Dairy Genomics in Application

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ABSTRACT

Implementation of genomic evaluation has caused profound changes in dairy cattle breeding. All young bulls bought by major artificial-insemination organizations now are selected based on these evaluation. Evaluation reliability can reach ~75% for yield traits, which is adequate for marketing semen of 2-yr-old bulls. Shortened generation interval from using genomic evaluations is the most important factor in increasing genetic improvement. Genomic evaluations are based on 42,503 single nucleotide polymorphisms (SNP) genotyped with technology that became available in 2007. The first unofficial USDA genomic evaluations were released in 2008 and became official for Holsteins, Jerseys, and Brown Swiss in 2009. Evaluation accuracy has increased steadily from including additional bulls with genotypes and traditional evaluations (predictor animals). Some of that increase occurs automatically as young genotyped bulls receive a progeny-test evaluation at 5 yr of age. Cow contribution to evaluation accuracy is increased by reducing mean and variance of their evaluations so that they are similar to bull evaluations. Integration of US and Canadian genotype databases was critical to achieving acceptable initial accuracy and continues to benefit both countries. Genotype exchange with other countries added predictor bulls for Brown Swiss and will add bulls for Holstein. In 2010, a low-density chip with 2,900 SNP and a high-density chip with 777,962 SNP were released. The low-density chip has increased greatly the number of animals genotyped and is expected to replace microsatellites in parentage verification. The high-density chip can increase evaluation accuracy by better tracking of loci responsible for genetic differences. To integrate information from chips of various densities, a method to impute missing genotypes was developed based on splitting each genotype into its maternal and paternal haplotypes and tracing their inheritance through the pedigree. The same method is used to impute genotypes of nongenotyped dams based on genotyped progeny and mates. Reliability of resulting evaluations is discounted to reflect errors inherent in the process. Gains in reliability from genomics above parent average ranged from 2.7 to 47.6 percentage units for Holsteins, 9.6 to 29.2 percentage units for Jerseys, and 3.0 to 25.8 percentage units for Brown Swiss demonstrating the contribution to accuracy from genomics.

(**Key Words:** genomic evaluation, SNP effects, reliability)

INTRODUCTION

Genetic evaluation of dairy cattle has provided the means for steady genetic improvement in production, fitness, and conformation traits. The evaluations have been based on milk recording and breed association programs for type traits. Widespread use of superior bulls through AI has been the primary vehicle for progress. Identification of superior bulls has been expensive and time consuming because of the need to wait for milking daughters and the cost of collecting their data to achieve an evaluation of adequate accuracy. The great

promise of DNA analysis has recently become a reality with the advent of low cost genotyping of large numbers of SNP markers.

The critical development was assays that can genotype large numbers of SNP at low cost. Although SNP are only biallelic (2 states), the large number available allows tracking the inheritance of short chromosomal segments. An international consortium of government, university, and industry cooperators worked with Illumina (San Diego, CA) to develop a set of SNP to be included on a chip (Van Tassell et al., 2008). A commercial set of 54,001 was included in the original release of the BovineSNP50 BeadChip (Illumina, 2010b). Consortium members had access to the new chip in fall 2007, and it became publicly available in late December 2007. In July 2010, Illumina released two new genotyping chips: a low-density chip (**Bovine3K**) with 2,900 SNP (Illumina, 2010c) and a high-density chip (**BovineHD**) with 777,962 SNP (Illumina, 2010a).

Some SNP were excluded because of low call rate, poor calling properties, or high correlation with other SNP (Wiggans et al., 2009). Procedures were developed to check for parent-progeny conflicts and other inconsistencies (Wiggans et al., 2010b). Extensive simulation work by VanRaden (2008), enabled development of genomic evaluation methods, which were applied once genotypes became available. The phenotypic and genotypic information for a predictor population is used to estimate SNP effects. Predictor animals are genotyped animals with traditional evaluations (i.e., ones that do not include genomic information). The SNP effects estimated from a predictor population are be used to calculate genomic evaluations for animals without traditional evaluations (VanRaden, 2008; VanRaden et al., 2009. The first unofficial USDA evaluations based on SNP genotypes were released in April 2008. Genomic evaluations became official for Holsteins and Jerseys in January 2009 and for Brown Swiss in August 2009.

The money to genotype thousands of animals came from research grants and contributions from AI and breed organizations. In return for their support, the AI organizations received the exclusive right to have males genomically evaluated until May 2013. The genotyping is done by GeneSeek (Lincoln, NE), DNA LandMarks (Quebec, Canada), and Genetic Visions (Middleton, WI).

EVALUATION PROCESS

Nomination

Genotypes that are usable for genetic evaluations have been received by USDA for >100,000 animals as of May 2011 (Table 1). The availability of the Bovine3K chip has greatly increased the number of animals genotyped, and its SNP are expected to replace microsatellites for parentage verification. Since September 2010, almost 33,800 Bovine3K chip genotypes have been received; 94% of those genotypes were for females. The 8 AI and 4 breed organizations that arrange for genotyping are designated as requesters. They arrange for a DNA sample to be collected and attached to a bar-coded mailer. That mailer is usually sent to the requester but may be sent directly to the genotyping laboratory. The bar code facilitates sample processing at the laboratory. The requester is expected to nominate each animal by making an entry in a database maintained by USDA's Animal Improvement Programs Laboratory (**AIPL**) before the sample reaches the genotyping laboratory. The nomination is either through a web interface or pedigree records containing the bar code (also known as sample identification). Requesters also can use the nomination query for nomination confirmation and update and for problem

resolution. The nomination process ensures that the pedigree for the animal is in the AIPL database before the genotype arrives at AIPL and simplifies matching the

Table 1. Numbers of genotyped animals by breed and evaluation date

		Predictor[2]		Young[3]			All
Breed	Evaluation date[1]	Bulls	Cows	Bulls	Cows	Imputed	animals
Holstein	**April 2009**	**7,600**	**2,711**	**9,690**	**1,943**	**—**	**21,944**
	August 2009	**8,512**	**3,728**	**12,137**	**3,670**	**—**	**28,047**
	January 2010	**8,974**	**4,348**	**14,061**	**6,031**	**—**	**33,414**
	April 2010	**9,770**	**7,415**	**16,007**	**8,630**	**1,471**	**41,822**
	August 2010	**10,430**	**9,372**	**18,652**	**11,021**	**2,029**	**49,475**
	December 2010	**11,293**	**12,825**	**21,161**	**18,336**	**2,172**	**63,615**
	January 2011	11,194	13,582	22,567	22,999	2,282	70,342
	February 2011	11,196	13,935	23,330	26,270	2,350	74,731
	March 2011	11,713	14,382	24,505	29,926	2,463	80,529
	April 2011	**12,152**	**11,733**	**25,204**	**36,047**	**2,342**	**85,136**
	May 2011	12,429	11,834	26,139	40,996	2,442	91,398
Jersey	February 2010	1,977	479	1,172	197	—	3,825
	April 2010	**2,072**	**637**	**1,250**	**202**	**97**	**4,161**
	August 2010	**2,145**	**792**	**1,476**	**258**	**152**	**4,671**
	December 2010	**2,217**	**2,189**	**1,754**	**1,924**	**178**	**8,084**
	January 2011	2,209	2,316	1,868	2,130	186	8,523
	February 2011	2,209	2,407	1,956	2,364	192	8,936
	March 2011	2,213	2,557	2,036	2,616	197	9,422
	April 2011	**2,265**	**2,775**	**2,096**	**2,884**	**183**	**10,020**
	May 2011	2,279	2,966	2,198	3,630	188	11,073
Brown Swiss	February 2010	1,168	54	179	15	—	1,416
	April 2010	**1,185**	**98**	**188**	**31**	**47**	**1,502**
	August 2010	**1,248**	**124**	**228**	**35**	**69**	**1,635**
	December 2010	**1,596**	**146**	**256**	**40**	**79**	**2,038**
	January 2011	1,593	149	265	42	78	2,049
	February 2011	1,593	152	271	50	78	2,066
	March 2011	1,593	154	275	55	79	2,077
	April 2011	**1,605**	**157**	**280**	**142**	**72**	**2,184**
	May 2011	1,612	165	285	221	75	2,283

[1]Evaluation dates in boldface are official USDA-DHIA evaluation releases.
[2]Animals with traditional evaluations (no genomic information included).
[3]Animals without traditional evaluations.

identification associated with the genotype with the animal's information in the AIPL database.

Genotyping

At the genotyping laboratories, DNA is extracted from the sample. In 2010, DNA sources included hair (82%), nasal swab (12%), blood (5%), semen (<1%), and ear punches (<1%). The process of DNA amplification and fragmentation, hybridization to the chip, labeling, and genotype detection takes 3 d. Data generated from the laser reader then are clustered to determine SNP genotypes (Illumina, 2010b). Those genotypes and identification information are transferred to AIPL.

Genotype Storage and Validation

The AIPL database can store multiple genotypes for an animal and relies on chip identification and sample location on the chip to identify a sample uniquely. Multiple samples arise from collection and labeling errors as well as upgrading from lower to higher density. Samples are checked on an animal basis for call rate and parent-progeny conflicts. In addition to conflicts with reported parents, a conflict also is designated if comparison with all other genotypes indicates that an animal has a parent-progeny relationship that is not found in the pedigree (usually the genomically correct parent). A report of SNP with a call rate of <90%, a departure from Hardy-Weinberg equilibrium (difference between number of expected and actual heterozygous SNP), or parent-progeny conflicts of >2% is returned to the submitting laboratory. Laboratories can run these checks using an automated process before they submit the genotypes for loading into the database. Based on the check runs, laboratories often are successful in reclustering problematic SNP to reduce the number of SNP conflicts in those categories. Those checks serve as a measure of the quality of the genotype calls. For BovineSNP50 genotypes, usually <10 SNP were outside those limits for any submission. For Bovine3K genotypes, considerable effort was required to determine which SNP were reliable and to adjust procedures to achieve results similar to those for BovineSNP50 genotypes.

The database allows for storage of genotypes from chips with differing numbers of SNP. Currently, the Bovine3K, BovineSNP50, and BovineHD chips are supported. Comparisons of SNP genotypes from different chips are supported but limited to SNP in common.

Many conflicts can be resolved. For most cases of sire conflict, an alternative sire is suggested. Identical genotypes often are the result of embryo splits or identical twins. Because bulls have only one X chromosome, their genotypes for X-specific SNP appear to be homozygous, and that characteristic is used in sex validation. Some cows inherit both of their X chromosomes from the same male ancestor and, therefore, appear to be males. If a common male ancestor can be found, genotypes for such cows are accepted. The Bovine3K chip includes Y-specific SNP, which are used in sex validation. Usability of genotypes is evaluated whenever pedigree of a genotyped animal changes.

Genotype Preparation

The SNP genotypes for each animal (42,503 SNP for BovineSNP50 genotypes, 38,201 SNP for BovineHD genotypes, and 2,614 SNP for Bovine3K genotypes) are extracted from the database. Because the number of animals with high-density genotypes is too few for routine evaluation, only the 38,201 SNP that match the BovineSNP50 chip currently are extracted. During extraction, multiple genotype calls for an individual animal are merged, with

preference given to the genotype with the highest call rate. Identical twins and animals from split embryos have their genotypes harmonized. For dams without genotypes, genotypes are imputed (constructed from relatives) if the number of genotyped progeny and mates is sufficient to reach a call rate of 90% on an allele basis. Since April 2010, dams with imputed genotypes have been included in genomic evaluations. Imputation also is used to add genotypes for SNP that are on the BovineSNP50 but not the Bovine3K chip. Imputation involves splitting the genotype into paternally and maternally contributed chromosomes (haplotypes). Haplotype inheritance is traced and used to fill in missing genotypes. When pedigree sources are not available, the most common consistent haplotype for the population is selected. Table 1 shows the number of usable genotypes by breed for some of the genomic evaluations released since April 2009.

Estimation of SNP Effects

The effects of SNP on traditional evaluations are estimated for >30 traits. The traditional evaluations are deregressed so that shrinkage based on amount of information, which is inherent in estimation of random effects, is undone to make the data more like individual records. Cow and bull evaluations must be comparable, because both are used to estimate SNP effects. Therefore, traditional evaluations of cows for milk, fat, and protein yields and component percentages are adjusted to remove overestimation usually associated with cow evaluations for yield traits (Wiggans et al., 2010a). That adjustment makes the mean and variance of the deregressed value for a cow similar to that for a bull with similar accuracy.

Deregressed traditional evaluations are regressed on each of the 42,503 SNP genotypes (VanRaden, 2008), where the genotypes are expressed as the quantity of one of the alleles (0, 1, or 2). Because the effects are considered to be random, a system with more effects than observations is solvable. The solution is the effect on each trait from replacing 1 allele in the SNP genotype with the other allele. In addition to SNP effects, a polygenic effect is estimated to capture genetic variation not accounted for by SNP.

Most SNP have small effects, which are distributed evenly across all chromosomes. For both Holsteins and Jerseys, the largest effects for milk and fat were found on chromosome 14 and were associated with the DGAT1 (diacylglycerol O-acyltransferase 1) gene (Grisart et al., 2004). An increased effect for protein yield was also found on chromosome 14 for Jerseys. Methods for the visualization of SNP effects were described by Cole and VanRaden (2010), and plots of the absolute values of effects for all 42,503 SNP on 31 traits of economic importance are available at the AIPL website (http://aipl.arsusda.gov/Report_Data/Marker_Effects/marker_effects.cfm).

Calculation of Genomic Evaluation

An animal's genomic evaluation includes a genomic prediction (estimates of SNP and polygenic effects) and information from traditional evaluations that is not already included in the genomic information. A traditional evaluation is calculated for just the subset of animals with genotypes to allow determination of the traditional information that was accounted for by genomics. A selection index is used to combine the genomic prediction, traditional evaluation, and subset evaluation (VanRaden et al., 2009).

Measure of Accuracy

Reliability measures how much information contributes to the evaluation.

For genomic evaluations, reliability combines daughter equivalents from genomics, parent average, and information from the traditional evaluation not accounted for through genomics. The genomic contribution is approximated by a function of the weighted sum of the genomic relationships of the animal with the predictor population. The weight is the reliability with the component for parent average removed. The genomic relationship with predictor animals and their evaluation reliability are the primary determinants of accuracy for genomic evaluations. Thus, the genomic contribution is lower for less related animals, such as those with foreign ancestors or subpopulations that contributed little to the current population (Wiggans and VanRaden, 2010).

The increase in evaluation reliability from including genomic information can be demonstrated by comparing August 2006 traditional parent averages for young bulls without daughter information, their August 2006 genomic evaluations that include SNP and polygentic effects estimated from the August 2006 predictor population in addition to their traditional parent average, and their June 2010 daughter deviations deregressed from their traditional evaluations (Table 2). Mean reliability for August 2006 genomic evaluations of young bulls across all yield, health, and fertility (where applicable) traits was 57% for Holsteins, 55% for Jerseys, and 52% for Brown Swiss. Gains in reliability above parent average (Table 2) ranged from 2.7 to 47.6 percentage units for Holsteins, 9.6 to 29.2 percentage units for Jerseys, and 3.0 to 25.8 percentage units for Brown Swiss. Reliability gains were lowest for stillbirth, which had the smallest predictor population because cow evaluations were not included and because fewer bulls had evaluations as data collection began more recently than for other traits. Coefficients of determination ($\mathbf{R^2}$) also are provided in Table 2 as a measure of the relationship between 2006 evaluations (either parent average or genomic evaluation) and 2010 daughter deviations (deregressed values). The R^2 ranged from 3.1 to 36.7 for parent average and from 9.6 to 62.1 for genomic evaluation. Reliabilities for both parent average and genomic evaluation are higher than their respective R^2, because reliability adjusts for error variance (differing amounts of information) and because selection had occurred in the genotyped population. Regression coefficients of June 2010 daughter deviation on August 2006 genomic evaluations ranged from 0.87 to 1.08 for Holsteins, 0.88 to 1.30 for Jerseys, and 0.84 to 1.09 for Brown Swiss; a coefficient close to 1 indicates that a 1-unit difference in the genomic evaluation results in a 1-unit change in the trait. For bias in genomic evaluation, a negative value indicates that the initial August 2006 genomic evaluation was higher than the June 2010 deregressed value.

Changes in methodology for genomic evaluation also impact the measure of evaluation accuracy. Implementation of the adjustment for cow evaluations in April 2010 increased the gain in reliability from genomics by about 3 percentage units for Holstein and Jersey yield traits (Wiggans et al., 2010a). In April 2011, a revised adjustment method was implemented for all cows that allowed genotyped and non genotyped animals to be comparable to each other (Wiggans et al., 2011). The accuracy loss from imputation required to include Bovine3K genotypes required a reliability adjustment. Reliabilities are converted to daughter equivalents and discounted by the lower call rate and loss in accuracy. The adjusted daughter equivalents then are converted back to reliabilities. Predictive ability of genetic merit with a low-density chip with 3,000 equally spaced SNP was

Table 2. Observed reliabilities (REL) in August 2006 for traditional parent averages and genomic evaluations[1] of young bulls without daughter information, coefficients of determination (R^2 x 100) between August 2006 evaluations and June 2010 daughter deviations deregressed from traditional evaluations, coefficients (b) for regression of June 2010 daughter deviations on August 2006 genomic evaluations, and bias in genomic evaluation by trait and breed.

		August 2006 REL, %			R^2			
Breed	Trait[2]	Parent average	Genomic evaluation	Gain[3]	Parent average	Genomic evaluation	b	Bias[4]
Holstein	Milk, kg	38.1	67.5	29.4	19.4	41.1	0.91	−4.0
	Fat, kg	38.1	73.1	35.0	17.5	43.3	0.96	−0.9
	Protein, kg	38.1	63.7	25.6	20.3	39.1	0.88	0.6
	Fat, %	38.1	85.7	47.6	26.9	62.1	1.02	0.0
	Protein, %	38.1	77.9	39.8	29.5	58.9	0.90	0.0
	PL, mo	31.0	64.2	33.2	16.4	31.4	1.04	−1.5
	SCS	33.9	60.4	26.5	15.8	31.7	0.88	0.0
	DPR, %	29.8	46.8	17.0	21.8	29.4	1.08	−0.2
	Sire CE	27.1	40.9	13.8	20.5	28.2	0.79	1.0
	Daughter CE	26.2	44.3	18.1	10.1	17.7	0.93	−1.0
	Sire SB	22.7	29.8	7.2	7.6	10.2	0.87	2.1
	Daughter SB	26.6	29.3	2.7	9.3	10.2	0.89	0.3
Jersey	Milk, kg	39.5	53.9	14.3	38.9	49.2	1.03	89.8
	Fat, kg	39.5	49.9	10.4	30.7	38.1	0.88	5.8
	Protein, kg	39.5	49.1	9.6	34.2	41.0	0.94	3.4
	Fat, %	39.5	64.9	25.3	40.2	58.1	0.97	0.0
	Protein, %	39.5	61.4	21.8	36.7	52.6	0.96	0.0
	PL, mo	24.2	50.8	19.1	10.6	19.2	0.97	−0.4
	SCS	18.7	48.9	13.8	10.4	18.3	0.70	0.1
	DPR, %	24.1	60.0	29.2	9.9	22.7	1.30	−0.1
Brown Swiss	Milk (kg)	37.2	53.8	16.7	5.1	24.4	0.61	−163.0
	Fat (kg)	37.2	53.1	16.0	7.5	21.3	0.54	−6.3
	Protein (kg)	37.2	53.0	15.9	6.2	22.4	0.52	−4.1
	Fat (%)	37.2	59.1	22.0	26.4	42.0	1.09	0.0
	Protein (%)	37.2	57.8	20.6	29.8	43.9	1.02	0.0
	PL (months)	28.3	54.2	25.8	9.7	22.0	1.07	−1.2
	SCS	32.2	53.4	21.2	12.1	23.0	1.02	0.0
	DPR (%)	24.9	28.1	3.0	3.1	9.6	0.48	0.0

[1]Includes SNP and polygenic effects estimated from the August 2006 predictor population (genotyped animals with traditional evaluations) and August 2006 traditional parent averages.
[2]PL = productive life, DPR = daughter pregnancy rate, CE = calving ease, and SB = stillbirth.
[3]Genomic REL – parent average REL.
[4]June 2010 daughter deviation – August 2006 genomic evaluation.

reported to be 84 to 89% of that with the BovineSNP50 chip for Holsteins (Vazquez et al., 2010) and around 95% for Jerseys (Weigel et al., 2010). In December 2010, reliabilities for official PTA for milk yield, which included all sources of information, ranged from 74 to 81% for most young Holstein bulls.

Distribution

Genomic evaluations are calculated monthly. At each triannual release of official USDA-DHIA evaluations, all genomic evaluations are released. Between those releases, genomic evaluations are released only for new animals or young bulls that are not being marketed so that evaluations of marketed bulls do not fluctuate between official evaluations. Evaluations of bulls that are less than 2 yr old and not enrolled in the cross-reference program of the National Association of Animal Breeders are distributed only to the owners and requesting AI organizations.

FUTURE

Genomic evaluations are expected to continue to increase in accuracy. The largest contributor to that increased accuracy will be additional predictor animals. Table 1 shows the natural increase in the US predictor population at each official evaluation from bulls with a first progeny-test result at approximately 5 yr of age. The US predictor population also increases the month following evaluation release when newly evaluated foreign bulls can contribute.

In July 2010, Illumina (2010a) released a high-density chip with 777,962 SNP, and Affymetrix (Santa Clara, CA; 2011) released a high-density chip with 648,855 SNP in January 2011. Although such chips can provide genotypes that increase accuracy of genomic evaluations by better tracking of the loci responsible for genetic differences, the accuracy gains are not expected to be large (VanRaden and Tooker, 2010). As with low-density SNP, high-density SNP would be imputed from current genotypes. The first step is to collect enough high-density genotypes so that most haplotypes are represented. Several thousand genotyped animals may be required. The ultimate density is full sequencing, and its cost has been dropping. With full sequencing for a substantial number of animals, SNP that are the causative mutation or are closely linked to it may be identified (Meuwissen, 2010). Identification of those SNP may enable an increase in evaluation accuracy and a reduced number of SNP needed for evaluation. The higher density genotypes may also support genomic evaluations of crossbred cattle, because the SNP may be close enough to the QTL that the phase of the association persists across breeds. However, even with accurate tracking of QTL alleles, their effects may differ between breeds.

Increased Accuracy through Collaboration

Collaboration is the least expensive way to increase the predictor population and thus increase accuracy. Collaboration between the United States and Canada was quite successful in initially increasing the size of the predictor population and continues to add to it. Research collaboration has helped to improve evaluation methodology, and coordination across countries has aided with producer acceptance by minimizing differences and explaining existing differences. Genotypes from the United States were traded with Switzerland, Germany, and Austria to increase the number of predictor bulls for Brown Swiss. Agreements with groups in Italy and Great Britain will provide more Holstein predictor bulls.

CONCLUSIONS

Genomic evaluations have revolutionized dairy cattle breeding by greatly increasing accuracy of estimates of genetic merit for young animals and could double the rate of genetic progress. Those evaluations are based on genotypes that are extensively checked for quality, and conflicts are resolved. They are becoming more accurate as animals are added to the predictor population. All young bulls purchased by major AI organizations now are selected based on genomic evaluations. The development, implementation, and acceptance of genomic evaluations have allowed extensive marketing of 2-yr-old bulls.

ACKNOWLEDGEMENTS

Materials for this article were excerpted from accepted Journal of Dairy Science publication "The Genomic Evaluation System in the United States: Past, Present, Future" Wiggans et al. 2011.

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