each trait of a bull, $\mathbf{D}$ to be a diagonal matrix containing $REL_M/(1 - REL_M)$, and $\mathbf{T}^{-1}$ to be the inverse of the genetic covariance matrix among traits. Matrix $\mathbf{T}^{-1}$ pre- and postmultiplied by the square roots of $\mathbf{D}$ (i.e., $\mathbf{D}^{0.5}\mathbf{T}^{-1}\mathbf{D}^{0.5}$) is then added to the bull's diagonal and

Table 2. Correlations of single-trait all-breed model evaluations from new and previous software for bulls born from 2000 through 2008 with >50 daughters by breed

Breed	Bulls (no.)	Milk yield	Fat yield	Protein yield	SCS	Daughter Pregnancy rate	Productive life	
							Single trait	Multi-trait
Holstein	9,476	0.996	0.996	0.995	0.999	0.995	0.988	0.967
Jersey	867	0.993	0.994	0.992	0.998	0.993	0.977	0.936
Brown Swiss	104	0.989	0.991	0.991	0.998	0.989	0.975	0.937
Guernsey	37	0.994	0.990	0.991	0.999	0.993	0.971	0.955
Ayrshire	21	0.985	0.971	0.974	0.998	0.963	0.982	0.976

$(\mathbf{D}^{0.5}\mathbf{T}^{-1}\mathbf{D}^{0.5})\mathbf{y}$ is added to the right hand side. Theoretical justification is that covariances between EBV_M for different traits are proportional to the REL_M and are mostly genetic rather than environmental if many daughters are included.

Validation

The new and previous software were compared in 2 main tests. The first determined if evaluations were the same or similar given the same model, pedigrees, and phenotypes but without genotypes. Genetic trends, Pearson correlations, and standard deviations of breeding values were compared. Numbers of the top 100 bulls in common using new and previous software were documented for the example traits protein, SCS, and DPR within breeds Holstein, Jersey, and Brown Swiss. The second test used truncation to investigate the predictive ability of multi-trait instead of single-trait models for national data. December 2012 evaluations were predicted using lactations initiated before October 2008 for bulls that had no daughter records before October 2008. Interbull genetic trend validation methods 1, 2, and 3 (Boichard et al., 1995) were applied to the multi-trait solutions. Method 1 tests whether first- and all-lactation trends are similar, method 2 tests whether daughter yield deviations are consistent across time within sire, and method 3 tests the trend in recent daughters added after truncation. Also, multi-trait HCR and CCR evaluations were submitted to the September 2013 Interbull test run. The resulting estimated genetic correlations between the US and all other country conception or nonreturn rates were compared with the corresponding February 2013 estimates that included single-trait, single-breed US evaluations.

Correlations of 2012 evaluations from previous software with single-trait, multi-trait, and previous evaluations from 2008 data were computed for bulls that had no daughters in 2008 (parent average evaluations) and for bulls that had 10 to 200 daughters in 2008 and >500 daughters in 2012. The previous evaluations were from January 2009 and included about 2 more months of daughters, whereas evaluations from new software included completed records instead of records in progress. Completed records for PL were from the lifetime instead of the lactation and provided much more information, so cows that first calved after October 2006 had their PL records removed. Similarly, DPR records were removed for calvings after May 2008 to mimic a 5-mo delay in receiving fertility compared with yield and SCS data. This provided a similar but not exactly equivalent amount of information for the new and previous software for each trait.

RESULTS AND DISCUSSION

Correlations

For the 7-trait all-breed animal model, evaluations from the new and previous software were very similar (Table 2). For recent Holstein bulls, correlations of single-trait with previous EBV were >0.995 for all

Table 3. Correlations of previous software single-trait evaluations with new software multi-trait evaluations for bulls born from 2000 through 2008 with >50 daughters in the all-breed model by breed

Breed	Bulls (no.)	Milk yield	Fat yield	Protein yield	SCS	Daughter Pregnancy rate	Productive life	
							Single trait	Multi-trait[1]
Holstein	9,476	0.994	0.994	0.993	0.996	0.971	0.951	0.967
Jersey	867	0.993	0.992	0.991	0.993	0.952	0.936	0.938
Brown Swiss	104	0.985	0.987	0.988	0.995	0.952	0.913	0.937
Guernsey	37	0.991	0.988	0.987	0.992	0.956	0.891	0.907
Ayrshire	21	0.981	0.972	0.972	0.996	0.906	0.948	0.951

[1]Correlation of previous approximate multi-trait with new multi-trait evaluations.

Table 4. Correlations of new software single-trait evaluations with new software multi-trait evaluations for bulls born from 2000 through 2008 with >50 daughters in the all-breed model by breed

	Bulls (no.)	Milk yield	Fat yield	Protein yield	SCS	Daughter pregnancy rate	Productive life
Holstein	9,476	0.998	0.998	0.998	0.996	0.976	0.974
Jersey	867	0.998	0.999	0.999	0.995	0.960	0.956
Brown Swiss	104	0.996	0.997	0.997	0.996	0.965	0.973
Guernsey	37	0.998	0.998	0.998	0.993	0.966	0.984
Ayrshire	21	0.996	0.997	0.997	0.997	0.966	0.988

traits, even with the revised heritability for yield traits, but were lower for PL because of model changes. Other breeds had correlations a little lower than Holstein except for SCS, which was 0.998 or 0.999 for all breeds. Correlations of multi-trait with previous EBV (Table 3) were slightly lower because the previous EBV were single-trait. From this comparison, numbers of the top 100 US Holstein bulls in common were 85 for protein, 87 for SCS, and 71 for DPR. Corresponding numbers were 88, 89, and 78 for Jersey, and 91, 86, and 80 for Brown Swiss. Correlations of new single-trait with new multi-trait EBV (Table 4) were high for yield traits and SCS of all breeds, but lower for DPR and PL as expected because those traits are less heritable and expressed later. Correlations for protein EBV in early years (results not shown) were also lower when multi-trait methods were used because both milk and fat were used to provide information for the missing protein records, whereas the approximate multi-trait method in the previous software used only milk as a correlated trait.

For the 3-trait fertility model, correlations of evaluations from previous and new software applied to the same data were about 0.995 within each breed for both HCR and CCR. Small differences occurred because the new software included all ancestors and unknown-parent groups, whereas the previous model truncated the pedigree and did not include groups. The lactation and individual breeding models were correlated by 0.972 for HCR and 0.986 for CCR in Holsteins and slightly less in other breeds (Table 5). Current evaluations had high correlations with either the new single-trait or multi-trait evaluations for Holsteins but lower correlations in other breeds because of additional crossbred daughters and contemporaries.

For Holstein sires with >90% reliability, correlations between the single-breed and multi-breed models (both single-trait) were 0.986 for HCR and 0.992 for CCR, indicating little change in rank when adding the other breeds. Correlations between single-trait and multi-trait evaluations from the new software were about 0.99 for HCR and about 0.96 for CCR, with lower correlations as expected for CCR because of its higher correlation with DPR.

Estimated regressions on inbreeding in the first analysis were nearly identical to previously assumed values, but estimated heterosis effects were smaller (Table 6). Compared with the previous heterosis estimates for yield traits, base heterosis was smaller but current heterosis was larger. The new estimates were larger for DPR and PL but smaller (less unfavorable) for SCS. Inbreeding depression per 1% inbreeding in the second analysis was estimated to be −0.21 for HCR, −0.10 for CCR, and −0.13 for DPR; the regression for inbreeding was more negative for DPR than in the first analysis. Heterosis was estimated to be 1.3 for HCR, 3.2 for CCR, and 1.4 for DPR.

Genetic trends within each breed were examined after adding the adjustment for expected future inbreeding, which measures the average inbreeding expected when an animal is randomly mated to the current population (VanRaden, 2005). The genetic bases for each

Table 5. Correlations of previous conception rate evaluations (EBV) with new single-breed and multi-breed EBV using single-trait (ST) and multi-trait (MT) lactation models by conception rate trait and breed for bulls with >50% reliability

			Correlation with previous evaluation				
Conception rate trait	Breed	Bulls (no.)	New software, same model	Lactation model	All-breed ST	All-breed MT	Correlation of ST and MT EBV from new software
Heifer	Holstein	2,107	0.995	0.972	0.980	0.961	0.986
	Jersey	157	0.991	0.973	0.910	0.892	0.988
	Brown Swiss	7	0.993	0.955	0.954	0.957	0.999
Cow	Holstein	15,556	0.996	0.986	0.973	0.952	0.958
	Jersey	1,390	0.995	0.984	0.943	0.904	0.954
	Brown Swiss	122	0.996	0.982	0.880	0.859	0.961

Table 6. Estimates of inbreeding depression and heterosis using previous and new software

Statistic	Software	Milk yield (kg)	Fat yield (kg)	Protein yield (kg)	SCS ($\log_2$)	Daughter pregnancy rate (%)	Productive life (mo)	
							Single-trait	Multi-trait
Inbreeding depression[1]	Previous	−29	−1.1	−0.95	0.0030	−0.078	−0.22	−0.22
	New	−30	−1.1	−0.91	0.0045	−0.071	−0.27	−0.25
Heterosis[2]	Previous	205	11.8	8.2	0.100	1.5	0.00	0.00
Base heterosis[3]	New	77	10.0	5.0	0.023	2.0	0.40	0.39
Current heterosis[4]	New	259	16.8	10.4	0.004	2.4	2.02	1.89

[1]Effect per 1% inbreeding.

[2]Effect for animals with 100% heterosis.

[3]Effect in base population for animals with 100% heterosis.

[4]Effect in current population for animals with 100% heterosis = base heterosis − 6(inbreeding regression).

breed were first expressed as differences from Holstein cows born in 2005 and were then adjusted to within-breed bases as is done for other yield and fitness traits. Trends were validated using Interbull tests 1 and 3 for CCR and test 3 for HCR (test 1 does not apply to HCR because it compares first-lactation with all-lactation trends). All breeds passed these tests for CCR and HCR. Test 2 estimates trend in DYD across time within sire and was also attempted for both traits, but only single-trait DYD were available, which differed from the multi-trait evaluations, and thus inconsistent results were observed. Multi-trait DYD were not yet programmed because diagonal blocks are regenerated from data during each iteration and not stored across iterations, but multi-trait contributions from daughters could be accumulated in memory for sires of interest instead of for all sires.

Genetic differences among breeds for fertility traits were fairly consistent with phenotypic differences (Table 7). For HCR, Holsteins had the highest phenotypic and genetic averages. For CCR, Jerseys and Milking Shorthorns exceeded Holsteins, with Brown Swiss and Guernseys being the lowest. Genetic differences among breeds for the other traits were very similar to previous estimates, with comparisons provided for the example trait milk (Table 8). Jersey genetic merit for milk yield was slightly more favorable, probably because of the revised heterosis estimate. Standard deviations of milk yield EBV were slightly smaller than previous estimates. For yield traits, this might be caused by the reduced heritability, but the estimated genetic trends were not reduced, probably because the trends are determined by bulls with high reliability and their EBV are not affected by the assumed heritability.

Inclusion of foreign information into the domestic evaluation gave correlations with MACE of 0.98 to 0.99 for Holstein bulls that had only foreign daughters compared with 0.45 to 0.69 if only domestic information was included (Table 9). Correlations after including foreign information were only 0.94 to 0.98 for Jerseys because most foreign bulls were from New Zealand, which has low genetic correlations with the United States. Thus, reliabilities of New Zealand bulls remained low on the US scale, and the domestic parent averages and unknown-parent group solutions had more effect on their evaluations.

Computation for the single-trait model with 7 traits took 500 iterations initially, and 3 min per iteration for a total of 25 h, using 7 processors. For subsequent updates with new data, prior solutions are used and only 100 to 200 iterations may be needed. Single-trait solutions were used as priors for the multi-trait model so that only 200 additional iterations were needed, which required 53 h with 7 processors and 16 min per

Table 7. Phenotypic means for conception rate of cows born in 2005 and breeding values expressed as difference from Holsteins by breed and conception rate trait[1]

Breed	Females with records (no.)		Phenotypic mean (%)		Breeding value mean (%)	
	HCR	CCR	HCR	CCR	HCR	CCR
Holstein	302,007	543,491	56.0	31.8	0.0	0.0
Jersey	11,533	32,007	50.9	37.8	−0.8	+5.7
Brown Swiss	1,620	4,449	44.1	28.3	−7.1	−4.5
Guernsey	612	1,742	44.8	26.1	−6.7	−7.1
Ayrshire	574	1,444	47.6	38.1	−4.7	+0.7
Milking Shorthorn	422	836	47.4	40.4	0.0	+4.0

[1]HCR = heifer conception rate; CCR = cow conception rate.

Table 8. Differences from Holstein EBV milk on an all-breed scale, EBV milk standard deviations in 2005, and genetic trends from 1965 through 2005 on a within-breed scale using previous and new software by breed

	Difference from Holstein EBV milk (kg)		2005 EBV milk SD (kg)		Genetic trend (kg)	
Breed	Previous	New	Previous	New	Previous	New
Holstein	0	0	622	595	3,195	3,504
Jersey	−2,965	−2,738	542	524	3,152	3,613
Brown Swiss	−1,985	−1,957	546	502	2,597	2,818
Guernsey	−2,870	−2,859	588	560	2,800	3,079
Ayrshire	−2,609	−2,619	430	406	2,036	2,195
Milking Shorthorn	−3,097	−2,832	393	375	2,233	2,452

iteration. Convergence rates were nearly the same for single-trait and multi-trait models, and the memory required was 35 GB for both, much less than the 256 GB available but somewhat large because hash tables to renumber the original effects into equation numbers are in the solving program instead of a separate preprocessing step.

Convergence tended to be slow for PL and fertility traits because of substantial genetic trend but low heritability. Correlations of single-trait PL genetic evaluations at 100, 200, 500, 1,000, and 2,000 iterations with those at 3,000 iterations were 0.964, 0.973, 0.985, 0.996, and 0.9998, respectively. The respective standard deviations of evaluations as a fraction of final SD were 0.944, 0.967, 0.977, 0.984, and 0.996. The variance of change in EBV divided by the variance of EBV was 4×10^{-10} at iteration 3,000. A correlation of 0.997 for evaluations at 500 and 1,000 iterations indicated near convergence, but more iteration may be needed routinely to ensure full convergence of all traits.

Predictive Ability

Correlations of truncated with current evaluations indicate better predictive ability for the new than for the previous software and for multi-trait than for single-trait models (Table 10). Single-trait evaluations were more accurate than previous evaluations for all traits of Holsteins, both for bulls with parent average and bulls that added daughters. One exception was fat yield for bulls with parent average, where the previous evaluation had a higher correlation. Multi-trait evaluations had correlations <0.01 higher than single-trait for both groups and all traits of Holstein bulls except for an increase of 0.023 for DPR of bulls that had daughter records. The small gains for multi-trait PL are because daughters had complete PL records in the truncated data, whereas current data include daughters with partial or no PL records. Correlations for single-trait evaluations were higher than with the previous software by 0.03 to 0.09 for Jerseys, probably because of fewer daughters per bull, the lower heritability used, and improved estimates of heterosis for crossbred daughters. Multi-trait evaluations were more variable, with small gains or losses as compared with single-trait, probably because of fewer bulls in the test.

Trend Validation

Genetic trends for each breed and trait in the first analysis were very similar to previous estimates (VanRaden et al., 2007) but extended 6 additional years. For example, differences for the trait milk between new multi-trait and previous single-trait trends are small (Table 8). Figures 1 and 2 provide breed differences for CCR and HCR, respectively, from the second analysis and genetic trends calculated as average breeding values by birth year for females with a phenotype for at least one trait. All breeds had negative genetic trends for CCR until recent years. For HCR, Holstein and Jersey had fairly steady merit across years, whereas the other breeds had negative genetic trends.

Table 9. Correlations of previous single-trait evaluations that included foreign information (multi-trait across-country evaluation, MACE) with new single-trait evaluations for Holstein and Jersey bulls with only foreign daughters before and after adding MACE

Breed	Bulls (no.)[1]	MACE	Milk yield	Fat yield	Protein yield	SCS	Daughter pregnancy rate	Productive life
Holstein	14,931	No	0.685	0.454	0.648	0.567	0.600	0.636
		Yes	0.993	0.991	0.993	0.996	0.980	0.976
Jersey	1,194	No	0.634	0.505	0.535	0.553	0.456	0.450
		Yes	0.941	0.968	0.956	0.963	0.976	0.918

[1]Not all bulls had evaluations for all traits.

Table 10. Correlations of truncated and current evaluations using previous and new software for bulls with no daughter records in July 2008 and bulls that gained daughter records after July 2008 by trait

		Bulls with no daughter records[1]			Bulls that gained daughter records[2]		
Breed	Trait	Previous	New single-trait	New multi-trait	Previous	New single-trait	New multi-trait
Holstein	Milk yield	0.579	0.577	0.584	0.792	0.812	0.820
	Fat yield	0.523	0.506	0.508	0.795	0.823	0.813
	Protein yield	0.559	0.560	0.561	0.792	0.827	0.813
	SCS	0.552	0.561	0.561	0.789	0.797	0.798
	Daughter pregnancy rate	0.528	0.606	0.601	0.659	0.694	0.704
	Productive life	0.661	0.641	0.658	0.818	0.744	0.790
Jersey	Milk yield	0.648	0.670	0.672	0.843	0.874	0.875
	Fat yield	0.616	0.637	0.641	0.692	0.687	0.681
	Protein yield	0.599	0.630	0.627	0.769	0.794	0.792
	SCS	0.458	0.478	0.465	0.652	0.700	0.688
	Daughter pregnancy rate	0.556	0.591	0.545	0.678	0.704	0.699
	Productive life	0.558	0.544	0.569	0.743	0.591	0.690

[1]Included 4,059 Holstein and 415 Jersey bulls with 0 daughters in 2008 and >50 in 2012.

[2]Included 444 Holstein and 66 Jersey bulls with 10 to 200 daughters in 2008 and >500 daughters in 2012.

Validation was conducted for trends from both analyses. All 30 breed–trait combinations passed trend validation method 1, which was applied to only 6 traits because PL is coded as a lifetime record rather than separate lactation records and because trait HCR does not include multiple lactations. For method 2, 26 breed–trait combinations passed but 4 did not: Holstein DPR, Jersey SCS and PL, and Brown Swiss PL. Method 2 was not applied to CCR or HCR because only single-trait daughter deviations were computed that did not contain the correlated information from DPR. For method 3, 26 combinations passed and 4 did not, those being Jersey fat yield, SCS, and PL, and Ayrshire CCR.

These validation results were slightly better than those for previous software, which did not pass some

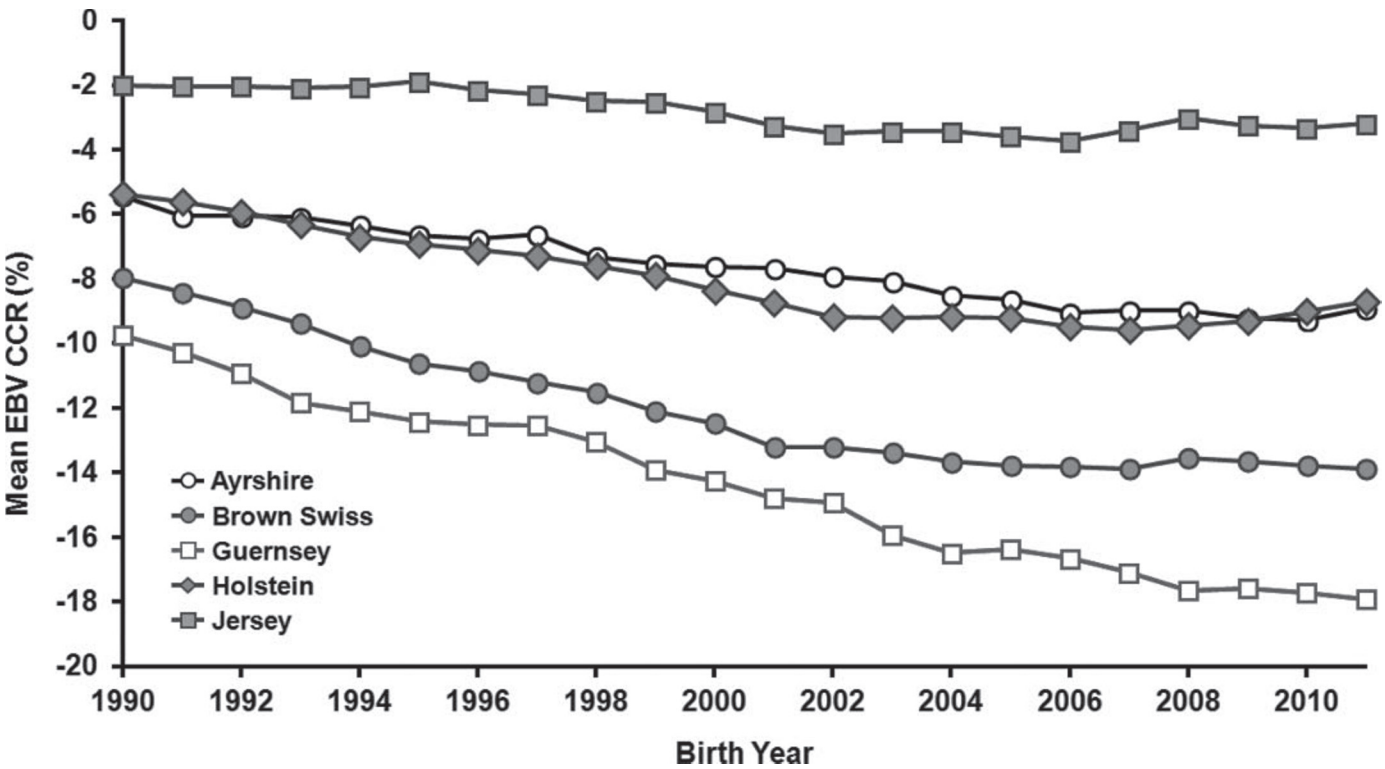

Figure 1. Genetic trends by breed for cow conception rate (%) on an all-breed scale. Color version available in the online PDF.

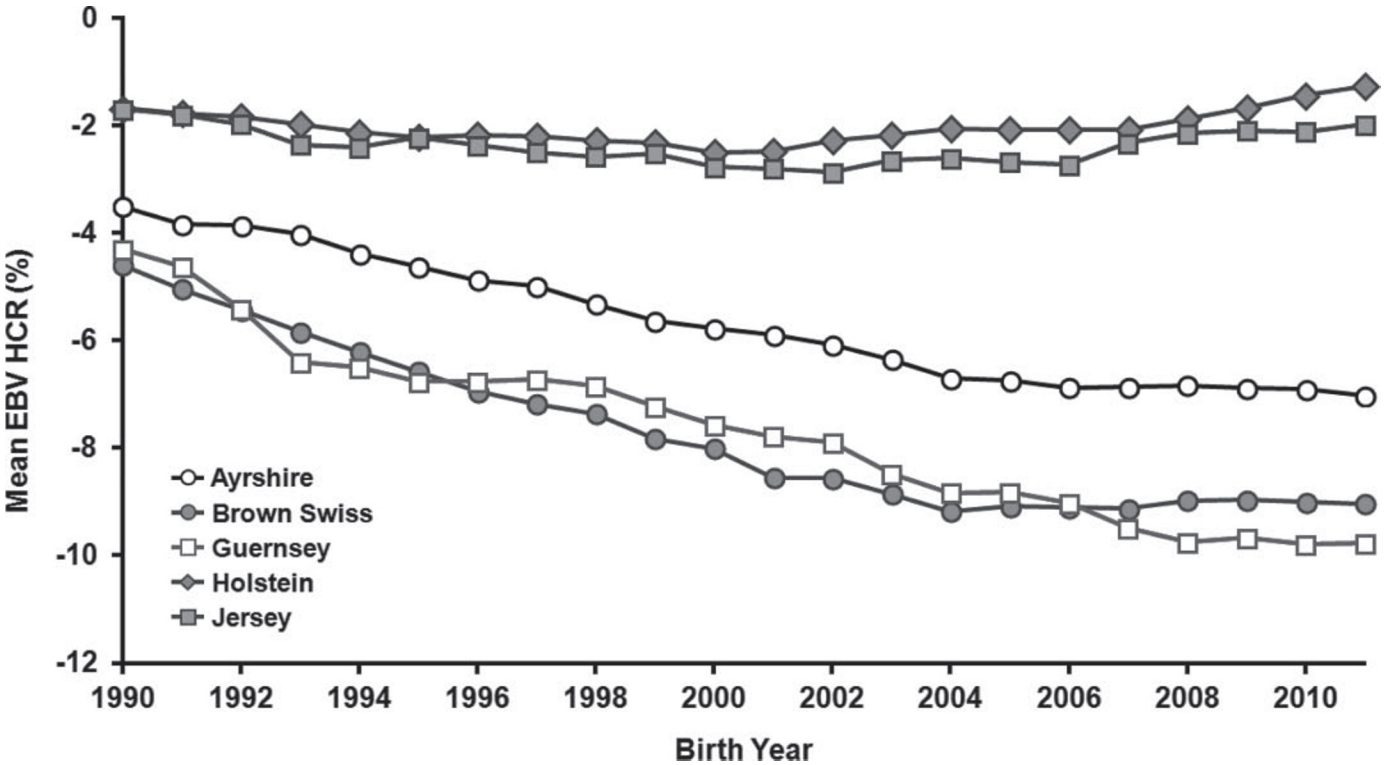

Figure 2. Genetic trends by breed for heifer conception rate (%) on an all-breed scale. Color version available in the online PDF.

of the same breed–trait combinations (Holstein and Guernsey DPR, Jersey SCS, and Brown Swiss PL for method 2; Holstein PL, Jersey fat yield and SCS, Brown Swiss milk yield and PL, and Guernsey PL for method 3). Improvements for PL such as multi-trait modeling, grouping by calving date rather than birth date, and the revised heterosis estimate improved validation results slightly. However, Interbull requires exchange of single-trait PL, which did not pass method 2 validation for Holsteins, whereas multi-trait PL did pass.

Genetic trend for CCR was more negative with multi-trait processing because of the correlated influence of DPR. Genetic trends were validated for all breeds using Interbull tests 1 and 3 for CCR and test 3 for HCR. Estimated genetic correlations with other countries from Interbull changed little for Holsteins and averaged 0.02 higher for HCR, 0.02 lower for CCR, and 0.04 higher for CFI. Results were more variable for other breeds, with average correlations that were lower for both HCR and CCR but higher for CFI because the multi-trait model improves the consistency of the back-calculation for CFI from CCR and DPR. A few recent bulls with numbers of observations that differed greatly for CCR versus DPR also had unexpected differences of multi-trait versus single-trait EBV. Future research could improve consistency by redefining DPR so that cows with more days open receive more weight, just as cows with more inseminations receive more weight.

Based on the small differences in accuracy and trend validation compared with the increased computation for the 7-trait model, implementation proceeded with the 3-trait fertility model first in December 2013. A 3-trait yield model and single-trait SCS and PL models are scheduled to switch to the new software in December 2014. Faster computation could allow larger multi-trait models in the future, such as including conformation traits to obtain exact rather than approximate multi-trait PL. Instead of including all conformation traits, including only 1 linear combination of conformation traits that best predicts PL could allow (effectively) multiple-trait PL with much less cost.

Remaining questions are how to include genotypes in the all-breed model, how to process nonnormal traits such as calving ease and stillbirth, and how to compute reliabilities for more general models. Models with more effects such as maturity rate could be solved now that more flexible programs are available, but such changes may not be a high priority compared with accounting for genomic preselection.

CONCLUSIONS

Flexible software was developed to allow model changes, multi-trait processing, and incorporation of

foreign data. New and previous software gave very similar EBV for 7 traits of 30 million cows; correlations with the previous single-trait, all-breed evaluations were >0.995. Multi-trait methods converged fairly quickly using a block diagonal solving strategy, with results almost identical to single-trait for milk, fat, and SCS but improved for protein because of missing data in early years and high correlation with milk. In the 3-trait fertility model, benefits were larger for HCR and CCR because those traits are missing before 2003 and had moderate to high correlations with DPR, which has been measured since 1960. Trend validation was conducted and 92 of 100 breed-trait-test combinations passed, a slight improvement over previous software. The new software was implemented in 2013 for HCR and CCR and is scheduled to be implemented for yield, SCS, single-trait PL, and DPR in 2014.

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