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Effects of polymorphisms at *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genes on fattening performance and carcass traits in Simmental bulls

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Abstract. The aim of this study was to investigate the effects of single nucleotide polymorphisms (SNPs) at six candidate genes (*LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1*) on fattening performance and carcass traits of Simmental bulls in Turkey. The analysis covered a total of 81 Simmental bulls grown on a private farm that were randomly selected for their fattening period for use in this study. Genotyping was performed using the PCR-RFLP method. The S20T polymorphism at the *CAST* gene and the G316A polymorphism at the *CAPN1* gene were associated with variation in final weight, fattening period, weight gain and average daily gain ($P < 0.05$). In addition, *LEP* A80V had a significant effect on hot and chilled carcass weight and dressing percentage ($P < 0.05$). There was no association between *GHR* S555G, *FABP4* V110M and *DGAT1* K232A markers with the traits analysed. These results suggested that focusing on the novel effects of *LEP*, *CAST* and *CAPN1* gene polymorphisms on meat production traits might be useful for marker-assisted selection in Simmental cattle.

1 Introduction

Fattening performance and carcass traits, which are under the control of polygenic inheritance, play a very important role in beef industry. Selection of animals with better performance and higher meat yield is one of the main objectives for breeders and beef farms. The majority of meat yield has a genetic as well as environmental component with varying heritability. Fattening performance and profitability are quite complex and are affected by housing type, season, initial weight, concentrate level, sex, and pen cattle population (Koknaroglu et al., 2005). In addition, the optimal slaughter ages and final weights vary widely among cattle breed types (Alberti et al., 2008). However, determining the expected yield and quality of meat that emerge in the later stages of life can be facilitated increasingly by the use of molecular studies.

A number of candidate genes have been identified as potentially associated with fattening performance and carcass traits varying on the specific trait analysed. The bovine leptin gene (*LEP*) is located on chromosome 4 and consists of three exons and two introns (Stone et al., 1996). The SNP reported in bovine *LEP* gene encodes alanine instead of valine at position 80 (Nkrumah et al., 2007; Giblin et al., 2010). A80V polymorphism (also known as A59V) in exon 3 has been shown to be a candidate marker for carcass and meat quality traits (Friedman and Halaas, 1998; Yazdani et al., 2010). In addition, polymorphisms in the bovine *LEP* gene (Gen Bank Acc. No.: AF536174.1) locus have been associated with serum leptin concentrations (Liefers et al., 2003; Nkrumah et al., 2005), meat quality (Buchanan et al., 2002; Nkrumah et al., 2005; Shin and Chung, 2007; Corva et al., 2009), milk yield and content (Clempson et al., 2011), dry matter intake (Banos et al., 2008), feed intake (Nkrumah et al., 2005; Banos et al., 2008), growth traits (Lusk, 2007; Kulig and Kmiec, 2009), energy storage (Corva et al., 2009; Kulig and Kmiec, 2009), and fat metabolism (Shin and Chung, 2007). The bovine calpastatin (*CAST*) gene (Gen Bank Acc. No: AF117813), mapped to chromosome 7, is considered a candidate gene for meat quality, especially postmortem tenderization (Schenkel et al., 2006). The serine/threonine substitution (S20T) in the *CAST* gene (exon 1C/1D) at position 20 has been shown to be associated with meat qual-

ity traits (Juszczuk-Kubiak et al., 2004). Calpain 1 (*CAPN1*) gene (Gen Bank Acc. No: AF252504), which is one of the most studied genes, encodes the large subunit of μ-calpain, an enzyme associated with the tenderization process (Page et al., 2004; Corva et al., 2007) and marbling (Cheong et al., 2008). Bovine *CAPN1* has been mapped to chromosome 29 (Page et al., 2004). The SNP G316A in exon 9 (alleles C/G) of the *CAPN1* gene determines the substitution of alanine by glycine in the amino acid 316 of the protein-domain II (Miquel et al., 2009; Soria et al., 2010). The G316A genotype has been shown to be associated with final weight (Miquel et al., 2009), average daily gain (Miquel et al., 2009; Tait et al., 2014) and meat quality traits (Gill et al., 2009; Miquel et al., 2009; Pinto et al., 2010). Post-natal growth, meat quality and fattening performance are under the control of multiple genes. However, growth hormone (GH), also known as somatotrophin, stimulates important physiological processes in cattle, and its effects on growth and metabolism play a key role which can not be overlooked. Nevertheless, the effect of GH is mediated by the GH receptor (*GHR*) (Waters et al., 2011). *GHR* (Gen Bank Acc. No: AF140284), mapped to chromosome 20, has been demonstrated as a candidate gene for meat and milk production in cattle (Di Stasio et al., 2005; Hradecka et al., 2008). The polymorphism at position 257 in exon 10 induced serine/glycine substitution at protein position 555 (S555G) of the *GHR* gene (Di Stasio et al., 2005). The S555G polymorphism has been associated with performance traits (Waters et al., 2011) and meat quality (Reardon et al., 2010). The bovine fatty acid binding protein 4 (*FABP4*) gene plays a role in lipid catabolism via changes in lipid hydrolysis and intracellular fatty acid (Casas et al., 2003). *FABP4* (Gen Bank Acc. No: NC_007312), which is found in the chromosome 14, is considered to be a genetic factor that affects the separation and storage of fat between muscles and tissues (Fortes et al., 2009). *FABP4* has been shown to affect properties such as back fat thickness, marbling score and carcass weight (Maharani et al., 2012; Shin et al., 2012). The SNP reported in bovine *FABP4* gene (exon 3) induces valine to methionine substitution at position 110 (nucleotide position 3691 = g.3691G>A) and is characterized and associated with desirable increases in marbling scores and meat quality grades (Shin et al., 2012). The diacylglycerol O-acyltransferase 1 (*DGAT1*) gene (Gen Bank Acc. No: AY065621) encodes the microsomal enzyme (*DGAT1*) in the triglyceride synthesis (Li et al., 2013). A lysine/alanine amino acid substitution in exon 8 region 232 (K232A) of *DGAT1* gene has been demonstrated to be associated with milk components (Banos et al., 2008; Hradecka et al., 2008; Cerit et al., 2014) and intramuscular fat content (Li et al., 2013; Tait et al., 2014) in different cattle breeds.

LEP, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genes have been shown to be important in regulating muscle and fat metabolism of cattle (Lagonigro et al., 2003; Schenkel et al., 2006; Sherman et al., 2008; Fortes et al., 2009; Curi et al., 2009; Li et al., 2013). The inconsistent association results between the markers used in this study and meat quality or growth traits have been reported in various cattle populations. Moreover, there is limited information about the association of these markers with fattening performance in the literature. We therefore based the study on the association of polymorphisms at *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genes with fattening performance and carcass traits belonging to Simmental bulls breeding in the South Marmara region of Turkey.

2 Material and methods

2.1 Animals and sampling

A total of 81 purebred Simmental bulls were used in the study. Ethical approval was received from Uludag University Local Ethical Committee of Animal Experiments (grant no. 2010-03/05). All animals belonged to the Pedigree Project of the Turkish Ministry of Food, Agriculture and Livestock, and Cattle Breeders Association.

The study was carried out under semi-open stall conditions. The animals were housed in concrete-floor pens and were fed ad libitum. The fattening period were initiated after 15 days of training. The experiment began after this period of adaptation of fattening, with the initial average body weight of animals being 200.21 kg. The weight of bulls was taken at the beginning of the fattening and then monthly during the fattening period. Based on these weights, average daily weight gains were calculated during the periods. According to this weight and weight gain, feed ration was revised.

Bulls were provided with corn silage and barley straw as roughage, barley butter, pasta, corn, corn gluten meal, corn bran, soybean meal, feed additive premix and sunflower meal 36 % as concentrates to obtain a target live weight gain (LWG) of minimum of 1.2 kg day^{-1} and designed according to live weight change of the animals. Animals had full access to water throughout the experiment. As the live weight of animals increased during the fattening period the portion of roughages and concentrate was adjusted of the diet ingredients. For this study, 4 mL blood samples were collected in EDTA tubes (Vacutest Kima, SRL, Italy) from the vena jugularis of each of the bulls.

2.2 Determination of fattening performance and carcass traits

To obtain efficient data for fattening performance, initial weight (IW), final weight (FW), fattening period (FP), total weight gain (TWG) and average daily gain (ADG) were recorded. Bulls were weighed individually to determine the fattening performance. At that time, average daily gain was calculated based on TWG and FP (Ozluturk et al., 2004; Mundan et al., 2012). When animals reached appropriate slaughter maturity, they were weighed while they were hungry and had no access to water for 12 h and sent to be slaugh-

tered. All animals were slaughtered in the same commercial abattoir according to standard routines. In the abattoir, FW and hot carcass weight (HCW) were recorded. Hot carcass weight was measured without removing the subcutaneous fat and keeping the kidney and pelvic fat. Chilled carcass weight (CCW) and chilling loss (CL) were measured after 24 h at 4 °C (Pfuhl et al., 2007). The dressing percentage (DP) was calculated based on both hot and chilled carcass weight (Journaux, 2007).

2.3 Genomic DNA extraction

DNA extraction was performed using a phenol-chloroform method as described by Green and Sambrook (2012). The amount and purity of the DNA samples were measured with a spectrophotometer (NanoDrop 2000c, Thermo Scientific, Wilmington, DE, USA). DNA samples were stored at −80 °C until PCR-RFLP was performed.

2.4 Genotyping

In this study, polymorphisms at six candidate genes were examined with the PCR-RFLP method. Primers used, PCR conditions and corresponding restriction enzymes are shown in Table 1. The DNA amplification reactions were performed in a thermal cycler (Palm Cycler GC1-96, Corbett Research, Sydney, Australia). The PCR amplification was performed in a total volume of 50 µL containing 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 *Taq* DNA polymerase (Biomatik, A1003-500 U, 5 U µL^{-1}), 1 µL (0.025 µM) of each primer and 3 µL of the DNA sample at a concentration of 100 ng µL^{-1}. After amplification, 15 µL of the PCR product with each SNP was digested in 15 units of the corresponding restriction enzyme. These reactions were incubated at 37 °C for 16 h. The digestion products were then electrophoresed in 3 % agarose gel (Sigma Aldrich, Steinheim, Germany) at 85–90 V for 1 h and photographed with a gel imaging system (DNR-Minilumi, DNR Bio-Imaging Systems, Israel) as shown in Figs. 1–6.

2.5 Statistical analysis

The Hardy–Weinberg equilibrium (HWE) was tested for all alleles by using the Court Lab HWE Calculator (Erken et al., 2010). The population genetic indexes including gene heterozygosity (He) and polymorphism information content (PIC) were estimated as described by Botstein et al. (1980). The effects of genotypes on the traits studied were analysed using the least-squares method as applied in a general linear model (GLM) procedure of Minitab (MINITAB®, USA, v17.1.0) according to the following listed mix models:

Model used for FW, TWG, ADG, HCW, CCW:

– $Y_{\text{ijklmnop}} = \mu + \beta\,\text{IW}_i + \text{FP}_j + A_k + B_l + C_m + D_n + E_o + F_p + e_{\text{ijklmnop}}$.

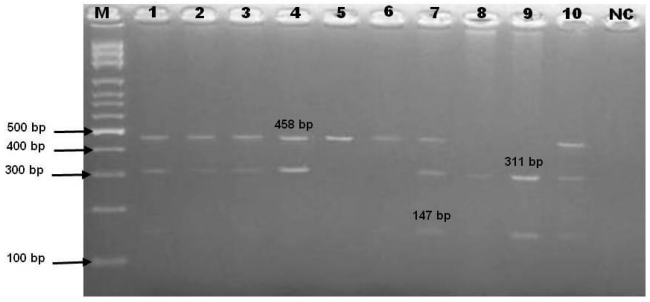

Figure 1. The electrophoresis pattern of A80V polymorphism within the bovine *LEP* gene in Simmental cattle. Note: CC = 458 bp; CT = 458, 311 and 147 bp; TT = 311 and 147 bp. (M: marker 100–1200 bp; lanes 5, 6: CC genotype; lanes 1–4, 7, 10: CT genotype; lanes 8, 9: TT genotype; NC: negative control.)

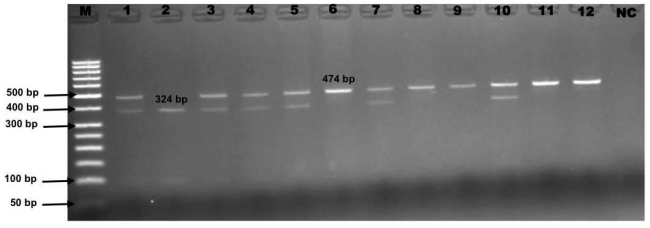

Figure 2. The electrophoresis pattern of S20T polymorphism within the bovine *CAST* gene in Simmental cattle. Note: CC = 474 bp; GC = 474 and 324 bp; GG = 324 bp. (M: marker 50–1000 bp; lanes 6, 8, 9, 11, 12: CC genotype; lanes 1, 3–5, 7, 10: GC genotype; lane 2: GG genotype; NC: negative control.)

Model used for FP:

– $Y_{\text{ijklmnop}} = \mu + \beta\,\text{IW}_i + \text{FW}_j + A_k + B_l + C_m + D_n + E_o + F_p + e_{\text{ijklmnop}}$.

Model used for DP:

– $Y_{\text{iklmnop}} = \mu + \beta\,\text{IW}_i + A_k + B_l + C_m + D_n + E_o + F_p + e_{\text{ijklmnop}}$.

Model used for CL:

– $Y_{\text{iklmnop}} = \mu + \beta\,\text{HCW}_i + A_k + B_l + C_m + D_n + E_o + F_p + e_{\text{ijklmnop}}$.

where $Y_{\text{ijklmnopr}}$ represents the studied traits, μ is the overall mean, β IW$_i$ is the regression effect of initial weight, FP$_j$ is the regression effect of fattening period, FW$_j$ is the regression effect of final weight, β HCW$_i$ is the regression effect of hot carcass weight, A_k is the fixed effect of the *LEP* genotype, B_l is the fixed effect of the *CAST* genotype, C_m is the fixed effect of the *CAPN1* genotype, D_n is the fixed effect of the *GHR* genotype, E_o is the fixed effect of the *FABP4* genotype, F_p is the fixed effect of the *DGAT1* genotype, and e_{ijklmnop} is random error. When significant associations were identified, the mean values for each genotype were contrasted using the Tukey test.

Table 1. Characteristics of polymorphisms in *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genes, primers used, PCR conditions and restriction enzymes.

SNP name*	Allele	PCR amplicon (bp)	Primers (5′ to 3′)	PCR conditions	Restriction enzyme	Reference
LEP A80V	C/T	458	F: 5'GGGAAGGGCAGAAAGATAG3' R: 5'CCAAGCTCTCCAAGCTCTC3'	94 °C 2′ (94 °C 30 s, 57 °C 1′, 72 °C 30 s) 35 cycles, 72 °C 15′	*Hph*I	Oztabak et al. (2010)
CAST S20T	G/C	624	F: 5'TGGGGCCCAATGACGCCATCGATG3' R: 5'GGTGGAGCAGCACTTCTGATCACC3'	94 °C 5′ (94 °C 30 s, 62 °C 45 s, 72 °C 45 s) 32 cycles, 72 °C 5′	*Alu*I	Juszczuk-Kubiak et al. (2004)
CAPN1 G316A	C/G	415	F: 5'GACTGGGGTCTCTGGACTT3' R: 5'GGAACCTCTGGCTCTTGA3'	95 °C 5′ (95 °C 45 s, 63 °C 45 s, 72 °C 45 s) 35 cycles, 72 °C 5′	*Btg*I	Lisa and Di Stasio (2009)
GHR S555G	G/A	342	F: 5'GCTAACTTCATCGTGGACAAC3' R: 5'CTATGGCATGATTTTGTTCAG3'	95 °C 5′ (94 °C 45 s, 53 °C 30 s, 72 °C 50 s) 35 cycles, 72 °C 5′	*Alu*I	Di Stasio et al. (2005)
FABP4 V110M	A/G	565	F: 5'ACCCCTATGATGCTATTCCACA3' R: 5'ATACGGTTCACATTGAGAGGGA3'	95 °C 4′ (94 °C 1′, 60 °C 1′, 72 °C 1.5 min^{-1}) 35 cycles, 72 °C 5′	*Nla*III	Shin et al. (2012)
DGAT1 K232A	A/K	411	F: 5'GCACCATCCTCTTCCTCAAG3' R: 5'GGAAGCGCTTTCGGATG3'	94 °C 4′, 10 cycles (94 °C 60 s, 66 °C 60 s; −1 °C per cycle, 72 °C 60 s), 25 cycles (94 °C 60 s, 56 °C 120 s, 72 °C 60 s), 72 °C 15′	*Cfr*I	Lacorte et al. (2006)

* SNP names were used according to translation.

Table 2. Allele and genotype frequencies of polymorphisms in *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genes, population genetic indices (He, PIC) and compatibility with the Hardy–Weinberg equilibrium.

SNP	*LEP* A80V			*CAST* S20T			*CAPN1* G316A			*GHR* S555G			*FABP4* V110M			*DGAT1* K232A		
Genotypes	CC	CT	TT	CC	GC	GG	CC	GC	GG	AA	AG	GG	AA	AG	GG	AA	KA	KK
N	7	31	43	18	53	10	0	12	69	52	12	17	4	19	58	67	14	0
%	8.64	38.28	53.08	22.22	65.44	12.34	0	14.81	85.19	64.19	14.82	20.99	4.94	23.45	71.61	82.72	17.28	0
MAF		0.28			0.45			0.07			0.28			0.17			0.09	
He		0.4092			0.4950			0.1302			0.4032			0.2822			0.1638	
PIC		0.3255			0.3724			0.1217			0.3219			0.2423			0.1503	
χ2(HWE)*		0.17			8.37*			0.51			32.73**			1.96			0.72	
P		0.677			0.003			0.471			0.000			0.161			0.394	

χ^2 (HWE) – Hardy–Weinberg equilibrium χ^2 value. * $P < 0.05$, ** $P < 0.001$ – not consistent with HWE. *N* – number of experimental bulls. MAF – minor allele frequency. He – heterozygosity. PIC – polymorphism information content.

3 Results and discussion

3.1 Genetic variability

The allele and genotype frequencies, population genetic indices (He, PIC) and compatibility with the Hardy–Weinberg equilibrium (HWE) are shown in Table 2. Results show that the population was determined to be compatible with either genotype in the HWE, except for *CAST* S20T and *GHR* S555G polymorphisms. This disequilibrium can be a result of indirect selection for these loci from the selection for dual-purpose production. Deviations from HWE can indicate inbreeding, population stratification related to the sampling of the genotyped sires (Lacorte et al., 2006). However, these results may reflect the actual allelic and genotypic frequencies for corresponding locus, especially for commercial herds. The PIC values indicate the quality of markers in genetic studies. A marker with a PIC value higher than 0.5 is considered to be very informative, whereas values between 0.25 and 0.5 are mildly informative, and values lower than 0.25 are not

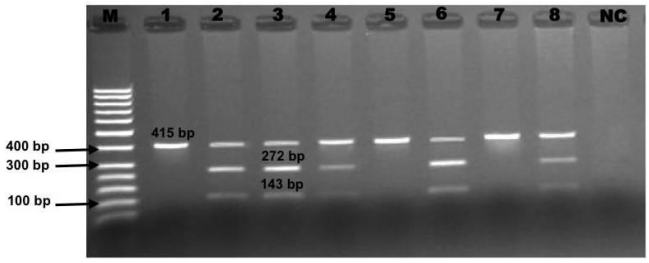

Figure 3. The electrophoresis pattern of G316A polymorphism within the bovine *CAPN1* gene in Simmental cattle. Note: CC = 272 and 143 bp; GC = 415, 272 and 143 bp; GG = 415 bp. (M: marker 50–1000 bp; lanes 2–4, 6, 8: GC genotype; lanes 1, 5, 7: GG genotype; NC: negative control.) CC genotype was not present in the current study.

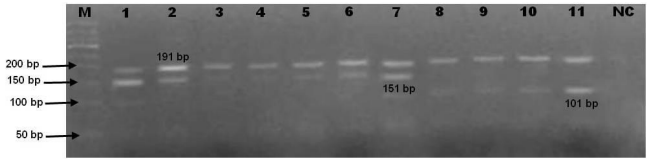

Figure 4. The electrophoresis pattern of S555G polymorphism within the bovine *GHR* gene in Simmental cattle. Note: AA = 191 and 101 bp; AG = 191, 151 and 101 bp; GG = 191 and 151 bp. (M: marker 50–1000 bp; lanes 8–11: AA genotype; lanes 1, 7: AG genotype; lanes 2–6: GG genotype; NC: negative control.)

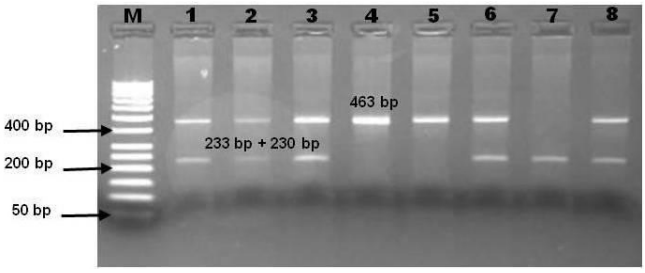

Figure 5. The electrophoresis pattern of V110M polymorphism within the bovine *FABP4* gene in Simmental cattle. Note: AA = 233 and 230 bp; AG = 463, 233 and 230 bp; GG = 463 bp. (M: marker 50–1000 bp; lane 7: AA genotype; lanes 1–3, 6, 8: AG genotype; lanes 4,5: GG genotype.)

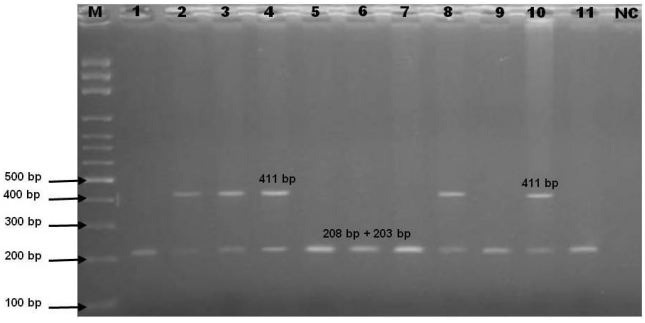

Figure 6. The electrophoresis pattern of K232A polymorphism within the bovine *DGAT1* gene in Simmental cattle. Note: AA = 208 and 203 bp; KA = 411, 208 and 203 bp; KK = 411 bp. (M: marker 100–1200 bp; lanes 1, 5–7, 9, 11: AA genotype; lanes 2–4, 8, 10: KA genotype; NC: negative control.) KK genotype was not present in the current study.

informative (Botstein et al., 1980). According to this classification, the PIC values found for *LEP* A80V, *CAST* S20T and *GHR* S555G indicated that the markers were mildly informative, whereas those for *CAPN1* G316A, *FABP4* V110M and *DGAT1* K232A were not informative. Among the 81 animals studied, the frequencies of the CC genotype in *LEP* A80V, GG genotype in *CAST* S20T, AG genotype in *GHR* S555G, and AA genotype in *FABP4* V110M polymorphisms were rather low compared to the other two genotypes. In addition, results indicated that the CC genotype of the *CAPN1* G316A polymorphism and the KK genotype of the *DGAT1* K232A polymorphism were absent in the present study.

In this study, the frequency of allele C of the *LEP* A80V polymorphism was 0.28 and the highest frequency was found for the TT genotype (53.08 %). Similar results have been reported by Oztabak et al. (2010) and Silva et al. (2014), who observed a higher genotypic frequency of allele C. In contrast, Lagonigro et al. (2003), Liefers et al. (2003), Kulig et al. (2010) and da Silva et al. (2012) reported that C allele frequency was very dominant over C allele frequency for Holstein × Charolais, Jersey, Nellore and Holstein populations respectively. The present results showed a higher frequency of heterozygous genotype of the *CAST* S20T polymorphism in Simmental population (65.43 %). Our results and those reported in other studies investigating the same polymorphism (Juszczuk-Kubiak et al., 2004; Yousefi and Azari, 2012) indicate that the frequency of heterozygous genotype is higher than that of two other genotypes.

The *CAPN1* CC genotype was not present in the present study. Moreover, C allele frequency was very low (0.07). Present results support the study that was carried out by Li et al. (2013), reporting that the CC genotype was absent in Hereford, Limousin and Simmental populations. Similarly, Curi et al. (2009), Soria et al. (2010) and Allais et al. (2011) reported that the C allele and accordingly the CC genotype were rather low or absent in different cattle populations. The major allele was A in *GHR* S555G polymorphism (0.72 %). Chessa et al. (2015) have reported the similar results in dual-purpose Simmental cattle. The AA genotype frequency is rather low compared to the other two genotypes (4.93 %) in *FABP4* V110M polymorphism. In a different study (Shin et al., 2012) performed in Hanwoo cattle, G and A allele frequencies are 0.79 and 0.21, respectively, for the same polymorphism, showing support for the results of the current study. In the K232A polymorphism, the genotype AA prevailed substantially over the KA (82.71 %), while the homozygous genotype KK was not found. Hanusova et

Table 3. Least-squares means for *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genotype effects on fattening performance traits.

Gene	G	IW (kg)	FW (kg)	FP (days)	TWG (kg)	ADG (kg)
LEP	CC	180.40 ± 16.50	601.50 ± 25.00	289.80 ± 20.30	401.30 ± 25.00	1.44 ± 0.10
	CT	200.10 ± 10.60	593.70 ± 15.80	276.60 ± 12.70	393.50 ± 15.80	1.42 ± 0.06
	TT	209.40 ± 9.340	602.50 ± 14.20	290.90 ± 11.60	402.30 ± 14.20	1.43 ± 0.05
	P	NS	NS	NS	NS	NS
CAST	CC	186.90 ± 11.00	617.30 ± 16.60^{a}	267.30 ± 13.50^{b}	417.10 ± 16.60^{a}	1.49 ± 0.06^{a}
	GC	208.30 ± 10.30	573.50 ± 15.50^{b}	305.50 ± 12.50^{a}	373.30 ± 15.50^{b}	1.32 ± 0.06^{b}
	GG	194.70 ± 15.60	606.90 ± 23.30$^{a, b}$	284.50 ± 19.00$^{a, b}$	406.70 ± 23.30^{a}	1.48 ± 0.09^{a}
	P	NS	0.032	0.028	0.032	0.036
CAPN1	GC	193.20 ± 13.20	575.00 ± 20.00^{b}	311.70 ± 16.00^{a}	374.80 ± 20.00^{b}	1.35 ± 0.08
	GG	200.00 ± 10.60	623.50 ± 15.90^{a}	259.80 ± 12.90^{b}	423.30 ± 15.90^{a}	1.52 ± 0.06
	P	NS	0.022	0.002	0.022	0.056
GHR	AA	197.00 ± 11.30	599.80 ± 16.90	291.20 ± 13.70	399.50 ± 16.90	1.44 ± 0.07
	AG	202.90 ± 14.30	617.80 ± 21.40	275.80 ± 17.50	417.60 ± 21.40	1.51 ± 0.09
	GG	189.90 ± 11.00	580.20 ± 16.40	290.30 ± 13.30	380.00 ± 16.40	1.34 ± 0.06
	P	NS	NS	NS	NS	NS
FABP4	AA	217.40 ± 19.60	617.80 ± 29.40	265.70 ± 23.80	417.60 ± 29.40	1.52 ± 0.12
	AG	180.50 ± 11.70	595.30 ± 18.10	296.70 ± 14.60	395.10 ± 18.10	1.40 ± 0.07
	GG	192.01 ± 8.81	584.60 ± 13.30	294.90 ± 10.70	384.40 ± 13.30	1.36 ± 0.05
	P	NS	NS	NS	NS	NS
DGAT1	AA	190.07 ± 9.84	593.80 ± 14.80	286.50 ± 12.00	393.60 ± 14.80	1.41 ± 0.06
	KA	203.20 ± 12.80	604.70 ± 19.20	285.00 ± 15.60	404.50 ± 19.20	1.46 ± 0.08
	P	NS	NS	NS	NS	NS

The data were expressed as least-squares means ± standard errors (mean ± SE).
G – genotype. IW – initial weight. FW – final weight. FP – fattening period. TWG – total weight gain. ADG – average daily gain. NS – non-significant.
$^{a, b}$ Means with different superscripts are significantly different at the 0.05 level.

al. (2014) in Czech Simmental sires gave supporting frequencies of K allele. By contrast, Lacorte et al. (2006) reported the KK genotype frequency was very dominant over AA and KA genotypes.

3.2 Genetic association

The least-squares means and their respective standard errors obtained for the fattening performance and carcass traits in Simmental bulls established are shown in Table 3 and 4 respectively. The marker *CAST* S20T affected ($P < 0.05$) with FW, FP, TWG and ADG. Animals with the CC genotype have higher rates of FW and TWG, whereas animals with the GC genotype have higher FP and also have the lowest ADG compared to the other two genotypes (Table 3). The marker G316A at the *CAPN1* gene had significant effects ($P < 0.05$) on FW, FP and TWG. Results indicate that animals with the GG genotype for the lowest FP also have the highest FW and TWG (Table 3). *LEP* A80V had a significant effect on HCW, CCW and DP ($P < 0.05$). Animals with the TT genotype have the highest rates of corresponding traits (Table 4).

In the variation analyses, *CAST* S20T and *CAPN1* G316A polymorphisms had significant effects on fattening performance traits ($P < 0.05$). The CC genotype of the S20T shows significant differences compared to the GG genotype and heterozygous animals in terms of FW, TWG, FP and ADG ($P < 0.05$). The mean FW for the CC genotype was 617.3 kg, which was an estimated 10.4 kg greater than the mean FW of GG genotype animals and 43.8 kg greater than the mean FW of heterozygous animals. Moreover, animals with CC have the lowest FP (267.3 days). These results indicated that animals which were homozygous for allele C grew faster during fattening and reached the highest FW and TWG in the lowest FP. In addition, the CC and GG genotypes were determined to have higher ADG compared to heterozygous animals. However, the *CAST* gene has profound effect on the meat quality, similar associations of S20T with fattening performance traits have not been reported in different cattle populations (Juszczuk-Kubiak et al., 2004; Corva et al., 2007). The *CAPN1* G316A genotype was significant for FW, FP and TWG ($P < 0.05$). For those traits of which the differences among genotypes were statistically significant, the GG means were different from those of GC. Thus, the CC genotype was not present in the present study. Animals with GG were determined to have 48.5 kg higher TWG. Moreover, these animals reached a higher FW and TWG in

Table 4. Least-squares means for *LEP*, *CAST*, *CAPN1*, *GHR*, *FABP4* and *DGAT1* genotype effects on carcass traits.

Gene	G	HCW (kg)	CCW (kg)	DP (%)[1]	DP (%)[2]	CL (%)
LEP	CC	320.21 ± 5.89^{b}	313.79 ± 5.79^{b}	$53.83 \pm 1.10^{a, b}$	$52.75 \pm 1.08^{a, b}$	2.00 ± 0.03
	CT	322.40 ± 3.76^{b}	315.94 ± 3.69^{b}	54.30 ± 0.70^{b}	53.21 ± 0.68^{b}	2.00 ± 0.02
	TT	332.73 ± 3.36^{a}	326.06 ± 3.30^{a}	55.95 ± 0.63^{a}	54.83 ± 0.61^{a}	2.00 ± 0.01
	P	0.006	0.006	0.018	0.019	NS
CAST	CC	321.01 ± 3.90	314.67 ± 3.83	53.99 ± 0.73	52.92 ± 0.71	1.97 ± 0.02
	GC	328.65 ± 3.65	322.04 ± 3.58	55.31 ± 0.68	54.20 ± 0.66	2.01 ± 0.01
	GG	325.68 ± 5.55	319.08 ± 5.45	54.78 ± 1.04	53.67 ± 1.02	2.02 ± 0.02
	P	NS	NS	NS	NS	NS
CAPN1	GC	328.48 ± 4.78	321.88 ± 4.70	54.96 ± 0.88	53.86 ± 0.86	2.01 ± 0.02
	GG	321.74 ± 3.83	315.32 ± 3.77	54.42 ± 0.70	53.33 ± 0.69	2.00 ± 0.02
	P	NS	NS	NS	NS	NS
GHR	AA	323.18 ± 4.05	316.63 ± 3.98	54.25 ± 0.75	53.15 ± 0.74	2.02 ± 0.02
	AG	328.90 ± 5.12	322.29 ± 5.03	55.45 ± 0.95	54.33 ± 0.94	2.01 ± 0.02
	GG	323.26 ± 3.92	316.87 ± 3.85	54.38 ± 0.73	53.30 ± 0.71	1.98 ± 0.02
	P	NS	NS	NS	NS	NS
FABP4	AA	328.88 ± 7.03	322.19 ± 6.90	55.79 ± 1.30	54.66 ± 1.28	2.03 ± 0.03
	AG	324.21 ± 4.24	317.78 ± 4.17	54.15 ± 0.78	53.07 ± 0.76	1.99 ± 0.02
	GG	322.25 ± 3.14	315.81 ± 3.09	54.15 ± 0.58	53.06 ± 0.57	2.00 ± 0.01
	P	NS	NS	NS	NS	NS
DGAT1	AA	328.27 ± 3.49	321.70 ± 3.43	55.16 ± 0.65	54.05 ± 0.64	2.00 ± 0.01
	KA	321.96 ± 4.56	315.49 ± 4.48	54.23 ± 0.85	53.14 ± 0.84	2.00 ± 0.02
	P	NS	NS	NS	NS	NS

The data were expressed as least-squares means ± standard errors (mean ± SE).
G – genotype. HCW – hot carcass weight. CCW – chilled carcass. DP – dressing percentage. CL – chilling loss. NS – non-significant.
[1] represents dressing percentage based on hot carcass weight. [2] represents dressing percentage based on chilled carcass weight.
[a, b] Means with different superscripts are significantly different at the 0.05 level.

the lower FP compared to heterozygous animals. Although shown to be statistically non-significant, animals with the GG animals tend to have higher ADG ($P = 0.056$). Similar results were reported by Miquel et al. (2009) who found a significant association of the marker genotype with FW. The *CAPN1* gene located on BTA29, and the specific inhibitor of the calpain family of endogenous proteases, *CAST* gene, located on BTA7 are functional and positional candidate genes for carcass and meat quality traits in beef cattle due to the physiological activity of their protein products (Koohmaraie, 1994; Curi et al., 2009). In addition, bovine *CAPN1* has been mapped to the telomeric end of the chromosomal region including considerable overlap of QTLs regulating not only beef tenderness but also growth (weaning weight, carcass weight) and feed efficiency (Casas et al., 2003; Pintos and Corva, 2011). Hence, focusing on this genomic region may be useful to obtain novel genetic associations among the mentioned traits.

The polymorphism of the *LEP* gene showed associations with variation of carcass traits. Animals with the TT genotype displayed a greater HCW (+12.52 kg) and CCW (+12.27 kg) than those with the homozygous for allele C and the heterozygotes ($P < 0.05$). Moreover, similar results were observed between the corresponding genotype and DP based on both HCW and CCW. Kulig and Kmiec (2009) reported a significant association of A80V polymorphism with live weight at 210 days and ADG in Limousin cattle, but carcass traits were not included in association analyses. In the study performed by Nkrumah et al. (2006), differences were observed among genotypes of A80V in carcass lean meat yield and carcass yield grade. In both studies, animals with the TT genotype were characterized by a significantly higher daily gain and *LEP* A80V was suggested as a useful marker for marker-assisted selection in beef cattle (Nkrumah et al., 2006; Kulig and Kmiec, 2009). However, no significant effect was observed in *LEP* A80V polymorphism on carcass weights in several studies (Nkrumah et al., 2007; Kulig and Kmiec, 2009; Melucci et al., 2012). Carcass traits such as HCW, CCW and DP, which are under the control of polygenic inheritance, may vary between breeds, to the best of our knowledge, genetic association studies, performed to determine the effects of A80V polymorphism on carcass traits in Simmental populations are insufficient. *LEP*, performs important roles in the control of body weight, fat deposition and feed intake (Buchanan et al., 2002; Nkrumah et al., 2007). The existence of an association between A80V polymor-

phism and carcass traits may be dependent on the overall fat content of the individual. However, further studies should be performed in various cattle populations to evaluate such novel associations.

No association was observed between the tested SNPs and CL. In addition, there was no association between the *GHR* S555G, *FABP4* V110M and *DGAT1* K232A markers and fattening performance traits, nor was there any association with variation in any carcass traits. However, Sherman et al. (2008) found that *GHR* S555G polymorphism was associated with body weight in Continental × British hybrid beef steers. The reason for the lack of corresponding result in the present study may be due to the breed genetic composition or polygenic effects associated with expression of this trait. Polymorphisms at *FABP4* and *DGAT1* genes have been associated with intramuscular fat content (Shin et al., 2012; Li et al., 2013). Nevertheless, adequate studies have not been conducted on the fattening performance in various breed of cattle. More studies should be carried out to confirm the present results and to test possible associations between markers and phenotypic traits in larger Simmental populations.

4 Conclusions

In this study, final weight, fattening period, total weight gain and average daily gain differentiated the *CAST* S20T and *CAPN1* G316A marker genotypes in Simmental bulls. Homozygous animals for allele C at the *CAST* S20T marker and homozygous animals for allele G at the *CAPN1* G316A marker reached the highest final weight and total weight gain in a shorter fattening period with higher average daily gain. Moreover, results indicated a novel effect of the *LEP* A80V on selected carcass traits. The TT genotype of the *LEP* A80V marker seemed to be favourable for evaluating carcass weights and dressing percentage in Simmental. Selecting animals with the favourable SNP genotypes may result in selecting animals with higher fattening performance and meat yield. Consequently, information on polymorphisms of the tested SNPs and significant associations may be used to improve selected traits in beef production.

Data availability. The original data are available upon request from the corresponding authors. Additional data can be found in the Supplement to this article.

The Supplement related to this article is available online at doi:10.5194/aab-60-61-2017-supplement.

Author contributions. Sena Ardicli and Hale Samli designed the study and wrote the paper. Sena Ardicli, Deniz Dincel and Hale Samli performed the experiments. Sena Ardicli and Deniz Dincel collected the samples. Faruk Balci analysed the data and did the statistical analysis. Sena Ardicli, Hale Samli and Faruk Balci edited and reviewed the paper.

Competing interests. The authors declare that they have no conflict of interest.

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