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# Influence of *SCD* and *FABP3* genetic markers on carcass traits and meat quality in Aberdeen Angus bulls

**Sena Ardicli[1]*, Nursen Senturk[1], Tugce Necla Selvi[2], Sena Yonga[3], Rumeysa Celik[4], Beyza Karalar[4], Aleyna Ozdeniz[5], Madina Aliyeva[6], Havvanur Aydin[7], Ozgur Toprak Ay[8], Ozge Ardicli[9], Muhammed Emin Sari[10], Berkay Bozkurt[11], Oliva Giannelli Viscardi[12], Huseyn Babayev[12], Hakan Ustuner[2]**

[1] Bursa Uludag University, Faculty of Veterinary Medicine, Department of Genetics, Bursa, Türkiye.
[2] Bursa Uludag University, Faculty of Veterinary Medicine, Department of Animal Science, Bursa, Türkiye.
[3] Izmir Institute of Technology, Faculty of Science, Department of Chemistry, Izmir, Türkiye.
[4] Bursa Uludag University, Faculty of Arts and Science, Department of Molecular Biology and Genetics, Bursa, Türkiye.
[5] Afyon Kocatepe University, Institute of Science, Department of Genetics, Afyonkarahisar, Türkiye.
[6] Bursa Uludag University, Institute of Science, Department of Molecular Biology and Genetics, Bursa, Türkiye.
[7] Hacettepe University, Graduate School of Health Sciences, Department of Bioinformatics, Ankara, Türkiye.
[8] Izmir Institute of Technology, Faculty of Science, Department of Molecular Biology and Genetics, İzmir, Türkiye.
[9] Bursa Uludag University, Karacabey Vocational School, Milk and Dairy Products Technology Program, Division of Food Processing, Bursa, Türkiye.
[10] Necmettin Erbakan University, Faculty of Medicine, Medical Department of Biology, Meram, Konya, Türkiye.
[11] Izmir Institute of Technology, Graduate School of Science and Engineering, Department of Biotechnology and Bioengineering, Izmir, Türkiye.
[12] University of Zurich, Swiss Institute of Allergy and Asthma Research, Davos, Switzerland.

***Corresponding author:**
sardicli@uludag.edu.tr

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**ABSTRACT** - This study evaluated the association of stearoyl-CoA desaturase (*SCD*) and fatty acid-binding protein 3 (*FABP3*) gene polymorphisms with carcass and meat quality traits in Aberdeen Angus bulls. Two hundred seventy-four Angus bulls were genotyped using PCR-RFLP and Sanger sequencing. Next, the association of *SCD* and *FABP3* genetic variants with traits such as live weight, average daily weight gain, carcass weight (both hot and cold), dressing percentage, carcass length, back fat thickness, carcass color score, pH, and marbling score was analyzed. Significant differences were observed in average daily weight gain among different *FABP3* genotypes, with the GG genotype showing the highest gains (P<0.01). Furthermore, novel associations between the *SCD* × *FABP3* interaction and key traits were identified, including dressing percentage and carcass pH. Notably, an epistatic pattern through this genotypic interaction was demonstrated, which may significantly influence postmortem pH decline in beef cattle. The results suggest a notable impact of the *FABP3* rs210042291 gene on growth rates. These findings highlight the complexity of genetic influences on meat quality traits.

**Keywords:** beef cattle, beef production, gene interaction, selection, SNP

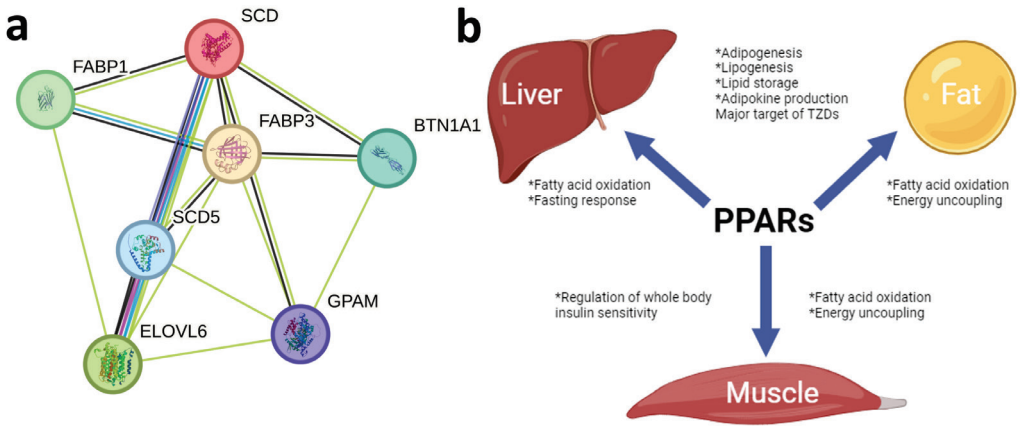
## 1. Introduction

Genomic technologies have helped identify genetic markers associated with carcass traits, supporting selective breeding to enhance meat quality and yield. Investigating these markers advances our understanding of the genetic architecture behind carcass traits, offering promising strategies for optimized meat production in cattle (Ardicli et al., 2017a; Purfield et al., 2019; Rafter et al., 2021).

Key genes such as stearoyl-CoA desaturase (*SCD*) and fatty acid-binding protein 3 (*FABP3*) are prominent candidates for carcass traits. The *SCD* gene, essential in fatty acid metabolism, regulates unsaturated fatty acid synthesis, influencing fat deposition and meat quality (Narukami et al., 2011; Mwangi et al., 2022). Polymorphisms of *SCD* have been linked to differences in intramuscular fat, a major quality factor in beef (Matsuhashi et al., 2011; Mwangi et al., 2022), and have shown significant impacts on carcass fatness, meat traits, live weight, total weight gain, and average daily weight gain (ADWG) (Ardicli et al., 2023). The *SCD* function offers insights into lipid accumulation within fat deposits, influencing both meat quality and animal health (Smith et al., 2006; Matsuhashi et al., 2011; Mwangi et al., 2022).

The bovine *FABP3* gene, part of the intracellular lipid-binding protein family, plays a significant role in lipid and glucose regulation (Cho et al., 2008; Ardicli et al., 2017b; Ardicli et al., 2021). Known as heart-type fatty acid-binding protein (H-FABP), FABP3 supports fatty acid transport to β-oxidation sites in mitochondria, affecting intramuscular fat (IMF) levels (Sweeney et al., 2015). Its influence on carcass traits, such as fat deposition and carcass yield, is well researched in pigs but less so in cattle. Although FABP3 gene polymorphisms have shown associations with backfat thickness and IMF, most studies focus on pigs (Tyra et al., 2013). The involvement of *FABP3* in lipid metabolism pathways (Figure 1a) underscores its potential relevance for carcass traits, although further studies in cattle are needed.

Meat quality in livestock is shaped by metabolic pathways like the peroxisome proliferator-activated receptor (PPAR) pathway, critical in lipid metabolism and fat composition in tissues (Fernyhough et al., 2007). The PPAR gamma (PPARγ), a primary regulator in this pathway, controls genes associated with adipogenesis, affecting fat content and distribution (He et al., 2013). Lim et al. (2015) showed that genes within the PPAR pathway, including *SCD* and *FABP3*, significantly influence IMF. These genes




*SCD* - stearoyl-CoA desaturase; *FABP3* - fatty acid binding protein 3; PPAR - peroxisome proliferator-activated receptor; TZDs - thiazolidinediones. (a) Bovine *SCD* and *FABP3* are crucial in pathways such as the biosynthesis of monounsaturated and unsaturated fatty acids, fatty acid metabolism, and the lipid biosynthetic process. https://string-db.org/ (b) Metabolic integration by PPAR: PPAR regulate lipid and glucose homeostasis through coordinated actions in the liver, muscle, and adipose tissue. Prepared based on the paper by Evans et al. (2004).

**Figure 1 -** *SCD* and *FABP3* are crucial components within the PPAR signalling pathway. These genes are instrumental in various metabolic processes, including lipid metabolism, fatty acid biosynthesis, and desaturation, as well as the development of adipose tissue, known as adipogenesis.

were differentially expressed between groups with low and high marbling. The PPAR activation affects lipid and glucose balance across liver, muscle, and adipose tissues (Evans et al., 2004), though specific gene roles in quality traits like marbling are not fully understood. This study aims to clarify the effects of *SCD* and *FABP3* gene polymorphisms on carcass traits and beef quality in Angus bulls, enriching the genetic selection framework for beef production.

## 2. Material and methods

### 2.1. Animals and sampling

Two hundred seventy-four Aberdeen Angus bulls from a commercial farm in the South Marmara region of Turkey (40°15'28.04" N, 29°30'50.18" E) were used. All cattle were housed for fattening in semi-open pens (approximately 20 bulls per paddock, providing 10 $m^2$ per animal) for approximately nine months, experiencing consistent environmental conditions and management procedures. The animals were fattened under consistent feeding conditions, and were adapted to their rations over a period of about two weeks. All animals were fed the same diet (including corn silage, wheat straw, macaroni pellets, corn bran, corn gluten feed, sunflower meal, vitamins, and minerals) *ad libitum* and had unrestricted access to water throughout the entire fattening period. The ADWG was calculated based on the total weight gained over the whole fattening period. After the fattening period, the animals were transported to a commercial slaughterhouse where they were humanely slaughtered and dressed according to standard national regulations and industry practices. After being housed in paddocks for 12 h without feed but with unrestricted access to water, the pre-slaughter live weight of the animals was recorded. During exsanguination, a precise 4-mL blood sample was collected from each animal using a sterile $K_3$EDTA tube (Vacutest Kima, SRL, Italy). The sample was drawn directly from the flowing blood to minimize contamination and ensure the integrity of the sample for subsequent analyses. The slaughtering process was routine, and no invasive procedures were applied to the animals during this study. Research on animals was conducted according to the Local Ethics Committee for Animal Experimentation at Bursa Uludağ University, Turkey (approval No: 2018-02/01).

### 2.2. Carcass measurements

Hot carcass weight (HCW) was recorded immediately after conventional slaughter processing. Measurements were taken without removing the subcutaneous fat and while retaining the kidney and pelvic fat. Following this, the carcasses were chilled at 4 °C for approximately 24 h. Subsequently, cold carcass weights (CCW) were recorded. Weights post-cooling were also assessed to determine the cooling loss (CL). Dressing percentage (DP) was calculated based on HCW. Carcass length (CLE) was measured as the distance from the *os pubis* to the tip of the first rib. Carcass fatness was based on visual examination of carcasses on a scale of 1 to 5, with 5 being the fattest (Hickey et al., 2007). Backfat thickness was measured on the lateral side of the *musculus longissimus dorsi*, precisely aligned three-quarters of the way along the 12th rib (Ardicli et al., 2018). The pH of the *m. longissimus dorsi* was determined between the 12th and 13th ribs using an electronic pH meter (Testo 205 pH meter). The marbling score was evaluated using a 10-level scale ranging from 1 (devoid) to 10 (abundant), with intermediate values indicating increasing amounts of fat: 2 = practically devoid, 3 = traces, 4 = slight, 5 = small, 6 = modest, 7 = moderate, 8 = slightly abundant, and 9 = moderately abundant (Zhao et al., 2004).

### 2.3. Genetic analysis

Genomic DNA was isolated using the standard phenol-chloroform method. The concentration and purity of the DNA samples were assessed using a NanoDrop 2000c spectrophotometer. Samples were then stored at –80 °C until needed for genetic analysis.

The PCR amplification was carried out in a total reaction volume of 50 µL, comprising 33.5 µL of $dH_2O$, 5 µL of 10× Buffer, 5 µL of $MgSO_4$, 1 µL of dNTPs (2.5 mM), 2.5 U of Taq DNA polymerase

(Biomatik, A1003-500U, 5U/µL), 1 µL of each primer (0.025 µM), and 3 µL of DNA sample at a concentration of 100 ng/µL. Oligonucleotide sequences (5' to 3') for the *SCD* rs41255691 marker were GTGTCCTGTTGTTGTGCTTCATCCTGCC as the forward primer and AATATTCTCTCGGGGGTTGATGGTCTTG as the reverse primer. Regarding the *FABP3* rs210042291 marker, the forward primer GTGAGTTGAGGAAGGGGCTGTG and the reverse primer TAGGTCTCCACCTCTTGTCCTTCAG were used.

After amplification, 15 µL of each PCR product was digested with 15 units of the corresponding restriction enzyme (*Nco*I for the *SCD* and *Aci*I for the *FABP3*). These reactions were incubated at 37 °C for 16 h. The digested products were then electrophoresed on a 3% agarose gel (Sigma Aldrich, Steinheim, Germany) at 90V for 1 h and visualized using a gel imaging system (DNR-Minilumi, DNR Bio-Imaging Systems, Israel).

Representative samples were sequenced from each genotype targeting the studied SNP using the FastStart High Fidelity PCR System DNTPack kit (Roche Diagnostics GmbH, Mannheim, Germany). The resulting PCR amplicons were purified with the Zymo DNA Clean & Concentrator-5 kit (Zymo Research, Irvine, CA, USA, #D4013) and subsequently sequenced using an ABI 3500 automated sequencer (Applied Biosystems, Foster City, CA, USA). The sequencing data were analyzed and edited using BioEdit software (v8.1.0). Finally, the findings were validated by cross-referencing with the cattle genome available on the Ensembl genome browser (https://www.ensembl.org/index.html). Figure 2 presents the Sanger sequencing analysis of targeted SNP in the *FABP3* and *SCD* genes from bovine samples, illustrating the genotypes represented for each variant.

Heterozygosity (He), effective number of alleles (Ne), and polymorphism information content (PIC) were calculated based on population genetics indices, following the methodologies described by Nei and Roychoudhury (1974) and Botstein et al. (1980). The Hardy-Weinberg equilibrium (HWE) for each SNP was evaluated using the chi-square ($\chi^2$) test. Additionally, the fixation index (FIS) was estimated by comparing theoretical ($H_{the}$) and experimental ($H_{exp}$) heterozygosities, as delineated by


For each SNP, the wild-type sequence is presented first, followed by 20 bp regions flanking the targeted variant. The sequences are displayed with the reference genome at the top, followed by the sequences from homozygous and heterozygous individuals below it. Sequence alignments were performed using the Benchling software (https://benchling.com/). Information on the reference genome can be accessed online at the Ensembl genome browser (https://www.ensembl.org/index.html).

**Figure 2 -** Sanger sequencing analysis targeted specified SNP in the *FABP3* and *SCD* genes of bovine samples, representing each genotype.

Crow and Kimura (2017). Additive and dominance effects were estimated according to Falconer and Mackay (1983) as follows:

The degree of dominance = d/a, in which additive effect (a) = (the difference between the means of the two homozygotes) / 2; dominance effect (d) = the deviation of the heterozygote from the mean of the homozygotes; and overdominance is indicated when d is greater than +a or less than −a.

### 2.4. Statistical analysis

Linear mixed models were selected based on the ANOVA coefficient of determination ($R^2$) values to assess the association between genotype and phenotype. The least-squares method, applied in the general linear model (GLM) procedure of Minitab software (v19), was used to test the significance of the association between *SCD* and *FABP3* gene polymorphisms and slaughter weight and carcass traits. Tukey's multiple comparison test was used if significant effects were detected. The selected statistical model is as follows:

$$Y_{ijklmn} = \mu + A_i + S_j + G_k + H_l + I_m + e_{ijklmn},$$

in which $Y_{ijklmn}$ = the studied traits, $\mu$ = the overall mean, $A_i$ = the fixed effect of slaughter age ($i$ = 14-16 months), $S_j$ = the fixed effect of slaughter season ($j$ = spring, summer, autumn, and winter), $G_k$ = *SCD* genotypes ($k$ = AA, GA, and GG), $H_l$ = *FABP3* genotypes ($l$ = AA, GA, and GG), $I_m$ = two-way interactions, and $e_{ijklmn}$ = random error.

## 3. Results

### 3.1. Genetic variation

All three potential genotypes were adequately represented for both markers (Table 1). The most predominant genotype for the *SCD* marker was heterozygous. For *FABP3*, the GG genotype was more frequent than other genotypes. The heterozygosity for the *FABP3* marker approached 0.50, and Ne was close to 2.00. The PIC values were 0.3444 for *SCD* and 0.3746 for *FABP3*, suggesting adequate genetic variability for both loci. Negative FIS values were observed for both markers. Notably, the *FABP3* locus deviated significantly from HWE, with a $\chi^2$ value of 59.6484 (P<0.001). In contrast, the *SCD* locus displayed no significant deviation from HWE ($\chi^2$ = 3.1704), suggesting equilibrium within this population segment.

**Table 1 -** *SCD* rs41255691 (g.21272246A>G; c.702A>G; p.Pro234=) and *FABP3* rs210042291 (g.122291188 G>A; c.246 + 323 G>A) genotypic/allelic frequencies, population genetic indices, and HWE test for genotypes in the Aberdeen Angus population (n = 274)

| Locus | *SCD* | | | *FABP3* | | |
|---|---|---|---|---|---|---|
| Genotype | AA | GA | GG | AA | GA | GG |
| n | 24 | 135 | 115 | 96 | 73 | 105 |
| % | 8.76 | 49.27 | 41.97 | 35.04 | 26.64 | 38.32 |
| MAF | | 0.33 | | | 0.48 | |
| He | | 0.4422 | | | 0.4992 | |
| Ne | | 1.7928 | | | 1.9968 | |
| PIC | | 0.3444 | | | 0.3746 | |
| FIS | | −2.0529 | | | −0.4623 | |
| χ2 (HWE) | | 3.1704 | | | 59.6484*** | |

n - number of experimental bulls; MAF - minor allele frequency; He - heterozygosity; Ne - effective number of alleles; PIC - polymorphism information content; FIS - fixation index; χ2 (HWE) - Hardy-Weinberg equilibrium χ2 value.
*** P<0.001.

### 3.2. Marker effects on traits

Results indicated that the *FABP3* marker was significantly associated with ADWG (P<0.01) (Table 2). In this context, bulls with the GG genotype exhibited remarkably higher ADWG than AA and heterozygous animals. While no significant effects were observed at the P<0.05 level for the *SCD* marker, a suggestive association with DP was identified (Table 2).

Notably, *SCD* × *FABP3* interaction was significantly associated with DP and carcass pH (P<0.05) (Table 3). Concerning the significant influence of the *FABP3* marker on ADWG, the additive effect of the genetic marker on ADWG was quantified at 0.085, indicating that the substitution of one allele for another at this locus is associated with a slight increase in the trait value. Furthermore, the dominance effect was measured at −0.075, suggesting that the interaction between different alleles at this locus results in a trait value below the expected additive contributions of the individual alleles.

## 4. Discussion

Selection based on the evaluation of phenotypic data and breeding values derived from pedigree records has achieved a certain level of success in improving desired traits. However, the advent of molecular techniques and their widespread application has significantly enhanced these traditional selection programs. The identification and validation of mutations and SNP with measurable effects on phenotypes have introduced a new dimension to genetic selection. These advancements have allowed for more precise and targeted breeding strategies, as the direct genetic contribution to traits can now be identified and utilized more effectively, improving both the accuracy and efficiency of selection (Goddard and Hayes, 2007; Hayes and Goddard, 2010; Ardicli et al., 2019b).

Variants in *FABP3* have garnered significant interest due to the pivotal role of the gene in regulating intracellular fatty acid availability, mobilization, and utilization, primarily for mitochondrial oxidation (Glatz et al., 2003; Gardan et al., 2007). This gene is especially important in metabolic pathways involving energy production and fat metabolism. In swine, *FABP3* has been identified as a potential candidate gene influencing fat deposition traits. However, the effects observed in different studies have been contradictory, with some showing a significant association with fat deposition traits, while others fail to replicate these findings (Nechtelberger et al., 2001; Chmurzynska et al., 2007). The limited number of studies in cattle conducted to date have produced equally inconsistent results, highlighting the need for further research to clarify the role of *FABP3* in fat deposition and metabolic regulation (Cho et al., 2008; Blecha et al., 2015). Sweeney et al. (2015) examined novel variations in the *FABP3* promoter region and their associations with fatness traits in pigs. While this is not in cattle, it demonstrates that *FABP3* polymorphisms can affect fat deposition, which is related to growth. Cho et al. (2008) found associations between two SNP in the *FABP3* gene (c.220A>G and c.328G>A) and backfat thickness and carcass weight in Korean Native cattle. While this does not directly focus on ADWG, it does show *FABP3* polymorphisms can affect growth-related traits. In our study, the *FABP3* rs210042291 polymorphism had a significant effect on ADWG. In this context, animals with the GG genotype exhibited higher ADWG compared with those with the heterozygous and AA genotypes. Specifically, GG animals had approximately 0.16 kg more ADWG. Concerning this novel genetic impact, the magnitude of the dominance effect (−0.075) is smaller than the additive effect (0.085), indicating that additive genetic effects play a more significant role in determining the trait value for this locus. Given that the heterozygote mean is closer to the AA than the GG mean and the dominance effect is negative, we can conclude that there is partial dominance of the A allele over the G allele for this trait. In this case, the genetic effect is best described as partial dominance rather than overdominance (Falconer and Mackay, 1983; Duenk et al., 2017; Xiang et al., 2018). Although previous studies suggest that *FABP3* may potentially influence growth traits such as ADWG, no studies were found that directly test this specific association in cattle. This highlights a gap in the current research, which warrants further investigation. To confirm this impact and definitively address this question, future studies should focus on examining the association between *FABP3* SNP and ADWG in beef cattle.

**Table 2 -** Levels of significance, least squares means, and standard errors for the effect of *SCD* rs41255691 and *FABP3* rs210042291 markers on carcass traits and meat quality

| Trait | Genotypes | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *SCD* | | | | *FABP3* | | | |
| | AA | GA | GG | Significance | AA | GA | GG | Significance |
| Live weight (kg) | 561.84±9.95 | 574.70±4.03 | 573.45±4.49 | NS | 567.67±5.65 | 565.71±8.50 | 576.61±5.59 | NS |
| Average daily weight gain (kg) | 1.55±0.08 | 1.57±0.03 | 1.54±0.04 | NS | 1.65±0.05b | 1.66±0.07b | 1.82±0.05a | P<0.01 |
| Hot carcass weight (kg) | 318.63±5.95 | 325.36±2.46 | 321.68±2.70 | NS | 320.11±3.41 | 320.99±5.04 | 324.57±3.43 | NS |
| Cold carcass weight (kg) | 313.25±6.24 | 319.93±2.57 | 316.30±2.00 | NS | 314.63±2.54 | 315.63±4.03 | 319.22±2.93 | NS |
| Cooling loss (kg) | 5.38±0.16 | 5.43±0.07 | 5.39±0.07 | NS | 5.48±0.09 | 5.36±0.13 | 5.35±0.09 | NS |
| Dressing percentage (%)[1] | 56.52±0.37 | 56.70±0.15 | 56.24±0.17 | P<0.1 | 56.38±0.21 | 56.56±0.31 | 56.52±0.21 | NS |
| Carcass length (cm) | 139.03±1.66 | 140.61±2.67 | 141.11±1.75 | NS | 140.89±0.94 | 140.09±1.42 | 139.78±193 | NS |
| Carcass fatness (1-5) | 3.58±0.17 | 3.50±0.06 | 3.50±0.07 | NS | 3.51±0.08 | 3.50±0.14 | 3.58±0.10 | NS |
| Back fat thickness (mm) | 11.48±0.55 | 11.51±0.21 | 11.42±0.24 | NS | 11.26±0.27 | 11.58±0.46 | 11.57±0.32 | NS |
| Carcass color score (1-5) | 3.62±0.20 | 3.48±0.07 | 3.51±0.08 | NS | 3.48±0.09 | 3.57±0.16 | 3.56±0.11 | NS |
| Carcass pH | 5.52±0.04 | 5.57±0.02 | 5.56±0.02 | NS | 5.56±0.02 | 5.53±0.04 | 5.56±0.02 | NS |
| Marbling score (1-10) | 7.32±0.29 | 7.10±0.11 | 7.06±0.13 | NS | 7.09±0.15 | 7.13±0.25 | 7.26±0.17 | NS |

NS: not significant.
[1] Dressing percentage was calculated based on hot carcass weight.
a,b - Different letters in the row indicate significant differences.

**Table 3 -** Levels of significance, least squares means, and standard errors for the effect of *SCD* × *FABP3* interaction on carcass traits and meat quality

| Haplotype | Phenotypic trait | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LW | ADWG | HCW | CCW | CL | DP | CLE | CF | BFT | CCS | pH | MS |
| AAAA | 561.50±11.80 | 1.51±0.10 | 314.75±6.97 | 309.27±4.11 | 5.48±0.18 | 55.81±0.43b | 140.99±1.97 | 3.58±0.17 | 11.16±0.58 | 3.62±0.20 | 5.54±0.04ab | 7.12±0.31 |
| AAAG | 546.20±22.70 | 1.49±0.18 | 311.90±13.41 | 306.60±13.17 | 5.26±0.35 | 56.69±0.83ab | 137.55±3.80 | 3.49±0.38 | 11.45±1.24 | 3.55±0.44 | 5.45±0.10c | 7.39±0.66 |
| AAGG | 577.80±13.32 | 1.68±0.11 | 329.29±8.30 | 323.88±4.67 | 5.41±0.22 | 57.04±0.51a | 138.56±2.23 | 3.67±0.24 | 11.83±0.80 | 3.69±0.28 | 5.56±0.05ab | 7.45±0.42 |
| GAAA | 574.73±6.94 | 1.42±0.06 | 326.50±4.32 | 320.99±3.33 | 5.51±0.11 | 56.95±0.27ab | 140.62±1.16 | 3.46±0.10 | 11.46±0.33 | 3.56±0.12 | 5.57±0.03ab | 7.13±0.18 |
| GAAG | 577.28±6.00 | 1.49±0.05 | 326.06±3.67 | 320.67±3.67 | 5.39±0.09 | 56.45±0.23ab | 140.42±1.01 | 3.58±0.09 | 11.63±0.32 | 3.40±0.11 | 5.53±0.02bc | 7.15±0.17 |
| GAGG | 572.10±5.83 | 1.53±0.04 | 323.53±3.67 | 318.14±5.44 | 5.38±0.08 | 56.71±0.23ab | 140.77±1.00 | 3.46±0.10 | 11.44±0.30 | 3.47±0.10 | 5.59±0.02a | 6.99±0.16 |
| GGAA | 566.74±6.58 | 1.44±0.05 | 319.09±3.98 | 313.64±6.77 | 5.45±0.11 | 56.38±0.25ab | 141.05±2.10 | 3.49±0.10 | 11.16±0.48 | 3.27±0.11 | 5.56±0.02ab | 7.01±0.16 |
| GGAG | 573.64±8.63 | 1.39±0.07 | 325.05±5.20 | 319.62±5.22 | 5.42±0.14 | 56.54±0.32ab | 142.30±3.44 | 3.42±0.15 | 11.60±0.33 | 3.76±0.17 | 5.61±0.04a | 6.84±0.25 |
| GGGG | 464.9±15.80 | 1.66±0.06 | 320.91±3.90 | 315.63±4.69 | 5.28±0.10 | 55.81±0.24ab | 139.97±3.04 | 3.60±0.09 | 11.44±0.78 | 3.51±0.11 | 5.53±0.02bc | 7.34±0.17 |

LW - live weight; ADWG - average daily weight gain; HCW - hot carcass weight; CCW - cold carcass weight; CL - cooling loss; DP - dressing percentage; CLE - carcass length; CF - carcass fatness; BFT - backfat thickness; CCS - carcass color score; MS - marbling score.
a,b - Different letters within a column indicate significant differences, P<0.05.

The bovine *SCD* gene has been widely studied for its potential effects on carcass and meat quality traits in beef cattle (Naserkheil et al., 2022). It encodes an enzyme that catalyzes the synthesis of monounsaturated fatty acids, playing a key role in fat metabolism (Li et al., 2020). Several studies have found associations between polymorphisms in the *SCD* gene and carcass fatness traits like marbling score, backfat thickness, and intramuscular fat content in various cattle breeds. For example, the T878C SNP in exon 5, which causes an amino acid change from valine to alanine, has been linked to differences in fatty acid composition and fat deposition in breeds like Japanese Black, Fleckvieh, and Chinese Simmental cattle (Zalewska et al., 2021). Some studies have also connected *SCD* variants to other economically important traits like carcass weight and meat tenderness (Taniguchi et al., 2004; Li et al., 2020; Zalewska et al., 2021). However, the effects appear to vary somewhat between different cattle populations. Overall, the *SCD* gene is considered a useful candidate gene for potential inclusion in breeding programs aimed at improving carcass quality traits in beef cattle, though more research is still needed to fully elucidate its effects across diverse breeds and production systems (Mannen, 2012). Although *SCD* is a very important gene for beef cattle breeding, the rs41255691 polymorphism did not show any significant effect at the $P<0.05$ level in the current study. Only heterozygous animals exhibited a slightly higher rate in DP, but the differences between genotypes were minimal. As a result, this was characterized as only a suggestive association ($P<0.1$). Therefore, further analyses should be conducted with a larger population. It is also important to note that this effect may either become more pronounced or completely disappear in studies involving a larger number of animals.

Understanding these SNP-SNP interactions could enhance our knowledge of the genetic and physiological mechanisms influencing lipid-related traits and meat production (Amorim et al., 2022). Most economic traits are governed by polygenic inheritance, proving to be more complex than initially anticipated. DNA markers are likely to explain only a small proportion of the genetic variance. Many effects are typically too minor to achieve statistical significance and are, therefore, often overlooked (Meuwissen et al., 2016). Analysis of interactions among marker loci, however, could yield valuable genotypic data. Such interactions might explain differences in genotype responses across various populations and genetic backgrounds, providing deeper insights into these complex traits (Tambasco et al., 2003). In this study, we identified novel genotypic interactions and their significant effects on key carcass traits. The genetic effects observed for the *SCD* × *FABP3* interaction reveal intriguing patterns of allele interactions. For the *SCD* gene, a negative additive effect of −0.135 indicates that the presence of the G allele is associated with a decrease in the trait value. Conversely, a positive dominance effect of 0.325 for the heterozygote suggests that its trait value exceeds the average of the two homozygotes, indicative of overdominance. In the case of the *FABP3* gene, a positive additive effect of 0.07 points to a slight increase in the trait value with the G allele. Additionally, a dominance effect of 0.11 for the heterozygote implies that its trait value is higher than that of the homozygotes, which is characteristic of partial dominance. These findings highlight a complex interaction between the genes, as the combined genotypes demonstrate a departure from simple additive effects, with *SCD* exhibiting a particularly pronounced dominance influence (Duenk et al., 2017). It may suggest that there might be epistatic interactions between *SCD* and *FABP3* for DP (Table 3). The analysis also reveals distinct genetic effects regarding the association between the *SCD* × *FABP3* interaction and carcass pH. For the *SCD* gene, a positive additive effect of 0.025 suggests that the presence of the G allele marginally increases the trait value. A positive dominance effect of 0.015 indicates that the G allele exhibits partial dominance, enhancing the trait value beyond what would be expected from additive effects alone. In contrast, the *FABP3* gene exhibits an additive effect of zero, indicating that neither allele directly affects the trait. However, a negative dominance effect of −0.03 suggests underdominance, in which the trait value of the heterozygote is lower than that of either homozygote. These findings illustrate that while the *SCD* gene contributes a small positive effect with partial dominance, the *FABP3* gene demonstrates no additive influence but presents underdominance. The interaction between these genetic factors is complex, as evidenced by the non-simple additive behavior of their combined genotypes.

The analysis of the *SCD* × *FABP3* genotypic interaction with regard to carcass pH reveals remarkable insights into their epistatic interactions. Specifically, the genotype combination GGAG exhibits the highest observed trait value at 5.61, which is not predictable based on the effects of the individual genes

alone. Conversely, the AAAG combination displays the lowest value at 5.45, similarly unexpected from the singular gene effects. The magnitude of this interaction, as evidenced by a 0.16 difference between the highest and lowest values, surpasses the additive individual impact of either gene, underscoring the presence of strong epistasis. In this context, there is substantial evidence of epistasis between the *SCD* and *FABP3* genes. The effects of each gene do not remain consistent when considering the genotypes of the other gene. Certain genotype combinations, such as GGAG and AAAG, present extreme values that defy explanation through additive effects alone. Additionally, the influence of one gene on the trait significantly varies depending on the genotype configuration of the other gene, further highlighting the complex interplay between these genetic factors. Although significant differences between genotypes were observed in our study, the carcass pH values remained within the normal range for 24 h postmortem. The lowest (5.45) and highest (5.61) values are still within acceptable limits (Table 3). However, the strong epistatic effects identified may carry critical implications. The extent of these genetic interactions may vary across different populations or breeds. Consequently, the impact on the phenotype could be more pronounced, potentially leading to a more distinct pH decline—an undesirable outcome, especially in cattle (Ardicli et al., 2019a). This complexity is often compounded by interactions with other biological mechanisms. First, genes involved in lipid metabolism and other metabolic pathways show epistatic interactions that could indirectly influence muscle pH through effects on energy utilization and glycogen storage (Amorim et al., 2022). Second, epistasis between genes determining muscle fiber type composition and those involved in glycolysis could influence the rate and extent of pH decline (Große-Brinkhaus, 2012). Ultimately, epistasis between genes involved in muscle metabolism, stress response, and glycogen storage may influence ultimate carcass pH. For instance, interactions between genes that regulate glycogen levels and those involved in stress response can affect the accumulation of lactic acid postmortem, impacting meat quality (Große-Brinkhaus et al., 2010; Mendes et al., 2024).

Interactions between multiple genes often influence complex carcass and meat quality traits (Ardicli et al., 2019b; Ardicli et al., 2023). Significant findings were obtained regarding carcass characteristics and epistatic interactions in pigs (Große-Brinkhaus, 2012; Banerjee et al., 2020), but in cattle, this cumulative genetic information is relatively scarce. One of the most comprehensive studies on epistatic interactions in beef cattle, conducted by Amorim et al. (2022), demonstrated substantial genetic interactions associated with lipid profiles, meat quality, carcass characteristics, and feed efficiency traits. In addition, different genetic models can be used to fit crossbreeding effects. Various models exist and are used to account for epistatic interactions, which express the loss of favorable genetic interactions within gametes (Hirooka et al., 1998). Interactions among genomic loci have often been overlooked in genetic association studies despite their role in revealing the combinatorial effects of variants on phenotypes or disease manifestations. A network biology approach could identify unexplained genetic variance, interactions among causal genes with minor effects, and relevant biological pathways (Banerjee et al., 2020). Our results suggest that epistatic interactions may play diverse roles in controlling genetic and phenotypic variation in carcass traits, specifically for DP and pH, among beef cattle. Although numerous genetic interactions are associated with various phenotypic traits, further research is necessary to determine whether the interacting loci perform biologically plausible functions, particularly in terms of functional mechanisms.

## 5. Conclusions

The results suggest a significant impact of the *FABP3* marker on growth rates in Angus cattle, with the GG genotype of this marker being associated with a higher average daily weight gain compared with other genotypes. Additionally, we identified novel associations involving the interaction between the *SCD* and *FABP3* genes, particularly in relation to dressing percentage and carcass pH levels. There is strong evidence of epistasis between these two genes, suggesting that they may be in collaboration to influence carcass traits. This interaction points to a more complex genetic architecture underlying key phenotypic traits than previously understood. Although these genes are closely related to fatty acid synthesis and lipid regulation mechanisms, we did not detect a significant relationship with marbling

in this study. These findings emphasize the intricate genetic mechanisms governing economically important traits in cattle, such as growth rates and meat quality. Understanding the genetic basis of these traits, including gene-gene interactions like those observed between *SCD* and *FABP3*, is crucial for improving selection strategies in breeding programs.

## Data availability

The data that support the results of this study are available from the corresponding author upon reasonable request.

## Author contributions

**Conceptualization:** Ardicli, S. and Ustuner, H. **Data curation:** Ardicli, S.; Senturk, N.; Selvi, T. N.; Yonga, S.; Celik, R.; Karalar, B.; Ozdeniz, A.; Aliyeva, M.; Aydin, H.; Ay, O. T.; Ardicli, O.; Sari, M. E.; Bozkurt, B.; Babayev, H. and Ustuner, H. **Formal analysis:** Ardicli, S. and Ustuner, H. **Funding acquisition:** Ardicli, S. and Ustuner, H. **Investigation:** Ardicli, S.; Senturk, N.; Selvi, T. N.; Yonga, S.; Celik, R.; Karalar, B.; Ozdeniz, A.; Aliyeva, M.; Aydin, H.; Ay, O. T.; Ardicli, O.; Sari, M. E.; Bozkurt, B.; Babayev, H. and Ustuner, H. **Methodology:** Ardicli, S.; Senturk, N.; Selvi, T. N.; Yonga, S.; Celik, R.; Karalar, B.; Ozdeniz, A.; Aliyeva, M.; Aydin, H.; Ay, O. T.; Ardicli, O.; Sari, M. E.; Bozkurt, B.; Babayev, H. and Ustuner, H. **Project administration:** Ardicli, S. and Ustuner, H. **Resources:** Ardicli, S. **Software:** Ardicli, O.; Bozkurt, B.; Viscardi, O. G. and Babayev, H. **Supervision:** Ardicli, S. and Ustuner, H. **Validation:** Ardicli, S.; Ardicli, O.; Bozkurt, B.; Viscardi, O. G.; Babayev, H. and Ustuner, H. **Visualization:** Ardicli, S.; Ardicli, O.; Viscardi, O. G. and Babayev, H. **Writing – original draft:** Ardicli, S.; Senturk, N.; Selvi, T. N.; Yonga, S.; Celik, R.; Karalar, B.; Ozdeniz, A.; Aliyeva, M.; Aydin, H.; Ay, O. T.; Ardicli, O.; Sari, M. E.; Bozkurt, B.; Viscardi, O. G.; Babayev, H. and Ustuner, H. **Writing – review & editing:** Ardicli, S.; Viscardi, O. G. and Babayev, H.

## Conflict of interest

The authors declare no conflict of interest.

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