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Use of the Illumina Bovine3K BeadChip in dairy genomic evaluation[1]

G. R. Wiggans,*[2] T. A. Cooper,* P. M. VanRaden,* K. M. Olson,† and M. E. Tooker*
*Animal Improvement Programs Laboratory, Agricultural Research Service, USDA, Beltsville, MD 20705-2350
†National Association of Animal Breeders, Columbia, MO 65205

ABSTRACT

Genomic evaluations using genotypes from the Illumina Bovine3K BeadChip (3K) became available in September 2010 and were made official in December 2010. The majority of 3K-genotyped animals have been Holstein females. Approximately 5% of male 3K genotypes and between 3.7 and 13.9%, depending on registry status, of female genotypes had sire conflicts. The chemistry used for the 3K is different from that of the Illumina BovineSNP50 BeadChip (50K) and causes greater variability in the accuracy of the genotypes. Approximately 2% of genotypes were rejected due to this inaccuracy. A single nucleotide polymorphism (SNP) was determined to be not usable for genomic evaluation based on percentage missing, percentage of parent-progeny conflicts, and Hardy-Weinberg equilibrium discrepancies. Those edits left 2,683 of the 2,900 3K SNP for use in genomic evaluations. The mean minor allele frequencies (MAF) for Holstein, Jersey, and Brown Swiss were 0.32, 0.28, and 0.29, respectively. Eighty-one SNP had both a large number of missing genotypes and a large number of parent-progeny conflicts, suggesting a correlation between call rate and accuracy. To calculate a genomic predicted transmitting ability (GPTA) the genotype of an animal tested on a 3K is imputed to the 45,187 SNP included in the current genomic evaluation based on the 50K. The accuracy of imputation increases as the number of genotyped parents increases from none to 1 to both. The average percentage of imputed genotypes that matched the corresponding actual 50K genotypes was 96.3%. The correlation of a GPTA calculated from a 3K genotype that had been imputed to 50K and GPTA from its actual 50K genotype averaged 0.959 across traits for Holsteins and was slightly higher for Jerseys at 0.963. The average difference in GPTA from the 50K- and 3K-based genotypes across trait was close to 0. The evaluation system has been modified to accommodate the characteristics of the 3K. The low cost of the 3K has greatly increased genotyping of females. Prior to the availability of the 3K (August 2010), female genotyping accounted for 38.7% of the genotyped animals. In the past year, the portion of total genotypes from females across all chip types rose to 59.0%.
Key words: 3K, dairy cattle, genomic evaluation

INTRODUCTION

Genomic evaluation of dairy cattle became available in the United States in 2008 (Wiggans et al., 2011). The BovineSNP50 BeadChip (**50K**; Illumina Inc., 2011b; Illumina Inc., San Diego, CA) was the only chip available for the first 2 yr of genomic evaluations. The high-density BovineHD (high-density) BeadChip (Illumina, 2010; Illumina Inc.) was introduced in January 2010 but is not used routinely due to cost and the small increases in accuracy of genomic evaluations (Harris et al., 2011; VanRaden et al., 2011a). The Illumina Bovine3K BeadChip (**3K**; Illumina Inc., 2011c) was introduced to increase the adoption of genomic testing. Currently, the cost of the 3K test is less than half that of the 50K test, making it financially attractive (Lawlor, 2011). The difference in cost between the 3K and 50K tests has diminished since the introduction of the 3K. Genomic evaluations using genotypes from the 3K became available in September 2010 and were used in the US Department of Agriculture official evaluations in December 2010. Rapid adoption of the technology was evidenced by the number of new genotypes tested monthly, which has averaged 5,000 and is steadily increasing. Unlike the 50K, which is mainly used for AI bulls, bull dams, and other elite animals, the lower cost of the 3K makes genotyping cows more affordable. Cow genotypes can be incorporated into a production system, used as an initial screening tool to determine where to invest in a higher-density test, or used solely for parentage validation. The chemistry used for the 3K (GoldenGate) is different from that of the 50K (Infinium). Single nucleotide polymorphism selection for the initial 50K eliminated approximately

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[2]Corresponding author: George.Wiggans@ars.usda.gov

20% of SNP from use in genomic evaluation because they were deemed to be of poor quality (Wiggans et al., 2009). Although only SNP from the 50K set that met call rate, parent-progeny compatibility, and Hardy-Weinberg equilibrium requirements were considered for the 3K, the different chemistry necessitated evaluating the 3K SNP separately because some SNP failed those requirements on the 3K. A genomic PTA (**GPTA**) for an animal tested on a 3K is calculated by using the 2,683 SNP to impute (VanRaden et al., 2011b) up to the 45,187 SNP used in the evaluation. The imputation process takes advantage of the relatedness of the genotyped population, and the accuracy of the imputed genotype is dependent on the number of genotyped relatives an animal has (Johnston et al., 2011). Including pedigree information in the imputation process also increases accuracy of the GPTA (Moser et al., 2009). In some cases, animals that were previously genotyped using the 3K were re-genotyped on a higher-density chip, in most cases the 50K. Because of the variability in imputation, the GPTA calculated from the 3K can be different from one from the 50K. The objective of the research was to describe the characteristics of the population genotyped using the 3K, SNP selection for the 3K, SNP quality measures, imputation methods to incorporate low-density genotypes into the genomic evaluation system, and comparison of the performance of the 50K and 3K.

MATERIALS AND METHODS

The majority of genotyped animals were Holstein (84.0%), followed by Jersey (15.0%) and Brown Swiss (1.0%). Other breeds such as Ayrshire and Guernsey are not currently genomically evaluated; however, their genotypes can be used for parentage validation and comprise a small (<1%) number of genotyped animals. The 3K is heavily used to test females (92.7% of females are genotyped with the 3K). Prior to the availability of the 3K (August 2010), females accounted for 38.7% of genotyped animals. In the past year, the portion of total genotypes from females across all chip types rose to 59.0%. Males not sponsored by AI organizations are now allowed to be genotyped for use in parentage validation, so the number of males genotyped may increase for this reason. Hair roots was the most popular sample source and accounted for 81.5% of the total samples submitted. The remaining samples were 9.5% nasal swabs, mostly from Canada, 8.6% blood, and <1% tissue and semen samples. Only 6.0% of animals genotyped using the 3K currently have daughter or lactation information. The low cost of the 3K has led to a large increase in the number of females genotyped. However, when a new family is tested, fewer relatives are available to assist with the imputation process. Overall, most of 3K-tested animals had at least 1 genotyped parent; 14.5% of the population had 0 genotyped parents, 60.8% had 1, and 24.7% had 2 genotyped parents. Most genotyped animals (68.2%) were in the high registry status group, which included animals that were ≥95% purebred based on pedigree information submitted by the American Jersey Cattle Association (Reynoldsburg, OH), Brown Swiss Association (Beloit, WI), Holstein Association USA (Brattleboro, VT), or Holstein Canada (Brantford, Ontario, Canada). The low registry status group included all other animals.

The difference in chemistry between the 3K and 50K genotypes causes greater variability in the accuracy of the genotypes. A consequence of this was first observed when a parent-progeny conflict was declared where microsatellite parentage testing had found that the sire did not conflict with the progeny. Investigation showed that the portion of conflicts was less than half the number usually found when the sire is wrong. This led to the designation of a new category of error referred to as unreliable genotype for those genotypes with an intermediate number of conflicts with its genotyped parent. Those genotypes are excluded from genomic evaluation, but the parent is not declared to be in conflict.

A SNP conflict for either sire or dam is determined by counting the number of opposite homozygous genotypes between the parent and progeny (e.g., AA vs. BB). Conflicts can only be detected for SNP on both the 3K and 50K. The expected number of conflicts between a parent and progeny is zero. Conflicts between sire and progeny SNP genotypes were analyzed for 51,637 animals with genotypes that were received through September 2011. The investigation was restricted to sires because of the higher portion of animals with a genotyped sire compared with those with a genotyped dam. Using the definitions from the official evaluation, to determine if a sire qualified, he must not have had more than 0.6% parent-progeny conflicts (to account for genotyping errors). Single nucleotide polymorphism conflicts in the range 0.6 to 4.5% caused the animal's entire genotype to be designated unreliable because the high number of conflicts indicated a problem in genotype quality. When SNP conflicts exceeded 4.5%, a sire conflict was declared. A subset of genotyped animals (n = 27,310) grouped by sex and registry status was analyzed to evaluate the status of the sire and dam relationships upon input of their 3K genotypes into the database. The relationship to the sire or dam was classified as confirmed, in conflict, unable to be determined (not genotyped or unknown parent), or no conflict with an unreliable genotype. Also reported is the number of cases where a suggested sire or dam was proposed. This relationship was declared when the genotype of

Table 1. Sire-progeny SNP conflicts for Bovine3K BeadChip (Illumina Inc., San Diego, CA)-genotyped Holsteins, Jerseys, and Brown Swiss

		SNP conflicts (%)				
Item	n	Mean	SD	Mode	Minimum	Maximum
Confirmed sire	50,327	0.0	0.01	0.0	0.0	0.5
Unreliable genotype	625	0.9	0.12	0.6	0.6	4.5
Sire conflict	685	23.0	5.51	28.0	5.0	43.0

the proposed parent had <0.6% parent-progeny SNP conflicts.

The minor allele frequency (**MAF**) distribution, mean, and mode and the percentage of SNP that were polymorphic for usable 3K SNP (n = 2,683) were determined for each breed using genotypes from 40,947 Holsteins, 7,309 Jerseys, and 297 Brown Swiss. The 3K SNP selection was based on 3 criteria using genotypes of 42,383 animals. Markers selected each had <20% missing genotypes and <2% parent-progeny conflicts (Wiggans et al., 2009), with proportionally stricter limits as MAF decreased (VanRaden et al., 2011c). Last, SNP were rejected if they did not fall within Hardy-Weinberg equilibrium limits. The weighted average across Brown Swiss (*BS*), Holstein (*HO*), and Jersey (*JE*) breeds for heterozygotes was calculated as

$$\frac{\left(NC_{BS}\times HWe_{BS}\right)+\left(NC_{HO}\times HWe_{HO}\right)+\left(NC_{JE}\times HWe_{JE}\right)}{NC_{TOT}},$$

and for minor homozygotes as

$$\frac{\left(NC_{BS}\times HWo_{BS}\right)+\left(NC_{HO}\times HWo_{HO}\right)+\left(NC_{JE}\times HWo_{JE}\right)}{NC_{TOT}},$$

where *NC* is the number of called SNP genotypes for each breed and in total (*TOT*), *HWe* is the ratio of observed heterozygous genotypes to expected heterozygote genotypes, and *HWo* is the ratio of observed minor homozygous genotypes to expected, calculated from the MAF of the evaluated SNP. The acceptance range for heterozygous SNP was 0.3 to 1.3 for heterozygous SNP and 0.1 to 10.0 for homozygous SNP.

Genotypes are submitted monthly by the commercial laboratories of GeneSeek (Lincoln, NE), DNA LandMarks (Saint-Jean-sur-Richelieu, QC, Canada), Genetic Visions (Middleton, WI), and Pfizer Animal Genetics (Kalamazoo, MI), and the quality of SNP genotypes is evaluated routinely. Statistics on 14 genotype data files submitted in September 2011, containing a total of 4,889 sample genotypes, were collected. The SNP that had ≥10% missing, exceeded HW limits as described above, or had ≥2% parent-progeny conflicts were counted. Such SNP are reported to the laboratories for further investigation. For an animal with 2 genotyped parents, a heterozygous genotype also is a conflict if both parents are the same homozygote. This trio test was used when possible to evaluate SNP quality. If an excessive number of SNP were found in any one category, the genotyping laboratories were requested to consider reclustering those SNP before final submission (Wiggans et al., 2011).

The accuracy of imputation was assessed by comparing imputed genotypes with 50K genotypes. The imputation was carried out with the second version of the Fortran program findhap.f90, which differs from version 1 (VanRaden et al., 2011b), by using multiple segment lengths instead of just 1 segment length, including population and pedigree haplotyping in 1 loop rather than 2 separate loops, and checking for haplotypes inherited from genotyped great-grandparents instead of just parents and grandparents. Haplotyping was done in 3 steps beginning with segments of 600 markers, then 200, and then 75. Computing time was 9 h for 109,286 Holsteins using 9.6 gigabytes of memory and 15 processors. The accuracy of imputation was assessed for 2,456 Holsteins and Jerseys that had been genotyped using both 3K and 50K. Their imputed SNP genotypes were compared with their actual 50K genotypes. This population was preferred over a simulation where 3K genotypes were constructed by setting some SNP on 50K genotypes to missing because it reflected the difference in the original SNP calls of the 3K genotype compared with the 50K. The effect of differing numbers of genotyped parents was assessed by creating 3 groups: neither parent genotyped (n = 6), 1 parent genotyped (n = 599), and both parents genotyped (n = 1,851). The numbers of identical genotypes and missing genotypes were counted.

A subset of the above population of animals with both 3K and 50K genotypes, including 2,197 Holsteins and 134 Jerseys, was analyzed to determine the correlation between GPTA based on 3K imputed to 50K and GPTA based on actual 50K for yield (milk, fat, protein, fat percentage, and protein percentage), fitness

Table 2. Initial parentage status by sex and registry status for animals genotyped using the Bovine3K BeadChip (Illumina Inc., San Diego, CA)

	Male		Female		
	Registry status[1]		Registry status		
Parentage status	High	Low	High	Low	Total
Sire					
Confirmed	1,071	559	16,175	6,329	24,134
Conflict	67	28	636	1,145	1,879
Unreliable confirmed	2	6	120	79	207
Nongenotyped	8	20	328	321	677
Unknown	1	0	19	393	413
Alternative suggested	63	28	601	1,239	1,931
Unreliable alternative suggested	1	0	4	17	22
Dam					
Confirmed	830	433	5,496	1,317	8,076
Conflict	36	19	96	29	180
Unreliable confirmed	4	3	48	21	76
Nongenotyped	278	157	11,604	4,412	16,451
Unknown	1	1	34	2,488	2,524
Alternative suggested	38	21	83	59	201
Unreliable alternative suggested	0	0	1	0	1

[1]Registry status high: ≥95% purebred or fully registered animals as submitted by a breed association; registry status low: all others.

(net merit, productive life, daughter pregnancy rate, and SCS) and conformation (final score and stature) traits. Differences in the 3K and 50K GPTA and genomic reliability are also reported. The SNP effects used to calculate the GPTA were calculated based on a predictor population, which included 31,038 Holsteins (14,304 females; 16,734 males) and 6,237 Jerseys (3,886 females; 2,351 males), using methods described by VanRaden et al. (2009).

RESULTS AND DISCUSSION

Sire SNP conflicts for 3K-genotyped animals are presented in Table 1. The mean SNP conflicts for animals with a confirmed sire were 0.0% and ranged from 0.0 to 0.5%. Approximately 2% of genotypes had >0.6% but <4.5% SNP conflicts, the range that defines an unreliable genotype. The mean percentage of SNP conflicts between a conflicting sire and progeny was 23.0%. Because of the high number of SNP that can be compared between a parent and progeny and the fact that a large difference exists in the number of conflicts between a true sire and a conflicting sire, the parentage validation is quite reliable. Some of the animals genotyped at 3K might have previously had their parentage verified by microsatellites; however, because these animals are predominately young and female, most would not have been verified.

Table 2 gives the initial parentage status for 3K genotypes by sex and registry status. For males, sire conflicts were similar between high and low registry status groups and were 5.8 and 4.6%, respectively. For females, a large difference was observed in sire conflicts: females in the high registry status group had 3.7% sire conflicts, whereas females in the low registry status group had 13.9% sire conflicts. For both males and fe-

Table 3. Selection of Bovine3K BeadChip (Illumina Inc., San Diego, CA) SNP and reason for exclusion

Description	Number of SNP
SNP on Bovine3K BeadChip[1]	2,886
Removed due to >20% missing[2]	151
Removed due to ≥2% parent-progeny conflicts	127
Removed due to exceeding Hardy-Weinberg equilibrium limits	5
Not usable on BovineSNP50 BeadChip	2
Usable Bovine3K BeadChip SNP	2,683

[1]Included 2,886 autosomal and X chromosome SNP plus 14 Y SNP for a total of 2,900 SNP.

[2]Eighty-one SNP had both >20% missing and >2% parent-progeny conflicts.

Table 4. Quality statistics for Bovine3K BeadChip (Illumina Inc., San Diego, CA) SNP genotypes from 4,889 samples submitted September 2011

	Number of SNP			
Item	≥2% Parent-progeny conflicts	≥10% Missing	Exceed Hardy-Weinberg limits	Animals per data file
Mean	7	4	10	350
Minimum	0	0	0	96
Maximum	35	14	23	1,326

males, the number of suggested or found sires and dams was similar to the number of sire and dam conflicts. In some cases, the number of suggested parents was higher than the number of conflicts. This occurred when the parent reported on the pedigree was not genotyped or was unknown and, therefore, could not be tested; however, the true parent was genotyped. Proportionally, the number of dam conflicts was similar to that of sire conflicts. However, 72% of males versus 27% of females had a genotyped dam. Within the females, only 0.2% of dams were unknown for animals in the high registry status group, whereas 30.0% of dams were unknown for females in the low registry status group and remained unknown after initial input of the genotype.

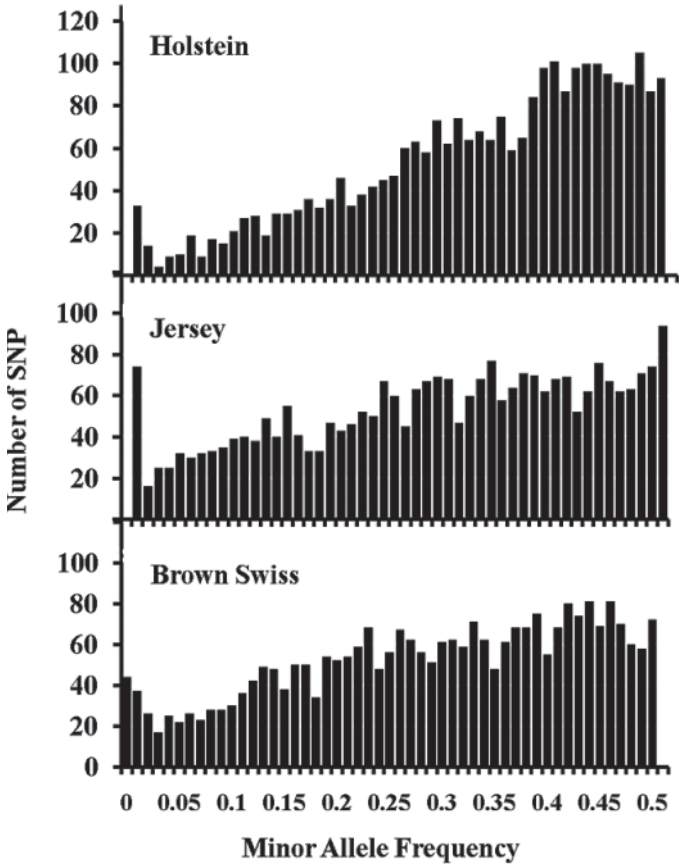

Figure 1. Minor allele frequency distribution of usable Bovine3K BeadChip (Illumina Inc., San Diego, CA) SNP by breed.

The MAF distribution of usable 3K SNP by breed is in Figure 1. For Holsteins, SNP tended to have a higher MAF with a steeper drop off toward rare alleles than observed in Jersey and Brown Swiss. The mean MAF for Holsteins, Jerseys, and Brown Swiss were 0.32, 0.28, and 0.29, respectively. The mode, however, was much higher than the mean for all the breeds: 0.48 for Holstein, 0.50 for Jersey, and a tie for Brown Swiss at 0.44 and 0.46. The percent of SNP that had ≥1% MAF was 94.4% for Holstein, 87.3% for Jersey, and 88.6% for Brown Swiss. The SNP that were chosen for the 3K had high MAF based on 50K genotypes. The monomorphic and rare alleles that do appear on the chip are used for breed identification (Wiggans et al., 2010).

Table 3 reports the number of SNP that were removed from use in genomic evaluation. A total of 2,900 SNP are manufactured on the 3K. Of those, 2,886 are available for use in genomic evaluation; 14 Y SNP are used only for sex determination. One hundred and fifty-one SNP were removed because of low call rate and 127 because of parent-progeny conflicts; 2 were not among those used from the 50K. Eighty-one SNP had both a high number of missing and a high number of parent-progeny conflicts, suggesting a correlation between call rate and accuracy. Last, 5 SNP were removed because they exceeded Hardy-Weinberg equilibrium limits.

Table 4 displays the quality statistics for genotypes submitted in September 2011. Only usable SNP are tested for quality control, so the expected number of SNP with low call rate, high parent-progeny conflicts, or Hardy-Weinberg equilibrium discrepancies is low. The mean number of SNP was <10 for each of the 3 characteristics.

Comparing the common SNP from animals genotyped with both 50K and 3K, 59 SNP genotypes were missing on the 50K on average. Of the called 50K SNP, an additional 13 were missing on the 3K, and the average concordance was 99.75%.

Table 5 gives the percentage of matching SNP genotypes from the comparison of genotypes after impu-

Table 5. Imputation accuracy for 2,456 animals genotyped with both the Bovine3K BeadChip and BovineSNP50 BeadChip (50K; Illumina Inc., San Diego, CA)

Genotyped parents	n	Match[1] (%)	Minimum (%)	Maximum (%)
0	6	93.0	91.0	96.7
1	599	95.2	88.0	99.6
2	1,851	96.7	89.5	100.0

[1]Portion of identical SNP genotypes excluding SNP missing on 50K.

tation from 3K and 50K genotypes. Imputation can make minor changes in 50K genotypes, filling missing SNP genotypes and correcting some inconsistencies. If a SNP genotype was missing in the 50K, it was not included in the calculation. Across SNP, on average, less than 1 SNP genotype was missing from the 50K imputation and 5.4 from the 3K imputation. Animals with 2 genotyped parents had the best imputation rate. As expected, on average, the accuracy of imputation increased with the number of genotyped parents.

The average correlation between GPTA calculated from 3K genotypes that were imputed to 50K and GPTA from actual 50K GPTA (Table 6) averaged 0.959 across traits for Holsteins and ranged from 0.947 to 0.969. The average correlation was slightly higher for Jerseys at 0.963 with a range of 0.954 to 0.978. Reliability of GPTA for yield and conformation traits based on an actual 50K genotype compared with reliability of GPTA from an imputed 3K was higher, on average, by 6 points for Holsteins and 2 to 3 points for Jerseys; corresponding differences for fitness traits were 4 to 5 points for Holsteins and 1 to 2 points for Jerseys. Differences in reliability were similar to simulated results of Chen et al. (2011). The lower reliability for the 3K-based GPTA reflects the accuracy loss due to imputation (Wiggans et al., 2011). A smaller difference in reliability between the 50K and 3K was found for Jerseys, because they were more closely related to the reference population and were less susceptible to imputation errors. The mean difference in the 50K and 3K GPTA across trait was close to zero. The largest difference was in Holstein net merit, which was $11.61 higher for an actual 50K versus an imputed 3K GPTA. Although the mean was close to 0, the range of differences of

Table 6. Comparison of genomic PTA (GPTA) and genomic reliability (GREL) from Bovine3K BeadChip (3K; Illumina Inc., San Diego, CA) genotypes imputed to BovineSNP50 BeadChip (50K; Illumina Inc.) and from actual 50K genotypes for 2,197 Holsteins and 134 Jerseys with both 3K and 50K genotypes

		Difference (50K – 3K)		
Trait[1]	Correlation	GPTA	GREL	Range of difference of GPTA
Holstein				
Milk (kg)	0.965	4.15	6	−295.0 to 319.5
Fat (kg)	0.954	0.03	6	−13.9 to 11.8
Protein (kg)	0.960	0.03	6	−6.4 to 6.5
Fat (%)	0.963	0.00	6	−0.1 to 0.1
Protein (%)	0.961	0.00	6	0.0 to 0.0
Net merit ($)	0.947	11.61	5	−166.0 to 209.0
PL (mo)	0.960	0.29	4	−1.5 to 2.7
DPR (%)	0.954	0.00	5	−0.2 to 0.2
SCS	0.962	−0.01	4	−1.2 to 1.4
Final score	0.956	0.04	5	−0.8 to 0.9
Stature	0.969	−0.01	6	−1.4 to 1.0
Jersey				
Milk (kg)	0.969	−10.6	3	−232.7 to 132.3
Fat (kg)	0.958	−0.49	3	−6.9 to 4.6
Protein (kg)	0.965	−0.47	3	−4.9 to 2.6
Fat (%)	0.967	0.00	3	−0.1 to 0.1
Protein (%)	0.968	0.00	3	0.0 to 0.0
Net merit ($)	0.959	1.34	2	−100.0 to 82.0
PL (mo)	0.958	0.19	1	−0.7 to 1.4
DPR (%)	0.954	0.01	2	−0.1 to 0.1
SCS	0.965	0.01	1	−0.4 to 0.7
Final score	0.978	0.01	2	−0.4 to 0.3
Stature	0.957	−0.03	2	−0.6 to 0.7

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

GPTA indicated that individual animals differed and the magnitude of those differences was proportional to the correlation for each trait, as expected.

CONCLUSIONS

The 3K has been successful in extending genotyping to a larger portion of the cow population. The number of new genotypes received monthly has almost doubled since the introduction of the 3K. All breeds can benefit from genomics through genomic PTA, parentage validation, or both. Single nucleotide polymorphism edits are an important part of quality control to ensure that SNP that might introduce error are removed, particularly where imputation could magnify the effect of an incorrect SNP genotype. The evaluation system has been modified to accommodate the characteristics of the 3K. The 50K is used as the industry standard; however, the 3K has proven to be a useful tool, yielding results of only slightly lower reliability at significantly lower cost. In September 2011, Illumina Inc. improved its low-density chip offering by replacing the 3K with the BovineLD BeadChip (Illumina Inc., 2011a). The BovineLD BeadChip includes 6,909 SNP, uses the same Infinium chemistry as the 50K, and costs the same as the 3K.

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