Prediction accuracy of carcass and carbon emission traits in Hanwoo cattle using genomic evaluation models.

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Abstract

This study estimated genetic parameters for carcass and carbon emission-related traits in Hanwoo cattle using various genomic analytic models, and explored methods for improving the accuracy of genetic evaluation based on these estimations. The analysis results across all models showed high prediction accuracy for carcass traits. Notably, the weighted single-step genomic best linear unbiased prediction (wssGBLUP) method significantly improved the accuracy by enhancing the utilization of genomic information through the application of weights. In contrast, carbon emission intensity, which is highly influenced by environmental factors, generally exhibited a lower prediction accuracy than other carcass traits. However, the wssGBLUP model demonstrated a significant improvement in accuracy, even in predictions of carbon emission intensity, demonstrating that the weighted application of genomic information contributes to improved predictive power, even for traits with substantial environmental influence. The findings of this study present a new strategy for effectively utilizing genomic information in Hanwoo cattle improvement programs to simultaneously achieve the dual goals of enhancing productivity and reducing environmental load, thereby providing a scientific foundation for the sustainable development of the livestock industry.

Keywords : Hanwoo cattle, Carcass traits, Carbon emission intensity, Genomic evaluation, wssGBLUP

Introduction

South Korea’s livestock industry must transition from a productivity-centric approach to new sustainability strategies. As environmental impacts, particularly greenhouse gas emissions, have emerged as an international issue, reducing the carbon emission intensity from livestock has become a significant challenge. Globally, there are 1.47 billion beef cattle and 290 million dairy cows, and ruminants, through enteric fermentation, emit substantial amounts of methane. Methane is a potent greenhouse gas with a global warming potential over 28 times greater than carbon dioxide, significantly impacting global warming [1]. Against this backdrop, it is crucial to establish breeding programs that consider not only productivity, but also environmental impacts, especially greenhouse gas emissions, for the sustainable development of the livestock industry. Numerous studies have suggested the potential for genetic improvement to reduce greenhouse gas emissions during livestock farming, which will be a key factor in securing future competitiveness of the livestock industry.

Breeding ruminants, including Hanwoo cattle, requires a genetic approach that goes beyond improving economic traits, focusing on carcass yield and quality, to consider greenhouse gas emissions. This approach contributes to achieving carbon neutrality in the livestock sector and is essential for reducing the environmental burden of farming. Specifically, breeding of Hanwoo cattle must shift towards reducing its carbon footprint and improving productivity, necessitating a multi-trait breeding strategy that comprehensively considers methane-related, carcass, and feed-efficiency traits [2]. The Hanwoo breeding program successfully reduced the carbon footprint of beef production by increasing carcass weight, supporting the positive effect of genetic approaches on greenhouse gas reduction. This genetic improvement has the potential to contribute to global greenhouse gas reduction by replacing a significant amount of beef imports, while maintaining livestock populations and improving productivity. This study aimed to establish a scientific basis for sustainable Hanwoo breeding by analyzing genetic correlations between major Hanwoo carcass traits and carbon emission-related traits and proposing an integrated model of genetic evaluation [3].

Genetics based evaluation methodologies for economic traits have continuously evolved from the traditional pedigree-based best linear unbiased prediction (BLUP) method to the genomic BLUP (GBLUP) model utilizing genomic information, the single-step GBLUP (ssGBLUP) model integrating genomic and pedigree information, and the weighted single-step GBLUP (wssGBLUP) method predicting the weight of each single nucleotide polymorphism (SNP). These advancements have enabled a more accurate evaluation of individual genetic merits, significantly enhancing the effectiveness of livestock breeding. GBLUP is a methodology developed to overcome the limitations of the traditional BLUP method and more accurately reflect the genetic relationships between individuals by estimating breeding values using genomic information, such as SNPs. ssGBLUP inherits the advantages of GBLUP while integrating pedigree information, contributing to the accuracy of estimations of breeding value for individuals lacking genomic information. Furthermore, wssGBLUP provides superior predictive performance compared with traditional BLUP or GBLUP by differentially reflecting the impact of specific genotypes on phenotypes [4]. These methodological advancements are expected to make significant contributions to sustainable livestock development, considering not only the improvement of livestock productivity and economic efficiency, but also environmental aspects [5, 6]. This study explored the potential for developing an integrated genetic evaluation model by precisely estimating the genetic parameters of Hanwoo carcass traits and carbon-emission-related traits using advanced genomic evaluation techniques. Such an integrated evaluation provides essential scientific evidence for establishing the direction of continuous Hanwoo cattle improvement and contributes to achieving breeding goals that simultaneously pursue economic benefits and environmental sustainability [7]. Specifically, the genetic improvement of various traits, such as feed efficiency, growth rate, and reproductive ability, is essential for sustainable beef production. Hanwoo is well known for its excellent meat quality, and genetic improvement has been accelerated through genomic selection [8–11].

In this context, this study aimed to estimate the genetic parameters of Hanwoo carcass traits and carbon emission-related traits by applying various models of genomic analysis, and to explore ways to enhance the accuracy of genetic evaluation based on these estimates. Through this study, we aimed to lay the foundation for new breeding strategies that can simultaneously achieve the dual goals of enhancing Hanwoo productivity and minimizing environmental impacts.

Materials and Methods

Materials

The genomic information used in this study was obtained from 18,352 Hanwoo cattle (all steers) born between 2012 and 2022 across the country (Table 1). Pedigree information was collected for the three generations by querying individual identification numbers from the Korea Animal Improvement Association. After verifying individual errors, a pedigree dataset comprising 292,111 individuals was constructed. Phenotypic information included carcass traits measured after 24 h of refrigeration post-slaughter according to the "Detailed Standards for Livestock Products Grading" (Ministry of Agriculture, Food, and Rural Affairs Notification No. 2025-23): carcass weight (CWT), eye muscle area (EMA), backfat thickness (BFT), and marbling score (MSC). Carbon emission intensity (CEI), calculated using the "Calculation Formula for Emission Intensity for Low-Carbon Livestock Products Certification" from the Livestock Products Quality Evaluation Institute, was used as an environmental trait.

$$Greenhouse\ gas\ emissions\ (CO_2\ eq)\ per\ kilogram\ of\ carcass\ weight = \frac{Slaughter\ month\ \times 198.2(CO_2 eq)}{carcass\ weight(kg)}$$

CEI is a trait that represents the efficiency of greenhouse gas emissions relative to production, allowing simultaneous consideration of environmental sustainability and production efficiency. Phenotypic information was collected using the OPEN API service provided by the Public Data Portal (data.go.kr). Phenotypic data for 115,256 individuals across three generations of pedigree information were collected. The materials used in this study are considered to be nationwide data that are not biased toward any specific region, and thus can be regarded as representative of the Hanwoo cattle population.

Quality control of genomic information

Genomic data quality control was performed using PLINK v1.9. SNPs were filtered based on call rates below 90%, minor allele frequencies below 1%, and Hardy-Weinberg equilibrium below 10^{-7} [12, 13]. After QC, 44,915 SNPs from 18,352 individuals were selected.

The GBLUP model

The GBLUP model is similar to the traditional pedigree-based BLUP method for estimating breeding values. However, it uses genomic information instead of pedigree information to construct a genetic relationship matrix among individuals. The mixed model equations used in the GBLUP were as follows:

$$Y = X\beta + Zu + E$$

where Y is the vector of observed trait values, β is the vector of fixed effects and covariates, u is the vector of additive genetic effects, E is the vector of residual effects, and X and Z are the incidence matrices for fixed effects (slaughterhouse - birth year - birth season and slaughter day) and random effect, respectively. The above equation is identical to the traditional BLUP model; however, it becomes a GBLUP model when genomic information is used instead of pedigree information. The matrix was expressed as follows:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1}/\sigma_u^2 \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}, \qquad G = \frac{ZZ'}{2\Sigma p_j(1-p_i)} = \frac{(M-P)(M-P)'}{2\Sigma p_j(1-p_i)}$$

where G is the genomic relationship matrix, R is the residual variance-covariance matrix, σ_u^2 is the additive genetic variance, M is the matrix of individual SNP genotypes, P is the matrix of expected genotype values, p_j is the frequency of the allele for the j-th locus. The centered genotype matrix Z was constructed by subtracting the expected genotype matrix P from the genotype matrix M [14]. Using the G matrix in this manner allows the estimation of additive effects by replacing the identical kinship coefficients between full-sib and half-sib relationships with genetic variation among individuals, leading to a more accurate estimation of breeding value compared to analyses using pedigree information.

The ssGBLUP model

The conventional BLUP and GBLUP methods analyze pedigree information and genomic information separately, whereas the ssGBLUP method integrates these data sources. By combining them, genetic relationships among individuals can be estimated more accurately, allowing for more precise genetic evaluation. The mixed linear model applied for the estimation of breeding values was identical to that used in the GBLUP method. The ssGBLUP method utilizes both pedigree and genomic information to construct an H matrix that represents genetic relationships among individuals. The H matrix represents an integrated relationship structure that includes individuals with genomic information and those connected through a pedigree but lacking genomic information, and was defined as follows:

$$H = \begin{bmatrix} H_{11} & H_{12} \\ H_{21} & H_{22} \end{bmatrix} = \begin{bmatrix} A_{11} + A_{12}A_{22}^{-1}(G - A_{22})A_{22}^{-1}A_{21} & A_{12}A_{22}^{-1}G \\ GA_{22}^{-1}A_{21} & G \end{bmatrix}$$

where H is the combined relationship matrix (pedigree + genome), A is the pedigree relationship matrix, and G is the genomic relationship matrix. For computational convenience, the inverse of the H matrix was used in the mixed model equations, as follows:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + H^{-1}/\sigma_u^2 \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}, \quad H^{-1} = A^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{bmatrix}$$

ssGBLUP has the advantage of being able to utilize the existing genetic evaluation process [15]. However, in the process of computing the inverse of the H matrix, efficient calculation of the inverse of the matrix (G^{-1}) is essential. Unlike the inverse of the pedigree relationship matrix (A^{-1}), there is no direct calculation method for the inverse of the G matrix (G^{-1}), and computation time can increase proportionally with the number of individuals with genomic information [14].

The wssGBLUP model

GBLUP and ssGBLUP methods assume that all SNPs contribute equally, whereas in reality, individual SNPs vary in their effects. The wssGBLUP method assigns iterative weights to SNPs, enabling a more accurate estimation of breeding value. The mixed linear model used for the estimation of breeding values was identical to that applied in the GBLUP method. The wssGBLUP method is based on the ssGBLUP method, which integrates genomic and pedigree information and assigns differential weights to SNP markers. This is achieved by introducing a diagonal matrix D which reflects the importance of each SNP marker during the construction of the genomic relationship matrix [5]. In the ssGBLUP method, D is set as the identity matrix. The equation used is as follows:

$$G_w = \frac{ZDZ'}{2\Sigma p_j(1-p_j)}$$

The process for predicting SNP weights (D matrix) was as follows. Initially, the weight matrix was set as the identity matrix, and breeding values were estimated using the ssGBLUP method. Based on this, the effect of each SNP was calculated and the SNP weights were computed using the square of the SNP effects and allele frequencies. The weight matrix was normalized to maintain the total genetic variance, and a new G matrix was generated using the updated weight matrix, followed by an iterative estimation of breeding values. This process can achieve sufficient analytical accuracy after 2-3 iterations [5].

Estimation of heritability and accuracy

Heritability was calculated using the estimated genetic and residual variances for each trait in each model (GBLUP, ssGBLUP, wssGBLUP). The formula used is as follows:

$$Heritability(h^2) = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_e^2}$$

where is heritability, σ_α^2 is the genetic variance, and σ_e^2 is the residual variance, with $\sigma_\alpha^2 + \sigma_e^2$ representing the phenotypic variance. Thus, heritability indicates the proportion of genetic components in the total phenotypic variation.

The accuracy of the breeding values for each model was estimated using the prediction error variance calculated for each individual during breeding value estimation. Additionally, the accuracy of the breeding values was estimated by analyzing the correlation between breeding values and actual phenotypic information.

$$Accuracy = \sqrt{1 - \frac{PEV}{\sigma_\alpha^2}}, \quad P_{X,Y} = \frac{cov(X,Y)}{\sigma_X \sigma_Y}$$

where PEV is the prediction error for each individual, σ_α^2 is the additive genetic variance for each trait. Correlation analysis was performed using the Pearson correlation coefficient between breeding values and phenotypic information. Realized accuracy theory posits that a correlation coefficient closer to 1 indicates a higher accuracy of the estimated breeding values.

Results

Descriptive statistical analyses

Descriptive statistics for phenotypic data are presented in Table 2. A total of 115,256 Hanwoo cattle raised nationwide were included in the analysis. The mean and standard deviation values for carcass traits, including CWT, EMA, BFT, and MSC, as well as estimated values for environmental traits, such as CEI, are presented. These values were 443.86±60.48 kg, 94.96±12.51 cm², 13.44±5.20 mm, 5.87±2.01 score, and 14.01±2.90 kg/CO_2eq, respectively.

Genetic parameter model estimations

Genetic parameters estimated for each trait derived from the GBLUP, ssGBLUP, and wssGBLUP models include additive genetic variance (σ_α^2), residual variance (σ_e^2), and phenotypic variance (σ_p^2). Heritability values (h^2) were calculated using the variance components (Table 3). The wssGBLUP model is based on the same H matrix as the ssGBLUP model and differs only in the iterative application of marker weights to the G matrix. Furthermore, since breeding values were estimated based on the same genetic parameters as the ssGBLUP model, the results were identical to those of the ssGBLUP model. The estimated heritability for CWT was 0.41 in the GBLUP model and 0.39 in the ssGBLUP/wssGBLUP models. For EMA, estimated heritability was 0.36 in the GBLUP model and 0.35 in the ssGBLUP/wssGBLUP models. Estimated heritability of BFT was 0.39 in the GBLUP model and 0.37 in, ssGBLUP/wssGBLUP, and for MSC, it was 0.48 and 0.49 in the GBLUP and ssGBLUP models, respectively. Finally, the estimated heritability of CEI was 0.35 and 0.34 in the GBLUP and ssGBLUP/wssGBLUP models, respectively. Examining the results by analysis model, heritability estimated by the GBLUP model was higher than that of the ssGBLUP and wssGBLUP models for all traits except MSC. The ssGBLUP and wssGBLUP models tended to estimate heritability more conservatively because they are based on both pedigree and genomic data. In addition, the GBLUP model used only a genomic-based G matrix, whereas the ssGBLUP/wssGBLUP models used an H matrix, which incorporated both pedigree and genomic information. Pedigree-based data may contain noise or low-accuracy information, potentially leading to a reduced accuracy. The MSC exhibited the highest heritability across all three models.

Analysis of accuracy of genetic evaluation

The accuracy of the genomic estimated breeding value (GEBV) based on the analysis models is listed in Table 4. Examining traits by trait, CWT recorded an accuracy of 0.67 for both GBLUP and ssGBLUP, while wssGBLUP showed the highest predictive capacity, at 0.75. This trend was similarly observed for EMA and BFT traits, with wssGBLUP consistently achieving higher accuracy than GBLUP and ssGBLUP, at 0.74 and 0.75, respectively. MSC had the highest accuracy across all models, with accuracies of 0.71, 0.70, and 0.77 for GBLUP, ssGBLUP, and wssGBLUP, respectively. CEI generally exhibited lower accuracy compared to other traits, with GBLUP and ssGBLUP models at 0.60 and 0.61, respectively, but wssGBLUP maintained a higher level of 0.71. Correlation analysis was performed between the breeding values of the test populations estimated by the analysis methods and the actual phenotypic information using the Pearson correlation coefficient. A correlation coefficient closer to 1 indicates that the estimation was more accurate and closer to the phenotype. The calculated correlation coefficients are shown as a heat map (Fig. 1). Overall, the ssGBLUP and wssGBLUP models showed a tendency towards higher correlation coefficients with phenotypes than the GBLUP models. For CWT, a gradual improvement was observed: 0.76 for GBLUP, 0.77 for ssGBLUP, and 0.78 for wssGBLUP. EMA also showed higher correlation coefficients with ssGBLUP and wssGBLUP than GBLUP. Although BFT showed a low correlation across all three models, the ssGBLUP and wssGBLUP models recorded slightly higher values (0.73) than GBLUP. MSC showed relatively high correlation coefficients across all three analysis models, with values of 0.80, 0.81, and 0.81 for GBLUP, ssGBLUP, and wssGBLUP, respectively. CEI had the lowest correlation coefficients overall, with values of 0.48, 0.52, and 0.47 for the GBLUP, ssGBLUP, and wssGBLUP models, respectively, with the ssGBLUP model showing the highest correlation coefficient. A comparative analysis of carcass traits and carbon emission intensity in Hanwoo cattle using the GBLUP, ssGBLUP, and wssGBLUP models revealed significant improvements in prediction accuracy with the latter two models.

Discussion

Comparing carcass performance with previous studies, Oh et al. [16] reported descriptive statistics for 1,905 Hanwoo cattle (steers), including CWT, EMA, BFT, and MSC, as 446.43±44.38 kg, 93.39±10.20 cm², 12.95±5.11 mm, and 6.10±1.94, respectively. Lee et al. [17], in their study of 186,332 Hanwoo cattle (steers), reported values of 432.70±54.85 kg, 93.04±12.27 cm², 13.51±5.46 mm, and 5.75±2.04, showing similar results to the present study. Kim et al. [18] analyzed 3,247,508 Hanwoo cattle slaughtered between 21 and 39 months of age, reporting an average CEI of 13.75 ± 1.4 kg/CO_2eq. The average CEI in this study was similar, at 14.01 ± 2.9 kg/CO_2eq.

In studies estimating genetic parameters through GBLUP modelling, Byun et al. [19] analyzed the heritability of 564 Hanwoo cattle (cows) and 13,000 Hanwoo steers raised nationwide, and reported 0.41, 0.38, 0.38, and 0.44 for CWT, EMA, BFT, and MSC, respectively. Mehrban et al. [20] reported heritabilities of 0.31, 0.44, 0.50, and 0.61 in an ssGBLUP analysis using 8,966 Hanwoo bulls and 6,313 Hanwoo cattle (steers). Mehrban et al. [21] reported heritability estimates of 0.28, 0.46, 0.57, and 0.59 using wssGBLUP for Hanwoo carcass traits in 5,134 animals, and Lopez et al. [6] reported 0.37, 0.35, 0.36, and 0.45 using the wssGBLUP model for 10,215 animals raised nationwide from 2006 to 2016. These findings indicate that heritability estimates vary significantly not only by the analysis model, but also by the characteristics of the herds used in the study. The heritability estimates most similar to those of the present study were found by Lopez et al. [6], sharing the commonality of analyzing commercial herds. Lassen & Løvendahl [22] defined methane emissions per liter of milk using 3,121 Holstein cattle, reporting a heritability of 0.21. Although a direct comparison with previous studies is challenging, because the CEI analyzed in this study reflects the carbon footprint across the entire rearing process rather than direct methane emissions, it provides insights into the impact of genetic factors across species on environmental efficiency [3]. These results underscore the importance of developing breeding strategies to enhance environmental sustainability in livestock breeding, and emphasize the need for research to identify and utilize genetic traits that contribute to reducing carbon emissions.

The accuracy of genetic evaluation was calculated based on the prediction error of estimated breeding values for each individual and the genetic variance of each trait; high values indicated greater consistency between actual genetic ability and estimated GEBV. The results showed that carcass traits exhibited high accuracy across all three models, with a significant improvement in the accuracy of the wssGBLUP method, which resulted from the increased utilization of genomic information through the application of weights. This accuracy improvement suggests that the weight-based wssGBLUP method can enhance the predictive power of traits with complex genetic backgrounds [4, 21]. CEI generally showed a lower predictive accuracy than other carcass traits, likely due to the influence of numerous environmental factors. This is presumed to be because CEI is heavily influenced by environmental factors. However, the wssGBLUP model demonstrated a significant improvement in accuracy, even for CEI prediction, demonstrating that the application of weights to genomic information can contribute to improved prediction even for traits heavily influenced by environmental factors.

High correlation coefficients between GEBV and phenotypic values were observed for carcass traits across all three models used in this study. However, CEI was poorly correlated across all three models, suggesting that CEI, which is significantly influenced by a complex set of environmental factors, has limitations in explaining the total phenotypic variation solely through genetic factors. Therefore, advanced modeling that considers the interaction between environmental factors and genomic data is needed to enhance the predictive accuracy of complex traits such as CEI.

CEI tended to decrease with higher carcass weight and younger slaughter month. Animals with greater growth efficiency and faster finishing times exhibited lower CEI values, indicating that a lower breeding value for CEI corresponds to a lower phenotypic CEI. This suggests a direction for genetic improvement of Hanwoo cattle that simultaneously achieves enhanced productivity and environmental load reduction, thereby contributing to the development of sustainable livestock farming. This integrated approach provides a pathway for more resource-efficient and ecologically responsible livestock production by integrating genetic selection with environmental sustainability

[2, 23, 24]. These findings highlight the importance of genomic-based breeding for achieving carbon footprint reduction goals in the livestock sector and provide essential scientific evidence for the future establishment of environmentally friendly livestock systems.

Conclusions

This study estimated the genetic parameters for carcass traits and CEI in Hanwoo cattle and compared the prediction accuracy of three genomic evaluation models: GBLUP, ssGBLUP, and wssGBLUP. The results showed that the ssGBLUP and wssGBLUP models exhibited higher accuracies than the GBLUP model, with the wssGBLUP model, which applied weights, demonstrating the best predictive performance across all traits. These findings represent significant progress in enhancing the prediction accuracy of complex quantitative traits using genomic information, particularly in weight-based models. Furthermore, this study confirmed the potential for reducing carbon footprints through Hanwoo cattle improvements, thereby suggesting a direction for genetic improvement that can contribute to the development of sustainable livestock farming. The findings of this study are expected to enhance the environmental sustainability of the Hanwoo cattle industry through precise breeding strategies and provide the scientific foundation necessary for achieving carbon neutrality goals in future livestock systems.

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Tables and Figures

Table 1. Detailed information on the genome population

Sex		Birth season		Birth region		Slaughter place		Slaughter month		Slaughter year	
Sets	Herds	Sets	Herds	Sets	Herds	Sets	Herds	Sets	Herds	Sets	Herds
Steer	18,327	Spring	5,796	Gangwon	1,720	A	14,396	24	11	2012	1
		Summer	2,918	Gyeonggi	1,199	B	1,087	25	80	2013	30
		Autumn	4,833	Gyeongnam	501	C	941	26	1,015	2014	20
		Winter	4,805	Gyeongbuk	3,133	D	649	27	2,476	2015	27
				Jeonnam	2,765	E	394	28	3,388	2016	7
				Jeonbuk	5,377	F	329	29	3,907	2017	2,222
				Chungnam	2,207	G	279	30	3,436	2018	8,061
				Chungbuk	1,435	H	77	31	2,625	2019	7,466
				Jeju	15	I	33	32	1,068	2020	507
						J	25	33	346	2021	3
						K	13			2022	8
						L	13				
						M	13				
						N	12				
						O	12				
						P	10				
						Q (≤10 heads)	69				
Total								18,352			

Table 2. Basic statistics for phenotype data in carcass traits and environmental impact trait (carbon emission intensity)

Type	Traits	No. of records	Mean	SD	Min	Max
Carcass traits	CWT (kg)	115,256	443.86	±60.48	113.00	760.00
	EMA (cm^2)		94.96	±12.51	2.00	184.00
	BFT (mm)		13.44	±5.20	1.00	59.00
	MSC (score)		5.87	±2.01	1.00	9.00
Environmental impact trait	CEI (kg/CO_2eq)	115,256	14.01	±2.90	5.95	69.42

CWT, carcass weight; EMA, eye muscle area; BFT, backfat thickness; MSC, marbling score; CEI, carbon emission intensity; mean, average; SD, standard deviation

Table 3. Estimated genetic parameters and heritability estimated using three models

Method	Traits	σ_α^2	σ_e^2	σ_p^2	h^2
GBLUP	CWT (kg)	909.0	1,319.1	2,228.1	0.41
	EMA (cm^2)	50.20	90.44	140.6	0.36
	BFT (mm)	9.33	14.82	24.1	0.39
	MSC (score)	1.58	1.73	3.3	0.48
	CEI (kg/CO_2eq)	0.86	1.62	2.5	0.35
ssGBLUP/ wssGBLUP	CWT (kg)	1,311.8	2,010.4	3,322.2	0.39
	EMA (cm^2)	54.57	99.53	154.1	0.35
	BFT (mm)	11.88	19.88	31.8	0.37
	MSC (score)	1.90	1.94	3.8	0.49
	CEI (kg/CO_2eq)	0.93	1.82	2.75	0.34

CWT, carcass weight; EMA, eye muscle area; BFT, backfat thickness; MSC, marbling score; CEI, carbon emission intensity; GBLUP, genomic BLUP; ssGBLUP, single-step genomic BLUP; wssGBLUP, weighted genomic BLUP.

σ_α^2: genetic variance, σ_e^2: residual variance, σ_p^2: phenotypic variance, h^2: heritability

Table 4. Comparison of prediction accuracy across three genomic evaluation models

Trait	Analysis method		
	GBLUP	ssGBLUP	wssGBLUP
CWT (kg)	0.67	0.67	0.75
EMA (cm^2)	0.65	0.66	0.74
BFT (mm)	0.66	0.66	0.75
MSC (score)	0.71	0.70	0.77
CEI (kg/CO_2eq)	0.60	0.61	0.71

CWT, carcass weight; EMA, eye muscle area; BFT, backfat thickness; MSC, marbling score; CEI, carbon emission intensity; GBLUP, genomic BLUP; ssGBLUP, single-step genomic BLUP; wssGBLUP, weighted single-step genomic BLUP; GEBV, genomic estimated breeding value

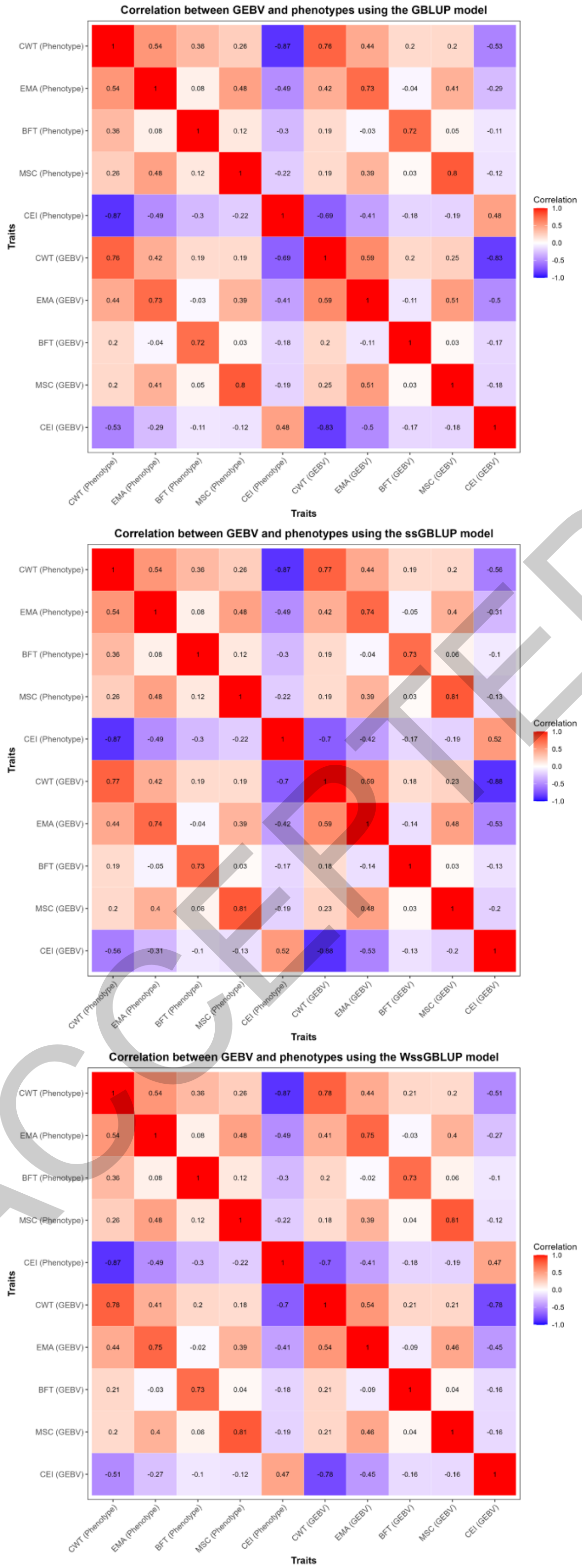

Fig. 1. Heatmaps of correlations between phenotypes and GEBVs estimated by GBLUP, ssGBLUP, and wssGBLUP models.