

Research Article

Analysis of the effects of inbreeding coefficients on carcass traits in Hanwoo steers within the Gyeongbuk region

Yangmo Koo^{1,†}, Soon Hwangbo^{2,†}, Ji-Hong Lee^{3,*}

¹Korea Animal Improvement Association, Seoul 06668, Republic of Korea

²Department of Companion Animal Industry, Daegu University, Gyeongsan 38453, Republic of Korea

³Department of Animal Biotechnology, Gyeongbuk National University, Yecheon 36830, Republic of Korea

[†]These authors contributed equally to this work and share first authorship.

*Corresponding author: ghlee2002@korea.kr

ABSTRACT

Background: Inbreeding in Hanwoo has become a growing concern as semen from a limited number of nationally proven bulls is widely used. This study investigated the effects of inbreeding on major carcass traits of Hanwoo steers and attempted to determine a threshold for inbreeding depression.

Methods: Pedigree-based inbreeding coefficients were calculated for 139,493 Hanwoo steers born from 2015 to 2024 in farms located in the Gyeongbuk region. The general linear model (GLM), linear regression model (LRM), linear mixed model (LMM), and quadratic mixed model (QMM) were used to analyze the effects of inbreeding on carcass weight (CWT), eye muscle area (EMA), backfat thickness (BF), and marbling score (MS). Animals were divided into five groups according to inbreeding level (F0, F1.25, F3.125, F6.25, and F6.25up), and least squares means were compared among groups.

Results: The average inbreeding coefficient was $1.36 \pm 1.56\%$, and it increased continuously from 0.728% in 2015 to 1.716% in 2024. The average inbreeding coefficient and carcass traits differed significantly among regions ($p < 0.05$), reflecting differences in the improvement level of cows and feeding management conditions of farms. Carcass traits gradually increased from F0 to F3.125, with CWT, EMA, and MS being highest in the F3.125 group (486.35 ± 0.25 kg, 101.14 ± 0.06 cm², and 6.45 ± 0.01 , respectively), but decreased significantly in the F6.25 and F6.25up groups, indicating inbreeding depression. In the GLM, the effects of inbreeding group, birth year, region, and slaughter age were significant for all carcass traits ($p < 0.001$). In the LMM, with birth year and slaughter age as fixed effects and region as a random effect, CWT, EMA, and MS showed positive linear slopes, which may reflect genetic improvement and environmental factors at low to moderate inbreeding levels. In the QMM, the linear coefficients of CWT, EMA, and MS were positive and the quadratic coefficients were negative ($p < 0.001$), showing an inverted U-shaped pattern. The turning points were estimated as 8.68% for CWT, 10.29% for EMA, and 11.20% for MS, all higher than the predefined 6.25% group boundary.

Conclusion: Carcass performance tended to decrease as the inbreeding level increased. An inbreeding coefficient of 6.25% may be used as a practical reference level for mating management, although it does not represent an exact biological threshold. These results can support mating decisions to reduce the risk of inbreeding depression in Hanwoo.

Keywords: carcass traits, Hanwoo, inbreeding coefficient, inbreeding depression, threshold

INTRODUCTION

The Hanwoo industry in Korea has shown remarkable growth based on the introduction of genetic evaluation systems and systematic selection techniques. With continuous selection of breeding bulls at the national level and supply of superior semen for artificial insemination to farms, major economic traits of Hanwoo such as carcass weight (CWT), eye muscle area (EMA), backfat thickness (BF), and marbling score (MS) have been greatly improved. These improvements have contributed to increasing the income of Hanwoo farms. However, there are also some structural limitations behind these improvements. Dependence on a small number of Korean proven bulls (KPN) has gradually increased, and some specific pedigree lines have been repeatedly used. For this reason, reduction of genetic diversity and increase of inbreeding coefficient in the Hanwoo population have recently become important factors that can affect the sustainability of the Hanwoo industry (Hwangbo et al., 2026).

Theoretically, when the level of inbreeding increases above a certain level, homozygosity of alleles in the population increases. In this process, the possibility of expression of deleterious recessive alleles also increases (Falconer and Mackay, 1996; Lynch and Walsh, 1998). This may reduce productivity, robustness, and reproductive efficiency of animals and may result in inbreeding depression. In particular, economic traits with relatively low heritability or those affected greatly by environmental factors may show a clear decrease in performance by inbreeding depression. This may finally result in decreased profitability of Hanwoo farms and reduced competitiveness of the Hanwoo industry (Kim et al., 2024).

Previous studies on inbreeding in Hanwoo have mainly examined genetic changes in the population and long-term changes in genetic diversity (Hwang et al., 2009; Koo et al., 2021). However, relatively few studies have used large-scale data from several regions to examine the relationship between inbreeding and carcass traits (Kim et al., 2024). These traits are closely related to the economic value of Hanwoo cattle. Environmental factors such as castration, fattening conditions, and feeding management can also affect these traits, especially in field data. For this reason, these factors should be considered together when carcass traits are analyzed (Kim et al., 2024). Gyeongbuk has the largest Hanwoo population in Korea, and farm conditions are not the same among farms. Inbreeding management in this region therefore needs to consider not only pedigree structure but also actual farm conditions (Kim et al., 2024).

In this study, we used pedigree and carcass records from 139,493 Hanwoo steers born and slaughtered in Gyeongbuk between 2015 and 2024. The inbreeding coefficient was calculated for each animal from pedigree information. Birth year, region, and slaughter age were included as fixed factors in the GLM for CWT, EMA, BF, and MS. For the LMM, region was treated as a random effect, while the inbreeding coefficient was included as a continuous variable. We also used the QMM because the relationship between inbreeding and carcass traits may not be simply linear. In addition, we examined the inbreeding level where the carcass traits started to decrease. The results of this study may be useful when managing inbreeding and maintaining pedigree diversity in Hanwoo breeding.

MATERIALS AND METHODS

Data preparation and cleaning

The data used in this study were pedigree and carcass records of 139,493 Hanwoo steers born in Gyeongbuk, which is the largest Hanwoo raising region in Korea. The animals were castrated, fattened, and then slaughtered. The data were limited to animals born from 2015 to 2024, which was the recent 10-year period when the Hanwoo improvement system was relatively stable.

Before statistical analysis, the data were cleaned. Only animals with complete records for inbreeding coefficient, CWT, EMA, BF, MS, birth year, slaughter age, and birth and fattening regions were used. Slaughter age was limited to 25–35 months ($25 \leq \text{AgeMonth} \leq 35$), which is the common slaughter age range for Hanwoo steers.

Outliers of CWT, EMA, BF, and MS were checked separately using the $1.5 \times \text{IQR}$ rule. Values lower than $Q1 - 1.5 \times \text{IQR}$ or higher than $Q3 + 1.5 \times \text{IQR}$ were considered as outliers. If an animal had an outlier value in any one of the four traits, the animal was removed from all later analyses. By this method, the same animals were used for comparison of the carcass traits.

This procedure removed records with possible measurement or recording errors. However, some highly inbred animals with low carcass performance may also have been removed. We did not check the distribution of the removed animals among the inbreeding groups. This is one limitation of this study. After data cleaning, 139,493 animals were used for the final analysis.

Inbreeding coefficients and categorization

The individual inbreeding coefficient (F) was calculated from pedigree records by using Wright's path-counting method (Wright, 1922; Lush, 1945). The calculation was done in Python v3.9.18 with custom scripts based on Wright's tabular method. Pandas v2.1.0 and NumPy v1.24.3 were used for processing the national Hanwoo pedigree data. Statistical analysis was done using Statsmodels v0.14.0, scipy v1.11.2, and Pymer4 v0.8.0.

Incomplete pedigree records can make F lower than the real value. Therefore, pedigree depth was also checked. The mean maximum pedigree depth was 5.42 ± 1.18 generations, and the complete generation equivalent was 3.85 ± 0.82 . Animals with less than three traced generations were removed during data filtering. Animals with no record for both parents were treated as base founders ($F=0$). When only one parent was unknown, the unknown parent was treated as unrelated and non-inbred. However, if a known common ancestor was found in another part of the pedigree, this was considered.

For comparison of carcass traits by inbreeding level, the F values were divided into five groups. These were F0 ($F=0\%$), F1.25 ($0\% < F \leq 1.25\%$), F3.125 ($1.25\% < F \leq 3.125\%$), F6.25 ($3.125\% < F \leq 6.25\%$), and F6.25up ($F > 6.25\%$).

The limits of the F3.125 and F6.25 groups were decided based on pedigree relationships used in Wright's method (Wright, 1922; Falconer and Mackay, 1996). For example, mating between first cousins gives an expected F of 6.25%. For half-first cousins or first cousins once removed, the expected value is 3.125%. The 1.25% level is different because it does not represent a standard pedigree relationship. We used this level mainly to separate animals with very low relatedness from those included in the F3.125 group. The actual F distribution of the study animals was also considered when this value was selected. In this population, the median F was 1.12%, while the 75th percentile was 1.87%.

Thus, F0 included animals with no detectable common ancestor in the recorded pedigree, F1.25 included animals with $0\% < F \leq 1.25\%$, F3.125 included $1.25\% < F \leq 3.125\%$, F6.25 included $3.125\% < F \leq 6.25\%$, and F6.25up included animals with $F > 6.25\%$.

Statistical models and computing environment

SAS 9.4 (SAS Institute Inc., Cary, NC, USA) and Python (v3.9+) under a Linux/Ubuntu environment were used for the analysis of the large-scale Hanwoo data. For data preprocessing and matrix calculation, pandas (v2.0+) and numpy (v1.24+) in Python were used. These packages were used for construction of the large data structure, removal of outliers based on IQR, and encoding of categorical variables.

PROC GLM in SAS and statsmodels (v0.14+) in Python were used for ANOVA and LSM estimation. Duncan's multiple range test was used to compare least squares means at the 5% significance level ($\alpha=0.05$) (Duncan, 1955). For the LMM (Model 3) and QMM (Model 4), fixed effects and variance components were estimated by restricted maximum likelihood (REML). The L-BFGS algorithm was used for optimization.

GLM parameters (Model 1) were estimated by ordinary least squares using PROC GLM. LRM parameters (Model 2) were also estimated by ordinary least squares using SAS PROC REG and Python scikit-learn. SAS PROC REG and Python scikit-learn were used for regression analysis and visualization and to estimate the linear regression coefficient for the continuous inbreeding coefficient.

The statistical models used in this study are as follows.

General linear model (Model 1)

To evaluate the effects of the Wright-based inbreeding groups and major environmental factors on carcass traits, the following GLM was analyzed (Falconer and Mackay, 1996).

$$Y_{ijkl} = \mu + F_Group_i + BirthY_j + Region_k + \beta_1 \cdot AgeMonth_{ijkl} + e_{ijkl}$$

where, Y_{ijkl} is the observed carcass trait value of an animal in the (i)th inbreeding group, (j)th birth year, (k)th region, and (l)th slaughter age, μ is the overall mean (Overall Mean/Intercept), F_Group_i is the fixed effect of the (i)th inbreeding group ((i)=F0, F1.25, F3.125, F6.25, F6.25up), $BirthY_j$ is the fixed environmental effect of the (j)th birth year ((j)=2015, 2016, ..., 2024), $Region_k$ is the fixed environmental effect of the (k)th region, $AgeMonth_{ijkl}$ is the slaughter age of the (l)th animal (25–35 months, continuous covariate), β_1 is the linear regression coefficient for the slaughter age covariate (Slope of Covariate), and e_{ijkl} is the random error term with a mean of 0 and variance of σ^2 .

Linear regression model (Model 2)

For the whole pedigree population, an LRM was analyzed to evaluate the linear relationship between changes in the inbreeding coefficient and major carcass traits without adjustment for other environmental factors (Lynch and Walsh, 1998).

$$Y_i = \beta_0 + \beta_1 \cdot inbed_i + e_i$$

where, Y_i is the observed carcass trait value (CWT, EMA, BF, MS) of the (i)th animal, β_0 is the regression intercept (Intercept, estimated value at 0% inbreeding), $inbed_i$ is the inbreeding coefficient (%) of the (i)th animal as a continuous variable, β_1 is the slope of each carcass trait according to a 1% increase in the inbreeding coefficient (Regression Slope), and e_i is the residual error term. In this model, the coefficient of determination (R^2) was calculated to quantify the contribution of the inbreeding coefficient as a single factor in explaining the total variation of each carcass trait.

Linear mixed model (Model 3)

To control regional environmental effects such as feeding management conditions and climatic variation among regions in Gyeongbuk and to estimate the pure marginal effect of the inbreeding coefficient as a continuous variable, an LMM was analyzed by setting the regional effect as a random effect (Lynch and Walsh, 1998; Searle et al., 1992).

$$Y_{ijk} = \mu + \beta_1 \cdot inbed_{ijk} + BirthY_j + \beta_2 \cdot AgeMonth_{ijk} + u_k + e_{ijk}$$

where, Y_{ijk} is the measured carcass trait value of animal (i), μ is the overall mean (Overall Mean), $inbed_{ijk}$ is the individual inbreeding coefficient (%) entered as a continuous variable, β_1 is the fixed regression coefficient (marginal effect) of each carcass trait for a 1% increase in the inbreeding coefficient, $BirthY_j$ is the fixed effect of birth year, $AgeMonth_{ijk}$ is the slaughter age of the animal (continuous covariate), β_2 is the fixed regression coefficient for slaughter age, u_k is the random effect of the region in Gyeongbuk, and e_{ijk} is the residual error term.

Quadratic mixed model (Model 4)

To test the nonlinear change in carcass traits with increasing inbreeding coefficient and the inbreeding depression effect occurring above a certain level of inbreeding, a QMM including the squared term of the inbreeding coefficient was constructed.

Although Model 4 includes a squared term of the inbreeding coefficient ($inbed^2$), the model is linear with respect to all regression parameters ($\beta_1, \beta_2, \beta_3$); only the fitted relationship between the inbreeding coefficient and each carcass trait is curved, not the model itself in a statistical sense.

$$Y_{ijk} = \mu + \beta_1 \cdot \text{inbed}_{ijk} + \beta_2 \cdot \text{inbed}_{ijk}^2 + \text{Birth}Y_j + \beta_3 \cdot \text{AgeMonth}_{ijk} + u_k + e_{ijk}$$

where, Y_{ijk} is the measured carcass trait value of animal (i), μ is the overall mean (Overall Mean), inbed_{ijk} is the individual inbreeding coefficient (%), β_1 is the first-order (linear) regression coefficient of the inbreeding coefficient, inbed_{ijk}^2 is the squared term of the inbreeding coefficient (Quadratic term), β_2 is the second-order nonlinear regression coefficient for the squared inbreeding coefficient, $\text{Birth}Y_j$ is the fixed effect of birth year, AgeMonth_{ijk} is slaughter age (covariate), β_3 is the fixed linear regression coefficient for slaughter age, u_k is the random effect of the region in Gyeongbuk, and e_{ijk} is the residual error term.

RESULTS AND DISCUSSION

Descriptive statistics of inbreeding and carcass traits

The descriptive statistics of the average inbreeding coefficient, carcass traits, and slaughter age of 139,493 Hanwoo steers in the Gyeongbuk region are shown in Table 1. The pedigree-based average inbreeding coefficient was $1.36 \pm 1.56\%$ (minimum 0%, maximum 28.12%). Considering the median value (1.12%) and the 75th percentile (1.87%), most animals showed a stable level of inbreeding, but some animals with high inbreeding levels were also found. The coefficient of variation (CV) was very high at 114.46%. This was because the inbreeding coefficients were widely distributed from many animals with 0% inbreeding to animals with high inbreeding levels. These results were found to be higher than those of Song et al. (2018), which reported an average inbreeding coefficient of 0.73% for Hanwoo from 1990 to 2017.

CWT and EMA were 477.45 ± 55.11 kg (CV 11.54%, minimum 311 kg, maximum 645 kg) and 99.10 ± 12.63 cm² (CV 12.75%, minimum 61 cm², maximum 137 cm²), respectively. These values were lower than reported by Kim et al. (2024) using large-scale field data. The average BF was 12.63 ± 4.60 mm (minimum 1 mm, maximum 26 mm). The average MS, a major economic trait related to meat quality, was 6.24 ± 1.85 based on a 1–9 scale (minimum 1, maximum 9). BF showed the highest coefficient of variation among the carcass traits at 36.42%.

The average slaughter age was 30.36 ± 2.03 months (CV 6.70%, minimum 25 months, maximum 35 months). Most animals were concentrated between 29 and 32 months of age.

Table 1. Descriptive statistics for inbreeding coefficient, carcass traits and slaughter age in Hanwoo steers

Item	Mean	SD	CV	Min	Max
Inbed	1.36	1.56	114.46	0	28.12
CWT	477.45	55.11	11.54	311	645
EMA	99.10	12.63	12.75	61	137
BF	12.63	4.60	36.42	1	26
MS	6.24	1.85	29.63	1	9
AgeMonth	30.36	2.03	6.70	25	35

Inbed: inbreeding coefficient (%); CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9); AgeMonth: slaughter age (months); SD: standard deviation; CV: coefficient of variation (%); Min: minimum value; Max: maximum value.

Analysis of inbreeding coefficient and carcass traits by birth year

The results of the analysis of changes in carcass traits and inbreeding coefficient according to birth year in Hanwoo steers in the Gyeongbuk region are shown in Table 2. The average inbreeding coefficient increased continuously every year from $0.728 \pm 0.016\%$ in 2015 to $1.716 \pm 0.032\%$ in 2024. The post-hoc test also showed a statistically significant increasing trend among birth years ($p < 0.05$). This shows that the inbreeding coefficient increased by about 0.988 percentage points during the last 10 years, and this result was consistent with the studies of Koo et al. (2021), which reported

an annual increase in the inbreeding coefficient of the national Hanwoo population. This result was also considered to be related to the simplified pedigree structure and increased pedigree duplication with increasing selection intensity in Hanwoo.

At the same time, changes in the major carcass traits showed that CWT increased from 450.65 ± 0.49 kg in 2015 to 489.31 ± 0.21 kg in 2023. EMA also increased from 93.56 ± 0.11 cm² in 2015 to 102.46 ± 0.26 cm² in 2024. BF showed a significant decreasing trend from 13.59 ± 0.05 mm in 2015 to 11.21 ± 0.09 mm in 2024 as the year increased. MS also increased from 5.75 ± 0.02 in 2015 to 6.45 ± 0.01 in 2023 and 6.44 ± 0.04 in 2024. These improvements in carcass traits were similar to the previous results of Kim et al. (2024), who used large-scale field pedigree data. These results suggest that systematic selection at the national and regional levels has been successfully conducted.

However, CWT of animals born in 2024 significantly decreased to 472.74 ± 1.06 kg. This was considered to be due to the combined effects of sampling bias caused by incomplete collection of slaughter data for the 2024 birth year compared with other years (N=3,372), and external feeding environmental factors such as recent changes in feed prices. Further verification will be needed with additional data in the future.

As a result, the changes in inbreeding coefficient and carcass traits by birth year showed that major carcass traits were improved through genetic improvement, but the inbreeding coefficient also continuously increased. Therefore, various mating plans and pedigree management strategies are needed to prevent inbreeding depression while maintaining the efficiency of genetic improvement.

Table 2. Least squares means for inbreeding coefficient and carcass traits by birth year in Hanwoo steers

Birth year	N	Inbed	CWT	EMA	BF	MS
2015	9,448	0.728 ± 0.016^i	450.65 ± 0.49^g	93.56 ± 0.11^g	13.59 ± 0.05^{ab}	5.75 ± 0.02^f
2016	8,836	0.851 ± 0.016^h	451.41 ± 0.52^g	94.38 ± 0.12^f	13.46 ± 0.05^{abc}	5.81 ± 0.02^{ef}
2017	8,701	0.901 ± 0.018^{gh}	451.88 ± 0.53^g	95.68 ± 0.13^e	13.20 ± 0.05^c	5.88 ± 0.02^{ef}
2018	7,582	0.969 ± 0.017^{gh}	456.04 ± 0.58^f	94.95 ± 0.13^f	13.30 ± 0.05^{bc}	5.82 ± 0.02^{ef}
2019	6,522	1.098 ± 0.020^f	466.16 ± 0.65^e	96.26 ± 0.15^e	12.88 ± 0.06^d	6.11 ± 0.02^d
2020	5,584	1.192 ± 0.022^e	472.93 ± 0.71^d	97.75 ± 0.17^d	12.45 ± 0.06^e	6.24 ± 0.03^{bcd}
2021	6,031	1.355 ± 0.021^d	481.22 ± 0.72^c	97.97 ± 0.16^d	12.50 ± 0.06^e	6.21 ± 0.02^{cd}
2022	15,560	1.483 ± 0.013^c	487.31 ± 0.46^b	99.68 ± 0.10^c	12.29 ± 0.04^e	6.32 ± 0.02^{bc}
2023	67,857	1.612 ± 0.006^b	489.31 ± 0.21^a	101.59 ± 0.05^b	12.38 ± 0.02^e	6.45 ± 0.01^a
2024	3,372	1.716 ± 0.032^a	472.74 ± 1.06^d	102.46 ± 0.26^a	11.21 ± 0.09^f	6.44 ± 0.04^a

Inbed: inbreeding coefficient (%); CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9).

Values represent least squares means $\pm$ standard errors.

^{a-i} Means with different letters within a column differ significantly according to Duncan's multiple range test ($p < 0.05$).

Analysis of inbreeding coefficient and carcass traits by region

The results of the analysis of changes in inbreeding coefficient and carcass traits according to region in Hanwoo steers in the Gyeongbuk region are shown in Table 3. Analysis of inbreeding level and carcass traits of Hanwoo steers in 22 cities and counties in Gyeongbuk showed clear differences among regions according to differences in genetic level and feeding environment. The average inbreeding coefficient was the lowest in region P at $1.008 \pm 0.016\%$ and the highest in region D at $1.500 \pm 0.017\%$. Although relatively stable levels of inbreeding were maintained among regions, significant differences were found in some regions ($p < 0.05$).

At the same time, among the major carcass traits, CWT was the highest in region U at 485.35 ± 1.07 kg and the lowest in region N at 467.38 ± 0.57 kg, showing a maximum difference of 17.97 kg among regions. EMA was the highest in region R at 100.65 ± 0.14 cm² and the lowest in region S at 97.08 ± 0.18 cm². BF was the thickest in region B at 13.10 ± 0.04 mm and the thinnest in region M at 11.90 ± 0.15 mm. MS was the highest in region B at 6.53 ± 0.01 and the lowest in region T at 5.94 ± 0.07 .

These significant regional differences in inbreeding level and carcass performance were similar to the results of Kim et al. (2024). They reported that even when nationally proven bulls (KPN) are used, final carcass performance can show large variation according to regional breeding improvement policies, the level of securing superior cow populations, and differences in feeding management conditions among farms. As a result, the relatively high improvement performance of some regions in major carcass traits showed that genetic and environmental factors acted together. This also supports the statistical use of an LMM, in which region was set as a random effect, to control biased environmental effects caused by regional differences and to estimate the pure effect of inbreeding.

Table 3. Least squares means for inbreeding coefficient and carcass traits by region in Hanwoo steers

Region	N	Inbed	CWT	EMA	BF	MS
A	10,957	1.434 ± 0.020 ^{abcdefg}	485.15 ± 0.77 ^{abcg}	99.76 ± 0.17 ^{bcdefg}	12.73 ± 0.06 ^{bc}	6.48 ± 0.02 ^{abcdeg}
B	8,594	1.446 ± 0.012 ^{abcdefg}	476.31 ± 0.42 ^{efg}	100.00 ± 0.10 ^{bcdeg}	13.10 ± 0.04 ^{abc}	6.53 ± 0.01 ^{abg}
C	16,663	1.341 ± 0.024 ^{defg}	479.92 ± 0.87 ^{bcdefg}	97.23 ± 0.20 ^g	12.83 ± 0.07 ^{abc}	5.97 ± 0.03 ^g
D	4,528	1.500 ± 0.017 ^{abcdeg}	481.88 ± 0.55 ^{abcdefg}	99.97 ± 0.12 ^{bcdeg}	12.23 ± 0.04 ^e	6.15 ± 0.02 ^{efg}
E	17,594	1.291 ± 0.164 ^{abcdefg}	478.95 ± 4.90 ^{abcdefg}	98.29 ± 1.20 ^{abcdefg}	12.93 ± 0.45 ^{abc}	6.17 ± 0.18 ^{abcdefg}
F	5,501	1.495 ± 0.018 ^{abcdeg}	482.39 ± 0.61 ^{abcdefg}	100.10 ± 0.14 ^{abcdeg}	12.72 ± 0.05 ^e	6.37 ± 0.02 ^{bcdeg}
G	2,801	1.339 ± 0.014 ^{defg}	471.85 ± 0.56 ^g	98.43 ± 0.13 ^{efg}	12.35 ± 0.05 ^e	6.15 ± 0.02 ^{efg}
H	9,410	1.357 ± 0.026 ^{cdefg}	476.60 ± 0.90 ^{defg}	99.91 ± 0.21 ^{abcdeg}	12.67 ± 0.07 ^e	6.36 ± 0.03 ^{bcdeg}
I	8,274	1.474 ± 0.011 ^{abcdefg}	483.12 ± 0.44 ^{abcdfg}	100.29 ± 0.10 ^{abcdg}	12.97 ± 0.04 ^{abc}	6.25 ± 0.01 ^{cdefg}
J	4,147	1.214 ± 0.021 ^{fg}	481.52 ± 0.78 ^{abcdefg}	98.68 ± 0.18 ^{efg}	12.60 ± 0.07 ^e	6.12 ± 0.03 ^{efg}
K	2,137	1.062 ± 0.024 ^g	471.76 ± 0.75 ^g	97.74 ± 0.18 ^{fg}	12.66 ± 0.07 ^e	6.03 ± 0.03 ^g
L	6,987	1.345 ± 0.031 ^{bcdefg}	468.66 ± 1.20 ^g	99.15 ± 0.28 ^{cdefg}	12.24 ± 0.10 ^e	6.08 ± 0.04 ^{efg}
M	3,941	1.286 ± 0.071 ^{bcdefg}	477.09 ± 1.70 ^{bcdefg}	98.22 ± 0.38 ^{defg}	11.90 ± 0.15 ^e	6.28 ± 0.06 ^{bcdefg}
N	9,569	1.390 ± 0.017 ^{bcdefg}	467.38 ± 0.57 ^g	97.73 ± 0.13 ^{fg}	12.38 ± 0.05 ^e	6.19 ± 0.02 ^{efg}
O	112	1.356 ± 0.021 ^{defg}	480.44 ± 0.69 ^{bcdefg}	97.96 ± 0.15 ^{fg}	12.83 ± 0.06 ^{bc}	6.20 ± 0.02 ^{defg}
P	950	1.008 ± 0.016 ^g	474.36 ± 0.57 ^g	97.50 ± 0.13 ^g	12.63 ± 0.05 ^e	6.01 ± 0.02 ^g
Q	2,410	1.245 ± 0.024 ^{efg}	479.18 ± 1.14 ^{bcdefg}	98.70 ± 0.25 ^{defg}	12.20 ± 0.09 ^e	6.05 ± 0.04 ^{efg}
R	5,005	1.380 ± 0.014 ^{bcdefg}	473.53 ± 0.60 ^g	100.65 ± 0.14 ^{abcg}	12.06 ± 0.05 ^e	6.52 ± 0.02 ^{abg}
S	4,763	1.482 ± 0.029 ^{abcdefg}	479.44 ± 0.85 ^{cdefg}	97.08 ± 0.18 ^g	12.74 ± 0.07 ^{bc}	5.99 ± 0.03 ^g
T	5,265	1.090 ± 0.054 ^g	478.72 ± 2.19 ^{abcdefg}	97.44 ± 0.48 ^{efg}	12.34 ± 0.19 ^{bc}	5.94 ± 0.07 ^{fg}
U	692	1.386 ± 0.033 ^{abcdefg}	485.35 ± 1.07 ^{abcg}	100.15 ± 0.24 ^{abcdeg}	12.29 ± 0.09 ^e	6.33 ± 0.04 ^{bcdefg}
V	9,193	1.107 ± 0.026 ^g	471.07 ± 0.81 ^g	97.95 ± 0.18 ^{fg}	12.56 ± 0.07 ^e	6.06 ± 0.03 ^{eg}

Inbed: inbreeding coefficient (%); CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9).

Values represent least squares means ± standard errors.

^{a–g} Means with different letters within a column differ significantly according to Duncan's multiple range test ($p < 0.05$).

Analysis of carcass traits according to inbreeding level

The results of the analysis of major carcass traits according to the level of inbreeding coefficient in Hanwoo steers in the Gyeongbuk region are shown in Table 4. The animals were classified into five groups according to the level of pedigree-based inbreeding coefficient. The average performance of major carcass traits was analyzed by inbreeding group. The results showed that carcass traits increased with increasing inbreeding level, but decreased when the inbreeding level was above a certain level ($p < 0.05$).

In the F0 group, in which inbreeding was not accumulated, CWT, EMA, BF, and MS were 461.72 ± 0.38 kg, 95.25 ± 0.08 cm², 13.02 ± 0.03 mm, and 5.75 ± 0.01 , respectively. As the groups changed to F1.25 (0% < F ≤ 1.25%) and F3.125 (1.25% < F ≤ 3.125%), in which inbreeding was induced to an appropriate level, the performance of carcass traits gradually increased. In the F3.125 group, CWT was the highest at 486.35 ± 0.25 kg, EMA at 101.14 ± 0.06 cm², and MS at 6.45 ± 0.01 . This improvement in carcass traits within the groups with an appropriate level

of inbreeding can be explained by the accumulation of superior genes in the population through intensive selection and mating mainly using proven bulls (KPN) with superior genetic ability. This result was similar to the results of Kim et al. (2024) who reported that a certain increase in genetic similarity was related to improvement of carcass traits in large-scale Hanwoo field data.

However, from the F6.25 group ($3.125\% < F \leq 6.25\%$), CWT, EMA, and MS began to decrease to 482.88 ± 0.66 kg, 100.64 ± 0.15 cm², and 6.40 ± 0.02 , respectively. In the F6.25up group ($F > 6.25\%$), CWT decreased to 470.26 ± 1.38 kg, EMA to 97.77 ± 0.31 cm², and MS to 6.29 ± 0.05 . These traits showed a significant decrease and a clear tendency of inbreeding depression, which reduced the improvement performance. In the case of BF, it gradually became thinner from 13.02 ± 0.03 mm in the F0 group as the inbreeding level increased, and remained at 12.41 – 12.64 mm after the F1.25 group.

In conclusion, the results of carcass traits by inbreeding coefficient level supported the inbreeding depression mechanism reported by McParland et al. (2007). An increase in the inbreeding coefficient above the threshold due to excessive pedigree duplication can increase the expression of harmful recessive homozygotes in both carcass quantity and quality traits of Hanwoo steers and can cause actual economic losses.

Table 4. Least squares means for carcass traits according to inbreeding coefficient level in Hanwoo steers

Level	N	CWT	EMA	BF	MS
F0	20,198	461.72 ± 0.38^e	95.25 ± 0.08^d	13.02 ± 0.03^a	5.75 ± 0.01^d
F1.25	56,098	474.17 ± 0.23^c	98.39 ± 0.05^c	12.64 ± 0.02^{bd}	6.19 ± 0.01^c
F3.125	51,980	486.35 ± 0.25^a	101.14 ± 0.06^a	12.51 ± 0.02^{cd}	6.45 ± 0.01^{ab}
F6.25	8,404	482.88 ± 0.66^b	100.64 ± 0.15^b	12.46 ± 0.05^{cd}	6.40 ± 0.02^{abc}
F6.25up	2,813	470.26 ± 1.38^d	97.77 ± 0.31^c	12.41 ± 0.12^{bcd}	6.29 ± 0.05^{bc}

F0: $F=0\%$; F1.25: $0\% < F \leq 1.25\%$; F3.125: $1.25\% < F \leq 3.125\%$; F6.25: $3.125\% < F \leq 6.25\%$; F6.25up: $F > 6.25\%$.

CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9).

Values represent least squares means $\pm$ standard errors.

^{a-e} Means with different letters within a column differ significantly according to Duncan's multiple range test ($p < 0.05$).

Analysis of inbreeding coefficient and carcass traits using the GLM

The results of the analysis of variance (ANOVA) using the GLM to test the effects and statistical significance of inbreeding group, birth year, region, and slaughter age on major carcass traits (CWT, EMA, BF, MS) and inbreeding coefficient of Hanwoo steers are shown in Table 5. All fixed effects and covariate factors included in the carcass trait models showed highly significant effects at the $p < 0.001$ level. Therefore, these factors were confirmed as important factors explaining changes in carcass trait performance.

For CWT ($R^2=0.122$), the F-value of slaughter age was the highest at 10,434.50, and the F-value of birth year was also high at 9,748.80. This showed that slaughter age (fattening period) and birth year had large effects on CWT. In addition, the inbreeding group also showed a high F-value of 4,139.19, indicating that the inbreeding group had a direct effect on CWT.

For EMA ($R^2=0.079$), the F-value of birth year was the highest at 563.64, followed by slaughter age at 123.26. The F-value of the inbreeding group was also high at 203.55. These results were considered to show that an increase in the inbreeding coefficient is greatly related to inbreeding depression, which directly restricts development and growth of the loin muscle as well as reducing body weight.

For BF ($R^2=0.021$), birth year and slaughter age showed large effects. The effect of the inbreeding group was also significant ($F=10.59$), but its F-value was lower than those of the other carcass traits.

For MS ($R^2=0.042$), which is a meat quality trait, the inbreeding group showed a highly significant F-value of 177.39 together with birth year and slaughter age. This showed that MS was greatly affected by increasing inbreeding compared with other carcass traits, and it was considered that an increase in inbreeding acted as a factor restricting marbling formation.

Meanwhile, for the inbreeding coefficient ($R^2=0.053$), birth year and city and county region showed very highly significant effects, whereas slaughter age showed an F-value of 1.53 ($p \geq 0.05$, NS) and was not statistically significant. The coefficient of determination (R^2), which

represents the overall explanatory power of the model, was the highest for CWT at 0.122, followed by EMA at 0.079, inbreeding coefficient at 0.053, MS at 0.042, and BF at 0.021.

Although the R^2 values were relatively low because of unavoidable environmental variation in large-scale field data, analysis of a large population of more than 100,000 animals showed that an increase in inbreeding had a highly significant statistical effect on variation in major carcass traits of Hanwoo. However, this GLM analysis considered only fixed effects. Therefore, there was a limitation in completely separating individual genetic variance and regional environmental bias from the residual term.

Table 5. Analysis of variance and coefficient of determination (R^2) for carcass traits and inbreeding coefficient

Source of Variation	CWT($R^2=0.122$)	EMA($R^2=0.079$)	BF($R^2=0.021$)	MS($R^2=0.042$)	Inbed($R^2=0.053$)
Birth year	9748.80 ^{***}	563.64 ^{***}	168.93 ^{***}	166.31 ^{***}	673.43 ^{***}
Inbreeding group	4139.19 ^{***}	203.55 ^{***}	10.59 ^{***}	177.39 ^{***}	–
Region	2143.09 ^{***}	36.54 ^{***}	25.92 ^{***}	55.55 ^{***}	66.00 ^{***}
Slaughter age (AgeMonth)	10434.50 ^{***}	123.26 ^{***}	72.91 ^{***}	89.38 ^{***}	1.53 ^{NS}

CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9); Inbed: inbreeding coefficient (%).

^{***} $p < 0.001$; NS: Not significant.

–: not applicable (variable not included as an independent factor in the model).

Analysis of inbreeding coefficient and carcass traits using the LRM

The results of regression analysis for evaluating the linear effect of increasing inbreeding coefficient on major carcass traits in Hanwoo steers are shown in Table 6. The results showed that the linear regression coefficient β of the inbreeding coefficient was highly significant at the $p < 0.001$ level for all carcass traits.

For each trait, CWT increased linearly by 0.728 ± 0.093 kg ($p = 6.85 \times 10^{-15}$), EMA by 0.311 ± 0.022 cm² ($p = 1.77 \times 10^{-45}$), and MS by 0.047 ± 0.003 ($p = 2.43 \times 10^{-46}$) as the inbreeding coefficient increased by 1%.

On the other hand, BF showed a negative regression coefficient of -0.028 ± 0.008 mm ($p = 0.00066$) for a 1% increase in the inbreeding coefficient. This result showed that BF became thinner as the inbreeding level increased, suggesting that increasing inbreeding may have an opposite effect on variation in fat accumulation.

Table 6. Linear regression coefficients of inbreeding coefficient on carcass traits using an LRM in Hanwoo steers

Trait	β (slope)	SE	p -value	R^2
CWT	0.728	0.093	<0.001	0.119
EMA	0.311	0.022	<0.001	0.075
BF	-0.028	0.008	<0.001	0.021
MS	0.047	0.003	<0.001	0.039

CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9); β : linear regression coefficient of inbreeding coefficient (per 1% increase in inbreeding); SE: standard error; R^2 : coefficient of determination.

Exact p -values before rounding: CWT (6.85×10^{-15}), EMA (1.77×10^{-45}), BF (0.000664), MS (2.43×10^{-46}).

Analysis of inbreeding coefficient and carcass traits using the LMM

Table 7 shows the marginal effect of the inbreeding coefficient on major carcass traits estimated using an LMM. Birth year and slaughter age were included as fixed effects, and region was treated as a random effect (Model 3). The A-matrix (pedigree relationship matrix) was used only to calculate the individual inbreeding coefficient from pedigree records (see “Inbreeding coefficients and categorization”). It was not included in the LMM as an additive genetic random effect. The regression coefficient (β) for inbreeding was significant for all carcass traits ($p < 0.05$).

For the estimated regression coefficient of each trait, CWT showed a regression change of 0.000235 ± 0.000098 kg ($p = 0.017$), EMA showed 0.002839 ± 0.000438 cm² ($p < 0.001$), and MS showed 0.024772 ± 0.002551 ($p < 0.001$) for a 1% increase in the inbreeding coefficient. On the other hand, BF showed a significantly negative regression coefficient of -0.005640 ± 0.000961 mm ($p < 0.001$) for a 1% increase in the inbreeding coefficient, showing a tendency for BF to become thinner as the inbreeding level increased.

The regression coefficients became much smaller in the mixed model when birth year, slaughter age, and region were included. Part of the relationship seen in the GLM and LRM may therefore come from these factors, not from inbreeding alone.

Model 3 did not have a separate pedigree-based additive genetic random effect. Because of this, the effect of inbreeding could not be clearly separated from other individual effects that were not included in the model. Even after adjustment, EMA ($\beta = 0.002839$, $p = 8.87 \times 10^{-11}$) and MS ($\beta = 0.024772$, $p = 2.74 \times 10^{-22}$) were still significantly related to the inbreeding coefficient. For some traits, however, the effect itself was very small. CWT was one example. In this analysis, genetic and environmental variation could not be completely separated. So, the results should not be taken as direct evidence for a specific additive genetic effect.

The LMM gave a more conservative estimate of the marginal effect of inbreeding than the GLM and LRM. The regression coefficient from Model 3 represents an adjusted marginal effect rather than a purely genetic effect. Region was the only random effect in the model, and individual additive genetic variance was not modeled separately.

Table 7. Linear regression coefficients of inbreeding coefficient on carcass traits using an LMM in Hanwoo steers

Trait	β (slope)	SE	p-value
CWT	0.000235	0.000098	0.017
EMA	0.002839	0.000438	< 0.001
BF	-0.005640	0.000961	< 0.001
MS	0.024772	0.002551	< 0.001

CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9); β : Estimates of linear regression coefficient per 1% increase in inbreeding coefficient (F); SE: Standard error.

Exact p-values before rounding: CWT (0.016967), EMA (8.87×10^{-11}), BF (4.27×10^{-9}), MS (2.74×10^{-22}).

Analysis of inbreeding coefficient and carcass traits using the QMM

The results of the analysis using a quadratic regression model to investigate the curved relationship between variation in carcass traits and increasing inbreeding coefficient, and whether a threshold exists in Hanwoo steers, are shown in Table 8. The results showed that for CWT, EMA, and MS, except for BF, the regression coefficients of both the first-order linear term (β_1) and the second-order nonlinear term (β_2) were highly significant at the $p < 0.001$ level.

For the linear and nonlinear regression coefficients of each trait, CWT was estimated as $\beta_1 = 2.795$ and $\beta_2 = -0.161$ ($p < 0.001$), EMA as $\beta_1 = 0.844$ and $\beta_2 = -0.041$ ($p < 0.001$), and MS as $\beta_1 = 0.112$ and $\beta_2 = -0.005$ ($p < 0.001$). All three traits showed a curved pattern of an inverted U-shaped curve, in which the first-order term β_1 had a positive (+) regression coefficient and the second-order term β_2 had a negative (−) regression coefficient.

This showed that carcass trait performance increased with genetic improvement in the low inbreeding range. However, when the inbreeding level exceeded a certain level (turning point), the negative effect of the second-order term increased, and carcass traits began to decrease.

On the other hand, in the BF model, the regression coefficient of the first-order term was $\beta_1 = -0.028$ ($p = 0.036$) and showed statistical significance, but the regression coefficient of the second-order term was $\beta_2 = 0.000037$ ($p = 0.965$, NS) and was not significant. This result means that BF did not show a nonlinear curved effect according to increasing inbreeding level and showed only a simple linear tendency of a small decrease.

The R^2 values of the quadratic regression model (CWT: 0.121, EMA: 0.077, MS: 0.040) slightly increased compared with the previous LRM, showing that the nonlinear model had better explanatory power. In particular, the negative second-order regression coefficients β_2 obtained for CWT, EMA, and MS clearly showed that there is an optimal threshold limit for management of the inbreeding coefficient to minimize damage from inbreeding depression when establishing Hanwoo mating plans.

The turning point of each inverted U-shaped curve was calculated from the QMM coefficients using $F^* = -\beta_1/(2\beta_2)$. It represents the inbreeding level at which the curve reaches the highest point (Table 8). The calculated values were 8.68% for CWT ($-2.795/(2 \times -0.161)$), 10.29% for EMA ($-0.844/(2 \times -0.041)$), and 11.20% for MS ($-0.112/(2 \times -0.005)$).

These values were all above 6.25%. The 6.25% value was already used as the upper boundary of the F6.25 group in Table 4 before the regression analysis was done. It was not a value obtained from the QMM. The turning point was different among traits and ranged from about 8.7% to 11.2%. So, the 6.25% group boundary and the QMM estimates do not mean exactly the same thing. This difference is discussed again in the Conclusion.

Table 8. Linear and quadratic regression coefficients of inbreeding coefficient for carcass traits using a QMM in Hanwoo steers

Trait	β_1 (linear)	β_2 (quadratic)	p -value (linear)	p -value (quadratic)	R^2
CWT	2.795	-0.161	< 0.001	< 0.001	0.121
EMA	0.844	-0.041	< 0.001	< 0.001	0.077
BF	-0.028	0.000037	0.036	0.965	0.021
MS	0.112	-0.005	< 0.001	< 0.001	0.040

CWT: carcass weight (kg); EMA: eye muscle area (cm²); BF: backfat thickness (mm); MS: marbling score (1–9); β_1 : linear regression coefficient for inbreeding coefficient (F); β_2 : Quadratic regression coefficient for squared inbreeding coefficient (F²); R^2 : Coefficient of determination.

Exact p -values before rounding:

CWT: $p_{\text{linear}} = 3.50 \times 10^{-73}$, $p_{\text{quadratic}} = 2.20 \times 10^{-63}$

EMA: $p_{\text{linear}} = 1.40 \times 10^{-119}$, $p_{\text{quadratic}} = 5.35 \times 10^{-76}$

BF: $p_{\text{linear}} = 0.036269$, $p_{\text{quadratic}} = 0.964989$ (not significant)

MS: $p_{\text{linear}} = 8.59 \times 10^{-95}$, $p_{\text{quadratic}} = 2.07 \times 10^{-51}$

CONCLUSION

This study analyzed the relationship between pedigree-based inbreeding coefficient and major carcass traits (CWT, EMA, BF, MS) using 139,493 Hanwoo steers born in Gyeongbuk from 2015 to 2024. The linear and nonlinear effects according to increasing inbreeding level were also evaluated. In animal genetics and breeding, inbreeding has been used as a breeding strategy to fix superior genotypes and improve genetic uniformity of a population (Wright, 1922; Falconer and Mackay, 1996). However, accumulation of inbreeding above a certain level is known to increase homozygosity of harmful recessive genes and cause inbreeding depression that reduces productivity (Charlesworth and Charlesworth, 1987; Croquet et al., 2006).

The results showed that the average inbreeding coefficient of the population was 1.36%, and the inbreeding coefficient continuously increased according to birth year. The average inbreeding coefficient of animals born in 2015 was 0.728%, but increased to 1.716% in 2024,

showing an increase of about 1.0 percentage point during the recent 10 years. These results suggest that the effective population size (N_e) has decreased because of intensive use of superior proven bulls (KPN) and repeated use of specific superior pedigree lines, and that the inbreeding level of the whole population has continuously increased. This tendency was also similar to results reported in beef and dairy cattle populations in other countries (Sørensen et al., 2005; Mc Parland et al., 2007).

Although semen from the same nationally proven bulls was used, the average inbreeding coefficient and carcass traits differed significantly among regions. These regional differences suggest that carcass traits were affected not only by genetic factors but also by feeding management, feeding systems, climate, and farm management conditions. To account for this variation, region was included as a random effect in the LMM.

The least squares means showed that carcass traits increased at low inbreeding levels. CWT, EMA, and MS were highest in the F3.125 group ($1.25\% < F \leq 3.125\%$). The values were 486.35 ± 0.25 kg, 101.14 ± 0.06 cm², and 6.45 ± 0.01 , respectively. Carcass traits started to decrease in the F6.25 group ($3.125\% < F \leq 6.25\%$). The F6.25up group ($F > 6.25\%$) showed lower carcass performance than the F3.125 and F6.25 groups. This result may show inbreeding depression at high inbreeding levels. In the field data, carcass performance decreased above the predefined 6.25% boundary. However, the QMM turning points were higher. They were 8.68% for CWT, 10.29% for EMA, and 11.20% for MS. Therefore, 6.25% can be used as a practical level for management, but it should not be considered as an exact biological threshold.

At a low level of inbreeding, genetic gain from intensive use of superior bulls may partly offset the negative effects of inbreeding. However, when inbreeding accumulates above a certain level, the effect of inbreeding depression may exceed the effect of genetic improvement because of increased homozygosity of harmful recessive genes. These results showed a tendency similar to the threshold levels of inbreeding depression reported in other livestock species (Carolino and Gama, 2008; Doekes et al., 2019). Previous studies mainly reported an average decrease in productivity according to increasing inbreeding. In contrast, this study presented an inbreeding level at which inbreeding depression begins to accelerate and suggested a quantitative management standard that can be used in Hanwoo breeding programs.

In conclusion, considering the continuously increasing trend of inbreeding in the recent Hanwoo population, future mating plans need a scientific mating strategy that goes beyond simply avoiding inbreeding. Individual inbreeding coefficients should be continuously monitored and managed so that the inbreeding coefficient does not exceed approximately 6.25%. In addition, optimum contribution selection and planned mating programs should be used together with efficient use of superior genetic resources to maintain genetic diversity within the population. Through these approaches, a sustainable Hanwoo breeding system should be established to maximize genetic improvement while minimizing inbreeding depression.

ACKNOWLEDGMENTS

Not applicable.

AUTHOR CONTRIBUTION

Conceptualization: Koo Y, Lee JH. Data curation: Koo Y. Formal analysis: Koo Y, Hwangbo S. Methodology: Hwangbo S, Lee JH. Writing – original draft: Koo Y, Hwangbo S. Writing – review & editing: Lee JH. Supervision: Lee JH. Funding acquisition: Lee JH. All authors read and approved the final manuscript.

CONFLICT OF INTERESTS

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

ETHICAL STATEMENT

This study did not involve any experimental procedures on live animals. All data analyzed were pedigree and carcass records routinely collected by the Korea Animal Improvement Association for national genetic evaluation and carcass grading. Therefore, approval from an Institutional Animal Care and Use Committee was not required.

FUNDING

This research was supported by the ANCHOR program through the Gyeongbuk ANCHOR CENTER, funded by the Ministry of Education (MOE) and Gyeongsangbuk-do, Republic of Korea (2026-ANCHOR-15-104; 2026031101).

USE OF ARTIFICIAL INTELLIGENCE

The authors declare that no generative artificial intelligence (AI) tools were used in the preparation of this manuscript.

REFERENCES

- Carolino N, Gama LT. 2008. Inbreeding depression on beef cattle traits: Estimates, linearity of effects and heterogeneity among sire-families. *Genetics Selection Evolution* 40:511–527. <https://doi.org/10.1186/1297-9686-40-5-511>
- Charlesworth D, Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237–268. <https://doi.org/10.1146/annurev.es.18.110187.001321>
- Croquet C, Mayeres P, Gillon A, et al. 2006. Inbreeding depression for global and partial economic indexes, production, type, and functional traits. *Journal of Dairy Science* 89(6):2257–2267. [https://doi.org/10.3168/jds.S0022-0302\(06\)72297-4](https://doi.org/10.3168/jds.S0022-0302(06)72297-4)
- Doekes HP, Veerkamp RF, Bijma P, et al. 2019. Inbreeding depression due to recent and ancient inbreeding in Dutch Holstein-Friesian dairy cattle. *Genetics Selection Evolution* 51:54. <https://doi.org/10.1186/s12711-019-0497-z>
- Duncan DB. 1955. Multiple range and multiple F tests. *Biometrics* 11(1):1–42. <https://doi.org/10.2307/3001478>
- Falconer DS, Mackay TFC. 1996. *Introduction to quantitative genetics*. 4th ed. Longman Group.
- Hwang JM, Park CJ, Choi JG. 2009. The inbreeding trend of Hanwoo cow population. *Annals of Animal Resources Sciences* 20:1–5.
- Hwangbo S, Koo Y, Lee JH. 2026. Evaluation of inbreeding and founder-based genetic diversity in Hanwoo cows. *Journal of Animal Breeding and Genomics* 10(1):1–11. <https://doi.org/10.12972/jabng.2026.10.1.1>
- Kim GE, Lee ED, Chung SU, et al. 2024. Effects of inbreeding coefficients on carcass traits for mating scheme in Hanwoo. *Journal of Korea Academia-Industrial Cooperation Society* 25(5):511–518. <https://doi.org/10.5762/KAIS.2024.25.5.511>
- Koo Y, Alam M, Park M, et al. 2021. Estimation of pedigree completeness index, inbreeding coefficient and effective population size of breeding stock for Hanwoo cows. *Journal of Animal Breeding and Genomics* 5(3):73–83. <https://doi.org/10.12972/jabng.20210007>
- Lush JL. 1945. *Animal Breeding Plans*. 3rd ed. Iowa State College Press, Ames, IA, USA.
- Lynch M, Walsh B. 1998. *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland, MA, USA.

- Mc Parland S, Kearney JF, Rath M. 2007. Inbreeding effects on milk production, calving performance, fertility, and conformation in Irish Holstein-Friesians. *Journal of Dairy Science* 90(9):4411–4419. <https://doi.org/10.3168/jds.2007-0227>
- Searle SR, Casella G, McCulloch CE. 1992. *Variance components*. John Wiley & Sons New York, NY, USA. <https://doi.org/10.1002/9780470316856>
- Song CW, Lopez BIM, Seo KS. 2018. Inbreeding coefficient and pedigree analysis of Hanwoo cattle population. *Journal of Animal Breeding and Genomics* 2(4):223–230. <https://doi.org/10.12972/jabng.20180037>
- Sørensen AC, Sørensen MK, Berg P. 2005. Inbreeding in Danish dairy cattle breeds. *Journal of Dairy Science* 88(5):1865–1872. [https://doi.org/10.3168/jds.S0022-0302\(05\)72861-7](https://doi.org/10.3168/jds.S0022-0302(05)72861-7)
- Wright S. 1922. Coefficients of inbreeding and relationship. *The American Naturalist* 56:330–338. <https://doi.org/10.1086/279872>