Comparison of economic returns among genetic evaluation strategies in a 2-tiered Charolais-sired beef cattle production system[1,2]

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ABSTRACT: The objective of this study was to estimate economic returns and costs associated with 4 scenarios of genetic evaluation that combine genotypes, phenotypes, and pedigree information from a vertically integrated purebred (**PB**) and commercial (**CM**) beef cattle system. Inference was to a genetic evaluation for a production system producing Charolais terminal sires for 10,000 CM cows. The first genetic evaluation scenario, denoted PB_A, modeled a genetic evaluation in which pedigree information and phenotypes are available for PB seedstock animals. Scenario PB_H contained the same information as PB_A with the addition of 25K density (GeneSeek Genomic Profiler LD) single nucleotide polymorphism (SNP) genotypes from PB animals. Scenario PBCM_A contained pedigree records and phenotypes from PB and CM cattle. Scenario PBCM_H contained phenotypes, pedigree, and genotypes from the PB and CM animals. Estimates of prediction error variance, (co)variance, and selection index parameters were used to estimate accuracy of selection candidates (r_{TI}) and genetic gain resulting from selection on an economic index in US dollars (ΔG). Annual costs and incomes were used to determine the 30-yr cumulative net present value (**CNPV**) per CM calf resulting from selection in these genetic evaluation scenarios. Adding genotypes and CM production phenotypes to genetic evaluation increased the r_{TI} of selection candidates and ΔG across all 4 scenarios. Scenario PBCM_H produced the highest annual ΔG in the PB herd at US$11.91 per head. Including CM phenotypes and parentage testing in the genetic evaluation increased the time to breakeven from 12 yr in PB_A to 19 years in PBCM_A after accounting for the cost of that information. Adding CM phenotypes and genotypes increased the breakeven time from 12 yr in PB_H to 18 yr in PBCM_H. Scenario PB_H produced the highest 30-yr CNPV per slaughtered CM calf at US$371.16. These results using field data indicate that economically relevant r_{TI} and ΔG can be realized by adding 25K SNP genotypes and CM phenotypes to genetic evaluation, but the additional cost of that data significantly delays the economic return to the enterprise.

Key words: accuracy, beef cattle, breeding objective, Charolais, single-step GBLUP

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[2]The authors declare that the commercial collaborator has an interest in the economic viability of various genotyping strategies. J.W.B. is currently in the employ of that collaborator and M.D.M. is a paid consultant to them. The findings or conclusions herein were not influenced by these interests.

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INTRODUCTION

Adoption of genomic technology in the beef cattle industry has improved selection accuracy (r_{TI}), which affects the rate of genetic gain (ΔG) and increases income when used in conjunction with an economic selection index (Dekkers, 2007; Meuwissen et al., 2013; Todd et al., 2014; MacNeil, 2016). In a vertically integrated production system, there is opportunity to capture value generated by implementing a genetic evaluation program using a combination of phenotypes, pedigree information, and genotypes from both nucleus animals and commercial (**CM**) offspring (Aguilar et al., 2010). The cost of collecting that information for the purpose of genetic evaluation also requires careful consideration, especially for expensive or difficult to measure traits that contribute variation to economic selection indexes. The objectives of this study were to compare r_{TI}, costs of genetic evaluation, and economic returns associated with the ΔG resulting from the combination of purebred (**PB**) and CM performance records with traditional pedigree relationships derived from parentage recording and with realized genomic relationships resulting from single nucleotide polymorphism (SNP) genotypes. Inference was to a genetic evaluation program for a vertically integrated, 2-tiered beef cattle production system producing Charolais terminal sires for 10,000 CM cows.

METHODS

Animal Care and Use Committee approval was not obtained for this study since all animals were owned and cared for by the commercial collaborator. All animals were under the supervision of a veterinarian for the duration of the study.

Population and Phenotypes

Cattle used in this study consisted of a PB Charolais herd with a terminal-sire breeding objective targeting growth and carcass traits to produce CM crossbred calves finished at a common feeding facility. The CM dam population primarily consisted of Angus x Hereford crossbred females. At the commencement of the study, traditional pedigree information was available for only the PB Charolais herd. Over a 3-yr period, 3,018 PB Charolais and 13,340 CM crossbred calves were genotyped. Sires and CM calves were genotyped using a combination of the GeneSeek Genomic Profiler (**GGP**) LD versions 1 to 4 (26K to 40K), GGP Bovine 50K (50K), and GGP HD version 1 (76K) SNP arrays (Neogen Genomics, Lincoln, NE).

All samples were imputed to a common density of 24,569 SNP markers (a subset of the 26K GGP LD commercial SNP array) using FImpute (Sargolzaei et al., 2014). This density has been demonstrated to be adequate for estimation of genomic relationship matrices in cattle (Rolf et al., 2010). The pool of 24,569 markers were chosen to optimize an imputation strategy utilizing population-wide haplotype information, with this set of real genotype calls represented across a reference population of 13,466 individuals. Genotype and pedigree information for CM dams was assumed to be missing. Markers chosen for imputation were required to have a call rate of >0.90, a minor allele frequency greater than 0.05, and consistent reference strand designation across marker panel versions. Markers on sex chromosomes and markers with missing or inconsistent map information (*Bos taurus* UMD 3.1) were also removed. Imputation accuracy was assessed on a per-chip basis by masking subsets of imputed markers from 20 randomly chosen individuals with real genotype calls across the 25K imputation pool. The average concordance between imputed and real marker calls was above 0.90 for every marker panel version in the analysis. The minimum observed concordance between real and imputed genotype calls on an individual basis was 0.82.

Genotypes were also used to pair sires with their progeny from a subset of available SNP markers (McClure et al., 2015; Strucken et al., 2016; Buchanan et al., 2016a). For the CM calves, sires were identified using a 1,000 SNP subset of the available marker panel and the SEEKPARENTF90 software to generate CM pedigree records (Aguilar et al., 2014; Buchanan et al., 2016a). For PB animals, historical 4-generation pedigree information was available containing 9,176 records.

Phenotypes collected from PB Charolais bulls included weaning weight (**WW**), average daily gain (ADG), dry matter intake (DMI; GrowSafe Systems, Ltd, Airdrie, AB Canada), ultrasound 12th-rib fat depth (**URFAT**), ultrasound intramuscular fat percentage (**UIMF**), and ultrasound longissimus muscle area (**UREA**). Phenotypes collected from CM calves finished in the feedlot included WW (collected at feedlot arrival), ADG, DMI, 12th-rib fat depth (**FAT**), marbling score (**MARB**) determined by image analysis (VBG 2000 E + V, Oranienburg, Germany), carcass ribeye area (**REA**), days to harvest (**D2H**), hot carcass weight (HCW), yield grade (**YG**), and bovine respiratory disease (**BRD**) treatment status (treated or not treated).

Variance Component Estimation

Estimates of genetic (co)variance components were obtained using REML procedures implemented in AIREMLF90 (Misztal et al., 2016). A bivariate animal model was used to estimate (co) variance components among traits in the breeding objective. The bivariate animal model is expressed as follows:

$$\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \quad (1)$$

where Y_i is the vector of observations for the ith trait, b_i is the vector of fixed effects for the ith trait, u_i is a vector of additive genetic effects for animals (random) for the ith trait, and X_i and Z_i are design matrices for the fixed and random animal effects, respectively. Subsequently, E(y) = Xb, and the (co) variance structure is represented by the following equation:

$$var\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a_1} & A\sigma_{a_{12}} & 0 & 0 \\ A\sigma_{a_{21}} & A\sigma^2_{a_2} & 0 & 0 \\ 0 & 0 & I\sigma^2_{e_1} & I\sigma_{e_{12}} \\ 0 & 0 & I\sigma_{e_{21}} & I\sigma^2_{e_2} \end{bmatrix} = \begin{bmatrix} A \times T & 0 \\ 0 & I \times E \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix} \quad (2)$$

where var(u) = G, var(e) = R, cov(u, e) = 0, var(y) = V = ZGZ' + R, var(a) is the additive genetic (co)variance, var(e) is the residual (co)variance, T is the additive genetic (co)variance matrix, A is the relationship matrix among animals (pedigree A, or combined H), and E is the residual (co) variance matrix. Estimates of genetic (co)variance for BRD were obtained using a threshold-linear model implemented in THRGIBBSF90b (Tsuruta and Misztal, 2006; Buchanan et al., 2016b).

Bivariate analysis of traits in the genetic evaluation proceeded as follows: BW and WW, DMI and ADG, FAT and URFAT, MARB and UIMF, REA and UREA, BRD and ADG, and D2H and ADG. Traits with records collected on both PB and CM animals included WW, DMI, and ADG. For all 3 traits, the genetic correlation between PB and CM records was greater than 0.90 when analyzed as a bivariate model. Consequently, WW, ADG, and DMI were considered the same trait when collected on PB or CM animals. Concatenated effects that were used to create contemporary groups for CM calves included ranch of origin, sex, implant protocol, and harvest date. Contemporary groups for PB animals included the concatenated effects of sex, birth year, birth month, and breeder. Measurement trial start date was included in the contemporary group effect for DMI. Age of dam preadjustments for BW and WW were applied according to the Beef Improvement Federation Guidelines (Beef Improvement Federation, 2016). Because dams of the commercial sired calves were not identified, models which included maternal effects could not be used in analyses of their phenotypes. Maternal additive effects for BW and maternal additive and permanent environmental effects for WW were included using BLUPF90 for the straightbred Charolais calves only (Meyer, 1992; Misztal et al., 2016). Phenotypes collected on individuals creating a contemporary group of less than 10 records or falling outside of 3 standard deviations from the contemporary group mean were removed from the evaluation. Adjustments for heterosis or breed composition of CM calves were not included due to missing genotype and pedigree information for CM dams. The final assembled genetic covariance matrix (G) was adjusted to a positive-definite matrix by adjusting the negative resulting eigenvalues following the methods described by Schaeffer (2014).

Relationship matrices were implemented with the default parameters in BLUPF90 using pedigree information (numerator relationship matrix, A) or with the single-step approach to simultaneously evaluate genotyped and nongenotyped animals with pedigree information (combined relationship matrix, H) (Misztal et al., 2016). In scenarios where genotypes were included on PB or CM animals, pedigree information was also included on those animals to assist with the compatibility of the G and A relationship matrices. Scaling factors for G and A_{22} were 0.95 and 0.05, respectively, according to the default parameters in BLUPF90 (Misztal et al., 2016).

Alternative Scenarios for Genetic Evaluation

The r_{TI} of selection candidates was estimated in 4 separate models using different combinations of phenotypes, genotypes, and pedigree information to simulate different production scenarios or data collection strategies that might be used to conduct genetic evaluations. This comparison of genetic evaluation strategies relies on the assumption that the benefit derived from genetic improvement in the purebred sector is expressed in the commercial sector. Thus, to measure gene flow from the purebred sector to the commercial sector, all of the purebred and commercial cattle were genotyped. However, 2

different subsets of the genotypic data were used in the evaluations that are reported here and these subsets were assumed to have different costs. In PB_A, a subset of 1k SNP genotypes was used only to verify parentage as a means of quality control for the pedigree. In PB_H, genotypes were used to enhance the accuracy of the genetic evaluation through the use of a blended relationship matrix (Legarra et al., 2014; Lourenco et al., 2015b), and thus, the cost of 25K SNP genotypes required for the purebred sector was considered in modeling this scenario. Only the Charolais seedstock had phenotypes that were considered in both of the aforementioned genetic evaluations. These evaluations were thus thought to reflect the current state of national cattle evaluations that are currently conducted by most, if not all, breed associations.

The third and fourth scenarios were assembled to model a vertically integrated beef production system where phenotypes and pedigree or genotypes were available from both PB and CM animals. In PBCM_A, 1K SNP genotypes were again used to verify parentage of both the purebred and commercial progenies. Phenotypes from these progenies were also used in the genetic evaluation. Finally, in PBCM_H, 25K SNP genotypes were used to again construct a blended relationship matrix (Legarra et al., 2014) for use in the genetic evaluation, which again incorporated phenotypes from both purebred and commercial progenies.

Economic Evaluation

Economic values for traits in the breeding objective were produced from an economic simulation of profit with parameters describing income and cost according to selection index theory following the method described by Buchanan et al. (2016b). The selection index was developed using a combination of economically relevant and indicator traits to maximize carcass-derived profit within a typical feedlot finishing system. Phenotypes were simulated using observed means and (co)variances for WW, DMI, D2H, HCW, YG, MARB, and BRD. Carcass income was generated using a market average carcass grid with premiums and discounts for YG, HCW, and MARB (MacNeil and Herring, 2005; Thompson et al., 2016). Economic values were expressed as the difference in profit per head as determined by independently perturbing each trait by 1 unit from the mean.

The standard deviation of the economic index (σ_I) and the r_{TI} of selection on the index for yearling selection candidates were estimated to assess the economic outcome of a particular genetic evaluation strategy. The standard deviation of the index was estimated from scenario PBCM_H as follows:

$$\sigma_I = \sqrt{v'Gv}, \tag{3}$$

where v is the vector of economic weights, and G is the genetic (co)variance matrix of traits in the index. Individual r_{TI} estimates obtained at the time of selection on young selection candidates (bull calves at 1 yr of age) are needed to estimate ΔG from selection on the index. The r_{TI} associated with each trait in the index for PB selection candidates was estimated from individual prediction error variance (σ^2_{PE}) obtained from BLUPF90 (Misztal et al., 2016) and additive genetic variance (σ^2_G) as follows:

$$r_{TI} = \sqrt{\frac{\sigma^2_G - \sigma^2_{PE}}{\sigma^2_G}} \tag{4}$$

The r_{TI} of the index for a selection candidate was calculated as the product of r_{TI} and the relative emphasis (%) in the index of an individual trait, and then summed across all traits in the index. The r_{TI} of the economic index was then used to estimate the selection response, ΔG, or expected genetic gain in profit per year in the PB herd (US$/hd) for each scenario as follows:

$$\Delta G = \frac{(i_s + i_d) r_{TI} \sigma_I}{(L_s + L_d)}, \tag{5}$$

where i_s and i_d equal the selection intensities of sires and dams, respectively, L equals the generation interval of sires and dams, and σ_I equals the standard deviation of the selection index. Selection intensities were chosen to create a replacement rate that would maintain the population structure as defined in Table 1. A discount rate of 5% and a 30-yr planning horizon were used to determine the cumulative net present value (**CNPV**) per CM calf resulting from selection on the economic index. Generation intervals were assumed constant across the 4 scenarios since the structure of the genetic evaluation would not affect the age at which bulls are selected or culled for natural service matings.

Enterprise scale, age classes, and selection intensities for a hypothetical combined PB nucleus herd and CM production system are shown in Table 1. Assumptions for age structure, population composition, and breeding scheme were adapted from Van Eenennaam et al. (2011). The genetic lag between selection decisions and the expression of profit in the CM calf crop was tracked according

Table 1. Enterprise scale and economic assumptions for a 2-tiered beef production model

Parameter	Value
No. of PB bull calves born each year[1]	270
PB bull:cow ratio	1:25
No. of PB cows	600
No. of PB bulls selected each year	12 (4.4%, i = 2.11)[2]
No. of bulls selected for CM use[3]	181 (70.2%, i = 0.50)
No. of PB and CM dams selected on index	0 (i = 0)
CM bull:cow ratio	1:20
No. of CM cows	10000
Planning horizon	30 yr
Discount rate for returns, d	5%
Maximum age of PB bull, yr	4
Maximum age of CM bull, yr	6
Generation interval PB bulls	3.24
Generation interval PB cows	4.89

[1]PB = purebred.
[2]i = selection intensity.
[3]CM = commercial.

to the population structure using simulation to model age classes, culling rates, and selection intensity for both PB and CM bull populations with simulation. The simulation utilized the population parameters in Table 1 to model the combined PB and CM breeding system that relies on the selection of PB sires (both terminal and herd sires) to drive the expression of profit in CM calves at slaughter. Herd sires were considered self-replacing, and terminal sires transferred to the CM sector passed on half of their average genetic merit to CM calves. Since CM dams were considered unknown with no recorded pedigree or genomic information, their contribution to genetic gain was considered zero. The CNPV expressed per CM calf produced annually (N = 8,000) in the system was calculated over a 30-yr planning horizon for each scenario. Estimates of the annual costs associated with parentage testing for pedigree recording, genotyping, and phenotyping the initial reference population were included in the economic model where appropriate in each scenario. Startup costs to phenotype, genotype, or assign parentage in the initial population were considered separately and jointly with the annual costs of genetic evaluation in the simulation of 30-yr CNPV.

Phenotypes included in the estimates of startup cost consisted of 3,018 PB animals (US$135 per head phenotype cost) and 13,340 CM animals (US$100 per head phenotype cost). Phenotype collection costs were provided by the commercial collaborator as an accurate estimate of materials plus labor and serve as an example for the real costs associated with the development and maintenance of a genetic evaluation strategy in the U.S. beef cattle industry. For all scenarios, 100% of the PB bull calves were phenotyped annually (N = 270). For scenarios where CM calf data were collected, 10% of the contemporary groups for CM calves were randomly phenotyped each year of the simulation (N = 800). Pedigree relationships based on SNP data were included at a purchase cost of US$15 per head, and genotypes were purchased for US$35 per head. The cost of genotyping/parentage for the CM animals was not included in the first 2 scenarios since this information is included only to model the genetic relationship between the 2 sectors of the production system. Total startup and annual costs for each genetic evaluation scenario are displayed in Table 2.

RESULTS AND DISCUSSION

Multiple strategies of genetic evaluation were compared under a breeding objective for profit to investigate the economic outcome associated with various strategies for combining phenotypes, genotypes, and relationships among animals. Figure 1 displays a model for combining indicator traits, carcass phenotypes, recorded pedigree information, and genotypes for genetic evaluation of terminal sires in a vertically integrated beef production system. Individual trait r_{TI} and the weighted r_{TI} of the selection index in each genetic evaluation strategy are displayed in Table 3. Scenario PB_H represents a genetic evaluation utilizing PB phenotypes where both pedigree and 25K genotypes are available for all PB animals in the genetic evaluation. The inclusion of genomic information for PB animals increased r_{TI} by approximately 26.5% over scenario PB_A (0.453 vs. 0.358). Improvement in r_{TI} from adding genomic information generally depends on population size, pedigree depth, genotype density, and trait heritability, but a previous study observed up to a 20% increase in r_{TI} from adding genomic information alone when moving to a single-step genetic evaluation (Lourenco et al., 2015b). Scenario PBCM_A and PBCM_H added growth and carcass phenotypes from 13,340 CM progeny to the genetic evaluation. The relationship matrix for PBCM_A was created from pedigree records for PB animals and CM pedigree records (sire-calf relationships only) generated through parentage assignment from genomic information representative of a commercial parentage test. Adding CM phenotypes to genetic evaluation PBCM_A increased r_{TI} by 35.5% over scenario PB_A. This

Table 2. Startup and annual costs for four scenarios of genetic evaluation

	Genetic evaluation scenario[2]			
Cost[1]	PB_A	PB_H	PBCM_A	PBCM_H
Startup cost				
PB genotyping	US$0	US$105,630	US$0	US$105,630
PB parentage	US$45,270	US$0	US$45,270	US$0
PB phenotyping	US$407,430	US$407,430	US$407,430	US$407,430
CM genotyping	US$0	US$0	US$0	US$466,900
CM parentage	US$0	US$0	US$200,100	US$0
CM phenotyping	US$0	US$0	US$1,334,000	US$1,334,000
Total startup cost	US$452,700	US$513,060	US$1,986,800	US$2,313,960
Number of PB	3,018	3,018	3,018	3,018
Number of CM	0	0	13,340	13,340
Total startup US$/head	US$150.00	US$170.00	US$121.46	US$141.46
Annual cost				
PB genotyping	US$0	US$9,450	US$0	US$9,450
PB parentage	US$4,050	US$0	US$4,050	US$0
PB phenotyping	US$36,450	US$36,450	US$36,450	US$36,450
CM genotyping	US$0	US$0	US$0	US$28,000
CM parentage	US$0	US$0	US$12,000	US$0
CM phenotyping	US$0	US$0	US$80,000	US$80,000
Total annual cost	US$40,500	US$45,900	US$132,500	US$153,900
Number of PB	270	270	270	270
Number of CM	0	0	800	800
Total annual US$/head	US$150.00	US$170.00	US$123.83	US$143.83

[1]PB = purebred, CM = commercial

[2]PB_A = PB phenotypes with PB pedigree; PB_H = PB phenotypes; PB pedigree and PB genotypes; PBCM_A = PB and CM phenotypes and pedigree; PBCM_H = PB and CM phenotypes, genotypes, and pedigree.

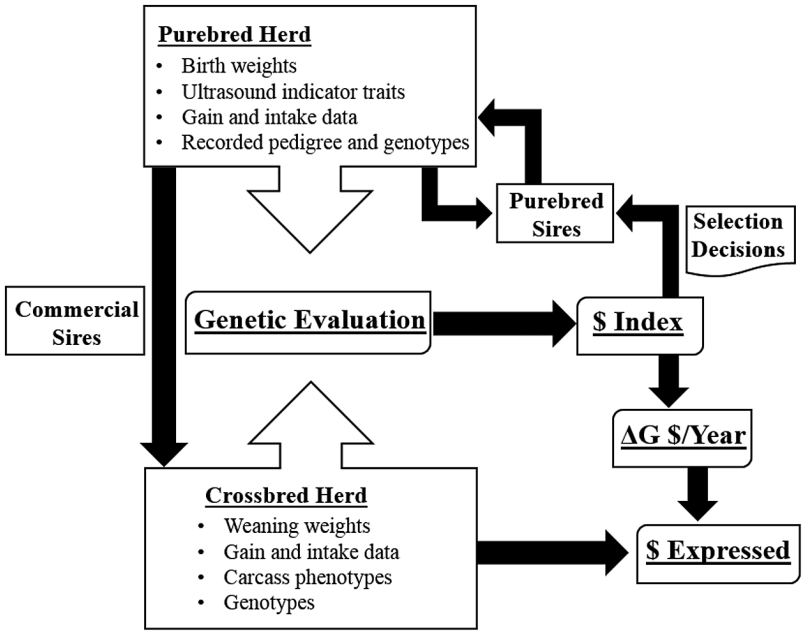

Figure 1. Model beef cattle production system to advance selection response (ΔG) in profitability.

result suggests the improvement in accuracy from adding CM phenotypes and pedigree information to the genetic evaluation is larger than adding genotypes on PB animals, but this finding does not suggest that parentage assignment or CM phenotyping should be prioritized for genetic evaluation without considering the additional costs involved in obtaining this information.

The highest estimates of r_{TI} were achieved when all information was included in the genetic

Table 3. Average accuracy (r_{TI}) for traits in the economic selection index

	Genetic evaluation scenario			
	PB_A	PB_H	PBCM_A	PBCM_H
r_{TI} Accuracy[1]				
BRD	0.307	0.339	0.373	0.567
D2H	0.210	0.444	0.512	0.570
DMI	0.439	0.530	0.542	0.647
HCW	0.356	0.486	0.515	0.667
MARB	0.345	0.448	0.536	0.643
WW	0.515	0.561	0.607	0.681
YG	0.305	0.429	0.473	0.653
Index	0.358	0.453	0.485	0.636
Selection outcome[2]				
ΔG/Yr	US$6.71	US$8.49	US$9.09	US$11.91
Yr to breakeven	12	12	19	18
30-Yr CNPV/CM calf	US$285.18	US$371.16	US$236.71	US$348.67

[1]BRD = bovine respiratory disease morbidity; D2H = days to harvest; DMI = dry matter intake; HCW = hot carcass weight; MARB = camera-based marbling score; WW = weaning weight; YG = yield grade. Increases in accuracy were obtained from genetic evaluation of the data available.

[2]ΔG = response to selection (US$/hd) on the index in the PB herd; PB = purebred; CM = commercial; 30-Yr CNPV = cumulative net present value per CM calf (US$) generated from 30 yr of selection on the economic index.

evaluation including PB and CM phenotypes, pedigree, and genotypes in scenario PBCM_H. Average r_{TI} of the index was 0.636 for selection candidates, which is a 31.1% improvement over PBCM_A and a 40.4% improvement over PB_H. These results indicate that an economically relevant improvement in selection accuracy can be achieved, at a cost, through the incorporation of genomic information and phenotypes from CM animals for this specific production system.

Increases in r_{TI} directly contribute to genetic gain in profitability in the context of an economic selection index, but the cost to achieve that gain must be accounted for in determining whether such improvements are cost-effective. Response to selection on the economic index, ΔG, years to breakeven, and 30-yr CNPV expressed in dollars per CM calf are displayed in Table 3. Figure 2 displays the annual CNPV per CM calf as a function of time. The standard deviation of the selection index as estimated from variance components was US$72.18, which was assumed a constant across the 4 scenarios. Selection intensity, i, was also a constant, so differences observed in ΔG are due to variation in r_{TI} as applied in the breeders equation (5).

Annual ΔG was greatest in scenario PBCM_H at US$11.91 per head, which resulted in a breakeven time of 18 yr. The highest rate of genetic gain in this 30-yr comparison did not result in the fastest time to breakeven or the greatest CNPV per CM calf due to the annual cost of phenotyping and genotyping 270 PB and 800 CM calves as displayed in Table 2 (US$153,900). However, the trend observed in Figure 2 indicates that scenario PBCM_H would result in the greatest value per CM calf given a longer planning horizon. This strategy of genetic evaluation represents the most accurate approach to evaluate candidates for selection and realize genetic improvement in CM production, but the time and cost of achieving that gain must be accounted for to calculate the return on investment.

Scenario PBCM_A had the least 30-yr CNPV relative to the genetic gain achieved, which was due to the marginal increase in r_{TI} compared with the cost of collecting CM phenotypes and parentage. This scenario produced a ΔG of US$9.09 per year in the PB herd but resulted in the least 30-yr CNPV per CM calf at US$236.71. When compared with PBCM_H, in the absence of genomic information, this scenario also had the longest time to breakeven at 19 yr. The economic outcome of this scenario highlights the significant cost of collecting phenotypes on CM animals and the added value resulting from a more accurate relationship matrix to join that CM information to the data collected in the PB herd.

Comparing economic returns, scenario PB_H offered the greatest 30-yr CNPV per CM calf and the fastest time to breakeven. The annual ΔG in this scenario was only 71% of that achieved in PBCM_H (US$8.48 vs. US$11.91), but the significantly lower annual costs allowed for a more rapid breakeven time (12 vs. 18 yr) and the greatest 30-yr CNPV per CM calf at US$371.16. Scenario PB_A also resulted in a breakeven time of 12 yr as a result of the low annual cost associated with that scheme.

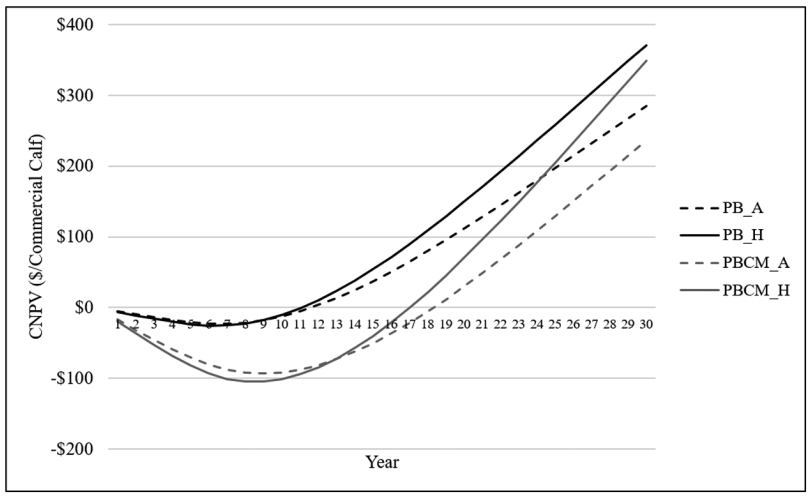

Figure 2. Cumulative net present value (CNPV) of per commercial (CM) calf (n = 8,000) over a 30-yr planning horizon for four scenarios of genetic evaluation.

The comparatively lower cost of PB_A also resulted in a higher 30-yr CNPV per CM calf compared with PBCM_A (US$285.18 vs. US$348.67). However, it is important to note that the genetic evaluation in PB_A produced the lowest r_{TI} for selection candidates and slowest annual ΔG in the PB herd at US$6.71.

The cost of phenotyping requires careful consideration when implementing genetic evaluation. The marginal benefit derived from an addition phenotype is a decreasing function, and thus, there is some threshold number of phenotypes for each trait that is optimal. The total cost of phenotyping can be reduced by sampling fewer CM progeny (up front in the development of a reference population, or annually thereafter) as in the present system, but this would negatively affect the r_{TI} and ΔG. Depending on their relative emphasis in the selection index, expensive to measure traits such as DMI might provide the greatest return when only collected on PB selection candidates once a substantial database of phenotypes has been established. There is a need for additional research to determine the optimal ongoing annual rate of collecting phenotypic information. It is noted that the highest rate of ΔG was observed with both PB and CM phenotypes in the genetic evaluation, but the cost of collecting such information in relation to the timing of the economic return needs consideration. This study assumed different phenotyping costs for PB and CM animals (US$135 per head vs. US$100 per head, respectively), which was mostly driven by recording ultrasound on all PB animals and DMI measurement for all PB and only a portion of CM animals. Once a sufficient population is established for genetic evaluation, an alternative annual strategy might be to phenotype and genotype all new selection candidates and only CM progeny from PB animals with r_{TI} in the genetic evaluation that is less than a critical threshold (Horton et al., 2014).

It should be noted that in these calculations all of the value derived from genetic improvement was assumed to be returned to the enterprise. Additionally, the startup cost to phenotype and genotype or collect parentage for the reference population in this comparison was not considered in the annual economic returns. When adding the startup costs to phenotype, genotype, or assign parentage in the initial reference population to the 30-yr CNPV simulation as shown in Figure 3, the time to break even is lengthened considerably, exceeding 30 yr in the case of PBCM_A. This highlights the "activation energy" and high startup costs required to enable an enterprise-specific private genomic selection program. The costs to develop a large genotyped and phenotyped reference population are typically absorbed by an entity such as a breed association or government-supported genetic evaluation unit with the intent to leverage the cost of obtaining such information over a large number of CM cattle to maximize the return on investment.

Terminal-sire selection in this scheme is designed to increase genetic gain and profitability in CM offspring where economic returns are realized. Capturing economically relevant and indicator phenotypes, pedigree records, and genomic information from PB and CM animals for inclusion in the prediction of economic merit is the primary objective of beef cattle genetic improvement (Garrick and Golden, 2009). Recent efforts in genetic evaluation have concluded that combining information

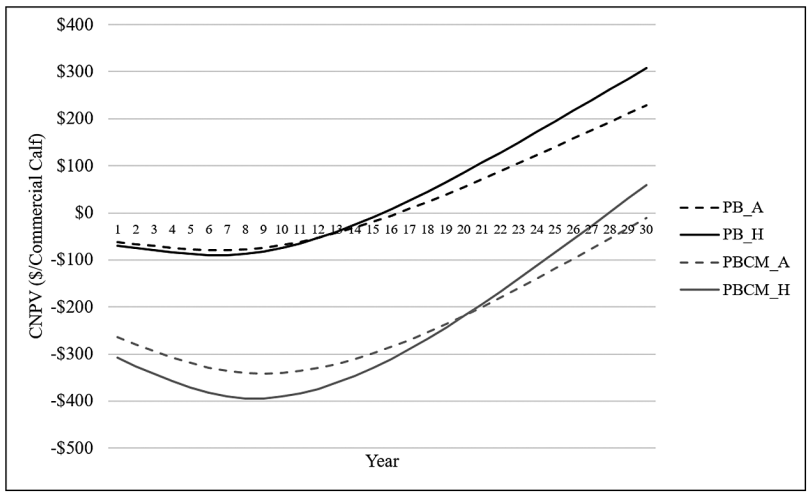

Figure 3. Cumulative net present value (CNPV) of per commercial (CM) calf (n = 8,000) over a 30-yr planning horizon for four scenarios of genetic evaluation including the startup costs to phenotype, genotype, or assign parentage in the initial reference population.

from various production segments using single-step GBLUP produces greater accuracy than multi-step methods due to the combined pedigree and genomic relationship matrix, especially for young unproven selection candidates (Christensen et al., 2014; Li et al., 2014; Lourenco et al., 2015a).

Income generated through increased genetic gain from the collection of genomic and phenotypic information from multiple production segments results from the increased r_{TI} of the predicted genetic merit of selection candidates. Additionally, if selected animals can consequently produce progeny at younger ages, the implementation of this strategy results in a reduction of generation interval (Buch et al., 2012; Meuwissen et al., 2013). The development of the single-step approach for genetic evaluation has enabled the combination of traditional pedigree relationships with genomic relationships into a combined relationship matrix, termed H (Legarra et al., 2009, 2014; MacNeil, 2016). This combined relationship matrix can be incorporated into the mixed model equations to estimate breeding values for genotyped and nongenotyped animals in a single model when pedigree information is partially missing (Meuwissen, 2009). In genetic evaluations using CM beef production data, this provides the opportunity to combine phenotypes typically collected only on PB animals, such as ultrasound indicator traits, with growth and carcass data from CM offspring to increase the accuracy of genetic evaluation (MacNeil and Northcutt, 2008; MacNeil et al., 2010; Christensen et al., 2014; Todd et al., 2014).

Increasing the r_{TI} of genetic evaluation can be accomplished in practice by increasing the number of phenotype and pedigree observations from recent generations, or by genotyping some proportion of individuals (Meuwissen et al., 2013; Lourenco et al., 2014; Wiggans et al., 2015; Boichard et al., 2016). Simulations have modeled the effect of adding different types of information to genetic evaluation systems (Santos et al., 2017). However, there is a need for additional field data associated with genetic evaluations produced using genomic predictions and actual carcass data from crossbred beef cattle production systems to enable modeling of the economic returns associated with an investment in genomics.

For some sectors of the beef cattle industry such as the cow–calf sector, it is still likely that the cost of genotyping commercial animals is greater than the economic return to that sector as commercial animals have few progeny upon which to obtain a return on investment (Van Eenennaam et al., 2012). In addition, an analysis of the cost of phenotyping vs. the return in genetic gain on an individual trait basis would aid in the design of optimal phenotyping strategies. For instance, the cost of measuring DMI far exceeds the cost of any other trait in the evaluation, but this trait does not carry the greatest importance in most terminal-sire selection indexes. The economic selection index used in this study included feedlot and carcass traits only, which would only be relevant to producers who retain ownership of their cattle through the supply chain. As such, care should be taken when interpreting the economic returns of genetic testing obtained in this study to the wider beef cattle industry, and especially to cow-calf producers who are selling their animals prior to entry into the feedlot as the traits in the feedlot index modeled in this study may have only indirect economic relevance to such operations.

CONCLUSIONS

This study provides an industry-based example of the economic considerations for the use of genomics and collection of CM carcass data for use in genetic evaluation in an integrated 2-tiered beef cattle production system focusing on terminal-sire selection. Differences in genetic gain may be realized through recording progeny performance and the incorporation of 25K SNP genomic information into genetic evaluation over pedigree (parentage or recorded pedigree) relationships alone. When implemented with an economic selection index, the increased response to selection in the breeding objective may result in a long-term positive economic return to the enterprise given an appropriate strategy for data collection and cost management. These results using field data indicate that the additional accuracy derived from adding CM phenotypes and 25K SNP genomic information data to the relationship matrix will maximize selection accuracy, but appropriate accounting measures are required to estimate the time and cost of achieving improved accuracy to calculate the return on that investment.

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