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The accuracies of DNA-based estimates of genetic merit derived from Angus or multibreed beef cattle training populations[1,2,3]

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ABSTRACT: Several organizations have developed prediction models for molecular breeding values (MBV) for quantitative growth and carcass traits in beef cattle using Bovine SNP50 genotypes and phenotypic or EBV data. Molecular breeding values for Angus cattle have been developed by IGENITY, Pfizer Animal Genetics, and a collaboration between researchers from Iowa State University and the University of Missouri-Columbia (ISU/UMC). The U.S. Meat Animal Research Center (USMARC; Clay Center, NE) has also developed MBV for 16 cattle breeds using 2 multibreed populations, the Germplasm Evaluation (GPE) Program and the 2,000 Bull Project ($2K_{ALL}$), and 2 single breed subpopulations of the 2,000 Bull Project, Angus ($2K_{AN}$) and Hereford ($2K_{HH}$). In this study, these MBV were assessed relative to commercial ranch EBV estimated from the progeny phenotypes of Angus bulls naturally mated in multisire breeding pastures to commercial cows: 121 for USMARC MBV, 99 for ISU/UMC MBV, and 29 for IGENITY and Pfizer MBV (selected based on number of progeny carcass records). Five traits were analyzed: weaning weight (WW), HCW, marbling score (MS), rib-eye muscle area (RE), and, for IGENITY and Pfizer only, feedlot ADG. The average accuracies of MBV across traits were 0.38 ± 0.05 for IGENITY, 0.61 ± 0.12 for Pfizer, 0.46 ± 0.12 for ISU/UMC, 0.16 ± 0.04 for GPE, 0.26 ± 0.05 for $2K_{ALL}$, 0.24 ± 0.04 for $2K_{AN}$, and 0.02 ± 0.12 for $2K_{HH}$. Angus-based MBV (IGENITY, Pfizer, ISU/UMC, and $2K_{AN}$) explained larger proportions of genetic variance in this population than GPE, $2K_{ALL}$, or $2K_{HH}$ MBV for the same traits. In this data set, IGENITY, Pfizer, and ISU/UMC MBV were predictive of realized performance of progeny, and incorporation of that information into national genetic evaluations would be expected to improve EPD accuracy, particularly for young animals.

Key words: beef cattle, genomic selection, marker-assisted selection

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INTRODUCTION

Marker-assisted selection for quantitative traits has evolved rapidly in the past 5 years. Mapping causative mutations has been successful for a number of Mendelian traits, including double muscling (McPherron and Lee, 1997) and deleterious recessive disorders (e.g., Neuropathic Hydrocephalus in Angus cattle; Beever, 2009; Teseling and Parnell, 2011). Although individual loci have been associated with a large proportion of genetic variance for some quantitative traits (e.g., *DGAT1* for milk fat percentage; Grisart et al., 2002), single marker selection has generally proved less useful for such traits. For example, Van Eenennaam et al. (2007) found that commercial marker tests using small marker panels associated with carcass traits were often

[1]Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the USDA and does not imply approval to the exclusion of other products that may be suitable.

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not significantly associated with the target trait in independent validation populations.

Meuwissen et al. (2001) proposed an approach called genomic selection to incorporate genotypic data from a large number of markers evenly distributed throughout the genome into breeding value estimation, by summing individual marker effects, creating molecular breeding values (**MBV**). This approach has been implemented in the dairy industry (VanRaden et al., 2009) using the Illumina Bovine SNP50 Bead Chip assay (**50K SNP**; Illumina, San Diego, CA; Matukumalli et al., 2009).

A number of organizations have developed MBV for quantitative growth and carcass traits in beef cattle based on 50K SNP. Two commercial companies are currently selling DNA test products for use in U.S. Angus cattle, and a collaboration between researchers at Iowa State University and the University of Missouri-Columbia (**ISU/UMC**) and the U.S. Meat Animal Research Center (**USMARC**; Clay Center, NE) have independently developed MBV based on the 50K SNP for use in Angus and multibreed beef cattle, respectively. In this study, the accuracies of these MBV were assessed relative to ranch-based EBV derived from commercial progeny phenotypes of purebred Angus bulls.

MATERIALS AND METHODS

Phenotypic Data

Individual progeny phenotypes were recorded for weaning weight (**WW**), feedlot in-weight (**In-WT**), HCW, marbling score (**MS**), and rib-eye muscle (LM) area (**RE**) from 5,170 Angus-sired progeny produced by 3 commercial ranches (Herds A, B, and C) located in Siskiyou County, CA, and 1 research herd (Herd D) maintained by the Sierra Field Research and Extension Center in Browns Valley, CA. Descriptive statistics for phenotypic records are provided in Table 1.

Weaning weight phenotypes (n = 4,702) were collected on progeny born between January 2009 and January 2011 in all herds and were pooled with those for progeny born between September 2007 and December 2008 in Herd A and September 2006 to December 2008 in Herd D. Weaning weights were adjusted for age at weaning and age of dam in accordance with Beef Improvement Federation standards (BIF, 2010) before analysis. Hair samples were collected on cattle at weaning and extracted DNA was genotyped with the 99 SNP Bovine SeekSire parentage panel (GeneSeek, a Neogen Company, Lincoln, NE). Paternity assignment was conducted using SireMatch software (John Pollak, Cornell University, Ithaca, NY), and sires were assigned if a single bull had no more than 1 genotype exclusion (sire and progeny possessing alternate homozygous genotypes). Electronic radio frequency identification (**RFID**) ear tags were placed on all calves at weaning to facilitate animal identification at feedlot and abattoir entry. Feedlot in-weights were collected for cattle from Herds A through C when they were shipped to Harris Feeding Co. (Coalinga, CA) between fall 2008 and 2011 and were incorporated into the data set based on RFID.

Table 1. Descriptive statistics for phenotypes collected from herds A through D

Trait[1]	Angus sires	Progeny phenotypes	Mean	SD	Minimum	Maximum
WW, kg	129	4,702	230.1	34.6	107.5	391.1
ADG, kg/day	75	1,902	1.44	0.26	0.53	2.87
HCW, kg	136	2,865	336.0	32.1	225.9	454.1
MS	136	2,864	5.83	0.95	3.00	9.33
RE, cm^2	136	2,864	81.4	7.6	23.2	111.0

[1]WW = weaning weight (205-d adjusted, kg); MS = marbling score (3 = traces, 4 = slight, 5 = small, 6 = modest, 7 = moderate, 8 = slightly abundant, and 9 = moderately abundant); RE = rib-eye muscle area.

Carcass records, including phenotypes for HCW, MS, and RE, were collected on cattle harvested between spring 2007 and summer 2011 at Harris Ranch Beef Co. (Selma, CA) for Herds A through C and at the Los Banos Abattoir (Los Banos, CA) for Herd D. Abattoir records were used to integrate live animal and carcass data, but for identity confirmation, meat samples were collected for DNA extraction and genotyping. Genotypes derived from DNA extracted from the hair and meat samples were directly compared to verify animal identification for each carcass record. As BW at slaughter was not measured, feedlot ADG was estimated using rate of BW gain from In-WT to estimated feedlot final BW derived from a function of CW, backfat thickness, and RE.

Genotyping of Angus Sires

The collective group of natural mating sires used in herds A through D are described here as the University of California-Davis (**UCD**) assessment population. The UCD sires (n = 127) of progeny born from 2009 to 2011 were genotyped with the 50K SNP at different times using different versions of the assay (Table 2) as new bulls were added to breeding groups between 2008 and early 2011. Illumina Bovine SNP50 Bead Chip assay genotypes for 95 of the 127 bulls were provided by collaborators at UMC using a noncommercial version of 50K SNP. Genotypes were provided for 55,074 SNP loci for 53 bulls (**UMC-A**) and 53,785 SNP loci for the remaining 42 bulls (**UMC-B**). Missing genotype values for the latter were imputed by UMC using fastPHASE (Scheet and Stephens, 2006). Illumina Bovine SNP50 Bead Chip assay (52,156 loci) genotypes for 6 Angus bulls used via AI at Herd D were provided by USMARC, as

Table 2. Differences between Illumina Bovine SNP50 Bead Chip assay (50K SNP) versions and number of markers imputed to obtain complete genotypes for predicting U.S. Meat Animal Research Center (USMARC) molecular breeding values

50K SNP genotype data sets	UMC-A[1]	UMC-B[1]	USMARC	C manifest
No. of bulls	53	42	6	26
No. of loci				
50,416	X	X	X	X
1,366	X	X	X	
180	X		X	X
159	X		X	
30			X	X
5			X	
Total 52,156	52,121	51,782	52,156	50,626
BEAGLE[2] imputation				
Loci imputed due to 50K SNP version	35	374	0	1,530

[1]UMC-A = first 50K SNP genotype set provided by collaborators at UMC; UMC-B = second 50K SNP genotype set provided by collaborators at UMC; C manifest = Illumina Bovine SNP50 v2

[2]Browning and Browning (2007).

they had been genotyped as part of the USMARC 2,000 Bull Project (Kuehn et al., 2011; Weber et al., 2012). The remaining 26 bulls were genotyped by GeneSeek (a Neogen Company, Lincoln, NE), which provided genotypes for 54,609 loci corresponding to the commercial C manifest (second commercial version of 50K SNP). Genotype datasets were combined based on unique SNP identification and, to generate complete genotypes for predicting USMARC MBV, missing values due to less than 100% call rate and differences in 50K SNP version (Table 2) in the combined dataset were imputed using BEAGLE version 3.3 (Browning and Browning, 2007). The distribution of animals genotyped per locus is provided in Supplementary Table 1 (see online version of the article at http://journalofanimalscience.org). Molecular breeding values derived from these imputed genotypes were compared with those derived from assuming the average genotype for each missing value for the purpose of comparing the effect on accuracy. Genotyping for predicting MBV for commercial products was performed at undisclosed laboratories by the respective companies, IGENITY (Merial, Duluth, GA), using DNA samples anonymously provided through Angus Genetics Inc. (St. Joseph, MO) or Pfizer Animal Genetics (Kalamazoo, MI).

Molecular Breeding Values Tested

The number of bulls tested for each MBV and the number of tested bulls with phenotyped progeny for each trait are presented in Table 3. A brief description of the source and derivation of the DNA test products that were evaluated is provided below.

Table 3. Number of University of California-Davis assessment bulls assayed for each DNA test

	Trait[1]		
DNA test	WW	ADG	HCW, MS, or RE
No. of tested bulls			
ISU/UMC[2]	99		99
MBV_{IG} or MVP[3]	29	29	29
GPE, $2K_{ALL}$, $2K_{AN}$, or $2K_{HH}$[4]	121		121
Subset of tested bulls with progeny			
ISU/UMC[2]	85		80
MBV_{IG} or MVP[3]	28	28	29
GPE, $2K_{ALL}$, $2K_{AN}$, or $2K_{HH}$[4]	96		85
Mean progeny number (range)			
ISU/UMC[2]	44 (1 to 151)		26 (1 to 130)
MBV_{IG} or MVP[3]	73 (21 to 151)	44 (15 to 105)	48 (11 to 130)
GPE, $2K_{ALL}$, $2K_{AN}$, or $2K_{HH}$[4]	42 (1 to 151)		25 (1 to 130)

[1]WW = weaning weight (205-d adjusted, kg); MS = marbling score (3 = traces, 4 = slight, 5 = small, 6 = modest, 7 = moderate, 8 = slightly abundant, and 9 = moderately abundant); RE = rib-eye muscle area.

[2]ISU/UMC = Iowa State University and the University of Missouri-Columbia [derived from genomic BLUP of 3,570 registered Angus bulls and deregressed American Angus Association EPD (Saatchi et al.,2011)].

[3]MBV_{IG} = IGENITY molecular breeding values [derived by IGENITY (Merial, Duluth, GA) using a 384-marker panel]; MVP = molecular value prediction [Illumina Bovine SNP50 Bead Chip assay (50K SNP) prediction derived by Pfizer Animal Genetics (Kalamazoo, MI) using GenSel (Fernando and Garrick, 2009) analysis of between 1,097 and 1,445 Angus cattle].

[4]GPE = Germplasm Evaluation; $2K_{ALL}$ = 2,000 Bull Project; $2K_{AN}$ = 2,000 Bull Project Angus; $2K_{HH}$ = 2,000 Bull Project Hereford. Illumina Bovine SNP50 Bead Chip assay prediction derived using GenSel analysis of the U.S. Meat Animal Research Center Germplasm Evaluation phenotypes, the 2000 Bull Project, Angus subset of the 2000 Bull Project, and the Hereford subset of the 2000 Bull Project, respectively (Weber et al. 2012).

IGENITY

IGENITY markets in the Angus breed a 384-SNP marker panel derived from 50K SNP based on associations with a suite of traits (residual feed intake, ADG, tenderness, MS, percent choice, yield grade, backfat thickness, RE, HCW, yearling weight, heifer pregnancy rate, stayability, maternal calving ease, and docility). The IGENITY MBV (**MBV_{IG}**) values used in this study refer to the estimates of genetic merit produced by IGENITY using only the genotypes and their effects. These are the same values used for incorporation into the Angus Genetics Inc. (**AGI**) genomic-enhanced EPD. The genetic correlations (MacNeil et al., 2010; Northcutt, 2011) used to incorporate MBV_{IG} results into Angus national cattle evaluations as correlated traits are shown in Table 4.

Table 4. Published estimates of accuracies of DNA-based genetic merit prediction equations

		Accuracy (± SE where available)				
		Trait[1]				
DNA test	Reference	WW	ADG	HCW	MS	RE
AN[2]						
MBV_{IG}[3]	Northcutt, 2011	0.45		0.54	0.65	0.58
MVP[3]	Pfizer Technical Summary, 2010[5]	0.53	0.52	0.50	0.49	0.49
	Northcutt, 2011	0.52		0.48	0.57	0.60
$2K_{AN}$[4,6]	Weber et al., 2012	0.05 ± 0.07		0.07 ± 0.06	0.24 ± 0.07	0.24 ± 0.06
MB[2]						
GPE[4,7]	Weber et al., 2012	0.12 ± 0.05		0.35 ± 0.10	0.23 ± 0.06	0.25 ± 0.07
$2K_{ALL}$[4,8]	Weber et al., 2012	0.24 ± 0.04		0.12 ± 0.05	0.23 ± 0.04	0.35 ± 0.05
HH[2]						
$2K_{HH}$[4,9]	Weber et al.,2012	0.24 ± 0.04			0.01 ± 0.04	0.22 ± 0.04

[1]WW = weaning weight; MS = marbling score; RE = rib-eye muscle area.

[2]AN = Angus; MB = multibreed; HH = Hereford.

[3]MBV_{IG} = IGENITY molecular breeding values [derived by IGENITY (Merial, Duluth, GA) using a 384-marker panel]; MVP = molecular value prediction [Illumina Bovine SNP50 Bead Chip assay (50K SNP) prediction derived by Pfizer Animal Genetics (Kalamazoo, MI) using GenSel (Fernando and Garrick, 2009) analysis of between 1,097 and 1,445Angus cattle].

[4]GPE = Germplasm Evaluation; $2K_{ALL}$ = 2,000 Bull Project; $2K_{AN}$ = 2,000 Bull Project Angus; $2K_{HH}$ = 2,000 Bull Project Hereford. Illumina Bovine SNP50 Bead Chip assay prediction derived using GenSel analysis of the U.S. Meat Animal Research Center Germplasm Evaluation phenotypes, the 2000 Bull Project, Angus subset of the 2000 Bull Project, and the Hereford subset of the 2000 Bull Project, respectively(Weber et al. 2012).

[5]50K Technical Summary (Pfizer Animal Health, 2010), accuracies estimated in yearling bull external assessment populations.

[6]Accuracy estimated in animals with at least 50% Angus breed composition in GPE Cycle VII and continuously sampled GPE.

[7]Accuracy estimated in Angus animals of 2000 Bull Project.

[8]Accuracy estimated in animals with at least 25% Angus breed composition in GPE Cycle VII and continuously sampled GPE.

[9]Accuracy estimated in GPE Cycle VII and continuously sampled GPE.

Pfizer Animal Genetics Molecular Value Predictions

Pfizer Animal Genetics markets a 50K SNP-based product that includes molecular value predictions (**MVP**) for 13 traits (birth weight, calving ease direct, WW, DMI, net feed intake, HCW, backfat thickness, RE, MS, tenderness, maternal calving ease, milk or maternal component of WW, and an index, $MVP feedlot). Pfizer MVP are genomic predictions derived using an unspecified GenSel model (Fernando and Garrick, 2009). The complete dataset used for training and internal evaluation included up to 5,101 Angus cattle records, with between 1,097 and 1,445 records used for training, depending on trait (Pfizer Animal Genetics, 2010). A technical summary including methodology and estimates of test accuracy was released by Pfizer Animal Genetics, and accuracies estimated by Pfizer Animal Genetics in internal yearling bull assessment populations are provided in Table 4. The genetic correlations used to incorporate these MVP into the Angus national cattle evaluation (Northcutt, 2011) are also in Table 4.

Iowa State University/University of Missouri-Columbia

A population of 3,570 registered Angus bulls with American Angus Association (**AAA**; St. Joseph, MO) pedigree and EPD data were genotyped using the 50K SNP panel at UMC (Saatchi et al., 2011). Expected progeny differences were deregressed according to Garrick et al. (2009), with appropriate residual weights applied. This dataset represents a population of animals spread over a 50-yr period (about 10 generations) during which selection had been applied to the breed. Quality control was performed to remove SNP with call rates of less than 90%, minor allele frequencies of less than 1%, or significant deviations from Hardy-Weinberg equilibrium ($P < 0.001$ genomewide) resulting in a total of 45,082 SNP used in the genomic selection analyses. All missing genotype values were imputed with fastPHASE (Scheet and Stephens, 2006). Molecular breeding values for 16 traits (birth weight, WW, milk or the maternal component of WW, yearling weight, yearling height, HCW, MS, RE, backfat thickness, mature weight, mature height, scrotal circumference, calving ease direct, maternal calving ease, heifer pregnancy rate, and docility) were derived using a genomic relationship matrix described by VanRaden [2008; genomic BLUP (**GBLUP**)]. Estimated accuracies for individual MBV were derived from inversion of the GBLUP coefficient matrix in the mixed model equations (Henderson, 1974) using a genomic relationship matrix (Nejati-Javaremi et al., 1997).

U.S. Meat Animal Research Center Germplasm Evaluation Program

United States Meat Animal Research Center Germplasm Evaluation (**GPE**) Program MBV were developed as described in Weber et al. (2012). Briefly, the training population included 3,358 cattle from Cycle VII of the GPE and the current continuously sampled GPE (2007 to 2008), consisting of F_1 and $F_1 \times F_1$ (F_1^2) crosses and backcrosses of 16 breeds: Angus, Red Angus, Brahman, Braunvieh, ChiAngus, Charolais, Gelbvieh, Hereford, Limousin, Maine-Anjou, MARCII (one-quarter Angus, one-quarter Hereford, one-quarter Gelbvieh, and one-quarter Simmental), MARCIII (one-quarter Angus, one-quarter Hereford, one-quarter Pinzgauer, and one-quarter Red Poll), Salers, Santa Gertrudis, Shorthorn, and Simmental. These cattle were genotyped using 50K SNP, and 52,156 SNP marker loci were used for genomic prediction analyses. The MBV were derived from phenotypic data adjusted for age, sex, contemporary group, breed, and heterosis for 6 traits (birth weight, WW, yearling weight, HCW, MS, and RE) using the BayesCπ model in GenSel (Fernando and Garrick, 2009; Habier et al., 2011).

U.S. Meat Animal Research Center 2,000 Bull Project Evaluation

The 2,000 Bull Project (**$2K_{ALL}$**) was developed by USMARC to evaluate genetic merit in 16 of the most widely used beef cattle breeds, using data from approximately 2,000 influential bulls submitted by participating breed associations. Its aim was to provide across-breed genomic predictions to the participating breed associations, and this was accomplished in 2011. Development of genomic prediction equations from these data was described by Weber et al. (2012). Briefly, the training population for $2K_{ALL}$ included EPD for 2,026 bulls from 13 breeds available at the time of the analysis: Angus, Red Angus, Beefmaster, Brangus, Brahman, Braunvieh, Charolais, Gelbvieh, Hereford, Limousin, Maine-Anjou, Shorthorn, and Simmental. Although the $2K_{ALL}$ was not designated for this purpose, subsets of Angus (n = 373) or Hereford bulls (n = 463) were used as training populations to produce prediction equations based on the 2,000 Bull Project Angus (**$2K_{AN}$**) or 2,000 Bull Project Hereford (**$2K_{HH}$**) breeds, respectively, to examine the efficacy of training in single breeds, using the largest single breeds available in $2K_{ALL}$. The American Hereford Association does not provide EPD for CW; therefore, no $2K_{HH}$ MBV were produced for this trait. The EPD were deregressed according to Garrick et al. (2009). The MBV prediction equations were derived using the Bayes Cπ model in GenSel (Fernando and Garrick, 2009; Habier et al., 2011). Weber et al. (2012) presented an analysis that excluded from $2K_{ALL}$ the 234 sires with progeny represented in the GPE population to minimize the genetic relationship between the population used to develop MBV ($2K_{ALL}$) and the population used for validation (GPE). The prediction equations used here were derived using the full $2K_{ALL}$ population including records for these 234 GPE sires and are those released to breed associations by USMARC in summer 2011.

Known Relationships between Training and Assessment Populations

Many bulls used for natural mating are the offspring of widely used AI sires. If those AI sires had been part of the training populations used to derive MBV, the predictive accuracies in their sons will be much greater than when validation is undertaken in distant relatives (Saatchi et al., 2011). Accordingly, the relationships between the bulls in the UCD assessment population and the bulls known to be used in development of a particular MBV were assessed. The ISU/UMC training population included bulls in the UCD assessment population and, in many cases, the sires of these bulls as well (Figure 1). However, none of the UCD assessment bulls had commercial progeny records sent to the AAA for inclusion in national evaluation, so the data available on these animals in the ISU/UMC training population included only ancestral information plus the phenotypic records of the bulls where available. Therefore, although their genotypes were present, these bulls contributed little information to the ISU/UMC analysis. In comparison, no members of the UCD assessment population were present in $2K_{AN}$ (and by extension $2K_{ALL}$); however, many sires of these bulls were included (Figure 1). The GPE training population was the least related to the UCD assessment population, with no UCD assessment bulls or their sires present. There were 10 bulls present in the $2K_{AN}$ population that were sires of both GPE and UCD assessment bulls; therefore, half-siblings are the greatest known relationship between the GPE and UCD assessment populations. It should be noted that the lack of information about the IGENITY and Pfizer training populations does not preclude the presence of close genetic relationships between them and the UCD assessment population.

Sire Breeding Value Estimation

The EPD and 4-generation pedigrees were obtained for all registered bulls from the AAA.

Single-trait genetic evaluations were conducted to generate ranch-based EBV using progeny phenotypic records and a relationship matrix based upon the 4-generation pedigree provided by AAA for the registered bulls that sired the commercial progeny. ASReml version 3 software (VSN International, Hemel

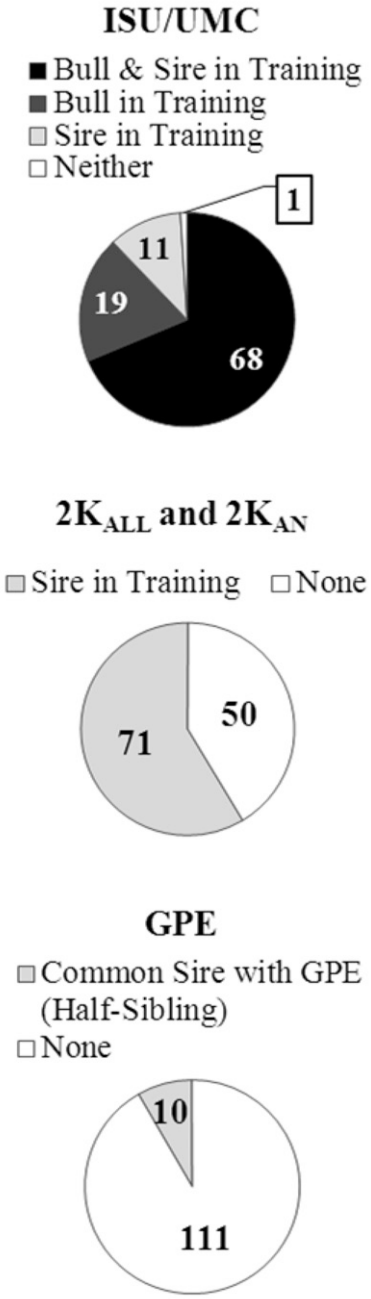

Figure 1. The number of bulls in the University of California-Davis (UCD) assessment population related to the training populations for Iowa State University and the University of Missouri-Columbia (ISU/UMC), 2,000 Bull Project ($2K_{ALL}$)/2,000 Bull Project Angus ($2K_{AN}$), or Germplasm Evaluation (GPE) Program through self and sire (black), self only (dark gray), sire only (medium gray), half-sibling (light gray), or neither (white).

Hempstead, UK; Gilmour et al., 2009) was used for all genetic evaluations, including estimation of variance components.

Analysis of WW was carried out using a maternal effects animal model following Quaas and Pollak (1980):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Z_m u_m} + \mathbf{e}, \qquad [1]$$

in which **y** is a vector of WW records preadjusted for days of age at weaning and age of dam (classified as 2, 3, 4, 5 to 10, and 11+ yr of age); **X**, **Z**, and $\mathbf{Z_m}$ are incidence matrices relating observations to fixed effects, direct genetic effects, and maternal effects; **b**, **u**, and $\mathbf{u_m}$ are vectors of fixed effects, direct additive genetic effects, and maternal effects; and **e** is a vector of residuals. Additive genetic, nonadditive genetic, and nongenetic maternal effects could not be partitioned due to a scarcity of dam pedigree information. Analyses of ADG, CW, MS, and RE were performed using a univariate animal model that omits the term $\mathbf{Z_m u_m}$ in Eq. [1]. Fixed effects associated with each trait were contemporary group for all traits, age for carcass traits, and sex for WW, HCW, and MS. Contemporary group was defined as herd, year, and season for WW; herd, year, season, and feedlot lot for ADG; and herd, year, season, and harvest lot for HCW, MS, and RE. Fixed effects were tested for significance ($P < 0.01$) as computed by ASReml from incremental Wald *F* statistics (Gilmour et al., 2009).

Derivation of Molecular Breeding Value Accuracy

In this context, accuracy is the genetic correlation estimated between the MBV and the ranch-based estimate of the genetic merit of the bulls as proposed by Kachman (2008). The proportion of genetic variance accounted for by the MBV was estimated as the square of the estimated genetic correlation (accuracy) as derived by Thallman et al. (2009). Furthermore, a regression analysis was performed of progeny means corrected for fixed effects on MBV.

For WW, Eq. [1] was expanded to accommodate MBV as follows:

$$\begin{bmatrix} y \\ MBV \end{bmatrix} = \begin{bmatrix} X_y & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} b_y \\ \mu_{MBV} \end{bmatrix} + \begin{bmatrix} Z_y & 0 \\ 0 & Z_{MBV} \end{bmatrix} \begin{bmatrix} u_y \\ u_{MBV} \end{bmatrix} + Z_m u_m + \begin{bmatrix} e \\ \varepsilon_{MBV} \end{bmatrix} \qquad [2]$$

in which **MBV** is a vector of MBV, **1** is a vector of ones, $\mathbf{Z_{MBV}}$ is an incidence matrix relating observations on the tested bulls to marker breeding values, $\boldsymbol{\mu}_{\mathbf{MBV}}$ and $\mathbf{u_{MBV}}$ are the MBV mean and the marker breeding values, and $\boldsymbol{\varepsilon}_{\mathbf{MBV}}$ is a vector of the MBV residuals. The variance-covariance structure is defined as

$$\text{var}\begin{bmatrix} \mathbf{u}_y \\ \mathbf{u}_{MBV} \\ \mathbf{u}_m \\ \mathbf{e} \\ \boldsymbol{\varepsilon}_{MBV} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{u_y} & \mathbf{A}\sigma_{u_y u_{MBV}} & \mathbf{A}\sigma_{u_y u_m} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}\sigma_{u_y u_{MBV}} & \mathbf{A}\sigma^2_{u_{MBV}} & \mathbf{A}\sigma_{u_{MBV} u_m} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}\sigma_{u_y u_m} & \mathbf{A}\sigma_{u_{MBV} u_m} & \mathbf{A}\sigma^2_{u_m} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma^2_e & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma^2_{\varepsilon_{MBV}} \end{bmatrix} \qquad [3]$$

in which **A** is the numerator relationship matrix including 4-generation Angus pedigree for sires, **I** is an identity matrix, σ_{uy}^2 is the additive genetic variance of WW direct, σ_{uMBV}^2 is the additive genetic variance of the WW MBV,

σ_{um}^2 is the variance of the maternal effects for WW, σ_{uyuMBV} is the additive genetic covariance between WW and MBV, σ_{uyum} is the covariance between WW direct and maternal effects, σ_{uMBVum} is the covariance between WW MBV and maternal effects, σ_e^2 is the residual variance for WW, and $\sigma_{\varepsilon MBV}^2$ is residual variance for WW MBV. For all other traits, the same model was used, with $\mathbf{Z_m u_m}$ excluded. The genetic correlation between MBV was estimated using a model and variance-covariance structure similar to Eq. [2], excluding $\mathbf{Z_m u_m}$, in which y is redefined as a correlated MBV with a single fixed effect (the MBV mean). For comparison, the genetic correlations between AAA EPD traits and ranch phenotypes were estimated using the same model after deregression of the EPD and using appropriate residual weights (Garrick et al., 2009; Weber et al., 2012).

The genotypes provided by USMARC corresponding to 6 bulls used via AI in Herd D and their AAA EPD were used directly in at least 2 of the training populations for MBV evaluated in this study. The accuracies corresponding to the AAA EPD of these bulls were very high, ranging from >0.99 for WW, 0.84 to 0.97 for CW, 0.87 to 0.97 for MS, and 0.88 to 0.98 for RE. As the focus of this study was to determine MBV accuracy for herd bulls with lower accuracy AAA EPD typical of yearling bulls, the MBV for these bulls were not included in the data used to estimate the MBV accuracy in the UCD assessment population but were included in analyses used to determine the correlation between MBV. The remaining genotyped Angus bulls (n = 121) represent the UCD assessment population used to evaluate MBV accuracy in this population.

RESULTS

Collection of Progeny Phenotypes

The DNA genotyping of both live progeny at weaning and their resultant carcasses at grading was necessary to verify animal–animal relationships for the genetic evaluation of growth and carcass traits and provided the opportunity to assess the average error rate in live animal to carcass matching in harvest records. In 5 consecutive cohorts produced by Herd A, we found carcass misidentification rates per cohort ranging from 3.5 to 19.3%, with an average misidentification rate of 10.8%.

Estimation of Ranch-Based Breeding Values

Estimates of variance components, trait heritabilities, and distributions of the accuracies of resulting EBV for tested bulls are presented in Table 5. Molecular breeding value heritabilities were consistently approximately 1. Rather than using fixed variance components provided by AGI and estimated using data in the AAA database, variance components used in the genetic evaluation of commercial ranch data were estimated to reflect this environment and the conditions under which phenotypes were collected as they influence trait definition. Data available on the dams of terminal progeny in commercial ranch evaluation is often scarce, as was the case here. There were 1,393 dams that produced 2 or more calves; however, maternal grandsire was known only for replacement heifers kept from the start of this trial (n = 117). The limited data available on dams did not allow maternal genetic and permanent environmental effects to be separated as is generally modeled in beef cattle evaluation (BIF, 2010), and although direct and maternal variances and covariances were estimable, standard errors were large. The covariance between direct and maternal effects was within a standard error of 0 rather than negative as typically found in beef cattle evaluation (Dodenhoff et al., 1999). An unusual feature of the results of the analyses was the high heritability of feedlot ADG, due to a large additive genetic variance relative to literature estimates (Arthur et al., 2001), al-

Table 5. Variance component estimates from ranch-based breeding value estimation and mean accuracy of ranch-based and American Angus Association (AAA) EPD for tested bulls

	Trait[2]				
Parameter[1]	WW	ADG	HCW	MS	RE
$\sigma_A^2 \pm$ SE	137.0 ± 31.0	0.0138 ± 0.004	321.5 ± 59.10	0.384 ± 0.05	17.4 ± 3.10
$\sigma_{AM} \pm$ SE	41.1 ± 58.1				
$\sigma_M^2 \pm$ SE	174.1 ± 60.8				
$\sigma_E^2 \pm$ SE	411.9 ± 22.1	0.0379 ± 0.0034	496.3 ± 47.6	0.398 ± 0.06	32.2 ± 2.6
$h_A^2 \pm$ SE	0.179 ± 0.04	0.267 ± 0.07	0.393 ± 0.07	0.509 ± 0.07	0.350 ± 0.06
Mean accuracy of sire EBV ± SE (minimum to maximum)	0.63 ± 0.02	0.54 ± 0.06	0.61 ± 0.02	0.63 ± 0.02	0.59 ± 0.02
	(0.11 to 0.90)	(0.08 to 0.88)	(0.10 to 0.93)	(0.11 to 0.94)	(0.11 to 0.92)
Mean accuracy of AAA EPD ± SE (minimum to maximum)	0.36 ± 0.01		0.29 ± 0.01	0.36 ± 0.01	0.41 ± 0.01
	(0.10 to 0.56)		(0.10 to 0.44)	(0.10 to 0.48)	(0.10 to 0.52)

[1]σ_A^2 = direct additive genetic variance; σ_{AM} = direct-maternal genetic covariance; σ_M^2 = maternal genetic variance; σ_E^2 = residual variance; h_A^2 = heritability.
[2]WW = weaning weight (205-d adjusted, kg^2); ADG = $(kg/day)^2$; HCW = kg^2; MS = marbling score ($units^2$), RE = rib-eye muscle area (cm^4).

though as feedlot final weight was estimated, these are slightly different traits. The additive genetic variance and heritability of MS were greater than reported by AAA (MacNeil and Northcutt, 2008), as was the heritability of RE although this was due to a small estimate of residual variance rather than a large estimate of additive genetic variance. This may be at least partially due to having corrected misidentification errors by genotyping carcasses at grading.

Molecular Breeding Value Accuracy

The accuracies of the MBV, as estimated by the additive genetic correlation between MBV and ranch performance, were variable between tests and traits, and large SE were observed for most estimates (Table 6). The ISU/UMC, MBV_{IG}, and MVP tests were the more accurate, explaining relatively large proportions of the genetic variance in WW (8 to 62%), CW (7 to 8%), MS (19 to 46%), and RE (9 to 41%) with the least accurately predicted trait being CW. Angus-trained MBV were more accurate than AAA EPD, on average. High correlations were also observed between MBV for these traits (Supplementary Table 2A and 2C through 2E; see online version of the article at http://journalofanimalscience.org), with ISU/UMC and MVP being highly correlated (r = 0.64 to 0.77) for all traits. Nearly all MBV underestimated change in progeny mean relative to change in MBV, with regression coefficients approaching one for the more accurate MBV (Supplementary Table 3; see online version of the article at http://journalofanimalscience.org). Realized accuracies for ADG were relatively low as was the correlation between ADG test results although care should be taken not to over-interpret these results due to the small size of that data set. The $2K_{AN}$ MBV (trained on about 10% as many AI sires as the ISU/UMC predictions) were by far the least among the Angus-trained predictions. They perhaps should not be considered in the average for that category of predictions, as the $2K_{ALL}$ was neither designed nor intended to be used for single breed prediction. The most important conclusion to be reached from this training on a subset of the data is that 373 AI sires is an insufficient training resource for genomic prediction. The GPE and $2K_{ALL}$ MBV were less accurate, with one-half the accuracy of Angus-trained MBV, on average. The GPE and $2K_{ALL}$ MBV were lowly to moderately correlated with each other and the other Angus-trained MBV. The $2K_{HH}$ MBV had the lowest average accuracies in this population. Although they were trained on slightly more AI sires than the $2K_{AN}$ MBV, they were far less effective predictions.

DISCUSSION

The carcass misidentification rate of 10.8% is similar to the 10% value reported by Thallman et al. (2003) in the carcass data collected for the Carcass Merit Project. We observed that misidentifications were primarily due

Table 6. The DNA test accuracy relative to ranch-based breeding value

		Accuracy ± SE						
		Trait[2]						
DNA test[1]		WW-d	WW-m	ADG	HCW	MS	RE	Average[3]
AAA data[4]		0.15 ± 0.08			0.14 ± 0.19	0.60 ± 0.20	0.53 ± 0.13	0.36 ± 0.14
AN	Average	0.45 ± 0.14		0.15 ± 0.26	0.25 ± 0.04	0.50 ± 0.12	0.49 ± 0.12	0.42 ± 0.05
ISU/UMC	Expected[5]	0.62 ± 0.005			0.56 ± 0.005	0.51 ± 0.008	0.54 ± 0.008	0.56 ± 0.03
	Realized[6]	0.29 ± 0.14	0.96 ± 0.43		0.27 ± 0.14	0.64 ± 0.10	0.64 ± 0.10	0.46 ± 0.12
MBV_{IG}	Realized	0.47 ± 0.20	–0.36 ± 0.79	0.33 ± 0.22	0.29 ± 0.23	0.44 ± 0.18	0.30 ± 0.21	0.38 ± 0.05
MVP	Realized	0.79 ± 0.10	–0.84 ± 0.43	–0.03 ± 0.24	0.29 ± 0.22	0.68 ± 0.12	0.68 ± 0.13	0.61 ± 0.12
$2K_{AN}$	Realized	0.24 ± 0.13	0.56 ± 0.44		0.15 ± 0.14	0.24 ± 0.12	0.32 ± 0.13	0.24 ± 0.04
MB	Average	0.16 ± 0.14			0.19	0.25 ± 0.18	0.19 ± 0.03	0.20 ± 0.03
GPE	Realized	0.06 ± 0.18	–0.68 ± 0.66		0.19 ± 0.15	0.18 ± 0.17	0.21 ± 0.13	0.16 ± 0.04
$2K_{ALL}$ HH	Realized	0.26 ± 0.13	0.40 ± 0.49		0.19 ± 0.14	0.37 ± 0.12	0.17 ± 0.14	0.26 ± 0.05
$2K_{HH}$	Realized	0.01 ± 0.17	1.04 ± 0.65			–0.14 ± 0.14	0.20 ± 0.13	0.02 ± 0.12

[1]AAA = American Angus Association; AN = Angus; ISU/UMC = Iowa State University and the University of Missouri-Columbia; MBV_{IG} = IGENITY molecular breeding values; MVP = molecular value prediction; $2K_{AN}$ = 2,000 Bull Project Angus; MB = ; GPE = Germplasm Evaluation; $2K_{ALL}$ = 2,000 Bull Project; HH = Hereford; $2K_{HH}$ = 2,000 Bull Project Hereford.

[2]WW-d = weaning weight direct; WW-m = weaning weight maternal; MS = marbling score; RE = rib-eye muscle area.

[3]Average across traits excluding ADG.

[4]Derived from EPD for registered bulls and then deregressed and weighted to account for differences in EPD accuracy.

[5]The average ± SE of genomic BLUP accuracy of 87 of the 99 sires with ISU/UMC molecular breeding values (MBV), calculated by the direct inversion of the linear mixed model equations using the genomic relationship matrix.

[6]The additive genetic correlation ± SE, estimated in a multivariate genetic model, between MBV and phenotypes.

to minor errors in animal order at slaughter with misidentification rates in particular harvests less than 10% due to incorrect ordering of groups of 2 or 3 animals whereas those harvests with greater than 10% errors were due to rail-outs, leading to a sequence of carcass records offset by 1 or 2 from the correct identification. Van Vleck (1970) determined that bias in variance component estimation due to misidentified records could reduce apparent genetic progress by up to 31% depending on the proportion misidentified, and Geldermann et al. (1986) demonstrated reductions in estimated heritability in experimental results for dairy cattle of up to 22%. Performing DNA genotyping of progeny meat samples in addition to hair samples collected earlier in life was a critical step to minimize bias in this analysis due to incorrect carcass to sire and live animal reconciliation.

The accuracy estimates of the IGENITY and Pfizer DNA test products derived in this study generally agreed with Northcutt (2011) based on an analysis of genotyped animals in the AAA phenotypic database, despite the large SE associated with the small sample size in our study. Although little is known regarding the genetic relationship between the training populations used to develop the commercial tests and the UCD assessment population, the accuracies observed here suggest that there is likely a high degree of genetic relationship between animals in the training and the UCD assessment populations. The ISU/UMC MBV accuracies were high and of similar scale to Pfizer MVP for carcass traits, with somewhat smaller SE due to the greater number of bulls evaluated with this test. Using ISU/UMC MBV as a correlated trait, the accuracy of ranch-based EBV improved for bulls without progeny but provided little improvement if progeny data were available.

The degree of relationship between the discovery or training population used to develop genotype-based prediction equations and the assessment population is a primary determinant in the observed accuracy of genomic breeding values (Habier et al., 2007, 2010). As the ISU/UMC and USMARC MBV were performed by researchers at collaborating institutions, information was available regarding pedigree relationships among the ISU/UMC, $2K_{ALL}$, and GPE populations and the UCD assessment population. Specifically, it was known which bulls were used directly for both training and assessment and whether the sires of the assessed animals were present in the training populations. In terms of known pedigree relationships between the training and UCD assessment population, the training populations can be ranked in order of most to least related: ISU/UMC, $2K_{ALL}$, and GPE. Animal and pedigree information are not published for the IGENITY and Pfizer training populations. However, as the herd bulls used in this study were sourced from the Angus seedstock sector, their sires were often influential AI sires with high accuracy EBV, and some of these AI bulls were likely selected for inclusion in training for IGENITY and Pfizer tests.

As the ISU/UMC MBV were developed using approaches previously reported in the dairy industry, it is of interest to compare the performance of these MBV to those derived from training populations of similar scale using Holstein cattle. In VanRaden et al. (2009), training genomic predictions on the records of 3,576 Holstein bulls with predicted transmitting abilitiy and genotypic data (38,416 SNP after quality control) resulted in accuracies of linear prediction (comparable to genomic relationship matrix approach) with first use ranging from 0.57 to 0.83 (mean 0.71) for 26 traits and the index Net Merit (mean heritability 0.25 ranging from 0.04 to 0.50). The ISU/UMC MBV were trained on a similar sized population of registered Angus bulls (3,570) but yielded decreased average expected accuracies (mean = 0.56; range by trait = 0.51 to 0.62 and by animal = 0.28 to 0.71; Table 6) and realized accuracies (mean 0.46; Table 6) for similar heritability traits in UCD assessment bulls. This is likely due to the reduced average accuracy of estimated genetic merits for beef compared with dairy cattle in the training populations and the relationship between the training and assessment populations. For example, the 6 AI bulls excluded from the UCD assessment population, which had greater accuracy EPD and greater genetic relationships to the training set, had greater expected accuracies (data not shown).

Another consideration is that the progeny used to estimate breeding values for the UCD assessment population were not purebred Angus in all cases due to the mixed breed composition of their dams. Although it has been shown that MBV can be developed specifically to select purebreds for performance in crossbred or admixed populations (Dekkers, 2007; Toosi et al., 2010), it is likely that for Angus-trained MBV, the greatest accuracies would be observed in a purebred Angus population. Non-Angus breeds contribute alternative haplotypes, influencing the extent and possibly the direction of marker–QTL linkage disequilibrium in the progeny population, and are also more genetically distant, with a reduced average relationship to an Angus-based training population. However, this study was designed to evaluate genomic prediction only of the contribution of Angus sires to the commercial progeny; therefore, the breed composition of the dams is relevant only to the extent of how the Angus haplotypes contributed by the sires would interact with the non-Angus haplotypes of the dams on both an intralocus (dominance) and interlocus (epistasis) basis.

Accuracies for GPE, $2K_{ALL}$, and $2K_{HH}$ MBV were less than those observed for Angus-trained MBV but comparable to those observed in other multibreed genomic prediction studies. In a simulation study modeled

on beef cattle, Kizilkaya et al. (2010) predicted multibreed-trained MBV to have accuracies ranging from 0.20 to 0.39 for 50 to 500 QTL underlying a trait of interest with a heritability of 0.5 for which no causative mutations were present on the genotyping panel. In the same study, Angus-trained MBV were expected to have accuracies of 0.39 to 0.51 given similar assumptions. Comparing our results to others for feedlot ADG, Mujibi et al. (2011) reported average genetic correlations of 0.22 and 0.37 for MBV derived using Bayes B and random regression models and trained on 721 crossbred beef steers. Harris et al. (2008) reported that Holstein-trained predictions were not effective in Jersey cattle, and Hayes et al. (2009) found realized accuracies from across-breed GBLUP with Holstein and Jersey breeds to be less than expected, but prediction of Jersey from a combined Holstein and Jersey reference population improved accuracies by up to 13%. Pryce et al. (2011) found genomic prediction accuracy to be greatest within breed in Holstein (**HO**), Jersey (**JE**), and Fleckvieh (**FLV**) but also noted that training in 2 breeds (**FLV+JE**) to predict a third (HO) improved genomic prediction accuracy from 0.22 to 0.42 relative to training in 1 breed (FLV) to predict another (HO).

In Weber et al. (2012), the accuracies of MBV trained in the USMARC GPE or 1,834 bulls of 13 breeds (including the 373 Angus and 143 Red Angus) and validated in the Angus bulls of the 2,000 Bull Project and GPE with at least 25% Angus breed composition, respectively, ranged from 0.12 to 0.35. In this study, the accuracies of the $2K_{ALL}$ MBV trained on 373 Angus bulls were roughly similar to those reported in Weber et al. (2012). This suggests that inclusion of bulls of different breeds (including Red Angus) neither helped nor detracted from the prediction accuracy of $2K_{ALL}$. However, this conclusion must be tempered by the condition that the training was done with models that considered the effects of SNP alleles on the trait of interest to be identical regardless of breed origin of the SNP. It is possible that SNP effects that are estimated as breed-specific deviations from overall effects and in which the variance is estimated from all breeds (so that other breeds contribute more to which genes have an effect than to the phase between markers and functional polymorphisms) may be much more effective. Furthermore, analyses based on haplotypes (especially with marker density greater than the 50K SNP) may also make contributions from other breeds to training much more effective. Therefore, although more sophisticated statistical models will be required to realize their benefits, multibreed and crossbred training populations will likely contribute more to genomic prediction than the results of this project suggest on the surface. As a practical matter, for most breeds of beef cattle, single breed training on purebred populations will be severely limited by the lack of availability of high accuracy AI sires.

A factor that may be confounding the findings of the current study regarding the $2K_{ALL}$ and GPE MBV is the imputation of genotypes using BEAGLE. Some loci with missing values may have a sufficient contribution to the variance explained by the $2K_{ALL}$ and GPE prediction equations that the choice of method used to fill those missing values may have been important. Although BEAGLE has been used to impute both sporadic missing values from unrelated individuals (Browning and Browning, 2007; Zhang et al., 2010) and to impute high density genotypes for low density genotypes of dairy cattle with high density genotyped relatives (Johnson et al., 2011), the accuracy of imputation of up to several thousand SNP genotypes per animal due to the different versions of the 50K SNP used to genotype these cattle has not been evaluated. In this dataset, the largest difference between 50K SNP versions were approximately 1,400 loci present in the USMARC and UMC (A and B) versions that were not present in the C manifest (Table 2). However, the SNP imputed due to differences between 50K SNP versions composed at most 3% of the MBV variance, and including missing values, 96.5% of loci in the USMARC 50K SNP version were genotyped for at least 80% of animals (Supplementary Table 1; see online version of the article at http://journalofanimalscience.org). Although the accuracy of imputation is not known, the average difference in MBV accuracy relative to assuming the average genotype for all missing values was small (data not shown). This will be a more significant problem in small datasets, for which the power to predict haplotypes is limited.

If training populations are confidential and assessment is performed independently, as in external validations of commercial genetic test products (Van Eenennaam et al., 2007; Johnston, 2010), it is not possible to directly determine the expected genomic prediction accuracy due to genetic relationship. This was the case for the IGENITY MBV and Pfizer MVP presented in this study. When training is performed by commercial entities with incentives for keeping their data proprietary, the accuracy observed in external assessment populations such as in the current study can be useful indicators of the accuracy that a typical commercial producer might expect. A simpler and more accurate approach would be to conduct the entire analysis in house and incorporate DNA test results into EPD evaluations. The AAA is the first U.S. beef cattle breed association to incorporate genomic predictions into national cattle evaluation in the form of genomic-enhanced EPD. Other breeds are moving in a similar direction. The American Hereford Association announced in September 2011 that they are preparing to use genomic predictions developed and implemented in house, available in conjunction with

parentage and genetic abnormality testing (AHA, 2011), which will facilitate both the development and updating of Hereford-specific prediction equations.

In conclusion, the aim of this study was to present an analysis of the accuracy of commercial DNA test products and MBV developed by prominent research institutions in the field of beef cattle genomics in a commercial ranch setting. Despite the relatively small assessment population size, MBV accuracies were similar to those reported for the Angus breed (Northcutt, 2011). The MBV derived in multibreed populations were less accurate than Angus-derived MBV but were comparable to those found in other studies and may improve in future research with greater density marker panels.

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