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Research Article

Genomic Evaluation and Genome-Wide Association Study of a Carbon Emission Proxy Trait Derived from Carcass Weight by Age in Hanwoo Cattle

Seunghwan Ko[1]†, Yoonji Chung[2], Hayeong Oh[1]†, Seung Hwan Lee[3]*, Phuong Thanh N. Dinh[1], JuHyeok Kim[3], Namuk Kim[3]
[1]Department of Bio-AI Convergence, Chungnam National University, Daejeon, 34134, Republic of Korea
[2]Institute of Agricultural Science, Chungnam National University, Daejeon, 34134, Republic of Korea
[3]Division of Animal & Dairy Science, Chungnam National University, Daejeon, 34134, Republic of Korea

*Corresponding author: slee46@cnu.ac.kr

ABSTRACT

Climate change mitigation and carbon neutrality have become global priorities, necessitating the reduction of greenhouse gas emissions in the livestock sector. However, the practical implementation of direct methane measurement is limited by high recording costs and the need for specialized equipment. This study investigated carcass weight by age (CWA) as a biologically meaningful proxy trait for carbon emission intensity in Hanwoo cattle. A reference population of 25,964 and a KPN population of 1,444 animals genotyped with the Hanwoo 50K SNP chip were utilized for genetic evaluation. The CWA-derived proxy trait was defined as the inverse of CWA (CWA^{-1}), representing the production time required per unit of carcass output. Genetic parameters and genomic estimated breeding values (GEBV) were estimated using a single-step genomic BLUP (ssGBLUP) framework. The heritability of CWA^{-1} was estimated at 0.343, which is comparable to or higher than conventional carcass traits such as carcass weight (0.327) and marbling score (0.291). Mean genomic prediction accuracy reached 0.783 in the reference population and 0.699 in the KPN population. Genome-wide association analysis identified significant genomic regions on chromosomes 4, 6, and 14, with candidate genes including *TOX, CALCR,* and *LCORL* associated with growth and production efficiency. Genetic trend analysis showed a consistent decrease in mean GEBV over birth years, indicating a favorable genetic tendency toward improved efficiency and reduced emission intensity. Incorporating the CWA^{-1} trait into the selection index demonstrated that environmental improvement can be pursued without sacrificing conventional genetic gain. These results suggest that CWA-derived traits serve as practical and candidate proxy trait for achieving both production efficiency and environmental sustainability in Hanwoo cattle.

Keywords: Hanwoo, Climate change, Carcass weight by Age, GEBV

INTRODUCTION

Climate change mitigation and the achievement of carbon neutrality have become major global policy priorities, and reducing greenhouse gas emissions is now an important goal in agricultural and livestock production systems (Lee et al., 2023). Among livestock species, ruminants are a major source of methane emissions because enteric fermentation produces substantial amounts of methane during feed digestion (Gerber et al., 2013). Since methane is a potent greenhouse gas, reducing emission intensity in beef production has become an important component of sustainable livestock breeding.

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Methane-related traits in cattle, including methane emission, methane yield, and methane intensity, have been reported to be heritable and genetically variable, suggesting that these traits can respond to selection (Ghavi Hossein-Zadeh, 2022; Brito et al., 2018; Kamalanathan et al., 2023). However, the practical implementation of these traits in routine breeding programs remains limited because direct measurement of methane emission at the individual level requires specialized equipment, such as GreenFeed systems (Hammond et al., 2016), repeated observations, and considerable recording costs (Kamalanathan et al., 2023; Garnsworthy et al., 2019). These constraints limit the feasibility of direct methane phenotyping in large-scale commercial populations and highlight the need for scalable proxy traits based on routinely collected production records.

To address these limitations, production efficiency-related proxy traits may provide a scalable alternative for indirectly evaluating emission intensity in beef cattle. Greenhouse gas emission intensity is influenced by the amount of carcass output produced relative to the time and resources required for production. Animals that achieve greater carcass output within a shorter production period are expected to use resources more efficiently and may generate lower cumulative emissions per unit of carcass output. In this context, carcass weight by age (CWA), defined as carcass weight produced per unit time, can be considered an indicator of production efficiency. Heo et al. (2025) provided a framework linking beef production efficiency with emission intensity, supporting the potential use of production-based proxy traits in emission-related studies. Therefore, the inverse of CWA, representing the production time required per unit of carcass output, may serve as an indirect proxy for emission intensity rather than a direct measure of methane emission or total greenhouse gas output.

Hanwoo is a native Korean cattle breed that has historically been used for draft purposes and was later intensively selected for beef production, particularly for superior marbling and meat quality (Lee et al., 2014). In the current Hanwoo breeding system, major carcass traits such as carcass weight (CWT), eye muscle area (EMA), backfat thickness (BF or BFT), and marbling score (MS) are included in the selection objective because they are directly related to carcass productivity and economic value (Lee et al., 2014). In contrast, environmental efficiency-related traits or proxy indicators for emission intensity have not yet been routinely incorporated into Hanwoo breeding objectives. This creates an important gap between conventional genetic improvement for productivity and emerging breeding goals for environmental sustainability.

The inclusion of environmental efficiency-related proxy traits in breeding programs requires the estimation of genetic parameters, such as additive genetic variance, residual variance, heritability, and genetic correlations with conventional economic traits. These parameters provide the basis for evaluating whether a trait is genetically variable and whether it can be improved without compromising existing breeding goals. In livestock populations, these parameters are commonly estimated using mixed model approaches based on restricted maximum likelihood (REML), while breeding values are predicted using Best Linear Unbiased Prediction (BLUP) and its genomic extensions (Patterson & Thompson, 1971; Henderson, 1984; VanRaden, 2008). Among genomic evaluation methods, single-step genomic BLUP (ssGBLUP) has become particularly useful because it integrates pedigree, phenotype, and genomic information within a single evaluation framework, thereby improving the accuracy of breeding value prediction (Aguilar et al., 2010; Christensen & Lund, 2010).

In addition to estimating breeding values, genome-wide association studies (GWAS) can be used to identify genomic regions associated with novel environmental efficiency-related proxy traits. In Hanwoo, previous GWAS have successfully detected loci associated with economically important carcass traits, including major loci on BTA14 affecting carcass weight (Lee et al., 2013). Similarly, the identification of genomic regions associated with CWA-derived proxy traits may improve our biological understanding of the trait and support future genomic selection for environmental efficiency.

Therefore, the objectives of this study were to: (1) define a CWA-derived efficiency proxy trait based on carcass weight by age; (2) estimate genetic parameters for this trait in Hanwoo cattle; (3) predict genomic breeding values and evaluate their accuracy using a genomic evaluation framework; (4) identify candidate genomic regions associated with the trait through GWAS; and (5) assess the potential incorporation of this trait into a selection index for Hanwoo breeding. Through these analyses, this study aimed to evaluate whether a CWA-derived proxy trait can serve as a practical breeding objective for improving both production efficiency and environmental sustainability in Hanwoo cattle.

MATERIALS AND METHODS

Animals and phenotypic data

A reference population consisting of 25,964 Hanwoo cattle and a KPN population consisting of 1,444 animals were used for the genetic evaluation of the CWA-derived proxy trait for emission intensity. All animals were genotyped using the Hanwoo 50K SNP chip (Illumina, San Diego, CA, USA), and phenotypic information was compiled from slaughter records and the Korea Animal Products Traceability System. The available phenotypic records included carcass weight (CWT, kg), eye muscle area (EMA, cm^2), backfat thickness (BF, mm), marbling score (MS, 1–9), birth year and month, slaughter year and month, sex, and age at slaughter (days). The reference population consisted of 25,610 steers and 354 cows, with slaughter ages concentrated around 29–31 months (Figure 1). These carcass and management variables were used to construct the CWA-derived proxy phenotype and to fit the genetic evaluation models.

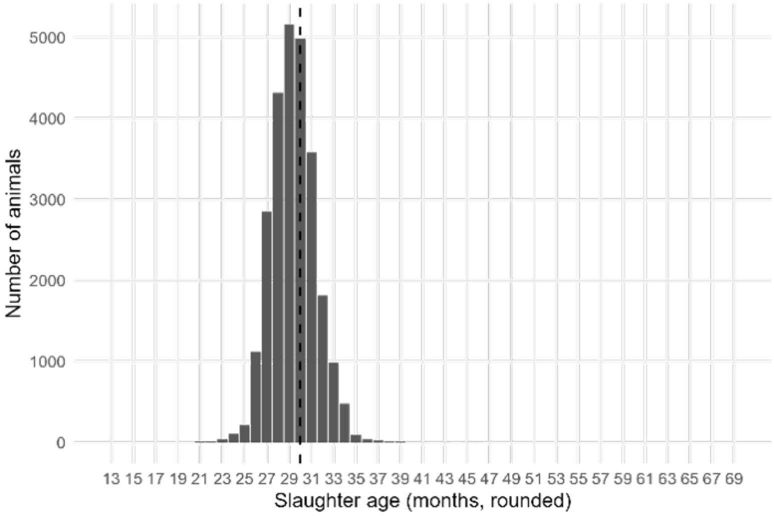

Figure 1. Distribution of slaughter age in the Hanwoo reference population

Definition of the CWA-derived efficiency proxy trait for emission intensity

In this study, carcass weight by age (CWA) was used as the biological basis for deriving a carbon emission-related proxy trait. Following the logic described in Heo et al. (2025), CWA represents carcass output per unit of production time and reflects individual production efficiency. It was calculated as:

$$\mathrm{CWA} = \frac{\text{Carcass weight (kg)}}{\text{Age at slaughter (days)}}$$

where carcass weight represents slaughter output and age at slaughter represents the total feeding or production period required to achieve that output. Animals with higher CWA values produce more carcass weight per unit time and are therefore interpreted as being more production efficient. Because emission intensity in beef systems is closely linked to the efficiency with which edible output is produced, a higher CWA corresponds to lower carbon burden per unit of production, whereas a lower CWA corresponds to a higher carbon burden. Based on this interpretation, the inverse of CWA was used in the present study as a carbon emission intensity-related phenotype. This trait was denoted as CWA^{-1}. Biologically, this transformed trait represents the amount of time required per unit carcass output and can be interpreted as an indirect index of carbon emission intensity, where higher values indicate lower efficiency and potentially greater emission intensity per unit product

(Heo et al., 2025). However, this trait should be interpreted as an indirect proxy based on production efficiency rather than a direct measure of methane emission, total greenhouse gas emission, feed intake, residual feed intake, or life-cycle carbon footprint.

Genotyping and quality control

All animals were genotyped using the Hanwoo 50K SNP chip. Marker quality control was performed using PLINK v1.9 (Purcell et al., 2007). SNPs and individuals with high missing genotype rates were excluded, and SNPs with minor allele frequency (MAF) less than 0.01 were removed. Specifically, genotype missingness was filtered using a threshold of less than 0.10, and only markers passing all quality control criteria were retained for downstream analyses. The resulting filtered SNP set was then used to construct the genomic relationship matrix and to perform genome-wide association analyses.

Genomic relationship matrix

A genomic relationship matrix was constructed using genome-wide SNP genotype information following the method of VanRaden (2008). In this approach, the genotype matrix is centered using allele frequencies, and genomic relationships are calculated so that realized genetic similarity among animals can be more accurately represented than with pedigree alone. Compared with the pedigree-based numerator relationship matrix, the genomic relationship matrix better captures Mendelian sampling and individual-specific allele sharing, which is particularly important for genomic evaluation of traits with complex inheritance (VanRaden, 2008).

If Z denotes the centered genotype matrix and p_i denotes the allele frequency of the i-th marker, the genomic relationship matrix G was constructed using the standard VanRaden formulation:

$$G = \frac{ZZ'}{2\sum p_i(1-p_i)}$$

where the denominator scales the matrix using expected marker heterozygosity. This genomic relationship matrix was used in the mixed model framework for genomic evaluation and variance component estimation.

Estimation of genetic parameters

Genetic parameters for the carbon emission-related trait and conventional carcass traits were estimated using a linear mixed model. A framework was adopted because the carbon-related proxy trait is biologically related to growth and carcass performance, and joint analysis can improve estimation efficiency by accounting for genetic and residual covariance among traits. In Hanwoo, carcass traits such as CWT, EMA, BF, and MS are continuous quantitative traits, and therefore a linear mixed model is appropriate.

The general linear mixed model can be written as:

$$y = Xb + Zu + e$$

where y is the vector of phenotypic observations for all analyzed traits, b is the vector of fixed effects, u is the vector of random additive genetic effects, and e is the vector of residuals. X and Z are the corresponding incidence matrices relating observations to fixed and random effects, respectively. The fixed effects included birth year-month, slaughter year-month, and sex. Age at slaughter was not fitted as an additional fixed effect in the CWA^{-1} model because it was already included in the definition of the derived trait.

The assumed variance structure was:

$$\mathrm{Var}(u) = H \otimes \Sigma_a \ \mathrm{Var}(e) = I \otimes \Sigma_e$$

where H is the pedigree-genomic relationship matrix, Σ_a is the additive genetic variance-covariance matrix among traits, Σ_e is the residual variance-covariance matrix among traits, I is an identity matrix, and $\otimes$ denotes the Kronecker product. This formulation allows the simultaneous estimation of additive genetic variances, residual variances, and covariance components among the analyzed traits. Variance components were estimated using REML implemented in the BLUPF90 family of programs (Patterson & Thompson, 1971; Henderson, 1984). Heritability for each trait was then calculated as the ratio of additive genetic variance to phenotypic variance. Genetic correlations were calculated from the estimated genetic covariance divided by the square root of the product of the corresponding genetic variances.

Genomic prediction of breeding values

Genomic estimated breeding values (GEBV) for the CWA-derived proxy trait were obtained using single-step genomic BLUP (ssGBLUP). The ssGBLUP approach integrates phenotypic, pedigree, and genomic information in a single evaluation system, and therefore allows information from both genotyped and non-genotyped relationships to contribute to prediction (Aguilar et al., 2010; Christensen & Lund, 2010). In the present study, this framework was used to estimate breeding values for the CWA-derived proxy trait and conventional carcass traits in Hanwoo.

Even when a target trait has limited direct records or relatively low heritability, prediction accuracy can be improved by borrowing information from correlated traits and from realized genomic relationships among animals. This is one of the key advantages of using genomic evaluation for newly proposed breeding objective traits. The mixed model equations were solved to obtain GEBV for all evaluated animals.

Accuracy of breeding values

The accuracy of breeding value prediction was evaluated using prediction error variance (PEV). In genetic evaluation, prediction accuracy is commonly interpreted as the correlation between the true breeding value and its estimate. Because true breeding values are unknown, this correlation can be approximated using the additive genetic variance and the PEV. Accuracy was calculated from additive genetic variance and PEV. The usual expression is:

$$\text{Accuracy} = \sqrt{1 - \frac{\text{PEV}}{\sigma_a^2}}$$

where σ_a^2 is the additive genetic variance of the trait. This statistic provides a practical measure of the reliability of genomic breeding values in both the reference and KPN populations.

Genome-wide association study

A genome-wide association study (GWAS) was performed to identify genomic loci associated with the CWA-derived carbon emission-related trait. Because the trait was analyzed in a structured population with related individuals, a linear mixed model was used to control for confounding due to relatedness and population structure. The model included fixed effects, the effect of the tested SNP, a random polygenic effect based on the genomic relationship matrix, and a residual term. This general model structure is consistent with mixed model GWAS commonly used in livestock populations.

The GWAS model may be expressed as:

$$y = Xb + Sa + Zu + e$$

where y is the vector of phenotypes for the carbon-related trait, b is the vector of fixed effects, a is the allele substitution effect of the tested SNP, S is the SNP genotype covariate, u is the vector of random polygenic effects assumed to follow $N(0,G\sigma_u^2)$, and e is the vector of residuals assumed to follow $N(0,I\sigma_e^2)$. Significant association signals were subsequently interpreted by examining nearby genes previously reported to be related to carcass growth, feed intake, or production efficiency.

Selection index analysis

To evaluate the potential use of the CWA-derived proxy trait in Hanwoo breeding, modified selection index scenarios were constructed by incorporating the standardized GEBV for CWA^{-1} into the conventional selection index used for KPN evaluation. Because CWA^{-1} represents the production time required per unit of carcass output and lower values are favorable, the CWA^{-1} component was included in the index in the favorable direction. Three weighting scenarios were examined: no CWA^{-1} weighting, moderate CWA^{-1} weighting, and maximum CWA^{-1} weighting, represented by weights of 0, 0.5, and 1.0, respectively. These weights were not derived from formal economic values but were used as hypothetical emphasis levels to evaluate how incorporation of the CWA-derived proxy trait could influence the direction of genetic change. The purpose of this analysis was to assess whether environmental efficiency could be considered in the selection framework without substantially compromising conventional genetic gain.

RESULTS AND DISCUSSION

Genetic parameters of the CWA-derived carbon emission trait

The CWA-derived proxy trait for carbon emission intensity (CWA^{-1}) exhibited substantial additive genetic variation in the Hanwoo population. As presented in Table 1, the additive genetic variance and residual variance were estimated at 0.896 and 1.712, respectively, resulting in a heritability (h^2) of 0.343. This estimate is comparable to, or slightly higher than, those of conventional carcass traits, including carcass weight (0.327), backfat thickness (0.279), eye muscle area (0.281), and marbling score (0.291). These results indicate that the CWA-derived proxy trait is genetically variable and has sufficient additive genetic variation to respond to selection.

From a breeding perspective, this finding is important because the practical use of a newly proposed efficiency-related proxy trait depends on whether it is heritable. The moderate heritability of CWA^{-1}(day/kg) suggests that indirect genetic improvement of production efficiency related to emission intensity may be feasible through selection. This result is consistent with previous studies reporting that methane-related and efficiency-related traits in cattle exhibit non-zero heritability and can respond to selection (Ghavi Hossein-Zadeh, 2022; Brito et al., 2018; Kamalanathan et al., 2023).

However, it is important to emphasize that CWA^{-1}(day/kg) represents an indirect proxy rather than a direct measurement of methane emission or total greenhouse gas output. Therefore, the biological interpretation of the heritability estimate should be linked to production efficiency, specifically carcass output relative to production time, rather than to methane emission physiology per se. The strength of this approach lies in its scalability, because it uses routinely recorded production data, whereas its limitation is that emission intensity is inferred indirectly through production efficiency (Heo et al., 2025).

Table 1. Summary of genetic parameter estimation for CWA-1, CWT, BF, EMA, MS

Parameters	CWA^{-1}	CWT	BF	EMA	MS
Genetic variance (σ_A^2)	0.896	1207.800	10.300	50.146	1.087
Residual variance (σ_e^2)	1.712	2487.700	26.642	128.53	2.642
Phenotypic variance (σ_P^2)	2.608	3695.5	36.942	178.67	3.729
Heritability(h^2)	0.343	0.327	0.279	0.281	0.291

Genetic relationship between CWA^{-1} and carcass weight

Because CWA^{-1}(day/kg) is a derived trait that includes carcass weight in its denominator, the genetic relationship between CWA^{-1} and CWT was additionally evaluated using a bivariate model. The genetic covariance between CWT and CWA^{-1} was estimated at −30.751, resulting in a strong negative genetic correlation of −0.997 (Table 2). This result indicates that animals genetically predisposed to greater carcass weight tend to have lower CWA^{-1} values, which is the favorable direction for the CWA-derived proxy trait.

The strong negative genetic correlation also suggests that a large proportion of the genetic variation in CWA^{-1} (day/kg) is related to the carcass weight component embedded in the trait definition. Therefore, CWA^{-1} should not be interpreted as an independent direct emission phenotype. Rather, it reflects production efficiency, particularly carcass output relative to production time, and may provide a practical proxy for emission intensity in the context of carcass-oriented Hanwoo breeding.

Table 2. Genetic covariance and genetic correlation between CWT and CWA^{-1}

Trait	Genetic variance of CWT	Genetic variance of CWA^{-1}	Genetic covariance	Genetic correlation
CWT −CWA^{-1}	1034.6	0.919	-30.751	-0.997

Distribution and accuracy of genomic breeding values

The distribution of genomic estimated breeding values (GEBV) for the CWA-derived proxy trait was highly consistent between the reference and KPN populations (Figure 2), indicating stability and robustness of the genomic evaluation model. The GEBV distributions were centered around zero, reflecting the polygenic architecture of the trait.

Prediction accuracy was evaluated using prediction error variance (PEV). The mean PEV-based accuracy was 0.783 in the reference population and 0.699 in the KPN population (Table 3). These accuracy levels are sufficiently high to support the application of genomic selection for environmental efficiency-related proxy traits in Hanwoo breeding programs.

This level of accuracy may be attributable to the use of genomic relationship information, which captures Mendelian sampling and realized relatedness more effectively than pedigree-based approaches (VanRaden, 2008), together with the large reference population size that supported stable genomic prediction.

Although accuracy in the validation population was slightly lower, this is expected due to reduced direct information. Nevertheless, the observed accuracy remains sufficiently high for practical use in selection decisions, particularly for early-stage candidate evaluation.

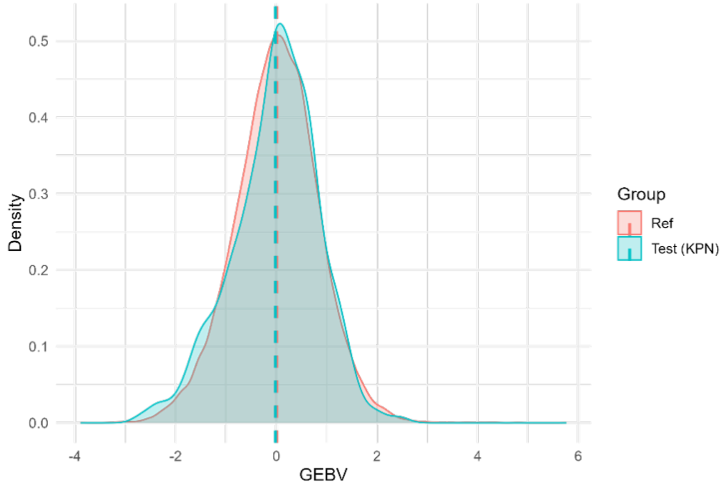

Figure 2. Distribution of breeding value CWA^{-1} in the reference and KPN populations

Table 3. Accuracy of breeding value for carcass traits and CWA^{-1}

trait	group	mean of accuracy	standard error of accuracy
CWT	reference	0.849	0.000188
	test	0.786	0.00443
BF	reference	0.813	0.000232
	test	0.738	0.00545
EMA	reference	0.762	0.000308
	test	0.653	0.00769
MS	reference	0.736	0.00038
	test	0.587	0.00897
CWA^{-1}	reference	0.783	0.000267
	test	0.699	0.00656

Genome-wide association analysis and candidate genes

The genome-wide association study (GWAS) identified several significant genomic regions associated with the CWA^{-1}(day/kg) on chromosomes 4, 6, and 14 (Figure 3). The most prominent signal was detected near the TOX gene on chromosome 14, with a −log10(p) value exceeding 20. Additional significant loci were identified near CALCR (BTA4) and LCORL (BTA6) (Table 4).

The genomic inflation factor ($\hat{\lambda} = 0.943$) indicated that population structure and relatedness were effectively controlled, minimizing false-positive associations. Most of the significant variants were located in intronic regions, suggesting that regulatory variation may contribute to phenotypic differences in the CWA-derived proxy trait.

Biologically, these candidate genes are strongly associated with growth, body size, and production efficiency. Previous studies have reported that LCORL and BTA14 loci are major determinants of carcass weight and growth-related traits in cattle (Lee et al., 2013; Lindholm-Perry et al., 2011; Grigoletto et al., 2020). Therefore, the present GWAS results suggest that genetic variation in the CWA-derived proxy trait may be linked to genomic regions involved in growth and carcass production efficiency.

However, it is important to interpret these findings cautiously. Because the analyzed trait is an inverse efficiency proxy rather than a direct emission phenotype, the identified loci should not be interpreted as “carbon emission genes” in a strict physiological sense. Instead, they represent genomic regions influencing biological processes that indirectly affect emission intensity through production efficiency.

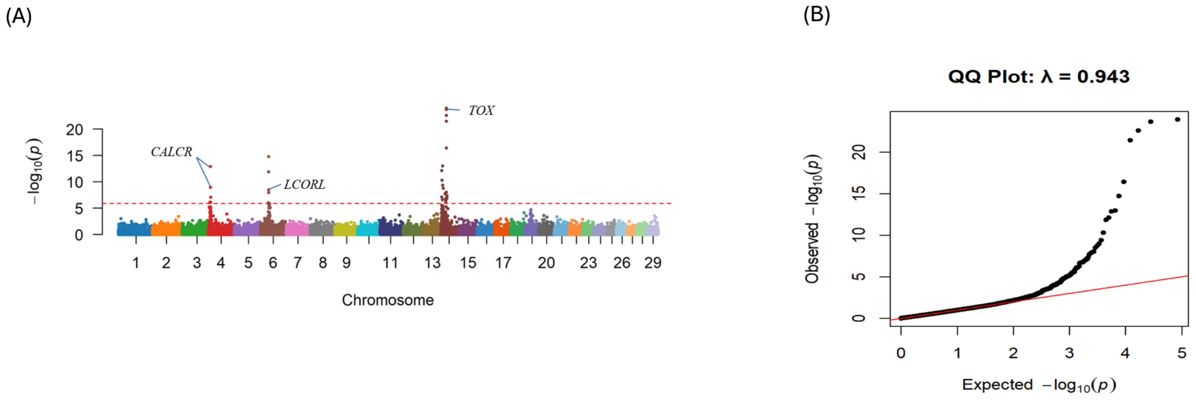

Figure 3. Genome-wide association results for the CWA-derived proxy trait (CWA^{-1}) in Hanwoo cattle. (A) Manhattan plot showing genome-wide association signals, with significant loci highlighted on chromosomes 4, 6, and 14. (B) Quantile–quantile (QQ) plot.

Table 4. Candidate genes associated with CWA^{-1}

Chr	SNP ID	Position(bp)	MAF	−log10(p)	Gene	Variant type
4	BTB-00166030	10,715,105	0.164	12.90	CALCR	Intron variant
6	Hapmap33628-BTC-041023	38,939,012	0.112	8.51	LCORL	Intron variant
14	Hapmap30932-BTC-011225	26,766,010	0.178	22.63	TOX	Intron variant

Genetic trends and implications for carbon-efficient breeding

The genetic trend analysis across birth years revealed important insights into the long-term dynamics of productivity and environmental efficiency in Hanwoo cattle (Figure 4).

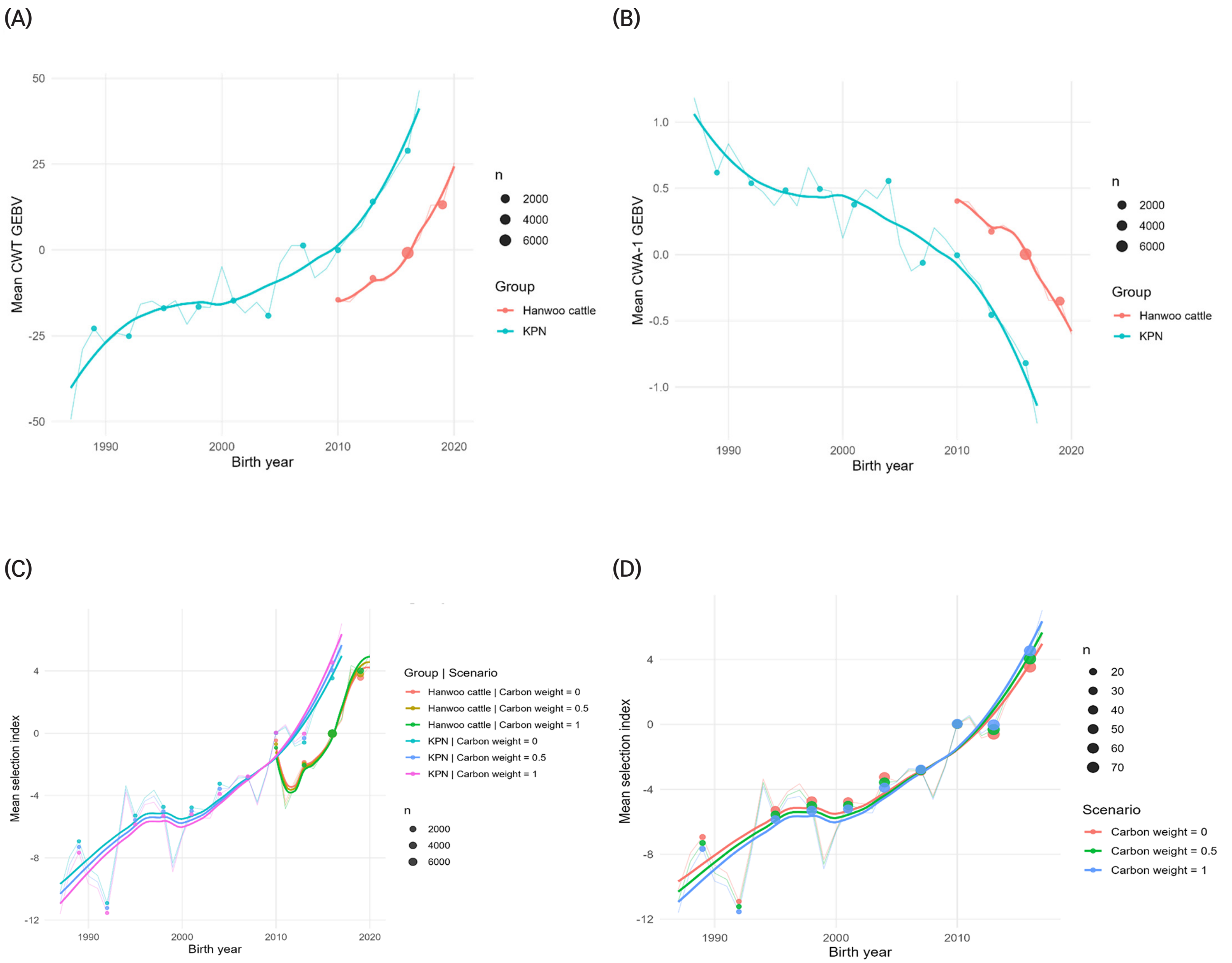

Figure 4. Genetic trends of GEBV and selection index in Hanwoo by birth year. (A) Genetic trends of CWT GEBV in the KPN and reference populations. (B) Genetic trends of mean GEBV for the CWA-derived proxy trait (CWA^{-1}) across birth years in the reference and KPN populations. (C) Genetic trends of selection index under different CWA^{-1} in the KPN population. (D) Genetic trends of selection index values under different CWA^{-1} weights in the KPN population.

First, the GEBV for carcass weight (CWT) showed a consistent increasing trend in both reference and KPN populations (Figure 4A), reflecting the success of long-term selection for production traits.

Second, the CWA^{-1}(day/kg) trait exhibited a clear decreasing trend over time (Figure 4B). Because lower values of CWA^{-1} correspond to higher production efficiency and lower emission intensity per unit output, this result indicates that past selection for growth and carcass traits has already resulted in a favorable correlated response for environmental efficiency.

This finding highlights a critical point in livestock breeding: improvements in productivity can indirectly reduce environmental impact at the system level. As proposed by Heo et al. (2025), carbon emission intensity is fundamentally linked to production efficiency. Animals that produce more output in less time require fewer resources and reduce the number of animals needed to achieve a given production target.

From a system perspective, total emission can be expressed as: Total emission $\propto$ Number of animals $\times$ Production period. Because the number of animals required is inversely proportional to carcass weight, total emission becomes proportional to: Total emission $\propto$ Age(days) / Carcass weight.

This relationship explains why the CWA^{-1} (day/kg) can serve as a proxy for carbon emission intensity. Therefore, selection for higher CWA (or lower CWA^{-1}) effectively reduces both production time and animal numbers, leading to lower cumulative emissions.

Selection index and breeding implications

The integration of the CWA-derived trait into the selection index did not compromise genetic gain for conventional traits (Figure 4C–D). Across different weighting scenarios (0, 0.5, and 1.0), the overall genetic trends remained positive and comparable to the conventional index.

This result demonstrates that environmental sustainability and productivity are not necessarily antagonistic breeding objectives. Instead, they can be simultaneously optimized when efficiency-based traits are incorporated into the selection framework.

However, it should be noted that the weighting factors used in this study were exploratory rather than derived from formal economic or policy-based values. Therefore, the current results should be interpreted as a proof of concept. Future research should aim to develop economically optimized weighting strategies and evaluate long-term correlated responses across multiple traits.

Overall implications

Taken together, the results of this study suggest that the CWA-derived trait is a practical and genetically informative indicator related to emission intensity in Hanwoo cattle. The trait exhibits moderate heritability, high genomic prediction accuracy, biologically relevant genetic associations, and favorable genetic trends over time.

Most importantly, this study provides a conceptual framework for carbon-efficient breeding based on production efficiency. Unlike direct methane measurements, which are costly and difficult to scale, the proposed approach enables immediate implementation using existing production data.

Although further validation using direct emission measurements is required, the present findings suggest that efficiency-based proxy traits can serve as a realistic and scalable pathway toward environmentally sustainable livestock breeding.

CONFLICT OF INTERESTS

No potential conflict of interest relevant to this article is reported.

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AUTHORS INFORMATION

Seung Hwan Lee: https://orcid.org/0000-0003-1508-4887
Seunghwan Ko: https://orcid.org/0009-0000-1367-6155
Yoonji Chung: https://orcid.org/0000-0002-6906-6468
Phuong Thanh N. Dinh: https://orcid.org/ 0000-0002-3057-0210
Hayeong Oh: https://orcid.org/ 0009-0007-9674-8599
JuHyeok Kim: https://orcid.org/0009-0005-4919-6811
Namuk Kim: https://orcid.org/0009-0008-1834-5425