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<b>Running Title</b>	Genetic correlations and prediction for Hanwoo reproductive and carcass traits
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3

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## 5 **Abstract**

6 This study estimated the heritabilities ( $h^2$ ) and genetic and phenotypic correlations between reproductive traits,  
7 including calving interval (CI), age at first calving (AFC), gestation length (GL), number of artificial  
8 inseminations per conception (NAIPC), and carcass traits, including carcass weight (CWT), eye muscle area  
9 (EMA), backfat thickness (BF), and marbling score (MS) in Korean Hanwoo cows. In addition, the accuracy of  
10 genomic predictions of breeding values was evaluated by applying the genomic best linear unbiased prediction  
11 (GBLUP) and the weighted GBLUP (WGBLUP) method. The phenotypic data for reproductive and carcass traits  
12 were collected from 1,544 Hanwoo cows, and all animals were genotyped using Illumina Bovine 50K SNP chip.  
13 The genetic parameters were estimated using a multi-trait animal model using the MTG2 program. The estimated  
14  $h^2$  for CI, AFC, GL, NAIPC, CWT, EMA, BF, and MS were 0.10, 0.13, 0.17, 0.11, 0.37, 0.35, 0.27, and 0.45,  
15 respectively, according to the GBLUP model. The GBLUP accuracy estimates ranged from 0.51 to 0.74, while the  
16 WGBLUP accuracy estimates for the traits under study ranged from 0.51 to 0.79. Strong and favorable genetic  
17 correlations were observed between GL and NAIPC (0.61), CWT and EMA (0.60), NAIPC and CWT (0.49), AFC  
18 and CWT (0.48), CI and GL (0.36), BF and MS (0.35), NAIPC and EMA (0.35), CI and BF (0.30), EMA and MS  
19 (0.28), CI and AFC (0.26), AFC and EMA (0.24), and AFC and BF (0.21). The present study identified low to  
20 moderate positive genetic correlations between reproductive and carcass weight traits, suggesting that a heavier  
21 body weight may lead to a longer CI, AFC, GL, and NAIPC. The moderately positive genetic correlation between  
22 CWT and AFC, and NAIPC, with a phenotypic correlation of nearly zero, suggesting that the genotype-  
23 environment interactions are more likely to be responsible for the phenotypic manifestation of these traits. As a  
24 result, the inclusion of these traits by breeders as selection criteria may present a good opportunity for developing  
25 a selection index to increase the response to the selection and identification of candidate animals, which can result  
26 in significantly increased profitability of production systems.

27 **Keywords:** Carcass traits; Correlation; Hanwoo; Heritability; Reproductive traits.

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## Introduction

Hanwoo is one of the oldest autochthonous cattle breeds in the world. Up to the 1960s, it was used primarily for farming on the Korean peninsula [1]. The Hanwoo has steadily been converted by Korean farmers from agricultural animals to beef cattle since the 1960s. The meat of choice in recent years has been locally raised Korean cattle, and it is priced accordingly. Hanwoo beef is renowned for its thick marbling, flavorful beefiness, and somewhat sweet flavor. It is also healthier than meat from other cattle breeds because it contains more omega-3 fatty acids with less cholesterol [2].

Reproduction traits play a vital role in the beef cattle industry as they directly influence the efficiency and profitability of production systems. Key reproductive traits, such as calving interval, age at first calving, gestation length, and number of artificial inseminations per conception, are of great importance in beef cattle breeding programs. These traits not only affect the reproductive performance of individual animals but also have significant impacts on overall herd productivity and management. A shorter calving interval enables more frequent calf production, leading to increased productivity and potential economic gains. It also facilitates efficient management practices such as grouping calves for marketing and optimizing nutrition management. Age at first calving influences lifetime productivity and profitability, as early maturing females have an extended reproductive lifespan, resulting in a higher cumulative number of calves produced. Achieving optimal age at first calving maximizes heifer utilization and minimizes costs associated with delayed breeding. Gestation length, influencing reproductive efficiency and overall management, demands accurate knowledge for optimal calving planning, timely calving assistance, postpartum care. Furthermore, comprehending the genetic control of gestation length informs breeding strategies to achieve desired calving seasons and synchronization protocols. The number of artificial inseminations per conception is crucial for reproductive success, with higher conception rates and fewer inseminations reducing costs while expediting genetic progress through more efficient use of superior sires. Improving fertility and reducing artificial inseminations enhance reproductive performance and drive increased profitability in beef cattle operations [3]. Challenges such as low reproductive capacity and infertility can result in extended durations between calvings, requiring additional interventions such as extra inseminations, increased veterinary attention, and hormonal treatments [4]. These interventions can disrupt current and subsequent lactations, leading to decreased productivity.

In cow breeding systems, the breed, sex, class, and location affect reproduction differently [5]. The outstanding

59 performance of male and female reproduction is a requirement for effective beef production techniques.  
60 Successfully incorporating reproductive features into genetic improvement projects requires advances in analysis  
61 techniques and whole-herd reporting [5]. The EBV and the reliability of anticipated breeding values (EBVs) are  
62 critical for selecting superior offspring to replace the present generation. The reliability of EBVs can be influenced  
63 by several factors, including selection intensity, pedigree errors, and generation interval [6]. According to the most  
64 recent studies, reproduction should be prioritized in a traditional cow-calf operation to maximize profitability.  
65 Even in a fully integrated cattle farm, reproduction necessitates an equal emphasis on attributes related to  
66 consumption and output. Genomic selection can give a large boost to the existing rates of genetic gain for beef by  
67 enhancing the accuracy of reproductive traits. The problem for cattle breeding is to improve the genetic variations  
68 identified by genomic estimations for those aspects of high genetic value that have less precision at the time of  
69 selection. The accuracy of genomic selection is currently poorer in beef cattle than in dairy cattle because of the  
70 relatively limited sample size with phenotypes and genotypes used to refine genomic prediction equations. For  
71 common heritable features, such as female reproductive traits, additional genotyped and phenotyped animals are  
72 needed to improve the accuracy of genomic predictions in beef cattle.

73 The Korean beef sector is seeing increased demand for genetically improving carcass qualities. The key  
74 qualities in the Hanwoo breeding program that were chosen and included in a selection index to boost the  
75 profitability of the meat industry were the carcass weight (CWT), back fat thickness (BF), eye muscle area (EMA),  
76 and marbling score (MS).

77 The genetic architecture of economically significant traits has been investigated regularly across many cattle  
78 populations since genotyping tools and enhanced genetic evaluation methodology emerged. Genome-wide  
79 association analyses have recently been used to find single nucleotide polymorphisms (SNPs) associated with  
80 reproduction traits in cows [7].

81 The correlations generally indicate how closely two traits are related [8]. A deeper knowledge of the common  
82 biological pathways and the causation linkages between two traits may be achieved by the genetic correlation,  
83 which explains the genetic relationship between two traits [9]. A strong correlation between two variables indicates  
84 their strong relationships and vice versa [10]. Typically, the correlation of the breeding values of traits is used to  
85 define the genetic correlation [11]. The genes contributing to the traits are typically co-inherited when two traits  
86 are significantly genetically connected. The phenotypic and genetic correlations are powerful tools for predicting

87 how one trait would respond to selection due to selection on another [8]. When selecting for overall merit  
88 incorporating multiple traits, the genetic correlation reflects the degree to which two traits are affected by the same  
89 genes or genes present within the same chromosome. According to calculations of the genetic correlation between  
90 two traits, selection for one trait may indirectly affect the genetic response for the other trait [12]. The pleiotropy  
91 of genes is the leading cause of the correlation, but linkage disequilibrium can also play a role [11]. A thorough  
92 understanding of the genetic variation of economically significant reproduction and production traits and precise  
93 estimation of genetic and phenotypic correlations of economically significant traits are also necessary for  
94 establishing effective genetic improvement programs [13]. Nevertheless, the genetic and phenotypic relationships  
95 between the reproductive and carcass traits of Korean Hanwoo cattle are poorly understood. The genetic  
96 parameters, genomic prediction accuracy, and correlations (phenotypic and genetic) among reproductive and  
97 carcass traits in Hanwoo cows were calculated to achieve these goals.

98

99

## **Materials and Methods**

### **Animal phenotypes**

100  
101 The data were collected using an existing database from 1,544 Hanwoo cows born between 2007 and 2020 and  
102 slaughtered between 2018 and 2022 and were part of nine (9) local livestock farms spread over the  
103 Gyeongsangbuk-do region in South Korea. All cows were slaughtered between 24 and 178 months of age. The  
104 analysis included reproductive traits, such as calving interval (CI), age at first calving (AFC), gestation length  
105 (GL), and the number of artificial inseminations per conception (NAIPC), as well as the carcass traits like carcass  
106 weight (CWT), eye muscle area (EMA), back fat thickness (BF), and marbling score (MS). The Animal Care and  
107 Use Committee's permission was not required for this study because all the data were obtained from the existing  
108 database. After a quality assessment, the remaining data included the values for CI ranging from 242 to 601 days,  
109 AFC between 499 and 999 days, GL between 252 and 337 days, CWT between 160 and 541 kg, EMA between  
110 22 and 131 cm<sup>2</sup>, BF between 2 and 39 mm, and MS scores between 1 and 9. The records of animals with a NAIPC  
111 above four were eliminated from the dataset. The Korean carcass grading procedure by the National Livestock  
112 Cooperatives Federation was used to record the phenotypic data for carcass traits, including CWT, EMA, BF, and  
113 MS. The CWT was measured on samples taken after 24 hours postmortem at the end of refrigeration. EMA was

114 measured using a dot-grid method with a cross-sectional slice between the 13<sup>th</sup> rib and the 1<sup>st</sup> lumbar vertebrae  
115 perpendicular to the vertebral column, where BF was also measured. A visual assessment of the marbling score  
116 was conducted using a categorical system of nine levels, based on the Korean Livestock Products Grading  
117 Guideline, ranging from 1 (no marbling) to 9 (high marbling). The details of phenotypic distribution information  
118 for the studied animals are presented in Fig. 1.

## 119 **Genotypic data**

120 The 1,544 Hanwoo cows used in this study were genotyped using Illumina Bovine 50K SNP Chip (Illumina  
121 Inc., San Diego, CA, USA), in which 52,116 SNPs were embedded. The blood samples collected by veterinarians  
122 were used to obtain the DNA. SNPs located on sex chromosomes and with unknown and duplicate positions were  
123 removed for further quality control procedures. Several QC thresholds were set to remove poor-quality SNPs for  
124 further analysis. SNPs were discarded from the analysis when the SNP call rate was less than 90%, individuals  
125 with a genotyping call rate less than 90%, and minor allele frequency (MAF) was less than 1% (monomorphic).  
126 The genotype frequency significantly deviated ( $p < 0.000001$ ) from Hardy–Weinberg Equilibrium (HWE). The  
127 identity-by-state (IBS) test was performed to determine if there were similar individuals or genotyping errors in  
128 the datasets. The pair of individuals showing a similarity rate >99% indicates an identical animal or error in  
129 genotyping. The entire QC process and IBS test were performed through PLINK v1.9 [14]. Furthermore, the  
130 missing alleles were imputed using Beagle v5.4 software [15]. After IBS and QC, 1,526 animals with genotypes  
131 of 41,445 SNPs were available for further analysis.

## 132 **Statistical analysis**

### 133 *Genomic best linear unbiased prediction (GBLUP)*

134 The dataset fit for an animal model with a genomic relationship matrix was performed to obtain the breeding  
135 values, including 1,103 complete records of all eight traits. The birth year and birth season were combined into  
136 one composite fixed effect. The fixed covariate of age at slaughter was also fitted with traits. The additive genetic  
137 effect of the animal was fitted as a random genetic component in the model. The genomic estimated breeding  
138 values (GEBV) were predicted using MTG2 v2.2 computer program [16]. The multi-trait animal model was  
139 implemented as follows [17]:

140 
$$y = Xb + Zu + e$$

141 where  $y$  represents the vector of phenotypic records (trait) for an  $n$ -animal sample;  $Xb$  is the fixed effects [18];  
 142  $Zu$  is the overall marker loci which are assumed to equal the vector of breeding values ( $a$ );  $e$  is the vector of  
 143 random residual effect which is assumed to be normally distributed with  $N(0, I\sigma_e^2)$ . In addition,  $\text{var}(u) = G\sigma_u^2$   
 144 where  $\sigma_u^2$  is the genetic variance, and  $G$  denotes the genomic relationship matrix (GRM), which was constructed  
 145 using the following equation [17]:

146 
$$G = \frac{(M - P)(M - P)'}{2 \sum_{i=1}^m p_i(1 - p_i)}$$

147 where the marker matrix  $M$  has dimensions of  $n \times m$ ;  $n$  is the number of individuals;  $m$  is the number of markers  
 148 used. The element of the  $P$  matrix was calculated using the formula,  $P_i = 2(p_i - 0.5)$ , where  $P_i$  represents the  
 149 minor allele frequency of the marker at locus  $i$ .  $(M - P)$  represents the incidence matrix ( $Z$ ) for markers.

150 The genomic relationship matrix (GRM) was constructed using the genome-wide complex trait analysis (GCTA)  
 151 tools developed by Yang [19], which effectively retains the genomic relationship between animals [17].

152 *Weighted genomic best linear unbiased prediction (WGBLUP)*

153 The WGBLUP model and inferences were the same as the above-described GBLUP technique, which had a  
 154 different way of constructing the matrix  $G$ . The  $G$ -matrix above was developed assuming that each SNP explains  
 155 the same proportion of genetic variance [20]. Wang [21] introduced the WGBLUP method and used the weighted  
 156  $G$  ( $G^*$ ) for significant SNPs with comparatively substantial effects. This genomic relationship matrix  $G^*$  was  
 157 constructed as follows [17]:

158 
$$G = \frac{ZDZ'}{2 \sum_{i=1}^m p_i(1 - p_i)}$$

159 where  $Z$ ,  $p_i$ , and  $n$  are the same as GBLUP, and  $D$  is the diagonal matrix in the WGBLUP technique, and its  
 160 values were determined by the weights derived from the SNP solutions discussed by Wang [21]. Following  
 161 Strandén and Garrick [22], the following can be derived:

162 
$$\hat{u} = DZ'G^{-1} \hat{g}$$

163 where  $\hat{u}$  is the vector of estimated SNP effects, and  $\hat{g}$  is a vector of GEBV from only genotyped individuals.  
 164 The weight for SNP  $i$  in this study was calculated as  $u_i^2$ . Constructing an algorithm for predicting  $D$  from GBLUP

165 is possible using the above equation. The algorithm was as follows for the iterative steps of the WGBLUP, as  
 166 stated by Wang [21]:

- 167 i. Set  $t = 0$ ,  $D_{(t)} = I$ , where  $t$  is the iteration number, and  $I$  denotes the identity matrix.
- 168 ii. The construct matrix  $G_t = ZD_{(t)}Z'\lambda$ , where  $t$  is the iteration number; The incidence matrix  $Z$   
 169 equals the matrix  $M$  minus matrix  $P$ , in which  $M$  is  $n \times m$  where  $n$  is the number of individuals and  $m$  is  
 170 the number of markers used, and  $P$  represents to  $2p_i$ .
- 171 iii. Compute genomic EBV (GEBV,  $\hat{g}$ ) utilizing the GBLUP method.
- 172 iv. Calculate SNP effects of all SNP as  $\hat{u}_{(t)} = \lambda D_{(t)} Z G_{(t)}^{-1} \hat{a}_g$ .
- 173 v. Calculate SNP weight as  $d_{i(t+1)} = \hat{u}_{i(t)}^2 / 2p_i(1 - p_i)$ , where  $i$  is the  $i^{\text{th}}$  SNP [23].
- 174 vi. Normalize matrix  $D_{(t+1)} = \frac{\text{tr}(D_{(0)})}{\text{tr}(D_{(t+1)})} D_{(t+1)}$ .
- 175 vii. Construct the matrix  $G_{(t+1)} = ZD_{(t+1)}Z'\lambda$ .
- 176 viii.  $t = t + 1$ .
- 177 ix. Exit or loop to steps iii or iv.

178 Breeding values were predicted using BLUPF90+ software [24], while the calculation of SNP effects for  
 179 WGBLUP was performed using the postGSf90 software [25].

#### 180 *Estimation of variance components and heritability*

181 The total phenotypic variance ( $\sigma_p^2$ ) was calculated as follows:

$$182 \quad \sigma_p^2 = \sigma_u^2 + \sigma_e^2$$

183 The heritability values for each trait were calculated using the following formula:

$$184 \quad h^2 = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_e^2} = \frac{\sigma_u^2}{\sigma_p^2}$$

185 where  $\sigma_u^2$  is the genetic variance;  $\sigma_e^2$  is the residual variance; and  $\sigma_p^2$  is the phenotypic variance.

#### 186 *Estimation of GEBV*

187 The GEBV of an animal  $i$  was calculated after estimating the marker effects using the following formula below:



188 
$$\text{GEBV}_i = \sum_{j=1}^m z_{ij} \hat{g}_j$$

189 where  $m$  is the number of markers;  $z_{ij}$  is the individual  $i$  genotype at marker loci  $j$ ;  $\hat{g}_j$  is the allele substitution  
 190 effect at locus marker  $j$ .

191 *Estimation of the model accuracy*

192 The following formula was used to estimate the GEBV accuracy for an animal  $i$  [26]:

193 
$$\text{Accuracy}_i = \sqrt{1 - \frac{\text{PEV}}{\sigma_g^2}}$$

194 where  $\sigma_g^2$  is the additive genetic variance of each trait, and PEV is the predicted error variance of the GEBV  
 195 for each animal. The inverse of the coefficient matrix of the mixed model equation, as previously defined [17],  
 196 can be used to calculate each PEV estimate in each individual. For each animal and trait, this study first calculated  
 197 the standard error of prediction (or the square root of PEV), which was transformed into an estimate of the PEV.  
 198 The only other element in the equation is the additive genetic variance or  $\sigma_g^2$ . Each trait was calculated  
 199 individually using the REML method from the same dataset.

200 *Genetic and phenotypic correlation*

201 The genetic and phenotypic (co)variances were estimated using pairwise bivariate animal model implemented  
 202 in MTG2 v2.22 software. The animal model for the analysis of two traits or bivariate analysis is written as [27]:

203 
$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

204 Where,  $y_1$  and  $y_2$  represents the observation vectors corresponding to individuals for traits 1 and 2. The  
 205 vectors  $b_1$  and  $b_2$  denotes the fixed effects for traits 1 and 2, while  $u_1$  and  $u_2$  are vectors representing the  
 206 additive genetic effects for traits 1 and 2, respectively. The  $e_1$  and  $e_2$  are the vectors of residual effects for traits  
 207 1 and 2.  $X$  and  $Z$  are the incidence matrices related to effects  $b$  and  $u$ , respectively.

208 The genetic ( $r_g$ ), and phenotypic ( $r_p$ ) correlations were estimated using the following formula:

209 
$$r_g = \frac{\sigma_{gX,Y}}{\sqrt{\sigma_{gX}^2 \sigma_{gY}^2}}; r_p = \frac{\sigma_{pX,Y}}{\sqrt{\sigma_{pX}^2 \sigma_{pY}^2}}$$

210 where  $\sigma_{gX,Y}$ , and  $\sigma_{pX,Y}$  are the genetic, and phenotypic covariance between traits  $X$  and  $Y$ ;  $\sigma_g^2$  represents the

211 additive genetic variance;  $\sigma_p^2$  is the phenotypic variance of the corresponding traits.

212 In addition, the coefficient of the genetic variation ( $CV_g$ ) was calculated as the square root of the additive  
213 genetic variance divided by the mean of the trait.

$$214 \quad CV_g \% = \frac{\sigma_g}{\bar{x}} \times 100$$

215

## 216 **Results and Discussion**

### 217 **Phenotypes and genotypes**

218 Table 1 lists the summary statistics (mean, maximum, minimum, standard deviations, and phenotypic  
219 coefficient of variation) of the studied traits of 1,103 animals consisting of the Hanwoo population. The mean  
220 values for CI, AFC, GL, NAIPC, CWT, EMA, BF, and MS in this study were 378.43 days, 741.19 days, 286.45  
221 days, 1.29, 374.86 kg, 87.81 cm<sup>2</sup>, 13.49 mm and 4.08, respectively. NAIPC (49.35%) showed the highest  
222 phenotypic variability. On the other hand, the phenotypic variability was lower in the GL among the reproductive  
223 traits and in the CWT among the carcass traits. The mean values for the reproductive traits are lower than those  
224 published earlier [28-32] and higher than in other studies [33, 34]. Noticeable differences in the sample sizes  
225 among studies were found, which might explain some of the variations of estimation in the present study and other  
226 reports. A longer calving interval is often related to lower fertility due to an undesirable conception rate. A recent  
227 report [35] found that the average values for CWT, EMA, BF, and MS were 447 kg, 93.75 cm<sup>2</sup>, 12.80 mm, and  
228 4.89, respectively, in the Hanwoo steer population. Another experiment on the Hanwoo population conducted over  
229 a period from 1989 to 2015 reported that the average for CWT, EMA, BF, and MS at approximately 24 months of  
230 slaughter age was 343.96 kg, 78.90 cm<sup>2</sup>, 8.71 mm, and 3.33, respectively [36].

231 A set of 41,445 common SNPs was selected after the quality control (QC) test, which covered 79.52% of initial  
232 SNPs on all 29 *Bos taurus* autosomes (BTA). The markers were unsteadily distributed with substantial over-  
233 representation on certain chromosomes. BTA 1 contains the highest number of SNP markers (2,614), covering a  
234 length of 52.10 Mb, while BTA 28 had the lowest number of SNPs (714). Finally, Table 2 lists the SNP information  
235 after the identity-by-state (IBS) test and QC procedure.

### 236 **Heritability estimation**

237 The  $h^2$  and variance components were estimated with standard errors for all reproductive and carcass traits  
238 using the markers and phenotypic information, as presented in Table 3. The estimates of heritability for CI, AFC,  
239 GL, NAIPC, CWT, EMA, BF, and MS were  $0.10 \pm 0.05$ ,  $0.13 \pm 0.05$ ,  $0.17 \pm 0.06$ ,  $0.11 \pm 0.04$ ,  $0.37 \pm 0.07$ ,  $0.35 \pm 0.07$ ,  
240  $0.27 \pm 0.06$ , and  $0.45 \pm 0.07$ , respectively. The average  $h^2$  values for the carcass and reproductive traits were  
241 estimated to be 0.13 and 0.36, respectively. Higher  $h^2$  values were observed in the GL among the reproductive  
242 traits and MS among the carcass traits. For the reproductive traits in this study, the estimated  $h^2$  values were in the  
243 range of low heritability. The observed low heritability estimates were comparable to previously reported  
244 estimates in other beef breeds. Lopez et al. [34] reported low  $h^2$  estimates for a CI of 0.01, GL of 0.14 in Hanwoo  
245 cattle, and high  $h^2$  estimates for an AFC of 0.08 in the same breed. In Japanese Black (Wagyu) cattle,  $h^2$  estimates  
246 of 0.049 [31] and 0.047 [37] for CI, 0.215 [37], and 0.158 [31] for AFC, and 0.020 for NAIPC [31] were described.  
247 Yague et al. [32] reported estimated  $h^2$  of 0.085, 0.037, and 0.071 for CI, GL, and NAIPC, respectively. Several  
248 studies reported the estimates of heritability for CI was 0.222 in Jersey x Red Sindhi [38], 0.105 [39], and 0.02  
249 [40] in Nelore cattle, and 0.09 in Brahman-Angus cattle [41]. Adonai et al. [42] reported a higher heritability of  
250 0.20 for AFC in Simmental cattle.

251 The heritability estimates for carcass traits in this study differ considerably from those obtained in previous  
252 studies by Naserkheil et al. [43]. They reported the  $h^2$  values for CWT, EMA, BF, and MS of 0.28, 0.46, 0.57, and  
253 0.59, respectively, using the pedigree-based GBLUP method. Another report on the genetic analysis of carcass  
254 traits for Hanwoo beef cattle on 6,092 animals from 2005 to 2017 showed corresponding  $h^2$  values of carcass  
255 weight as  $0.35 \pm 0.04$ ,  $0.43 \pm 0.05$ ,  $0.48 \pm 0.05$ , and  $0.56 \pm 0.05$ , respectively, using a pedigree-based GBLUP model  
256 [35].

257 Heritability estimates based on the 50K SNP Chip for CWT, EMA, BF, and MS in this present study agreed  
258 with those observed by Srivastava et al. [44] for a population of 7,324 Korean Hanwoo cattle. On the other hand,  
259 Lopez et al. [45] suggested that the estimated  $h^2$  with 50K SNP panel in Korean Hanwoo cattle for carcass traits  
260 was medium to high, ranging from 0.32 to 0.40 based on GRM.

261 According to  $CV_g$ , the results showed significant additive genetic variation for NAIPC (15.50%), BF (22.34%),  
262 and MS (31.58%), compared to relatively lower additive genetic variation for the other traits (0.96 to 8.59%). The  
263 evolvability of a trait is determined by its genetic variability [46], which impacts how easily traits can be altered  
264 by breeding. In other words, the predicted genetic gain for NAIPC, BF, and MS will be higher than other traits

265 (using the standardized scale).

266 The low  $h^2$  estimate observed in our study can be attributed to several factors that warrant further discussion.  
267 Firstly, it is important to highlight that in our study, the  $h^2$  was calculated using markers and phenotypic  
268 information without access to pedigree records. The absence of pedigree information can impact the accuracy of  
269  $h^2$  estimates, as pedigree records play a crucial role in capturing true genetic relationships among individuals.  
270 Studies that utilized pedigree information or a complete dataset of individuals have reported higher  $h^2$  estimates  
271 for carcass traits. Moreover, our study was limited by a relatively small sample size, and this factor can also  
272 influence the estimation of  $h^2$ . A reduced sample size may result in diminished statistical power to accurately  
273 detect genetic effects. Given these limitations, it is expected that the  $h^2$  estimates for carcass traits in our study  
274 would be lower compared to investigations with pedigree information and larger sample sizes. Furthermore, there  
275 may be differences in the slaughter age of the animals, such as the number of records, the breed, differences in the  
276 fixed effects, and the statistical models used for analyses, which could account for the disparity between the  
277 estimates of this study and those of previous studies. In addition, the differences in heritability can be explained  
278 by the varying genotype-environment interactions. However, despite these challenges, our study provides valuable  
279 insights into the heritability of carcass traits using marker-based methods and highlights the need for more  
280 comprehensive studies with larger sample sizes and pedigree information to obtain more accurate heritability  
281 estimates.

#### 282 **Estimation of GEBV prediction accuracy**

283 The GEBV accuracy for reproductive and carcass traits in Hanwoo cows was estimated using the GBLUP and  
284 WGBLUP models with a complete data set. Generally, the predictive accuracy for most traits slightly varied  
285 between GBLUP and WGBLUP models (Table 4). The accuracy of the genomic predictions ranged from 0.51 to  
286 0.60 in reproductive traits and 0.68 to 0.74 in carcass traits using the GBLUP model, whereas the accuracy ranged  
287 between 0.51 and 0.66 in the reproductive traits, and 0.72 and 0.79 in the carcass traits in WGBLUP model,  
288 respectively. The average accuracy for reproductive traits in the studied population was approximately 0.54  
289 (GBLUP)–0.57 (WGBLUP) and approximately 0.71 (GBLUP)–0.76 (WGBLUP) for carcass traits. The average  
290 GEBV accuracy in the WGBLUP indicated more positive changes than GBLUP (5.6% in the reproductive traits  
291 and 6.7% in the carcass traits) among the GEBV estimates of all studied traits. In this study, the WGBLUP showed  
292 obvious superiority over the GBLUP method. Currently, the genomic selection is applied in beef cattle on a large

293 scale, focusing mainly on the carcass traits [47, 48].

294 Some studies have been conducted to evaluate the average prediction accuracy of genomic evaluations using  
295 GBLUP and ssGBLUP methods for the reproductive traits on different populations, such as Canadian Holstein  
296 (Guarini et al., 2018) and Nelore cattle (Alves et al., 2021). The genomic evaluation accuracy for the reproductive  
297 traits varied among breeds, the genetic architecture of the traits studied, statistical method, effects of SNPs, and  
298 the used SNP set. For AFC, Laodim et al. [49] reported that the accuracy performance of the ssGBLUP model was  
299 0.297 and between 0.23 and 0.33 for Thai crossbreed animals and Nelore cattle, respectively, using another three  
300 different Bayesian statistical methods [50] and appeared to be a lower value compared to the present findings.

301 In Nelore cattle, the average prediction accuracy ranged between 0.38 and 0.42 by GBLUP and Bayesian  
302 method for the same trait [51], which partially supports our results for AFC accuracy. Boddhireddy et al. [52]  
303 showed a higher accuracy of prediction in Nelore cattle using the BayesC method for reproductive traits, which  
304 was 0.64.

305 Some studies reported the performance of genomic prediction models for various traits in different breeds [53-  
306 56]. Kim et al. [57] observed high prediction accuracy using 919 Hanwoo cattle by the GBLUP method, and the  
307 prediction accuracies obtained for CWT, EMA, BF, and MS were 0.779, 0.758, 0.766, and 0.791, respectively. On  
308 the other hand, the genomic prediction accuracy varied among traits while using GRM constructed on a 50K SNP  
309 panel; the genomic prediction accuracy for CWT, EMA, BF, and MS were 0.63, 0.58, 0.55, and 0.56, respectively  
310 [45]. By contrast, lower accuracy was also observed using a 50K SNP chip for Korean Hanwoo cattle in the  
311 GBLUP method, with EMA, BF, and MS values ranging from 0.27 to 0.30, respectively [1].

## 312 **Genetic and phenotypic correlation**

313 Table 5 lists the genetic and phenotypic correlations among the reproductive and carcass traits. The genetic and  
314 phenotypic correlations between traits were analyzed using the genetic and phenotypic variance and the  
315 covariance of the two traits. The estimates of the genetic correlation between reproductive and carcass traits were  
316 low to high, ranging from  $-0.56 \pm 0.03$  to  $0.61 \pm 0.03$ . According to Dahliani et al. [58], the correlation values  
317 were divided into the following categories: very low (0.00 to 0.19), low (0.20 to 0.39), moderate (0.40 to 0.59),  
318 strong (0.60 to 0.79), and very strong (0.80 to 1.00). Strong positive genetic correlations were found between GL  
319 and NAIPC ( $0.61 \pm 0.03$ ) and CWT and EMA ( $0.60 \pm 0.02$ ), as represented in Table 5, which were the highest

320 correlations among the trait pairs. Furthermore, the strength of the associations between NAIPC and CWT ( $0.49$   
321  $\pm 0.03$ ) and AFC and CWT ( $0.48 \pm 0.03$ ) were moderate and positive. Hence, the selection of these traits could be  
322 advantageous. This strong positive genetic correlation could be due to pleiotropy, wherein a gene or a set of genes  
323 influences two traits and results in the genetic correlation between these traits [59].

324 Positive phenotypic ( $0.05 \pm 0.02$ ) and genetic correlations ( $0.26 \pm 0.01$ ) were observed between CI and AFC.  
325 The genetic associations between CI and AFC were stronger than the phenotypic correlations. Shin et al. [60]  
326 reported a comparable positive association between these traits in Hanwoo cows, which strongly supports the  
327 present study. The moderate genetic associations between reproductive traits have the same sign as patterns that  
328 can be observed phenotypically [61, 62]. Gutiérrez et al. [63] reported a favorable genetic correlation ( $0.233$ ) in  
329 beef cattle between CI and AFC. In contrast to the genetic association, which was only weakly positive ( $0.10$ ),  
330 Lôbo [64] discovered a high positive phenotypic correlation between AFC and CI ( $0.43$ ). In these results, AFC  
331 appears to be an important characteristic reflecting the reproductive health of cows. An improvement in the CI  
332 performance would result from the selection for a shorter AFC. Berry and Evans [65] estimated a positive genetic  
333 association of  $0.22$ , while Lopez et al. [66] reported a correlation of  $0.52$ ; however, the genetic correlation between  
334 AFC and CI was only found to be between  $0.09$  [67] and  $-0.25$  during the first 42 days of the calving season. In  
335 contrast, CI with AFC was a low negative correlation, which is not an agreement reported elsewhere [68, 69].  
336 They reported negative correlations between CI and AFC of  $-0.13$  for Brahman cattle and  $-0.06$  for Nelore cattle.

337 The calculated weak positive associations between GL and CI also agree with Lopez et al. [66]. The phenotypic  
338 correlation of  $0.04$  between GL and AFC is consistent with earlier investigations [66]. These outcomes resembled  
339 those in Nelore cows, as reported by Magnabosco et al. [70]. Oyama et al. [71] also mentioned the genetic  
340 relationships between GL and CI of  $0.16$ . Bekele et al. [72] reported strong positive genetic correlations between  
341 GL and CI in Fogera cattle,  $0.72$ .

342 The strongest correlation among all the trait pairs in this analysis was obtained between GL and NAIPC ( $0.61$   
343  $\pm 0.03$ ), which showed a significant genetic relationship. On the other hand, the CI showed the highest negative  
344 correlation with NAIPC ( $-0.56 \pm 0.03$ ) and AFC with GL ( $-0.41 \pm 0.02$ ). Similar findings have been achieved in  
345 Japanese Black cattle by Setiaji and Oikawa [73], who reported the positive genetic and phenotypic correlation  
346 between NAIPC and GL. NAIPC was recorded before conception, and GL represents a heifer's ability to sustain  
347 the pregnancy until the day of calving. As a result, the strong genetic link shows that these two traits are related

348 genetically and might be influenced by a group of genes. As a result, choosing one of the traits would have a  
349 significant impact on the other.

350 This study found that estimates of genetic association between traits ranged widely. The traits of Hanwoo cows,  
351 CWT and EMA, are highly and positively associated, suggesting that animals with a higher EMA will result from  
352 selection for increasing the CWT. This correlation estimate was similar to that of Park et al. [74] and Choi et al.  
353 [75], who used Hanwoo males to report values between  $0.52 \pm 0.08$  and  $0.55$  using similar features. Other Hanwoo  
354 research revealed the same positive association [43, 76-79]. The association between CWT and EMA was  
355 supported by several different studies involving Angus [80-83], Brangus [84, 85], Angus–Brahman [86], Canadian  
356 crossbred cattle [87], Nellore cattle [88], Heriford, Simmental [89], Brazilian Nelore [90], Brahman [91, 92], and  
357 other crossbred cattle [93].

358 The genetic correlation of BF with CWT ( $-0.12 \pm 0.03$ ) and EMA ( $-0.18 \pm 0.03$ ) was negative, which is  
359 financially feasible for the beef industry because CWT and EMA will increase if BF decreases and make the  
360 carcass profitable. Davoli et al. [94] obtained similar results in Large White pigs and revealed negative genetic  
361 correlations between CWT and BF. In the case of the fat content, BF is associated with MS ( $0.35 \pm 0.02$ ), which  
362 increases the juiciness of the meat.

363 According to these findings, the genetic correlation between EMA and MS was determined to be positive and  
364 fairly moderate ( $0.28 \pm 0.03$ ), similar to the results from other research [75, 92, 95, 96], but significantly lower  
365 than the estimate of 0.65 published by Hwang et al. [97] in Hanwoo population.

366 In this study, the findings of the genetic correlation between reproductive and carcass traits were moderate to  
367 low, or negative. All reproductive traits have moderate to weak positive genetic correlations with CWT. MacNeil  
368 et al. [98] also reported a lower correlation of GL with CWT, which was also close to zero. On the other hand,  
369 EMA showed positive genetic correlations between AFC ( $0.24 \pm 0.03$ ) and NAIPC ( $0.35 \pm 0.03$ ). Furthermore,  
370 BF also showed a weakly positive genetic correlation with CI and AFC. The highest positive genetic correlations  
371 between the reproductive and carcass traits were between NAIPC and CWT ( $0.49 \pm 0.03$ ) and AFC and CWT  
372 ( $0.48 \pm 0.03$ ). In contrast, negative genetic correlations were found between AFC and MS. Negative results have  
373 also been reported [99, 100], showing that the age at first calving can be lowered by increasing the meat and fat  
374 deposition. Higher subcutaneous fat deposition may signal faster maturation and make animals more sexually  
375 precocious, but more research is needed. A lower fat content is better for reproduction in cows.

376 These studies showed that the strong phenotypic correlation of  $0.66 \pm 0.02$  between CWT and EMA, which  
377 was the strongest correlation among all pairs of reproductive and carcass traits, followed by the weak positive  
378 correlations between EMA and MS, AFC, and NAIPC, between CWT and BF, and between CWT and MS which  
379 were 0.33, 0.30, 0.29, and 0.29, respectively. In the present study, the phenotypic correlation was within the range  
380 of estimates made previously for Korean Hanwoo [95], Angus [80, 81], Brangus [84, 85], Angus-Brahman [86],  
381 Canadian crossbred cattle [87], and Nellore cattle [88].

382 This study found low to moderate genetic correlations between the attribute of reproductive and carcass weight,  
383 which may explain why choosing a heavier body weight may result in longer CI, AFC, GL, and increased NAIPC.  
384 The genotype-environment interaction is a more likely cause of the phenotypic manifestation of these traits  
385 because of the near-zero phenotypic association and the marginally favorable genetic correlation between CWT,  
386 AFC, and NAIPC. After producing a reference population for carcass and reproductive traits, the application of  
387 genomic selection would be preferable to address the limitations of this study. These findings on variance  
388 components, heritability estimates, GEBV accuracy, and correlation coefficients for reproductive and carcass traits  
389 offer important insights into the genetic merits of Hanwoo cows. They may benefit future research on them and  
390 their incorporation into the Hanwoo National Evaluation for genomic selection.

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## Tables

642 **Table 1.** Descriptive statistics of the reproductive and carcass traits.

<b>Traits</b>	<b>N</b>	<b>Mean</b>	<b>SD</b>	<b>Max</b>	<b>Min</b>	<b>CV (%)</b>
CI (days)	1,103	378.43	53.82	601	242	14.22
AFC (days)	1,103	741.19	73.86	999	499	9.97
GL (days)	1,103	286.45	6.72	337	252	2.35
NAIPC (1-4)	1,103	1.29	0.64	4	1	49.35
CWT (kg)	1,103	374.86	49.93	541	160	13.32
EMA (cm <sup>2</sup> )	1,103	87.81	12.81	131	22	14.58
BF (mm)	1,103	13.49	5.84	39	2	43.28
MS (1-9)	1,103	4.08	1.93	9	1	47.31

643 N, number of individuals; SD, standard deviations; CV, coefficient of variation; CI, calving interval; AFC, age at  
644 first calving; GL, gestation length; NAIPC, number of artificial inseminations per conception; CWT, carcass  
645 weight; EMA, eye muscle area; BF, backfat thickness; MS, marbling score.

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656 **Table 2.** SNP statistics after QC for Hanwoo autosomes.

<b>BTA</b>	<b>No. of SNPs before QC</b>	<b>No. of SNPs after QC</b>	<b>Remove frequency</b>	<b>Average distance (kb)</b>	<b>Standard deviation (kb)</b>	<b>Min distance (kb)</b>	<b>Max distance (kb)</b>	<b>Total distance (Mb)</b>
1	3221	2614	0.23	60.50	54.60	0.05	936.23	52.10
2	2756	2181	0.26	62.70	68.00	0.08	1087.31	84.73
3	2579	2038	0.27	59.50	62.30	0.01	863.15	42.65
4	2477	1932	0.28	62.10	53.20	0.03	507.93	83.84
5	2154	1662	0.30	72.90	70.60	0.04	818.54	113.01
6	3157	2526	0.25	47.10	56.80	0.03	1601.81	83.13
7	2478	2020	0.23	55.70	66.30	0.13	1177.03	63.54
8	2243	1776	0.26	63.70	54.20	0.08	547.23	51.10
9	2073	1623	0.28	65.00	62.70	0.45	642.76	62.10
10	2355	1872	0.26	55.70	92.80	0.07	3259.34	118.98
11	2179	1717	0.27	62.50	58.90	0.13	833.19	121.14
12	1650	1252	0.32	72.60	120.60	0.24	2470.22	46.18
13	1681	1331	0.26	63.00	55.20	0.07	715.70	65.16
14	2266	1806	0.25	46.10	46.50	0.01	505.77	157.88
15	1665	1312	0.27	64.60	64.90	0.01	969.41	45.33
16	1598	1241	0.29	65.70	70.20	0.18	1360.52	74.85
17	1567	1229	0.28	61.00	65.50	0.16	1301.14	136.66
18	1301	1041	0.25	62.70	63.10	0.51	966.71	71.10
19	1377	1120	0.23	56.80	53.30	0.73	586.98	107.18
20	1568	1237	0.27	57.90	52.00	0.47	559.10	90.83
21	1397	1149	0.22	61.90	70.30	0.49	1322.35	112.38
22	1209	969	0.25	63.20	52.80	0.09	494.16	61.22
23	1124	924	0.22	56.40	53.80	0.32	488.53	81.41
24	1229	1000	0.23	62.20	52.90	0.06	454.80	50.95
25	937	783	0.20	54.50	45.50	0.07	332.62	120.01
26	1030	825	0.25	61.80	47.50	0.28	394.54	105.46
27	917	745	0.23	60.90	60.20	0.15	587.19	121.08
28	902	714	0.26	64.80	56.70	0.02	555.53	104.17
29	1026	806	0.27	63.50	65.40	0.03	1060.19	71.59
<b>Total</b>	<b>52116</b>	<b>41445</b>	<b>0.26</b> (Average)	<b>60.93</b> (Average)	<b>61.96</b> (Average)	<b>0.17</b> (Average)	<b>944.83</b> (Average)	<b>2499.76</b>

657 BTA, *Bos taurus* autosomes (29); kb, kilobases; Mb, megabases.

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660 **Table 3.** Estimates of heritability, additive genetic variance, residual variance, phenotypic variance, and  
 661 coefficient of genetic variance for reproductive and carcass traits in Hanwoo cows.

Traits	$h^2$	$\sigma_a^2$	$\sigma_e^2$	$\sigma_p^2$	$CV_g$ (%)
CI	0.10 (0.05)	280.41 (143.80)	2616.93 (170.65)	2902.65 (127.75)	4.42
AFC	0.13 (0.05)	697.16 (275.85)	4689.72 (311.90)	5383.78 (236.91)	3.56
GL	0.17 (0.06)	7.54 (2.58)	37.51 (2.72)	45.44 (2.05)	0.96
NAIPC	0.11 (0.04)	0.04 (0.02)	0.37 (0.02)	0.41 (0.02)	15.50
CWT	0.37 (0.07)	918.70 (185.23)	1546.92 (152.21)	2491.93 (118.34)	8.09
EMA	0.35 (0.07)	56.87 (12.19)	105.91 (10.20)	163.64 (7.68)	8.59
BF	0.27 (0.06)	9.08 (2.28)	24.08 (2.06)	33.33 (1.54)	22.34
MS	0.45 (0.07)	1.66 (0.29)	2.07 (0.22)	3.74 (0.18)	31.58

662  $h^2$ , heritability;  $\sigma_a^2$ , genetic variance;  $\sigma_e^2$ , residual variance;  $\sigma_p^2$ , phenotypic variance;  $CV_g$ , coefficient of genetic  
 663 variance. The numbers in parentheses are standard errors.

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675 **Table 4.** Accuracy of the genomic predictions of Hanwoo cows.

Traits	GBLUP				WGBLUP			
	Mean	SD	Max	Min	Mean	SD	Max	Min
<b>Reproductive Traits</b>								
CI	0.51	0.04	0.62	0.14	0.56	0.03	0.66	0.43
AFC	0.52	0.04	0.62	0.15	0.55	0.03	0.64	0.42
GL	0.60	0.04	0.69	0.23	0.66	0.03	0.74	0.48
NAIPC	0.53	0.04	0.62	0.16	0.51	0.03	0.62	0.37
<b>Carcass Traits</b>								
CWT	0.73	0.03	0.79	0.33	0.77	0.02	0.81	0.57
EMA	0.68	0.03	0.75	0.29	0.74	0.02	0.79	0.54
BF	0.68	0.03	0.74	0.29	0.72	0.02	0.79	0.55
MS	0.74	0.03	0.80	0.34	0.79	0.02	0.84	0.61

676 GBLUP, genomic best linear unbiased prediction; WGBLUP, weighted GBLUP; SD, standard deviation.

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687 **Table 5.** Estimates of the genetic (above the diagonal) and phenotypic (below the diagonal) correlations (standard  
 688 error in parentheses) among reproductive and carcass traits in Hanwoo cows.

Trait	CI	AFC	GL	NAIPC	CWT	EMA	BF	MS
CI	<b>1.00</b>	0.26 (0.01)	0.36 (0.03)	-0.56 (0.03)	0.09 (0.02)	-0.03 (0.03)	0.30 (0.03)	-0.21 (0.03)
AFC	0.05 (0.02)	<b>1.00</b>	-0.41 (0.02)	-0.01 (0.03)	0.48 (0.03)	0.24 (0.03)	0.21 (0.01)	-0.04 (0.03)
GL	-0.06 (0.03)	0.04 (0.03)	<b>1.00</b>	0.61 (0.03)	0.04 (0.03)	-0.14 (0.06)	-0.09 (0.08)	0.07 (0.03)
NAIPC	-0.03 (0.08)	0.30 (0.02)	0.05 (0.03)	<b>1.00</b>	0.49 (0.03)	0.35 (0.03)	-0.04 (0.05)	-0.15 (0.03)
CWT	0.01 (0.03)	-0.01 (0.03)	0.01 (0.03)	0.04 (0.03)	<b>1.00</b>	0.60 (0.02)	-0.12 (0.03)	0.13 (0.03)
EMA	-0.02 (0.01)	0.03 (0.04)	-0.00 (0.02)	0.05 (0.03)	0.66 (0.02)	<b>1.00</b>	-0.18 (0.03)	0.28 (0.03)
BF	0.04 (0.03)	-0.04 (0.03)	0.03 (0.07)	-0.02 (0.01)	0.29 (0.03)	0.09 (0.03)	<b>1.00</b>	0.35 (0.02)
MS	-0.01 (0.03)	-0.03 (0.01)	0.07 (0.03)	0.03 (0.03)	0.29 (0.03)	0.33 (0.03)	0.14 (0.03)	<b>1.00</b>

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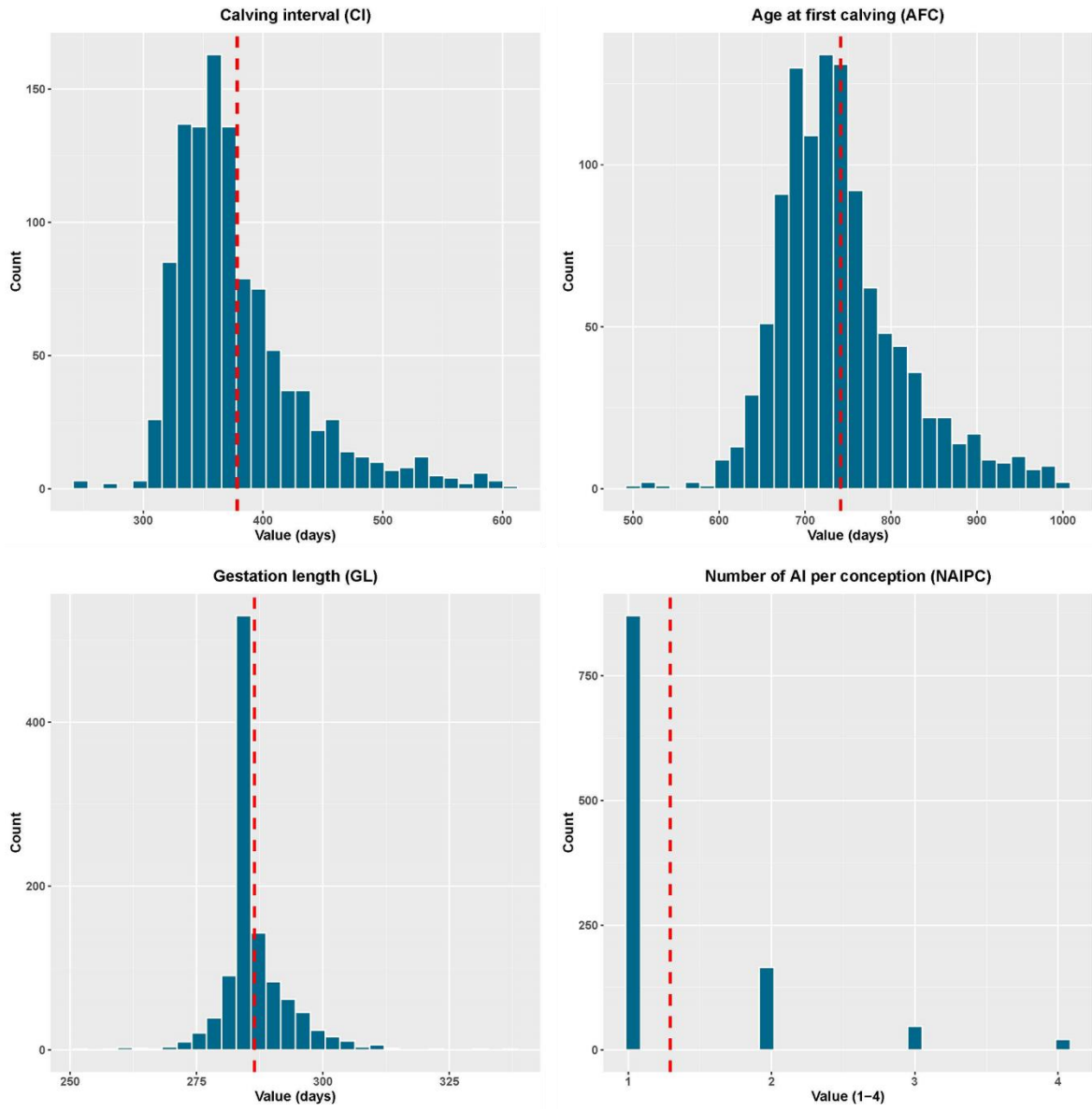
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# Figures

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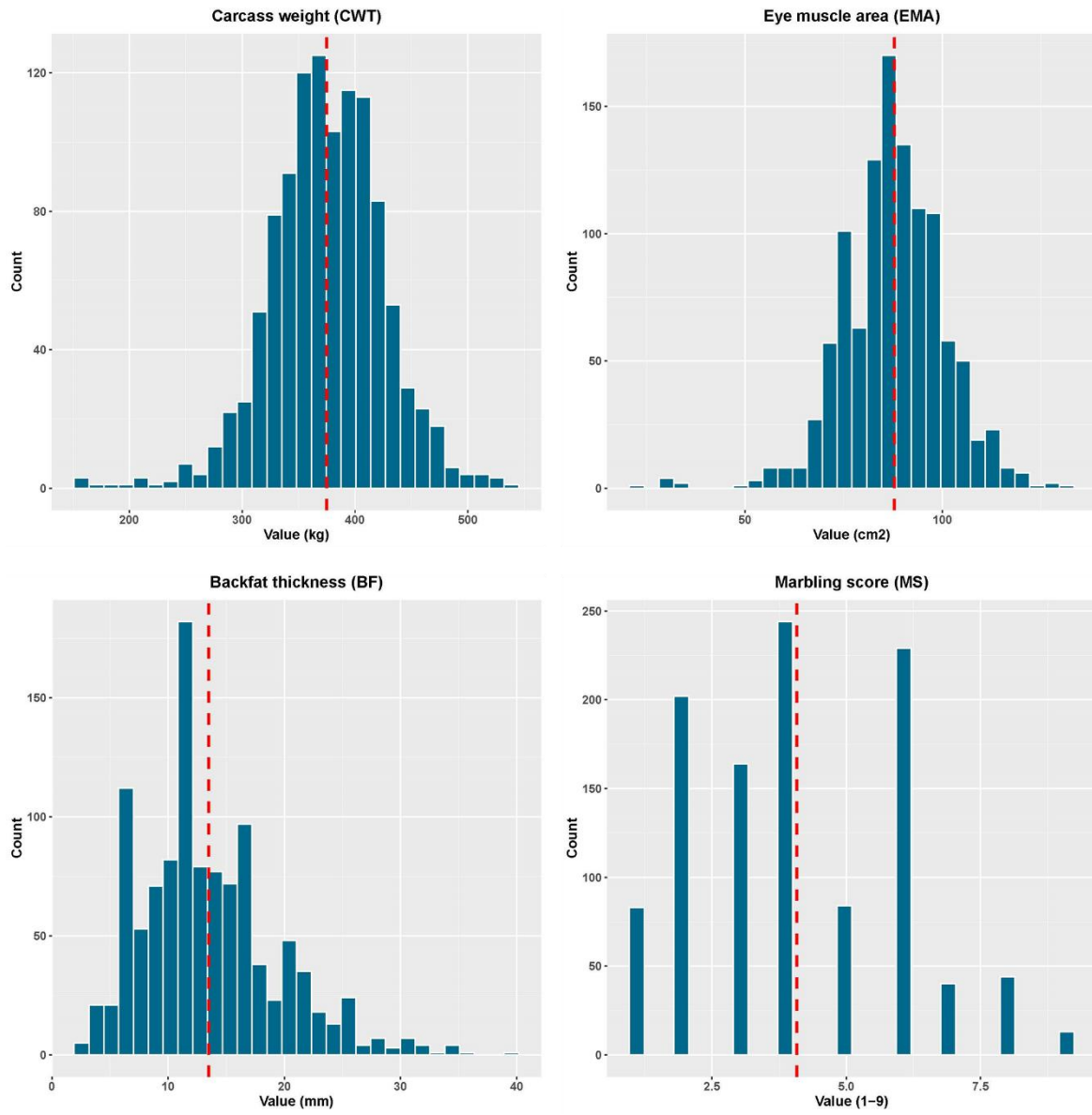
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703 **B**



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705 **Fig. 1. Phenotypic distribution: (A) Reproductive traits; and (B) Carcass traits in Hanwoo cows. The red**

706 dashed lines indicate the mean of the trait.

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