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Investigating genotype-by-sex interaction in genomic predictions for beef cattle growth traits

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Introduction

Sexual dimorphism is well established in natural populations. Through improvements in management and genetics, the beef industry continues to see significant increases in feedlot growth and carcass weights. Selection for increased yearling weight and carcass weight, coupled with little selection to moderate cow weight, has resulted in the production of larger mature cows. Larger cows lead to increased maintenance costs, reduced stocking and calving rate and higher production costs per unit of weaned calf produced (Ziegler *et al*., 2020). Currently, genetic evaluation models adjust for sex differences when making genetic predictions, selecting for the same alleles in both males and females. However, could one select for different genetic effects in female, maternal context and male, terminal context? This study aims to investigate the influence of genotype-by-sex interaction effect (G×S) on growth traits of beef cattle and to evaluate the development of a sex-based genomic predictions models. Ultimately, the goal would be to intentionally select larger steers and smaller cows by using sex-specific selection indices, thus creating increased sexual dimorphism via artificial selection.

Materials & Methods

The phenotypic, pedigree and genomic data used for this study were transferred from American Simental Association to the University of Missouri and included birth weight (BW, kg), 205-d adjusted weaning weight (WW, kg), and 365-d yearling weight (YW, kg) records of 46,234, 44,456, and 30,153 animals, linked to 1,536, 1,490 and 1,277 known sires, respectively, born in continental United States between 1986 and 2019.

Statistical models and analysis. Each trait that went into the downstream analyses were pre-adjusted for fixed effect of contemporary group (breeder zip code, birth year, season and sex). All trait records of contemporary groups with less than ten individuals were excluded. Phenotypic records outside the intervals of mean±4 standard deviation units were dropped. Quality control of genotype data was performed with PLINK v1.9 (Chang *et al*., 2015). Pedigree and genotype data were available for all animals and was used to create either a numerator relationship or H matrix for subsequent analyses. A single trait animal or sire model was initially applied, ignoring G×S, to estimate baseline heritability for the traits studied and as a proxy model for Simmental national genetic evaluation system. The model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \quad (1)$$

where **y** is the vector of pre-adjusted phenotypic values of BW, WW, and YW; **b** is the vector of trait means (data were pre-adjusted); **u** is the vector of random genetic effect of the animal or sire; **e** is the random residual error; **X** and **Z** are the incidence matrices associated with the fixed and random genetic effects, respectively. A two-trait animal or sire model that fits the same growth trait observed in males and females as distinct dependent variables was used to evaluate G×S. Both models were tested because an animal model provides a standard approach for Simmental national genetic evaluations while a sire model allows for evaluation of replication of sire genetic effects across both sexes.

The model was:

$$\begin{bmatrix} \boldsymbol{y}_f \\ \boldsymbol{y}_m \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_f & 0 \\ 0 & \boldsymbol{X}_m \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_f \\ \boldsymbol{b}_m \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_f & 0 \\ 0 & \boldsymbol{Z}_m \end{bmatrix} \begin{bmatrix} \boldsymbol{u}_f \\ \boldsymbol{u}_m \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_f \\ \boldsymbol{e}_m \end{bmatrix} \quad (2)$$

where $\mathbf{y}_f$ and $\mathbf{y}_m$ are the vectors of pre-adjusted phenotypic values for the same trait observed in females and males, respectively; $\mathbf{X}_f$ and $\mathbf{X}_m$ = incidence matrices for the fixed effects; $\mathbf{b}_f$ and $\mathbf{b}_m$ = vectors of trait means; $\mathbf{Z}_f$ and $\mathbf{Z}_m$ = incidence matrices for the random genetic effects; $\mathbf{u}_f$ and $\mathbf{u}_m$ = vectors of the unknown animal or sire genetic effects; and $\mathbf{e}_f$ and $\mathbf{e}_m$ = vectors of unknown random residual errors for females and males, respectively. Three statistical methods including animal BLUP, sire BLUP, and sire single-step GBLUP were analysed using blupf90 family of programs. Estimates of variance components, heritability and genetic correlation among sex groups were generated for each trait.

Validation of genomic predictions. The linear regression method (LR) proposed by Legarra and Reverter (2018) was used for validation. A 3-fold validation approach was adopted by masking the phenotype of sire progenies born in 2014, 2015, or 2016 to create a partial dataset, such that the progeny information for these sires was not utilized in the estimation of breeding values thus reducing the amount of data used in the estimation of EPDs. Although, these sires can have at least one progeny record in the whole dataset. Similarly, for animal model, records of animals born in 2014, 2015, or 2016 were masked to create 3-fold partial datasets. The linear regression statistics including bias, slope and accuracy were estimated to assess the performance of each model between the whole and partial datasets.

Results & Discussion

Heritability estimates of growth traits. Over the past few decades, the beef industry has seen a significant increases in feedlot growth and carcass weights that are consistent with directional selection, however, commercial cow-calf sector has also witnessed a substantial increase in mature cow size. Studies have shown that larger cows wean off a lower percentage of their mature weight with no additional calf crop (Beck *et al*., 2016) which provided the motivation to develop a sex-based genomic prediction model for increasing carcass weights while moderating mature cow size. The result shows that heritability estimates were moderate to high and similar between and across sexes for all traits and methods evaluated (Table 1).

Table 1. Heritability estimates from single and two-trait estimation using animal and sire BLUP models across sexes.

			Single Trait Model		Two-Trait Model	
Trait[1]	Sex	N	Animal BLUP	Sire BLUP	Animal BLUP	Sire BLUP
BW	Female	24677	0.59±0.004	0.23±0.014	0.61±0.004	0.24±0.011
	Male	21557	0.58±0.013	0.26±0.015	0.61±0.014	0.26±0.013
	Across	46234	0.61±0.006	0.24±0.011		
WW	Female	23240	0.56±0.011	0.21±0.015	0.56±0.012	0.23±0.015
	Male	21216	0.58±0.013	0.26±0.016	0.59±0.013	0.27±0.014
	Across	44456	0.56±0.008	0.24±0.019		
YW	Female	14072	0.57±0.014	0.19±0.018	0.58±0.011	0.20±0.014
	Male	16081	0.49±0.020	0.19±0.018	0.52±0.019	0.19±0.014
	Across	30153	0.53±0.019	0.18±0.014		

[1]BW = Birth weight in kg; WW = Weaning weight in kg; YW = Yearling weight in kg.

This empirical evidence may provide explanation for the spikes in mature cow size observed over the years in the beef industry as high heritability in cattle leads to a stronger genetic response to selection. Further, when a two-trait model that accounts for G×S is used for analyses (Table 1), heritability estimates tended to increase slightly which can speed up genetic progress by producing more accurate EBVs, thus, the use of a proper breeding program that addresses mature cow size relative to growth can be accomplished.

Evidence of G×S and sire reranking. Considering a genetic correlation from a two-trait animal or sire model that have values less than 0.80 as substantial evidence of G×S on any trait evaluated (Silva Neto *et al*., 2024), yearling weight, which is a strong proxy for mature weight in cattle, had lower genetic correlations than weaning weight and birth weight (Table 2). The low genetic correlation means that sires can produced different end target weights in males and females if enough selection pressure to artificially increase sexual dimorphism is implemented. This is further corroborated by the low Spearman's rank correlation (< 0.9) observed for yearling weight EPDs when using a sire model (Table 2). These findings suggest potential re-ranking of sire EBVs for YW (Silva Neto *et al*., 2024) and possible differences in the performance of sons and daughters of the sire at advanced ages. A Spearman rank correlation of 1 for Animal BLUP versus a Spearman rank correlation of 0.87 also motivates the use of sire models, as they allow re-ranking of sires depending on sex of progeny. In general, as sexual dimorphism show more divergent characteristics at advanced age in males and female, genetic correlation is likely to become smaller, thus, breeders can mitigate against spike in mature cow size by continuing measuring mature weight for use in genetic evaluation system.

Table 2. Genetic correlations and Spearman rank correlations of EBVs between sexes treated as two-traits using animal and sire models in BLUP evaluations.

Trait	Methods	Genetic	Spearman rank
Birth weight, kg	Animal BLUP	0.97	1.00
	Sire BLUP	0.91	0.98
Weaning weight, kg	Animal BLUP	0.86	1.00
	Sire BLUP	0.89	0.97
Yearling weight, kg	Animal BLUP	0.78	1.00
	Sire BLUP	0.71	0.87

Genomic prediction validation. This study evaluated strategy for developing a two-trait genomic selection model that accounts for G×S and compared the LR statistics from this model to across sex proxy model that mimics the national evaluation (Table 3). As expected, prediction accuracy from a two-trait model were greater than those from single trait and matched the baseline accuracy from across sex evaluation (Table 3). Because complete pedigree was available for use in this analysis, there were little or no difference between prediction accuracy from single-step GBLUP and BLUP. Model bias and slope were very close to their expectations of zero and unity, respectively, for all methods tested, indicating that predicted EBV and GEBV were unbiased and properly dispersed (Table 3). Thus, accounting for G×S in the genomic evaluation model improved prediction accuracy across sexes and can create opportunity for implementing a sex-based genomic prediction for moderating mature cow size and increasing carcass weight in beef cattle.

Table 3. Average bias, slope and accuracy across 2014, 2015, and 2016 validation groups from single and two-trait analysis using animal and sire BLUP models.

			Single trait model			Two-trait model		
Trait[1]	Model	Sex	Bias	Slope	Accuracy	Bias	Slope	Accuracy
BW	Animal BLUP	Female	0.016	0.989	0.28	0.005	0.999	0.42
		Male	0.001	0.986	0.30	0.007	1.000	0.42
		Across	0.011	0.992	0.37			
	Sire BLUP	Female	0.001	1.006	0.44	-0.001	0.998	0.52
		Male	0.000	0.994	0.44	-0.002	0.995	0.52
		Across	-0.001	0.994	0.51			
WW	Animal BLUP	Female	0.014	0.990	0.28	0.019	0.998	0.38
		Male	-0.015	0.991	0.31	0.008	0.996	0.38
		Across	0.031	0.992	0.38			
	Sire BLUP	Female	-0.013	0.972	0.37	0.023	0.982	0.50
		Male	0.030	0.974	0.40	0.023	0.983	0.50
		Across	0.026	0.979	0.48			
YW	Animal BLUP	Female	0.040	0.993	0.25	0.020	1.005	0.36
		Male	-0.082	0.991	0.35	-0.025	0.998	0.36
		Across	0.019	0.991	0.38			
	Sire BLUP	Female	0.021	1.005	0.26	0.020	1.001	0.38
		Male	0.001	0.994	0.37	-0.001	0.989	0.38
		Across	0.013	0.993	0.36			

[1]BW = Birth weight in kg; WW = Weaning weight in kg; YW = Yearling weight in kg.

Conclusions

This study investigated the rising concern regarding the increasing size of mature beef cows by developing a sex-based genomic prediction model that accounts for G×S. Empirical evidence shows that a G×S model can potentially lead to different end weights in males and females if different selection pressure are utilised, thus, sexed-based genetic prediction may effectively create increased sexual dimorphism for growth traits of beef cattle.

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