

1  
2

JAST (Journal of Animal Science and Technology) TITLE PAGE

ARTICLE INFORMATION	Fill in information in each box below
Article Type	Research article
Article Title (within 20 words without abbreviations)	Parameter Estimation and Assessment of Bias in Genetic Evaluation of Carcass Traits in Hanwoo Cattle Using Real and Simulated Data
Running Title (within 10 words)	Assessment of Bias in Genetic Parameter Estimates of Carcass Traits
Author	Mohammed Bedhane <sup>1</sup> , Julius van der Werf <sup>2</sup> , Sara de las Heras-Saldana <sup>2,3</sup> , Leland Ackerson IV <sup>1</sup> , Dajeong, Lim <sup>4</sup> , ByoungHo Park <sup>4</sup> , Mi Na Park <sup>4</sup> , Seung Roh <sup>5</sup> , Samuel Clark <sup>2</sup>
Affiliation	<sup>1</sup> College of Agriculture & Natural Resources, Michigan State University, East Lansing, USA <sup>2</sup> School of Environmental and Rural Science, University of New England, Armidale, Australia <sup>3</sup> AGBU, a joint venture of NSW Department of Primary Industries and University of New England, 2351, Armidale, Australia <sup>4</sup> National Institute of Animal Science, RDA, Republic of Korea <sup>5</sup> Hanwoo Genetic Improvement Center, NAGI, Republic of Korea
ORCID (for more information, please visit <a href="https://orcid.org">https://orcid.org</a> )	Mohammed Bedhane 0000-0003-4149-4118
Competing interests	The authors declare that they have no competing interests
Acknowledgements	The project was supported by the National Institute of Animal Science, Rural Development Administration (RDA), Republic of Korea.
Availability of data and material	Upon a reasonable request, the datasets of this study can be available from the corresponding author.
Authors' contributions Please specify the authors' role using this form.	Conceptualization: Bedhane MN, Samuel AC., Julius W, Sara HS. Data curation: Bedhane MN, Samuel AC., Julius W, Park MN. Hee RS., Park B., Lim D. Formal analysis: Bedhane MN Methodology: Bedhane MN, Samuel AC., Julius W. Software: Bedhane MN, Samuel AC. Validation: Bedhane MN, Samuel AC., Ackerson IV L Investigation: Bedhane MN, Samuel AC, Julius W., Sara HS. Writing - original draft: Bedhane MN. Writing - review & editing: Bedhane MN, Samuel AC., Julius W, Sara HS., Ackerson IV L.
Ethics approval and consent to participate	This article does not require IRB/IACUC approval because performance data was collected from standard slaughterhouses in South Korea

3  
4

5 CORRESPONDING AUTHOR CONTACT INFORMATION

For the corresponding author (responsible for correspondence, proofreading, and reprints)	Fill in information in each box below
First name, middle initial, last name	Mohammed N. Bedhane
Email address – this is where your proofs will be sent	benegash@gmail.com
Secondary Email address	bedhanem@msu.edu
Address	1132 Poplar Lane, Apt.103, East Lansing, 48823, Michigan, USA.
Cell phone number	+1 (763)-339-0735
Office phone number	-
Fax number	-

6

7 **Abstract**

8 Most carcass and meat quality traits are moderate to highly heritable, indicating that they can be improved through  
9 selection. Genetic evaluation for these types of traits is performed using performance data obtained from commercial  
10 and progeny testing evaluation. The performance data from commercial farms are available in large volume, however,  
11 some drawbacks have been observed. The drawback of the commercial data is mainly due to sorting of animals based  
12 on live weight prior to slaughter, and this could lead to bias in the genetic evaluation of later measured traits such as  
13 carcass traits. The current study has two components to address the drawback of the commercial data. The first  
14 component of the study aimed to estimate genetic parameters for carcass and meat quality traits in Korean Hanwoo  
15 cattle using a large sample size of industry-based carcass performance records (n=469,002). The second component  
16 of the study aimed to describe the impact of sorting animals into different contemporary groups based on an early  
17 measured trait and then examine the effect on the genetic evaluation of subsequently measured traits. To demonstrate  
18 our objectives, we used real performance data to estimate genetic parameters and simulated data was used to assess  
19 the bias in genetic evaluation. The results of our first study showed that commercial data obtained from  
20 slaughterhouses is a potential source of carcass performance data and useful for genetic evaluation of carcass traits to  
21 improve beef cattle performance. However, we observed some harvesting effect which leads to bias in genetic  
22 evaluation of carcass traits. This is mainly due to the selection of animal based on their body weight before arrival to  
23 slaughterhouse. Overall, the non-random allocation of animals into a contemporary group leads to a biased estimated  
24 breeding value in genetic evaluation, the severity of which increases when the evaluation traits are highly correlated.

25 **Keywords:** Hanwoo, carcass traits, heritability, genetic evaluation, commercial data, simulation study.

26

27 **1. INTRODUCTION**

28 In South Korea, genetic evaluation was performed with data obtained from progeny testing and commercial data to  
29 improve carcass and meat quality traits of Hanwoo beef cattle (1). Recently, a genetic breeding program has started,  
30 and many studies assess the use of genomics in small sample sizes (1-7). Higher to moderate heritabilities were  
31 reported for most carcass traits and marbling scores (2-5, 7-12). Other traits such as meat and fat colour were moderate  
32 to lower heritable in Hanwoo cattle (2, 3, 5, 7-11). Carcass and meat quality traits have a major influence on the  
33 profitability of beef production but represent a challenge since they are often hard to measure and select for. This is  
34 because carcass traits cannot be recorded on selection candidates and therefore time-consuming progeny tests are often  
35 used to gain selection accuracy. Due to this cost, breeders often look to commercial animals recorded for carcass  
36 performance. Performance records on commercial animals are interesting because the large number of animals being  
37 harvested, which presents opportunities to improve accuracy at a perceived low cost (13). However, there are often  
38 drawbacks to this commercial data due to the production management strategies. For instance, animals are usually  
39 recruited or sorted into management groups according to their weight, and similarly, they arrive in abattoirs in  
40 homogenized cohorts. Such selective formation of contemporary groups referred to as 'harvesting' could lead to  
41 biased evaluation of genetic merit.

42 Sources of bias in genetic evaluation have been discussed widely in literature (14). The main sources of bias in animal  
43 breeding are non-random selection of animals for breeding (parental selection), sequential selection, culling of animals  
44 before records, preferential treatment, selective reporting, and misclassification or manipulation of contemporary  
45 groups (15). Regardless of the source of information, genetic evaluation methods can be used to account for non-  
46 genetic effects (14). Various methods have been deployed for genetic evaluation in livestock and mixed model  
47 evaluation of single and multiple traits (16-19). For unbiased genetic evaluation, fixed effects, such as a contemporary  
48 group, and covariates such as age, live weight and carcass weight are fitted in the model to account for non-genetic  
49 factors (20). For instance, adjustment of slaughter endpoints such as harvesting age and weight has an impact on  
50 genetic evaluation, Pollott, Guy (21) found that the heritability for daily carcass weight gain was higher with slaughter  
51 at fixed weight ( $h^2 = 0.63$ ) than at fixed age ( $h^2 = 0.11$ ), indicating that animals can attain similar slaughter weight at  
52 different age. In general, field data are consistently provided by herds in which artificial selection is continuously  
53 occurring and where heavier animals are sent first to slaughterhouses. Consequently, the usual assumption of random  
54 sampling invoked for estimation and prediction (22) is no longer valid in genetic evaluation. The extent of a possible

55 bias in genetic evaluation can be evaluated using simulated data instead of field data. The first component of this study  
56 aimed to estimate genetic parameters for carcass and meat quality traits in Korean Hanwoo cattle using industry-based  
57 carcass performance records. Following, we aimed to assess the impact of sorting animals based on early measured  
58 traits on the genetic evaluation of subsequently measured traits using simulated data.

## 59 **2. MATERIALS AND METHODS**

### 60 **2.1. Commercial data**

61 All phenotypic and pedigree data used in the present study were obtained from the Republic of South Korea.  
62 Individuals without a record of sire or dam were discarded from the data. After filtering the raw data, 469,002 Hanwoo  
63 cattle from 3,464 distinct farms were used in the analysis. The pedigree file comprised 1.23 million ancestors over 13  
64 generations, including 646 sires and 390,166 dams in the analysis. The animals were born between the year of 2008  
65 and 2014, and slaughtered between the ages of 28 and 35 months. All studied traits were recorded between the years  
66 2010 and 2016.

#### 67 **2.1.1. Modelling of fixed effects**

68 A preliminary analyses of variance was performed using the linear model in R (R-Core-Team, 2018) to identify the  
69 most appropriate fixed effects (contemporary groups) to be used in the subsequent analyses for all studied traits. The  
70 most significant factor was the interaction between herd (3,646 herds), birth-year (7-levels), and birth-season (4-  
71 levels), which were combined to form the contemporary group. The final dataset consisted of 469,002 animals from  
72 31,403 contemporary groups (Table 1). A contemporary group of herd-year-season (HYS) with less than five records  
73 was omitted from the analysis. The distribution of animals across various ages and herds, as well as animals born in  
74 each year, and season, are shown in Figure 1. The description of population structure, as well as the distribution of  
75 animals across age, herd, birth year, and season are summarized in Table 1 and Figure 1. [*Insert Table 1 and Figure*  
76 *1*]

#### 77 **2.1.2. Carcass traits**

78 All individuals were slaughtered at various ages (28-35 months), and phenotypic measurements were taken on the  
79 chilled carcass. Phenotypic data on carcass traits included carcass weight (CWT), eye muscle area (EMA), backfat  
80 thickness (BFT), bodyweight at slaughter (BW), and meat-index (MI). EMA and BFT were measured at the 12<sup>th</sup> and  
81 13<sup>th</sup> rib junction after a 24-h chill, and cold CWT measurement was taken at that time. The fasted live body weight  
82 (BW) in kilogram was taken prior to transport to the abattoirs. Only 52% of animals in the dataset had bodyweight

83 records at slaughter. The meat index (MI) represents the retail cut percent, which is predicted from a linear index of  
84 carcass weight (kg), eye muscle area (cm<sup>2</sup>), and backfat thickness (mm).  $MI=68.184-[0.625 * BFT] + [0.130 * EMA]-$   
85  $[0.024 * CWT] + 3.23$

### 86 **2.1.3. Meat quality traits**

87 Meat quality traits included marbling score (MS), meat colour (MC), fat colour (FC), and meat texture (MT) which  
88 were each graded at the time when carcass traits were measured. Marbling score was recorded based on visual  
89 inspection by trained technicians using the Beef Marbling Standard (BMS) for grading the carcass. The BMS system  
90 classifies the meat from 1 to 9 scale of marbling, with a 2% intramuscular fat content difference between each point  
91 score (23). Similarly, trained technicians graded the other three traits (MC, FC, and MT) manually. Meat colour was  
92 assessed and graded from very light red (grade 1) to dark red (grade 7). Similarly, the FC was assessed and graded  
93 from polar white (grade 1) to creamy yellow (grade 6). The texture of the meat was evaluated on a scale from very  
94 fine (grade 1) to coarse (grade 3). [Insert Table 2]

### 95 **2.1.4. Statistical model**

96 Variance components and heritabilities were estimated with a series of univariate animal models. For each trait, the  
97 model included the contemporary group (as defined above) fitted as a fixed effect and age fitted as a linear covariate  
98 in the model. Genetic and phenotypic correlations were estimated using a bivariate model with similar fixed and  
99 random effects as the univariate model. ASReml version 4.1 software (24) was used for the entire data analysis. Prior  
100 to the main analysis, we performed a model comparison between a model with and without maternal (permanent  
101 environmental) effect. Based on the *Akaike* information criterion (AIC) value, the model without maternal effect best  
102 fitted the data (25). The model was represented as:

$$103 \quad y = Xb + Zu + e \quad (1)$$

104 where X is an incidence matrix for observations y. Age as a linear covariate and contemporary groups (HYS) as a  
105 fixed effect in vector b, Z is an incidence matrix for random animal additive genetic values in u, and e represents  
106 random environmental effects. u and e were assumed to be distributed as  $u|\sigma_a^2 \sim N(0, A\sigma_a^2)$ ,  $e|\sigma_e^2 \sim N(0, I\sigma_e^2)$ ,  
107 respectively where  $\sigma_a^2$  is the additive genetic variance and  $\sigma_e^2$  is the residual. Where A is a numerator relationship  
108 matrix for all animals using 13 generations and I is an identity matrix.

109 **2.2. Simulated data**

110 A stochastic simulation was used to study how the genetic evaluation of the carcass traits was affected when the  
111 animals were sorted based on early age performance traits such as yearling weight. A beef cattle population was  
112 simulated with the input parameters described in Table 3, using R (26). The simulated base population consisted of  
113 100 sires and 2,000 dams, which were assumed unrelated and not in-bred. The mating ratio of sire to dam was 1 to 20.  
114 A total of 4,000 progeny were produced in a single generation. All progenies had an early age measurement (EM) for  
115 yearly body weight and were subsequently measured for carcass traits later in the production cycle (Late measurement  
116 (LM)). All progenies were split into 10 contemporary groups (CG), each with 400 animals. The CGs were generated  
117 using two alternatives to sort the progeny; 1) based on the early trait measurement (EM), 2) randomly assigned to the  
118 CG. The simulated data was consisted of ten replications for each scenario. In each scenario, the genetic evaluation  
119 was performed on carcass traits (LM). To examine the range of possibilities for EM and LM traits, a variety of  
120 heritability and correlation values were used for data simulation (Table 3). [Insert Table 3]

121 **2.2.1. Model and data analysis**

122 Linear mixed models were used to estimate the breeding values and variance components (16) implemented in  
123 ASReml version 4.1 (24) using the model described in equation 1. The fixed effect (CG) was fitted only to the LM  
124 trait in the sorted scenario. The bias in the variance of the estimated breeding values was measured through the  
125 regression coefficient (slope) of the true breeding values of 100 base sires on their estimated breeding values (EBV)  
126 in each replication. The estimated bias in EBV was the mean of the 10 replications.

127 **3. RESULTS**

128 **3.1. Commercial data**

129 Variance components and heritabilities for the studied traits are shown in Table 4. In the current study, the estimated  
130 heritabilities for carcass traits ranged from 0.37 for EMA to 0.45 for MI. However, meat quality traits showed low to  
131 high heritability and the estimates ranged from 0.004 for FC to 0.55 for MS. The phenotypic and genetic correlations  
132 between studied traits are shown in Table 5. The genetic and phenotypic correlations within carcass traits varied from  
133 0.05 to -0.94, and 0.03 to -0.94, respectively. Similarly, the genetic and phenotypic correlations within meat quality  
134 traits ranged from 0.42 to -0.94, and 0.04 to -0.61, respectively. The genetic correlations between carcass and meat  
135 quality traits varied from low (0.04) to medium (0.44). All correlations were estimated with small standard errors  
136 ranging from 0.00 to 0.08. [Insert Tables 4 and 5]

137 **3.2. Simulated data**

138 **3.2.1. The impact of sorting animals in genetic evaluation**

139 As expected, the random allocation of animals to CG was unbiased; however, bias was observed when animals were  
140 sorted into CG based on EM traits. The degree of bias varied depending on the heritability and the correlations  
141 between EM and LM traits.

142 **3.2.2. The impact of correlations between traits with the same heritability**

143 As indicated in Figure 2 A, the EBV was biased (overestimated) when the genetic and residual correlations between  
144 the simulated traits were -0.8 and 0.8 respectively. Slight underestimated EBV was observed when the genetic and  
145 residual correlation between the EM and LM traits was higher (0.8). These results indicated that the bias was higher  
146 for the sorting scenario when the correlation between the two studied traits was higher. But slightly biased EBV was  
147 observed when the genetic and residual correlation was lower (-0.2 and 0.2) (Figure 2 A). The result showed that  
148 changes in genetic and residual correlations affected the magnitude of bias in the EBV. The current results showed  
149 that the EBV was highly biased when the correlation between the sorting (EM) and the subsequent evaluation (LM)  
150 trait was higher, and sorting bias was lesser when the correlation between the two traits was weaker. At higher genetic  
151 (0.8) and residual (-0.8) correlations, considerably overestimated EBV with a bias of 0.54 was observed (Figure 2 D).  
152 However, less biased EBV was observed when the residual correlations were lower (Figure 2 D). Overall,  
153 overestimated, and underestimated breeding values were observed at the combination of high genetic and residual  
154 correlations (Figure 2 D). With similar genetic and residual correlations, a slight increment of bias was observed when  
155 the heritabilities of both simulated traits changed from high (0.5) to low (0.2).

156 **3.2.3. The impact of correlations with different heritability**

157 We assessed the bias generated by sorting animals in the genetic evaluation using traits with different heritabilities  
158 (high-low and low-high). In the randomly sampled scenario, the regression coefficients (slopes) in all alternatives  
159 were equal to one and no change of bias was observed with changing of input parameters including heritability of the  
160 traits (results not shown). However, we observed different magnitudes of bias with the changing of input parameters  
161 between the two studied traits when animals were sorted into various CG depending on the EM trait (yearly weight).  
162 Highly biased estimated breeding values of 0.15 ( $\pm 0.01$ ) and 0.20 ( $\pm 0.02$ ) were observed when genetic and residual  
163 correlations were 0.8 and -0.8, respectively (Figure 2, B). These highly biased EBV (overestimated) were observed  
164 when the heritability of the LM trait (evaluation trait) was low (0.2). However, relatively less biased EBV were



165 observed when the heritability of the LM trait was higher (Figure 2, C). The highly biased EBV with low heritability  
166 of LM trait indicated that at constant genetic and residual correlations, genetic evaluation is further affected by the  
167 heritability of the evaluation (LM) trait than the sorting (EM) trait. Relatively less biased EBV was observed at low  
168 correlations with both high and low heritability of the evaluation (LM) trait (Figure 2, B & C). The low genetic and  
169 residual correlations may be responsible for the less biased EBV even though the heritability of the LM trait varied.  
170 Overall, with the low heritability (0.2) of the LM trait, the EBV was highly biased (overestimated), however, when  
171 the heritability of the LM trait was higher (0.5) the EBV was less biased. In addition, the bias of EBV was less when  
172 the difference between the genetic and residual correlations was lower whereas highly biased EBV was observed when  
173 the difference between the two correlations was bigger. Overall, our results indicate that the magnitude of the sorting  
174 bias depends on the genetic architecture of the two traits. [Insert Figure 2]

## 175 **4. DISCUSSIONS**

### 176 **4.1. Commercial data**

177 The estimated heritability for carcass weight was  $0.44 \pm 0.01$ , which is higher than most other reports in Hanwoo where  
178 the reported estimates ranged from 0.25 to 0.39 (9, 11, 27, 28). The main reason for the difference is the weights of  
179 the animals used in the current study were obtained from commercial farm and had higher weight. Similarly, the  
180 heritability of EMA in the current study was higher ( $0.37 \pm 0.01$ ) than estimates in previous reports which ranged from  
181 0.27 to 0.36 (8, 11). The estimated heritability for BFT in the current study ( $0.44 \pm 0.01$ ) is very close to previous  
182 reports on Hanwoo cattle ranging from 0.44 to 0.45 (2, 9, 11). However, the MI trait showed high heritability compared  
183 to previous findings (0.26) reported by Do, Park (8) in Hanwoo cattle. This is because the MI trait in the current study  
184 was predicted from carcass traits such as carcass weight which were obtained from commercial data. In Hanwoo cattle,  
185 previously reported heritabilities for meat quality traits ranged from 0 for FC to 0.65 MS (2, 8, 9, 11, 27, 28).

186 Slight variations have been observed between current and previous estimated heritabilities in Hanwoo beef cattle.  
187 These inconsistencies mainly have arisen from the data type used in each report. Most of the previous reports used  
188 small data set obtained from well-deigned progeny testing experiments that showed low variation compared to the  
189 data used in the current study obtained from slaughterhouses. Compared to previous reports, the data used in the  
190 current study is larger (half a million animals) and were obtained from more than three thousand farms in the Republic  
191 of South Korea. Types of information such as pedigree and/or genomic data used in the analysis may lead to different  
192 values of parameter estimates. Some traits such as marbling score had different heritability estimates in different

193 breeds because the traits have shown different genetic variation in different populations. For instance, the currently  
194 estimated heritability for MS was 0.55 and it is higher than the estimated in other beef cattle breeds reported by Davis  
195 and Simmen (29) ( $0.27 \pm 0.17$ ), Ríos-Utrera, Cundiff (30) ( $0.40 \pm 0.09$ ) and Nephawe, Cundiff (31)  $0.46 \pm 0.06$  in Angus  
196 and US purebred and composite steers respectively.

197 In the current study, CWT showed moderate and positive genetic (0.51) correlation with EMA, which is lower than  
198 the previous estimates ranged from 0.63 to 0.80 in Hanwoo cattle (8, 9, 28). In agreement with the current results,  
199 Hwang et al. (2008) reported a negative genetic correlation (-0.24) between EMA and BFT in Hanwoo cattle. In the  
200 current study, the estimated phenotypic and genetic correlations between CWT and BFT were 0.27 and 0.05,  
201 respectively; however, with small data set, Do, Park (8) reported a lower genetic correlation of 0.17 and higher  
202 phenotypic correlation of 0.31 between CWT and BFT. The highest genetic (0.94) and phenotypic (0.93) correlations  
203 were observed between BW at slaughter and CWT in the current study. These two traits are extensively studied in  
204 other breeds and they show high correlation (32). Low genetic correlations of BW with EMA (0.30) and BFT (0.10)  
205 had been reported by Smith, Domingue (32) in Brahman cattle, which is in range with the current study. In the current  
206 study, the genetic correlation of MI with CWT was lower and moderate with EMA while higher (-0.94) with BFT. In  
207 agreement with our current study, high negative genetic (-0.95) and phenotypic (-0.97) correlations between MI and  
208 BFT had been reported in Hanwoo cattle (8). This is because MI trait was predicted from the three traits (CWT, EMA  
209 and BFT), as a result, MI showed a high genetic and phenotypic correlations with CW, EMA and BFT traits.

210 In the current study, genetic and phenotypic correlations between meat quality traits varied from high to low.  
211 Previously, similar genetic and phenotypic correlations were reported between MS and MT traits in Hanwoo cattle  
212 using pedigree and genomic data (4, 5, 8), however, the phenotypic correlation between MS and MT reported by these  
213 authors were lower compared to current estimates. The high genetic correlation between MS and MT traits suggests  
214 that the traits are highly dependent. Given this strong correlation and the fact that MS has more genetic variation (high  
215 heritability), it is the easiest trait to use to select for high meat quality or both traits can be improved simultaneously.  
216 Compared with the current study, Do, Park (8) reported lower (-0.42 and -0.40) genetic correlations of MS with meat  
217 and fat colour traits, respectively using small sample size data obtained from progeny testing experiments of Hanwoo  
218 cattle. Slightly higher genetic correlation between colour traits (meat and fat colour) was reported using genomic data  
219 in Hanwoo cattle (4). The genetic correlations of MT with MC and FC traits in the current study were similar to the  
220 previous reports in Hanwoo cattle (4, 8). In the current study, we observed low genetic correlation between carcass

221 and meat quality traits. Similarly, several studies reported low genetic and phenotypic correlation estimates between  
222 carcass and meat quality traits in Hanwoo cattle (8, 9, 11, 27).

223 Overall, the currently estimated genetic parameters laid within the range of previous reports in Hanwoo cattle, however,  
224 slight differences have been observed for some traits. The main reasons for the observed difference are the sample  
225 size used in the study, source of performance data (commercial farms versus well-designed progeny testing  
226 experiments) and type of the information used to estimate the relationship among animals (pedigree versus genomic  
227 data). In addition, various models were used to analyse the data, the random and fixed effects that are fitted in the  
228 model, and the random or non-random allocation of animals into contemporary group leads to different value of  
229 parameter estimation in the genetic evaluation of carcass traits. Furthermore, the scoring or grading system of meat  
230 quality is very subjective across studies and has an impact on the genetic evaluation of such traits.

#### 231 **4.1.1. The use and implication of commercial data in genetic evaluation**

232 The phenotypic data used in the current study was obtained from slaughterhouse and these carcass performance data  
233 were recorded on various age groups of animals ranged between 28 and 35 months. The estimated parameters in the  
234 current study are closer to previously reported estimates obtained from progeny testing experiment. This is indicating  
235 that commercial data obtained from slaughterhouse are useful and can be used to estimate genetic parameters in the  
236 evaluation of carcass traits. The commercial carcass performance data can be available in large amount from  
237 slaughterhouse compared to progeny testing experiment data, but we have observed some drawback in the commercial  
238 data. This is because, in most commercial farms, the desired carcass quantity and quality is specified by abattoirs  
239 based on the weight of animals, which is suitable for slaughter. As a result, most animals have arrived in abattoirs in  
240 homogenized weight which is called harvesting effect. Such selective formation of contemporary groups might lead  
241 to biased evaluation of genetic merit of animals for carcass trait. However, this type of bias in the genetic evaluation  
242 can be controlled using various models depending on the source of the bias. For instance, bias due to sorting of animals  
243 based on weight can be reduced or eliminated using multitrait genetic evaluation methods. The multitrait model can  
244 account for harvesting effect and thus produce more accurate and less biased parameter estimation in genetic  
245 evaluation.

#### 246 **4.1.2. Simulated data**

247 Sorting of animals based on yearling weight potentially affected the genetic evaluation of the latter measured traits.  
248 The current study has verified that the non-random evaluation of animals led to a bias in genetic evaluation.

249 **4.1.3. The impact of sorting in genetic evaluation**

250 The sorting bias observed in the current simulation study has a similar effect to the selection bias described in the  
251 literature (14, 15, 33). The theory of selection bias was established clearly by Pollak, van der Werf (15). They  
252 demonstrated that potential bias was found in the genetic evaluation of the second trait, which was selected based on  
253 the first trait. Similarly, in the current simulation study, when animals were sorted based on the early measured trait,  
254 sorting bias was detected in the subsequent evaluation of the latter measured trait. Also, Pollak and Quaas (33)  
255 observed a selection bias in the predictors in single-trait analysis and the magnitude of the bias of the EBV depends  
256 on the correlation among studied traits which is in agreement with the current findings.

257 A recent study by Macedo, Reverter (34) has studied a selection bias in genetic evaluation models. They found a  
258 selection bias in genetic evaluation using data with environmental trends compared to randomly sampled data into  
259 different contemporary groups. Similarly, in the current study, we found biased EBV when animals were non-  
260 randomly assigned into various contemporary group. Selection bias has been studied in sheep, Eiríksson and  
261 Sigurdsson (35) demonstrated that a selected group of the lambs was kept for replacement and therefore not measured  
262 for carcass traits, led to bias in the genetic evaluations. The authors demonstrated that the bias was higher for the  
263 selected ram group, indicating that this group consisted of rams that had higher genetic merit for carcass conformation  
264 trait than the rest groups. Similarly, we found biased EBV when animals with higher yearling weight were assigned  
265 into same group.

266

267 **4.1.4. The impact of traits' heritability, genetic and residual correlations in genetic evaluation**

268 In the current simulation study, the structures of input parameters including heritability, genetic and residual  
269 correlations, and the difference between the two correlations influenced the genetic evaluations. The genetic and  
270 phenotypic correlation of traits potentially affects the genetic evaluation of animals in breeding program (15, 33, 36,  
271 37). Our results showed that highly biased EBV was observed when the genetic correlations were higher which  
272 coincided with a report by Author et al (33). In addition, our result showed that highly biased EBV was observed  
273 when the difference between genetic and residual correlation was higher. Conversely, when the difference between  
274 genetic and residual correlation was smaller, the EBV was less biased and the regression coefficient was closer to one.  
275 In the current simulation study, the bias of the EBV was assessed by allocating unequal heritabilities (high-low and  
276 the vice versa) for the two simulated traits. In this case, the observed bias of the EBV was not the same as a similar

277 heritability (high-high and low-low) was assigned to the studied traits. Highly biased EBV was observed when the  
278 heritability of the LM (evaluation) trait was lower. This could be explained as genetic evaluation is more affected by  
279 the heritability of the LM trait than the EM (sorting) trait with the constant genetic and residual correlations. A recent  
280 study showed that allocating wrong heritability for the trait in a genetic evaluation led to a biased EBV in simulation  
281 study (34). These authors established that in pedigree-based predictions, the use of incorrect heritability generates a  
282 strong bias in genetic evaluation using simulation data. Our result showed that different magnitude of bias was  
283 observed with two different heritabilities assigned to the LM (evaluation) trait. However, we have not proven that the  
284 observed bias linked to incorrect heritability that was allocated to the evaluation trait during data simulation. Knowing  
285 the source of bias and then using appropriate models for the genetic evaluation of animals is a key component of the  
286 process to estimate accurate breeding values. For instance, to overcome selection bias in genetic evaluation,  
287 multivariate evaluations methods had been proposed (16). The decision to use a multitrait model versus a single trait  
288 model depends on correlations among the studied traits. In the first scenario of the current study, the sorting bias that  
289 was observed in the single-trait model was reduced by the bivariate model (results not shown). Similarly, Pollak, van  
290 der Werf (15) showed that the observed bias associated with selection in the univariate model was reduced or  
291 eliminated by multiple traits evaluation methods.

292 A recent study by Macedo et al (34) has studied a selection or sorting bias in genetic evaluation models. They found  
293 a selection or sorting bias in genetic evaluation using data with environmental trend compared to a randomly sampled  
294 data into different contemporary groups. Similarly, in the current study, we found biased EBV when animals were  
295 non-randomly assigned into various contemporary group. Selection bias has been studied in sheep, Eiríksson and  
296 Sigurdsson (35) demonstrated that a selected group of the lambs was kept for replacement and therefore not measured  
297 for carcass traits, led to bias in the genetic evaluations. The authors demonstrated that the bias was higher for the  
298 selected ram group, indicating that this group consisted of rams that had higher genetic merit for carcass conformation  
299 trait than the rest groups. Similarly, we found biased EBV when animals with higher yearling weight were assigned  
300 into same group.

301

## 302 **5. CONCLUSIONS**

303 The genetic parameters estimated for carcass and meat quality traits in Hanwoo cattle population indicate the extent  
304 of genetic variability among the studied traits that could be exploited through selection programs. Particularly, carcass

305 traits showed high genetic variation in Hanwoo population. On the other hand, results from the current study have  
306 revealed the existence of negative (unfavorable) genetic associations between a carcass and most of meat quality traits.  
307 This implies that long-term selection for carcass traits could negatively affect meat quality traits, which are highly  
308 valuable in Hanwoo cattle. Moderate genetic correlations between EMA and MS suggest that genetic progress for  
309 carcass traits such as EMA may result in more marbled meat. This is important because, marbling is the major price-  
310 determining factor in the Korean beef industry. Very low or near-zero correlations between CWT and most of the  
311 meat quality traits, suggest that selection based on CWT may have little or no influence on the performance of meat  
312 quality traits. In addition, negative genetic and phenotypic correlations between carcass and few meat quality traits  
313 reflect the adverse effects in a single trait selection program. Commercial data obtained from slaughterhouse is a  
314 potential source of carcass performance data and useful for genetic evaluation of carcass traits to improve beef cattle  
315 performance. However, using commercial data could produce biased EBV because in this data, animals are mainly  
316 sorted based on live weight prior to slaughter and this non-random selection of animals to slaughterhouse affects the  
317 genetic evaluation of carcass traits which is obtained from abattoir. Overall, the current simulation study contributed  
318 fundamental information on harvesting effect and how the genetic architecture of studied traits affects the genetic  
319 evaluation of carcass traits.

## 320 **6. ACKNOWLEDGMENTS**

321 The project is funded by Rural Development Administration (RDA), Republic of Korea with the collaborative of  
322 Cooperative Research of Next Generation BioGreen 21 with the Project number BG21.

323

324

325

326 **7. REFERENCES**

- 327 1. Park B, Choi T, Kim S, Oh S-H. National genetic evaluation (system) of Hanwoo (Korean native cattle).  
328 Asian-Australasian journal of animal sciences. 2013;26(2):151.
- 329 2. Choi T, Alam M, Cho C, Lee J, Park B, Kim S, et al. Genetic parameters for yearling weight, carcass  
330 traits, and primal-cut yields of Hanwoo cattle. Journal of animal science. 2015;93(4):1511-21.
- 331 3. Bhuiyan MSA, Kim HJ, Lee DH, Lee SH, Cho SH, Yang BS, et al. Genetic parameters of carcass and  
332 meat quality traits in different muscles (longissimus dorsi and semimembranosus) of Hanwoo (Korean  
333 cattle)1. Journal of Animal Science. 2017;95(8):3359-69.
- 334 4. Bedhane M, van der Werf J, Al Kalaldehy M, Lim D, Park B, Park M, et al., editors. Assessment of  
335 genomic prediction accuracy for meat quality traits in Hanwoo cattle. Proc Assoc Advmt Anim Breed  
336 Genet; 2019.
- 337 5. Bedhane M, van der Werf J, Gondro C, Duijvesteijn N, Lim D, Park B, et al. Genome-Wide  
338 Association Study of Meat Quality Traits in Hanwoo Beef Cattle Using Imputed Whole-Genome  
339 Sequence Data. Frontiers in Genetics. 2019;10:1235.
- 340 6. Mehrban H, Lee DH, Moradi MH, IlCho C, Naserkheil M, Ibáñez-Escriche N. Predictive performance  
341 of genomic selection methods for carcass traits in Hanwoo beef cattle: impacts of the genetic  
342 architecture. Genetics Selection Evolution. 2017;49(1):1.
- 343 7. Bedhane M, van der Werf J, de las Heras-Saldana S, Lim D, Park B, Na Park M, et al. The accuracy  
344 of genomic prediction for meat quality traits in Hanwoo cattle when using genotypes from different  
345 SNP densities and preselected variants from imputed whole genome sequence. Animal Production  
346 Science. 2022;62(1):21-8.
- 347 8. Do C, Park B, Kim S, Choi T, Yang B, Park S, et al. Genetic parameter estimates of carcass traits  
348 under national scale breeding scheme for beef cattle. Asian-Australasian journal of animal sciences.  
349 2016;29(8):1083.
- 350 9. Hwang J-M, Kim S, Choy Y-H, Yoon H-B, Park C-J. Genetic parameter estimation of carcass traits  
351 of Hanwoo steers. Journal of Animal Science and Technology. 2008;50(5):613-20.
- 352 10. Park G, Moon S, Ko Y, Ha J, Lee J, Chang H, et al. Influence of slaughter weight and sex on yield  
353 and quality grades of Hanwoo (Korean native cattle) carcasses. Journal of Animal Science.  
354 2002;80(1):129-36.

- 355 11. Srivastava S, Lopez BI, Heras-Saldana Sdl, Park J-E, Shin D-H, Chai H-H, et al. Estimation of Genetic  
356 Parameters by Single-Trait and Multi-Trait Models for Carcass Traits in Hanwoo Cattle. *Animals*.  
357 2019;9(12):1061.
- 358 12. Strucken EM, Al-Mamun HA, de las Heras-Saldana S, Bedhane MN, Lim D, Park B, et al. Finding  
359 the marble—The polygenic architecture of intramuscular fat. *J Anim Breed Genom*. 2017;1.
- 360 13. Englishby T, Banos G, Moore K, Coffey M, Evans R, Berry D. Genetic analysis of carcass traits in  
361 beef cattle using random regression models. *Journal of animal science*. 2016;94(4):1354-64.
- 362 14. Schaeffer L, Schenkel F, Fries L, editors. Selection bias on animal model evaluation. *Proceedings of*  
363 *the 6th World Congress on Genetics Applied to Livestock Production*; 1998.
- 364 15. Pollak EJ, van der Werf J, Quaas RL. Selection Bias and Multiple Trait Evaluation. *Journal of Dairy*  
365 *Science*. 1984;67(7):1590-5.
- 366 16. Henderson CR. Best linear unbiased estimation and prediction under a selection model. *Biometrics*.  
367 1975:423-47.
- 368 17. VanRaden PM, Tooker ME, Wright JR, Sun C, Hutchison JL. Comparison of single-trait to multi-trait  
369 national evaluations for yield, health, and fertility1. *Journal of Dairy Science*. 2014;97(12):7952-62.
- 370 18. Wiggans G, Misztal I, Van Vleck L. Implementation of an animal model for genetic evaluation of  
371 dairy cattle in the United States. *journal of Dairy Science*. 1988;71:54-69.
- 372 19. Liu Z, Jaitner J, Reinhardt F, Pasma E, Rensing S, Reents R. Genetic evaluation of fertility traits of  
373 dairy cattle using a multiple-trait animal model. *Journal of Dairy Science*. 2008;91(11):4333-43.
- 374 20. Quaas RL, Pollak E. Mixed model methodology for farm and ranch beef cattle testing programs.  
375 *Journal of Animal Science*. 1980;51(6):1277-87.
- 376 21. Pollott G, Guy D, Croston D. Genetic parameters of lamb carcass characteristics at three end-points:  
377 fat level, age and weight. *Animal Science*. 1994;58(1):65-75.
- 378 22. Henderson CR. *Applications of linear models in animal breeding*: University of Guelph Guelph; 1984.
- 379 23. Jo C, Cho S, Chang J, Nam K. Keys to production and processing of Hanwoo beef: a perspective of  
380 tradition and science. *Animal frontiers*. 2012;2(4):32-8.



- 381 24. Gilmour A, Gogel B, Cullis B, Welham S, Thompson R. ASReml user guide release 4.1 structural  
382 specification. Hemel Hempstead: VSN international ltd. 2015.
- 383 25. Self SG, Liang K-Y. Asymptotic properties of maximum likelihood estimators and likelihood ratio  
384 tests under nonstandard conditions. *Journal of the American Statistical Association*.  
385 1987;82(398):605-10.
- 386 26. R-Core-Team. R: A Language and Environment for Statistical Computing. R Foundation for  
387 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>. 2018.
- 388 27. Lee D. Methods for genetic parameter estimations of carcass weight, longissimus muscle area and  
389 marbling score in Korean cattle. *Journal of Animal Science and Technology*. 2004;46(4):509-16.
- 390 28. Roh S, Kim B, Kim H, Min H, Yoon H, Lee D, et al. Comparison between REML and Bayesian via  
391 gibbs sampling algorithm with a mixed animal model to estimate genetic parameters for carcass traits  
392 in Hanwoo (Korean native cattle). *Journal of Animal Science and Technology*. 2004;46(5):719-28.
- 393 29. Davis M, Simmen R. Genetic parameter estimates for serum insulin-like growth factor-I concentration  
394 and carcass traits in Angus beef cattle. *Journal of Animal Science*. 2000;78(9):2305-13.
- 395 30. Ríos-Utrera A, Cundiff LV, Gregory KE, Koch RM, Dikeman ME, Koohmaraie M, et al. Genetic  
396 analysis of carcass traits of steers adjusted to age, weight, or fat thickness slaughter endpoints1. *Journal*  
397 *of Animal Science*. 2005;83(4):764-76.
- 398 31. Nephawe K, Cundiff L, Dikeman M, Crouse J, Van Vleck LD. Genetic relationships between sex-  
399 specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body  
400 condition score of cows, and carcass traits of their steer relatives. *Journal of animal science*.  
401 2004;82(3):647-53.
- 402 32. Smith T, Domingue JD, Paschal JC, Franke DE, Bidner TD, Whipple G. Genetic parameters for  
403 growth and carcass traits of Brahman steers1,2. *Journal of Animal Science*. 2007;85(6):1377-84.
- 404 33. Pollak EJ, Quaas RL. Monte Carlo Study of Genetic Evaluations Using Sequentially Selected Records.  
405 *Journal of Animal Science*. 1981;52(2):257-64.
- 406 34. Macedo FL, Reverter A, Legarra A. Behavior of the Linear Regression method to estimate bias and  
407 accuracies with correct and incorrect genetic evaluation models. *Journal of Dairy Science*.  
408 2020;103(1):529-44.
- 409 35. Eiríksson JH, Sigurdsson Á. Sources of bias, genetic trend and changes in genetic correlation in carcass  
410 and ultrasound traits in the Icelandic sheep population. 2017.

411 36. Massender E, Brito LF, Cánovas A, Baes CF, Kennedy D, Schenkel FS. A genetic evaluation of  
412 growth, ultrasound, and carcass traits at alternative slaughter endpoints in crossbred heavy lambs.  
413 Journal of animal science. 2019;97(2):521-35.

414 37. Rios Utrera A, Van Vleck LD. Heritability estimates for carcass traits of cattle: a review. 2004.

415

416

417  
418 Table 1. Description of the population structure.

Unit	Mean	Minimum	Maximum	Total
Progeny per sire	726	1	7685	-
Progeny per dam	1.2	1	9	-
Animals	-	-	-	469,002
Sires	-	-	-	646
Dams	-	-	-	390,166
Number of contemporary group (HYS)	-	-	-	31,403
Animal per contemporary group (HYS)	15	5	1578	-
Progeny per sire per contemporary group	2	1	98	-

419  
420 Table 2. Descriptive statistics for carcass and meat quality traits of Hanwoo cattle.

Traits	Sample size	Mean	SD	Minimum	Maximum	CV
<b>CWT (kg)</b>	469002	432.4	42.8	303	551	0.10
<b>EMA (cm<sup>2</sup>)</b>	469002	91.2	9.7	65	116	0.12
<b>BFT (mm)</b>	469002	13.2	4.5	1	25	0.34
<b>BW (Kg)</b>	223839	722.7	65	450	979	0.01
<b>MI (%)</b>	469002	64.6	3.3	52.4	77	0.01
<b>MS (1-9)</b>	469002	5.7	1.87	1	9	0.33
<b>MC (1-7)</b>	469002	4.83	0.48	2	7	0.10
<b>FC (1-6)</b>	469002	2.9	0.29	1	6	0.10
<b>MT (1-3)</b>	469002	1.2	0.38	1	3	0.32

421 CWT = carcass weight, EMA = eye muscle area, BFT = back fat thickness, BW = body weight, MI = meat index, MS  
422 =marbling score, MC = meat colour, FC = fat colours and MT = meat texture, SD = standard deviation and CV =  
423 coefficient of variation.  
424  
425

426 Table 3. Alternatives of input parameters for the two studied traits.

<b>Heritability alternatives</b>	<b>Genetic correlation alternatives</b>	<b>Residual correlation alternatives</b>
0.5, 0.5 (H-H)	-0.8, -0.2, 0.2, 0.8	-0.8, -0.2, 0.2, 0.8
0.2, 0.2 (L-L)	-0.8, -0.2, 0.2, 0.8	-0.8, -0.2, 0.2, 0.8
0.5, 0.2 (H-L)	-0.8, -0.2, 0.2, 0.8	-0.8, -0.2, 0.2, 0.8
0.2, 0.5 (L-H)	-0.8, -0.2, 0.2, 0.8	-0.8, -0.2, 0.2, 0.8

427 H =high and L =low

428  
429 Table 4. Variance components and heritability for the carcass and meat quality traits in univariate animal model  
430 analysis.

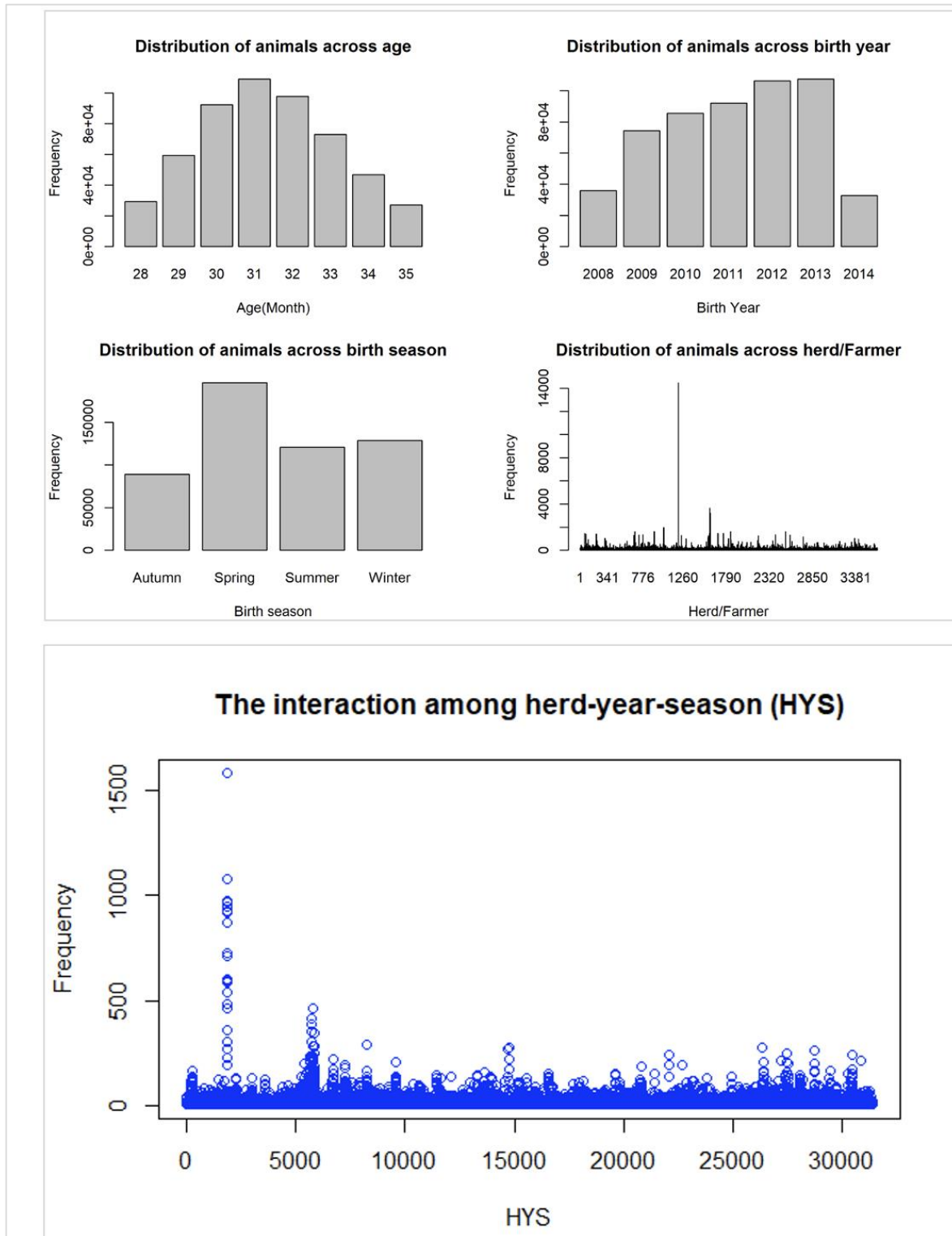
<b>Trait</b>	<b>Genetic variance</b>	<b>Residual variance</b>	<b>Heritability</b>
<b>Carcass traits</b>			
Carcass weight	701.01(20.8)	909.7 (14.5)	0.44 (0.01)
Eye muscle area	33.19 (1.15)	56.7 (0.8)	0.37 (0.01)
Back fat thickness	8.7 (0.26)	11.31 (0.18)	0.44 (0.01)
Bodyweight	1245.6 (77.5)	2288.6 (54.6)	0.35 (0.02)
Meat index	4.8(0.14)	5.8(0.09)	0.45(0.01)
<b>Meat quality traits</b>			
Marbling score	1.90 (0.04)	1.60 (0.03)	0.55 (0.01)
Meat colour	0.017 (0.00)	0.196 (0.00)	0.08 (0.01)
Fat colour	0.0003 (0.00)	0.071 (0.00)	0.004 (0.00)
Meat texture	0.041 (0.00)	0.100 (0.00)	0.29 (0.01)

431  
432

433 Table 5. Phenotypic correlations (below diagonal) and genetic correlations (above diagonal) among studied traits in  
 434 bivariate model analysis.

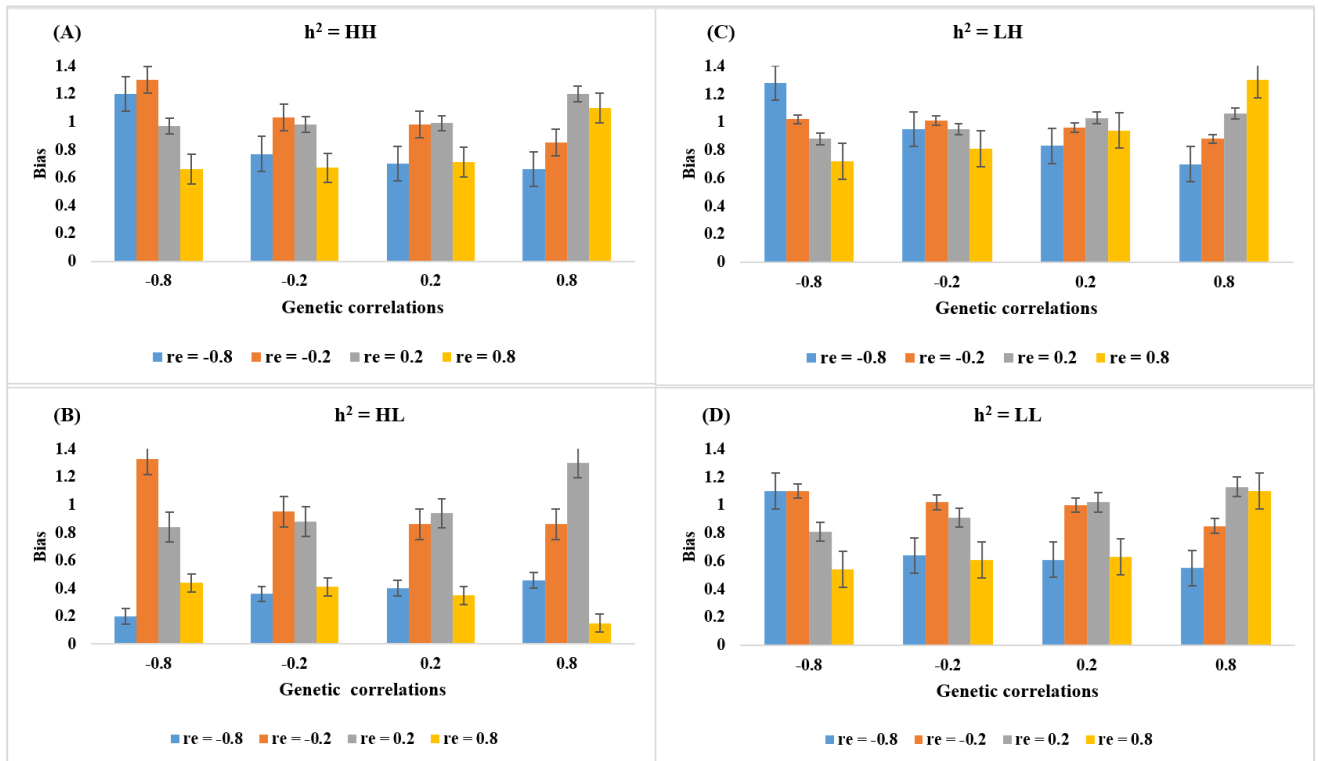
Studied traits	CWT	EMA	BFT	BW	MI	MS	MC	FC	MT
<b>Carcass traits</b>									
CWT	-	0.38 (0.06)	0.05 (0.07)	0.93 (0.01)	-0.18 (0.07)	0.13 (0.00)	-0.22 (0.07)	-0.11 (0.11)	-0.16 (0.07)
EMA	0.45 (0.00)	-	-0.24 (0.07)	0.31 (0.07)	0.45 (0.06)	0.39 (0.01)	-0.31 (0.07)	-0.09 (0.06)	-0.44 (0.06)
BFT	0.27 (0.00)	0.03 (0.00)	-	-0.06 (0.07)	-0.94 (0.01)	0.04 (0.00)	-0.13 (0.07)	0.28 (0.09)	0.08 (0.07)
BW	0.94 (0.00)	0.41 (0.00)	0.21 (0.00)	-	-0.08 (0.06)	0.04 (0.07)	-0.18 (0.06)	-0.10 (0.11)	-0.07 (0.06)
MI	-0.36 (0.00)	0.24 (0.00)	-0.94 (0.00)	-0.30 (0.00)	-	0.23 (0.07)	0.06 (0.06)	-0.25 (0.10)	-0.18 (0.07)
<b>Quality traits</b>									
MS	0.13 (0.07)	0.51 (0.07)	-0.11 (0.07)	0.08 (0.00)	0.07 (0.00)	-	-0.61 (0.05)	-0.57 (0.08)	-0.98 (0.00)
MC	-0.10 (0.00)	-0.10 (0.00)	-0.12 (0.00)	-0.07 (0.00)	0.09 (0.00)	-0.26 (0.00)	-	0.42 (0.09)	0.64 (0.05)
FC	-0.00 (0.00)	-0.01 (0.00)	0.02 (0.00)	-0.00 (0.00)	-0.02 (0.00)	-0.06 (0.00)	0.11 (0.00)	-	0.54 (0.09)
MT	-0.11 (0.00)	-0.20 (0.00)	-0.05 (0.00)	-0.07 (0.00)	0.00 (0.00)	-0.61 (0.00)	0.21 (0.00)	0.04 (0.00)	-

435  
 436  
 437  
 438



440

441 Figure 1. Distribution of animals across age, birth year, birth season, and herd top panel, and distribution of animals  
 442 across contemporary group (HYS), lower panel.



444  
 445 Figure 2. Change in bias due to sorting of animals and impact of the correlations and heritabilities of the EM and LM  
 446 traits in genetic evaluation.  $h^2$  = heritability, HH = high-high (0.5, 0.5), HL = high-low (0.5, 0.2), LH = low-high (0.2, 0.5),  
 447 LL = low-low (0.2, 0.2),  $re$  = residual correlations, used genetic correlations on the X-axis and bias on the Y-axis.  
 448  
 449