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Association analyses of SNPs in candidate genes with body fat deposition and carcass merit traits in beef cattle

by

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Dedication

“To the people who believe in Science”

Abstract

A candidate gene approach was used to identify single nucleotide polymorphisms (SNPs) and their associations with body fat deposition and carcass merit traits in beef cattle. In total, 37 SNPs from 9 candidate genes have been genotyped on 463 hybrid, 206 Angus and 187 Charolais steers for association analyses with 10 different fat deposition and carcass merit traits. In single SNP analyses, 28 SNPs of 9 genes have been found significantly ($P<0.05$) associated with different traits in the cattle populations. Gene-specific linkage disequilibrium assessment of SNPs revealed the existence of haplotype blocks within 4 genes. Haplotype analyses have identified 31 haplotypes of 6 genes having significant associations ($P<0.05$) with different fat deposition and carcass merit traits in the cattle populations. These findings will provide insight into the genetic mechanism regulating body fat deposition in beef cattle and will assist the beef industry to improve beef quality through marker assisted selection.

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List of Abbreviations

ACSF3=acyl-CoA synthetase family member 3

AUBF = Average daily gain of ultrasound backfat, mm

AUREA = Average daily gain of ultrasound rib eye area, cm^2

AVBF = Average backfat, mm

CMAR = Carcass marbling score (USDA)

CREA= Carcass rib eye area, cm^2

CWT = Carcass weight, kg

FABP3= fatty acid binding protein-3

FASN= bovine fatty acid synthase

FDR = False discovery rate

GPAM= mitochondrial glycerol 3-phosphate acyltransferase

IDH1= isocitrate dehydrogenase 1 (NADP+), soluble

IGF1= insulin-like growth factor 1

IGGA = Illumina GoldenGate Assay

INS= Insulin

LD = Linkage disequilibrium

LIPE= lipase, hormone-sensitive

LMY = Lean meat yield, %

MAF = Minor allele frequency

OLR1= oxidized low density lipoprotein (lectin-like) receptor 1

SNP = Single nucleotide polymorphism

SWT = Slaughter weight, kg

TF = Transcription factor

UBF = Ultrasound backfat, mm;

UREA = Ultrasound rib eye area, cm^2

USDA = United States Department of Agriculture

UTR = Un-translated region

1. Chapter One: Introduction and Literature Review

1.1. General introduction

The process of domestication was established on mutualism and selective benefit for partners (Zeder et al., 2006) accompanied with severe and novel selective pressure on cattle populations (Freeman et al., 2008). Likewise, the improvement of beef cattle carcass traits perhaps was initiated at the ancient times, following cattle domestication and likely through the implementation of “classical breeding strategies” (Kadarmideen et al., 2006). In time, with the development of cattle farming and emergence of beef industries, these strategies were adopted as an integral part of the modern age agricultural sciences as a branch named “cattle breeding”. Production capacity expansion, quality enhancement of carcass products and consumer satisfaction are the key factors for the sustainable development of beef industries throughout the globe. Age-old great efforts of beef cattle breeders have devoted to meet these demands by the beef industries, so that, beef can hold its position as a source of protein in the food chain for the growing human civilization. Cattle farmers benefited from the traditional breeding and selection program based on phenotypic measurements of economically important traits and pedigree information. However, the progress of traditional genetic improvement, which is based on animal’s phenotype or genetic merit e.g. breeding value derived from the phenotype, has not been optimal for traits that have a low heritability, such as reproductive traits or for traits that are difficult and/or expensive to measure, such as disease resistance, feed efficiency, nutrition, fatty acid contents in milk and meat, and for traits that are measured at a later stage, such as fat deposition, carcass and meat quality traits.

Studies have showed that incorporating genetic markers or DNA markers to calculate the breeding values, namely marker assisted selection (MAS), will accelerate the genetic improvement rates for traits described above by increasing the accuracy of genetic prediction even at the early stage of the life, and by shortening the generation interval (Lande and Thompson, 1990; Meuwissen and Van Aredonk, 1992; Meuwissen et al., 2001; Gianola et al., 2003). Subsequently, a concept of genomic selection has been developed, which utilizes genome-wide genetic markers to estimate breeding values (GEBV) and has been considered as a variant of marker assisted selection (Meuwissen et al., 2001; Schaeffer, 2006; Goddard and Hayes, 2007), with an aim to predict an animal's genetic merit based only on genetic markers.

The recent release of more than 2 million bovine SNPs by the international bovine genome sequencing project (Matukumalli et al., 2009), in coupling with the development of cost-effectively high-throughput SNP genotyping platforms, has greatly enabled researchers to identify, characterize and validate SNP markers influencing the quantitative traits of interest in cattle.

This thesis reports an association study of 37 SNPs within 9 genes with fat deposition and carcass merit traits in three beef cattle populations. Firstly, the thesis presented a comprehensive literature review of candidate gene association analyses and the objectives of this study. Subsequently, the thesis reports SNP genotyping, least square means of 10 fat deposition and carcass traits for different SNP genotypes in three beef cattle populations and SNP effects including allele substitution effect, additive effect and dominance effect for each single SNP.
The thesis also reports haplotype blocks, reconstructed haplotypes and SNP haplotype effetcs on the traits in the beef cattle populations. The data presented in the thesis will provide insight into the genetic controls of body fat deposition and carcass merit traits in beef cattle and the gene-specific SNP markers identified to have associaitons with the thaits will assist the beef industry to speed up the genetic improvement rate for the production and quality traits through successfully implementing marker assisted selection or genomic selection.

1.2. Literature review

1.2.1. Fat deposition and carcass merit traits of beef cattle

Fat cells are essential components of an animal's body composition and play important roles in metabolism. Fat deposition takes place in four common physiological body parts of beef cattle in different stages of life, which includes; (i) internal fat or kidney fat; (ii) intermuscular fat or seam fat; (iii) subcutaneous fat; (iv) intramuscular fat, chronologically and with the maturity in respect to age (Boggs et al., 1998; Fiems et al., 2000).

Carcass subcutaneous fat thickness or backfat thickness, which is usually measured at the 12th rib over the rib eye muscle (*m longissimus thoracis et lumborwn*) and three-quarters of the distance from its medial to its lateral border (Johnson, 1996), eventually covers approximately 30% of the beef carcass, and as a result, has importance to beef production. Small amount of external fat mainly protects beef carcasses from discoloration, dehydration and quick drying in the freezer as well as rapid cooling of the meat in the cooler and subsequently enhances the tenderization (May et al., 1992; Boggs et al., 1998). However, excessive amount of subcutaneous fat is considered as waste fat and needs to be removed from carcasses in the slaughterhouse which increases the labour investment and cost of beef production (Reckless, 1987; Ulbricht & Southgate, 1991; Fiems et al., 2000).

On the other hand, the intramuscular fat, which is known as "marbling", comprises approximately 15% of total fat in beef carcasses and is considered as "good fat". There are some benefits of intramuscular fat, i.e., (i) marbling improves meat tenderness by reducing bulk density and by decreasing the strength of the connective tissue, known as bite and strain; (ii) marbling improves quality through increased juiciness, known as lubrication; (iii) marling protects meat from drying out, when it is cooked too long or too rapidly, known as insurance (Savell and Cross, 1988; Fiems et al., 2000). Greater amount of intramuscular fat can also increase the attractiveness of meat colour (Boucque, 1982). Therefore, carcass marbling score is viewed as the major determinate of quality grades (QG) of marketed beef. Authorized by USDA and Canadian market grading systems, marbling is a desirable trait and a higher grade on carcasses is determined by increased amounts of marbling. However, beef cattle usually deposit excessive backfat during the finishing stage in order to achieve a higher marbling score (Wilson, 1992 & 1994; Whittaker et al., 1992).

Rib eye area (REA) is one of important carcass merit traits that are related to beef production and is measured as area of *longissimus* dorsi muscle or rib eye muscle. Measurement is usually taken between the 12th and 13th ribs and square inches (inch^2) or square centimetres (cm^2) are the unit of area .Within a specific carcass weight range, REA may significantly contribute to the beef carcass yield grades variation, within a specific carcass range (Wilson, 1994).

Although carcass backfat, carcass marbling and carcass rib eye area are ultimate measures of the traits, the development of ultrasound technology has allowed these traits to be measured when animals are alive. These ultrasound measures, e.g. ultrasound backfat (UBF), ultrasound marbling (UMAR) and ultrasound rib eye area (UREA) have been used as early indicators of the performance of the traits (Crews and Kemp, 2001; Devitt and Wilton, 2001; Crews et al., 2003)

Other important carcass merit traits include hot carcass weight (HCW) and lean meat yield. Hot carcass weight is considered as a reduced animal's slaughter weight (SWT) by removing the hide, head, feet, tail, entrails and gut fill. Lean meat yield (LMY) is an estimation of the total muscle in a carcass, free of all dissectible fat (estimated saleable meat %) and is considered as amount of saleable meat (Johnson, 1996; Agriculture Canada, 1992;www.omafra.gov.on.ca).

1.2.2. Genetic parameters of fat deposition and carcass merit traits

Starting in the 1950's, estimates of genetic parameters such as heritability were reported for different carcass traits by approximately 40 independent research works (Shelby et al., 1955 & 1963; Blackwell et al., 1962; Cundiff et al., 1964; Brackelsberg et al., 1971; Bertrand et al., 2001; Crews and Kemp, 2001; Utrera and Vleck, 2004; Nkrumah et al., 2007; Smith et al., 2007), and the genetic parameters were summarized in Table 1.1. In general, theses studies confirmed the heritability of fat related traits from carcass and ultrasound measurements resides within the range of moderate to high (0.33-0.61), indicating a great potential of genetic improvement on the traits (Table 1.1.).

Along with the heritability of the carcass traits, genetic correlations of carcass traits were also reported in recent studies (Bertrand et al., 2001; Crews and Kemp, 2001; Devitt and Wilson, 2001; Smith et al., 2007) and the estimates were summarized in Table 1.1.. Overall, the genetic correlations between fat deposition and carcass merit traits are ranged from extremely low (r=0.04 bewteen average backfat thickness (AVBF) and carcass marbling score (CMAR)) to very high (r=0.94 between slaughter weight (SWT) and carcass weight (CWT). The low genetic correlation between backfat thickness and carcass marbling score suggests that the genes affecting fat thickness and marbling may be different and it is possible to increase marbling without necessarily increasing the fat depth in beef cattle (Bertrand et al., 1998 & 2001; Fiems et al., 2000). In addition, ultrasound back fat thickness (UBF) from feedlot steers has a high genetic correlation (0.79±0.13) with average backfat (AVBF) from carcass after slaughter (Crews et al., 2003) suggests that ultrasound measures of backfat may be a good indicator of backfat at slaughter. That also supports the hypothesis from Arnold et al. (1991) that the fat thickness in seedstock cattle (UBF) could be an indicator of growth while in slaughter cattle (AVBF) it could be an indicator of maturity (Bertrand et al., 2001). Also, higher genetic correlation between the ultrasound rib-eye area (UREA) and carcass rib-eye area (CREA) (0.71±0.11) (Crews and

Kemp, 2001) and between ultrasound marbling (UMAR) and carcass marbling score (CMAR) (0.68±0.18) (Devitt and Wilton, 2001) have been found. Therefore, due to the higher genetic correlation between ultrasound and carcass traits, it is possible to make genetic progress of carcass traits through genetic selections based on ultrasound measurements (Devitt and Wilton, 2001).

1.2.3. Genetic improvement of fat deposition and carcass merit traits of beef cattle

In livestock industries including the beef cattle, the practices for the genetic improvement of animals began with the development of systems like animal identification, pedigree recording, and performance recording (Garrick and Golden, 2009). Genetic evaluation and selection is a major tool that has been used to improve the performance of economically relevant traits in beef cattle. In the early stage of beef cattle improvement program, selection index was employed to predict genetic merit of a potential parent, and later a best linear unbiased prediction called BLUP was developed and used to predict the genetic merit. Selection index was developed in 1930's and 1940's (Hazel and Lush, 1942) and was implemented as the best linear predictor of the breeding value of an animal, which was set with the primary goal to achieve maximum genetic progress toward a stated economic goal i.e., to improve the performance of economically important traits (Hazel, 1943; Hazel, 1993). However, the assumptions of the selection index i.e., the genetic uniformity of cattle herd and systematic effects can be estimated without errors are seldom true. Therefore, it was later replaced by the BLUP animal model (Henderson, 1963). BLUP successfully accommodated the fixed effects and accounted for the genetic differences between the animal and successfully implemented the animal models that can account for changes in the genetic mean and variance and therefore has been considered as an optimal way to analyze genetic data from populations with artificial selection records (Henderson 1973, 1975, 1984, 1988; Thompson 1979, 1989; Kennedy and Sorenson, 1988; Van Vleck, 1993).

As the computational power increased in the 1990s, BLUP became a standard way to estimate genetic merits for quantative traits in animal breeding. As a result, great genetic improvements have been made for traits that have moderare to high heritbility and are reglaurly measured such as milk production in dairy cattle. However, the progress of the genetic improvements has not been optimal for traits that have a low heritability, such as reproductive traits, for traits that are difficult and/or expensive to measure, such as disease resistance, feed efficiency, and for traits that are measured at a later stage, such as fat deposition and carcass and meat quality traits.

1.2.4. QTL detection and candidate gene identification

Identification of DNA markers assocaited with the traits descibed above holds a great promise to accelerate their genetic improvement rates through integrating DNA markers into the traditional breeding and selection programs, i.e. marker assisted selection or genome selection. In 1990s, search for genomic areas of bovine chromosomes affecting economically important traits in beef cattle was launched. These genomic areas were called as quantitative trait loci (QTLs), which is defined as the chromosomal location of a single gene or group of genes showing a significant association with a complex trait of interest (Beever et al. 1990; Lander and Kruglyak, 1995). In beef cattle, QTLs have been reported in a number of chromosomes for several fat deposition and carcass merit traits, which includes fat depth on BTA 2, 3, 7, 5, 8, 14 ,16, 19 (Casas et al., 2000, 2001 & 2003; MacNeil and Grosz et al., 2002; Moore et al., 2003; Li et al., 2004); marbling score on BTA 2, 3, 4, 5, 6, 8, 9, 10, 13, 14, 16, 17, 18, 23, 26, 27 and 29 (Stone et al., 1999; Casas et al., 2001, 2003 & 2004; MacNeil and Grosz et al., 2002; Kim et al., 2003; Mizoshita et al., 2004; Mizoguchi et al., 2006; Imai et al., 2007; Abe et al., 2008); rib eye area on BTA 12, 14, 19 and 21 (Taylor et al., 1998; MacNeil and Grosz et al., 2002); lean meat area on BTA 2, 4 and 12 (MacNeil and Grosz et al., 2002; Alexander et. al., 2007); hot carcass weight on

BTA 1, 2, 4, 5, 6, 10, 13, 14, 16, 18, 22, 23, 24 and 29 (Casas et al., 2000 & 2003; MacNeil and Grosz et al., 2002; Kim et al., 2003); slaughter weight on BTA 1, 2, 14, 17 and 23 (Kim et al., 2003; Mizoshita et al., 2004). The QTLs that have been reported for economically relevant traits in beef cattle have also been summarized in website databases i.e., http://bovineqtl.tamu.edu. (Polineni et al., 2006) http://www.animalgenome.org/QTLdb/ (Hu et al., 2007). These databases provide important references for searching positional candidate genes under the QTL regions those are the carriers for causative and functional polymorphisms.

With the advantage of robust heterogeneity of DNA markers that reside within candidate genes, and the ability to detect small QTL effects using advacned statstical tools (Craddock et al., 2001; Wu et al., 2005) positional candidate gene association analysis has been commonly used to identify DNA variants of candidate genes under the QTL regions that are associated with the traits of interest. In cattle, a number of positional candidate genes have been evaluated for the traits of interest, which included Metallothionein 2A (MT2A) (Ryan & Womack, 1994; Barendse et al., 1997), Melancortin receptor 1(MC1R) (Klungland et al., 1995; Werth et al., 1996; Barendse et al., 1997), Carboxypeptidase E (CPE) (Konfortov & Miller, 1998), growth hormone 1 (GH1) gene (Taylor et al., 1998), CCAAT/enhancer binding protein, alpha (CEBPA) (Barendse & Fries, 1999), thyroglobulin (TG) (Barendse, 1999; Moore et al., 2003), uncoupling protein 1 (UCP1) (Sonstegard & Kappes, 1999), leptin (LEP) (Buchanan et al., 2002), fatty acid binding protein (heart) 3 (FABP3) gene (Roy et al., 2003), diacylglycerol-O- acyltransferase 1 (DGAT1) gene (Moore et al., 2003; Thaller et al., 2003; Grisart et al., 2004), hormone-sensitive lipase (LIPE), pyruvate dehydrogenase-beta (PDHB) (Haegeman et al., 2003). In addition, QTL mapping is an ongoing task and genes from other species i.e., human, swine etc. which were found associated with a phenotypic trait of interest, has also been evaluated as candidates for similar traits in cattle (Haegeman et al., 2003), such as, caveolin-3 (McNally et al., 1998) and metallothionein 2A (Beattie et al., 1998).

In addition to the positional candidate gene approach, a functional candidate gene approach has also been undertaken to identify genes underlying the expression of economically important phenotypic traits like carcass traits (Kadarmideen et al., 2006). The functional candidate gene association analyses target polymorphisms of genes that have potential functions that cause variations for traits of interest with or without a prior knowledge of QTL regions. For example, mitochondrial transcription factor A (TFAM), which is a nuclear gene and plays an important role in lipid metabolism, was found associated with marbling and subcutaneous fat depth in Wagyu x Limousin cross breed cattle; subsequently, that gene was suggested as a strong candidate gene for obesity in mammals (Jiang et al., 2005). Previous studies indicated that both of the positional and functional candidate gene approaches or the combination of the two methods provided a powerful means to identify gene variants that influence the quantitative traits of interest.

1.2.5. Superiority of SNP as a genetic marker

A single nucleotide polymorphism (SNP) is a source of variance in the genome. As suggested by the acronym, a SNP ("snip") is a single base mutation in DNA with a usual alternative of two possible nucleotides at a given position. SNPs are the simplest form and the most common source of genetic polymorphisms (Vignal et. al., 2002).

There are four major reasons for an increasing interest to use SNPs as DNA markers for genetic analyses. Firstly, they are prevalent and abundant and thus provide more potential markers near or in any locus of interest than other types of polymorphism such as microsatellites. For example, in human genomic DNA there appears to be an SNP approximately every 1000 bases (Landegren et. al., 1998). In cattle, about 2.2 million SNPs have been reported so far, which yields approximately 1 SNP per 1300 bases. Secondly, some SNPs are located in coding regions and may directly affect secondary structure of mRNA (Nacley et al., 2006) or substitute amino acids during protein synthesis. Thirdly, SNPs are more stably inherited than microsatellite markers, making them more suited as DNA markers for long term selection purposes. Finally, SNPs are more suitable than microsatellites for high throughput genotyping.

Genome-wide linkage scans tend to employ high density maps of SNPs because both the theoretical and simulation studies (Goddard and Wijsman, 2002; Evans and Cardon, 2004), as well as real data application (John et al., 2004), indicate that SNPs can achieve a superior power to detect and localize linkages (Chao et al., 2005) in comparison to other makers. All these characteristics of SNPs made it suitable DNA variant for association analyses of quantitative traits in beef cattle.

The key properties of SNPs can be summarized as below which made them as a promising marker tool for linkage and association analyses.

- ➢ SNPs usually contain two alleles per marker. It has only one locus containing two bases.
- ➢ SNPs are more abundant throughout the genome (Approx. 1 per 1000 base pairs in human) (Landegren et. al., 1998) in comparison to other markers.
- ➢ Two mutation mechanisms are found for SNPs

  ----Transitions : A transition substitution occurs within purines i.e., adenine (A), guanine (G) (A<=> G alternatively called R) or within pyrimidines i.e., cytosine (C), tyrosine (T) (C<=>T alternatively called Y).

  ----Transversions : A transversion substitution occurs between a purine and a pyrimidine. (purine<=>pyrimidine; A<=>T (W), A<=>C (M), G<=>C (S), G<=> T (K)).
- ➢ SNPs can be classified on nature of affected nucleotide.

----Noncoding SNP : This type of SNPs are found in the 5′ or 3′ nontranscribed region (NTR) or in promoter binding sites (can affect specific promoter binding or alter it so that other promoter can bind), 5′ or 3′ untranslated region (UTR) of mRNA, intron, or intergenic region of a chromosome.

----Coding SNP : A SNP in a coding region are named based on their activity on protein synthesis. One is called non-synonymous or missense or non-conservative polymorphism (change the amino acid on protein) and the other called synonymous or conservative polymorphism or silent mutation (don`t change the amino acid within protein but may affect secondary structure of mRNA).

- ➢ More stable inheritance pattern than other markers with very low mutation rate of 1×10^{-9} (Martinez-Arias et. al., 2001).

- ➢ Suitable for high throughput genotyping using DNA microarray technologies. High-throughput SNP genotyping is the process of quickly and cost-effectively identifying the SNP values in as many different individual genomes as possible.
- ➢ Genotyping accuracy is very high (Havill and Dyer, 2005) in comparison to other DNA variants (no creation of false allele and easy to determine size). Moreover, SNP genotyping is easily automated, cost effective with a low error rate (Kennedy et. al., 2003).

- ➢ Estimating the gene position using SNPs is far less biased than using the usual panel of microsatellites (biases of 0-2 cM for SNPs vs. 8.9 cM for microsatellites). Using dense maps of SNPs in linkage analyses is more powerful and less biased than using the 10 cM maps of microsatellites (Jeremie et al., 2005).
- ➢ SNPs have greater linkage information content by creating local haplotypes of SNPs that function as “super alleles” and SNP panels provide sufficient meiotic information for linkage analyses (Daniel et. al., 2004).

In summary, SNPs at the 5′near gene region exposed to promoters and other transcriptional regulators and likely are the first choice for association analyses. Depending on the presence of alternative alleles, the SNP locus may affect the rate of transcription which can even be tissue specific for different breeds of cattle (Maj et al., 2009). It is evident in several studies that one allele of SNP creates a binding site for the transcription factor which may disrupt in case of other, i.e., A allele of somatostatin (SST) SNP g.447A>G provides a binding site for myocyte-specific enhancer factor 2A (Morsci et al., 2006), "A" allele of pro-melanin-concentrating hormone (POMC) SNP g. −134A>T provides a binding site for transcriptional repressor, adenovirus E4 promoter binding protein (E4BP4) (also known as NFIL3) (Helgeson et al., 2008). Also, some SNPs may be responsible for loss or gain of binding sites for many transcription factors or transcription regulatory elements, for example, SNP c.−1220C>A and c.−1212C>T result a discrepancy of binding sites of tal-1α/E47 heterodimer, cAMP-responsive element binding protein 1, heterodimers of the bHLH transcription factors HAND2 and E12, nuclear factor 1, RAR-related orphan receptor α1, zinc finger protein RP58 in mitochondrial transcription factor A (TFAM) (Jiang et al., 2005) and adinopectin (ADIPOQ) SNP g.1596G>A is located in the initiator element of the type II promoter, which is binding site for transcription factor TAF_{II}150 and TAF_{II}250. The ADIPOQ mutation was predicted to affect the transcription factor complex (Morsci et al., 2006). For all the above mentioned SNPs of SST, POMC, TEAM, ADIPOQ genes, it was found that they were significantly associated with one or more fat deposition related carcass traits (Table 1.2.). Therefore, the SNPs of the promoter binding site area of a gene should be included in priority for association studies if the allelic alternation affects transcription factor binding sites.

Next to the promoter region of a gene, 5′ untranslated region (UTR) is considered as a major site for translational regulation. In many cases, internal ribosome entry sites (IRESs) and upstream open-reading frames (uORFs) are found in this area of a gene (Pickering and Willis, 2005). In human gene studies, it was found that mutations in the 5′UTR area may have a profound impact on cellular functions, (Velden and Thomas, 1999; Cazzola and Skoda, 2000). The first study of 5′UTR SNP c. −537C>T of thyroglobulin (TG) in beef cattle revealed significant association with carcass marbling in Angus, Shorthorn and Wagyu cattle (Barendse et al., 1998). Later, 5′UTR SNPs c.−4241A>T of growth hormone releasing hormone (GHRH) (Cheong et al., 2006) SNP c.−292C>T of insulin-like growth factor 2 (IGF2) (Goodall & Schmutz, 2007; Sherman et al., 2008) were found to have significant associations with carcass weight (CWT) carcass rib eye area (CREA) and ultrasound backfat (UBF), ultrasound marbling (UMAR), respectively. Indeed, the mechanisms behind these associations could be the direct impairment of translational regulations or be linked with the causative SNP, which is subject to further functionality analyses. Also, the encouraging findings of association studies suggest that more SNPs from the 5′UTR area of different genes should be included for future association studies.

Obviously, it is plausible that SNPs causing amino acid substitution can directly affect the protein structure and functional variations of the protein that could have significant effects on the phenotypic traits. Supported by this hypothesis, missense SNPs were taken for association studies for traits of interest in beef cattle by many scientists (Buchanan et al., 2002, 2005 & 2007; Thaller et al., 2003; Nkrumah et al., 2004; Kononoff et al., 2005; Schenkel et al., 2005 & 2006; Barendse et al., 2006; Stasio et al., 2007; Cho et al., 2008; Esmailizadeh et al., 2008), and SNPs of eight different candidate genes have been reported to have associations with body fat deposition and carcass merit traits including, ultrasound rib eye area (UREA), final weight (FWT), hot carcass weight (HCW), average backfat thickness (AVBF), lean meat yield (LMY) and carcass marbling score (CMAR) etc (Table 1. 2). Interestingly, for most of the nonsynonymous SNPs, the association was versatile covering different traits (Table 1.2.), which also in many cases supports the correlation of the carcass traits as well as the pleiotropic action of the candidate genes. As an example, SNP C73T in Exon2 of leptin gene reported to have significant association with eight different carcass traits in six different cattle breeds. In an investigation by Buchanan et al, (2002), it was revealed that the allele of SNP C73T was associated with the mRNA concentration in blood, which may be an indication of functionality of a nonsynonymous SNP. Undoubtedly, more missense SNPs should be screened through association studies to detect functional candidate genes for carcass traits in beef cattle.

Synonymous SNPs are very frequent throughout the cattle genome but next to intronic SNPs in number. Apparently nonfunctional attribute made these SNPs less likely to be chosen for association studies. However, in spite of the unknown effect on the gene function, some association studies used intronic as well as synonymous SNPs as markers and highly significant associations with several carcass traits, i.e., UMAR, HCW, AVBF, LMY, CMAR, yield grade were observed in different cattle breeds (Buchanan et al., 2005; Cho et al., 2008; Sherman et al., 2008; Tian et al., 2007). Linkage of the SNP genotypes with the functional SNPs of the same or other candidate genes was the most popular explanation of the association events of synonymous SNPs and intronic SNPs. However, recently, it was discovered that the allelic variation in synonymous SNP locus can alter mRNA secondary structure and modulate protein expression (Nacley et al., 2006). Also, tissue specific expression of functional intron has been reported in human gene studies (Guilloux et al. 1996), implying that the huge intronic genetic area, flanking the exons of a gene may have significant contributions at the biological level, yet to be identified.

Lastly, the SNPs of the 3′UTR of a candidate gene is considered as valuable DNA markers for association studies because of the allelic discrimination that could provide possible binding sites for micro-RNAs and subsequently the interference on protein production can occur following mRNA degradation. In Texel sheep, a guanine (G) to adinine (A) transition in the 3′UTR of the myostatin (GDF8) gene that potentially creates a target site for mir1, mir206 and microRNAs (miRNAs) , which are highly expressed in skeletal muscle, showed a significantly association with muscular hypertrophy (Clop et al., 2006). In Korean native cattle, a SNP c.2151*479C>T at 3′UTR was found associated with carcass marbling score (Cheong et al., 2008). Also, in TG gene, 4 SNPs from 3′flanking region was found to significantly affect carcass marbling in different cattle populations (Gan et al., 2008).

Overall, polymorphisms from any region of a gene might have associations with phenotypic traits. However, to properly explain the association as a phenomenon at the physiological and biological level it is necessary to discern the functional SNPs from non-functional ones. Therefore, for association analyses, the priority should be given to SNPs that could potentially influence gene transcription, translation and/or amino acid distribution on the synthesized protein.

1.2.6. Candidate genes-SNPs association analyses with fat related carcass merit traits in beef cattle

1.2.6.1. Single SNP association

In beef cattle, many studies have been conducted so far to assess associations between SNPs within candidate genes and economically relevant traits, and significant associations of gene specific SNPs with many fat related carcass merit traits were reported. By summarizing candidate gene-specific SNPs associated with carcass merit and fat related carcass traits in different beef cattle breeds that have been reported so far, it was found that 40 different SNPs of 26 candidate genes have been associated with 17 different fat deposition and carcass merit traits in 14 different cattle breeds have been reported in 31 different single SNP association studies (Table 1.2.).

In total, 15 gene-specific SNPs of 10 candidate genes including ADIPOQ (Morsci et al., 2006), CRH (Wibowo et al., 2007), FABP4 (Cho et al., 2008), LEP

(Buchanan et al, 2002 & 2007; Kononoff et al., 2005; Nkrumah et al., 2004; Schenkel et al., 2005 & 2006; Stasio et al., 2007), MSTN (Esmailizadeh et al., 2008), PMCH (Helgeson et al., 2008), TFAM (Jiang et al., 2005), TG (Casas et al., 2005), UCN3 (Jiang et al., 2008) and UCP2 (Sherman et al., 2008) have been identified to have significant associations with average backfat thickness in Angus, Charolais, Hereford, Korean native cattle and Simmental beef cattle populations (Table 1.2). Additionally, SNPs under the gene region of IGF2 (Goodall and Schmutz, 2007; Sherman et al., 2008) and LEP (Nkrumah et al., 2005) has been found associated with the ultrasound backfat thickness in hybrid cattle populations.

Likewise, 18 gene-specific SNPS from 12 candidate genes i.e., CAPN1 (Cheong et al., 2008), CRH (Wibowo et al., 2007), DGAT1 (Thaller et al., 2003), FABP4 (Park et al., 2006), GH1 (Barendse et al., 2006), LEP (Stasio et al., 2007), NPY (Sherman et al., 2008), SST (Morsci et al., 2006), TFAM (Jiang et al., 2005), TG (Barendse, 1999; Thraller et al., 2003; Gan et al., 2008), UCN3 (Jiang et al., 2008) and UCP3 (Sherman et al., 2008) have been found associated with carcass marbling score in different cattle breeds including Angus, Blonde d'Aquitaine (Italian bulls), Brahman, Charolais, Hanwoo, Hereford and hybrid etc. cattle populations (Table 1.2). Moreover, some of these genes along with the other genes also have associations with other fat related carcass traits, such as, SNP c.−292C>T of IGF2 is associated with CREA (Goodall and Schmutz, 2007); SNPs g.1431C>T , g.1596G>A and g.2606T>C of ADIPOQ (Morsci et al., 2006) and SNP C22G in Exon1 of CRH (Buchanan et al., 2005) are associated with UREA ; SNPs E2JW & E2FB of LEP (Schenkel et al., 2005 & 2006), c. −537C>T of TG (Casas et al., 2005), SNP2 of UCP3 (Sherman et al., 2008) are associated with LMY ; SNPs c.73+67G>C in FABP3 (Cho et al., 2008), c.−4241A>T in GHRH (Cheong et al., 2006), g.1069C>G in MC4R (Buchanan et al., 2005), g.433C>A in MSTN (Esmailizadeh et al., 2008), g.254C>T in POMC (Buchanan et al., 2005) are associated with HCW in different beef cattle populations (Table 1.2).

Among the SNP associations reported, 22 single SNPs from 15 candidate genes were found to have significantly effects on multiple fat deposition and carcass merit traits. As an example, in spite of very low genetic correlation between backfat thickness and marbling score of beef cattle, SNPs of 5 candidate genes (FABP4, LEP, TFAM, TG, UCN3) were identified to have effects on both the backfat thickness and marbling score (Table 1.2) All these single SNPs association analyses results suggest that the fat deposition and carcass merit traits are parhaps controlled by the multiple genes and can be regarded as complex traits. Consequently, the single SNPs under the gene region may have effects on more than one trait as well as different SNPs of a single gene can be significantly associated with one or more traits. Overall, identification and characterization of genetic markers like gene specific SNPs can facilitates the association analyses of candidate genes with body fat deposition and carcass merit traits across different beef cattle populations. Therefore, to improve beef cattle carcass traits through the implementation of marker assisted selection, more and more gene specific SNPs from candidate genes must be identified and verified for their associations with fat deposition and carcass merit traits in beef cattle (Cheong et al., 2006).

1.2.6.2. Haplotype association

1.2.6.2.1. What is haplotype and why the haplotype association is needed?

The specific set of alleles observed on a single chromosome, or part of a chromosome, is called a haplotype (The International HapMap Consortium, 2003).

It is likely that, the haplotypes explicitly incorporate genetic information provided by the multiple SNPs of a candidate gene and could be more informative in comparison to a single SNP (Judson et al., 2000; Judson and Stephens, 2001; Zhang et al., 2002; Garner and Slatkin, 2003; The International HapMap

Consortium 2005, Hayes et al., 2007). Therefore, the attempt to locate the haplotype blocks on the BTA chromosomes, and underlying genes, has proved to be very useful to detect important genetic regions linked with traits of interest (Morsci et al., 2006). Additionally, the construction of haplotypes could reveal the localized LD pattern which in turn also could be effective to identify haplotype interference on the secondary structure of mRNA (Wibowo et al., 2007) as well as gene expression.

In beef cattle, gene specific SNPs from different genes and also non-functional genomic SNPs were used to construct haplotypes for association studies with fat related carcass traits in beef cattle populations. Haplotype association analyses studies facilitated the detection of candidate genes and/or chromosomal regions affecting beef cattle body fat deposition and carcass traits (Thraller et al., 2003; Moore et al., 2003; Stone et al., 2005, Cheong et al., 2006). As an example, to find out candidate genes for fat traits in hybrid beef cattle, Stone et al. (2005) analyzed haplotypes based on seven SNPs (db38340689, db38340690, db38340691, db38340692, db38340805, db38340806, db38340810) from three positional candidate genes HEM1 (hematopoietic protein 1), PDE1B (phosphodiesterage 1B) and NOL1 (Nuclear antigen 1) and found significant haplotype associations with traits related to carcass fat, i.e., fat thickness, rib fat, predicted fat yield, and yield grade. Theses SNPs spaning the haplotypes covered a wide range of area from BTA 5 (approximately 30cM to 113cM) which also harbours many other positional and functional candidate genes i.e., IGF1 (Li et al., 2004) and PMCH (Helgeson et al., 2008) for subcutaneous fat deposition.

Some haplotypes on several positional and functional candidate genes were found to have significantly effects on fat deposition and carcass traits in different beef cattle populations. Backfat thickness (AVBF) and whole body fat deposition were found to be significantly affected by haplotypes AGTC (comprising of alleles from SNPs c. −1557C>A, c. −823G>A, 21T>C, c.40G>C) of candidate gene FABP3 (Fatty acid binding protein 3) (Cho et al., 2008) in Hanwoo cattle and CC (produced by SNPs c.−1220C>A and c.−1212C>T) of TFAM (mitochondrial transcription factor A) (Jinag et al., 2005) gene in Wagyu x Limousin crossbred cattle, respectively. Also, haplotypes GGGG and CCGG (reconstructed by SNPs g.9657C>T, c.10718G>C, c.10841G>A and c.10936G>C) of CRH (corticotrophin releasing hormone) was found significantly associated with subcutaneous fat depth in Wagyu x Limousin crossbreed cattle populations (Wibowo et al., 2007).

Likewise, the haplotypes of TFAM was significantly associated with the variation in marbling in the Wagyu x Limousin crossbreed cattle population (Jiang et al., 2005). Additionally, the leptin gene haplotype CCTT (by SNP UASMS1, UASMS2, E2JW and E2FB) had associations with lean meat yield (LMY) and grade fat (GF) which were detected by Schenkel et al., (2005) in commercial hybrid cattle populations. Lastly, haplotype ATACAC reconstructed by SNPs c. −4241A>T, c. −3195T>A, c. −618T>A, c.114C>A, c.2042A>G, c.2279C>T within the candidate gene GHRH (growth hormone releasing hormone) was detected to have a significant association with the longissimus muscle area in Korean native cattle population (Cheong et al., 2006).

In consideration of these evidences, haplotype association analyses could be as effective as single SNPs association and sometimes can be more explanatory providing the historical recombination information of a cattle population. So, selection decision can be made using haplotype structures of candidate genes to upgrade beef cattle carcass traits (Henderson et al., 2005; White et al., 2005). Recently, 50K SNP markers has been genotyped spanning the whole bovine genome under the action of “International Bovine HapMap Project”, which likely will facilitate to identify the founder haplotype blocks across different cattle populations and to infer the signature of selection as well as domestication (Van Tassel et al., 2008; Bovine HapMap Consortium, et al. 2009). Therefore, construction of haplotype blocks using gene specific SNPs could effectively be used to narrow down the haplotype search at the individual candidate gene level which could accelerate haplotype association analyses to reveal the genes associations with fat related carcass merit traits in beef cattle populations.

1.3. Scope of research and statement of objectives

In recent years, significant progress of QTL identificantion and fine mapping has provided appropriate references to search for causative DNA polymorphisms for the quantitative traits of interest including fat deposition related carcass merit traits in beef cattle. Also, more than 23,000 genes have been reported to reside within in bovine genome (www.ncbi.nlm.nih.gov/sites/entrez) and more progress of the bovine gene annotation is expected (http://www.hgsc.bcm.tmc.edu/projects/bovine/). Additionally, the Human genome project reported and characterized many genes which appear in the bovine genome and may play similar roles in beef cattle phenotypic development and yet to be analyse (Tabor et al. 2002). All these genomic information could facilitate the candidate gene approach to further search for the functional genetic markers which also could play significant roles in major metabolic processes. Although some gene specific SNPs have been identified and reported to have associations with fat deposition and carcass merit traits in beef cattle, many more SNPs are needed to be identified for their associations with the traits and the associations also need to be verified to solve the mistry behind the genetic control of body fat deposition and carcass merit traits of beef cattle.

Notably, most of the previous SNP association studies used one single cattle population, and most of the studies were performed using hybrid cattle population (Table 1.2.). However, cattle breeds are biologically and physiologically distinct, such as, continental breeds, including Charolais and Simmental, are leaner than their British (Angus and Hereford) counterparts. In contrast, British breeds are early maturing with more subcutaneous fat depth (Gregory et al., 1994; Helgeson et al., 2008). Also, due to hybrid vigour and complementarity (Hickman, 1991; Marshall, 1994) hybrid cattle may have diversified body composition with intensified polygenic effects behind the carcass composition and body fat deposition which may provide advantageous background for marker discovery through association analyses of candidate genes. Therefore, it is worthwhile to include different cattle populations i.e., hybrid and purebred to identify and validate SNPs associated with fat deposition and carcass merit traits in different beef cattle populations before the implementation of these SNPs in marker assisted selection program (Dekker, 2004).

Therfore, the objectives of the current study are:

i. To compile and discover SNPs underlying gene specific regions of positional and functional candidate gene(s) for fat deposition and carcass merit traits.
ii. To examine the associations between the gene SNPs and fat deposition and carcass merit traits in experimental beef cattle populations.
iii. To evaluate haplotype blocks within a gene and to assess the haplotype effects on fat deposition and carcass merit traits in experimental beef cattle populations.

2. Chapter Two: Materials and Methods

2.1. Animal Resources

The present study used one hybrid and two purebred beef cattle populations from two different locations of Alberta, Canada. All animals were managed according to the guidelines established by the Canadian Council of Animal Care (CCAC, 1993).

The two purebred populations include 206 Angus steers of 18 sires and 187 Charolais steers of 19 sires from the Onefour Research Substation of the Agriculture and Agri- Food Canada Research Centre at Lethbridge. The environment at the Onefour site is mentioned as semi-arid short grass prairie system (Crews and Kemp, 2001). The calves of the purebred animals were born between late February and mid-May in calving year 2004 and 2005. The parentage identification of the animals sire was recorded based on the artificial insemination (AI) of the dam while the maternal parentage identification was recorded at birth. To identify each animal under the experiment, they were assigned an ear tag number such as, A001P or C001R which was formatted as A/C=Angus/Charolais, 001=sequence number of animal at birth, and P/R= letter assigned indicate a specific year of birth. All animals were assigned a 9 digit identification number starting with the year of birth (first four digits) to be included in the respective association databases, e.g., Angus for the Canadian Angus Association and Charolais for the Canadian Charolais Association. Subsequently, the pedigree history was tracked following the sire and dam’s identification and registration numbers from both of the cattle association databases. For Angus, 9 generations pedigree were available where the oldest animal was dated back to the year 1964 and for Charolais, 6 generations pedigree were available including the oldest parent dated back to the year 1959. Typical postweaning ration made of alfalfa hay and rolled barley range cube were provided and animals had free-choice access to water and mineral supplements at the postweaning period. Later, at the feedlot of Lethbridge Research Centre (LRC) animals were fed a background ration followed by a finishing ration till to the endpoint, when the animals were transported to commercial slaughter house and were processed. According to Crews and Kemp (2001) at LRC the composition of the background diet consists of 80% barley silage, 17.5% steam-rolled barley and 2.5% mineral supplement whereas, finishing diet contains 39% barley silage, 60.3% rolled barley and 0.7% mineral mix.

The hybrid population consisted of 463 steers of 88 sires from the University of Alberta Kinsella Research Station. The population has been previously described by Nkrumah et al., (2007). The sires for the population were Angus, Charolais or Hybrid bulls of the University of Alberta and the dams were produced over more than 10 years by crossing three composite lines, namely Beef synthetic 1 (33% angus and Charolais, 20% Galloway and 47% other beef breeds), Beef synthetic 2 (60% Hereford and 40% other beef breeds), Dairy Beef Synthetic (approximately 60% Holstein, Brown Swiss/Simmental, and approximately 40% other beef bred) (Goonewardene et al., 2003). A multiple-sire breeding system was used and the animals were born in three consecutive years of 2002, 2003 and 2004. The sire of each animal was identified later based on a panel of microsatellite markers. Pedigree of this population was available for only one generation. The typical postweaning diet was followed by the background diet at feedlot which was composed of alfalfa-brome hay with oats and supplemented with corn grain and feedlot mineral supplement. This diet followed by test diet with an interval of 30 days adjustment period while the final composition was 64.5% barley grain, 20% oat grain, 9.0% alfalfa hay pellet, 5.0% beef feedlot supplement, and 1.5% canola oil, supplying 14.0% CP and 2.91 Mcal/kg of ME, on a DM basis (Nkrumah et al., 2004 & 2007). The author has not performed the maitainance and collection of the phenotypic data from any of the animal populations.

2.2. Phenotype data

We analyzed in total, 10 ultrasound and carcass measurement traits, which includes ultrasound backfat (UBF), ultrasound rib-eye area (UREA), average daily gain of ultrasound backfat (AUBF), average daily gain of ultrasound rib-eye area (AUREA), slaughter weight (SWT), carcass weight (CWT), average backfat (AVBF), carcass rib-eye area (CREA), lean meat yield (LMY) and carcass marbling score (CMAR), respectively.

Ultrasound measurements were taken for the amount of fat thickness and longissimus muscle area between the 12-13th ribs for the traits UBF and UREA, respectively. Aloka 500V real-time ultrasound with a 17cm, 3.5-MHz linear array transducer (Overseas Monitor Corp. Ltd., Richmond, British Columbia, Canada) (Nkrumah et al., 2004, 2005) was used for hybrid and Aloka SSD-1100 Flexus real-time ultrasound unit (Aloka Co. Ltd., Tokyo, Japan) was used for Angus and Charolais populations to collect ultrasound data (Crews and Kemp 2001). Ultrasound measurements of traits (UBF and UREA) were conducted every 28 days during the feedlot tests while the BIF guidelines (BIF, 1996) were followed for ultrasound scanning and image analyses. Final UBF, UREA as well as AUBF and AUREA, which were obtained by regression analyses of ultrasound measurements upon time (day), were analysed in this study. SWT was measured as the live weight before slaughtering the animal. The average kill-age of the hybrid, Angus and Charolais cattle breed were 390, 450 and 437 days, respectively.

Carcass data was collected 24 hours postmortem. While evaluating carcass traits, the Canadian beef carcass grading system (Agriculture Canada, 1992) was followed, which also meet Canadian meat industry carcass measurements. In brief, CWT was measured as the weight from the left and right half of the carcass. AVBF and CREA were measured at the 12th to 13th rib interface over the longissimus muscle area. For LMY, which is an estimate of saleable meat measured as LMY%=57.96 + (0.202 × CREA) – (0.027 × CWT) – (0.703 × AVBF) (Jones et al., 1984; Nkrumah et al., 2004). Lastly, CMAR was measured as visible intramuscular fat content, following the Canadian beef grading system in a scale of “A”, “AA”, “AAA” and “Canada Prime” (Nkrumah et al., 2007). However, later we converted the marbling score to the United States Department of Agriculture (USDA) numerical scores (Table 2.1.). Canadian standards consider muscling, color and fat thickness for the four grades to assign during carcass evaluation, whereas, the USDA system are weighted and one factor may compensate for a deficiency in another factor, the Canadian system allows no “quality attribute offsets” (BIF, 1996, Appendix 3.2, pp. 121-122). As an example, the average marbling score of USDA, which is termed as “low USDA choice” (score 5 to < 6) correspond to the Canadian “AAA” grade (Crews and Kemp, 2001) as well as “high USDA choice” (score 7 to < 8). Thus, the USDA system accounts for variation in the degree of marbling, which may be useful to detect the CMAR for trait variation within animals more effectively.

For hybrid steers, carcass data were available for only 381 animals. But ultrasound measurements were available for all the steers in the same population. Both the ultrasound and carcass merit data were available for all of the steers in Angus and Charolais bred. A summary of phenotypic data is given in Table 2.2. In addition, a 10 ml blood sample was collected and preserved by venipuncture for each steer during the feedlot tests for subsequent genotyping analyses.

2.3. Animal genotyping

2.3.1. Selection of candidate genes.

We selected candidate genes based on the literature search, gene position under the QTL and their reported function in cattle body metabolism. In total 9 positional and functional candidate genes, i.e., ACSF3, FABP3, FASN, GPAM, IDH1, IGF1, INS, LIPE and OLR1 were selected from different bovine chromosomes (BTA), i.e., BTA2 (FABP3), BTA5 (IGF1), BTA18 (ACSF3), BTA19 (FASN), BTA26 (GPAM) and BTA29 (INS). The six candidate genes (FABP3, FASN, GPAM, IDH1, IGF1 and INS) were located under the QTL region for fat deposition and carcass merit traits in beef cattle and they also have functional significance in body metabolism. The other three candidate genes (ACS, LIPE and OLR1) were well known for their participation in body metabolism in cattle as well as in human and were described previously as fat related functional candidate genes in many species, i.e., cattle, human, pig etc (www.ncbi.nlm.nih.gov/sites/entrez) (KEGG metabolic pathways-www.genome.jp). The candidate genes name, corresponding BTA chromosomal position, their public database accession number, positional or functional candidacy status are given in the Table 2.3.

2.3.2. SNP identification and genotyping.

DNA samples were prepared using a QuickGene DNA whole blood kit S (DB-S; Intermedico, Markham, Canada) from blood samples collected from each animal. A SNP discovery steer panel was constructed consisting of 8 pair of half-sib steers on the basis of low-high values of fat traits from purebred Angus and Charolais populations. This panel of 16 animals was used to discover new SNPs and confirm previously reported SNPs within the gene-specific region of the selected genes. By direct sequencing of PCR products following a big-dye sequencing protocol in ABI 3730 DNA analyser (Applied Biosystems Inc., CA, USA) using primers that were designed based on the gene sequences, and by comparing these sequences among the steers in the panel, 14 new SNPs were discovered in house from the selected 9 gene regions (Table 2.4). Additinally, we have compiled another 23 SNPs that were previously reported in the public databases or journal articles (Table 2.4.) for further genotyping. In total, 37 gene SNPs were genotyped for the 9 genes (SNP name and location, accession no. in database or reported authors name, positional and/or functional information is provided in table 2.4.). Ten SNPs (Table 2.4.) were genotyped by a PCR-RFLP method using appropriate primers (Table 2.5) that were designed in-house and supplied by Invitrogen (Invitrogen Corporation, Carlsbad, CA, USA). The PCR reaction mixture included 2.5 µl 10x buffer, 1.5 µl 25mM $MgCl_2$, 2 µl 2.5mM dNTPs, 1.25 µl 5µM primer mix, 0.2 µl Amplitaq gold, 1.25 µl PCRx, 11.3 µl H_2O, 5 µl 2.5 ng/µl DNA template A touch down method was used for DNA amplification which consisted of 95°c, 5mins.; 12 cycle of 3 temp 94°c 35sec, 61°c−55°c 30sec, 72°c 30sec; 25 cycle of 3 temp, 94°c 30sec, 55°c 30sec, 72°c 30sec; 72°c 7mins., 4°c ∞ for SNPs except the c. −397T>C SNP in INS gene, where the primer annealing temperature was 65°c (95°c, 5mins.; 37 cycle of 3 temp, 94°c 30sec, 65°c 30sec, 72°c 30sec; 72°c 7mins., 4°c ∞). Eight different restriction enzymes (Table 2.5.) were used according to the protocol supplied by the manufacturer (New England Biolabs, Pickering, Canada) for restriction digestion of the amplified fragments for SNP genotyping. Agarose gels ranging from 1% to 4% were prepared using 0.5xTBE buffer to separate the restriction enzyme digested fragments. The images of the gels were analyzed and the genotypes were determined considering allele “cut” versus “uncut” DNA bands by restriction digestion. Three SNPs (Table 1) were genotyped by using Step One RT-PCR system (Applied Biosystems Inc., CA, USA). The TaqMan® Genotyping Master Mix and primers were designed and supplied by Applied Biosystems based on the SNP sequences using the allele discrimination method. Genotypes of animals were displayed and called based on the intensities of the FAM and VIC dyes. Seven SNPs from LIPE gene were genotyped directly by sequencing using the Big Dye DNA sequencing protocol and the 3730 DNA analyser (Applied Biosystems Inc., CA, USA). All PCR-RFLP, RT-PCR and sequencing genotypes were checked by a second person to make sure the genotypes were accurately called and recorded for each animal. The author performed the genotyping of 20 SNPs through the above mentioned protocols by himself. While the remaining SNPs (17) were genotyped using the Illumina GoldenGate assay on the Beadstation 500G genotyping system (Illumina Inc. San Diego, CA, USA) and the author participated in the process of genotyping along with the other members

of the research group. In addition 3 SNPs that were previously genotyped using the PCR-RFLP and DNA sequencing techniques were also genotyped using the the Illumina GoldenGate assay as positive controls. It was found that the genotypes determined by the the Illumina GoldenGate assay were verified with an accuracy> 99%.

2.4. Statistical Analyses.

2.4.1. Single SNP association analysis by ASREML

Associations between individual SNPs and the 10 ultrasound and carcass traits were examined separately for each population by fitting the following mixed linear regression model or animal model (Henderson, 1984, 1988; Kennedy et al.,1992) using ASReml (Gilmour et al., 2000):

$$y = Xb + Za + e$$

Y is the vector of phenotypes for the trait analysed; X is the design matrix for fixed effects; and b is the vector of coefficients of the regression on the fixed effects including the SNP effects. For the hybrid population, other fixed effects included feedlot test batch over 3 years (six levels) and breed (three levels by breed of sire as Angus, Charolais and Hybrid). For the Angus and Charolais populations, other fixed effects included the feedlot test batch over 2 years (eight levels). Z is the incidence matrix for the random animal effects and a is the vector of the polygenic effects, and e is the vector of residuals. For the proposed animal model, the expectation of the random vector E(a) and residual error E(e) are equals to 0 [E(a)=E(e)=0], so, the expectation of the model is, E(y) = Xb and $Var(y) = V = ZAZ' + I\sigma^2_{e.}$ The model assumes distributions as: $y \sim N(Xb,V)$, $a \sim N(0, A\sigma^2_g)$ and $e \sim N(0,I_e\sigma^2_e)$, where, A is the additive genetic relationship matrix, σ^2_g is additive direct genetic variance (contributed by a) and σ^2_e is residual error variance (contributed by e) with identity matrix (I_e). One, nine and six generations of pedigree information were incorporated in the model to construct A matrix for hybrid, Angus and Charolais populations, respectively.

To perform analyses in ASReml, the three SNP genotypes were coded as 0, 1 and 2, respectively and the SNP allele substitution effect was estimated via the regression analysis. The additive effect and dominance effects were estimated by subtracting the solution for the one homozygous genotype from that for the other homozygous genotype and by subtracting the average of solutions for homozygous genotypes from that of heterozygous genotypes, respectively (Falconer and Mackay, 1996). To adjust the animal's age effect, animal age at slaughter was included in the model as a linear covariate. In the absence of a SNP homozygous genotypes for one allele, we didn't calculate additive and dominance effect. However, additive effects were estimated in the absence of the heterozygous genotype of a SNP under test.

2.4.2. Haplotype association analyses

2.4.2.1. Haplotype blocks identification by HAPLOVIEW

A haplotype is defined as two or more linked marker allele on a chromosome (Zhao et al., 2003; Schaid, 2004). Linkage between markers canbe explained by the linkage disequilibrium (LD), which is a non-random allelic association and statistically is defined as the correlation coefficient between the pairs of SNP loci denoted by the r-square value (Hill and Robertson, 1968). Recent advancement in the Human Hapmap Project emphasized on the local linkage disequilibrium measurement of SNPs to identify the SNPs alleles that may inherited together, forming a common haplotype pattern, also called haplotype blocks (Daley et al., 2001; Patil et al., 2001; Zhang et al., 2002; Schulze et al., 2004; http://www.genome.gov/10001688). This haplotype blocks contain SNP alleles with less diversity following the population-wise common arrangement at the chromosomal level. Haplotypes blocking likely provides information about the historical recombination pattern of SNP alleles as well as it may be informative for genome-wise meiotic recombination hot spots detection (Gabriel et al., 2002; Wang et al., 2002; Stumpf and Goldstein et al., 2003). To predict the haplotype blocks and structures, we used the software HAPLOVIEW (Barrett et al., 2005). The hybrid, Angus and Charolais SNP genotypes were used to construct gene specific input file, where sire based half-sib family was analyzed and only one generation pedigree was added for each population with the parent SNP alleles as missing value. The pair-wise SNP LD values were calculated as r^2. These r^2 values (0—1) were determinants, whether the pairs of SNPs genotypes are in weak or strong LD with each other. To partition the haplotype blocks, the software used multiple block definitions (Gabriel et al., 2002; Wang et al., 2002). The software also calculated general status information of SNP alleles, i.e., Herdy-Weinberg Equilibrium (HWE) p-values, observed heterozygosity (OHET) of a SNP and minor allele frequencies from SNP genotypes. Consequently, haplotype blocks at the population level. The haplotype blocks were used to predict haplotypes structures at the next step of our analyses.

2.4.2.2. Haplotype reconstruction by HAPLORE

Following the LD and haplotype block analyses by HAPLOVIEW, HAPLORE was used to reconstruct haplotypes for each animal in the population. HAPLORE (Zhang et al., 2005) is capable to reconstruct haplotypes using SNP genotypes when general pedigrees are available and reportedly, outperform some contemporarily used software for haplotypes reconstruction (Zhang and Zhao, 2006). Animal haplotypes within the haplotype blocks that were identifed using HAPLOVIEW as well as haplotypes spanning the haplotype blocks were constrcuted for each gene using HAPLORE via the haplotype-elimination algorithm. This haplotype-elimination algorithm provides likelihood of haplotypes in a population with general pedigree where haplotypes can be treated as an allele at a single locus (Lange and Weeks, 1989; O’Connell, 2000; Cox et al., 2002). Additionally, the haplotype-elimination algorithm in HAPLORE is guaranteed to exclude all inconsistent haplotypes (Zhang et al., 2005).

2.4.2.3. Haplotypes random effect test

SNP haplotypes for each gene were treated as alleles and their random effects on the fat deposition and carcass merit trait were examined using the likelihood-ratio (LR) test (Kendall and Stuart, 1979; Lynch and Walsh, 1998). The test provides information on the goodness-of-fit of a full model versus a reduced model, where the LR test statistic is a χ^2 distribution (Wald 1943).

$$\chi^2 = -2\ (\ \text{lnLoglikelihood}_{\text{Reduced Model}} - \text{lnLoglikelihood}_{\text{Full Model}}\ )$$

The log likelihood values for the full and reduced mixed linear regression model was obtained using the ASReml program (Gilmour et al., 2000) for following two models.

The full model was, $\mathbf{y=Xb + Za + Z_1h + e}$
The reduced model was, $\mathbf{y=Xb + Za + e}$

These model components and particulars were previously defined for single SNP association analyses model description, with only exception is the absence of SNP as a fixed effect in both the full and the reduced models. Alternatively, the SNP fixed effect was replaced by the haplotype random effect in the full model, and Z_1 is the incidence matrix for haplotypes and h is the vector for haplotypes random effects with distribution h ~ $N(0, \sigma^2_h A)$, where, σ^2_h is genetic variance due to haplotypes and A matrix is previously defined and identical to the matrix structure used for single SNP analyses (the population structure in same for SNP and haplotypes association analyses), for the tested animal population. Therefore, joint estimation of the vectors of animal's additive genetc effect and haplotype random effects were performed in full model, whereas, only random animal's additive effects were present in the reduced model. For each populaitn, the same pdigree information was used as that for the single SNP association analyses.

Overall, in LR test, the degree of freedom was the number of additional parameters in the full model in comparison to the reduced model. In our analyses, the haplotype distribution was the only parameter added in the full model and consequently, the degree of freedom was 1. Following the probability of χ^2 distribution, at the P-value of 5% (χ^2 >3.84 = 0.05) or less, the null hypothesis, which was defined as the reconstructed haplotypes of a single population don't have a random effect over the phenotypic trait, was rejected.

2.4.2.4. Haplotypes association analyses by ASReml

Haplotypes having significant random effects on any of the 10 fat deposition and carcass merit traits in hybrid, Angus and Charolais cattle populations were subjected to further association analyses to estimate their fixed effects on respective traits. Major haplotypes were defined as frequency $\geq$ 0.03 in the specific animal population and considered for fixed effect analyses. Minor haplotypes (frequency < 0.03) were ignored due to a small number of animals having these haplotypes. Fixed effect estimation using a very small number of animals may result in a high rate of false positives. To estimate the fixed effect for a particualr haplotype under test, haplotype genotypes were grouped and haplotype genotype was assigned for each animal as (i) haplotype homozygous animals i.e., containing pair of a particular haplotype under test, (ii) haplotypes heterozygous animals i.e, containing one particular haplotype under test along with any other haplotype in the genome and (iii) animals other haplotypes i.e., absence of the haplotype which is under test.

Associations between the haplotypes and the 10 ultrasound and carcass traits were examined by fitting the following mixed linear regression model using ASReml (Gilmour et al., 2000):

$$y = Xb + Za + e$$

This model component and the notations were described earlier as in the single SNP association analyses. While, in this case haplotypes were included as a fixed effect instead of a single SNP. For analyses, similar model assumptions, animal pedigree and covariate were used. To estimate a single haplotype effect, the three haplotype groups or haplotype genotypes were coded as 0, 1 and 2, respectively, and the haplotype substitution effect was estimated via the regression analysis. The haplotypes additive effects and dominance effects were estimated using the similar method as applied in the single SNP association analysis, considering a haplotype as a single allele (Falconer and Mackay, 1996).

2.4.3. Calculation of false discovery rate (FDR)

Considering multiple-tests were carried out in this study, we preformed a candidate gene based FDR calculation. FDR can be defined as the proportion of false-positive test results out of all positive (significant) tests (Calborg and Haley, 2004). The FDR calculation was as described by Benjamini and Hochberg (1995) and it was applied in QTL analyses (Weller et al., 1998). The FDR at a candidate gene level was calcualted using the the formula $FDR=mP_{(i)} / I$, where m is the total number of tests within a gene for a trait, $P_{(i)}$ is the SNP P-value at rank i when the P-values are ranked from lowest to highest and I is the rank of the SNP under test (Benjamini and Hochberg, 1995; Weller et al., 1998).

3. Chapter Three: Results and Discussions

3.1. Acetyl-CoA synthetase family member 3 (ACSF3)

3.1.1. Single SNP association

A novel polymorphism, c.−757C>T in the promoter area of ACSF3 was identified in-house and the SNP was genotyped in the three breed populations with the allele “T” as the minor allele having the allele frequency (MAF) 0.216, 0.296 and 0.056 in the Hybrid, Angus and Charolais populations (Table 3.1). The intralocus SNP allele frequencies were confirmed at Hardy-Weinberg equilibrium (P>0.05) (Table 3.1.) in the hybrid, Angus and Charolais cattle populations. Among the 10 fat deposition and carcass merit traits examined, the SNP was found to have a slightly significant allele substitution effect on ultrasound rib eye area (UREA) (P<0.059), carcass marbling (CMAR) (P<0.061) and significant allele substitution efect on on carcass rib eye area (CREA) (P<0.045) in the hybrid cattle population (Table 3.2.). The substitution effects of the “C” allele on the three fat-related traits were −1.29 cm^2, −1.55 cm^2 and 0.12 for UREA, CREA and CMAR, respectively. The SNP showed a significant additive effect (P<0.005) and dominance effect (P<0.023) on CMAR in the hybrid population. Animals with the “TT” genotypes have 9.63% higher CMAR in comparison to animals with the “CC” genotypes. However, no significant association of c.−757C>T was observed for other traits across all three beef cattle populations.

3.1.2. Discussion

ACSF3, which is an isoform of acetyl CoA synthatase (ACS), is considered as an enzyme located on the cytosolic surface of peroxisomes, endoplasmic reticulum and outer mitochondrial membranes. ACS has a regulatory role in the entry of fatty acids into synthetic or oxidative pathways for oxidation, elongation and desaturation of fatty acids. Therefore the isoform ACSF3 is likely a very necessary enzyme for the elongation, de-saturation of fatty acids and it is also found on cytosolic surfaces of the outer mitochondrial membranes, endoplasmic reticulum and peroxisomal membranes (Coleman and Bell, 1983; Hesler et al., 1990). It also acts at the entry point of triacylglycerol synthesis reaction. The enzyme helps to add a CoA thioester to the fatty acids of 10-20 carbons to form long-chain acyl-CoAs (Brecher, 1983; Waku, 1992). Also, ACS activity was found predominant in liver and adipose tissues, while, isoforms (e.g., ACSF3) showed a higher gene expression during the differentiation of preadipocytes to adipocytes associated with the higher level of activity during this period (Coleman et al., 1978). ACS is also abundant in liver, adipocytes and small intestinal mucosal cells and responsible for activating fatty acids to generate phospholipids and proved critical for TAG synthesis (Oikawa et al., 1998). ACSF3 is located on BTA 18 within 13.32cM to 13.37cM where no QTL region for fat deposition and carcass merit traits were reported. However, we considered its functional importance. Therefore, due to the importance in lipogenesis, we investigated ACSF3 as a candidate gene for fat deposition and carcass merit traits in beef cattle populations.

A preliminary analysis of the ACSF3 gene sequence using TESS (Transcription element search system) (http://www.cbil.upenn.edu/tess) (Schug 2003) revealed that the "C" allele of the SNP c.−757C>T introduces a putative binding site (CCTGG) for a cellular DNA binding protein, LBP-1 (Toohey and Jones, 1989; Kato et al., 1991), while "T" allele provide a binding site (CTTGGC) for NF-1 (like proteins) (Pastorcic et al., 1989; Bradshaw et al., 1988). In *Bos taurus* LBP-1 is known as "similar to Upstream-binding protein 1" (LOC785419). As a transcription factor, LBP-1 binds with the TATA box binding factor (TFIID) and subsequently, represses transcription (Kato et al., 1991), however, variation of activity is reported with the presence of the isoforms, i.e., LBP-1a, LBP-1b, LBP-1c in human. In cattle, the activity of LBP-1 on gene expression is yet to be studied, but it is likely that LBP-1a and LBP1c might have influence over the ACSF3, if they are available in cytoplasm like human (Sato et al., 2005). In contrast, NFI can act as an activator or repressor for many genes that are ubiquitously expressed as well as hormonally, nutritionally and developmentally regulated (Gronostajski 2000). In bovine, three NFI transcription factors (NFIA, NFIB and NFIC) have been reported in the databases (http://www.ncbi.nlm.nih.gov), although, their functional specificity on gene expression is subjected to further study.

In this study, it was found that the ACSF3 SNP only showed some associations with rib-eye area and carcass marbling in the hybrid population.The SNP effect might due to the activity difference of different transcription factor and subsequent its influence over the ACSF3 gene expression in hybrid cattle. However, the SNP effects were not detected in the purebred Angus and Charolais population, which may due to a smaller size of the population with distinct body composition in comparison to hybrid cattle. On the other hand, the SNP c.−757C>T may not be a causal mutation but in linkage disequilibrium (LD) with the causative DNA makers for traits. Overall, our findings need to be validated and the results also suggest that the ACSF3 is a potential functional candidate gene for further SNP marker discovery for fat related carcass traits including fatty acids composition in different beef cattle breeds.

3.2. Fatty acid binding protein 3 (FABP3)

3.2.1. Single SNP association

Three FABP3 SNPs were genotyped that included c.21T>C, c.4593C>G and c.7627T>C. “C”, “G” and “C” were minor alleles for c.21T>C, c.4593C>G and c.7627T>C, respectively across all three breeds with an exception that “T” allele of c.7627T>C was fixed in the Angus population (Table 3.1). Also, MAF of c.21T>C (0.041) and c.4593C>G (0.041) were low in Angus. Allele frequencies of SNPs were in Hardy-Weinberg equilibrium (P>0.05) (Table 3.1) across all three populations. Single marker association results showed that in hybrid and Angus cattle, c.21T>C and c.4593C>G both had significant allele substitution effects (ASE) (P<0.05 and P<0.1, respectively) on UREA (Table 3. 3). In hybrid, “T” allele of c.21T>C and “C” allele of c.4593C>G increased UREA by 1.5 and1.2%, while in Angus the same alleles from SNPs increased UREA by 2.9%. Additionally, in Angus, slaughter weight (SWT) and carcass weight (CWT) were found associated with SNPs c.21T>C (SWT, P<0.017; CWT, P<0.008) and c.4593C>G (SWT, P<0.017; CWT, P<0.007, respectively). “T” allele of c.21T>C and “C” allele of c.4593C>G both increased SWT by 1.7% and CWT by 2.28%. In Charolais, the significant ASE of SNP c.7627T>C was found on AUREA (P<0.089) as well as on carcass marbling (CMAR) (P<0.023) (Table 3.3). For both of the traits animals with the “C” allele containing animals showed increased trait values and especially when “T” allele was subdtituted by “C” allele, CMAR increased by 7%.

3.2.2. Haplotype blocks and haplotype association

HAPLOVIEW analyses revealed that SNP c.21T>C and c.4593C>G are in complete linkage disequilibrium (LD) with each other across three different breeds, which established the same haplotype block covering 4kb region of the FABP3 gene (Figure 3.1, 3.2 & 3.3.). Also, it was found that alleles of c.7627T>C are not in pair-wise LD in hybrid (r^2= 0) and has very low (r^2= 0.05) pair-wise LD in Charolais with other SNPs. The major reason of low LD is due to the low MAF of "G" allele. Further reconstruction of haplotypes using SNP c.21T>C and c.4593C>G within the haplotype blocks, explored similar haplotype pattern for three breeds. In result, haplotype T-C was the most frequent haplotype having haplotype frequency 0.608 in hybrid, 0.917 in Angus and 0.527 in Charolais. This was followed by both C-G and C-C in hybrid and Charolais but T-G and C-C in Angus. Corresponding haplotypes names were given sequentially according to their frequencies in Table 3.4.

Random effect of haplotypes on the 10 fat deposition and carcass merit traits in three breeds were presented in Table 3.5. Significant random effects ($P<0.05$) were found in hybrid cattle for all the traits except carcass marbling ($P<0.22$). However, no significant effects were found for any of the traits in Angus and Charolais cattle breeds. Further estimation of the fixed effects of haplotypes in hybrid cattle population revealed significant haplotype substitution effects (HSE) of HFABP3_01 ($P<0.031$), HFABP3_03 ($P<0.030$) and HFABP3_04 ($P<0.064$) on UREA while HFABP3_01 ($P<0.083$) and HFABP3_03 ($P<0.055$) had significant HSE on AUREA (Table 3.6.). Haplotype HFABP3_01 (T-C) homozygous animals had increased the UREA by 2.28% in comparison to animals containing other haplotypes and when other haplotypes substituted by HFABP3_03 (C-C) UREA decreased by 2.39%.

3.2.3. Discussion

Fatty acid metabolism involves the intracellular flux of fatty acids while inside the cell fatty acid binding proteins (FABP) regulate the movement of fatty acids between the cell membrane and mitochondria and/or peroxisomes for beta-oxidation, and also includes other cellular organelles for lipid synthesis (gene function from www.ncbi.nih.nlm.gov/sites/entrez). Moore et al. (1991) first suggested that the correlation observed between FABP activity and marbling score in beef muscle, which was the first indication that FABP might be a candidate gene for fat related carcass traits in beef cattle. Three major FABPs which were found in mammalian cells include hepatic-, intestinal- and cardiac-type FABPs (Spener et al., 1990). More specifically, in bovine three types of FABP are available i.e., fatty acid binding protein 3 (FABP3), muscle and heart (mammary-derived growth inhibitor), brain (B-FABP) (brain lipid-binding protein) (BLBP) (Mammary derived growth inhibitor related) and fatty acid binding protein, heart like (FABP-HL) (www.ncbi.nih.nlm.gov/sites/entrz). According to the peroxisome proliferator activated receptors (PPARs) signalling pathway, FABP was reported as a lipid transporter for liver, skeletal muscle cell, adipocyte cells (KEGG gene pathways- www.genome.jp/KEGG). Functional activities of the FABP3 were referred it as a functional candidate gene for fat deposition and carcass merit traits in beef cattle. Additionally, FABP3 is located on BTA 2 within 100.795 to 100.801cM where the QTL region for fat thickness was reported in crossbred beef cattle populations (Stone et al., 1999; http://genomes.sapac.edu.au/bovineqtl/). Therefore, the positional and functional importance of FABP3 denoted its significance as a candidate gene and subsequently incorporated for the gene-specific SNPs search and further association studies with fat deposition in different beef cattle populations.

Several studies in cattle have already been done proving the activity of FABP3 in the fat metabolism and carcass merit traits in dairy and beef cattle, respectively. In spite of the availability of the other isofroms i.e., FABP4, FABP5 and FABP3 plays a major role in lactating dairy cows for milk fat synthesis. The mRNA of FABP3 is predominant in mammary gland and highly coordinates fatty acids intracellular channelling in mammary glands (Bionaz and Lore, 2008). In beef cattle, a gene specific SNP association study performed by Cho et al., (2008) in a Korean native cattle population revealed a significant effect of a intronic SNP of

FABP3 (c.73+67G>C) on carcass weight (CWT) and haplotypes of FABP3 on backfat thickness (AVBF). One of our SNP c.21T>C was reported by them but no significant association has been found with the phenotypic traits (CWT and AVBF). Here, we found significant association of c.21T>C with SWT and CWT in Angus with a larger animal population size and different cattle breed than Cho et al. (2008), who used only 22 Hanow cattle data.

Hybrid, Angus and Charolais cattle differ biologically as well as genetically, therefore, the trend of FABP3 SNPs association were different for different cattle breeds. In Angus, we found the association of FABP3 with SWT and CWT, which is in agreement with the positional effect of FABP3 on the QTL for slaughter weight (Stone et al, 1999). Here, c.21T>C is a synonymous (Gly7Gly) polymorphism and how it could affect the traits is subject to further research. The effect of FABP3 on UREA is very distinct findings and no functional relation with FABP3 and muscle development can be established based on the current literature.

In the current study, the haplotypes HFABP3_01 and HFABP3_03 shared “C” allele from SNP c.4593C>G but differ by the alleles of SNP c.21T>C, while, HFABP3_01 contain “T” allele and HFABP3_03 contain “C” allele. The significant HSE of these haplotypes on UREA may link to this single allelic difference between haplotypes. This represents that the presence of “T” allele is likely desirable to increase UREA, which is also supported by the single marker result.

Recently, Jurie et al. (2007) reported that mRNA and proteins from isoforms of FABP gene differs in cattle breeds and also, H-FABP (FABP3) has a significant correlation with muscle triacylglycerol (TAG) content. They also suggested that FABP3 expression at the protein and mRNA levels might be one of the best indicators of intramuscular TAG depositions in beef cattle. TAG deposition may contribute to marbling score which supports the association of FABP3 with marbling in the Charolais cattle populaton. Overall, our finding suggests that FABP3 potentially plays important role in body fat deposition and carcass merit traits in different beef cattle breeds. Different SNPs from the gene specific region of FABP3 should be developed for further association studies with fat related carcass traits to support this hypothesis and also based on our findings functionality analyses of FABP3 SNPs is recommended.

3.3. Fatty acid synthase (FASN)

3.3.1. Single SNP association

We genotyped total 5 SNPs of FASN which included one synonymous (c.8581G>A), three nonsynonymous (c.10388C>T, c.12794A>C, c.14169T>C) and one intronic (c.12865G>A) SNP covering the gene region from exon 21 to exon 37 (Table 2.4.). The MAF of SNPs was given in Table 3.1. All of the SNPs were found to be polymorphic except for c.8581G>A in the Angus and the Charolais populations. The SNPs were in HWE equilibrium in the hybrid and the Charolais (P>0.05) but not in Angus cattle population (Table 3.1.). In hybrid, SNP c.14169T>C had a significant allele substitution effect on CREA (P<0.042) while, the "T" allele can increased the CREA by 1.28 cm^2 in "CC" or "CT" animal. In Angus, c.10388C>T and c.12865G>A were slightly significantly associated with AVBF, LMY and CMAR (P<0.10) while the additive effects were significant for only CMAR (P<0.056 for c.10388C>T, P<0.047 for c.12865G>A). For c.10388C>T, the "CC" animals have increase AVBF by 9.06%, decrease LMY by 2.82% and increase CMAR by 9.83% in comparison to "TT" animals. Similarly, "AA" animals of c.12865G>A have increased AVBF by 8.66%, decreased LMY by 2.79% and increased CMAR by 10.2% in comparison to the "GG" animals. In addition, c.14169T>C had an effect on CWT and CMAR (P<0.10) with "T" allele increased CWT by 1.13% and CMAR by 3.94%, while a significant additive effect was only found for CMAR (P<0.039) in the Angus cattle. In Charolais, the association of c.12794A>C was found slightly significantly associated with the SWT (P<0.083) while, "AA" allele containing animals had lower SWT by 1.2% in comparison to animals having "CC" genotype. Additionally, c.12865G>A was significantly associated with UREA (P<0.055), AUBF (P<0.099), AUREA (P<0.080) and SWT (P<0.035) but the additive effect was only significant for SWT (P<0.024). Animals containing "GG" genotype had increased UREA by 1.79%, increased AUBF by 13.57%, increased AUREA by 6.62% and increased SWT 2.01% in comparison to the "AA" genotype containing animals. The synonymous SNP c.8581G>A (Glu1112Glu) was not associated with any of the traits we analyzed in all the three cattle populations (Table 3.7.).

3.3.2. Haplotype blocks and haplotype association

HAPLOVIEW analyses of the SNPs in the three cattle populations revealed that each of the breed contains one haplotype block (Figure 3.4., 3.5 & 3.6.). The haplotype blocks of the hybrid and Angus cattle were the same as constructed by the four SNPs c.10388C>T, c.12794A>C , c.12865G>A and c.14169T>C. In hybrid cattle, the SNP c.8581G>A was out of the block due to low pairwise LD ($r^2<0.05$) with the other SNPs and the same SNP was out of analyses in Angus because its "G" allelic monomorphism. However, within the haplotype block of the hybrid cattle the pairwise LD between the SNPs were moderate to high ($r^2>0.50$-0.99), while the Angus haplotype block spanning four SNPs (c.12794A>C, c.12794A>C, c.12865G>A and c.14169T>C) that were completely linked ($r^2=1.0$) with each other. Interestingly, in Charolais, the SNP block was completely different and shortened to cover c.10388C>T, c.12794A>C, c.12865G>A, while the SNPs were in complete LD with each other ($r^2=1.0$). In this case, c.14169T>C was out of the block due to its low pairwise LD ($r^2<0.50$) with other SNPs. Further analyses to reconstruct the haplotypes within the haplotype blocks discovered in total 12 haplotypes for hybrid, 8 haplotypes for Angus and 7 haplotypes for Charolais (Table 3.8). However, only 5 haplotypes in hybrid, 4 haplotypes in Angus and 4 haplotypes in Charolais were considered as major haplotypes (Frequency>0.03).

Random effects of haplotypes on the 10 fat related carcass merit traits from different breeds have been presented in Table 3.9. Haplotypes of hybrid cattle had significant ($P<0.01$) haplotypes random effects over all the traits examined except for CMAR. But no significant haplotypes random effects were found for the Angus and Charolais populations breed for any of the traits analyzed. An extended estimation of the fixed effects for major haplotypes (frequency>0.03) in the hybrid cattle population showed that HFASN_02 (T-C-G-C) decreased CREA (P<0.10) by 1.07 cm^2 and HFASN_05 (T-C-G-T) increased CREA (P<0.10) by 2.76 cm^2, while only HFASN_05 affected AUREA (P<0.10) and increased it by 8.26% (Table 3.10.). Hybrid cattle having other haplotypes had increased 2.09% CREA in comparison to animals having the HFASN_02 haplotypes.

3.3.3. Discussion

Bovine FASN is a key enzyme that plays an important role in lipogenesis and has been well studied in mammals for fat related phenotypic traits and obesity. Earlier studies in human identified FASN as a candidate gene for body fat deposition (Berndt et al. 2007) and a novel non-synonymous polymorphism under the coding region of this gene was found to be associated with percentage of body fat (Kovacs et al. 2004). In beef cattle, fat deposition related carcass traits were not thoroughly studied for associations with FASN. However, it was reported that the FASN gene region contain seven acyl carrier protein (ACP) domains which may cause differential catalytic activity (Sul and Wang, 1998; Roy et al. 2005a) leading towards differential rate of lipogenesis. In further studies, two silent point mutations were identified in the enoyl reductase and β-keto reductase domains of FASN and found associated with milk fat including the composition of fatty acids and milk fat content respectively (Roy et al. 2006). Moreover, five other single nucleotide polymorphisms (SNPs) associated with fatty acids profiles were identified in dairy cattle (Morris et al. 2007). Recently, the associations of SNPs in the thioesterase domain of FASN was reported with the fatty acid composition of longissimous dorsi muscle in pure breed Angus cattle (Zhang et al., 2008) and polymorphisms at exon 34 which is in the enoyl reductase and β-keto reductase domain were reported to affect the fatty acid composition in intramuscular fat of Japanease black cattle (Abe et al., 2009). This association of FASN with fatty acid profiles of beef implies that FASN could be considered as a functional candidate gene for fat traits in beef cattle. Additionally, FASN is located within 73.51 to 73.65cM on BTA 19 and is under the QTL region for subcutaneous fat which has been finely mapped in the chromosomal region of 65.7 to 99.5 cM (Casas et al. 2000; Li et al. 2004a). Consequently, FASN is considered as a positional and functional candidate gene for fat related carcass traits in beef cattle while it was previously speculated that FASN might have effect on fat related carcass traits and should be investigated (Roy et. al., 2005b). Therefore, in the current study, association analyses of FASN were carried out with fat deposition and carcass merit traits in hybrid, Angus and Charolais beef cattle using gene-specific SNPs.

In the current study, three SNPs c.12794A>C, c.12865G>A and c.14169T>C which resides under the enoyl reductase and β-keto reductase catalytic domain of FASN, while SNPs c.8581G>A and c.10388C>T located upstream of the region at exon 21 and exon 24. None of these SNPs were analyses in earlier studies were investigated in previous studies. The c.10388C>T (His1390Tyr) which has slight association with AVBF, LMY and CMAR in the Angus population is a nonsynonymous polymorphism introduces a change of amino acid for the FASN protein that has different characteristics, i.e., histidine is basic and tyrosine is polar in nature. When we look at the amino acid's potential functional role on enzymatic activities, we observe that histidine supports the catalytic reaction steps with the advantage of acting as charged or neutral at physiological p^H to stabilize to transition state of a catalytic reaction (Bartlett et al., 2002). In contrast, tyrosine has unique ability to perform homolytic reactions and acts as hydrogen atom shuttle, while these processes are very necessary for the enzymes functional activity (Holliday et al., 2009). However, both of the amino acids likely support the enzymatic activity of FASN but the enzymatic propensity in presence of histidine is reportedly higher than tyrosine (Bartlett et al., 2002). Therefore, a higher FASN activity associated with the "C" allele in Angus cattle may lead to higher backfat thickness as AVBF as well as CMAR but less LMY.

The SNP c.12794A>C (Ile1856Lue) which has association with SWT in the hybrid cattle is a missense polymorphism in exon 32 which altered the amino acid isoleucine to leucine. Both of these amino acids are nonpolar (www.en.wikipedia.org) and the side chains of these amino acid are never been found to participates in enzyme catalytic activities, although rarely they may participate in electron transfer (Holliday et al., 2009). In comparison, leucine is more frequent in catalytic residues than isoleucine with more enzyme catalytic propensity (Bartlett et al., 2002), which likely contribute to the FASN activities. However, it is still unclear why leucine favours to increase SWT in presence of "C" allele in Charolais cattle.

The intronic c.12865G>A SNP had slight associations with AVBF, LMY and CMAR in the Angus and with UREA, AUBF, AUREA and SWT in the Charolais cattle populations and it resides very closly to the c.12794A>C. This SNP may be in LD with the causative mutation resides nearby gene region and likely not a fuctional one due to its intronic origin.

The SNP c.14169T>C (Val2007Ala) had slight associations with CREA in the hybrid and CWT, CMAR in the Angus populations is a nonsynonymous polymorphism. The association may be explained by its substitution of amino acid valine to alanine in FASN enzyme. Both of these two amino acids have similar physiochemical properties as isoleucine and leucine with likely similar enzymatic propensity. However, valine (8.85 g/100g at 25°C) has less solubility than alanine (16.65g/100g at 25°C) (TMI 1989; CRCHCP 1977, www.prowl.rockefeller.edu/aainfo), which may contribute to the discrimination in the enzymatic activity or stability in the cell cytoplasm. It was observed that valine which originated by the "T" allele is favourable to increase trait values across different populations, i.e., CREA for hybrid as well CWT and CMAR for Angus. The exact mechanisms of amino acids substitution and the differential activities of FASN which may affect the fat deposition in cattle are yet to be discovered.

Haplotypes diversity and the larger population size in hybrid cattle population may be the key for the significant random and fixed effect which were absent in Angus and Charolais cattle breed. Interestingly, the two haplotypes i.e., HFASN_02 (T-C-G-C) and HFASN_05 (T-C-G-T) those had effects on the trait CREA share the same alleles from the SNPs c.10388C>T, c.12794A>C and c.12865G>A. From single marker analyses, the “T” allele was associated with less fat in Angus, while the “C” allele increases SWT in Angus and the “G” allele as found to increase UREA in Charolais, which may set a common platform to affect CREA in hybrid cattle. However, these two haplotypes differ by the “C” versus “T” allele from c.14169T>C and this SNP was already found associated with CREA in hybrid ($P<0.05$). Therefore, the consequence of the effect of “C” allele to decrease the CREA traits value has been detected at the haplotype level.

SNPs c.10388C>T, c.12794A>C and c.12865G>A were not in HWE in the Angus population as well as the major alleles of these three SNPs in the hybrid and Charolais populations appeared as minor in the Angus population. These events indicate that these SNPs of FASN may be under the slection pressure in the experimental Angus cattle population. Also, these SNPs of FASN could have specific roles in a breed like Angus which deposite more body fat than other breeds like the hybrid and Charolais which are leaner.

It is noteworthy that most of the abovoe described SNP had a weak associations ($P<0.10$) with the traits. Therefore, the SNP association need to be validated using a larger population size and more SNPs from the FASN gene specific area should be tested. In addition, functional analyses of the nonsynonymous SNPs will likely increase our understanding of the FASN regulation on cattle body fat deposition and carcass merit traits.

3.4. Glycerol 3-phosphate acyltransferase, mitochondrial (GPAM)

3.4.1. Single SNP association

One novel SNP c.−1564G>A at the promoter region and four previously reported SNPs c.−345C>T , c.18088G>C, c.26006A>G, c.35863A>C from public databases were genotyped in three cattle breeds. For SNPs c.−1564G>A and c.−345C>T allele “A” and allele “T” were minor alleles respectively across all the three breed populations (Table 3.1.). SNPs c.18088G>C and c.26006A>G were polymorphic only for hybrid cattle while “G” allele of c.18088G>C and “A” allele of c.26006A>G were fixed in Angus and Charolais populations. Allele “A” of c.35863A>C was fixed in Angus population while this SNP was polymorphic in hybrid and Charolais. SNPs were in Hardy-Weinberg equilibrium (P>0.05) except for c.−1564G>A and c.26006A>G in hybrid cattle population (Table 3.1.). Interestingly, it has been found that SNP c.−1564G>A had very low number of “AA” homozygous animals across three cattle breeds, i.e., 5, 8 and 1 for the hybrid, Angus and Charolais cattle populations, respectively. Also, c.−345C>T had only 3 animals in the Angus and 2 animals in the Charolais populations that had “TT” genotypes.

In the hybrid cattle population, significant allele substitution effects were observed for c.−1564G>A on UBF (P<0.026) and CMAR (P<0.015). Significant additive effects of c.−1564G>A were found on UBF (P<0.018), AUBF (P<0.006) with a dominance effect on AUBF (P<0.017). Animals having “AA” genotype had increased UBF by 26.59%, increased AUBF by 37% and increased CMAR by 8.24% in comparison to animals having “GG” genotypes. SNP c.18088G>C had significant allele a substitution effect on CREA (P<0.026), while substitution of “G” allele by “C” allele increased the CREA by 2.53cm^2. SNP c.26006A>G had a significant allele substitution effect on SWT (P<0.009) and CWT (P<0.0.019) with siginifcant additive effects for both of the traits (SWT, P<0.003; CWT, P<0.008). Animals having “GG” genotype of c.26006A>G had 4.44% higher

SWT and 4.16% higher CWT in comparison to “AA” genotype containing animals. Lastly, c.35863A>C had a significant allele substitution effect on AUBF (P<0.016).

In Angus, c.−1564G>A had a significant additive effect on SWT (P<0.018), CWT (P<0.013) and CREA (P<0.010) with a significant dominance effect on CREA (P<0.033). Animals having “AA” genotypes had 4.17% increased SWT, 4.96% increased CWT and 8% increased CREA in comparison to “GG” genotype containing animals. Significant allele substitution effects of c.−345C>T were found on AUREA (P<0.044) and a slightly significant effect on CMAR (P<0.082), while, “CC” animals had increased AUREA by 30% in comparison to “TT” animals and had 5% increased marbling for “C” allele substitution. In Charolais, only c.35863A>C was associated with UBF (P<0.053). Interestingly, in Charolais, we had no “CC” animal for SNP c.35863A>C, however, “A” allele substitution had decreased the UBF by 13.55% (Table 3.11.).

3.4.2. Haplotype blocks and haplotype association

Results of HAPLOVIEW analyses of the SNPs in hybrid, Angus and Charolais cattle breeds are presented in figure 3.7., 3.8. and 3.9. The SNPs were found in low ($r^2<0.5$) and/or no ($r^2=0$) pair-wise LD with each other across three breeds and were unable to produce haplotype blocks in any of the populations. Further haplotype reconstruction revealed that in total 19 different haplotypes spanning 5 SNPs in hybrid, 4 haplotypes spanning 2 SNPs in Angus and 6 haplotypes spanning 3 SNPs in Charolais (Table 3.12.). Based on the frequencies (freq.>0.03), 3 haplotypes were major in hybrid and 3 were major in Charolais and 1 (A-T) was found minor in Angus.

Random effects of the haplotypes were tested and results are presented in Table 3.13. In hybrid, all traits have been found significantly affected (P<0.001) by the haplotype random effect, whereas, in Angus haplotypes random effects were significant (P<0.027) only for CREA. No significant haplotype random effects were found in the Charolais cattle population. Furthermore, we tested the fixed effects of the major haplotypes from hybrid and Angus cattle populations (Table 3.14.). Haplotype HGPAM_01 (G-C-G-A-A) had significant haplotype substitution effects on UBF (P<0.022), SWT (0.011), CWT (P<0.010), AVBF (P<0.008), LMY (P<0.013) and CMAR (P<0.004) with significant haplotype additive effects on UBF (P<0.027), SWT (P<0.014), CWT (P<0.014), AVBF (P<0.013), LMY (P<0.016) and CMAR (P<0.004). For HGPAM_01, haplotype homozygous animals had 9.7% lower UBF, 3.22% lower SWT, 3.47% lower CWT, 11% lower AVBF, 2.3% increased LMY and 6.4% decreased CMAR in comparison to animals have other haplotypes. Also, HGPAM_03 (A-C-G-A-A) has significant haplotype substitution effects on UBF (P<0.003), AUBF (P<0.067), AVBF (P<0.023), LMY (P<0.041) and CMAR (P<0.015) with significant additive effects on UBF (P<0.004) and AUBF (P<0.001). For haplotype HGPAM_03, haplotype homozygous animals had 33% more UBF, 44% more AUBF, 18.95% more AVBF, 2.47% decreased LMY and 4.19% less CMAR in comparison to animals have other hapltypes.

In Angus, the result of the haplotypes fixed effect test revealed a slightly significant haplotype substitution effect of AGPAM_01 (G-C) on CREA (P<0.073) with a significant additive effect (P<0.010). AGPAM_01 haplotype homozygous animals have 6.92% lower CREA in comparison to animals have other haplotypes. On the other hand, haplotype AGPAM_02 had significant haplotype additive effects on SWT (P<0.020) and CWT (P<0.016) whereas, AGPAM_03 (G-T) showed significant haplotype substitution effects on UREA (P<0.038) and AUREA (P<0.031). AGPAM_02 haplotype homozygous animals had 4.11% higher SWT and 4.77% higher CWT while AGPAM_03 haplotype homozygous animals had 1.73% lower UREA and 29.26% lower AUREA in comparison to animals with other haplotypes.

3.4.3. Discussion

GPAM is considered as a key enzyme of *de novo* lipid synthesis as well as a candidate gene for fat deposition and carcass merit traits and milk fat content in bovine (Roy et al., 2005). Synthesis of triacylglycerol from fatty acids is the determinant of intramuscular fat (Pethick et al., 2004) in muscle which likely affects the fat related carcass traits, i.e., marbling. GPAM catalyzes the esterification process of glycerol-3-phosphate with acyl-coA in mitochondria, which is also considered as the rate-limiting step of triacylglycerol synthesis (Bell and Coleman et al., 1980; Roy et al., 2005). In addition to the functional importance in lipogenesis, GPAM it is also located (41.3 - 41.40cM) under the QTL for fat yield and yield grade (2.839cM - 41.65cM) on BTA 26 (Casas et al., 2003b), that provides its status as a positional candidate gene for fat deposition related carcass traits in beef cattle. Therefore, we considered GPAM gene specific SNPs for association analyses with fat deposition and carcass merit traits in hybid, Angus and Charolais beef cattle populations.

The SNP c.−1564G>A was located in the promoter region of the GPAM gene and a preliminary analyses to predict transcription binding factor binding site by TESS (Transcription element search system) (www.cbil.upenn.edu/tess) (Schug 2003) suggests that the “A” allele provides a binding site for two types of transcription factors noted as “integration host factor” (IHF) and “C/EBP beta (CEBPβ) or delta (C/EBPδ)” while no transcription factor binding site was found for “C” allele. However, the affinity was higher for “C/EBP beta or delta”. The IHF was first described by Giladi et al., (1990) as a small dimeric protein that binds to a specific DNA consensus sequence and produces DNA bending, subsequently enhances the formation of RNA polymerase-promoter closed complexes. Later, IHF was described as an asymmetric histone-like protein that binds and bends the DNA at specific sequences and an accessory factor for replication, site-specific recombination and transcription (Goosen and van de Putte, 1995) as it can initiate and stimulate transcription via a direct interaction with RNA polymerase. Detailing the study on IHF, it has been found that precise promoter sequence geometry is necessary for IHF to positively regulate transcription (Dworkin et al., 1997). The other transcription binding factors C/EBPβ and/or C/EBPδ are the family member of C/EBP transcription regulatory DNA binding proteins, first named by Cao et al., (1991) and called as CCAAT/binding protein (C/EBP). Out of the six member of the C/EBP protein family, only three are available in bovine includes C/EBPα (Ramji and Foka, 2002), C/EBPβ (Yamaoka et al., 1997) and C/EBPδ (Taniguchi and Sasaki et al., 1997). Due to the similarity in the sequence of amino acids produced in the basic region, C/EBPβ and C/EBPδ has similar DNA binding pattern and interact with virtually identical DNA sequences (Williams et al., 1991; Osada et al., 1996; Cassel and Nord, 2003). Also, isoforms of C/EBP i.e., C/EBPβ and C/EBPδ genes are expressed early in adipocyte differentiation found in 3T3-L1 cell lines (Cao et al., 1991; Yeh et al., 1995; Taniguchi and Sasaki et al., 1997; Yamaoka et al., 1997). Additionally, C/EBPβ has a regulatory role in cellular activities in a number of cell types i.e., adipocytes (Cao et al., 1991; Lin et al., 1992 and Darlington et al., 1998), hepatocytes (Diehl, 1998), the hematopoietic (Scott et al., 1992; Tanaka et al., 1995), and mammary gland (Robinson et al., 1998; Piwien-Pilipuk et al., 2002), with a functional role in gene transcriptions. Therefore, it is high likely that the “A” allele of c.−1564G>A may speed up the transcription of GPAM during early stage differentiation of bovine adipocyte cells and consequently increase the lipid synthesis leading to more backfat deposition which measured as UBF, when animals are in feedlot. In addition, the consequences of this accelerated adipocyte differentiation is likely responsible for more TAG deposition in muscle, increasing the intramuscular fat and that is why, allele “A” of c.−1564G>A significantly increase CMAR in hybrid cattle. These assumptions is further supported by one study, where, C/EBPβ and C/EBPδ double knockout mice did not accumulate lipid droplets in brown adipose tissue and had significantly reduced epidydimal fat pads in surviving adults (Tanaka et al., 1997; Lekstrom-Himes and Xanthopoulos, 1998). However, no significant effect of this SNP on carcass marbling was seen in purebred Angus and Charolais, which may be due to their biological differences with distinct breed specific fat deposition related gene mechanism. Also, small size of Angus and Charolais populations and very low count of “AA” homozygous animals in these populations may also be the reasons for no significant association of c.−1564G>A with any of the carcass traits. Additionally, the action of C/EBP isoforms may be pleiotropic and tissue specific (Julie and Kleanthis, 1998) that could contribute to cattle breed specific gene activation. Conclusively, we can say, this SNP could be an ideal candidate for further validation study with larger animal populations of different beef cattle breeds.

Another SNP at the promoter of GPAM was c.−345C>T. The SNP was found to have a slightly significantly association with carcass marbling in the Angus population ($P<0.10$). Transcription factor binding analyses using TESS (Schug, 2003) revealed that both the alleles share binding site for transcription factor (TF) HNF3-alpha (liver specific nuclear factor) (Grange et al., 1991) but only “C” allele provides additional binding sites for the POU family transcription factor with octamer members (OCT) along with the SP1 transcription factor binding site. In bovine, 23 of POU family members genes have been reported in public databases (www.ncbi.nih.nlm.gov) and these TFs mainly interact with other proteins in transcription initiation complex (Deev and Polianovskii, 2004) to exert their regulation over transcription. Tissue-specific isoforms are the special feature of POU protein family mediated gene expression regulation (Pankratova et al., 2004), and interestingly, the GPAM in bovine has tissue specific transcriptional discrepancies, while in mesenteric adipose and heart tissue the GPAM transcript activity seems to be slightly weaker than in muscle and liver (Roy et al., 2006). In addition, SP1 can play its transcriptional regulatory role on the binding site given by the “C” allele and it may increase the GPAM expression in Angus leading to less intramuscular fat deposition. Several other nearby predicted SP1 binding sites were previously reported previously and this is a common TF in the promoter of other genes related to fat metabolism i.e., FASN and leptin (Fukuda and Iritani, 1999; Roy et al., 2005 & 2006). The significant effect of the SNP c.−345C>T on carcass marbling found in Angus, a breed that deposits more body fat than hybrid and Charolais, does not necessarily indicate that the SNP activity is absent in hybrid and Charolais. Instead, it should be subjected to further validation in other populations.

Three other SNPs i.e., c.18088G>C, c.26006A>G, c.35863A>C were located on different introns (Table 2.2) of the GPAM. The SNPs showed significant associations with the different fat related carcass traits in hybrid and Charolais cattle breeds. The functional aspects of these SNPs are unclear but they may be in LD with other causative SNP(s) in the GPAM gene-specific area and/or nearby genomic area. Also, these SNPs should be further evaluated through validation studies.

SNPs of GPAM showed very low LDs with each other in all the three populations with a range of LD (r^2) from 0 to 0.31, indicating a higher recombination rate between the SNPs of the gene. Haplotype spanning 5, 2, and 3 SNPs in the hybrid, Angus and Charolais populations, respectively, have been constructed for each animal with haplotypes HGPAM_01, AGPAM_01, and CGPAM_01 dominanted in the populations. However, haplotypes were more diversified in the hybrid cattle population than in the Angus and Charolais population.

The haplotypes showed significantly random effects on all the fat and carcass traits examined in the hybrid cattle population and haplotype fixed effects were also detected for UBF, AVBF, LMY and CMAR in the population. GPAM haplotypes HGPAM_01 (G-C-G-A-A) and HGPAM_03 (A-C-G-A-A) in the hybrid cattle population were different only by the single allele obtained from SNP c.−1564G>A while predicted trait values (LS means) of theses haplotypes showed completely opposite trend of association with UBF, AVBF, LMY and CMAR. In the presence of, the “G” allele from c.−1564G>A in the haplotype HGPAM_01, animals had lower UBF, AVBF and increased LMY while opposite effects were prevailed for haplotype HGPAM_03 which contains the “A” allele leading to increased body fat deposition. This indicates that c.−1564G>A may be important SNP having effects on fat related carcass traits in hybrid cattle at both the single marker as well as the haplotype level.

For the Angus population, a significant random haplotype effect on CREA was detected and haplotype AGPAM_01 (G-C) showed a slightly significant fixed effect on CREA ($P<0.073$). CREA was significantly lowered for AGPMA_01 homozygous cattle indicating that the haplotype may be or may be linked to SNPs that have functional impacts on the longissimus muscle development in Angus cattle.

GPAM is mostly expressed in lipogenic tissues, such as, liver and adipose tissues and likely regulates the rate-limiting step in TAG and phospholipid biosynthesis, along with hormonal and nutritional controls over its activity (Sul and Wang, 1998). Therefore, GPAM is potentially a very good candidate gene to be screened for its effect on beef cattle economically important fat related traits. All the results presented in the current study support the candidature of GPAM gene for bovine fat deposition and carcass merit traits. Different SNPs from the gene specific region of GPAM should be developed and further association analyses across different beef cattle breeds with a larger population size is warranted.

3.5. Isocitrate dehydrogenase 1 (NADP+), soluble (IDH1)

3.5.1. Single SNP association

One novel SNP c.−4145C>T at the promoter and two other intronic SNPs i.e., c.4208T>G, c.9970A>G of the IDH1 gene have been genotyped. Across all the three breed populations, the “T”, “G” and “G” alleles were found as minor alleles respectively for SNPs c.−4145C>T, c.4208T>G and c.9970A>G. Additionaly, it was found that these SNP genotypes were in Hardy-Weinberg equilibrium in all breeds except for c.9970A>G in Charolais (Table 3.1.), in which SNP genotype “GG” had only 2 animals.

Single marker association analyses revealed that SNP c.9970A>G had significant allele substitution effects on UBF ($P<0.043$), SWT ($P<0.043$) and CWT ($P<0.033$) in the hybrid cattle population (Table 3.15.). Allele substitution effects showed that animals substituted by the “A” allele have 0.51mm more UBF depth and 8.80 Kg and 4.97 Kg more weight in SWT and CWT, respectively. The additive effects of c.9970A>G were significant for UBF ($P<0.038$), SWT ($P<0.008$), CWT ($P<0.020$), AVBF ($P<0.032$) and LMY ($P<0.023$), while the dominance effects were significant for AVBF ($P<0.019$), LMY ($P<0.010$) and CMAR ($P<0.043$) in the hybrid population. The “AA” animal had 15% more UBF, 5.59% more SWT, 5.02% more CWT, 17.37% more AVBF and 3.41% less LMY in comparison to the “GG” animals. In Angus, a significant dominance effect was found for c.4208T>G on CMAR ($P<0.042$) while the heterozygous animals had a 0.33 unit increase in CMAR relative to the average trait value of the homozygous animals.

3.5.2. Haplotype blocks and haplotype association

Extended analyses of the SNP genotypes using the software HAPLOVIEW revealed that the SNPs are not in strong pair-wise LD ($r^2<0.5$) with each other across the three cattle populations (Figure 3.10., 3.11. & 3.12.) Therefore, no distinct haplotype blocks have been found for any of the populations. Further reconstruction of haplotypes using HAPLORE revealed that all the major haplotypes (frequency>0.03) were similar among the three cattle population (Table 3.16). Additionally, in likelihood ratio tests results it was found that haplotypes random effects were significant (P<0.05) for all the phenotypic traits examined except for CMAR in hybrid cattle but the haplotype random effects were not significant for the traits in the Angus and Charolais population (Table 3.17.).

Fixed haplotype effect analyses were performed for five major haplotypes (frequency>0.03) in the hybrid cattle population (Table 3.18) while slightly significant haplotype substitution effects were found for HIDH1_02 (P<0.098), HIDH1_03 (P<0.087) and a significant haplotype substitution effect was found for HIDH1_05 (P<0.045) on UBF with −0.40 mm, 0.44 mm and −1.09 mm estimated effects, respectively. However, only HIDH1_03 had a significant additive effect on the UBF (P<0.046) while haplotype homozygous animals had 14.58% lower UBF than the animals having other haplotypes. Additionally, HIDH1_03 had significant allele substitution effects on SWT (P<0.021) and CWT (P<0.049) with significant additive effects on SWT (P<0.008) and CWT (P<0.026). For both of the associated traits, animals having a homozygous genotype of haplotype HIDH1_03 showed lower trait values, i.e., 5.44% lower SWT and 4.74% lower CWT in comparison to animals with other haplotypes (Table 3.19.).

3.5.3. Discussion

Like any other mammals, bovine body metabolism is a complex process and lipogenesis and gluconogenesis are not independent but interrelated metabolic processes behind the formulation of the adipose tissue depots (Smith et al., 1983).

In beef cattle, lipogenic adipose tissue carbon sources are mainly acetate, lactate and glucose. However, independent of diet, acetate provides 70-80% of the acetyl units to in vitro lipogenesis in subcutaneous adipose tissue, but only 10-25% in intramuscular adipose tissue and glucose provides 1-10% of the acetyl units in subcutaneous adipose tissue, but 50-75% in the intramuscular depot, while the contribution of lactate to lipogenesis was found similar in both tissues (15-30%) (Smith and Grouse, 1984). It was found that enzymes of the gluconogenesis and glycolysis, i.e., NADP-malate dehydrogenase, NADP-isocitarte dehydrogenase, ATP citrate lyase may supply NADPH required for lipogenesis (Smith and Grouse, 1984). Later, Shechter et al. (2003) mentioned that IDH1 activity is co-ordinately regulated with the cholesterol and fatty acid biosynthetic pathways and subsequently suggested that IDH1 is likely the source of cytosolic NADPH required by these pathways. IDH1 is a NADP+ dependent cytosolic enzyme, which catalyzes the decarboxylation of isocitrate into alpha-ketoglutarate (Nekrutenko et al., 1998) in the citric acid cycle. Recently, in dairy cattle, it was found that IDH1 generated NADPH which was a primary source of reducing equivalents for *de novo* fatty acid synthesis in mammary gland (Liu et al., 2006). Therefore, we considered IDH1 as a functional candidate gene to study gene specific SNPs associations with body fat deposition and carcass merit traits in hybrid, Angus and Charolais beef cattle. IDH1 is located on BTA 2 between 81.15cM to 81.16cM (http://genomes.sapac.edu.au/bovineqtl/) where QTL regions for fat thickness (Stone et al., 1999), CMAR (Casas et al., 2003b) and SWT (Kim et al., 2003) were identified. The chromosomal location of IDH1 indicates its positional candidature of IDH1 as well, which gave us confidence to screen this gene for SNPs markers and subsequent association studies.

Among all three SNPs examined c.9970A>G had significant associations with UBF, SWT, CWT, AVBF, LMY, and CMAR in the hybrid cattle population. SNP c.9970A>G is an intronic polymorphism having no involvement in the protein synthesis and may be in LD with nearby causative DNA variants. However, no associations of IDH1 SNP markers with fat deposition and carcass merit traits were observed in the Angus and Charolais cattle populations except for c.4208T>G having a significant dominace effect with CMAR in Angus, which likely indicates that this IDH1 gene activity may be more conserved in purebred cattle populations. Also, it is reasonable to assume that the rate of glucose metabolism differs within different cattle breeds with the activity of the enzymes. Therefore, with the relatively small population size of Angus and Charolais it might be difficult to get significant associations of IDH1 SNPs that we used in the study.

SNPs of IDH1 showed relatively low LDs with each other in all the three populations with a range of LD (r^2) from 0.2 to 0.47, indicating a higher recombination rate between the SNPs of the gene. Significnat random haplotype effects were detected on all the fat and carcass merit traits examined in the hybrid cattle populations but not in the Angus and Charolais population and haplotypes including HIDH1_03 were found to have effects on some of the traits examined. The haplotype HIDH1_03 (C-T-G) contains the "C" allele from the SNP c.−4145C>T which is located at the upstream from the transcriptional start site of the gene. The site provides multiple putative binding site for transcription factors Sp1, activator protein 1 (Ap-1), GC-rich sequence DNA binding factor (GCF) and CP1. Sp1 and Ap-1 are well known transcription activator (Dunah et al., 2002; Bakiri et al., 2002; Hess et al., 2004; Hazelton et al., 2008) and in contrast the GCF activity is related to the down regulation or repression of gene transcription (Kageyama and Pastan, 1989). Notably, these transcription factors binding sites are absent in presence of "T" allele of c.−4145C>T, which may contribute to the association of haplotype HIDH1_03 with several carcass traits, i.e., UBF, SWT and CWT in the hybrid cattle population. However, associations between the SNP c.−4145C>T with the traits were not significant in all the three populations in the single SNP marker analysis. Instead, SNP c.9970A>G, a intronic SNP, was found to have significant associations with UBF, SWT and CWT in the hybrid cattle population.

Our findings from both the single marker and the haplotype studies were in agreement with the positional candidature of IDH1 under the QTL regions for SWT (Kim et al., 1999), fat thickness (Stone et al., 1999) and CMAR (Casas et al., 2003b). The reported QTL studies was conducted in hybrid and or in commercial cattle populations, and in the current study, we found significant associations in the hybrid cattle population but not in the pure bred cattle populations indicates that the IDH1 gene activity may be conserved for different breeds of cattle. Conclusively, it is fair to assume that availability of multiple transcription factors for promoter SNP of IDH1 such as c. −4145C>T may cause recruitment of the more transcriptional machineries (Landry et al., 2003) for IDH1 transcriptional regulation which could be responsible for differential gene expression. This assumption is further supported by the findings of Wang et al. (2005) which showed that Japanease black cattle had more cytosolic NADP+ IDH gene expression in comparison to Holstein steers. So, it is not surprising that IDH1's influence on body fat deposition will vary due to the breed differences. Recently, Jurie et al. (2007) reported that greater intramuscular TAG content was associated with greater ICDH (Isocitrate dehydrogenase) enzyme activities. Therefore, more SNP association study on IDH1 along with other isofroms like IDH2 is recommended as a candidate gene for fat deposition and carcass merit traits in different beef cattle populations.

3.6. Insulin like growth factor-I (IGF1)*

3.6.1. Single SNP association

We have genotyped two SNPs of IGF1, c.−512C>T and c.47807T>C. SNP c.−512C>T is located at the promoter region and c.47807T>C is located at the intron 2 of IGF1. c.−512C>T had minor allele “C” for the hybrid and Charolais populations while allele “T” was the minor allele in the Angus population. For c.47807T>C, “C” was the minor allele across all three populations (Table 3.1.). The intralocus genotypic frequencies of c.−512C>T and c.47807T>C were conformed to Hardy–Weinberg equilibrium proportions for all three populations ($P > 0.05$) (Table 3.1.). Among the 10 fat deposition and carcass merit traits examined in the three cattle populations, the alleles of the SNP c.−512C>T were found to have significant allele substitution effects on UBF ($P<0.027$), AVBF ($P<0.011$) and LMY ($P<0.017$) in the Angus cattle population (Table 3.19.), The estimated allele substitution effects were −0.57 mm, −1.13 mm and 0.93% on the UBF, AVBF and LMY respectively. The “C” allele, which has a frequency of 0.56 in the Angus population, is associated with significantly higher UBF, higher AVBF and lower carcass LMY in comparison to the “T” allele. The additive effects of c.−512C>T were significant for UBF ($P<0.022$), AVBF ($P<0.015$) and LMY ($P<0.022$). Animals with the “CC” genotype have about 13% more carcass average fat and 3.3% less LMY than animals carrying the “TT” in the Angus population. Also in Angus, SNP c.47807T>C had significant allele substitution effect on SWT ($P<0.009$) and CWT ($P<0.002$) while additive and dominance effects were not estimated due to the absence of the “CC” animals.

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* A version of this section “Association analyses of a SNP in the promoter of IGF1 with fat deposition and carcass merit traits in hybrid, Angus and Charolais beef cattle” has been published in Animal Genetics. Islam et al., 2009. 40(5):766-769.

In Charolais, significant allele substitution effects of c.47807T>C was found on UREA ($P<0.014$) with a slightly significant effect on AUREA ($P<0.067$). For c.47807T>C in Angus, the "T" allele was responsible for 2.18% increase in SWT and 3.52% increase in CWT while the minor allele "C" increased the trait values for UREA by 4% and AUREA by 14% in the Charolais population. No association of both of the IGF1 SNPs with fat deposition and carcass merit traits have been found in the hybrid cattle population.

3.6.2. Haplotype blocks and haplotype association

We further analyzed both of the IGF1 SNP genotypes by HAPLOVIEW to examine the LD between the two SNPs in the there the cattle populations. We observed that the SNPs are in very low LD in Angus ($r^2=0.02$) and Charolais ($r^2=0.03$) and in no LD ($r^2=0$) in hybrid cattle populations. (Figure 3.13., 3.14. & 3.15.). We further reconstructed haplotypes using the two SNPs genotypes for each animal for the different cattle breeds (Table 3.20.). The most frequent haplotypes i.e., <u>T-T</u> and <u>C-T</u> were found to be dominant and the other two infrequent haplotypes i.e., <u>T-C</u> and <u>C-C</u> were at very low frequencies across all three cattle populations. Haplotypes were found to have significant random effect ($P<0.05$) for all of the phenotypic traits in the hybrid cattle population but none of the traits in Angus and Charolais populations. However, no significant fixed effect associations of the haplotypes were found for any of the haplotypes with any of the traits in the hybrid population (Table 3.22.).

3.6.3. Discussion

Insulin like growth factor-1 (IGF1) is one of the insulin-like growth factors that have an essential role in regulating animal growth and metabolism (Hossner et al.

1997). In beef cattle, serum IGF1 concentration has been found to have significant correlations with fat deposition and carcass merit traits (Anderson et al. 1988; Davis & Simmen 2000). The IGF1 gene was mapped on bovine chromosome (BTA) 5 at 73.5 cM (Grosse et al. 1999) and several studies have identified quantitative trait loci regions associated with fat level and carcass traits in the vicinity of IGF1 in beef cattle (Casas et al. 2000; Li et al. 2004a). Ge et al. (1997) reported a single nucleotide polymorphism (SNP) (C>T) in the promoter region of IGF1 (Gene bank accession no. AF017143) and located 512 bp upstream from the start codon (c. −512C>T). The SNP c.−512C>T was later evaluated for its association with growth traits in beef cattle, with significant associations for weight gain during the first 20 days after weaning and on-test weight in Angus (Ge et al. 2001), and a small dominance effect on birth weight in commercial lines of Bos taurus (Li et al. 2004b). SNP c.47807T>C is located in intron 2 of IGF1 and no association study was reported in beef cattle. In this study, we further investigated the association of the IGF1 SNPs c.−512C>T and c.47807T>C with fat deposition and carcass merit traits in three unrelated cattle populations including hybrid, Angus and Charolais populations.

A preliminary analysis of the IGF1 gene sequence using Transcription element search system (TESS, http://www.cbil.upenn.edu/tess) (Schug 2003) revealed that the “C” allele of the c.−512C>T introduces a putative binding site (TCCA) for nuclear factor I (NFI) (Nagata et al. 1983). This NFI is a family of multifunctional transcription factors occurring in four isoforms in vertebrates and acting as transcriptional activators or repressors (Gronostajski, 2000). In bovine, three NFI transcription factors (NFIA, NFIB and NFIC) have been reported in the databases (http://www.ncbi.nlm.nih.gov/sites/entrez). In general, NFI can act as an activator or repressor for many genes that are ubiquitously expressed as well as hormonally, nutritionally and developmentally regulated (Gronostajski 2000). The adipocyte-specific NFI regulation over gene expression was demonstrated using the 3T3-F442A cell line (Graves et al. 1991). Miura et al. (2004) also reported the regulatory role of NFI on white adipose tissue-specific gene expression in transgenic mice. In addition, NFI controls the expression of stearoyl CoA desaturase gene 1 during preadipocyte differentiation in the mouse 3T3 cell line (Singh & Ntambi, 1998). This stage of differentiation of precursor cells into mature fat cells is accompanied by enhanced expression of IGF1 in transgenic mice (Rajkumar et al. 1999), which indicates the role of IGF1 in fat cell developmental processes. In Angus beef cattle, Davis & Simmen (2000) reported that bulls with lower IGF1 concentration had higher backfat thickness. Similarly, circulating IGF1 was found to correlate negatively with carcass fat percentage, fat accretion rate and fat thickness in Simmental crossbred bulls (Anderson et al. 1988). In this study, the promoter SNP c.−512C>T of IGF1 was found to be significantly associated with ultrasound and carcass backfat thickness in Angus steers but not in the hybrid and Charolais populations. The three unrelated populations used in this study represent different biological types. In comparison to the hybrid and Charolais breeds, Angus has greater fat depth on average (Table 1), presumably due to the early maturity in Angus, which allows the steers to produce more fat at a younger age (Gregory et al. 1994). It remains undetermined, however, whether the significant IGF1 SNP association in the Angus population is due to the linkage phase change between the SNP and the causative SNP or SNPs across the populations, or whether it is due to an adipose tissue related regulatory role of the IGF1 promoter SNP on fat deposition.

SNP c.47807T>C was found associated with SWT and CWT in the Angus population. Association of IGF1 polymorphisms with body weight (Bian et al., 2008), improved growth and muscle weight (Zhou et al., 2005) have been reported in chicken which also suggests the potential effect of IGF1 on animals body weight as well and supports the association of IGF1 with SWT and CWT in Angus.

Interestingly, the IGF1 haplotypes showed significant random effects on all the fat and carcass weight related trait in the hybrid population but not in the two pure bred populations. However, no significant haplotype fixed effect was observed for the traits. Further association study using a larger sample size is needed to discern the IGF1 haplotype effect.

Overall, we found that different SNP alleles of c.−512C>T and c.47807T>C can affect fat related carcass traits in Angus and Charolais cattle and the haplotypes of SNPs have potential effects. A recent study on IGF1 in dairy cattle revealed that c.−512C>T affect IGF1 gene expression while the “CC” genotype has the highest expression level in blood and this likely affects milk and meat production traits (Maj et al., 2008). Therefore, it is expected that the IGF1 expression difference may also present in beef cattle and IGF1 SNPs could be a valuable tool for marker assisted selection in beef industries.

Recently, Helgeson & Schmutz (2008) reported that an A>T SNP in pro-melanin-concentrating hormone (PMCH), located in close proximity to IGF1, was significantly associated with average fat and grade fat in two crossbred populations of *Bos taurus*. The SNP, which is located in the regulatory region of PMCH, has been proposed to introduce a binding site for transcriptional repressor, adenovirus E4 promoter binding protein and consequently affects fat deposition in beef cattle (Helgeson & Schmutz 2008). Therefore, further validation of the SNP associations in different cattle populations and functionality analyses of the IGF1 SNPs as well as the PMCH SNP will likely provide insight into the genetic mechanisms regulating the deposition of backfat in beef cattle.

3.7. Insulin (INS)

3.7.1. Single SNP association

We genotyped two previously reported SNPs, c.−526T>C and c.−397T>C from the public databases. Both SNPs are located in the promoter region of INS. The “C” allele for both of the SNPs was found as minor alleles across all three cattle breeds. In Angus, only two specific steers (A187P and A843R) were found as heterozygous and rest of the animals were homozygous for “T” allele for both of the SNPs. Therefore, both of the SNPs were excluded from further analyses in the Angus population due to the extremely low minor allele frequencies (0.005). In hybrid and Charolais, both the SNPs were in Hardy-Weinberg equilibrium ($P>0.05$) (Table 3.1.).

In the hybrid population, significant and slightly significant additive effects of c.−526T>C have been found on UBF ($P<0.056$), AUBF ($P<0.052$), SWT ($P<0.036$) while dominance effects of the sSNP were found on UBF ($P<0.051$), SWT ($P<0.005$), CWT ($P<0.025$), CMAR ($P<0.072$). Animals having the “TT” genotype had 12% higher UBF, 17% higher AUBF, 3.77% more SWT in comparison to the “CC” genotype containing animals. Also, heterozygous “CT” animals had higher UBF, higher SWT, higher CWT and more CMAR than homozygous “CC” or “TT” animals. For c.−397T>C, slightly significant allele substitution effect has been found on AUBF ($P<0.060$) while homozygous “TT” animals had 17% more AUBF in comparison to the homozygous “CC” animals, accompanied by significant additive effect ($P<0.028$) on the trait. In addition, significant and slightly significant additive effects of c.−397T>C have been found on UBF ($P<0.047$), AUBF ($P<0.052$), SWT ($P<0.016$) while dominance effects of c.−397T>C were found on UBF ($P<0.088$), SWT ($P<0.005$), and CWT ($P<0.044$) in the hybrid population. Homozygous “TT” animals had 12.43% higher UBF, 19.19% higher AUBF and 4.33% more SWT in comparison to the “CC” animals, whereas heterozygous “CT” animals had higher UBF, SWT and CWT in comparison to the homozygous animals.

In the Charolais population, no significant allele substitution effects, additive effects or dominance effects were found at the P<0.05 for INS SNPs under investigation, however, c.−526T>C had slightly significant additive effects on AUBF (P<0.054) with 15% increased trait value for the “CC” animals.

3.7.2. Haplotype blocks and haplotype association

Assessment of LD between SNPs and search for potential haplotype blocks using HAPLOVIEW revealed that the pairwise LD between the two SNPs was very high in hybrid (r^2=0.95) while in Charolais the SNPs were in complete LD (r^2=1), forming a strong haplotype block Further reconstruction of haplotypes was performed by HAPLORE and four haplotypes were found among the animals (Table 3.24.). Haplotype T-T (HINS_01 and CINS_01) was found as the most frequent haplotype in both the hybrid and Charolais populations. Frequencies of other three haplotypes i.e., T-C, C-T and C-C were very comparable for two breeds.

Random effects of haplotypes (LR test) were estimated and the haplotype random effects significant in the hybrid population for all the phenotypic traits except for CMAR, while in the Charolais population, no significant random effects were found (Table 3.25.). Further assessment of the fixed effect of haplotypes in the hybrid cattle population revealed that HINS_01 (T-T) had a slightly significant haplotype substitution effect (P<0.077) and additive effect (P<0.078) on CMAR although the haplotype random effect was not significant (P<0.2878).
HINS_03 (C-T) had significant and slightly significant haplotype substitution effects on SWT (P<0.034), CWT (P<0.029) and CMAR (P<0.062). Animals substituted by HINS_03 can increase SWT by 1.85%, CWT by 1.98% and CMAR by 3.18%. However, the additive and dominance effects were not estimated for

HINS_02 and HINS_03 haplotypes due to the absence of haplotype homozygous animals. Lastly, HINS_04 (C-C) had significant and slightly significant haplotype substitution effects on UBF ($P<0.050$), AUBF ($P<0.049$) and SWT ($P<0.027$) with significant haplotype additive effects on UBF ($P<0.026$), AUBF ($P<0.027$), SWT ($P<0.004$) and CWT ($P<0.065$). Haplotype HINS_04 homozygous animals had 14.26% lower UBF, 19.88% lower AUBF, 5.31% lower SWT and 3.59% lower CWT in comparison to animals containing other haplotypes (Table 3.26.).

3.7.3. Discussion

Beef cattle body fat deposition is an ultimate consequence of various metabolic reactions. Fat cells from different location of the body can utilize different energy source and nutrients for lipid synthesis and subsequent deposit as fat.
As an example, glucose is the primary substrate for intramuscular adipocyte cells, whereas acetate is utilized by subcutaneous adipocyte cells to synthesis fatty acids. Therefore, diets rich in starch may accelerate intramuscular fat deposition in contrast to subcutaneous fat deposition (Smith and Crouse, 1984; Choat et al., 2003). Conversion of glucose to fat indicates that the enzymes and hormones of the glyconogenesis pathway e.g., insulin can be a determinant of fat deposition and carcass merit traits in beef cattle.

Insulin is a pancreatic hormone and well-known for its hypoglycaemic effect. Concentration of insulin in plasma was reported to be positively correlated with the food and energy intake (Bassett, 1974; Brockman and Laarveld, 1996). The effect of insulin was previously demonstrated in several studies as the measurement of insulin sensitivity on different tissues. It is evident that insulin stimulates glucose conversion to glyceride-glycerol in intramuscular adipose tissue instead of subcutaneous adipose tissue (Gilbert et al., 2003) may contribute to increase intramuscular fat. Additionally, INS also can upregulate the lipogenic enzymes, affecting transcription factor SREBP-1c activity (Repa et al., 2000; Shao et al., 2002) and/or down regulate the rate of lipolysis by stimulating either cyclic adenosine monophosphate (cAMP) to generate adenosine monophosphate kinase (AMPK) or protein phosphatise-1 (Ragolia and Begum, 1998; Duncan et al., 2007) to deactivates hormone-sensitive lipase (HSL). INS activity in lipid metabolism supports that it could be a potential functional candidate gene for fat deposition related carcass traits in beef cattle. Moreover, INS is located at 55.38 cM on BTA29 (http://genomes.sapac.edu.au/bovineqtl/) which resides under a QTL region for CMAR (30 to 58cM) (MacNeil and Grosz, 2002) and HCW (50 to 62 cM) (Casas et al., 2003a). This signify the potential importance of INS as a positional candidate gene for further investigation to identify the gene specific SNP markers associated with fat deposition related traits in beef cattle.

Both of the SNPs examined in this study were located in the promoter region of the INS. A search for putative transcription factor binding site in the area of respective gene sequence by using TESS (Transcription element search system) (http://www.cbil.upenn.edu/tess) (Schug 2003) found that for c.−526T>C, the "T" allele has no binding site for any promoters but "C" allele provides RAF (v-raf murine oncogene homolog) (Pfeifer et al., 1987) binding site. For c.−397T>C, the "T" allele provides a binding site for nuclear factor I (NF-I) (Nagata et al., 1983) and the "C" allele introduces a binding site for transcription factor 9 (TF9), alternatively known as GC factor (GCF) (Kageyama and Pastan, 1989). In bovine, three family members of RAF (RAF-1, ARAF and BRAF) (Avruch et al., 1994, Daum et al., 1994), three isoforms of NFI transcription factors (NFIA, NFIB and NFIC) and a pseudo gene similar to GC-rich DNA binding factor (GCF) has been reported (www.ncbi.nih.nlm.gov).

From the single marker and haplotype results, it is evident that the SNP c.−397T>C affects AUBF in the hybrid cattle population with the "C" allele associated with lower fat growth rate, and haplotype C-C (HINS_04) was also associated with lower UBF and AUBF. Lowering the fat depth may be due to the repression of the INS expression caused by the transcriptional factor GCF. Interestingly, the promoter region of INS is very rich in "G" and "C" nucleotides.

The 50 bases upstream and downstream of SNP c.−397T>C has about 75% “G” and “C” nucleotides. Therefore, it is high likely that GC rich transcription factor, GCF may harbour in this area and repress the INS transcription rate. Moreover, Gilbert et al. (2003) demonstrated that insulin stimulates glucose conversion to glyceride-glycerol which supports the development of intramuscular adipose tissue instead of subcutaneous adipose tissue. Therefore, it is not clear how INS concentration in plasma may affect the subcutaneous fat depth related trait like UBF.

In previous studies, it was found that tissue specific insulin sensitivity can affect fat production in cattle (McCann and Reimers, 1985a; Eisemann and Huntington, 1994) and sheep (McCann et al., 1986; Bergman et al., 1989). Variation in insulin sensitivity may affect caloric partitioning among tissues and tissue development which may change with age of the animal **(**Rhoades et al., 2007). This may be the reason behind the lack of significant effect of INS on carcass average backfat thickness (Eisemann et al., 1997). Additionally, for SWT and CWT lower trait values were observed for <u>C-C</u> (HINS_04) haplotypes with significant additive effects, which could be the consequence of the INS transcriptional repression followed by the decreased rate of glucose uptake by peripheral tissues (Schoonmaker et al., 2003). This finding is also supported by the INS position under the QTL for HCW (50 to 62 cM) (Casas et al., 2003a) in beef cattle. Lastly, the effect of RAF is not clear as a transcriptional factor, although it may contribute to the variation of trait values through serine/threonine kinase based differential regulation in activities (Morrison and Culter et al., 1997).

The significant haplotype fixed effect on CMAR in the hybrid population may be false positive due to the absence of significant haplotype random effect on the trait. However, it is speculated that the insulin may have effects over marbling via glucose metabolism as the negative correlation between carcass adiposity and plasma glucose concentration has been found (Matsuzaki et al., 1997; Schoonmaker et al., 2003). Dunshea et al. (1995) reported that beef steers reduce glucose level by 55% in response to the very high levels of serum insulin (>600 mU/L), and Schoonmaker et al. **(**2003) suggested that increased serum insulin may increase marbling score. Moreover, INS is located under the QTL region for CMAR, which is in agreement with our result and supports its potential functional influence on intramuscular fat deposition and carcass marbling.

However, the significant effects of INS on the fat and carcass traits were only found in the hybrid cattle population. That could be due to a larger population size used for association analyses in comparison to the Charolais population. Breed specific body metabolism differences also likely contribute to the non-significant INS associations with fat related traits in Charolais. This assumption is supported by the previous study, where breed differences in plasma levels of insulin and carcass composition was found between Japanese cattle breeds and Holstein (Matsuzaki et al., 1997).

Conclusively, we can say that more research is needed to uncover the functional effect of SNPs, c.−526T>C and c.−397T>C over INS gene expression and to validate the significant effects on the different fat deposition and carcass merit traits. Further study may also provide insight into the breed specific functional role of the INS gene specific SNPs which could be valuable for the implantation of marker assisted selection programs in beef industries.

3.8. Hormone sensitive lipase (LIPE)

3.8.1. Single SNP association

In total, 15 SNPs which included 7 previously reported SNPs in the public databases and 8 novel SNPs discovered in-house were genotyped on the steers of the three cattle populations. All SNP's minor alleles, minor allele frequencies (MAF), observed heterozygosity (OHET) has been presented in Table 3.1. Remarkably for SNPs c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A, c.8560C>T and c.8731G>A, the minor alleles were "G", "G", "A", "C", "G", "C", "G", "C", respectively in the Angus population while these alleles were found as major alleles in the hybrid and Charolais populations, i.e. allele frequencies are greater than 0.50. SNP c.8782G>C was found monomorphic and the "G" allele was fixed in the Angus cattle population. Except for SNPs c.2692C>T in the Angus population, c.5332G>A and c.8563C>T in the Charolais population, all other SNPs were in HWE (P>0.05) (Table 3.1.).

In the hybrid cattle population, significant and slightly significant allele substitution effects were found for c.8782G>C (P<0.018) on AUREA and c.8689A>G (P<0.079), c.9937A>T (P<0.037) on AVBF. Significant additive effects were found for c.8782G>C on CMAR (P<0.024), c.9937A>T on SWT (P<0.046) while significant dominance effects were found for c.8689A>G on CREA (P<0.014), c.8782G>C on CMAR (P<0.003) and c.9937A>T on SWT (P<0.030) and CREA (P<0.013). Animals having "AA" genotypes of c.8689A>G had 7.4% less AVBF than "GG" animals, and the "AG" animals had lower CREA than homozygous animals. Animals containing "GG" genotypes of c.8782G>C had 34.45% more AUREA, 11% more CMAR than the "CC" animals. Also, "AA" animals of c.9937A>T had 4.53% more SWT and 10.85% more AVBF while heterozygous "AT" animals had lower SWT and CREA than homozygous animals.

In the Angus population, significant and slightly significant allele substitution effects were found for c.276A>G (P<0.092) and c.8731G>A (P<0.090) on AUREA, c.8563C>T (P<0.049) on CMAR. Significant additive effects were found for c.8782G>C on CMAR (P<0.024), c.9937A>T on SWT (P<0.046) while significant dominance effects were found for c.8689A>G on CREA (P<0.014), c.8782G>C on CMAR (P<0.003) and c.9937A>T on SWT (P<0.030) and CREA (P<0.013). Significant and slightly significant dominance effects were found for c.−11470G>A (P<0.081), c. −9627G>A (P<0.093), c.276A>G (P<0.072), c.7195C>T (P<0.040), c.7324G>A (P<0.052), c.8560C>T (P<0.085) and c.8731G>A (P<0.044) on AVBF. For all of the SNPs having the dominance effect on AVBF increased the trait value for heterozygous animals in comparison to the homozygous genotype of respective SNPs.

In the Charolais population, significant and slightly significant allele substitution effects were found for c.8549A>G (P<0.011), c.8560C>T (P<0.074) and c.8563C>T (P<0.042) on UREA, c.8782G>C (P<0.041) and c.9937A>T (P<0.097) on AUBF, c.8563C>T (P<0.064) on AUREA, c.8563C>T (P<0.032) on SWT, c.8782G>C (P<0.081) on CWT. Significant and slightly significant additive effects were found for c.8549A>G (P< 0.004) on UREA, c.8563C>T (P<0.084) on AUREA, and c.8549A>G (P<0.095), c.8560C>T (P<0.073), c.8731G>A (P<0.085) on CWT, while dominance effects were found significant for c.7195C>T (P<0.043), c.8560C>T (P<0.029), c.8689A>G (P<0.031), c.8731G>A (P<0.042), c.9937A>T (P<0.019) on UBF, c.8549A>G (P<0.040) on SWT, c.8731G>A (P<0.011) on CWT and c.8560C>T (P<0.038) on CMAR. Animals having the “AA” genotypes of c.8549A>G decreased UREA by 4.32%, “CC” genotypes of c.8560C>T increased UREA by 2.12%, “CC” genotypes of c.8563C>T increased UREA by 3.82% in comparison to the minor allele homozygous animals of respective SNPs. Animals containing the “CC” genotype of c.8563C>T had 1.89% increased SWT in comparison to the “TT” genotypes.

Least square means of traits values for different SNPs genotypes and their estimated effects have been given in Table 3.27).

3.8.2. Haplotype blocks and haplotype association

Further analyses of LIPE SNPs using HAPLOVIEW revealed one haplotype block (hybrid block 1) spanning 8 SNPs at the upstream of the gene including c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A, c.8549A>G in the hybrid cattle population. High pair wise LD (r^2>0.5) were prominent for SNPs under the gene region covered by the haplotype block. In the Charolais cattle population, a similar haplotype block spanning the SNPs at the beginning of the gene was observed but the haplotype block structure was shortened by 1 SNP excluding c.8549A>G from the haplotype block. For the Angus population, the haplotype block with high LD between SNPs was interrupted by SNP c.5332G>A, splitting the haplotype block into two haplotype blocks, which includes Angus haplotype block 1 (c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T) and Angus haplotype block 2 (c.7195C>T, c.7324G>A, c.8549A>G, c.8560C>T). The SNP (c.5332G>A) had lower LD (r^2<0.50) with other SNPs. For all the three populations, SNPs at the downstream of the gene showed low pair-wise LD (r^2<0.5). However, for the purpose of haplotye reconstruction, SNPs with lower LD at the downstream region of LIPE were considered as another haplotype blocks, i.e. hybrid haplotype block 2 spaning c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T; Angus haplotype block 3 spanning c.8563C>T, c.8689A>G, c.8731G>A, c.8893G>A, c.9937A>T and Charolais haplotype block 2 spanning c.8549A>G, c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T. In addition, we assumed a haplotype block named as Angus block 4 spanning SNPs c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A (Figure 3.19.) in order to capture the effect of the SNP c.5332G>A which resides between Angus block 1 and Angus block 2 and has low pairwise LD (r^2<0.5) with other SNPs,.

Haplotype reconstruction using HAPLORE revealed, 64 types of haplotypes for the hybrid haplotype block 1 where 5 haplotypes were considered as major (freq. ≥ 0.03) and 51 types of haplotypes for hybrid block 2 where 6 haplotypes were considered as major haplotype (freq. ≥ 0.03). For the Angus population, 11, 12, 17 and 25 types of haplotype were found for haplotype block 1, block 2, block 3 and block 4 respectively. Within these blocks the numbers of major (freq. ≥ 0.03) haplotypes were 5, 4, 7 and 6 respectively. Finally, for the Charolais block 1 and block 2 we had 30 haplotypes with 7 major and 61 haplotypes with 6 major (freq. ≥ 0.03), respectively (Table 3.28.).

Random effects (P<0.05) of haplotypes from different haplotypes blocks were found to be significant on all fat deposition and carcass merit traits in the there populations except for haplotypes ALIPEB1 from Angus haplotype block 1 and haplotype ALIPEB2 from Angus haplotype block 2. Consequently, estimation of the hapotype fixed effects was conducted for major haplotypes (freq.≥0.03) under the haplotype blocks which had significant random effects on the traits (Table 3.29.)

In the hybrid cattle population, no haplotypes from haplotype block 1 had significant fixed effects on any of the phenotypic traits. In the haplotype block 2, significant and slightly significant haplotype substitution effects were found for haplotype HLIPEB2_01 (T-C-A-A-G-G-A) on UBF (P<0.072), haplotype HLIPEB2_03 (C-C-G-G-G-G-T) on AVBF (P<0.024) and haplotype HLIPEB2_06 (T-C-A-G-G-G-A) on UBF (P<0.001), AUBF (P<0.023), SWT (P<0.007), CWT (P<0.033), AVBF (P<0.002), LMY (P<0.014), CMAR (P<0.096). Significant and slightly significant additive effects of haplotypes were found for HLIPEB2_02 (C-C-A-G-G-G-A) on AUREA (P<0.024), CMAR (P<0.049) and for HLIPEB2_03 on SWT (P<0.041), CREA (P<0.057) while dominance effects were found for HLIPEB2_02 on AUREA (P<0.024), CMAR (P<0.049) and for HLIPEB2_03 on SWT (P<0.041), CREA (P<0.057). Haplotype homozygous animals for

HLIPEB2_01 had 9.17% increased UBF; HLIPEB2_03 had 12.21% more AVBF in comparison to animals having other haplotypes. Lastly, haplotype HLIPEB2_06 showed consistent effects over different traits while the substitution of HLIPEB2_06 had a decreased UBF (20.7%), lower SWT (4.8%), lower CWT (3.8%), lower ABVF (21.34%), higher LMY (3.33%) and lower CMAR (5.36%) (Table 3.30.).

In the Angus population, we have analyzed major haplotypes (freq.≥0.03) from Angus haplotype block 3 and Angus haplotype block 4 to estimate fixed effects of haplotypes (Table 3.31.). In Angus haplotype block 3, significant and slightly significant haplotype substitution effects were found on UBF for ALIPEB3_02 (C-A-G-G-T) (P<0.063) and ALIPEB3_06 (C-G-G-G-A) (P<0.099); on UREA for ALIPEB3_05 (P<0.012); on AUREA from ALIPEB3_01 (C-A-A-G-A) (P<0.086); on SWT for ALIPEB3_05 (P<0.034); on CWT for ALIPEB3_05 (0.033); on AVBF for ALIPEB3_01 (P<0.009) and ALIPEB3_05 (P<0.073); on LMY for ALIPEB3_01 (P<0.019); on CREA for ALIPEB3_05 (C-A-G-G-A) (P<0.099); on CMAR for ALIPEB3_03 (C-G-A-G-A) (P<0.022) and ALIPEB3_04 (P<0.084). Significant and slightly significant additive effects were found on AUREA for ALIPEB3_01 (P<0.060) and ALIPEB3_04 (P<0.022); on SWT for ALIPEB3_04 (C-G-G-G-T) (P<0.015); on CWT for ALIPEB3_04 (P<0.008); on AVBF for ALIPEB3_01 (P<0.047); on LMY for ALIPEB3_01 (P<0.072); on CMAR for ALIPEB3_03 (P<0.007). Significant and slightly significant dominance effects were found on UBF for ALIPEB3_01 (P<0.038); on AUREA for ALIPEB3_04 (P<0.036); on SWT for ALIPEB3_04 (P<0.007); on CWT for ALIPEB3_04 (P<0.005); on CMAR for ALIPEB3_04 (P<0.019). No haplotype homozygous animal was available for ALIPEB3_05, therefore, we didn't calculate the additive or dominance effects and ALIPEB3_07 was not associated with any of the traits we analyzed. ALIPEB3_01 haplotype homozygous animals increased the AVBF by 11.42% and LMY by 3.02%; ALIPEB3_03 haplotype homozygous animals inceased CMAR by 16.06%; ALIPEB3_04 haplotype homozygous animals inceased SWT by 5.89%, icreased CWT by 7.11% and CMAR by 4.41% in comparison to animals having other haplotypes. Also, substitution of other haplotypes by haplotype ALIPEB3_05 can increase UREA by 4.52%, increase SWT by 2.54%, icrease CWT by 2.91%, increase AVBF by 10.98%, and increase CREA by 3.61%.

In Angus Haplotype block 4, out of 6 major haplotypes (freq≥0.03) significant and slightly significant haplotype substitution effects were found for ALIPEB4_01 on CWT (P<0.072) and ALIPEB4_06 on LMY (P<0.048) and CREA (P<0.093). None of the additive and dominance effects were significant for ALIPEB4_01 (G-T-A-T-A) and ALIPEB4_02 (A-C-G-C-G) while additive and dominance effects were not calculated for ALIPEB4_03 (A-T-G-T-G), ALIPEB4_04 (G-T-G-T-A), ALIPEB4_05 (G-C-A-C-A) and ALIPEB4_06 (A-T-G-C-G) due to absence of haplotype homozygous animal (Table 3.31.). Haplotype ALIPEB4_01 homozygous animals decreased the CWT by 1.46% in comparison to animals containing other haplotypes. Also, substitution of other haplotypes by haplotype ALIPEB4_06 can decrease LMY by 3.77% and decreased CREA by 4.09%.

In the Charolais population, major haplotypes (frequency>0.03) were tested for fixed effects from Charolais haplotype block 1 and Charolais haplotype block 2. In Charolais haplotype block 1, significant and slightly significant haplotype substitution effects were found on UREA for CLIPEB1_04 (A-A-A-T-G-T-G) (P<0.084); on SWT for CLIPEB1_02 (A-A-G-T-A-T-A) (P<0.023) and CLIPEB1_03 (A-A-G-T-G-T-A) (P<0.015); on CWT for CLIPEB1_02 (P<0.035); on LMY for CLIPEB1_04 (P<0.021) and CLIPEB1_05 (G-G-G-T-A-C-A) (P<0.037); on CREA for CLIPEB1_03 (P<0.074), CLIPEB1_04 (P<0.010) and CLIPEB1_05 (P<0.025). Significant and slightly significant additive effects were found on UBF for CLIPEB1_03 (P<0.033); on AUBF for CLIPEB1_03 (P<0.034); on SWT for CLIPEB1_03 (P<0.077); on CWT for CLIPEB1_03 (P<0.015); on CREA for CLIPEB1_03 (P<0.042). Significant dominance effects were found on UBF for CLIPEB1_03 (P<0.005); on AUBF for CLIPEB1_02

(P<0.044) and CLIPEB1_03 (P<0.002); on UREA for CLIPEB1_01 (G-G-A-C-G-C-G) (P<0.038); on CWT for CLIPEB1_03 (P<0.019). Haplotype homozygous animals of CLIPEB1_02 decreased SWT by 2.08%, decreased CWT by 3.25%; CLIPEB1_03 increased SWT by 9.28%, decreased CREA by 19% in comparison to animals containing other haplotypes. Also, substitution of other haplotypes by haplotype CLIPEB1_04 can increase UREA by 2.98%, increase LMY by 3.10% and increased CREA by 6.20%; CLIPEB1_05 can increase LMY by 2.85% and increased CREA by 5.47%.

In Charolais haplotype block 2, significant and slightly significant haplotype substitution effects were found on UBF for CLIPEB2_03 (P<0.052); on UREA for CLIPEB2_01 (A-C-C-A-G-G-G-A) (P<0.003); on AUBF for CLIPEB2_03 (A-T-C-A-A-G-G-A) (P<0.026); on SWT for CLIPEB2_03 (P<0.081), CLIPEB2_05 (G-C-C-A-G-G-G-A) (P<0.096) and CLIPEB2_06 (A-C-T-A-G-G-G-A) (P<0.097); on CWT for CLIPEB2_06 (P<0.057); on AVBF for CLIPEB2_01 (P<0.021); on LMY for CLIPEB2_01 (P<0.015). Significant and slightly significant additive effects were found on UBF for CLIPEB2_02 (G-C-C-G-G-G-G-T) (P<0.012); on UREA for CLIPEB2_01 (P<0.009); on AVBF for CLIPEB2_01 (P<0.045); on LMY for CLIPEB2_01 (P<0.076). Significant dominance effects were found on UBF for CLIPEB2_02 (P<0.003); on SWT for CLIPEB2_01 (P<0.016). Haplotype homozygous animals of CLIPEB2_01 decreased UREA by 5.75%, increased AVBF by 2.14%, decreased LMY by 2.91%; CLIPEB2_02 decreased UBF by 29.87%; CLIPEB2_03 increased UBF by 9.66%, increased AUBF by 25.6%, decreased SWT by 0.76%; CLIPEB2_06 increased CWT by 9.88% in comparison to animals containing other haplotypes. No other haplotypes from these two blocks were found associated with any other traits analyzed. Additive and dominance effects for CLIPEB1_04, CLIPEB1_05, CLIPEB1_06 (A-G-G-T-G-T-G), CLIEPB1_07 (G-A-A-C-A-C-A) and CLIPEB2_05 were not estimated due to absence of haplotype homozygous animal (Table 3.32).

3.8.3. Discussion

LIPE is an enzyme which catalyzes the breakdown of triglycerides in adipose tissue cells and thus controls the rate of lipolysis (Holm et al., 1988). It is mainly available in cell cytoplasm and abundant in adipose tissues including other tissues i.e., skeletal muscle, cardiac muscle, ovarian and adrenal tissues. LIPE activity has a special feature to degrade specifically diacylglycerol rather than triacylglycerol by eleven fold while it can also function as cholesterol esters and retinyl esters hydrolases (Holm, 2003; Yeaman, 2004). It is also termed as hormone sensitive lipase (HSL) due to its sensitivity against some hormones including catecholamine, glucagon, insulin, leptin and adrenocorticotropin hormone (ACTH) (Holm et al., 1988, 2000 & 2003; Kraemer and Shen 2002). In the mouse model, it was found that the LIPE-independent lipolysis can’t produce adequate amount of free fatty acids to release in plasma and mobilization of the free fatty acids may affect cellular energy level. Conversely, in the absence of LIPE recruitment of fatty acid is reduced within the cytosol preventing re-esterification of fatty acids and regeneration of TAG (Haemmerle et al., 2002a and 2002b; Voshol et al., 2003).

Due to all the above mentioned functions, LIPE is considered to be a functional gene of lipid metabolism in animals (Ma et al., 2007, Holm et al., 1988). LIPE was studied as a candidate gene for fatness in pig (Wu, 1998), and Steffen et al., (1981) showed that LIPE could be a rate-limiting enzyme for lipolysis in swine. Recently, LIPE gene expression was studied in bovine mammary gland and it was assumed that it plays a pivotal role in lipid and energy metabolism in lactating mammary gland (Yonezawa et al., 2008, Xu et al., 2008). However, LIPE resides on the BTA 18, within 51.10cM to 51.12cM (http://genomes.sapac.edu.au/bovineqtl/) and no QTL has been so far reported at that chromosomal region. However, we selected LIPE as a functional candidate gene for fat deposition and carcass merit traits in beef cattle, considering the rate-limiting catalytic activity on lipolysis and functional significance in animal fat metabolism.

From single SNP association analyses, it was found that, c.8563C>T, c.8782G>C and c.9937A>T were associated with different traits across three cattle populations. The c.8563C>T is a synonymous SNP (Leu565Leu) and the “C” allele showed increased trait values (CMAR, UREA, AUREA and SWT) for all associated traits in both the Angus and the Charolais populations. The unfavourable “T” allele is the minor allele for all the three populations and a significant deviation in HWE allele frequencies was observed in the hybrid (P=5.0E-4), Angus (P=0.0605) and Charolais (P=0.0097) populations, suggesting a phenotypic trait based selection pressure on cattle populations leading to only 4, 2 and 7 “TT” animals in the hybrid, Angus and Charolais populations, respectively. SNP c.8782G>C is a nonsynonymous polymorphism which changes Ala 638 to Pro, and “G” is the favourable allele which increases trait values in the hybrid population (AUREA) and Charolais (AUBF and CWT) cattle. Alanine and proline both have least catalytic propensity and due to their inert nature they almost never participate in catalytic activity of enzymes (Bartlett et al., 2002; Holliday et al., 2007 & 2009). However, these two amino acids are nonpolar amino acids but proline has a higher molecular mass, and contains an unusual ring to the N-end amine group and can disrupt α-helical secondary structure of protein (Zhang and Peng, 2000; www.en.wikipedia.org), which likely affect LIPE activity. SNP c.9937A>T is located 3′ near gene while the “A” allele is the favourable allele to reduce fat depth in the hybrid (AVBF) and Charolais (AUBF) population. Further study is needed to valide the valide the SNP association and to examine the possible functionality of the SNP.

SNP c.8689A>G which is associated with the fat thickness in the hybrid cattle population is a nonsynonymous SNP causing a change Ile607Val. Both of the amino acids is nonpolar in nature, having aliphatic side chain with very low enzymatic propensity and rarely participate in enzyme catalytic activity (Bartlett et al., 2002; Holliday et al., 2009), while valine has lower molecular mass and more solubility in water (g/100g, 25 ºC) in comparison to isoleucine (TMI, 1989; CRCHCP, 1977; www.prowl.rockefeller.edu/aainfo/), which is the product of unfavourable "G" allele causing more AVBF. For the synonymous SNP c.276A>G (Tyr92Tyr) and the nonsynonymous SNP c.8731G>A (Glu621Lys), minor alleles "A" and "G" were favourable for AUREA in the Angus populaiton, respectively. The biological significance of c.276A>G is unpredictable due to no change in amino acid in the LIPE protein. But for c.8731G>A, the change in animo acid may have significant consequences at the protein level which may cause differential LIPE enzymatic activity, because the glutamic acid (mass 57.05 dalton) is acidic in nature but the lysine (mass 128.17 dalton) has basic properties. However, both of them have flexible side chains and their catalytic propensity in the enzymatic reaction are similar (Bartlett et al., 2002; Holliday et al., 2007 & 2009). Two other SNPs c.8549A>G and c.8560C>T are nonsynonymous and changes Gln560Arg and Ser564Pro, respectively. These two SNPs showed associations with UREA in Charolais. For Gln560Arg, the amino acid change is from polar to basic (glutamine to arginine) and it may double the catalytic propensity while for Ser564Pro the change is from polar to nonpolar (serine to proline) and it may reduce the catalytic propensity to half (Bartlett et al., 2002). All these changes may affect the catalytic properties of LIPE, because the glutamine and serine are comparatively less soluble than arginine and proline, and arginine may facilitate binding to molecules, e.g., facilitate DNA binding of proteins in comparison to glutamine, whereas, serine acts as hydrogen donor to enzymes but proline disrupts protein folding structure like α-helix or β-sheet (TMI, 1989; CRCHCP, 1977; www.en.wikipedia.org; www.prowl.rockefeller.edu/aainfo; Zhang and Peng, 2000). Therefore, "A" allele of c.8549A>G which produces "glutamine"and "T" allele of c.8560C>T which produces "proline" are the unfavourable alleles and likely affect the LIPE enzymatic activity which cause decreased UREA and CWT in Charolais beef cattle.

Interestingly, haplotype reconsturction showed that two most frequent haplotypes of hybrid haplotype block 1, i.e., HLIPEB1_01 & HLIPEB1_02 (G-G-A-C-G-C-G-G & A-A-G-T-A-T-A-A) and Charolais haplotype block 1, i.e., CLIPEB1_01 & CLIPEB1_02 (G-G-A-C-G-C-G & A-A-G-T-A-T-A) shared the alleles from the corresponding SNPs, while, the haplotypes in Angus haplotype block 1 were shortendend to span four SNPs, i.e., ALIPEB1_01 and ALIPEB1_02 (A-A-G-T & G-G-A-C) but still sharing the same SNP alleles of the four SNPs The similarity of this haplotype block may be an indicator of the evolutionary consereved region of LIPE gene that exists across different cattle populations. LD analyses supports this assumption while the SNP alleles are in high LD ($r^2>0.5$) with each other. However, the break point of haplotype block 1 and block 2 in the Angus population caused by SNP c.5332G>A, which had a low pairwise LD ($r^2<0.5$) with other SNPs, could be a recently introduced recombination hot spot in the experimental Angus cattle population. Within each haplotype block, the haplotype diversity was low in the Angus population that results in less number of haplotypes within each haplotype block than that in the hybrid and Charolais populations (Table 3.28). In contrast, the hybrid populations had the highest haplotype diversity which may be due to a larger population size used in the study and/or their biological origin from different breeds of cattle that had likely contributed to the versatile allelic combination in haplotypes.

Haplotypes random effects have been found for all of the haplotype blocks except Angus haplotype block 1 and Angus haplotype block 2, those cover the upstream region to middle part of the LIPE gene region. The same region also covered by the Hybrid haplotype block 1 and Charolais haplotype block 1 having significant random effects. The absence of the random effects in Angus may be due to the breakage of the common haplotype block (hybrid and Charolais blocks) into two blocks in presence of c.5332G>A. Supporting this assumption we constructed Angus haplotype block 4 to capture the effect of c.5332G>A which had significant random effects on fat related traits.

In hybrid cattle haplotype associations, the effect of HLIPEB2_06 (T-C-A-G-G-G-A) which decreases UBF was found to be completely opposite to the effect of HLIPEB2_01 (T-C-A-A-G-G-A) and these two haplotypes differed from each other only by the “G” versus “A” allele donated by missense SNP c.8731G>A (Glu621Lys). The average molecular mass differences of amino acids along with their differences in chemical properties, i.e., glutamic acid is acidic while lysine is basic in nature, may cause the enzymatic activity differences of LIPE, which could be the possible reason for the controversial effect from these two haplotypes. Additionally, glutamic acid has higher catalytic propensity than lysine which may increase LIPE activity in presence of HLIPEB2_06 leading to higher rate of lipolysis and subsequently reduce UBF and AVBF, CMAR as well as increase LMY with significant association with these traits. However, SNP c.8731G>A was not associated with UBF in the single marker association analysis, indicating the haplotype associations may due to other SNPs that is in LD with the haplotype. On the other hand, HLIPEB2_03 (C-C-G-G-G-G-T) which contains “G” allele from c.8689A>G (Ile607Val) and “T” allele from c.9937A>T increased the AVBF by 6.61% in comparison to other haplotypes. In the single marker analyses of SNP c.8689A>G and c.9937A>T, these two alleles, i.e. “G” and “T” were found to significantly increase ABVF in the hybrid cattle population. Therefore, significant association of HLIPEB2_03 with AVBF may be attributed to the effect of the single SNPs.

Similarly, the haplotypes associated with the traits in the Angus and Charolais populatins were also supported by their single SNP associations. However, most of the haplotype associated with the traits were not in the agreement with single SNP associations, indicating that other polymorphisms with the haplotype blocks may responsible for the associations. For example, haplotypes under Angus haplotype block 3 were found to have significant or slightly significant association with UBF, URA, AUREA, SWT, CWT, AVBF, LMY, CREA and CMAR while SNPs which constructed this block had association with AUREA, SWT, AVBF, LMY and CMAR. Also, in Angus haplotype block 4 haplotypes were found to have significant or slightly significant association with CWT, LMY and CREA while the SNP c.276A>G under this block had slight association with AUREA and none of the other SNPs had any association. Therefore, some of the traits have been found associated with haplotypes as well as single SNPs and some of the traits had association with only haplotypes but none of the SNPs which constructed haplotype block.

Likewise in the Charolais population, different haplotypes under the haplotype block 1 were found to have significant or slightly significant association with the UBF, UREA, AUBF, SWT, CWT, LMY and CREA, while, the SNP c.7195C>T under this block had associated with UBF and no other association of single SNPs were found. Also, different haplotypes of Charolais haplotype block 2 have been found associated with UBF, UREA, AUBF, AUREA, SWT, CWT, AVBF and LMY, while SNPs under this block were associated with UBF, UREA, AUBF, AUREA, SWT, CWT and AVBF. Interestingly, across the hybrid, Angus and Charolais population it has been observed that the haplotypes were associated with the more traits than the SNPs under the haplotype blocks. This indicates that the actual effect of haplotype on a single trait might be independent of single SNP effect on the trait. Also, haplotype effects on the traits could be accounted as the effect of multiple SNP alleles which constructed a particular haplotype.

LIPE is a rate limiting gene of lipolysis (Belfrage, 1984) and it is highly expected that this gene could affect the fat deposition and carcass merit traits in beef cattle. Previously, Kazala et al. (2003) showed that LIPE activity in intramuscular adipose tissue of *longissimous* muscle may be a biochemical marker for marbling score in Wagyu hybrid cattle. SNPs and haplotypes identified to have associations with the fat and carcass merit traits will provide tools for further marker validation. In addition, additional polymorphisms of the gene should be discovered and evaluated for associations with fat related traits in beef cattle.

3.9. Oxidized low density lipoprotein (lectin-like) receptor 1 (OLR1)

3.9.1. Single SNP association

In the current study, we have analyzed a previously reported polymorphism c.10463C>A at the 3′UTR of OLR1 (Khatib et al., 2006). The SNP was in HWE equilibrium ($P>0.05$) across three cattle populations with allele "A" as the minor allele in the hybrid (MAF<0.158), Angus (MAF<0.073) and Charolais (MAF<0.163) populations (Table 3.1.). We found association of this SNP with CREA ($P<0.041$) in the hybrid cattle population with a significant additive effect ($P<0.085$) and CMAR ($P<0.064$). The "C" allele of the SNP was found to increase the CREA by 1.57 cm^2, while the "CC" animal had 4.67% increased CREA in comparison to the "AA" animals. In Angus, the "AA" genotype containing animals had 13.36% more CMAR in comparison to the "CC" animals (Table 3.33.).

3.9.2. Discussion

OLR1 acts as a receptor of oxidized form of the low density lipoprotein (oxLDL) found on the surface of the vascular endothelium and participate in a number of cellular functions including the secretory activities of the endothelium following apoptosis (Sawamura et al., 1997; Imanishi et al., 2002). OLR1 also can affect the endothelial cell function which may cause atherosclerosis (Dun et al., 2008; Metha and Li, 1998). OLR1 was first identified by Sawamura et al., (1997) in bovine aortic endothelial cells and known as a protein which binds, internalizes and degrades oxidized low-density lipoprotein (Khatib et al., 2006). OLR1 is located at 105.5cM on BTA5 (http://genomes.sapac.edu.au/bovineqtl/) but no QTL for fat related traits of beef cattle has been reported in this area. Due to its association with milk fat traits in dairy cattle (Khatib et al., 2006) and the vital role in lipid metabolism, the gene was considered as a functional candidate gene for beef cattle fat deposition and carcass merit traits.

We used NCBI nucleotide sequence blast and found that the bovine OLR1 gene sequence (Gene bank accession no. NW_001495095) has an 88% sequence similarity with the *Homo sapiens* oxidized low density lipoprotein (lectin-like) receptor transcript (NM_002543.3). It has been previously reported that the first three exons of the human OLR1 correspond to the N-terminal cytoplasmic domain, the transmembrane domain and the neck domain, while exon 4 to 6 provide a lectin-like domain (Aoyama et al., 1999). It is high likely that bovine has the similar lectin-like domain which facilitates the binding of the C-type lectin like molecules (Sawamura et al., 1997). The SNP c.10463 C>A is located at the 3′ UTR of OLR1 which could be a regulatory site of the gene. Several polymorphisms of this region of OLR1 were studied in human as well as in animals and the studies confirmed the differential gene activity of OLR1 in presence of SNPs. For example, Lambert et al., (2003) reported the association of OLR1 3′UTR SNP with Alzheimer’s disease whereas Mango et al., (2003) reported the association of the SNP with myocardial infraction. Chen et al., (2003) found an association of OLR1 with coronary artery disease and predicted that the SNP impaired mRNA stability of human OLR1 gene.

It is also mentionable that, the SNP c.10463C>A was previously assessed in dairy cattle and significant associations were reported with the alternation of gene expression. Khatib et al., (2006) found that “AA” animals reduced the expression of OLR1 in comparison to the “AC” or “CC” animals and suggested that this SNP might be a functional SNP which affect fat metabolism in tissues other than mammary gland. Furthermore, a recent study conducted by Komisarek and Dorynek, (2009) in Polish Holstein-Friesian bulls revealed that “AA” animals decreased milk fat percentage and speculated that the lower OLR1 expression in these animals may associated with lower plasma OxLDL concentration. The same study also reported that the “C” allele of SNP c.10463C>A provided a putative binding site for transcription factor SP1/GC binding site whereas “A” allele diminished it. Therefore, it is likely that discrepancies of OLR1 expression may affect the body fat deposition in beef cattle and in the results we have seen that the “C” allele increases the CREA in the hybrid population. Additionally, in the Angus population, the “A” allele containing animals had higher CMAR, which suggests that impairment in OLR1 expression may be associated with the deposition of intramuscular fat.

Moreover, breed specific frequency differences of SNP c.10463C>A has been reported by Khatib et al. (2006) and supported by Komisarek and Dorynek, (2009). The frequency of “C” allele was found associated with an increase in fat yield and fat percentage across different dairy cattle populations. In the current study we found that, the Angus population had higher frequency of “C” allele (0.927) than hybrid (0.842) and Charolais (0.837). It is noteworthy that the fatness is higher in Angus among the three breeds and Charolais contain less fat. The actual role of OLR1 on fat deposition may be caused through the impairment of glucose metabolism and influence over lipid metabolism in liver and mammary glad (Komisarek and Dorynek, 2009; Ringseis et al. 2007; Liao et al. 2008, Khatib et al., 2006). In dairy cattle studies, it was found that oxidized fat can inhibit lipoprotein lipase activity and fatty acid transporter genes which may cause reduction in triacylglycerol in milk (Komisarek and Dorynek, 2009; Ringseis et al. 2007). The exact mechanism of OLR1 through which it affects the fatness traits in beef cattle is subject to further study. However, previous studies supported the regulatory role of mutations at 3′UTR of genes through the effect on mRNA stability, polyadenylation, rates of translation and gene silencing (Khatib et al., 2006; Conne et al., 2000). Therefore, the association of c.10463C>A we reported here should be further validated and functionality analyses of this SNP could be valuable to get insight on OLR1 function as a candidate gene for fat deposition and carcass merit traits in different beef cattle breeds.

3.10. Summary of candidate genes association analyses

In the current study we analyzed in total 37 gene-specific SNPs from 9 candidate genes that include 14 newly identified SNPs in house and 23 previously reported SNPs located at the different regulatory, coding and non-coding region of genes. The genes we analyzed are reportedly had importance on fat deposition due to either their positions under the QTL regions for beef cattle fat deposition and carcass merit traits and/or functional roles in glucose or lipid metabolism. The SNPs were assessed for association analyses with 10 different fat deposition and carcass merit traits at the single SNP level for SNP with MAF >0.005 and at the haplotype level for genes with multiple SNPs. In the single SNP analyses, 27 SNPs of 9 genes have been found significantly ($P<0.05$) associated with different traits in the three cattle populations. Linkage disequilibrium assessment of SNPs within a gene revealed the existence of haplotype blocks within 4 genes. Haplotype analyses have identified 31 haplotypes of 6 genes having significant associations with different fat deposition and carcass merit traits in the populations (Table 3.34.).

All of the SNPs and haplotypes associations were breed specific. None of the SNPs has effects on the same traits across all three cattle populations, however, OLR1 SNP c.10463C>A has association with CREA in the hybrid and Charolais populations. Haplotypes were uniqe in allele arrangement, therefore, not comparable across breeds. However, UREA, SWT and CWT were affected by the GPAM haplotypes in the hybrid and Angus populations while SWT, CWT, AVBF, LMY and CMAR were affected by the LIPE haplotypes across all three cattle populations. Obviously the hybrid, Angus and Charolais cattle breeds have the similar genetic background but are different in their body composition (Gregory et al, 1994) as well as different phenotypic trait values with each other. The fat deposition and carcass traits are the physiological manifestation of cattle genes functions. The association study we conducted supports the hypothesis that the genes act differently and likely in a breed specific manner to deposit body fat in beef cattle and subsequently the phenotypic trait values differ between breeds.

Furthermore, we assessed LD between SNPs within a gene and explored haplotype blocks (Gabriel et al., 2002) in 7 genes using 35 gene specific SNPs. In general, haplotype blocks were found in FABP3, FASN, INS and LIPE and correlations between the SNPs alleles within these genes were high across the three cattle breeds, however, decay of LD was found at the front part of the gene i.e., FASN in the hybrid and LIPE in Angus cattle population, while decay of LD sometimes also found at the lower part of the gene i.e., LIPE in the hybrid cattle population. These correlations were measured as pair-wise linkage disequilibrium (LD) while SNPs with strong LD with (r^2>0.5) each other are confined together as a founder of haplotype blocks. Haplotype blocks are preferably confined at the point where the appearances of the recombination hot spots are found (Jeffreys et al., 2004; Greenawalt et al., 2006). Likewise, we found considerable breakage of haplotype blocks at the different genes, while the break point also determined the breed specific haplotype blocks and the coverage of SNPs under each block. For GPAM, IDH1 and IGF1, we found very low LD (r^2<0.5) between the SNPs within the genes and consequently no distinguished haplotype blocks were found. Similarly, most of the LIPE SNPs from exon 8 and the 3′ near gene was out of the haplotype blocks across three cattle breeds due to their low pair-wise LD with other SNPs, suggesting a high recombination rate in this gene area. Haplotype blocks can be generated in gene region with low recombination rate and may be less affected by the genetic drift (Liu et al., 2004), genes or gene regions with no haplotype blocks indicate that a higher recombination rate prevails between the SNP alleles such as in GPAM, IDH1, IGF1 and LIPE, which necessarily increased the chance of haplotype diversity followed by the significant association of haplotypes of these genes with different fat traits across cattle breeds (Table 3.36.).

In general, LDs between SNPs within gene were low in the hybrid population, for example, in FASN within haplotype block the pairwise LD (r^2) between SNPs were ranges from 0.97 to 0.69 while in the haplotype block of the purebred Angus and Charolais populations the SNPs were in complete pairwise LD (r^2=1) with each other. Due to the presence of low LD between SNPs we have found greater number of haplotypes under the haplotype blocks and in the hybrid cattle population in comparison the Angus and Charolais cattle populations. Subsequently, increasing number of haplotypes as well as their versatile distribution among animals facilitated to discover significant haplotypes random effects on the fat related traits for the entire 7 genes we investigated in the hybrid cattle population. As an example, for FASN we found 12 and 8 haplotypes for the hybrid and Angus populations, respectively arises from the same SNPs, however, significant haplotype random effects have been found in the hybrid cattle but not in the Angus population. Also, in some cases we found non-significant (P<0.05) random effects of haplotypes but the fixed effects analyses revealed significant effects on the trait, as an example, INS haplotypes had non-significant haplotypes random effects on CMAR (P<0.2878), however, the fixed effect analyses revealed significant effect (P<0.034) of HINS_02. This indicates that the association may be a false positive and should be subject to validation experiments. Indeed, with the increasing empirical understanding about the haplotype structure in a gene, we are still well behind to properly address and estimate the effects of genetic drift, recombination, mutation and migration which may cause decay of LD between SNPs (Gu et al., 2007; Carvajal-Rodríguez, 2009) and subsequently alter the founder haplotype blocks of genes. Therefore, haplotypes block identification and haplotypes association analyses using more gene-specific SNPs in different cattle breeds could be plausible to get new insight in the future.

We conducted association analyses on multiple SNPs and used P<0.10 to declare it as slightly significantly associated with the traits. To adjust our significant threshold (P<0.10) of allele substitution effects from multiple markers under the 7 candidate genes, we performed 10 individual trait- based false discovery rate

(FDR) calculation for each gene, assuming that carcass traits are independent of each other (Benjamini and Hochberg, 1995; Weller et al., 1998; Sherman et al., 2008; Marques et al., 2009). In the current study, we had single SNP analyzed from candidate gene ACS and OLR1; therefore, FDR was not calculated for those genes. The FDR ranged from 0.004 to 1.00 while 5 SNPs adopted the correction at the significant level ($P<0.05$) and 8 SNPs sustained after the correction at the slightly significant level ($P<0.10$) from three genes including FABP3, GPAM and IGF1 (Table 3.35). This correction of the P-values does not nullify the importance of SNPs which is nonsignificant after FDR because the number of the SNPs in a multiple test severly affects the FDR calculation. Also, we didn't calculate FDR for additive and dominance effects because thses effects were discreately found and difficult to consider as multiple tests for a single trait. However, we studied candidate genes based on their positional status under QTL, as well as functional candidature on cattle body fat deposition and carcass merit traits through different metabolic pathways. Therefore, the genes we studied are tagged with potential functional significance which supports our results and implies that the gene specific SNP markers having significant allele substitution effect should not be excluded from further analyses based on FDR findings. Instead, verification of SNPs effects through functional analyses and validation studies in other populations are recommended (Sherman et al., 2008). For haplotype random effects, we performed LR test which likely controls the false discovery rate (Gilmour, 2007). Therefore, adjustment of P-values from haplotypes substitution effects was not implemented.

4. Chapter Four: Conclusion

4.1. Candidate gene approach vs genome-wide association

There are two methodologies familiarly used to characterize genes of economically important quantitative traits in beef and dairy cattle, i.e., genome wide association (GWA) analyses and candidate gene approach. In genome-wide association studies, a panel of SNPs are used in which SNPs are evenly distributed throughout the whole genome in order to capture LD with the causative SNPs. The SNPs of GWA or “tagSNPs” can serve as proxies for causative SNPs in the neighbourhood based on the assumption that the SNPs are in high LD with nearby SNPs in genome. In the contrary, candidate gene approaches obtain the highest possible coverage of genetic variation within specified gene boundaries (Pettersson et al., 2009) irrespective of the LD values of gene specific SNPs. In the current study, we have found that LD structure may vary within gene SNPs for different cattle populations. These findings lead us to assume that multiple SNPs within a candidate gene may not be in high LD with the “tagSNPs” but still can be a cusative SNP for phenotypic traits and it can also have very low minor allele frequency (MAF), which may be difficult to capture in GWA studies. On the other hand, the candidate gene approach, which targets specific genes and often includes multiple SNPs within a gene, is more effective and feasible to detect to detect the causative SNPs with low LD with other SNPs and/or with low minor allele frequencies (Wilkening et al., 2009).

Nevertheless, there are considerable debate that the candidate gene approach has some drawbacks such as selection of SNPs may be biased by selecting markers base on functional annotation, whereas, causative polymorphisms may be in the regions considered as non-functional (Evans et al., 2008). For example, evolutionary conserved regions may contain functionally important element like cis-regulatory elements (Hughes et al., 2005) and microRNA coding genes (Altuvia et al., 2005). However, with the completion of the bovine genome project, the functional annotation of the genes now largely covers the genome of the *Bos taurus*, which could greatly facilitate canadiate gene associations analyses for complex traits.

4.2. Future research consideration

In beef cattle, DNA marker association analyses are targeted to develop markers that could be implemented in maker assisted selection programs of beef industries. Like many other economically important traits, fat deposition related carcass traits are considered as complex traits and controlled by many genes.

We have identified SNPs and haplotypes associations using relatively small size of cattle populations. To scale up the SNP markers or haplotypes from the discovery population to commercial population it is important to perform the validation trial of markers in different cattle herd to further verify the concurrent responses from the associated phenotypic traits (Barendse, 2005a). It is strongly recommended that unbiased and independent validation studies are necessary to build confidence on SNPs markers commercialization as well as to maximize the reliability of DNA variants research (Eenennaam et al., 2007).

In this study, the analyses results of 37 SNPs from 9 genes with fat deposition and carcass merit tarits that may indicates the existance of genetic control on the traits. To improve the beef quality through maker assisted selection programs in beef industries more genes and gene-specific SNPs from the regulatory as well as non-regulatory regions is needed to be examined to discover association with different fat traits i.e, fat related carcass traits, fatty acids composition etc.

The fat deposition and carcass merit traits are quantitative in nature and trait value variations are the ultimate consequence of the function of candidate genes. The transcriptional profiles of genes may vary in presence of the SNPs at the regulatory regions that are necessary to be verified through gene expression analyses *in vitro* (Zhu and Zhao, 2007). Therefore, functional tests of SNPs are recommended to improve the reliability of the association analyses that also could provide insight into the genetic basis of fat deposition in beef cattle.

Table 1.1. Heritability and genetic correlation of a few commonly measured fat deposition and carcass merit traits.

Trait*	UBF	UREA	SWT	CWT	AVBF	LMY	LMA	CREA	CMAR
UBF	**0.59**[a]	0.34[c]	---	−0.27±0.23[b]	0.79±0.13[f]	−0.33±0.21[b]	−0.39±0.10[e]	−0.22±0.21[b]	−0.27±0.21[b]
UREA		**0.61**[b]	---	0.31±0.21[b]	0.16±0.22[b]	0.35±0.20 [b]	---	0.71±0.11 [b]	0.31±0.19 [b]
SWT			**0.50**[a]	0.94±0.03[d]	0.10±0.27[d]	---	0.30±0.21[d]	---	0.33±0.42[d]
CWT				**0.33**[a]	0.08±0.26[d]	---	0.45±0.19[d]	0.47[c]	0.09[c]
AVBF					**0.34**[c]	---	−0.25±0.27[d]	−0.21[c]	0.04±0.33[d]
LMY						**0.63**[a]	---	---	---
LMA							**0.45**[a]	---	0.17±0.28[d]
CREA								**0.47**[c]	−0.01[c]
CMAR									**0.49**[a]

*UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; LMA= Lean meat area, cm^2; CREA= Carcass rib eye area, cm^2; CMAR = Carcass marbling score.

Heretabilities are on the diagonal **as Bold letters.**

Genetic correlations are above the diagonal.

[a] Nkrumah et al., 2007; [b] Crews and Kemp, 2001; [c] Bertrand et al., 2001; [d] Smith et al., 2007; [e] Devitt and Wilton, 2001; [f] Crews et al., 2003.

Table 1.2. A summary of candidate genes and gene-specific SNPs associated with fat deposition and carcass merit traits in different beef cattle breeds.

Candidate Gene[a]	Gene-specific SNPs	SNP functional class/Location	Cattle breed[b]	Associated fat deposition and carcass merit traits[c]
ADIPOQ	g.1431C>T	5′near gene	AN	AVBF, UREA (Morsci et al., 2006)
	g.1596G>A	Promoter	AN	AVBF, UREA (Morsci et al., 2006)
	g.2606T>C	5′near gene	AN	AVBF, UREA (Morsci et al., 2006)
CAPN1	c.2151*479C>T	3′ Utranslated region	HC	CMAR (Cheong et al., 2008)
CAST	---	---	HY	FY (Schenkel et al., 2006)
CRH	C22G in Exon1	Nonsynonymous (Pro-Arg)	HY	HCW, UREA (Buchanan et al., 2005)
	c.10936G>C	Nonsynonymous (Asp-His)	HY	CMAR, SF (Wibowo et al., 2007)
DGAT1	K232A	Nonsynonymous (Lys-Ala)	CH	CMAR (Thaller et al., 2003)
FABP3	c.73+67G>C	Intron1	KNC	CW (Cho et al., 2008)
FABP4	c.2821G>C, c.3520A>T, c.3678A>G	---	HC	CMAR (Park et al., 2006)
	c.220A>G	Nonsynonymous (Ile-Val)	KNC	BF (Cho et al., 2008)
	c.348+303T>C	Intron3	KNC	BF (Cho et al., 2008)

GH1	c.457C>G	Nonsynonymous (Leu-Val)	AN, SH	CMAR, RF (Barendse et al., 2006)
GHR	ss86273136 (tag)	Promoter	BRA	RIF (Garret et al., 2008)
	SNP2	Intron4	HY	QG (Sherman et al., 2008)
GHRH	c.−4241A>T	5′ Untranslated region	KNC	CWT (Cheong et al., 2006)
IGF2	c.−292C>T	5′ Untranslated region	HY	CREA, PCF, UBF, UMAR (Goodall and Schmutz, 2007; Sherman et al., 2008)
IGFBP3	c.299C>A	---	QC	FC (Sun et al., 2003)
LEP	UASMS1	5′near gene	HY	FY (Schenkel et al., 2005 & 2006)
	UASMS2	5′near gene	HY	UBF, UMAR (Nkrumah et al., 2005)
	UASMS3	5′near gene	HY	UBF (Nkrumah et al., 2005)
	C73T in Exon2	Nonsynonymous (Arg-Cys)	AN, BdA, CH, HE, HY, SI	AVBF, CMAR, CWT, FWT, GF, LMY, UREA, YG (Buchanan et al, 2002 & 2007; Kononoff et al., 2005; Nkrumah et al., 2004; Schenkel et al., 2005; Stasio et al., 2007)
	E2JW	Exon2	HY	FY, GF, LMY, SF (Schenkel et al., 2005 & 2006)
	E2FB	Exon2	HY	FY, GF, LMY, SF (Schenkel et al., 2005 & 2006)
LEPR	T115C in Exon20	Nonsynonymous (T945M)	HY	FY, GF, SF, IMF (Schenkel et al., 2006)

MC4R	g.1069C>G	Nonsynonymous (Val-Leu)	HY	HCW (Buchanan et al., 2005)
MSTN	g.433C>A	Nonsynonymous (Phe-Leu)	HY	AVBF, CWT, IMF, LMA (Esmailizadeh et al., 2008)
MyoD	C39T, C112G	Intron2	HY	CWT, LEA (Tian et al., 2007)
NPY	SNP1	Intron2	HY	CMAR, UMAR (Sherman et al., 2008)
PMCH	g. −134A>T	Promoter	HY	AVF, GF (Helgeson et al., 2008)
POMC	g.254C>T	Synonymous (Ser)	HY	HCW (Buchanan et al., 2005)
SST	g.447A>G	Promoter	AN	CMAR (Morsci et al., 2006)
TFAM	c.−1220C>A, c.−1212C>T	Promoter	HY	CMAR, SF (Jiang et al., 2005)
TG	c. −537C>T	5′Untranslated region	AN, BR, CH, SH	AVBF, CMAR, FC, LMY (Barendse, 1999; Thraller et al., 2003; Casas et al., 2005)
	G133C, G156A, C220T, A506C	3′flanking region	AN, CH, HE, JI, LI, LU, UC	CMAR (Gan et al., 2008)
UCN3	---	---	HY	CMAR, SF (Jiang et al., 2008)
UCP2	SNP3	Synonymous in Exon4	HY	AVBF, LMA, YG (Sherman et al., 2008)
UCP3	SNP2	Intron3	HY	CMAR, LMY (Sherman et al., 2008)

[a] ADIPOQ = Adinopectin (produce adipocytokine adinopectin); CAPN1 = Calcium activated neutral protease; CAST = Calpastatin gene; CRH = Corticotrophin releasing hormone; DGAT1 = Diacylglycerol 0-acyltransferage 1; GH1= Growth hormone1; GHR= Growth hormone receptor; GHRH = Growth hormone releasing hormone; IGF2=Insulin like growth factor 2; IGFBP3 = Insulin-like growth factor binding protein 3; LEP = Leptin; LEPR = Leptin receptor; MC4R = Melancortin-4-recptor ; NPY= Neuropeptide Y; PMCH = Pro-melanin-concentrating hormone; POMC = Pro-opimelancortin; SST = Somatostatin; TFAM = Mitochondrial transcription factor A; TG = Thyroglobulin; UCN3=Urocortin 3; UCP2/3= Uncoupling protein 2/3.

[b] AN=Angus, BdA=Blonde d'Aquitaine (Italian bulls); BR=Brahman; BAR=Brangus; CH=Charolais; HE=Hereford; HY=Hybrid/Crossbreed; JI=Jinan; KNC/HC=Korean native cattle (Hanwoo); LI=Limousin; LU=Luxi; QC= Qinchuan cattle; SH=Shorthorn; SI=Simmental.

[c] AVF/AVBF= Average fat/backfat; CMAR= Carcass marbling score; CREA= Carcass rib eye area; CWT= Carcass weight; FY/FC=Fat yield/content; GF= Grade fat; IMF=Intramuscular fat content; LEA=Loin eye area; LMY/LMA= Lean meat yield/area; PF= Per cent fat; RF= Rump fat; RIF = Rib fat; SF = Subcutaneous fat depth; SWT/FWT= Slaughter weight or final weight; UBF= Ultrasound backfat thickness; UMAR= Ultrasound marbling score; UREA= Ultrasound rib eye area; YG= Yield grade.

Table. 2.1. Data conversion scale of Canadian marbling Score to USDA marbling score used in this study*.

Marbling score	Canadian Grade[a]	Canadian Score[a]	USDA Grade	USDA Score
Abundant	Canada Prime	≥4	USDA Prime	10−10.99
Moderately abundant				9 − <10
Slightly abundant				8 − <9
Moderate	Canada AAA	3 − <4	USDA Choice	7 − <8
Modest				6 − <7
Small				5 − <6
Slight	Canada AA	2 − <3	USDA Select	4 − <5
Traces	Canada A	1 − <2	USDA Standard	3 − <4
Practically devoid				2 − <3
Devoid	---	---	---	1 − <2

*http://www.canadianbeef.info/ca/en/rt/quality/default.aspx; American Angus Association® (www.angus.org); Agriculture Canada, 1992; Agricultural Marketing Service (AMS), (Department of Agriculture) Rules and Regulations, 1996, USA; [a](Nkrumah et al., 2007).

Table 2.2. Summary of fat deposition and carcass merit traits phenotypic data used for the association analyses study.

Trait[a]	Population	Mean	Standard Deviation	Minimum	Maximum
UBF	Hybrid	9.34	3.51	1.8453	26.8055
	Angus	15.69	2.72	7.180943	23.78494
	Charolais	8.37	2.24	4.175348	14.08938
UREA	Hybrid	83.39	10.62	61.0505	119.8249
	Angus	81.09	6.16	62.03167	100.3934
	Charolais	83.88	7.06	68.45767	114.5146
AUBF	Hybrid	0.03	0.02	−0.0126	0.1244
	Angus	0.07	0.03	0.006595	0.190934
	Charolais	0.03	0.02	−0.02688	0.093252
AUREA	Hybrid	0.17	0.07	0.0021	0.4053
	Angus	0.20	0.09	−0.1525	0.407523
	Charolais	0.22	0.08	−0.06033	0.459502
SWT	Hybrid	536.91	54.96	377.16	705.34
	Angus	566.06	43.17	445.9	667.90
	Charolais	564.58	54.79	417.3	688.7
CWT	Hybrid	312.30	31.92	207.20	401.2531
	Angus	330.15	28.86	267.86	408.5092
	Charolais	335.15	32.18	248.792	422.7648
AVBF	Hybrid	12.32	4.26	2.67	27.3333
	Angus	17.2	4.04	5.67	27.67
	Charolais	8.10	3.31	3.33	26.00
LMY	Hybrid	57.82	3.81	44.2377	66.1785
	Angus	53.68	3.6	44.09869	65.8105
	Charolais	62.15	3.32	44.64849	68.15204
CREA	Hybrid	83.94	9.20	53.00	113.00
	Angus	82.59	7.76	64.00	110.00
	Charolais	93.72	9.35	65.00	130.00

CMAR	Hybrid	4.63	0.73	3.10	7.63
	Angus	6.30	1.21	3.50	9.30
	Charolais	4.54	0.72	3.20	9.00

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

Table 2.3. Selected candidate genes information.

Gene name[a]	BTA no.[b]	Position (bp) on BTA[b]	Accession number[c]	QTL location[d]	Functional role in metabolism[c]
ACSF3	18	13,212,191 — 13,250,827	NM_001035068	---	Lipogenesis
FABP3	2	126,260,500 — 126,268,108	NM_174313	FT (Stone et al., 1999)	Lipid transport
FASN	19	52,171,722 — 52,190,007	AF285607	SFD (Li et al., 2004)	Lipogenesis
GPAM	26	33,097,552 — 33,137,508	NW_001494373	FY, YG (Casas et al., 2003b)	Lipogenesis
IDH1	2	101,647,000 — 101,668,024	NW_001494667	FT (Stone et al., 1999); CMAR (Casas et al., 2003b); SWT (Kim et al., 2003)	Gluconogenesis
IGF1	5	71,126,213 — 71,198,012	NW_001495053	SFD (Casas et al., 2000; Li et al., 2004); CMAR (Casas et al., 2003a)	Glucose metabolism
INS	29	51,247,435 — 51,248,568	NW_001494548	CMAR (MacNeil and Grosz, 2002); HCW (Casas et al., 2003a)	Glucose and lipid metabolism
LIPE	18	50,646,216 — 50,657,593	NW_001493616	---	Lipolysis
OLR1	5	107,285,874 — 107,297,179	NW_001495095	---	Lipid transport

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= bovine fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b] Source: http://www.genome.ucsc.edu/cgi-bin/hgGateway (Cow genome browsing gateway).

[c] Source: http://www.ncbi.nlm.nih.gov/sites/entrez (Bovine gene search).

[d]Source: http://genomes.sapac.edu.au/bovineqtl/ (Bovine QTL viewer—Texas A & M University); CMAR = Carcass marbling score; FT = Fat thickness; FY = Fat yield; HCW = Hot carcass weight; SFD = Subcutaneous fat depth; SWT = Slaughter weight.

Table 2.4. Gene-specific SNPs used for association analyses with carcass merit and fat related carcass traits.

Gene name[a]	Marker name[b]	Gene-specific position	Base position[c]	Functional class[d]	SNP source	Genotyping method[f]
ACSF3	c.−757C>T	5′ near gene	−757	Promoter	Discovered in house	RT-PCR
FABP3	c.21T>C	Exon_1	+21	Synonymous (Gly→Gly)	Cho et al. (2008)	RT-PCR
	c.4593C>G	Intron_2	+4593	Intronic	NCBI (rs41579156)	IGGA
	c.7627T>C	3′ near gene	+7627	Genomic	Discovered in house	IGGA
FASN	c.8581G>A	Exon_21	+8581	Synonymous (Glu→Glu)	NCBI (rs41919996)	IGGA
	c.10388C>T	Exon_24	+10388	Non-synonymous (His→Tyr)	NCBI (rs41919993)	IGGA
	c.12794A>C	Exon_32	+12794	Non-synonymous (Ile→Lue)	Discovered in house	PCR-RFLP
	c.12865G>A	Intron_32	+12865	Intronic	Discovered in house	IGGA
	c.14169T>C	Exon_37	+14169	Non-synonymous (Val→Ala)	NCBI (rs41919984)	IGGA
GPAM	c.−1564G>A	5′ near gene	−1564	Promoter	Discovered in house	PCR-RFLP
	c. −345C>T	5′ near gene	−345	Promoter	NCBI (rs41606739)	PCR-RFLP
	c.18088G>C	Intron_7	+18088	Intronic	NCBI (rs42102081)	IGGA
	c.26006A>G	Intron_11	+26006	Intronic	NCBI (rs42102079)	IGGA

	c.35863A>C	Intron_19	+35863	Intronic	NCBI (rs42102077)	IGGA
IDH1	c. −4145C>T	5′ near gene	−4145	Promoter	Discovered in house	RT-PCR
	c.4208T>G	Intron_3	+4208	Intronic	NCBI (rs41641851)	IGGA
	c.9970A>G	Intron_6	+9970	Intronic	NCBI (rs29001855)	IGGA
IGF1	c. −512C>T	5′ near gene	−512	Promoter	Ge et al. (1997)	PCR-RFLP
	c.47807T>C	Intron_2	+9970	Intronic	NCBI (rs29012855)	IGGA
INS	c. −526T>C	5′ near gene	−526	Promoter	NCBI (rs42194738)	IGGA
	c. −397T>C	5′ near gene	−397	Promoter	NCBI (rs42194737)	PCR-RFLP
LIPE	c.−11470G>A	5′ near gene	−11470	Promoter	NCBI (rs41887425)	PCR-RFLP
	c. −9627G>A	5′ near gene	9627	Promoter	NCBI (rs41887424)	IGGA
	c.276A>G	Exon_1	276	Synonymous (Tyr→Tyr)	NCBI (rs41887418)	IGGA
	c.2692C>T	Intron_2	2692	Intronic	NCBI (rs41887414)	IGGA
	c.5332G>A	Exon_7	5332	Synonymous (Val→Val)	NCBI (rs41887411)	PCR-RFLP
	c.7195C>T	Intron_7	7195	Intronic	NCBI (rs41887410)	PCR-RFLP
	c.7324G>A	Intron_7	7324	Intronic	NCBI (rs41887409)	PCR-RFLP
	c.8549A>G	Exon_8	8549	Non-synonymous (Gln→Arg)	Discovered in house	DNA Sequencing
	c.8560C>T	Exon_8	8560	Non-synonymous (Pro→Ser)	Discovered in house	DNA Sequencing
	c.8563C>T	Exon_8	8563	Synonymous (Lue→Lue)	Discovered in house	DNA Sequencing
	c.8689A>G	Exon_8	8689	Non-synonymous (Ile→Val)	Discovered in house	DNA Sequencing
	c.8731G>A	Exon_8	8731	Non-synonymous (Glu→Lys)	Discovered in house	DNA Sequencing

	c.8782G>C	Exon_8	8782	Non-synonymous (Ala→Pro)	Discovered in house	DNA Sequencing
	c.8893G>A	Exon_8	8893	Non-synonymous (Asp→Asn)	Discovered in house	DNA Sequencing
	c.9937A>T	3′ near gene	9937	3′ near gene	Discovered in house	IGGA
OLR1	c.10463C>A	Exon_6	10466	3′ UTR	Khatib et al. (2006)	PCR-RFLP (PstI)

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b] Nomenclature of SNPs is according to den Dunnen and Antonarakis (2000).

[c] Relative to the start codon position (start codon first base = +1).

[d] Standard amino acids abbreviations are used for synonymous and non-synonymous SNPs.

[e] UTR = Un-translated region.

[f] IGGA = Illumina GoldenGate Assay; PCR-RFLP (Enzyme name) = Polymerase chain reaction (PCR) restriction fragment length polymorphism (RFLP) (restriction enzyme name is given for respective SNP) ; RT-PCR = Real-time PCR.

Table 2.5. Primers and restriction enzymes used for PCR-RFLP genotyping.

Gene[a]	SNP[b]	Froward primer (5′ -3′)	Reverse primer (5′ -3′)	Restriction enzyme
FASN	c.12794A>C	GAGGACGCCTTCCGCTAG	CCTGTTCACGCACTGCTG	AvaII
GPAM	c.−1564G>A	gtgcgtgatcgccctttc	ctgcctgggaaaatgaagact	RsaI
	c. −345C>T	TGACCAAAAATTCCCAGCAC	tcaccctatttcaggtatgtgac	BstCI
IGF1	c. −512C>T	ATTACAAAGCTGCCTGCCCC[1]	ACCTTACCCGTATGAAAGGAATATACGT[1]	SnaBI
INS	c. −397T>C	AGTGCAGGAGACACAAGTTCAGT	GGACACTGAGGGACTGAACC	HinP1I
LIPE	c.−11470G>A	ccctgctccagtatttttgc	tgaagcccttttcagagtgg	ApoI
	c.5332G>A	gcctgaggttgtgtgtgttg	AAGAAGGAGTTGAGCCACGA	RsaI
	c.7195C>T	gctacagggcacctaagcag	catcccttccctttgaatga	BssSI
	c.7324G>A	gctacagggcacctaagcag	catcccttccctttgaatga	PstI
OLR1	c.10466C>A	AAGGCGAATCTATTGAGAGC[2]	acttctctgaagtcctgca[2]	PstI

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b] Nomenclature of SNPs is according to den Dunnen and Antonarakis (2000). Relative to the start codon position (start codon first base = +1).

[1] Ge et al., 1997; [2] Khatib et al., 2006.

Table 3.1. SNPs genotypes counts, minor allele, minor allele frequency (MAF), observed heterozygosity (OHET) and Hardy-Weinberg equilibrium (HWE) P value in the hybrid, Angus and Charolais cattle populations obtained from gene-specific SNPs used for association analyses.

Gene name[a]	Marker name[b]	Animal	Homozygous animals for major allele	Haterozygous animals	Homozygous animals for minor allele	Minor allele	MAF[c]	OHET[d]	HWE P-value[e]
ACSF3	c.−757C>T	Hybrid	280	155	21	T	0.216	0.340	1
		Angus	105	80	21	T	0.296	0.388	0.3932
		Charolais	166	21	0	T	0.056	0.112	1
FABP3	c.21T>C	Hybrid	237	182	37	C	0.280	0.398	0.8335
		Angus	188	17	0	C	0.041	0.083	1
		Charolais	84	80	23	C	0.337	0.428	0.6459
	c.4593C>G	Hybrid	234	180	37	G	0.282	0.399	0.8396
		Angus	189	17	0	G	0.041	0.083	1
		Charolais	86	77	23	G	0.331	0.414	0.4483
	c.7627T>C	Hybrid	448	7	0	C	0.008	0.015	1
		Angus	206	0	0	0	0	0	0
		Charolais	180	7	0	C	0.019	0.037	1
FASN	c.8581G>A	Hybrid	416	37	1	A	0.043	0.081	1
		Angus	205	0	0	0	0	0	0

		Charolais	184	0	0	0	0	0	0
	c.10388C>T	Hybrid	153	210	90	T	0.430	0.464	0.2759
		Angus	72	116	18	C	0.369	0.563	0.0042
		Charolais	167	0	19	T	0.102	0.398	0.5385
	c.12794A>C	Hybrid	154	91	71	C	0.425	0.471	0.4918
		Angus	74	114	18	A	0.364	0.553	0.008
		Charolais	93	76	18	C	0.299	0.406	0.764
	c.12865G>A	Hybrid	149	213	91	G	0.436	0.470	0.3878
		Angus	72	115	18	A	0.368	0.561	0.0051
		Charolais	105	0	81	A	0.436	0.441	0.8434
	c.14169T>C	Hybrid	183	200	71	C	0.377	0.441	0.2145
		Angus	67	120	19	T	0.383	0.583	0.0014
		Charolais	115	0	72	C	0.385	0.342	1
GPAM	c.−1564G>A	Hybrid	305	145	5	A	0.170	0.319	0.0062
		Angus	121	75	8	A	0.223	0.368	0.5357
		Charolais	147	38	1	A	0.107	0.204	0.6958
	c.−345C>T	Hybrid	220	182	50	T	0.310	0.404	0.2264
		Angus	159	43	3	T	0.119	0.210	1
		Charolais	153	32	2	T	0.096	0.171	1
	c.18088G>C	Hybrid	391	61	3	C	0.074	0.134	0.8932

		Angus	206	0	0	0	0	0	0
		Charolais	187	0	0	0	0	0	0
	c.26006A>G	Hybrid	415	0	40	G	0.088	--	4.25E-59
		Angus	206	0	0	0	0	0	0
		Charolais	187	0	0	0	0	0	0
	c.35863A>C	Hybrid	424	30	0	C	0.033	0.066	1
		Angus	206	0	0	0	0	0	0
		Charolais	173	14	0	C	0.037	0.075	1
IDH1	c.−4145C>T	Hybrid	331	116	9	T	0.147	0.255	0.9347
		Angus	152	50	4	T	0.141	0.243	1
		Charolais	124	61	2	T	0.173	0.326	0.0981
	c.4208T>G	Hybrid	176	220	58	G	0.370	0.485	0.4751
		Angus	65	88	53	G	0.471	0.427	0.0514
		Charolais	98	75	14	G	0.275	0.401	1
	c.9970A>G	Hybrid	310	122	20	G	0.179	0.270	0.1115
		Angus	169	36	1	G	0.092	0.175	0.9396
		Charolais	111	73	2	G	0.207	0.392	0.0087
IGF1	c.−512C>T	Hybrid	165	232	58	C	0.382	0.510	0.1148
		Angus	60	106	38	T	0.446	0.520	0.5767
		Charolais	56	97	33	C	0.438	0.522	0.5339

	c.47807T>C	Hybrid	421	32	0	C	0.035	0.071	1
		Angus	198	8	0	C	0.019	0.039	1
		Charolais	169	17	1	C	0.051	0.091	0.764
INS	c.−526T>C	Hybrid	213	201	38	C	0.306	0.433	0.7346
		Angus	203	2	0	C	0.005	--	--
		Charolais	87	87	12	C	0.294	0.455	0.4783
	c.−397T>C	Hybrid	218	197	40	C	0.304	0.445	0.3968
		Angus	204	2	0	C	0.005	--	--
		Charolais	87	85	15	C	0.308	0.468	0.1616
LIPE	c.−11470G>A	Hybrid	170	205	80	A	0.401	0.451	0.2102
		Angus	66	104	36	G	0.427	0.505	0.783
		Charolais	69	89	29	A	0.408	0.476	1
	c.−9627G>A	Hybrid	177	199	75	A	0.387	0.441	0.1587
		Angus	67	103	33	G	0.406	0.507	0.6545
		Charolais	65	88	33	A	0.414	0.473	0.8205
	c.276A>G	Hybrid	177	198	78	G	0.391	0.437	0.0952
		Angus	67	104	34	A	0.419	0.507	0.6767
		Charolais	65	95	25	G	0.392	0.514	0.3886
	c.2692C>T	Hybrid	179	124	123	T	0.434	0.291	3.32E-17
		Angus	91	75	33	C	0.354	0.377	0.0183

	Charolais	66	43	63	T	0.491	0.250	4.39E-11
c.5332G>A	Hybrid	178	213	63	A	0.373	0.469	1
	Angus	39	130	36	G	0.492	0.634	2.0E-4
	Charolais	77	96	14	A	0.332	0.513	0.0466
c.7195C>T	Hybrid	166	208	82	T	0.408	0.456	0.2645
	Angus	63	110	32	C	0.424	0.537	0.218
	Charolais	61	100	26	T	0.406	0.535	0.1946
c.7324G>A	Hybrid	177	202	77	A	0.390	0.443	0.1603
	Angus	66	104	35	G	0.424	0.507	0.7107
	Charolais	70	93	24	A	0.377	0.497	0.5423
c.8549A>G	Hybrid	106	226	105	G	0.499	0.517	0.5496
	Angus	71	96	34	G	0.408	0.478	0.9594
	Charolais	62	79	39	G	0.436	0.439	0.1829
c.8560C>T	Hybrid	188	194	57	T	0.351	0.442	0.5854
	Angus	71	98	34	C	0.409	0.483	1
	Charolais	91	73	19	T	0.303	0.399	0.5304
c.8563C>T	Hybrid	417	18	4	T	0.029	0.041	5.0E-4
	Angus	188	12	2	T	0.039	0.059	0.0604
	Charolais	146	29	7	T	0.118	0.159	0.0097
c.8689A>G	Hybrid	248	181	26	G	0.256	0.398	0.4277

		Angus	93	87	26	G	0.337	0.422	0.4975
		Charolais	99	77	11	G	0.265	0.412	0.5776
	c.8731G>A	Hybrid	200	192	47	A	0.326	0.437	0.9914
		Angus	64	103	35	G	0.428	0.510	0.6840
		Charolais	103	59	14	A	0.247	0.335	0.2498
	c.8782G>C	Hybrid	385	48	1	C	0.058	0.111	1
		Angus	203	0	0	0	0	0	0
		Charolais	157	23	0	C	0.064	0.128	0.9446
	c.8893G>A	Hybrid	232	192	31	A	0.279	0.422	0.3703
		Angus	179	26	1	A	0.068	0.126	1
		Charolais	103	67	17	A	0.270	0.358	0.2716
	c.9937A>T	Hybrid	247	152	20	T	0.229	0.363	0.7056
		Angus	92	83	29	T	0.346	0.407	0.1885
		Charolais	94	62	9	T	0.242	0.376	0.9799
OLR1	c.10466C>A	Hybrid	325	118	13	A	0.158	0.259	0.6561
		Angus	178	26	2	A	0.073	0.126	0.5721
		Charolais	129	55	3	A	0.163	0.294	0.4607

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b]Nomenclature of SNPs is according to Dunnen and Antonarakis (2000).

[c,d,e]In case of monomorphic state of SNP no information is given. Also, in absence of heterozygous genotype, OHET and HWE P value is not mentioned. Data obtained by the HAPLOVIEW analyses of the SNP genotypes from three different animal populations.

Table 3.2. Least square means of fat deposition and carcass merit traits and estimated effects of ACS c.−757C>T SNP in hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Domina-nce effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.−757C>T	9.0720	9.3360	8.6917	0.5337	0.708	0.1902	0.585	0.4541	0.267
			±0.2411	±0.2940	±0.6748	±0.2679		±0.3460		±0.4080	
	Angus	c.−757C>T	15.8313	15.5131	15.7100	0.1432	0.668	-0.6064	0.843	-0.2576	0.530
			±0.3581	±0.3641	±0.6022	±0.2729		±0.3044		±0.4081	
	Charolais	c.−757C>T	8.0575	8.4590	--	−0.4014	0.356	--	--	--	--
			±0.3138	±0.5458		±0.4938					
UREA	Hybrid	c.−757C>T	83.7286	82.5326	80.8795	−1.297	**0.059†**	1.425	0.101	0.2286	0.826
			±0.4893	±0.6538	±1.6703	±0.6481		±0.8647		±1.034	
	Angus	c.−757C>T	80.7083	81.3792	80.6634	−0.2046	0.689	-0.2247	0.975	0.6934	0.479
			±0.8494	±0.8637	±1.4350	±0.6523		±0.7269		±0.9749	
	Charolais	c.−757C>T	83.6642	83.4187	--	0.2455	0.762	--	--	--	--

			±0.7359	±1.5407		±1.495					
AUBF	Hybrid	c.−757C>T	0.0330	0.0348	0.0333	0.1022	0.398	-0.1484	0.935	0.1632	0.448
			±0.0012	±0.0015	±0.0035	±0.1392		±0.1811		±0.2139	
	Angus	c.−757C>T	0.0682	0.0684	0.0673	0.2240	0.953	-0.4309	0.893	0.6227	0.887
			±0.0033	±0.0034	±0.0061	±0.2853		±0.3205		±0.4352	
	Charolais	c.−757C>T	0.0321	0.0313	--	0.7392	0.861	--	--	--	--
			±0.0020	±0.0046		±0.4640					
AURE-A	Hybrid	c.−757C>T	0.1630	0.1641	0.1644	0.9097	0.950	-0.7045	0.899	0.3697	0.956
			±0.0030	±0.0041	±0.0107	±0.4115		±0.5530		±0.6637	
	Angus	c.−757C>T	0.1955	0.2077	0.2142	−0.1032	0.252	0.9363	0.334	0.2833	0.832
			±0.0092	±0.0095	±0.0182	±0.8502		±0.9644		±0.1332	
	Charolais	c.−757C>T	0.2187	0.2086	--	0.1008	0.536	--	--	--	--
			±0.0062	±0.0173		±0.1792					
SWT	Hybrid	c.−757C>T	545.5844	538.6060	550.3255	−2.463	0.804	-2.371	0.679	-9.349	0.164
			±5.1471	±5.8183	±11.4902	±4.532		±5.698		±6.692	
	Angus	c.−757C>T	565.6093	563.9702	567.6707	−0.1717	0.714	1.031	0.765	-2.670	0.563
			±4.1257	±4.1257	±6.8348	±3.080		±3.432		±4.595	
	Charolais	c.−757C>T	565.3782	565.1326	--	0.2455	0.977	--	--	--	--
			±4.1444	±8.3134		±7.955					
CWT	Hybrid	c.−757C>T	314.5925	311.3142	319.1875	−0.5894	0.956	-2.297	0.501	-5.576	0.164

			±3.0480	±3.4502	±6.8386	±2.699		±3.395		±3.987	
	Angus	c.−757C>T	329.3547±2	328.5011	331.8710	−0.5750	0.542	1.258	0.579	-2.112	0.488
			.5510	±2.5801	±4.3998	±2.028		±2.260		±3.034	
	Charolais	c.−757C>T	334.9504	329.5838	--	5.367	0.351	--	--	--	--
			±2.3436	±5.6648		±5.709					
AVBF	Hybrid	c.−757C>T	11.9437	12.1807	11.9256	0.1269	0.637	0.9067	0.985	0.2460	0.675
			±0.2852	±0.3771	±0.9470	±0.3690		±0.4899		±0.5840	
	Angus	c.−757C>T	16.8580	17.3970	17.8734	−0.5176	0.249	0.5077	0.310	0.3129	0.963
			±0.5381	±0.5494	±0.9636	±0.4455		±0.4989		±0.6739	
	Charolais	c.−757C>T	7.8074	7.8982	--	−0.9078	0.884	--	--	--	--
			±0.3428	±0.7995		±0.7990					
LMY	Hybrid	c.−757C>T	58.2410	57.6762	57.9969	−0.3606	0.238	0.1221	0.789	-0.4427	0.411
			±0.3117	±0.3821	±0.8835	±0.3502		±0.4535		±0.5351	
	Angus	c.−757C>T	54.1507	53.3476	53.0931	0.6143	0.120	-0.5288	0.234	-0.2743	0.651
			±0.4436	±0.4546	±0.8407	±0.3934		±0.4422		±0.6038	
	Charolais	c.−757C>T	62.3626	62.2040	--	0.1586	0.824	--	--	--	--
			±0.2912	±0.7768		±0.7993					
CREA	Hybrid	c.−757C>T	84.9033	82.3652	84.0104	−1.553	**0.045***	0.4465	0.648	-2.092	**0.069†**
			±0.7459	±0.8800	±1.9138	±0.7623		±0.9721		±1.143	
	Angus	c.−757C>T	82.7147	81.7226	82.6366	0.3668	0.702	-0.3906	0.965	-0.9530	0.438

			±0.8443	±0.8670	±1.6688	±0.7839		±0.8848		±1.222	
	Charolais	c.−757C>T	94.2517	93.4826	--	0.7691	0.683	--	--	--	--
			±1.0158	±2.2229		±2.184					
CMAR	Hybrid	c.−757C>T	4.5307	4.5457	5.0136	0.1207	**0.061†**	-0.2414	**0.005***	-0.2265	**0.023***
			±0.0631	±0.0750	±0.1652	±0.6599		±0.8411		±0.9893	
	Angus	c.−757C>T	6.1579	6.3777	6.2061	−0.8743	0.549	0.3355	0.819	0.1743	0.373
			±0.1930	±0.1956	±0.3083	±0.1367		±0.1458		±0.1948	
	Charolais	c.−757C>T	4.5170	4.4612	--	0.5585	0.780	--	--	--	--
			±0.1075	±0.1948		±0.1795					

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b]Least square means and SE for genotypes AA, AB and BB.

[c]AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d]Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e]Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996). *P < 0.05. †P<0.10

Table 3.3. Least square means of fat deposition and carcass merit traits and estimated effects of FABP3 SNPs in hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Dominance effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.21T>C	9.0261 ±0.2581	9.3652 ±0.2644	8.7669 ±0.5149	−0.7072 ±0.2320	0.540	−0.1296 ±0.2734	0.637	0.4687 ±0.3386	0.168
		c.4593C>G	9.0834 ±0.2606	9.3296 ±0.2671	8.7561 ±0.5178	0.9505 ±0.2343	0.716	0.1637 ±0.2753	0.554	0.4099 ±0.3419	0.232
		c.7627T>C	9.1570 ±0.2054	8.2678 ±1.2091	--	0.8892 ±1.206	0.345	--	--	--	--
	Angus	c.21T>C	15.7660 ±0.3036	14.8925 ±0.6580	--	0.8734 ±0.6589	0.106	--	--	--	--
		c.4593C>G	15.7753 ±0.3033	14.8970 ±0.6575	--	−0.8782 ±0.6583	0.101	--	--	--	--
	Charolais	c.21T>C	8.0844 ±0.3590	8.0316 ±0.3587	8.3077 ±0.5117	−0.6292 ±0.2329	0.915	0.1116 ±0.2527	0.660	−0.1644 ±0.3205	0.609
		c.4593C>G	8.0993 ±0.3607	8.0191 ±0.3613	8.2987 ±0.5125	0.4867 ±0.2335	0.985	−0.9970 ±0.2525	0.694	−0.1799 ±0.3259	0.582

		c.7627T>C	8.0798	8.6844		−0.3023	0.459	--	--	--	--
			±0.3079	±0.8206		±0.3916					
UREA	Hybrid	c.21T>C	84.2011	82.2188	82.7833	−1.248	**0.047***	−0.7089	0.292	−1.273	0.139
			±0.5507	±0.5814	±1.2405	±0.5689		±0.6712		±0.8575	
		c.4593C>G	84.0359	82.3288	82.7896	−1.074	**0.090†**	0.6232	0.357	−1.084	0.211
			±0.5532	±0.5846	±1.2428	±0.5720		±0.6734		±0.8637	
		c.7627T>C	83.2281	85.3294	--	−2.101	0.573	--	--	--	--
			±0.4178	±3.0687		±3.077					
	Angus	c.21T>C	81.2284	78.8717	--	−2.357	**0.078†**	--	--	--	--
			±0.7318	±1.5720		±1.571					
		c.4593C>G	81.2677	78.8896	--	−2.378	**0.073†**	--	--	--	--
			±0.7347	±1.5753		±1.574					
	Charolais	c.21T>C	84.6990	82.8330	82.4701	−1.334	0.109	−1.114	0.144	−0.7515	0.448
			±0.9144	±0.9201	±1.4367	±0.6975		±0.7586		±0.9858	
		c.4593C>G	84.6238	82.9289	82.4816	−1.242	0.154	1.071	0.159	−0.6238	0.535
			±0.9101	±0.9236	±1.4339	±0.6968		±0.7568		±1.002	
		c.7627T>C	83.5685	85.7635	--	−1.098	0.342	--	--	--	--
			±0.7176	±2.4073		±1.191					
AUBF	Hybrid	c.21T>C	0.0333	0.0347	0.0307	0.1409	0.924	−0.1284	0.369	0.2688	0.132
			±0.0013	±0.0013	±0.0027	±0.1203		±0.1420		±0.1776	

		c.4593C>G	0.0336 ±0.0013	0.0346 ±0.0013	0.0307 ±0.0027	−0.4154 ±0.1211	0.904	0.1446 ±0.1425	0.311	0.2455 ±0.1788	0.171
		c.7627T>C	0.0336 ±0.0010	0.0318 ±0.0063	--	0.1819 ±0.6337	0.667	--	--	--	--
	Angus	c.21T>C	0.0685 ±0.0027	0.0656 ±0.0067	--	0.2905 ±0.6887	0.631	--	--	--	--
		c.4593C>G	0.0685 ±0.0027	0.0656 ±0.0067	--	−0.2916 ±0.6870	0.626	--	--	--	--
	Charolais	c.21T>C	0.0330 ±0.0025	0.0323 ±0.0025	0.0279 ±0.0043	0.1955 ±0.2150	0.395	−0.2516 ±0.2344	0.285	0.1872 ±0.3132	0.552
		c.4593C>G	0.0332 ±0.0024	0.0322 ±0.0025	0.0279 ±0.0042	−0.2157 ±0.2153	0.351	0.2634 ±0.2341	0.263	0.1638 ±0.3182	0.608
		c.7627T>C	0.0317 ±0.0019	0.0405 ±0.0074	--	−0.4375 ±0.3712	0.239	--	--	--	--
AURE-A	Hybrid	c.21T>C	0.1674 ±0.0033	0.1586 ±0.0036	0.1641 ±0.0078	0.4694 ±0.3595	0.112	−0.1631 ±0.4250	0.702	−0.7136 ±0.5502	0.196
		c.4593C>G	0.1660 ±0.0033	0.1597 ±0.0036	0.1642 ±0.0078	−0.3165 ±0.3572	0.231	0.9323 ±0.4231	0.826	−0.5439 ±0.5521	0.328
		c.7627T>C	0.1636 ±0.0023	0.1543 ±0.0196	--	0.9285 ±0.1970	0.797	--	--	--	--

	Angus	c.21T>C	0.2042 ±0.0069	0.1943 ±0.0198	--	0.9943 ±0.2041	0.776	--	--	--	--
		c.4593C>G	0.2036 ±0.0072	0.1937 ±0.0201	--	−0.9841 ±0.2076	0.813	--	--	--	--
	Charolais	c.21T>C	0.2267 ±0.0085	0.2146 ±0.0088	0.1964 ±0.0158	0.1427 ±0.8157	0.187	−0.1517 ±0.8944	**0.092†**	0.3050 ±0.1227	0.804
		c.4593C>G	0.2253 ±0.0085	0.2163 ±0.0090	0.1964 ±0.0159	−0.1284 ±0.8200	0.281	0.1441 ±0.8965	0.110	0.5446 ±0.1247	0.663
		c.7627T>C	0.2158 ±0.0060	0.2650 ±0.0284	--	0.2464 ±0.1447	**0.089†**	--	--	--	--
SWT	Hybrid	c.21T>C	542.5847 ±5.4320	546.4082 ±5.4740	533.7967 ±9.2044	0.7916 ±3.934	0.790	−4.394 ±4.620	0.345	8.218 ±5.539	0.140
		c.4593C>G	543.1402 ±5.5504	546.7316 ±5.5971	533.2540 ±9.2754	−1.243 ±3.965	0.853	4.943 ±4.637	0.287	8.534 ±5.563	0.127
		c.7627T>C	543.2578 ±4.6648	546.6633 ±20.1031	--	−3.405 ±19.81	0.881	--	--	--	--
	Angus	c.21T>C	566.1666 ±3.5126	556.3409 ±7.4694	--	−9.826 ±7.452	**0.017***	--	--	--	--
		c.4593C>G	566.1441 ±3.5103	556.3352 ±7.4561	--	−9.809 ±7.435	**0.017***	--	--	--	--

	Charolais	c.21T>C	569.9247 ±4.8906	559.7225 ±4.9183	567.5900 ±7.6413	3.884 ±3.724	0.254	−1.167 ±4.022	0.772	−9.035 ±5.219	**0.086†**
		c.4593C>G	569.7854 ±4.8662	559.9572 ±4.9331	567.5546 ±7.6177	−3.654 ±3.716	0.272	1.115 ±4.007	0.781	−8.713 ±5.294	0.102
		c.7627T>C	565.3989 ±4.1049	564.1298 ±12.9269	--	0.6345 ±6.346	0.909	--	--	--	--
CWT	Hybrid	c.21T>C	312.8577 ±3.2232	315.9075 ±3.2485	307.7274 ±5.4709	0.9089 ±2.342	0.691	−2.565 ±2.748	0.354	5.615 ±3.296	**0.090†**
		c.4593C>G	313.1268 ±3.3053	316.1589 ±3.3332	307.4468 ±5.5242	−0.2785 ±2.364	0.731	2.840 ±2.762	0.305	5.872 ±3.314	**0.078†**
		c.7627T>C	313.6347 ±2.7673	313.7209 ±11.9681	--	−0.8627 ±11.79	0.770	--	--	--	--
	Angus	c.21T>C	329.9948 ±2.1139	322.4561 ±4.8008	--	−7.539 ±4.852	**0.008***	--	--	--	--
		c.4593C>G	330.0159 ±2.1066	322.4675 ±4.7886	--	−7.548 ±4.840	**0.007***	--	--	--	--
	Charolais	c.21T>C	337.2571 ±3.0035	330.7083 ±3.0696	336.7019 ±5.2128	2.244 ±2.634	0.397	−0.2776 ±2.881	0.924	−6.271 ±3.857	0.106
		c.4593C>G	337.0997 ±2.9769	331.0343 ±3.0901	336.6474 ±5.1953	−2.026 ±2.622	0.443	0.2261 ±2.870	0.938	−5.839 ±3.907	0.137

		c.7627T>C	334.0855 ±2.2269	345.1604 ±9.0938	--	−5.537 ±4.589	0.230	--	--	--	--
AVBF	Hybrid	c.21T>C	11.9654 ±0.3084	12.2436 ±0.3265	11.3394 ±0.7000	0.6037 ±0.3208	0.951	−0.3130 ±0.3790	0.412	0.5912 ±0.4853	0.225
		c.4593C>G	11.9991 ±0.3064	12.2209 ±0.3260	11.3317 ±0.7006	−0.9911 0.3229	0.949	0.3337 ±0.3800	0.383	0.5555 ±0.4901	0.258
		c.7627T>C	12.0422 ±0.2365	10.4595 ±1.7266	--	1.582 ±1.731	0.282	--	--	--	--
	Angus	c.21T>C	17.2443 ±0.4584	16.3902 ±1.0610	--	0.8542 ±1.074	0.461	--	--	--	--
		c.4593C>G	17.2780 ±0.4609	16.4100 ±1.0667	--	−0.8679 ±1.080	0.441	--	--	--	--
	Charolais	c.21T>C	7.7237 ±0.4609	7.4148 ±0.4662	9.0565 ±0.7548	−0.3642 ±0.3725	0.385	0.6664 ±0.4070	0.104	−0.9754 ±0.5351	**0.071†**
		c.4593C>G	7.6887 ±0.4596	7.4643 ±0.4701	9.0600 ±0.7551	0.4115 ±0.3728	0.329	−0.6856 ±0.4069	**0.094†**	−0.9101 ±0.5444	**0.097†**
		c.7627T>C	7.8173 ±0.3381	7.7846 ±1.2822	--	0.1636 ±0.6430	0.973	--	--	--	--
LMY	Hybrid	c.21T>C	58.2018 ±0.3327	57.6932 ±0.3415	58.7591 ±0.6713	0.5809 ±0.3041	0.643	0.2787 ±0.3574	0.438	−0.7873 ±0.4437	**0.078†**

		c.4593C>G	58.1506 ±0.3334	57.7402 ±0.3428	58.7649 ±0.6742	0.5019 ±0.3072	0.795	−0.3072 ±0.3600	0.396	−0.7175 ±0.4488	0.112
		c.7627T>C	62.3514 ±0.2878	62.3350 ±1.2782	--	0.8207 ±0.6490	0.994	--	--	--	--
	Angus	c.21T>C	53.6608 ±0.3764	54.3640 ±0.9390	--	−0.7032 ±0.9592	0.474	--	--	--	--
		c.4593C>G	53.6431 ±0.3747	54.3520 ±0.9383	--	0.7089 ±0.9588	0.460	--	--	--	--
	Charolais	c.21T>C	62.5785 ±0.4193	62.6128 ±0.4293	61.1496 ±0.7332	0.4795 ±0.3709	0.253	−0.7145 ±0.4063	0.081	0.7488 ±0.5454	0.172
		c.4593C>G	62.5842 ±0.4194	62.6062 ±0.4359	61.1485 ±0.7349	−0.4921 ±0.3722	0.251	0.7178 ±0.4066	**0.080†**	0.7399 ±0.5543	0.184
		c.7627T>C	58.0183 ±0.2715	59.8260 ±1.5851	--	−1.808 ±1.581	0.185				
CREA	Hybrid	c.21T>C	84.3431 ±0.7787	83.3550 ±0.7926	84.8933 ±1.4854	0.2686 ±0.6632	0.705	0.2751 ±0.7797	0.725	−1.263 ±0.9562	0.188
		c.4593C>G	84.2166 ±0.7804	83.5199 ±0.7952	84.9044 ±1.4864	−0.9726 0.6669	0.905	−0.3439 ±0.7818	0.662	−1.041 ±0.9618	0.281
		c.7627T>C	83.9568 ±0.6523	87.2690 ±3.4070	--	−3.312 ±3.385	0.337	--	--	--	--

	Angus	c.21T>C	82,2537 ±0.6470	82.0660 ±1.8399	--	0.1877 ±1.898	0.694	--	--	--	--
		c.4593C>G	82.2888 ±0.6528	82.0982 ±1.8421	--	−0.1906 ±1.900	0.679	--	--	--	--
	Charolais	c.21T>C	95.4313 ±1.3003	93.5106 ±1.3117	92.3241 ±2.0870	1.658 ±1.023	0.143	−1.554 ±1.114	0.166	−0.3671 ±1.457	0.801
		c.4593C>G	95.2913 ±1.2842	93.6459 ±1.3095	92.3252 ±2.0774	−1.526 ±1.022	0.188	1.483 ±1.111	0.184	−0.1623 ±1.481	0.913
		c.7627T>C	94.1483 ±1.0070	95.1453 ±3.5214	--	−0.4985 ±1.751	0.766	--	--	--	--
CMAR	Hybrid	c.21T>C	4.5524 ±0.0666	4.5804 ±0.0678	4.4771 ±0.1283	0.9340 ±0.5729	0.956	−0.3762 ±0.6756	0.579	0.6562 ±0.8304	0.432
		c.4593C>G	4.5627 ±0.0670	4.5828 ±0.0684	4.4762 ±0.1287	−0.1627 ±0.5777	0.869	0.4324 ±0.6788	0.526	0.6335 ±0.8366	0.451
		c.7627T>C	4.5590 ±0.0545	4.4820 ±0.2967	--	0.7691 ±0.2952	0.741	--	--	--	--
	Angus	c.21T>C	6.2638 ±0.1679	6.1819 ±0.3390	--	0.8191 ±0.3342	0.922	--	--	--	--
		c.4593C>G	6.2691 ±0.1679	6.1840 ±0.3389	--	−0.6362 ±0.3200	0.971	--	--	--	--

Charolais	c.21T>C	4.5239	4.4849	4.5573	0.2508	0.962	0.1668	0.857	−0.5572	0.636
		±0.1238	±0.1238	±0.1816	±0.8456		±0.9179		±0.1172	
	c.4593C>G	4.5223	4.4834	4.5556	0.4119	0.957	−0.1667	0.854	−0.5549	0.639
		±0.1215	±0.1221	±0.1787	±0.8351		±0.9040		±0.1176	
	c.7627T>C	4.4919	5.1289		0.3185	**0.023***	--	--	--	--
		±0.1009	±0.2864		±0.1383					

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b]Least square means and SE for genotypes AA, AB and BB.

[c]AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d]Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e]Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

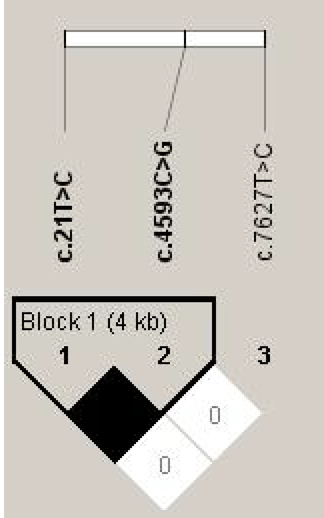

Figure 3.1. Haplotype block for FABP3 SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Figure 3.2. Haplotype block for FABP3 SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

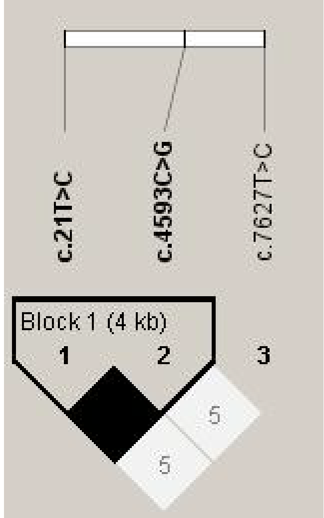

Figure 3.3. Haplotype block for FABP3 SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.4. FABP3 haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype block[a]	Haplotype name[b]	Allele arrangement[c,d]	Frequency[d]
Hybrid	HFABP3B1	HFABP3_01	T-C	0.608
		HFABP3_02	C-G	0.160
		HFABP3_03	C-C	0.117
		HFABP3_04	T-G	0.114
Angus	---	AFABP3_01	T-C	0.917
		AFABP3_02	C-C	0.041
		AFABP3_03	T-G	0.041
Charolais	CFABP3B1	CFABP3_01	T-C	0.527
		CFABP3_02	C-G	0.198
		CFABP3_03	C-C	0.139
		CFABP3_04	T-G	0.136

[a] Haplotype block is obtained from HAPLOVIEW analyses of SNP genotypes. Name is given by the Author, while last two digit indicate block no. i.e., B1 is block one.

[b] Haplotype name is given by the Author. Haplotypes were named with last two digit assigned based on frequency, i.e., H_01 is equal or more frequent than H_02.

[c] SNPs c.21T>C and c.4593C>G were used chronologically to set the allele arrangement

[d] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.5. Log likelihood ratio (LR) test result for FABP3 haplotypes in the hybrid, Angus and Charolais cattle populations.

Animal	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square value[d]	Chi-square test P-value[d]
Hybrid	UBF	−566.678	−568.994	10.66	0.0011
	UREA	−911.962	−915.633	16.906	0.00004
	AUBF	1376.37	1379.58	14.782	0.0001
	AUREA	954.764	957.85	14.21	0.0002
	SWT	−1605.84	−1611.51	26.112	<0.0001
	CWT	−1413.82	−1421.29	34.402	<0.0001
	AVBF	−699.202	−701.414	10.186	0.0014
	LMY	−667.365	−669.456	9.628	0.0019
	CREA	−951.766	−954.045	10.494	0.0012
	CMAR	−47.4918	−47.1706	1.48	0.2238
Angus	UBF	−287.271	−287.372	0.46	0.4976
	UREA	−457.832	−458.054	1.02	0.3125
	AUBF	602.504	602.504	0	1.0
	AUREA	381.786	381.786	0	1.0
	SWT	−761.658	−761.750	0.42	0.5169
	CWT	−676.868	−677.133	1.22	0.2694
	AVBF	−386.267	−386.267	0	1.0
	LMY	−365.816	−365.816	0	1.0
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.703	−142.703	0	1.0
Charolais	UBF	−225.126	−225.126	0	1.0
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.664	599.664	0	1.0
	AUREA	354.899	354.899	0	1.0
	SWT	−722.287	−722.287	0	1.0
	CWT	−668.033	−668.033	0	1.0
	AVBF	−316.704	−316.704	0	1.0
	LMY	−319.990	−319.990	0	1.0

CREA	−494.255	−494.255	0	1.0
CMAR	−42.7920	−42.7920	0	1.0

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait.

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.6. Least square means of fat deposition and carcass merit traits and estimated effects of FABP3 haplotypes in the hybrid beef cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozyg-ous[b]	Haplotype heterozyg-ous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HFABP3_01	9.0000 ±0.2554	9.4468 ±0.3928	9.1579 ±0.2892	0.9291 ±0.1605	0.335	−0.7897 ±0.1613	0.626	0.3679 ±0.4059	0.367
		HFABP3_02	8.8011 ±0.5135	9.5151 ±0.4063	9.0900 ±0.2254	0.2567 ±0.2512	0.898	−0.1444 ±0.2674	0.591	0.5695 ±0.4461	0.203
		HFABP3_03	--	9.3401 ±0.3266	9.0587 ±0.2254	−0.2814 ±0.3410	0.272	--	--	--	--
		HFABP3_04	--	9.2732 ±0.3295	9.0845 ±0.2237	−0.1887 ±0.3446	0.423	--	--	--	--
UREA	Hybrid	HFABP3_01	84.0544 ±0.5528	82.7409 ±0.8990	82.1319 ±0.6592	−0.9756 ±0.4023	**0.031***	0.9612 ±0.4048	0.019*	−0.3522 ±0.9774	0.719
		HFABP3_02	82.8391 ±1.2547	82.6851 ±0.9379	83.3316 ±0.4739	0.3446 ±0.6038	0.654	−0.2462 ±0.6630	0.711	−0.4003 ±1.109	0.719
		HFABP3_03	--	81.6854 ±0.7707	83.6900 ±0.4836	2.005 ±0.8532	**0.030***	--	--	--	--
		HFABP3_04	--	81.8737	83.6116	1.738	**0.064†**	--	--	--	--

				±0.7782	±0.4791	±0.8621					
AUBF	Hybrid	HFABP3_01	0.0331	0.0351	0.0334	0.2232	0.595	−0.1498	0.859	0.1851	0.379
			±0.0013	±0.0020	±0.0015	±0.8384		±0.8425		±0.2095	
		HFABP3_02	0.0309	0.0356	0.0334	0.4753	0.833	−0.1234	0.376	0.3443	0.139
			±0.0026	±0.0020	±0.0011	±0.1295		±0.1385		±0.2313	
		HFABP3_03	--	0.0344	0.0333	−0.1092	0.426	--	--	--	--
				±0.0017	±0.0011	±0.1779					
		HFABP3_04	--	0.0342	0.0333	−0.8565	0.517	--	--	--	--
				±0.0017	±0.0011	±0.1797					
AURE-A	Hybrid	HFABP3_01	0.1663	0.1608	0.1595	−0.3519	**0.083†**	0.3426	0.189	−0.2115	0.727
			±0.0033	±0.0055	±0.0040	±0.2580		±0.2598		±0.6039	
		HFABP3_02	0.1645	0.1617	0.1633	−0.3013	0.844	0.5977	0.886	−0.2158	0.758
			±0.0079	±0.0056	±0.0027	±0.3677		±0.4156		±0.6968	
		HFABP3_03	--	0.1564	0.1653	0.8982	**0.055†**	--	--	--	--
				±0.0046	±0.0027	±0.5380					
		HFABP3_04	--	0.1582	0.1647	0.6471	0.151	--	--	--	--
				±0.0047	±0.0027	±0.5436					
SWT	Hybrid	HFABP3_01	541.7962	555.4014	539.9526	−0.3588	0.672	0.9218	0.734	14.53	0.037*
			±5.2861	±7.3961	±5.7083	±2.693		±2.695		±6.909	
		HFABP3_02	536.9660	556.6281	541.4466	−0.8979	0.588	−2.240	0.622	17.42	0.022

			±9.1788	±7.7272	±4.9442	±4.346		±4.525		±7.516	
		HFABP3_03	--	541.9399	543.8336	1.894	0.950	--	--	--	--
				±6.2146	±4.8689	±5.712					
		HFABP3_04	--	542.3132	543.6896	1.376	0.906	--	--	--	--
				±6.2782	±4.8694	±5.775					
CWT	Hybrid	HFABP3_01	312.1999	321.9907	311.4910	0.4181	0.583	0.3544	0.825	10.15	0.014*
			±3.0934	±4.3555	±3.3484	±1.602		±1.599		±4.099	
		HFABP3_02	310.0453	323.1964	311.9994	−1.226	0.431	−0.9771	0.717	12.17	0.007*
			±5.4150	±4.5433	±2.8798	±2.581		±2.683		±4.457	
		HFABP3_03	--	312.6478	313.8594	1.212	0.988	--	--	--	--
				±3.6634	±2.8503	±3.398					
		HFABP3_04	--	312.9764	313.7357	0.7593	0.908	--	--	--	--
				±3.7019	±2.8513	±3.436					
AVBF	Hybrid	HFABP3_01	11.9607	12.1467	12.0112	0.2920	0.658	−0.2524	0.912	0.1607	0.775
			±0.3234	±0.5201	±0.3807	±0.2277		±0.2293		±0.5602	
		HFABP3_02	11.3570	12.1769	12.0589	0.2376	0.606	−0.3510	0.349	0.4689	0.454
			±0.7061	±0.5312	±0.2710	±0.3415		±0.3728		±0.6235	
		HFABP3_03	--	12.2643	11.9274	−0.3368	0.361	--	--	--	--
				±0.4338	±0.2712	±0.4813					
		HFABP3_04	--	12.2152	11.9468	−0.2683	0.451	--	--	--	--

				±0.4384	±0.2697	±0.4858					
LMY	Hybrid	HFABP3_01	58.1680	57.5617	58.0756	−0.6956	0.503	0.4623	0.828	−0.5601	0.292
			±0.3267	±0.5074	±0.3726	±0.2107		±0.2114		±0.5294	
		HFABP3_02	58.7324	57.5238	58.0558	−0.1648	0.769	0.3383	0.336	−0.8703	0.138
			±0.6699	±0.5272	±0.2895	±0.3305		±0.3497		±0.5836	
		HFABP3_03	--	57.7523	58.1331	0.3807	0.276	--	--	--	--
				±0.4292	±0.2967	±0.4477					
		HFABP3_04	--	57.8502	58.0956	0.2454	0.446	--	--	--	--
				±0.4326	±0.2939	±0.4523					
CREA	Hybrid	HFABP3_01	84.1738	83.4365	83.8507	−0.1836	0.702	0.1615	0.726	−0.5758	0.623
			±0.7638	±1.1497	±0.8532	±0.4563		±0.4588		±1.163	
		HFABP3_02	85.0361	83.5465	83.8826	−0.4058	0.572	0.5767	0.454	−0.9129	0.477
			±1.4875	±1.2017	±0.6946	±0.7245		±0.7657		±1.276	
		HFABP3_03	--	83.1931	84.2081	1.015	0.303	--	--	--	--
				±0.9606	±0.6918	±0.9690					
		HFABP3_04	--	83.5293	84.0806	0.5513	0.584	--	--	--	--
				±0.9693	±0.6877	±0.9800					
CMAR	Hybrid	HFABP3_01	4.5403	4.6618	4.5251	−0.1869	0.928	0.7633	0.848	0.1292	0.197
			±0.0633	±0.0970	±0.0715	±0.3957		±0.3966		±0.9991	
		HFABP3_02	4.5088	4.6727	4.5361	−0.1409	0.761	−0.1368	0.837	0.1503	0.173

	±0.1270	±0.1011	±0.0567	±0.6244		±0.6592		±0.1099	
HFABP3_03	--	4.5392	4.5600	0.2076	0.882	--	--	--	--
		±0.0817	±0.0575	±0.8406					
HFABP3_04	--	4.5437	4.5581	0.1437	0.937	--	--	--	--
		±0.0827	±0.0575	±0.8495					

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b]Least square means and SE for haplotype homozygous (animal contain same haplotype at both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c]Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d]Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*$P<0.05$, †$P<0.10$.

Table 3.7. Least square (LS) means of fat deposition and carcass merit traits and estimated effects of FASN SNPs in the hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Dominance effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.8581G>A	9.1097 ±0.2075	9.4137 ±0.5345	--	−0.3041 ±0.5320	0.443	--	--	--	--
		c.10388C>T	8.9067 ±0.2847	9.3576 ±0.2517	9.0938 ±0.3717	0.1516 ±0.2149	0.446	−0.9356 ±0.2194	0.671	0.3573 ±0.2894	0.218
		c.12794A>C	8.9297 ±0.2843	9.3367 ±0.2503	9.1083 ±0.3823	0.1501 ±0.2150	0.473	−0.8933 ±0.2217	0.688	0.3177 ±0.2887	0.272
		c.12865G>A	9.0143 ±0.3696	9.3718 ±0.2511	8.9097 ±0.2891	−0.1152 ±0.2156	0.583	0.5233 ±0.2194	0.812	0.4098 ±0.2868	0.155
		c.14169T>C	8.8921 ±0.2669	9.3958 ±0.2605	9.1585 ±0.4075	−0.2245 ±0.2168	0.256	0.1332 ±0.2286	0.562	0.3705 ±0.2990	0.217
	Angus	c.10388C>T	15.6700 ±0.6361	15.6634 ±0.3319	15.7121 ±0.3871	0.3284 ±0.3007	0.944	−0.2104 ±0.3424	0.951	−0.2766 ±0.3823	0.943
		c.12794A>C	15.6539 ±0.6367	15.6265 ±0.3355	15.7672 ±0.3788	0.9190 ±0.3004	0.790	−0.5662 ±0.3418	0.869	−0.8400 ±0.3835	0.827

		c.12865G>A	15.7442 ±0.3894	15.6183 ±0.3408	15.6345 ±0.6389	−0.8463 ±0.3019	0.811	0.5486 ±0.3424	0.873	−0.7102 ±0.3803	0.852
		c.14169T>C	15.6798 ±0.6208	15.6304 ±0.3288	15.7721 ±0.3917	−0.8356 ±0.3024	0.814	0.4615 ±0.3372	0.891	−0.9552 ±0.3760	0.800
	Charolais	c.10388C>T	8.1312 ±0.3218	--	7.5994 ±0.5350	−0.2659 ±0.2370	0.287	0.5318 ±0.4740	0.264	--	--
		c.12794A>C	7.8415 ±0.3506	8.4864 ±0.3652	7.7376 ±0.5362	0.1899 ±0.2327	0.506	0.5194 ±0.2542	0.838	0.6968 ±0.3227	**0.033***
		c.12865G>A	8.3487 ±0.3344	--	7.7939 ±0.3472	−0.2774 ±0.1577	0.123	0.5548 ±0.3155	**0.081†**	--	--
		c.14169T>C	7.9177 ±0.3255	--	8.4035 ±0.3629	−0.2429 ±0.1592	0.143	0.4858 ±0.3184	0.129	--	--
UREA	Hybrid	c.8581G>A	83.2042 ±0.4367	84.3470 ±1.3148		−1.143 ±1.343	0.337	--	--	--	--
		c.10388C>T	83.3813 ±0.6188	82.7624 ±0.5442	84.2336 ±0.8588	0.2428 ±0.5199	0.626	−0.4261 ±0.5262	0.420	−1.045 ±0.7276	0.153
		c.12794A>C	83.4327 ±0.6410	82.8855 ±0.5568	83.8509 ±0.9076	0.4764 ±0.5312	0.920	−0.2091 ±0.5450	0.702	−0.7563 ±0.7319	0.302
		c.12865G>A	84.0667 ±0.8513	82.9139 ±0.5399	83.2746 ±0.6279	−0.2639 ±0.5203	0.612	0.3961 ±0.5263	0.453	−0.7568 ±0.7234	0.296

		c.14169T>C	83.4414	82.8987	83.8122	0.6693	0.967	0.1854	0.739	−0.7281	0.340
			±0.5844	±0.5795	±0.9626	±0.5302		±0.5561		±0.7582	
	Angus	c.10388C>T	82.1425	81.0128	80.6667	−0.5721	0.407	0.7379	0.368	−0.3918	0.668
			±1.5176	±0.7933	±0.9119	±0.7178		±0.8165		±0.9112	
		c.12794A>C	81.9959	80.6847	81.1761	−0.3144	0.937	0.4099	0.616	−0.9013	0.327
			±1.5150	±0.7946	±0.8979	±0.7182		±0.8143		±0.9147	
		c.12865G>A	80.7178	80.9131	82.0571	0.4703	0.490	−0.6697	0.413	−0.4744	0.604
			±0.9026	±0.7854	±1.5093	±0.7177		±0.8142		±0.9103	
		c.14169T>C	82.2662	80.8885	80.8115	0.4731	0.490	−0.7273	0.368	−0.6503	0.470
			±1.4805	±0.7849	±0.9348	±0.7222		±0.8040		±0.8962	
	Charolais	c.10388C>T	83.6393	--	83.6740	0.1738	0.951	−0.3464	0.982	--	--
			±0.7334		±1.5339	±0.7433		±1.487			
		c.12794A>C	83.1452	84.2284	83.9496	0.6414	0.259	−0.4022	0.614	0.6810	0.513
			±0.8509	±0.9139	±1.5544	±0.7069		±0.7957		±1.036	
		c.12865G>A	84.2693	--	82.7629	−0.7532	**0.055†**	1.506	0.114	--	--
			±0.8226		±0.8740	±0.4731		±0.9461			
		c.14169T>C	83.4800	--	83.9334	−0.2267	0.588	0.4534	0.642	--	--
			±0.7982		±0.9455	±0.4846		±0.9693			
AUBF	Hybrid	c.8581G>A	0.0335	0.0349	--	−0.1466	0.511	--	--	--	--
			±0.0010	±0.0028		±0.2789					

	c.10388C>T	0.0328 ±0.0014	0.0342 ±0.0013	0.0335 ±0.0019	0.5098 ±0.1107	0.621	−0.3543 ±0.1134	0.756	0.9772 ±0.1513	0.520
	c.12794A>C	0.0330 ±0.0014	0.0340 ±0.0013	0.0339 ±0.0020	0.5882 ±0.1116	0.589	−0.4725 ±0.1154	0.694	0.5990 ±0.1516	0.683
	c.12865G>A	0.0332±0.0019	0.0343±0.0013	0.0330±0.0015	−0.3140 ±0.1114	0.772	0.1269 ±0.1139	0.912	0.1190 ±0.1504	0.431
	c.14169T>C	0.0322 ±0.0013	0.0351 ±0.0013	0.0334 ±0.0021	−0.1136 ±0.1117	0.280	0.5844 ±0.1178	0.621	0.2278 ±0.1565	0.147
Angus	c.10388C>T	0.0625 ±0.0065	0.0678 ±0.0031	0.0702 ±0.0036	0.3259 ±0.3136	0.305	−0.3855 ±0.3581	0.283	0.1457 ±0.4115	0.724
	c.12794A>C	0.0626 ±0.0065	0.0682 ±0.0031	0.0696 ±0.0036	0.2592 ±0.3130	0.415	−0.3464 ±0.3573	0.335	0.2119 ±0.4131	0.609
	c.12865G>A	0.0703 ±0.0037	0.0677 ±0.0031	0.0624 ±0.0066	−0.3435 ±0.3156	0.283	0.3955 ±0.3596	0.273	0.1291 ±0.4124	0.755
	c.14169T>C	0.0624 ±0.0064	0.0677 ±0.0031	0.0709 ±0.0038	−0.3855 ±0.3163	0.229	0.4239 ±0.3532	0.232	0.1026 ±0.4041	0.800
Charolais	c.10388C>T	0.0319 ±0.0019	--	0.0312±0.0046	−0.3174 ±0.2304	0.880	0.6347 ±0.4609	0.891		
	c.12794A>C	0.0304 ±0.0024	0.0341 ±0.0026	0.0323 ±0.0048	0.1977 ±0.2193	0.352	−0.9387 ±0.2496	0.708	0.2810 ±0.3292	0.395

		c.12865G>A	0.0339±0.0022	--	0.0293±0.0024	−0.2307 ±0.1447	**0.099†**	0.4613 ±0.2895	0.114	--	--
		c.14169T>C	0.0306 ±0.0022	--	0.0344 ±0.0027	−0.1870 ±0.1501	0.211	0.3741 ±0.3002	0.215	--	--
AUREA	Hybrid	c.8581G>A	0.1638 ±0.0024	0.1637 ±0.0082	--	0.6360 ±0.8523	0.834	--	--	--	--
		c.10388C>T	0.1626 ±0.0038	0.1625 ±0.0034	0.1695 ±0.0054	0.2947 ±0.3237	0.384	−0.3447 ±0.3305	0.298	−0.3521 ±0.4633	0.450
		c.12794A>C	0.1623 ±0.0038	0.1620 ±0.0033	0.1696 ±0.0056	0.2971 ±0.3282	0.378	−0.3636 ±0.3377	0.283	−0.3913 ±0.4650	0.403
		c.12865G>A	0.1679 ±0.0053	0.1623 ±0.0034	0.1627 ±0.0039	−0.2201 ±0.3256	0.499	0.2605 ±0.3318	0.435	−0.3010 ±0.4624	0.517
		c.14169T>C	0.1615 ±0.0035	0.1653 ±0.0035	0.1647 ±0.0060	−0.2096 ±0.3288	0.585	0.1591 ±0.3465	0.648	0.2255 ±0.4839	0.643
	Angus	c.10388C>T	0.2040 ±0.0197	0.1982 ±0.0087	0.2093 ±0.0104	0.6133 ±0.9474	0.500	−0.2688 ±0.1086	0.805	−0.8480 ±0.1278	0.509
		c.12794A>C	0.2030 ±0.0197	0.1945 ±0.0089	0.2146 ±0.0103	0.1161 ±0.9460	0.211	−0.5790 ±0.1082	0.594	−0.1429 ±0.1274	0.264
		c.12865G>A	0.2097 ±0.0104	0.1973 ±0.0088	0.2035 ±0.0197	−0.6884 ±0.9481	0.451	0.3113 ±0.1086	0.775	−0.9368 ±0.1277	0.465

		c.14169T>C	0.2060 ±0.0192	0.1981 ±0.0086	0.2097 ±0.0107	−0.5538 ±0.9581	0.543	0.1879 ±0.1072	0.861	−0.9746 ±0.1256	0.440
	Charolais	c.10388C>T	0.2167 ±0.0062	--	0.2245 ±0.0178	0.3876 ±0.9221	0.742	−0.7751 ±0.1844	0.675		
		c.12794A>C	0.2118 ±0.0081	0.2239 ±0.0091	0.2246 ±0.0182	0.8456 ±0.8505	0.203	−0.6370 ±0.9800	0.517	0.5665 ±0.1314	0.667
		c.12865G>A	0.2235 ±0.0078	--	0.2087 ±0.0087	−0.7407 ±0.5649	**0.080†**	0.1481 ±0.1130	0.192	--	--
		c.14169T>C	0.2126 ±0.0072	--	0.2274 ±0.0096	−0.7420 ±0.5779	0.174	0.1484 ±0.1156	0.201	--	--
SWT	Hybrid	c.8581G>A	542.9646 ±4.7352	546.2387 ±9.5657	--	−3.274 ±8.941	0.513	--	--	--	--
		c.10388C>T	541.3180 ±5.7598	541.4358 ±5.2415	550.7669 ±6.9833	3.935 ±3.661	0.237	−4.724 ±3.757	0.210	−4.607 ±4.800	0.340
		c.12794A>C	541.1131 ±5.6943	542.5579 ±5.1775	549.1374 ±7.0988	3.485 ±3.643	0.321	−4.012 ±3.777	0.289	−2.567 ±4.788	0.594
		c.12865G>A	551.0277 ±6.9175	542.1323 ±5.1952	540.2483 ±5.7845	−4.832 ±3.665	0.176	5.390 ±3.750	0.152	−3.506 ±4.748	0.463
		c.14169T>C	541.0175 ±5.4460	542.3248 ±5.3116	551.5190 ±7.5076	−4.219 ±3.700	0.194	5.251 ±3.914	0.181	−3.943 ±4.938	0.427

	Angus	c.10388C>T	567.4442	567.0788	561.3313	−4.196	0.173	3.056	0.429	2.691	0.529
			±7.2253	±3.9097	±4.4577	±3.389		±3.849		±4.258	
		c.12794A>C	567.4219	567.0452	561.6531	−3.940	0.198	2.884	0.455	2.508	0.559
			±7.2260	±3.9303	±4.4061	±3.388		±3.845		±4.279	
		c.12865G>A	561.3726	567.0263	567.3915	4.119	0.182	−3.009	0.438	2.644	0.538
			±4.4698	±3.9249	±7.2461	±3.414		±3.866		±4.277	
		c.14169T>C	567.1504	567.1608	560.7568	4.449	0.151	−3.197	0.401	3.207	0.445
			±7.0538	±3.8820	±4.5686	±3.402		±3.786		±4.185	
	Charolais	c.10388C>T	565.4805	--	566.1673	0.3434	0.903	−0.6868	0.930	--	--
			±4.1143		±8.1991	±3.915		±7.831			
		c.12794A>C	559.7424	572.4034	566.7403	6.856	**0.083**	−3.499	0.402	9.162	0.092
			±4.5710	±4.8894	±8.1769	±3.718		±4.157		±5.398	
		c.12865G>A	570.5706	--	559.0670	−5.752	**0.035***	11.50	**0.024***	--	--
			±4.5521		±4.8074	±2.511		±5.022			
		c.14169T>C	563.3500	--	568.8335	−2.742	0.301	5.483	0.288	--	--
			±4.3471		±5.1030	±2.568		±5.135			
CWT	Hybrid	c.8581G>A	313.3806	316.0671	--	−2.686	0.440	--	--	--	--
			±2.7953	±5.6817		±5.322					
		c.10388C>T	313.2019	312.4906	316.8132	1.366	0.469	−1.806	0.422	−2.517	0.382
			±3.4149	±3.1051	±4.1475	±2.181		±2.237		±2.860	

	c.12794A>C	313.0817	313.1175	315.9221	1.133	0.577	−1.420	0.530	−1.384	0.626
		±3.3871	±3.0788	±4.2251	±2.170		±2.250		±2.853	
	c.12865G>A	317.3351	312.9599	312.4361	−2.137	0.310	2.450	0.274	−1.926	0.498
		±4.1079	±3.0776	±3.4298	±2.183		±2.233		±2.829	
	c.14169T>C	314.0710	312.3237	315.8814	−0.1952	0.811	0.9052	0.700	−2.653	0.371
		±3.2575	±3.1774	±4.4843	±2.208		±2.335		±2.944	
Angus	c.10388C>T	331.6829	330.4649	326.5084	−3.178	0.120	2.587	0.308	1.369	0.630
		±4.6714	±2.3971	±2.7856	±2.226		±2.529		±2.835	
	c.12794A>C	331.5969	330.3160	326.9339	−2.781	0.168	2.332	0.358	1.051	0.713
		±4.6732	±2.4088	±2.7517	±2.225		±2.527		±2.850	
	c.12865G>A	326.5363	330.4279	331.6473	3.126	0.127	−2.556	0.316	1.336	0.640
		±2.7931	±2.4075	±4.6842	±2.241		±2.538		±2.846	
	c.14169T>C	331.4810	330.7262	325.6976	3.737	**0.072†**	−2.892	0.247	2.137	0.444
		±4.5528	±2.3789	±2.8678	±2.239		±2.487		±2.780	
Charolais	c.10388C>T	334.7396	--	332.4358	−1.152	0.694	2.304	0.692	--	--
		±2.3722		±5.7669	±2.898		±5.796			
	c.12794A>C	333.0671	336.8339	332.0109	1.061	0.701	0.5281	0.864	4.295	0.295
		±2.8474	±3.1337	±5.8501	±2.711		±3.090		±4.089	
	c.12865G>A	335.9204	--	332.7997	−1.560	0.401	3.121	0.392	--	--
		±2.7541		±3.0056	±1.814		±3.629			

		c.14169T>C	334.2975 ±2.6047	--	334.8275 ±3.2768	−0.2650 ±1.852	0.888	0.5300 ±3.704	0.887	--	--
AVBF	Hybrid	c.8581G>A	11.9835 ±0.2454	12.2523 ±0.7407	--	−0.2686 ±0.7568	0.609	--	--	--	--
		c.10388C>T	11.8283 ±0.3578	12.2665 ±0.3143	11.9156 ±0.4917	0.1021 ±0.2953	0.704	−0.4366 ±0.3002	0.885	0.3946 ±0.4113	0.341
		c.12794A>C	11.8752 ±0.3593	12.1719 ±0.3120	11.9684 ±0.5091	0.9079 ±0.2972	0.748	−0.4661 ±0.3058	0.879	0.2501 ±0.4109	0.545
		c.12865G>A	11.9873 ±0.4901	12.2205 ±0.3145	11.8108 ±0.3660	−0.1341 ±0.2963	0.649	0.8825 ±0.3014	0.770	0.3214 ±0.4089	0.435
		c.14169T>C	11.9758 ±0.3392	12.0201 ±0.3347	12.1248 ±0.5505	−0.6732 ±0.2999	0.765	0.7448 ±0.3168	0.815	−0.3021 ±0.4279	0.944
	Angus	c.10388C>T	18.0745 ±1.0158	17.5299 ±0.4932	16.4371 ±0.5762	−0.9316 ±0.4865	**0.058†**	0.8187 ±0.5551	0.142	0.2741 ±0.6327	0.666
		c.12794A>C	18.0503 ±1.0205	17.4636 ±0.5018	16.5790 ±0.5750	−0.7965 ±0.4873	0.105	0.7356 ±0.5561	0.188	0.1490 ±0.6362	0.815
		c.12865G>A	16.4715 ±0.5856	17.4769 ±0.5039	18.0335 ±1.0205	0.8721 ±0.4892	**0.077†**	−0.7810 ±0.5566	0.163	0.2244 ±0.6321	0.723
		c.14169T>C	17.9761 ±1.0001	17.3496 ±0.4979	16.6777 ±0.6046	0.6575 ±0.4939	0.186	−0.6492 ±0.5515	0.241	0.2266 ±0.6246	0.971

	Charolais	c.10388C>T	7.8128 ±0.3395	--	7.9954 ±0.8062	0.9130 ±0.4032	0.802	−0.1826 ±0.8063	0.821	--	--
		c.12794A>C	7.9381 ±0.4086	7.6225 ±0.4474	8.0759 ±0.8201	−0.6870 ±0.3796	0.802	−0.6889 ±0.4308	0.873	−0.3845 ±0.5683	0.500
		c.12865G>A	7.7316 ±0.3990		7.8606 ±0.4319	0.6951 ±0.2536	0.724	−0.1390 ±0.5071	0.785		
		c.14169T>C	7.8843 ±0.3803	--	7.7035 ±0.4699	0.9038 ±0.2588	0.711	−0.1808 ±0.5177	0.728	--	--
LMY	Hybrid	c.8581G>A	58.0758 ±0.2765	57.7904 ±0.7048	--	0.2854 ±0.7000	0.561	--	--	--	--
		c.10388C>T	58.3375 ±0.3770	57.8011 ±0.3336	58.0095 ±0.4905	−0.2265 ±0.2823	0.394	0.1640 ±0.2886	0.571	−0.3725 ±0.3800	0.330
		c.12794A>C	58.3354 ±0.3718	57.8461 ±0.3272	57.9209 ±0.5009	−0.2634 ±0.2819	0.342	0.2073 ±0.2910	0.478	−0.2820 ±0.3793	0.460
		c.12865G>A	57.9697 ±0.4870	57.8428 ±0.3314	58.3397 ±0.3813	0.2347 ±0.2831	0.401	−0.1850 ±0.2888	0.524	−0.3119 ±0.3772	0.411
		c.14169T>C	58.2953 ±0.3561	57.9020 ±0.3473	57.7440 ±0.5395	0.3054 ±0.2851	0.247	−0.2756 ±0.3014	0.363	−0.1176 ±0.3930	0.766
	Angus	c.10388C>T	52.7278 ±0.9004	53.4948 ±0.4157	54.2612 ±0.4906	0.7662 ±0.4327	**0.079†**	−0.7667 ±0.4953	0.124	0.2609 ±0.5741	0.999

		c.12794A>C	52.7382 ±0.9024	53.5331 ±0.4210	54.1812 ±0.4877	0.6914 ±0.4327	0.112	−0.7215 ±0.4954	0.148	0.7340 ±0.5764	0.899
		c.12865G>A	54.2533 ±0.4954	53.5170 ±0.4214	52.7411 ±0.9045	−0.7477 ±0.4354	**0.088†**	0.7561 ±0.4974	0.131	0.1980 ±0.5757	0.972
		c.14169T>C	52.7906 ±0.8843	53.6449 ±0.4181	54.0766 ±0.5156	−0.5625 ±0.4398	0.202	0.6430 ±0.4920	0.193	0.2113 ±0.5656	0.710
	Charolais	c.10388C>T	62.3409 ±0.2895	--	62.278 5±0.7975	−0.3122 ±0.4099	0.916	0.6244 ±0.8199	0.939		
		c.12794A>C	62.2797 ±0.3729	62.4753 ±0.4162	62.1614 ±0.8157	0.3472 ±0.3806	0.855	0.5916 ±0.4367	0.893	0.2548 ±0.5829	0.663
		c.12865G>A	62.4469 ±0.3556	--	62.2662 ±0.3963	−0.9032 ±0.2527	0.635	0.1806 ±0.5055	0.721	--	--
		c.14169T>C	62.3024 ±0.3366	--	62.4383 ±0.4388	−0.6793 ±0.2590	0.773	0.1359 ±0.5181	0.794	--	--
CREA	Hybrid	c.8581G>A	83.9963 ±0.6589	84.0324 ±1.5502	--	−0.3605 ±1.513	0.974	--	--	--	--
		c.10388C>T	84.8071 ±0.8827	83.4566 ±0.7906	83.8229 ±1.1103	−0.6480 ±0.6148	0.293	0.4921 ±0.6297	0.437	−0.8584 ±0.8155	0.293
		c.12794A>C	84.9783 ±0.8823	83.4668 ±0.7887	83.4616 ±1.1424	−0.9191 ±0.6171	0.138	0.7583 ±0.6384	0.236	−0.7532 ±0.8187	0.361

	c.12865G>A	83.9739	83.5980	84.6154	0.4404	0.477	−0.3208	0.612	−0.6966	0.392
		±1.0990	±0.7805	±0.8862	±0.6166		±0.6298		±0.8096	
	c.14169T>C	85.2026	83.1012	83.2482	1.280	**0.042***	−0.9772	0.137	−1.124	0.182
		±0.8344	±0.8127	±1.2069	±0.6208		±0.6586		±0.8386	
Angus	c.10388C>T	81.1461	82.9527	81.5938	−0.4231	0.596	−0.2239	0.822	1.583	0.177
		±1.7988	±0.7984	±0.9490	±0.8650		±0.9925		±1.167	
	c.12794A>C	81.1369	82.8961	81.7224	−0.3018	0.694	−0.2927	0.769	1.466	0.212
		±1.8019	±0.8081	±0.9435	±0.8642		±0.9927		±1.171	
	c.12865G>A	81.6003	82.8734	81.1119	0.3724	0.635	0.2442	0.806	1.517	0.197
		±0.9371	±0.7891	±1.7929	±0.8623		±0.9900		±1.170	
	c.14169T>C	81.0479	83.0708	81.3256	0.5747	0.484	0.1389	0.887	1.884	0.102
		±1.7476	±0.7840	±0.9810	±0.8744		±0.9776		±1.144	
Charolais	c.10388C>T	94.1877	--	94.1917	0.2004	0.971	−0.4009	0.999	--	--
		±1.0201		±2.2298	±1.093		±2.187			
	c.12794A>C	94.0597	94.4257	93.8627	0.6596	0.867	0.9849	0.933	0.4645	0.763
		±1.2051	±1.3021	±2.2699	±1.038		±1.173		±1.534	
	c.12865G>A	94.6136	--	93.6895	−0.4620	0.423	0.9241	0.510	--	--
		±1.1873		±1.2663	±0.6990		±1.398			
	c.14169T>C	94.1737	--	94.2094	−0.1783	0.953	0.3566	0.980	--	--
		±1.1263		±1.3514	±0.7096		±1.419			

CMAR	Hybrid	c.8581G>A	4.5614	4.4927	--	0.6867	0.649	--	--	--	--
			±0.0548	±0.1334		±0.1312					
		c.10388C>T	4.5014	4.5892	4.5909	0.5205	0.317	−0.4475	0.415	0.4301	0.547
			±0.0746	±0.0665	±0.0949	±0.5319		±0.5457		±0.7104	
		c.12794A>C	4.5108	4.5818	4.5949	0.4785	0.366	−0.4207	0.445	0.2896	0.684
			±0.0731	±0.0649	±0.0963	±0.5291		±0.5479		±0.7072	
		c.12865G>A	4.6231	4.5806	4.4868	−0.7227	0.175	0.6815	0.213	0.2566	0.717
			±0.0942	±0.0660	±0.0753	±0.5334		±0.5457		±0.7045	
		c.14169T>C	4.5071	4.6074	4.5525	−0.4218	0.416	0.2270	0.690	0.7763	0.291
			±0.0696	±0.0678	±0.1030	±0.5371		±0.5676		±0.7332	
	Angus	c.10388C>T	6.7645	6.2779	6.0995	−0.2660	**0.081†**	0.3135	**0.056†**	−0.1367	0.450
			±0.3193	±0.1739	±0.1979	±0.1498		±0.1628		±0.1801	
		c.12794A>C	6.7593	6.2659	6.1272	−0.2401	0.115	0.2995	**0.068†**	−1565	0.389
			±0.3196	±0.1752	±0.1961	±0.1500		±0.1627		±0.1810	
		c.12865G>A	6.0900	6.2918	6.7816	0.2846	**0.063†**	−0.3263	**0.047***	−0.1267	0.484
			±0.1963	±0.1724	±0.3183	±0.1503		±0.1629		±0.1805	
		c.14169T>C	6.8095	6.2526	6.1094	0.2680	**0.080†**	−0.3336	**0.039***	−0.1936	0.276
			±0.3116	±0.1727	±0.2028	±0.1504		±0.1600		±0.1769	
	Charolais	c.10388C>T	4.5159	--	4.4600	−0.2839	0.759	0.5584	0.746	--	--
			±0.1035		±0.1868	±0.8728		±0.1720			

c.12794A>C	4.5064	4.5410	4.4167	−0.1836	0.799	0.4552	0.625	0.7582	0.525
	±0.1192	±0.1253	±0.1928	±0.8477		±0.9277		±0.1188	
c.12865G>A	4.5321	--	4.4796	−0.2829	0.665	0.5243	0.647	--	--
	±0.1180		±0.1227	±0.5783		±0.1139			
c.14169T>C	4.5374	--	4.4652	0.3747	0.512	−0.7216	0.530	--	--
	±0.1116		±0.1259	±0.5817		±0.1146			

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10

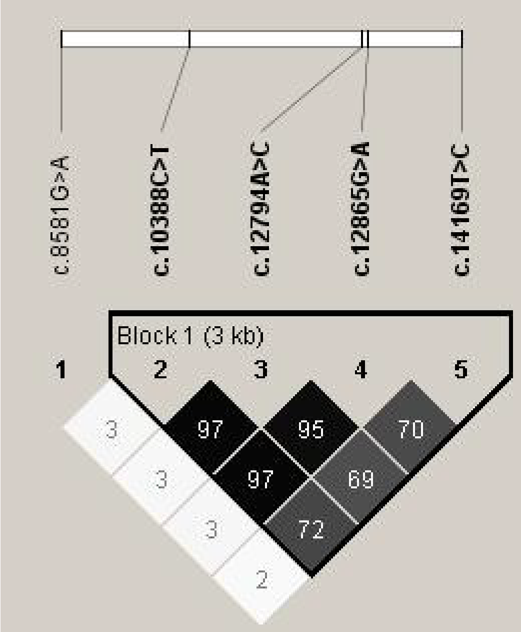

Figure 3.4. Haplotype block for FASN SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

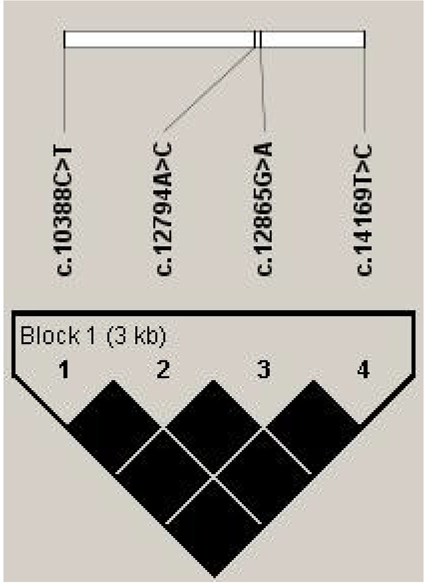

Figure 3.5. Haplotype block for FASN SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

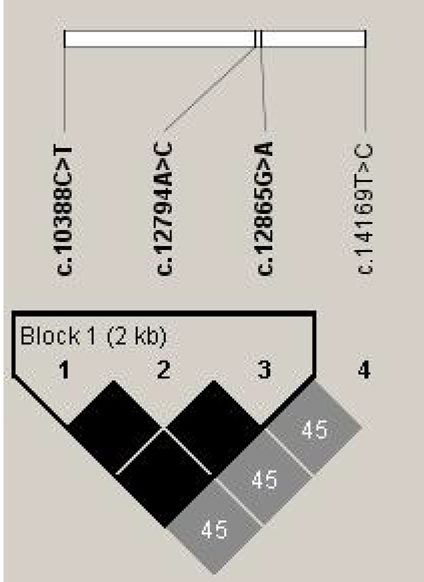

Figure 3.6. Haplotype block for FASN SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.8. FASN haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype block[a]	Haplotype name[b]	Allele arrangement[c,d]	Frequency[d]
Hybrid	HFASNB1	HFASN_01	C-A-A-T	0.412
		HFASN_02	T-C-G-C	0.259
		HFASN_03	T-A-A-T	0.135
		HFASN_04	C-C-G-C	0.116
		HFASN_05	T-C-G-T	0.037
		Others 7 types	---	0.040
Angus	AFASNB1	AFASN_01	T-C-G-C	0.422
		AFASN_02	C-A-A-T	0.187
		AFASN_03	T-C-A-T	0.175
		AFASN_04	C-A-G-C	0.169
		Other 4 types	---	0.046
Charolais	CFASNB1	CFASN_01	C-A-A	0.580
		CFASN_02	T-C-G	0.219

	CFASN_03	C-C-G	0.072
	CFASN_04	T-A-A	0.069
	Other 3 types	---	0.058

[a] Haplotype block is obtained from HAPLOVIEW analyses of SNP genotypes. Name is given by the Author, while last two digit indicate block no. i.e., B1 is block one.

[b] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[c] SNPs c.10388C>T , c.12794A>C, c.12865G>A, c.14169T>C were used chronologically to set the allele arrangement for hybrid and Angus. SNPs c.10388C>T , c.12794A>C, c.12865G>A were used chronologically to set the allele arrangement for Charolais.

[d] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.9. Log likelihood ratio (LR) test result for FASN haplotypes in the hybrid, Angus and Charolais cattle populations.

Cattle population	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	UBF	−566.678	−568.994	10.66	0.0011
	UREA	−913.253	−915.633	10.96	0.0009
	AUBF	1376.74	1379.58	13.08	0.0003
	AUREA	955.601	957.85	10.36	0.0013
	SWT	−1605.59	−1611.51	27.26	<0.0001
	CWT	−1413.82	−1421.29	34.40	<0.0001
	AVBF	−699.202	−701.414	10.19	0.0014
	LMY	−667.366	−669.456	9.62	0.0019
	CREA	−951.766	−954.045	10.49	0.0012
	CMAR	−47.329	−47.1706	0.73	0.3928
Angus	UBF	−287.372	−287.372	0	1.0
	UREA	−458.054	−458.054	0	1.0
	AUBF	602.508	602.504	0.02	0.8875

	AUREA	381.785	381.786	0.004	0.9496
	SWT	−761.750	−761.750	0	1.0
	CWT	−677.133	−677.133	0	1.0
	AVBF	−386.235	−386.267	0.15	0.6985
	LMY	−365.524	−365.816	1.34	0.247
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.162	−142.703	2.49	0.1146
Charolais	UBF	−225.042	−225.126	0.386	0.5344
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.661	599.664	0.014	0.9058
	AUREA	354.899	354.899	0	1.0
	SWT	−722.277	−722.287	0.046	0.8302
	CWT	−668.033	−668.033	0	1.0
	AVBF	−316.704	−316.704	0	1.0
	LMY	−319.990	−319.990	0	1.0
	CREA	−494.255	−494.255	0	1.0
	CMAR	−42.7920	−42.7920	0	1.0

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait.

Details of

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.10. Least square means of fat deposition and carcass merit traits and estimated effects of FASN haplotypes in the hybrid beef cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HFASN_01	8.8769 ±0.2874	9.5632 ±0.3652	9.1394 ±0.2538	0.1175 ±0.1645	0.548	−0.1312 ±0.1645	0.428	0.5550 ±0.3791	0.145
		HFASN_02	9.0272 ±0.4037	9.3537 ±0.3505	9.0836 ±0.2346	−0.2028 ±0.2025	0.921	−0.2816 ±0.2117	0.895	0.2983 ±0.3768	0.431
		HFASN_03	--	9.3037 ±0.3187	9.0726 ±0.2217	−0.2310 ±0.3323	0.505	--	--	--	--
		HFASN_04	--	9.3435 ±0.3449	9.0776 ±0.2165	−0.2659 ±0.3527	0.475	--	--	--	--
		HFASN_05	--	9.0930 ±0.5647	9.1361 ±0.2064	0.4305 ±0.5608	0.842	--	--	--	--
UREA	Hybrid	HFASN_01	83.3861 ±0.6658	82.7205 ±0.8559	83.2307 ±0.5817	−0.4966 ±0.4110	0.857	0.7769 ±0.4134	0.852	−0.5880 ±0.9314	0.529
		HFASN_02	82.9497 ±0.9747	82.9306 ±0.8217	83.3192 ±0.5130	0.2168 ±0.4988	0.666	−0.1847 ±0.5264	0.727	−0.2039 ±0.9409	0.829
		HFASN_03	--	83.0122	83.2339	0.2217	0.778	--	--	--	--

				±0.7404	±0.4627	±0.8216					
		HFASN_04	--	82.9761	83.2299	0.2538	0.760	--	--	--	--
				±0.8105	±0.4509	±0.8774					
		HFASN_05	--	84.5621	83.0870	−1.475	0.341	--	--	--	--
				±1.3947	±0.4230	±1.420					
AUBF	Hybrid	HFASN_01	0.0329	0.0365	0.0328	−0.1508	0.803	0.5000	0.954	0.3688	0.062†
			±0.0015	±0.0019	±0.0013	±0.8578		±0.8561		±0.1960	
		HFASN_02	0.0330	0.0358	0.0329	−0.5474	0.601	0.6817	0.951	0.2786	0.156
			±0.0021	±0.0018	±0.0011	±0.1045		±0.1095		±0.1953	
		HFASN_03	--	0.0329	0.0337	0.8072	0.628	--	--	--	--
				±0.0016	±0.0011	±0.1724					
		HFASN_04	--	0.0337	0.0335	−0.2467	0.913	--	--	--	--
				±0.0018	±0.0011	±0.1836					
		HFASN_05	--	0.0350	0.0334	−0.1553	0.661	--	--	--	--
				±0.0029	±0.0010	±0.2932					
AUREA	Hybrid	HFASN_01	0.1626	0.1697	0.1605	−0.1349	0.681	0.1034	0.691	0.8197	0.150
			±0.0039	±0.0051	±0.0034	±0.2586		±0.2592		±0.5670	
		HFASN_02	0.1630	0.1712	0.1604	−0.3118	0.308	0.1285	0.694	0.9458	0.107
			±0.0059	±0.0049	±0.0028	±0.3059		±0.3255		±0.5831	
		HFASN_03	--	0.1568	0.1652	0.8438	0.105	--	--	--	--

				±0.0045	±0.0026	±0.5126					
		HFASN_04	--	0.1597 ±0.0049	0.1640 ±0.0026	0.4324 ±0.5501	0.448	--	--	--	--
		HFASN_05	--	0.1768 ±0.0088	0.1622 ±0.0024	−0.1459 ±0.9036	**0.079†**	--	--	--	--
SWT	Hybrid	HFASN_01	540.7334 ±5.8120	542.8225 ±7.1165	545.1787 ±5.2764	2.227 ±2.790	0.519	−2.223 ±2.796	0.429	−0.1336 ±6.574	0.984
		HFASN_02	548.9735 ±7.4274	542.8791 ±6.7094	542.0704 ±4.9738	−3.050 ±3.474	0.392	3.452 ±3.605	0.341	−2.643 ±6.353	0.679
		HFASN_03	--	540.6827 ±6.1893	544.3638 ±4.9001	3.681 ±5.690	0.502	--	--	--	--
		HFASN_04	--	542.6618 ±6.5823	543.5301 ±4.8240	0.8683 ±5.973	0.854	--	--	--	--
		HFASN_05	--	547.5816 ±9.9087	543.0742 ±4.6741	−4.507 ±9.303	0.728	--	--	--	--
CWT	Hybrid	HFASN_01	312.7404 ±3.4202	313.9515 ±4.1990	313.8970 ±3.0996	0.5670 ±1.660	0.842	−0.5783 ±1.664	0.729	0.6328 ±3.909	0.872
		HFASN_02	314.2492 ±4.4136	313.1791 ±3.9836	313.4809 ±2.9463	−0.2801 ±2.068	0.904	0.3841 ±2.147	0.859	−0.6860 ±3.785	0.857
		HFASN_03	--	311.8350	314.1896	2.355	0.471	--	--	--	--

				±3.6397	±2.8597	±3.380					
		HFASN_04	--	311.4200	314.1201	2.700	0.427	--	--	--	--
				±3.8675	±2.8041	±3.549					
		HFASN_05	--	318.9345	313.2041	−5.730	0.368	--	--	--	--
				±5.8678	±2.7285	±5.532					
AVBF	Hybrid	HFASN_01	11.8249	12.1528	12.0913	0.1280	0.643	−0.1332	0.568	0.1947	0.711
			±0.3753	±0.4823	±0.3281	±0.2308		±0.2320		±0.5236	
		HFASN_02	12.1904	11.7768	12.0478	−0.1122	0.967	0.7133	0.810	−0.3423	0.520
			±0.5505	±0.4661	±0.2940	±0.2803		±0.2963		±0.5294	
		HFASN_03	--	12.2098	11.9477	−0.2621	0.586	--	--	--	--
				±0.4205	±0.2669	±0.4629					
		HFASN_04	--	12.0853	11.9954	−0.8993	0.877	--	--	--	--
				±0.4603	±0.2609	±0.4944					
		HFASN_05	--	11.5620	12.0393	0.4771	0.482	--	--	--	--
				±0.7889	±0.2517	±0.7986					
LMY	Hybrid	HFASN_01	58.3458	57.7760	57.9179	−0.2056	0.395	0.2139	0.326	−0.3559	0.478
			±0.3801	±0.4826	±0.3359	±0.2161		±0.2165		±0.4994	
		HFASN_02	57.6458	57.9562	58.1493	0.2417	0.366	−0.2517	0.368	0.5864	0.906
			±0.5319	±0.4628	±0.3111	±0.2661		±0.2783		±0.4951	
		HFASN_03	--	57.8610	58.0939	0.2328	0.611	--	--	--	--

				±0.4190	±0.2918	±0.4365					
		HFASN_04	--	57.8924	58.0699	0.1775	0.726	--	--	--	--
				±0.4536	±0.2852	±0.4634					
		HFASN_05	--	58.7951	57.9850	-0.8101	0.229	--	--	--	--
				±0.7427	±0.2766	±0.7354					
CREA	Hybrid	HFASN_01	84.7506	83.3247	83.6403	−0.5394	0.252	0.5552	0.240	−0.8707	0.430
			±0.8807	±1.1050	±0.7861	±0.4705		±0.4712		±1.098	
		HFASN_02	82.8621	82.6168	84.6380	1.069	**0.068†**	−0.8880	0.144	−1.133	0.292
			±1.1881	±1.0512	±0.7370	±0.5819		±0.6049		±1.072	
		HFASN_03	--	83.4629	84.1127	0.6498	0.497	--	--	--	--
				±0.9455	±0.6881	±0.9521					
		HFASN_04	--	83.1071	84.1632	1.056	0.294	--	--	--	--
				±1.0168	±0.6729	±1.006					
		HFASN_05	--	86.5373	83.7729	−2.764	**0.084†**	--	--	--	--
				±1.6195	±0.6454	±1.584					
CMAR	Hybrid	HFASN_01	4.4936	4.6379	4.5630	0.3246	0.450	−0.3470	0.397	0.1096	0.247
			±0.0737	±0.0931	±0.0655	±0.4071		±0.4072		±0.9445	
		HFASN_02	4.5278	4.6625	4.5246	−0.2325	0.645	0.1574	0.976	0.1363	0.144
			±0.1009	±0.0883	±0.0603	±0.5023		±0.5227		±0.9287	
		HFASN_03	--	4.5347	4.5614	0.2677	0.740	--	--	--	--

		±0.0806	±0.0577	±0.8233					
HFASN_04	--	4.5465	4.5563	0.9861	0.901	--	--	--	--
		±0.0871	±0.0566	±0.8724					
HFASN_05	--	4.6364	4.5491	-0.8730	0.556	--	--	--	--
		±0.1401	±0.0539	±0.1379					

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b] Least square means and SE for haplotype homozygous (animal contain same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c] Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d] Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

[†] P<0.10

Table 3.11. Least square means of fat deposition and carcass merit traits and estimated effects of GPAM SNPs in hybrid, Angus and Charolais beef cattle population.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Domina-nce effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.−1564G>A	8.9603 ±0.2252	9.4471 ±0.2917	12.2068 ±1.3547	0.6500 ±0.2875	**0.026***	−1.623 ±0.6807	**0.018***	−1.136 ±0.7196	0.116
		c. −345C>T	9.2239 ±0.2519	9.0829 ±0.2707	9.1531 ±0.5014	−0.7677 ±0.2409	0.686	0.3538 ±0.2743	0.898	−0.1056 ±0.3329	0.752
		c.18088G>C	9.2193 ±0.2127	8.7602 ±0.4326	7.9702 ±1.5943	0.4941 ±0.3992	0.183	−0.6246 ±0.8000	0.438	0.1655 ±0.8797	0.851
		c.26006A>G	9.1397 ±0.2099	--	9.2161 ±0.5083	−0.3823 ±0.2548	0.910	0.7646 ±0.5095	0.881	--	--
		c.35863A>C	9.0750 ±0.2097	10.0376 ±0.5653	--	0.9625 ±0.5685	0.105	--	--	--	--
	Angus	c.−1564G>A	15.7926 ±0.3330	15.5185 ±0.3681	15.2199 ±0.9237	−0.2786 ±0.3128	0.296	0.2863 ±0.4638	0.539	0.1221 ±0.5241	0.981
		c. −345C>T	15.5252 ±0.3147	16.2492 ±0.4564	14.7426 ±1.4179	0.4589 ±0.4088	0.314	0.3913 ±0.7108	0.583	1.115 ±0.7625	0.146

	Charolais	c.−1564G>A	8.0996 ±0.3261	8.0432 ±0.4656	7.6356 ±2.0130	−0.7607 ±0.4010	0.725	0.2320 ±1.008	0.818	0.1757 ±1.039	0.866
		c. −345C>T	8.1355 ±0.3206	7.7727 ±0.4660	9.8260 ±1.4417	−0.9769 ±0.3859	0.740	−0.8452 ±0.7164	0.240	−1.208 ±0.7740	0.121
		c.35863A>C	8.1724 ±0.3130	7.0642 ±0.6417	--	−1.108 ±0.6055	**0.053†**	--	--	--	--
UREA	Hybrid	c.−1564G>A	83.1246 ±0.4832	83.3961 ±0.6839	86.6234 ±3.4515	0.4853 ±0.7276	0.509	−1.749 ±1.736	0.315	−1.478 ±1.845	0.426
		c. −345C>T	83.0217 ±0.5695	83.6393 ±0.6309	83.0582 ±1.2323	0.2525 ±0.6038	0.710	−0.1825 ±0.6854	0.979	0.5993 ±0.8501	0.483
		c.18088G>C	83.2417 ±0.4400	83.3630 ±1.0528	82.6302 ±4.0056	−0.2926 ±1.004	0.974	−0.3057 ±2.013	0.880	0.4271 ±2.223	0.848
		c.26006A>G	83.2012 ±0.4259	--	83.8055 ±1.2411	−0.3021 ±0.6392	0.750	0.6042 ±1.278	0.638	--	--
		c.35863A>C	83.1716 ±0.4212	84.3108 ±1.4061	--	1.139 ±1.447	0.459	--	--	--	--
	Angus	c.−1564G>A	80.4938 ±0.7938	81.4127 ±0.8770	83.6489 ±2.1947	1.148 ±0.7435	0.167	−1.578 ±1.101	0.154	−0.6587 ±1.244	0.598
		c. −345C>T	81.3598 ±0.7744	79.7770 ±1.1076	80.0626 ±3.3924	−1.370 ±0.9793	0.136	0.6486 ±1.699	0.704	−0.9342 ±1.817	0.608

	Charolais	c.−1564G>A	83.4270	84.4178	86.5224	1.049	0.255	−1.548	0.623	−0.5569	0.865
			±0.7541	±1.2214	±6.2551	±1.180		±3.139		±3.260	
		c. −345C>T	83.8322	82.7289	83.5612	−0.8905	0.541	0.1355	0.951	−0.9678	0.691
			±0.7599	±1.2760	±4.4296	±1.149		±2.217		±2.429	
		c.35863A>C	83.7881	81.7780	--	−2.010	0.381	--	--	--	--
			±0.7504	±1.8423		±1.826					
AUBF	Hybrid	c.−1564G>A	0.0331	0.0340	0.0529	0.2116	0.165	−0.9884	**0.006***	−0.9070	**0.017***
			±0.0011	±0.0015	±0.0071	±0.1508		±0.3565		±0.3772	
		c. −345C>T	0.0342	0.0326	0.0350	−0.3823	0.716	−0.3901	0.786	−0.1991	0.255
			±0.0013	±0.0014	±0.0026	±0.1256		±0.1429		±0.1747	
		c.18088G>C	0.0340	0.0317	0.0296	0.2238	0.254	−0.2167	0.606	−0.9006	0.984
			±0.0010	±0.0022	±0.0083	±0.2085		±0.4177		±0.4602	
		c.26006A>G	0.0335	--	0.0344	−0.4472	0.880	0.8943	0.738	--	--
			±0.0010		±0.0026	±0.1330		±0.2660			
		c.35863A>C	0.0331	0.0405	--	0.7364	**0.016***	--	--	--	--
			±0.0010	±0.0029		±0.2965					
	Angus	c.−1564G>A	0.0695	0.0660	0.0697	−0.2214	0.487	−0.1107	0.982	−0.3591	0.528
			±0.0031	±0.0035	±0.0098	±0.3339		±0.4964		±0.5670	
		c. −345C>T	0.0667	0.0737	0.0615	0.4605	0.290	0.2626	0.730	0.9534	0.254
			±0.0028	±0.0045	±0.0151	±0.4223		±0.7591		±0.8323	

	Charolais	c.−1564G>A	0.0334 ±0.0020	0.0272 ±0.0035	0.0293 ±0.0196	−0.5784 ±0.3565	0.121	0.2032 ±0.9837	0.837	−0.4198 ±0.1024	0.683
		c. −345C>T	0.0324 ±0.0021	0.0295 ±0.0038	0.0348 ±0.0139	−0.2059 ±0.3560	0.583	−0.1181 ±0.6965	0.866	−0.4149 ±0.7675	0.590
		c.35863A>C	0.0320 ±0.0020	0.0321 ±0.0055	--	0.4552 ±0.5647	0.966	--	--	--	--
AURE-A	Hybrid	c.−1564G>A	0.1632 ±0.0027	0.1634 ±0.0042	0.1780 ±0.0219	0.1206 ±0.4602	0.797	−0.7374 ±0.1103	0.506	−0.7227 ±0.1176	0.541
		c. −345C>T	0.1611 ±0.0034	0.1664 ±0.0039	0.1659 ±0.0077	0.3477 ±0.3804	0.321	−0.2370 ±0.4321	0.585	0.2879 ±0.5433	0.598
		c.18088G>C	0.1638 ±0.0025	0.1626 ±0.0066	0.1441 ±0.0255	0.3048 ±0.6373	0.723	−0.9857 ±0.1280	0.444	0.8680 ±0.1415	0.542
		c.26006A>G	0.1636 ±0.0024	--	0.1622 ±0.0078	0.6661 ±0.4057	0.905	−0.1332 ±0.8115	0.870	--	--
		c.35863A>C	0.1630 ±0.0024	0.1705 ±0.0089	--	0.7596 ±0.9240	0.369	--	--	--	--
	Angus	c.−1564G>A	0.1999 ±0.0083	0.2052 ±0.0097	0.2295 ±0.0292	0.8654 ±0.1003	0.322	−0.1478 ±0.1497	0.326	−0.9504 ±0.1730	0.584
		c. −345C>T	0.2092 ±0.0072	0.1851 ±0.0126	0.1459 ±0.0453	−0.2603 ±0.1222	**0.044***	0.3169 ±0.2278	0.166	0.7525 ±0.2546	0.768

	Charolais	c.−1564G>A	0.2172	0.2183	0.2356	0.1953	0.661	−0.9220	0.814	−0.8078	0.843
			±0.0067	±0.0127	±0.0779	±0.1358		±0.3913		±0.4078	
		c. −345C>T	0.2185	0.2119	0.2648	−0.3466	0.775	−0.2318	0.396	−0.2978	0.328
			±0.0066	±0.0136	±0.0541	±0.1348		±0.2721		±0.3032	
		c.35863A>C	0.2165	0.2304	--	0.1389	0.347	--	--	--	--
			±0.0063	±0.0205		±0.2163					
SWT	Hybrid	c.−1564G>A	542.1310	544.7159	560.7794	3.508	0.507	−9.324	0.414	−6.740	0.573
			±4.9469	±5.7936	±22.7396	±4.828		±11.35		±11.90	
		c. −345C>T	540.6455	543.6585	554.5039	5.299	0.231	−6.929	0.139	−3.916	0.474
			±5.3179	±5.5040	±8.9956	±4.070		±4.662		±5.437	
		c.18088G>C	542.4774	548.2371	547.7938	−5.140	0.503	2.658	0.846	3.102	0.835
			±4.7948	±7.8976	±27.2613	±6.753		±13.62		±14.79	
		c.26006A>G	541.0421	--	566.1901	−12.97	0.009*	25.15	**0.003***	--	--
			±4.5667		±8.9256	±4.219		±8.438			
		c.35863A>C	543.0382	546.5240	--	3.486	0.755	--	--	--	--
			±4.7192	±9.9039		±9.463					
	Angus	c.−1564G>A	563.3939	565.1739	587.9573	5.403	0.321	−12.28	**0.018***	−10.50	**0.072†**
			±3.8479	±4.2224	±10.2710	±3.493		±5.130		±5.781	
		c. −345C>T	565.9399	563.8992	538.3254	−4.843	0.160	13.81	0.087†	11.77	0.172
			±3.6760	±5.2416	±16.0013	±4.643		±8.013		±8.565	

	Charolais	c.−1564G>A	565.7169 ±4.1997	561.6055 ±6.6292	621.5882 ±32.8818	−0.5641 ±6.361	0.848	−27.94 ±16.50	**0.093†**	−32.05 ±17.11	**0.063†**
		c. −345C>T	566.3659 ±4.3279	560.1939 ±6.9751	570.1775 ±23.5099	−4.396 ±6.148	0.441	−1.906 ±11.75	0.871	−8.078 ±12.83	0.530
		c.35863A>C	565.3135 ±4.1461	565.8851 ±9.8969	--	0.5717 ±9.744	0.979	--	--	--	--
CWT	Hybrid	c.−1564G>A	313.4494 ±2.9504	313.5079 ±3.4549	322.8350 ±13.5560	0.6922 ±2.879	0.854	−4.693 ±6.769	0.490	−4.634 ±7.092	0.516
		c. −345C>T	311.7745 ±3.1531	314.1543 ±3.2653	320.4257 ±5.3510	3.516 ±2.424	0.177	−4.326 ±2.777	0.121	−1.946 ±3.242	0.550
		c.18088G>C	312.8172 ±2.8545	318.6851 ±4.6974	316.8901 ±16.2086	−5.116 ±4.017	0.234	2.036 ±8.101	0.802	3.831 ±8.794	0.665
		c.26006A>G	312.4535 ±2.7643	--	326.0026 ±5.3495	−6.775 ±2.519	**0.019***	13.55 ±5.039	**0.008***	--	--
		c.35863A>C	313.3529 ±2.7998	317.0899 ±5.8900	--	3.737 ±5.631	0.542	--	--	--	--
	Angus	c.−1564G>A	327.8164 ±2.3708	329.5604 ±2.6262	344.9106 ±6.7494	4.127 ±2.311	0.245	−8.547 ±3.399	**0.013***	−6.803 ±3.854	**0.080†**
		c. −345C>T	329.7828 ±2.2516	327.6880 ±3.3341	319.5626 ±10.6049	−2.826 ±3.032	0.183	5.110 ±5.322	0.339	3.015 ±5.742	0.601

	Charolais	c.−1564G>A	333.9547	335.0721	351.0095	1.924	0.685	−8.527	0.477	−7.410	0.553
			±2.4054	±4.2305	±23.8143	±4.326		±11.96		±12.45	
		c. −345C>T	334.8708	332.2009	337.9997	−1.719	0.691	−1.564	0.857	−4.234	0.657
			±2.4849	±4.6207	±17.1568	±4.363		±8.613		±9.519	
		c.35863A>C	334.2344	337.4804	--	3.246	0.645	--	--	--	--
			±2.2910	±6.7247		±6.928					
AVBF	Hybrid	c.−1564G>A	11.8228	12.4171	13.9126	0.6602	0.107	−1.045	0.283	−0.4506	0.664
			±0.2620	±0.3777	±1.9312	±0.4064		±0.9716		±1.033	
		c. −345C>T	11.8647	12.2214	12.3974	0.3004	0.403	−0.2663	0.483	0.9038	0.850
			±0.2954	±0.3355	±0.6745	±0.3326		±0.3780		±0.4766	
		c.18088G>C	11.9985	12.1702	12.4933	−0.1880	0.809	0.2474	0.827	−0.7566	0.951
			±0.2491	±0.5932	±2.2553	±0.5650		±1.133		±1.251	
		c.26006A>G	11.9888	--	12.4416	−0.2264	0.686	0.4528	0.531	--	--
			±0.2386		±0.6981	±0.3597		±0.7194			
		c.35863A>C	11.9419	13.1383	--	1.196	0.160	--	--	--	--
			±0.2386	±0.7904		±0.8127					
	Angus	c.−1564G>A	16.9439	17.4586	16.8984	0.3264	0.516	0.2278	0.976	0.5374	0.537
			±0.5088	±0.5705	±1.5090	±0.5145		±0.7636		±0.8675	
		c. −345C>T	17.2033	17.1209	15.0459	−0.3228	0.639	1.079	0.362	0.9963	0.436
			±0.4774	±0.7241	±2.3439	±0.6650		±1.177		±1.275	

	Charolais	c.−1564G>A	7.7076 ±0.3717	8.1948 ±0.6292	6.4179 ±3.3951	0.3597 ±0.6252	0.631	0.6448 ±1.704	0.706	1.132 ±1.773	0.525
		c. −345C>T	7.8603 ±0.3682	7.5149 ±0.6598	7.7361 ±2.3925	−0.2819 ±0.6128	0.606	0.6208 ±1.200	0.959	−0.2833 ±1.322	0.831
		c.35863A>C	7.8590 ±0.3537	7.1250 ±0.9616	--	−0.7339 ±0.9751	0.412	--	--	--	--
LMY	Hybrid	c.−1564G>A	58.2209 ±0.2884	57.6663 ±0.3790	57.1278 ±1.7888	−0.5533 ±0.3784	0.149	0.5465 ±0.8991	0.545	−0.8007 ±0.9515	0.993
		c. −345C>T	58.2083 ±0.3211	57.9611 ±0.3472	57.2951 ±0.6513	−0.3745 ±0.3146	0.265	0.4566 ±0.3578	0.204	0.2094 ±0.4363	0.633
		c.18088G>C	57.9953 ±0.2828	58.3521 ±0.5703	57.6844 ±2.0975	−0.2489 ±0.5249	0.577	−0.1554 ±1.052	0.883	0.5122 ±1.157	0.659
		c.26006A>G	58.0564 ±0.2745	--	57.8576 ±0.6665	0.9938 ±0.3342	0.949	−0.1988 ±0.6685	0.767	--	--
		c.35863A>C	58.1224 ±0.2751	56.9971 ±0.7424	--	−1.125 ±0.7466	0.149	--	--	--	--
	Angus	c.−1564G>A	53.8804 ±0.4267	53.4196 ±0.4863	54.9323 ±1.3546	−0.1122 ±0.4654	0.811	−0.5259 ±0.6900	0.448	−0.9868 ±0.7886	0.213
		c. −345C>T	53.6851 ±0.3937	53.7606 ±0.6276	55.8323 ±2.1144	0.3212 ±0.5903	0.588	−1.074 ±1.063	0.314	−0.9980 ±1.164	0.393

	Charolais	c.−1564G>A	62.5413 ±0.3210	61.7578 ±0.5816	60.6498 ±3.4499	−0.8007 ±0.6135	0.237	0.9457 ±1.732	0.586	0.1623 ±1.805	0.929
		c. −345C>T	62.3694 ±0.3099	62.2687 ±0.6205	62.2097 ±2.4122	−0.9641 ±0.6039	0.943	0.7986 ±1.213	0.948	−0.2086 ±1.348	0.988
		c.35863A>C	62.3564 ±0.2967	62.3169 ±0.9287	--	−0.3946 ±0.9690	0.956	--	--	--	--
CREA	Hybrid	c.−1564G>A	84.0747 ±0.7086	83.6017 ±0.8819	86.9879 ±3.8791	−0.1966 ±0.8236	0.811	−1.457 ±1.946	0.457	−1.930 ±2.051	0.350
		c. −345C>T	83.9371 ±0.7856	84.3013 ±0.8296	82.7951 ±1.4652	−0.1937 ±0.6913	0.774	0.5710 ±0.7874	0.471	0.9352 ±0.9407	0.323
		c.18088G>C	83.5752 ±0.6651	86.6324 ±1.2488	84.6958 ±4.5072	−2.535 ±1.127	**0.026***	0.5603 ±2.259	0.805	2.497 ±2.475	0.314
		c.26006A>G	83.7888 ±0.6553	--	86.1390 ±1.4610	−1.175 ±0.7189	0.108	2.350 ±1.438	0.104	--	--
		c.35863A>C	84.0781 ±0.6632	82.9977 ±1.6244	--	−1.080 ±1.608	0.502	--	--	--	--
	Angus	c.−1564G>A	81.9160 ±0.7699	82.0797 ±0.8993	89.0583 ±2.6741	1.383 ±0.9300	0.208	−3.571 ±1.372	**0.010***	−3.407 ±1.583	**0.033***
		c. −345C>T	81.9889 ±0.6470	82.7345 ±1.1632	84.9941 ±4.2303	0.9325 ±1.128	0.486	−1.503 ±2.128	0.482	−0.7570 ±2.393	0.753

	Charolais	c.−1564G>A	94.6102	92.3203	83.8381	−2.618	0.152	5.386	0.242	3.096	0.518
			±0.9677	±1.6640	±9.1373	±1.675		±4.588		±4.774	
		c. −345C>T	94.4986	92.8097	94.2378	−1.344	0.472	0.1304	0.968	−1.558	0.664
			±1.0833	±1.8510	±6.5030	±1.681		±3.257		±3.574	
		c.35863A>C	94.3278	92.5604	--	−1.767	0.577	--	--	--	--
			±1.0281	±2.6592		±2.667					
CMAR	Hybrid	c.−1564G>A	4.5006	4.6704	4.9048	0.1744	**0.015***	−0.2021	0.228	−0.3226	0.855
			±0.0592	±0.0745	±0.3333	±0.7063		±0.1673		±0.1765	
		c. −345C>T	4.5267	4.5493	4.7777	0.8458	0.163	−0.1255	**0.065†**	−0.1029	0.205
			±0.0652	±0.0693	±0.1246	±0.5928		±0.6744		±0.8102	
		c.18088G>C	4.5551	4.5582	4.7890	−0.2723	0.806	0.1169	0.556	−0.1139	0.601
			±0.0568	±0.1087	±0.3943	±0.9855		±0.1977		±0.2168	
		c.26006A>G	4.5496	--	4.6522	−0.5128	0.467	0.1026	0.415	--	--
			±0.0548		±0.1262	±0.6260		±0.1252			
		c.35863A>C	4.5537	4.6106	--	0.5691	0.700	--	--	--	--
			±0.0555	±0.1405		±0.1399					
	Angus	c.−1564G>A	6.3033	6.1665	6.5334	−0.5114	0.796	−0.9996	0.652	−0.2226	0.373
			±0.1783	±0.1946	±0.4625	±0.1558		±0.2208		±0.2485	
		c. −345C>T	6.1679	6.5073	6.9503	0.3523	**0.082†**	−0.4044	0.235	−0.9152	0.800
			±0.1751	±0.2412	±0.7083	±0.2062		±0.3395		±0.3605	

Charolais	c.−1564G>A	4.4919 ±0.1052	4.6211 ±0.1581	4.4868 ±0.7349	0.1131 ±0.1439	0.472	0.2536 ±0.3684	0.993	0.1318 ±0.3811	0.729
	c. −345C>T	4.5249 ±0.1085	4.4518 ±0.1643	4.5678 ±0.5275	−0.5227 ±0.1395	0.692	−0.2142 ±0.2628	0.935	−0.9452 ±0.2852	0.741
	c.35863A>C	4.5240 ±0.1026	4.3552 ±0.2251	--	−0.1688 ±0.2167	0.417	--	--	--	--

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

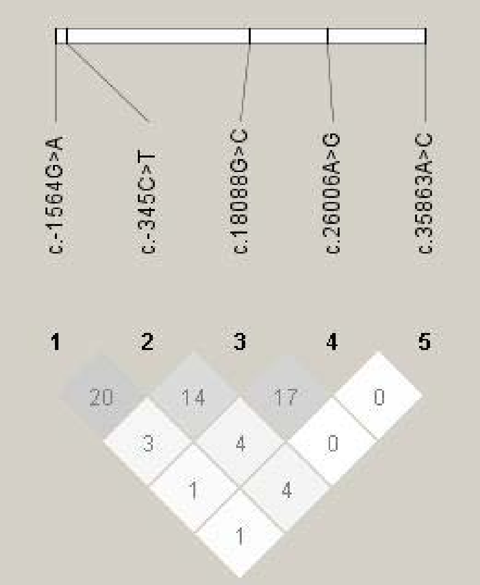

Figure 3.7. Haplotype block for GPAM SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Figure 3.8. Haplotype block for GPAM SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

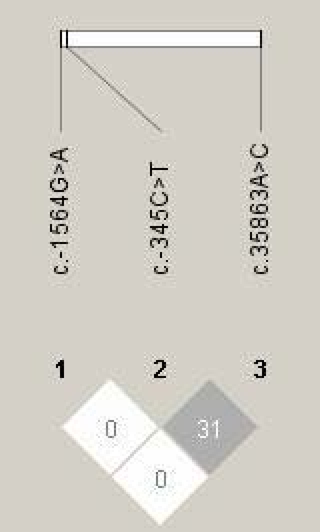

Figure 3.9. Haplotype block for GPAM SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.12. GPAM haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype name[a]	Allele arrangement[b,c]	Frequency[c]
Hybrid	HGPAM_01	G-C-G-A-A	0.524
	HGPAM_02	G-T-G-A-A	0.199
	HGPAM_03	A-C-G-A-A	0.131
	Others 16 types	---	0.145
Angus	AGPAM_01	G-C	0.682
	AGPAM_02	A-C	0.199
	AGPAM_03	G-T	0.097
	AGPAM_04	A-T	0.022
Charolais	CGPAM_01	G-C-A	0.765
	CGPAM_02	A-C-A	0.104
	CGPAM_03	G-T-A	0.091
	Other 3 types	---	0.040

[a] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[b] SNPs c.−1564G>A, c. −345C>T, c.18088G>C, c.26006A>G, c.35863A>C were used chronologically to set the allele arrangement for hybrid. SNP c.−1564G>A, c. −345C>T were used chronologically to set the allele arrangement for Angus. And SNP c.−1564G>A, c. −345C>T, c.35863A>C were used chronologically to set the allele arrangement for Charolais.

[c] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.13. Log likelihood ratio test (LR test) result for GPAM haplotypes in the hybrid, Angus and Charolais cattle populations.

Cattle population	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	UBF	−550.945	−568.994	83.12	<0.0001
	UREA	−889.159	−915.633	121.92	<0.0001
	AUBF	1337.95	1379.58	191.72	<0.0001
	AUREA	927.696	957.85	138.87	<0.0001
	SWT	−1563.21	−1611.51	222.43	<0.0001
	CWT	−1376.27	−1421.29	207.33	<0.0001
	AVBF	−681.931	−701.414	89.72	<0.0001
	LMY	−651.697	−669.456	81.78	<0.0001
	CREA	−928.510	−954.045	117.59	<0.0001
	CMAR	−44.4736	−47.1706	12.42	0.0004
Angus	UBF	−287.372	−287.372	0	1.0
	UREA	−458.054	−458.054	0	1.0
	AUBF	602.504	602.504	0	1.0
	AUREA	381.786	381.786	0	1.0
	SWT	−761.750	−761.750	0	1.0
	CWT	−677.133	−677.133	0	1.0
	AVBF	−386.267	−386.267	0	1.0
	LMY	−365.764	−365.816	0.24	0.6242
	CREA	−502.583	−503.640	4.87	0.0273
	CMAR	−142.702	−142.703	0.006	0.9383
Charolais	UBF	−225.083	−225.126	0.2	0.6547
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.664	599.664	0	1.0
	AUREA	354.899	354.899	0	1.0
	SWT	−722.287	−722.287	0	1.0
	CWT	−668.033	−668.033	0	1.0
	AVBF	−316.704	−316.704	0	1.0

LMY	−319.990	−319.990	0	1.0
CREA	−493.831	−494.255	1.95	0.1626
CMAR	−42.7920	−42.7920	0	1.0

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait. Details of model description is given in materials and methods (page…).

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.14. Least square means of fat deposition and carcass merit traits and estimated effects of GPAM haplotypes in the hybrid and Angus beef cattle populations.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HGPAM_01	8.6961	9.1520	9.6373	0.4687	**0.022***	−0.4706	**0.027***	−0.1471	0.959
			±0.2960	±0.2604	±0.3428	±0.2073		±0.2109		±0.2848	
		HGPAM_02	9.2287	9.0373	9.1590	0.5494	0.968	0.3482	0.927	−0.1566	0.725
			±0.7335	±0.3170	±0.2338	±0.2801		±0.3781		±0.4427	
		HGPAM_03	13.3624	9.6569	8.9093	−0.9433	**0.003***	2.227	**0.004***	−1.479	**0.071†**
			±1.5362	±0.3126	±0.2129	±0.3048		±0.7707		±0.8141	
	Angus	AGPAM_01	15.7353	15.6850	15.2011	−0.1437	0.477	0.2671	0.512	0.2168	0.618
			±0.3699	±0.3376	±0.7759	±0.3211		±0.4052		±0.4328	
		AGPAM_02	15.2055	15.3946	15.8535	0.4083	0.145	−0.3240	0.483	−0.1349	0.800
			±0.9203	±0.3879	±0.3269	±0.3157		±0.4597		±0.5319	
		AGPAM_03	14.6105	16.1740	15.6047	−0.2804	0.586	−0.4971	0.483	1.066	0.178
			±1.4151	±0.4880	±0.3053	±0.4125		±0.7059		±0.7878	
UREA	Hybrid	HGPAM_01	82.0604	83.9861	83.0357	0.6715	0.196	−0.4876	0.362	1.438	**0.049***
			±0.6933	±0.5997	±0.8291	±0.5272		±0.5318		±0.7258	
		HGPAM_02	83.4613	83.1644	83.0959	−0.1177	0.786	0.1827	0.849	−0.1142	0.920

			±1.8371	±0.7499	±0.5171	±0.7024		±0.9548		±1.130	
		HGPAM_03	85.5008	83.4303	83.0100	−0.5286	0.522	1.245	0.534	−0.8251	0.697
			±3.9658	±0.7732	±0.4889	±0.7850		±1.991		±2.110	
	Angus	AGPAM_01	81.1277	80.7713	82.3174	0.5297	0.852	−0.5948	0.540	−0.9513	0.359
			±0.8805	±0.8035	±1.8506	±0.7674		±0.9668		±1.033	
		AGPAM_02	83.6394	81.2392	80.7349	−0.8585	0.337	1.452	0.188	−0.9479	0.457
			±2.1973	±0.9251	±0.7790	±0.7548		±1.098		±1.270	
		AGPAM_03	80.0114	79.0429	81.4221	1.935	**0.038***	−0.7054	0.675	−1.674	0.372
			±3.3612	±1.1734	±0.7491	±0.9791		±1.675		±1.864	
AUBF	Hybrid	HGPAM_01	0.0320	0.0334	0.0356	0.1714	0.109	−0.1766	0.113	−0.4083	0.787
			±0.0015	±0.0013	±0.0018	±0.1089		±0.1108		±0.1502	
		HGPAM_02	0.0369	0.0317	0.0340	0.6717	0.763	0.1465	0.459	−0.3743	0.108
			±0.0038	±0.0016	±0.0011	±0.1462		±0.1969		±0.2318	
		HGPAM_03	0.0594	0.0344	0.0329	−0.3053	**0.067†**	0.1329	**0.001***	−0.1180	**0.007***
			±0.0081	±0.0016	±0.0011	±0.1614		±0.4061		±0.4292	
	Angus	AGPAM_01	0.0691	0.0675	0.0691	−0.8605	0.751	−0.4660	0.991	−0.1603	0.733
			±0.0035	±0.0031	±0.0081	±0.3362		±0.4276		±0.4677	
		AGPAM_02	0.0695	0.0644	0.0701	0.3735	0.252	−0.3031	0.951	−0.5496	0.340
			±0.0097	±0.0037	±0.0030	±0.3358		±0.4908		±0.5731	
		AGPAM_03	0.0606	0.0723	0.0676	−0.2427	0.600	−0.3476	0.647	0.8191	0.342

			±0.0151	±0.0049	±0.0027	±0.4353		±0.7566		±0.8575	
AURE-A	Hybrid	HGPAM_01	0.1591	0.1649	0.1652	0.3379	0.338	−0.3064	0.367	0.2736	0.561
			±0.0041	±0.0035	±0.0051	±0.3332		±0.3379		±0.4677	
		HGPAM_02	0.1721	0.1657	0.1614	−0.4712	0.410	0.5335	0.383	−0.1099	0.880
			±0.0116	±0.0045	±0.0029	±0.4426		±0.6075		±0.7242	
		HGPAM_03	0.1710	0.1637	0.1628	−0.1377	0.737	0.4114	0.747	−0.3169	0.815
			±0.0253	±0.0047	±0.0027	±0.5009		±0.1270		±0.1351	
	Angus	AGPAM_01	0.2092	0.1982	0.1972	−0.8807	0.532	−0.1371	0.644	−0.5074	0.729
			±0.0099	±0.0087	±0.0243	±0.1008		±0.1940		±0.2055	
		AGPAM_02	0.2289	0.2040	0.2005	−0.7505	0.380	0.1416	0.352	−0.1069	0.550
			±0.0296	±0.0107	±0.0083	±0.1028		±0.1513		±0.1780	
		AGPAM_03	0.1472	0.1783	0.2081	0.3001	**0.031***	−0.3047	0.188	0.6518	0.980
			±0.0458	±0.0145	±0.0073	±0.1309		±0.2302		±0.2637	
SWT	Hybrid	HGPAM_01	534.7190	541.7542	552.5266	8.628	**0.011***	−8.904	**0.014***	−1.869	0.695
			±5.9815	±5.4538	±6.5826	±3.513		±3.588		±4.747	
		HGPAM_02	554.0917	540.0485	542.5598	−0.9556	0.618	5.766	0.374	−8.277	0.264
			±12.8034	±6.1337	±5.0174	±4.795		±6.452		±7.390	
		HGPAM_03	560.9721	546.6556	540.7590	−6.410	0.258	10.11	0.449	−4.210	0.763
			±26.5565	±6.2105	±4.9132	±5.180		±13.26		±13.89	
	Angus	AGPAM_01	564.2495	564.8518	574.0129	2.425	0.818	−4.882	0.285	−4.279	0.380

			±4.2005	±3.8415	±8.7324	±3.617		±4.551		±4.852	
		AGPAM_02	588.0353	564.8990	563.8537	−5.151	0.392	12.09	**0.020***	−11.05	0.064†
			±10.2506	±4.3189	±3.6381	±3.547		±5.121		±5.925	
		AGPAM_03	538.6727	563.9219	565.7512	5.010	0.134	−13.54	**0.089†**	11.71	0.186
			±15.8957	±5.5703	±3.5771	±4.642		±7.917		±8.808	
CWT	Hybrid	HGPAM_01	308.7324	312.0624	319.8395	5.226	**0.010***	−5.554	**0.010***	−2.224	0.434
			±3.5127	±3.1953	±3.8773	±2.092		±2.134		±2.828	
		HGPAM_02	320.1191	311.3572	313.2663	−0.3122	0.695	3.426	0.375	−5.335	0.227
			±7.5923	±3.5998	±2.9186	±2.853		±3.836		±4.404	
		HGPAM_03	325.4435	313.7216	312.7144	−1.662	0.661	6.365	0.423	−5.357	0.520
			±15.8269	±3.6646	±2.8762	±3.093		±7.907		±8.289	
	Angus	AGPAM_01	328.8343	328.6927	337.8808	1.895	0.838	−4.523	0.132	−4.665	0.150
			±2.6429	±2.3807	±5.6869	±2.378		±2.986		±3.219	
		AGPAM_02	344.8282	329.1379	328.3739	−3.563	0.391	8.227	**0.016***	−7.463	**0.060†**
			±6.7389	±2.7443	±2.2824	±2.343		±3.385		±3.932	
		AGPAM_03	319.4880	326.6438	329.8598	3.760	**0.092†**	−5.186	0.327	1.970	0.739
			±10.5347	±3.5744	±2.1812	±3.055		±5.262		±5.894	
AVBF	Hybrid	HGPAM_01	11.2650	12.2364	12.7583	0.7738	**0.008***	−0.7467	**0.013***	0.2247	0.583
			±0.3744	±0.3217	±0.4556	±0.2928		±0.2967		±0.4073	
		HGPAM_02	12.1349	11.9523	12.0582	0.4412	0.934	0.3838	0.943	−0.1443	0.821

			±1.0318	±0.4172	±0.2844	±0.3943		±0.5368		±0.6361	
		HGPAM_03	14.5625	12.7767	11.8034	−1.028	**0.023***	1.380	0.214	−0.4062	0.731
			±2.2036	±0.4138	±0.2396	±0.4364		±1.107		±1.176	
	Angus	AGPAM_01	17.2432	17.2154	16.4679	−0.1838	0.743	0.3876	0.563	0.3599	0.619
			±0.5779	±0.5226	±1.2691	±0.5277		±0.6683		±0.7216	
		AGPAM_02	16.9008	17.2973	17.1487	−0.4538	0.924	−0.1240	0.872	0.2725	0.759
			±1.5190	±0.6074	±0.4982	±0.5244		±0.7659		±0.8905	
		AGPAM_03	14.8802	16.6789	17.3227	0.8022	0.243	−1.221	0.299	0.5775	0.662
			±2.3459	±0.7864	±0.4669	±0.6790		±1.173		±1.317	
LMY	Hybrid	HGPAM_01	58.6431	57.9937	57.2908	−0.6729	**0.013***	0.6762	**0.016***	0.2672	0.944
			±0.3836	±0.3362	±0.4472	±0.2732		±0.2779		±0.3760	
		HGPAM_02	57.4933	57.9065	58.1157	0.2528	0.380	−0.3112	0.536	0.1020	0.862
			±0.9689	±0.4179	±0.3075	±0.3699		±0.4997		±0.5852	
		HGPAM_03	56.8090	57.3682	58.2521	0.8627	**0.041***	−0.7216	0.486	−0.1624	0.882
			±2.0529	±0.4149	±0.2796	±0.4058		±1.030		±1.089	
	Angus	AGPAM_01	53.5899	53.6864	55.0030	0.3627	0.440	−0.7066	0.238	−0.6100	0.352
			±0.4882	±0.4372	±1.1242	±0.4689		±0.5959		±0.6518	
		AGPAM_02	54.9368	53.5752	53.7124	−0.1498	0.747	0.6122	0.376	−0.7494	0.354
			±1.3553	±0.5168	±0.4126	±0.4709		±0.6882		±0.8044	
		AGPAM_03	55.9469	54.1812	53.5884	−0.7558	0.214	1.179	0.266	−0.5864	0.625

			±2.1075	±0.6854	±0.3799	±0.6071		±1.057		±1.196	
CREA	Hybrid	HGPAM_01	83.6767	84.1838	83.7684	0.1081	0.856	−0.4582	0.940	0.4612	0.575
			±0.8936	±0.7939	±1.0188	±0.5986		±0.6094		±0.8184	
		HGPAM_02	82.7183	82.7769	84.4494	1.323	0.103	−0.8655	0.425	−0.8070	0.524
			±2.0961	±0.9196	±0.6898	±0.7997		±1.078		±1.258	
		HGPAM_03	87.5838	83.1908	84.1054	0.5731	0.517	1.739	0.441	−2.654	0.263
			±4.4733	±0.9455	±0.6781	±0.8836		±2.242		±2.363	
	Angus	AGPAM_01	81.3168	82.3954	87.3629	1.949	**0.073†**	−3.023	**0.010***	−1.944	0.139
			±0.8457	±0.7440	±2.1554	±0.8964		±1.149		±1.308	
		AGPAM_02	89.1393	82.2458	81.9189	−1.621	0.137	3.610	**0.009***	−3.283	0.043
			±2.6698	±0.9674	±0.7472	±0.9403		±1.364		±1.606	
		AGPAM_03	84.9644	83.0545	82.0101	−1.163	0.408	1.477	0.489	−0.4328	0.860
			±4.2258	±1.3106	±0.6255	±1.199		±2.124		±2.453	
CMAR	Hybrid	HGPAM_01	4.4296	4.5495	4.7325	0.1474	**0.004***	−0.1514	**0.004***	−0.3156	0.651
			±0.0715	±0.0627	±0.0831	±0.5054		±0.5140		0.6949	
		HGPAM_02	4.6849	4.6004	4.5296	−0.7366	0.248	0.7764	0.404	−0.6922	0.950
			±0.1795	±0.0774	±0.0569	±0.6852		±0.9257		±0.1084	
		HGPAM_03	4.7036	4.7076	4.5067	−0.1874	**0.015***	0.9844	0.607	0.1024	0.613
			±0.3801	±0.0774	±0.0527	±0.7515		±0.1907		0.2014	
	Angus	AGPAM_01	6.1714	6.2578	6.4457	0.1078	0.417	−0.1379	0.481	−0.1191	0.806

	±0.1859	±0.1711	±0.3748	±0.1541		±0.7483		±0.7993	
AGPAM_02	6.4650	6.0997	6.2857	0.8545	0.631	0.8961	0.684	−0.2756	0.278
	±0.4425	±0.1937	±0.1660	±0.1513		±0.2194		±0.2530	
AGPAM_03	6.8731	6.3989	6.1882	−0.2463	0.194	0.3424	0.311	−0.1318	0.725
	±0.6776	±0.2419	±0.1596	±0.1973		±0.3368		±0.3735	

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b]Least square means and SE for haplotype homozygous (animal contain same haplotype at both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c]Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d]Additive effect was estimated by subtracting the solution for the "haplotype homozygous" genotype from that for the "other haplotypes". It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for "haplotype homozygous and other haplotypes" from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10

Table 3.15. Least square means of fat deposition and carcass merit traits and estimated effects of IDH1 SNPs in the hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Domina-nce effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c. −4145C>T	9.0635 ±0.2283	9.3921 ±0.3168	8.8242 ±0.9737	0.2040 ±0.2908	0.541	0.1196 ±0.4903	0.808	0.4482 ±0.5494	0.417
		c.4208T>G	8.8464 ±0.2806	9.3750 ±0.2581	9.1766 ±0.4316	−0.2578 ±0.2230	0.252	0.1651 ±0.2366	0.488	0.3636 ±0.3029	0.231
		c.9970A>G	9.3006 ±0.2295	8.9723 ±0.3148	7.8716 ±0.6676	−0.5147 ±0.2607	**0.043***	0.7145 ±0.3406	**0.038***	0.3862 ±0.4236	0.365
	Angus	c. −4145C>T	15.7166 ±0.3138	15.5547 ±0.4471	15.6568 ±1.2410	−0.1276 ±0.3796	0.771	0.2991 ±0.6212	0.962	−0.1321 ±0.6884	0.848
		c.4208T>G	15.9999 ±0.4004	15.6448 ±0.3546	15.3534 ±0.4226	0.3244 ±0.2410	0.209	−0.3233 ±0.2418	0.183	−0.3186 ±0.3424	0.926
		c.9970A>G	15.5680 ±0.3090	16.1065 ±0.4855	16.7311 ±2.4401	0.5435 ±0.4557	0.216	−0.5815 ±1.224	0.636	−0.4302 ±1.282	0.973
	Charolais	c. −4145C>T	8.0985 ±0.3235	8.0595 ±0.4076	8.7289 ±1.3940	0.1885 ±0.3301	0.940	−0.3152 ±0.6911	0.649	−0.3541 ±0.7234	0.626

		c.4208T>G	8.0755 ±0.3349	8.0963 ±0.3758	8.3021 ±0.6118	−0.7513 ±0.2531	0.824	0.1133 ±0.2933	0.700	−0.9251 ±0.3564	0.796
		c.9970A>G	8.1380 ±0.3401	8.0504 ±0.3729	6.5783 ±1.4667	−0.1839 ±0.3061	0.547	0.7799 ±0.7256	0.284	0.6922 ±0.7652	0.368
UREA	Hybrid	c. −4145C>T	83.1986 ±0.4752	83.3459 ±0.7400	83.0498 ±2.4517	0.8380 ±0.7244	0.955	0.7443 ±1.241	0.952	0.2217 ±1.411	0.876
		c.4208T>G	83.1367 ±0.6147	83.5505 ±0.5560	82.5836 ±1.0312	0.9307 ±0.5505	0.854	−0.2765 ±0.5878	0.639	0.6904 ±0.7736	0.375
		c.9970A>G	83.5062 ±0.4761	82.7849 ±0.7137	82.3941 ±1.6431	−0.6416 ±0.6406	0.309	0.5560 ±0.8545	0.517	−0.1653 ±1.084	0.879
	Angus	c. −4145C>T	80.8139 ±0.7411	81.3707 ±1.0602	83.8054 ±2.9557	0.8283 ±0.9030	0.341	−1.496 ±1.480	0.314	−0.9390 ±1.641	0.569
		c.4208T>G	81.1327 ±0.9550	80.7807 ±0.8449	81.1889 ±1.0088	−0.1955 ±0.5783	0.912	0.2813 ±0.5797	0.961	−0.3801 ±0.8219	0.645
		c.9970A>G	80.9119 ±0.7435	81.2981 ±1.1657	81.8898 ±5.8461	0.3974 ±1.093	0.682	−0.4890 ±2.932	0.868	−0.1027 ±3.072	0.973
	Charolais	c. −4145C>T	83.6158 ±0.7916	83.5769 ±1.0709	87.0071 ±4.3261	0.2282 ±0.9907	0.637	−1.696 ±2.165	0.436	−1.735 ±2.281	0.449
		c.4208T>G	83.9616 ±0.8190	82.6720 ±0.9478	86.0634 ±1.7605	−0.4609 ±0.7666	0.820	1.051 ±0.8956	0.243	−2.340 ±1.106	0.036

		c.9970A>G	83.3875	83.9530	87.0106	0.7358	0.411	−1.812	0.418	−1.246	0.597
			±0.8125	±0.9248	±4.4558	±0.9179		±2.225		±2.347	
AUBF	Hybrid	c. −4145C>T	0.0333	0.0348	0.0307	0.7052	0.689	0.1296	0.615	0.2780	0.339
			±0.0011	±0.0016	±0.0051	±0.1514		±0.2565		±0.2889	
		c.4208T>G	0.0325	0.0348	0.0330	−0.7881	0.506	0.2568	0.836	0.2039	0.202
			±0.0014	±0.0013	±0.0022	±0.1161		±0.1233		±0.1592	
		c.9970A>G	0.0341	0.0330	0.0290	−0.1803	0.173	0.2556	0.153	0.1467	0.513
			±0.0011	±0.0016	±0.0035	±0.1351		±0.1779		±0.2229	
	Angus	c. −4145C>T	0.0697	0.0648	0.0494	−0.6330	0.112	0.1011	0.126	0.5301	0.472
			±0.0029	±0.0044	±0.0131	±0.3940		±0.6564		±0.7343	
		c.4208T>G	0.0704	0.0676	0.0665	0.1945	0.457	−0.1926	0.451	−0.8843	0.812
			±0.0038	±0.0033	±0.0041	±0.2535		±0.2542		±0.3711	
		c.9970A>G	0.0670	0.0715	0.1053	0.6133	0.196	−0.1917	0.149	−0.1463	0.291
			±0.0027	±0.0048	±0.0263	±0.4763		±0.1321		±0.1381	
	Charolais	c. −4145C>T	0.0315	0.0337	0.0140	0.4884	0.841	0.8743	0.202	0.1093	0.132
			±0.0022	±0.0031	±0.0136	±0.3046		±0.6821		±0.7203	
		c.4208T>G	0.0318	0.0320	0.0341	−0.7284	0.737	0.1143	0.689	−0.9454	0.791
			±0.0023	±0.0027	±0.0055	±0.2373		±0.2844		±0.3553	
		c.9970A>G	0.0312	0.0331	0.0349	0.1931	0.491	−0.1864	0.789	0.7110	0.992
			±0.0022	±0.0026	±0.0139	±0.2826		±0.6954		±0.7337	

AURE-A	Hybrid	c. −4145C>T	0.1630 ±0.0027	0.1639 ±0.0046	0.1675 ±0.0155	0.1265 ±0.4540	0.698	−0.2251 ±0.7863	0.776	−0.1382 ±0.9029	0.879
		c.4208T>G	0.1622 ±0.0037	0.1651 ±0.0033	0.1617 ±0.0064	−0.5881 ±0.3452	0.834	−0.2589 ±0.3702	0.945	0.3146 ±0.4948	0.527
		c.9970A>G	0.1645 ±0.0029	0.1626 ±0.0044	0.1606 ±0.0104	−0.1941 ±0.4014	0.649	0.1971 ±0.5413	0.717	0.5042 ±0.6929	0.994
	Angus	c. −4145C>T	0.1980 ±0.0072	0.2155 ±0.0122	0.2439 ±0.0398	0.1912 ±0.1149	0.103	−0.2297 ±0.2006	0.254	−0.5405 ±0.2278	0.813
		c.4208T>G	0.2022 ±0.0111	0.2020 ±0.0095	0.2046 ±0.0120	−0.1184 ±0.7717	0.936	0.1222 ±0.7740	0.875	−0.1423 ±0.1149	0.902
		c.9970A>G	0.2011 ±0.0076	0.2053 ±0.0140	0.2849 ±0.0815	0.8658 ±0.1426	0.578	−0.4186 ±0.4104	0.309	−0.3769 ±0.4292	0.382
	Charolais	c. −4145C>T	0.2142 ±0.0070	0.2269 ±0.0106	0.2065 ±0.0540	0.1034 ±0.1159	0.208	0.3812 ±0.2716	0.889	0.1657 ±0.2874	0.566
		c.4208T>G	0.2157 ±0.0078	0.2157 ±0.0094	0.2459 ±0.0208	−0.8316 ±0.9116	0.224	0.1512 ±0.1109	0.175	−0.1513 ±0.1406	0.284
		c.9970A>G	0.2141 ±0.0077	0.2240 ±0.0090	0.1768 ±0.0540	0.6077 ±0.1090	0.520	0.1867 ±0.2717	0.494	0.2853 ±0.2869	0.322
SWT	Hybrid	c. −4145C>T	541.6669 ±4.8685	548.1022 ±6.0560	534.1282 ±16.2613	3.631 ±4.861	0.505	3.769 ±8.053	0.641	10.20 ±8.891	0.252

		c.4208T>G	537.8241	547.7125	544.1456	−4.950	0.181	3.161	0.427	6.728	0.175
			±5.5663	±5.2479	±7.7842	±3.750		±3.957		±4.941	
		c.9970A>G	545.3494	542.8146	514.8418	−8.803	**0.033***	15.25	**0.008***	12.72	**0.067†**
			±4.7505	±5.9355	±11.4058	±4.385		±5.639		±6.908	
	Angus	c. −4145C>T	564.7924	565.1636	575.6775	1.818	0.567	−5.443	0.437	−5.071	0.512
			±3.6851	±5.1424	±13.9706	±4.285		±6.979		±7.711	
		c.4208T>G	566.7234	565.3648	562.5426	2.068	0.628	−2.090	0.446	0.7318	0.850
			±4.5268	±4.0115	±4.7748	±2.721		±2.729		±3.863	
		c.9970A>G	565.6145	563.8314	545.1711	−2.709	0.712	10.22	0.456	8.439	0.558
			±3.7503	±5.6599	±27.2828	±5.162		±13.66		±14.33	
	Charolais	c. −4145C>T	565.4971	563.9796	593.1713	0.8549	0.948	−13.84	0.227	−15.35	0.202
			±4.4304	±5.8834	±22.8073	±5.278		±11.39		±11.99	
		c.4208T>G	567.4159	560.4684	573.0192	1.289	0.707	2.802	0.558	−9.749	**0.098†**
			±4.6422	±5.3229	±9.5085	±4.081		±4.767		±5.857	
		c.9970A>G	564.2758	567.1884	537.9419	0.6772	0.896	13.17	0.265	16.08	0.197
			±4.4639	±5.0511	±23.5865	±4.898		±11.76		±12.41	
CWT	Hybrid	c. −4145C>T	313.0399	315.2032	312.4452	1.488	0.659	0.2974	0.951	2.461	0.644
			±2.9070	±3.6150	±9.7022	±2.896		±4.804		±5.304	
		c.4208T>G	311.1701	316.3159	311.4945	−1.491	0.494	0.1622	0.945	4.984	0.092
			±3.3525	±3.1650	±4.6643	±2.238		±2.359		±2.941	

		c.9970A>G	314.9522	312.8993	299.1163	−4.973	**0.043***	7.918	**0.020***	5.865	0.156
			±2.8471	±3.5495	±6.8024	±2.608		±3.360		±4.114	
	Angus	c. −4145C>T	328.8319	329.8824	336.8825	1.912	0.412	−4.025	0.385	−2.975	0.564
			±2.2244	±±3.2721	±9.1900	±2.811		±4.607		±5.135	
		c.4208T>G	329.3864	330.1391	327.3571	0.9729	0.819	−1.015	0.577	1.767	0.493
			±2.8588	±2.5102	±3.0798	±1.810		±1.815		±2.569	
		c.9970A>G	329.4304	329.1903	308.9612	−1.314	0.841	10.23	0.265	9.995	0.298
			±2.2635	±3.5790	±18.2195	±3.413		±9.150		±9.561	
	Charolais	c. −4145C>T	336.3202	329.2248	356.6998	−4.598	0.217	−10.19	0.227	−17.29	0.054
			±2.4289	±3.5439	±16.7040	±3.690		±8.397		±8.878	
		c.4208T>G	337.1237	329.7694	336.0586	3.532	0.227	−0.5326	0.879	−6.822	0.120
			±2.8006	±3.3075	±6.6806	±2.907		±3.485		±4.357	
		c.9970A>G	331.9963	338.4372	322.5284	4.918	0.159	4.734	0.579	11.17	0.215
			±2.5689	±2.9945	±16.9437	±3.467		±8.506		±8.977	
AVBF	Hybrid	c. −4145C>T	12.0019	12.0146	12.8671	0.1342	0.806	−0.4326	0.536	−0.4199	0.598
			±0.2645	±0.4142	±1.3756	±0.4067		±0.6962		±0.7921	
		c.4208T>G	11.7963	2.0870	12.4234	−0.3075	0.333	0.3135	0.345	−0.2287	0.959
			±0.3441	±0.3112	±0.5786	±0.3087		±0.3301		±0.4347	
		c.9970A>G	12.0374	12.4317	9.9500	−0.2946	0.402	1.044	**0.032***	1.438	**0.019***
			±0.2809	±0.4120	±0.9288	±0.3635		±0.4809		±0.6064	

	Angus	c. −4145C>T	17.2186 ±0.4747	16.9515 ±0.7059	18.6441 ±2.0434	0.7852 ±0.6207	0.991	−0.7128 ±1.026	0.489	−0.9799 ±1.144	0.394
		c.4208T>G	17.4418 ±0.6362	17.2619 ±0.5581	16.7525 ±0.6757	0.3401 ±0.3983	0.393	−0.3446 ±0.3995	0.390	0.1648 ±0.5717	0.774
		c.9970A>G	17.1089 ±0.4730	17.5753 ±0.7776	15.9986 ±4.0785	0.3532 ±0.7509	0.641	0.5552 ±2.049	0.787	1.022 ±2.144	0.635
	Charolais	c. −4145C>T	7.8322 ±0.3729	7.7202 ±0.5285	8.8836 ±2.3525	−0.1445 ±0.5250	0.991	−0.5257 ±1.181	0.657	−0.6376 ±1.247	0.610
		c.4208T>G	7.7792 ±0.3991	7.9080 ±0.4703	7.6666 ±0.9410	−0.2324 ±0.4091	0.995	−0.5629 ±0.4897	0.909	0.1851 ±0.6114	0.763
		c.9970A>G	7.7581 ±0.4046	7.9235 ±0.4657	4.5097 ±2.3924	−0.7120 ±0.4910	0.876	1.624 ±1.197	0.177	1.790 ±1.263	0.159
LMY	Hybrid	c. −4145C>T	58.0907 ±0.2932	57.9741 ±0.4115	56.9893 ±1.2768	−0.2387 ±0.3809	0.585	0.5507 ±0.6434	0.395	0.4341 ±0.7220	0.550
		c.4208T>G	58.2918 ±0.3540	57.9908 ±0.3238	57.4964 ±0.5559	0.3711 ±0.2903	0.206	−0.3977 ±0.3085	0.199	0.9673 ±0.3973	0.809
		c.9970A>G	58.0417 ±0.3014	57.6159 ±0.4125	60.0895 ±0.8729	0.2761 ±0.3433	0.392	−1.024 ±0.4450	**0.023***	−1.450 ±0.5533	**0.010***
	Angus	c. −4145C>T	53.6403 ±0.3916	54.1205 ±0.6073	52.0061 ±1.8282	0.1171 ±0.5503	0.833	0.8171 ±0.9198	0.377	1.297 ±1.032	0.211

		c.4208T>G	53.3416 ±0.5480	53.6482 ±0.4759	54.3120 ±0.5855	−0.4795 ±0.3555	0.181	0.4852 ±0.3566	0.176	−0.1786 ±0.5159	0.730
		c.9970A>G	53.8208 ±0.3876	53.2606 ±0.6718	53.4640 ±3.6912	−0.5190 ±0.6665	0.436	0.1784 ±1.856	0.924	−0.3818 ±1.941	0.845
	Charolais	c. −4145C>T	62.3743 ±0.3271	62.3139 ±0.4881	61.8669 ±2.3990	−0.8993 ±0.5201	0.956	0.2537 ±1.207	0.834	0.1933 ±1.277	0.880
		c.4208T>G	62.4576 ±0.3580	62.1083 ±0.4305	62.6750 ±0.9335	0.9573 ±0.4076	0.889	0.1087 ±0.4947	0.827	−0.4580 ±0.6249	0.465
		c.9970A>G	62.4729 ±0.3569	62.1085 ±0.4167	65.3607 ±2.4022	−0.1250 ±0.4880	0.817	−1.444 ±1.206	0.233	−1.808 ±1.273	0.158
CREA	Hybrid	c. −4145C>T	84.0159 ±0.7051	84.0274 ±0.9390	81.8694 ±2.7692	−0.2921 ±0.8275	0.721	1.073 ±1.388	0.442	1.085 ±1.547	0.486
		c.4208T>G	84.0105 ±0.8253	84.3544 ±0.7637	82.6881 ±1.2384	0.3989 ±0.6314	0.530	−0.6612 ±0.6682	0.325	1.005 ±0.8497	0.238
		c.9970A>G	84.2874 ±0.7046	83.1141 ±0.9322	84.6962 ±1.9090	−0.5034 ±0.7433	0.499	−0.2044 ±0.9641	0.833	−1.378 ±1.192	0.249
	Angus	c. −4145C>T	82.1184 ±0.6775	82.9305 ±1.1334	79.8355 ±3.6661	0.2942 ±1.077	0.765	1.141 ±1.848	0.539	1.954 ±2.096	0.354
		c.4208T>G	81.9606 ±1.0274	82.4572 ±0.8735	82.4028 ±1.1085	−0.2364 ±0.7086	0.665	0.2211 ±0.7103	0.755	0.2755 ±1.052	0.794

		c.9970A>G	82.2494	82.4987	80.1369	0.1304	0.868	1.056	0.780	1.306	0.741
			±0.6923	±1.2846	±7.4863	±1.310		±3.769		±3.942	
	Charolais	c. −4145C>T	94.4351	93.2589	98.4381	−0.6690	0.731	−2.002	0.532	−3.178	0.348
			±1.0505	±1.4687	±6.3613	±1.436		±3.191		±3.369	
		c.4208T>G	94.8142	92.8475	96.2106	0.4860	0.727	0.6982	0.599	−2.665	0.106
			±1.1848	±1.3754	±2.5880	±1.118		±1.322		±1.637	
		c.9970A>G	94.2223	93.9883	96.6343	−0.3759	0.987	−1.206	0.713	−1.440	0.677
			±1.1680	±1.3336	±6.5433	±1.346		±3.270		±3.449	
CMAR	Hybrid	c. −4145C>T	4.5693	4.5032	4.8568	−0.7189	0.899	−0.1438	0.232	−0.2098	0.119
			±0.0590	±0.0797	±0.2390	±0.7158		±0.1200		±0.1340	
		c.4208T>G	4.5405	4.5551	4.6111	−0.2994	0.588	0.3531	0.546	−0.2066	0.782
			±0.0709	±0.0655	±0.1073	±0.5488		±0.5822		±0.7419	
		c.9970A>G	4.5130	4.6934	4.4523	0.7694	0.246	0.3035	0.718	0.2107	**0.043***
			±0.0621	±0.0816	±0.1659	±0.6464		±0.8360		±0.1032	
	Angus	c. −4145C>T	6.3193	6.0586	6.1350	−0.2123	0.259	0.9060	0.760	−0.1820	0.578
			±0.1703	±0.2329	±0.6184	±0.1904		±0.2955		±0.3258	
		c.4208T>G	6.1786	6.4520	6.0320	0.7132	0.517	−0.7954	0.492	0.3315	**0.042***
			±0.2094	±0.1876	±0.2194	±0.1161		±0.1152		±0.1614	
		c.9970A>G	6.1696	6.4705	6.5253	0.2861	0.200	−0.1779	0.758	0.1230	0.839
			±0.1629	±0.2425	±1.1521	±0.2187		±0.5766		±0.6053	

Charolais	c. −4145C>T	4.5382 ±0.1126	4.4260 ±0.1437	4.6037 ±0.5080	−0.8860 ±0.1195	0.440	−0.3273 ±0.2524	0.897	−0.1449 ±0.2647	0.586
	c.4208T>G	4.5190 ±0.1135	4.4931 ±0.1284	4.5182 ±0.2162	0.1117 ±0.9058	0.883	−0.3839 ±0.1055	0.996	−0.2551 ±0.1287	0.844
	c.9970A>G	4.4745 ±0.1139	4.5754 ±0.1262	4.1369 ±0.5245	0.6333 ±0.1092	0.565	0.1688 ±0.2602	0.518	0.2697 ±0.2745	0.328

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b]Least square means and SE for genotypes AA, AB and BB.

[c]AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d]Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e]Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10

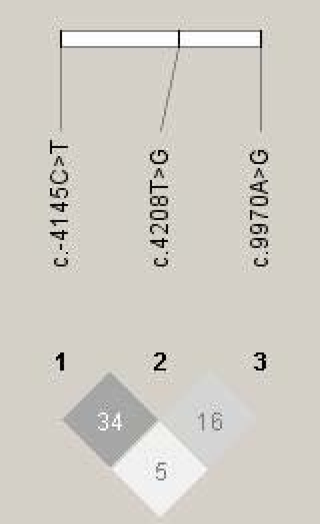

Figure 3.10. Haplotype block for IDH1 SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

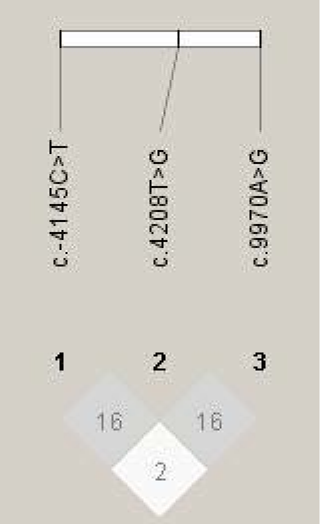

Figure 3.11. Haplotype block for IDH1 SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

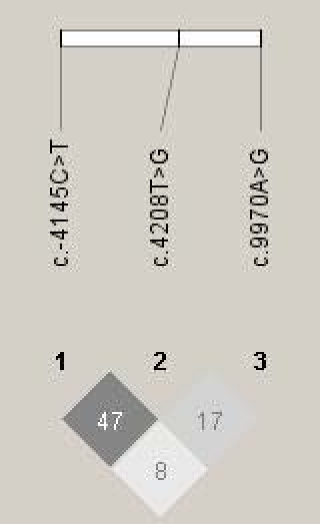

Figure 3.12. Haplotype block for IDH1 SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.16. IDH1 haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype name[a]	Allele arrangement[b,c]	Frequency[c]
Hybrid	HIDH1_01	C-T-A	0.443
	HIDH1_02	C-G-A	0.257
	HIDH1_03	C-T-G	0.142
	HIDH1_04	T-G-A	0.087
	HIDH1_05	T-T-A	0.039
	Others 3 types	---	0.033
Angus	AIDH1_01	C-T-A	0.408
	AIDH1_02	C-G-A	0.371
	AIDH1_03	T-G-A	0.087
	AIDH1_04	C-T-G	0.075
	Other 4 types	---	0.058
Charolais	CIDH1_01	C-T-A	0.452
	CIDH1_02	C-G-A	0.206
	CIDH1_03	C-T-G	0.168
	CIDH1_04	T-G-A	0.069
	CIDH1_05	T-T-A	0.067
	CIDH1_06	T-T-G	0.037

[a] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[b] SNPs c. −4145C>T, c.4208T>G and c.9970A>G were used chronologically to set the allele arrangement for hybrid, Angus and Charolais animal populations.

[c] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.17. Log likelihood (LR) ratio test result for IDH1 haplotypes in the hybrid, Angus and Charolais cattle populations.

Animal	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	UBF	−565.420	−568.994	5.79	0.0161
	UREA	−910.685	−915.633	11.83	0.0006
	AUBF	1372.64	1379.58	17.96	0.00002
	AUREA	951.624	957.85	14.32	0.0002
	SWT	−1602.08	−1611.51	17.31	0.00003
	CWT	−1410.51	−1421.29	15.24	0.00009
	AVBF	−697.669	−701.414	7.06	0.0079
	LMY	−666.112	−669.456	5.77	0.0163
	CREA	−949.141	−954.045	12.09	0.0005
	CMAR	−47.6839	−47.1706	1.24	0.2655
Angus	UBF	−287.326	−287.372	0.21	0.6468
	UREA	−458.054	−458.054	0	1.0
	AUBF	602.504	602.504	0	1.0
	AUREA	381.786	381.786	0	1.0
	SWT	−761.750	−761.750	0	1.0
	CWT	−677.133	−677.133	0	1.0
	AVBF	−386.267	−386.267	0	1.0
	LMY	−365.795	−365.816	0.1	0.7518
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.703	−142.703	0	1.0
Charolais	UBF	−225.126	−225.126	0	1.0
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.664	599.664	0	1.0
	AUREA	354.899	354.899	0	1.0
	SWT	−722.287	−722.287	0	1.0
	CWT	−668.033	−668.033	0	1.0

AVBF	−316.704	−316.704	0	1.0
LMY	−319.990	−319.990	0	1.0
CREA	−494.255	−494.255	0	1.0
CMAR	−42.7920	−42.7920	0	1.0

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait. Details of model description is given in materials and methods (page…).

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.18. Least square means of fat deposition and carcass merit traits and estimated effects of IDH1 haplotypes in the hybrid beef cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HIDH1_01	9.0284 ±0.3418	9.1351 ±0.2627	9.2037 ±0.2839	0.8549 ±0.1977	0.594	−0.8766 ±0.2004	0.663	0.1903 ±0.2876	0.947
		HIDH1_02	9.2554 ±0.7222	9.4374 ±0.2716	8.8932 ±0.2507	−0.4005 ±0.2789	**0.098†**	0.1811 ±0.3754	0.631	0.3631 ±0.4169	0.387
		HIDH1_03	7.8884 ±0.6617	9.0636 ±0.3471	9.2355 ±0.2208	0.4409 ±0.2606	**0.087†**	−0.6735 ±0.3341	**0.046***	0.5016 ±0.4505	0.267
		HIDH1_04	8.8462 ±0.9703	9.3737 ±0.4072	9.1035 ±0.2138	−0.1102 ±0.3336	0.824	−0.1287 ±0.4870	0.793	0.3989 ±0.5957	0.505
		HIDH1_05	--	10.1295 ±0.5501	9.0341 ±0.2133	−1.095 ±0.5608	**0.045***	--	--	--	--
UREA	Hybrid	HIDH1_01	83.4217 ±0.7961	83.2068 ±0.5746	83.0139 ±0.6418	−0.2038 ±0.4941	0.725	0.2039 ±0.5011	0.685	−0.1098 ±0.7283	0.988
		HIDH1_02	83.6972 ±1.8176	83.2122 ±0.6146	83.1415 ±0.5496	−0.1486 ±0.6809	0.736	0.2778 ±0.9488	0.771	−0.2072 ±1.068	0.847
		HIDH1_03	82.4482	82.9067	83.3169	0.4231	0.522	−0.4343	0.610	0.2417	0.983

			±1.6448	±0.8222	±0.4573	±0.6562		±0.8485		±1.157	
		HIDH1_04	83.0922	83.3776	83.1617	−0.1159	0.951	−0.3475	0.978	0.2506	0.870
			±2.4456	±0.9696	±0.4428	±0.8224		±1.234		±1.530	
		HIDH1_05	--	82.9286	83.2131	0.2844	0.881	--	--	--	--
				±1.3577	±0.4267	±1.405					
AUBF	Hybrid	HIDH1_01	0.0333	0.0333	0.0341	0.4373	0.622	−0.3919	0.709	−0.3747	0.804
			±0.0017	±0.0013	±0.0014	±0.1030		±0.1044		±0.1504	
		HIDH1_02	0.0351	0.0348	0.0325	−0.1918	0.140	0.1299	0.509	0.1014	0.645
			±0.0038	±0.0014	±0.0012	±0.1437		±0.1959		±0.2187	
		HIDH1_03	0.0289	0.0329	0.0341	0.1921	0.156	−0.2561	0.145	0.1377	0.563
			±0.0034	±0.0018	±0.0011	±0.1359		±0.1749		±0.2367	
		HIDH1_04	0.0307	0.0340	0.0336	0.2849	0.805	−0.1445	0.572	0.1943	0.537
			±0.0051	±0.0021	±0.0010	±0.1728		±0.2546		±0.3129	
		HIDH1_05	--	0.0378	0.0332	−0.4594	0.104	--	--	--	--
				±0.0028	±0.0010	±0.2910					
AURE	Hybrid	HIDH1_01	0.1620	0.1639	0.1640	0.2772	0.979	−0.7660	0.981	−0.1890	0.686
-A			±0.0035	±0.0049	±0.0040	±0.3142		±0.3185		±0.4652	
		HIDH1_02	0.1666	0.1636	0.1625	−0.1448	0.908	0.2043	0.736	−0.9441	0.891
			±0.0116	±0.0036	±0.0032	±0.4220		±0.6036		±0.6849	
		HIDH1_03	0.1608	0.1631	0.1633	0.7681	0.842	−0.1233	0.821	0.1005	0.893

			±0.0104	±0.0051	±0.0027	±0.4181		±0.5421		±0.7448	
		HIDH1_04	0.1671	0.1633	0.1630	−0.9858	0.713	0.2036	0.797	−0.1736	0.861
			±0.0156	±0.0060	±0.0025	±0.5138		±0.7877		±0.9855	
		HIDH1_05	--	0.1612	0.1633	0.2095	0.727	--	--	--	--
				±0.0086	±0.0024	±0.8893					
SWT	Hybrid	HIDH1_01	543.8772	543.2998	543.0349	−0.4059	1.000	0.4212	0.901	−0.1563	0.974
			±6.5013	±5.3963	±5.6789	±3.325		±3.366		±4.748	
		HIDH1_02	555.0642	545.2656	540.8334	−5.539	0.147	2.325	0.260	−0.5708	0.697
			±12.3663	±5.5279	±5.2749	±4.845		±3.751		±4.088	
		HIDH1_03	515.6733	541.5545	545.3443	9.731	**0.021***	−14.84	**0.008***	11.05	0.138
			±11.3514	±6.4147	±4.6408	±4.362		±5.545		±7.424	
		HIDH1_04	533.0466	549.4054	542.5939	−2.087	0.761	−4.774	0.555	11.59	0.233
			±16.3034	±7.5244	±4.7257	±5.655		±8.035		±9.681	
		HIDH1_05	--	551.3614	542.4338	−8.928	0.307	--	--	--	--
				±9.7014	±4.7122	±9.476					
CWT	Hybrid	HIDH1_01	313.8503	314.7612	311.9902	−1.119	0.654	0.9300	0.644	1.841	0.517
			±3.8396	±3.1770	±3.3464	±1.977		±2.000		±2.824	
		HIDH1_02	317.2385	314.3422	312.5875	−1.986	0.328	7.115	0.537	−2.683	0.889
			±7.3517	±3.2461	±3.0919	±2.879		±6.297		±6.852	
		HIDH1_03	299.6554	312.6363	314.5739	4.923	**0.049***	−7.459	**0.026***	5.522	0.214

			±6.7619	±3.8087	±2.7430	±2.599		±3.308		±4.430	
		HIDH1_04	312.4118	316.4762	313.0871	−1.875	0.625	−0.3377	0.944	3.727	0.521
			±9.7035	±4.4395	±2.7499	±3.362		±4.792		±5.780	
		HIDH1_05	--	313.2804	313.5694	0.2890	0.979	--	--	--	--
				±5.7547	±2.7558	±5.642					
AVBF	Hybrid	HIDH1_01	11.7235	12.2409	11.9274	0.5818	0.767	−0.1020	0.720	0.4155	0.311
			±0.4567	±0.3352	±0.3705	±0.2787		±0.2827		±0.4095	
		HIDH1_02	12.1712	12.1108	11.9383	−0.1513	0.565	0.1165	0.828	0.5606	0.926
			±1.0216	±0.3482	±0.3122	±0.3838		±0.5332		±0.5993	
		HIDH1_03	9.9621	12.6707	11.9814	0.2200	0.552	−1.010	**0.034***	1.699	**0.009***
			±0.9221	±0.4657	±0.2682	±0.3700		±0.4733		±0.6430	
		HIDH1_04	12.9113	12.2070	11.9638	−0.3357	0.545	0.4738	0.497	−0.2306	0.789
			±1.3749	±0.5502	±0.2575	±0.4647		±0.6934		±0.8575	
		HIDH1_05	--	12.0743	12.0131	−0.6116	0.879	--	--	--	--
				±0.7660	±0.2484	±0.7916					
LMY	Hybrid	HIDH1_01	58.2678	57.9064	58.0316	−0.9284	0.654	0.1181	0.655	−0.2433	0.522
			±0.4472	±0.3429	±0.3709	±0.2594		±0.2630		±0.3776	
		HIDH1_02	58.2365	57.8328	58.1708	0.1933	0.466	0.3287	0.947	−0.3708	0.502
			±0.9512	±0.3570	±0.3293	±0.3662		±0.4945		±0.5493	
		HIDH1_03	60.1002	57.4250	58.0583	−0.2533	0.449	1.021	**0.021***	−1.654	**0.006***

			±0.8616	±0.4493	±0.2821	±0.3432		±0.4361		±0.5885	
		HIDH1_04	56.9329	57.8320	58.0898	0.3876	0.433	−0.5785	0.369	0.3206	0.684
			±1.2729	±0.5315	±0.2759	±0.4367		±0.6393		±0.7828	
		HIDH1_05	--	57.8710	58.0479	0.1769	0.761	--	--	--	--
				±0.7238	±0.2761	±0.7394					
CREA	Hybrid	HIDH1_01	84.1646	84.2143	83.4890	−0.3804	0.501	0.3378	0.555	0.3875	0.635
			±0.9993	±0.7846	±0.8407	±0.5616		±0.5691		±0.8129	
		HIDH1_02	86.1447	83.4163	84.2091	0.8633	0.916	0.9678	0.368	−1.761	0.136
			±2.0653	±0.8259	±0.7730	±0.8049		±1.068		±1.177	
		HIDH1_03	84.8707	82.9836	84.1442	0.3399	0.649	0.3633	0.703	−1.524	0.234
			±1.8968	±1.0141	±0.6709	±0.7427		±0.9499		±1.278	
		HIDH1_04	81.9176	84.2411	83.9500	0.2421	0.800	−1.016	0.463	1.307	0.438
			±2.7582	±1.1911	±0.6644	±0.9525		±1.378		±1.677	
		HIDH1_05	--	83.5359	83.9917	0.4558	0.778	--	--	--	--
				±1.5862	±0.6565	±1.603					
CMAR	Hybrid	HIDH1_01	4.4456	4.5776	4.5897	0.6515	0.171	−0.7205	0.146	0.5997	0.397
			±0.0868	±0.0683	±0.0731	±0.4869		±0.4935		±0.7047	
		HIDH1_02	4.5359	4.5977	4.5211	−0.4873	0.435	0.7402	0.937	0.6921	0.503
			±0.1790	±0.0696	±0.0647	±0.6946		±0.9280		±0.1026	
		HIDH1_03	4.4444	4.7386	4.5093	−0.8888	0.173	−0.3245	0.694	0.2618	**0.019***

	±0.1636	±0.0875	±0.0579	±0.6436		±0.8189		±0.1101	
HIDH1_04	4.8622	4.4808	4.5577	−0.1606	0.874	0.1522	0.204	−0.2292	0.117
	±0.2388	±0.1022	±0.0561	±0.8256		±0.1195		±0.1456	
HIDH1_05	--	4.4848	4.5605	0.7573	0.606	--	--	--	--
		±0.1370	±0.0552	±0.1390					

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for haplotype homozygous (animal contains same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c] Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d] Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10.

Table 3.19. Least square means of fat deposition and carcass merit traits and estimated effects of IGF1 SNPs in the hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Domina-nce effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c. −512C>T	9.0115 ±0.4241	9.1603 ±0.2469	9.1934 ±0.2881	0.7377 ±0.2258	0.772	−0.9094 ±0.2429	0.709	0.5783 ±0.2987	0.847
		c.47807T>C	9.1017 ±0.2079	9.9194 ±0.5787	--	−0.8177 ±0.5735	0.145	--	--	--	--
	Angus	c. −512C>T	16.0092 ±0.3966	15.7633 ±0.3269	14.7353 ±0.4851	−0.5760 ±0.2692	**0.027***	0.6369 ±0.2743	**0.022***	0.3911 ±0.3430	0.256
		c.47807T>C	15.6504 ±0.2978	16.5312 ±1.0293	--	−0.8808 ±1.021	0.730	--	--	--	--
	Charolais	c. −512C>T	8.0080 ±0.4683	8.1944 ±0.3448	7.9572 ±0.3945	−0.6520 ±0.2435	0.678	0.2540 ±0.2504	0.919	0.2118 ±0.3069	0.492
		c.47807T>C	8.0462 ±0.3082	9.0177 ±0.6155	4.5451 ±1.9505	−0.3475 ±0.5165	0.609	−1.751 ±0.9689	0.073	2.722 ±1.082	**0.013***
UREA	Hybrid	c. −512C>T	83.9411 ±1.0263	82.7637 ±0.5326	83.6827 ±0.6386	0.1746 ±0.5642	0.781	0.1292 ±0.6036	0.831	−1.048 ±0.7572	0.168

		c.47807T>C	83.3145	81.6006	--	1.714	0.254	--	--	--	--
			±0.4170	±1.4336		±1.460					
	Angus	c. −512C>T	80.7917	80.8899	81.4544	0.2950	0.721	−0.3313	0.620	−0.2332	0.779
			±0.9706	±0.8034	±1.1833	±0.6506		±0.6650		±0.8284	
		c.47807T>C	80.9437	82.9173	--	−1.974	0.751	--	--	--	--
			±0.7237	±2.4695		±2.447					
	Charolais	c. −512C>T	81.5005	84.3054	83.7500	0.8420	0.160	−1.125	0.127	1.680	**0.075†**
			±1.2690	±0.8323	±0.9952	±0.7218		±0.7326		±0.9364	
		c.47807T>C	83.4363	86.2352	93.4328	−3.294	**0.014***	4.998	0.101	−2.199	0.520
			±0.6442	±1.6697	±6.0536	±1.478		±3.024		3.406	
AUBF	Hybrid	c. −512C>T	0.0331	0.0338	0.0336	0.1301	0.935	−0.2651	0.835	0.4546	0.773
			±0.0022	±0.0012	±0.0015	±0.1178		±0.1267		±0.1566	
		c.47807T>C	0.0335	0.0361	--	−0.2566	0.382	--	--	--	--
			±0.0010	±0.0030		±0.3017					
	Angus	c. −512C>T	0.0702	0.0681	0.0630	−0.3353	0.232	0.3600	0.215	0.1574	0.673
			±0.0040	±0.0032	±0.0049	±0.2831		±0.2892		±0.3721	
		c.47807T>C	0.0681	0.0717	--	−0.3591	0.824	--	--	--	--
			±0.0027	±0.0105		±0.1051					
	Charolais	c. −512C>T	0.0309	0.0333	0.0305	−0.5986	0.817	0.1953	0.932	0.2603	0.383
			±0.0039	±0.0024	±0.0030	±0.2228		±0.2278		±0.2971	

		c.47807T>C	0.0315 ±0.0019	0.0392 ±0.0052	0.0223 0.0192	−0.4908 ±0.4643	0.275	−0.4635 ±0.9600	0.630	0.1228 ±0.1082	0.258
AUREA	Hybrid	c. −512C>T	0.1648 ±0.0065	0.1624 ±0.0032	0.1643 ±0.0039	0.3545 ±0.3573	0.869	0.2491 ±0.3835	0.949	−0.2111 ±0.4853	0.665
		c.47807T>C	0.1629 ±0.0024	0.1704 ±0.0091	--	−0.7523 ±0.9363	0.458	--	--	--	--
	Angus	c. −512C>T	0.2115 ±0.0109	0.1961 ±0.0085	0.2074 ±0.0140	−0.3810 ±0.8351	0.692	0.2047 ±0.8442	0.809	−0.1331 ±0.1143	0.246
		c.47807T>C	0.2024 ±0.0071	0.2114 ±0.0307	--	−0.9043 ±0.3099	0.540	--	--	--	--
	Charolais	c. −512C>T	0.2137 ±0.0141	0.2155 ±0.0081	0.2230 ±0.0104	0.5024 ±0.8405	0.354	−0.4638 ±0.8573	0.590	−0.2874 ±0.1169	0.806
		c.47807T>C	0.2155 ±0.0061	0.2428 ±0.0193	0.2510 0.0760	−0.2525 ±0.1760	**0.067†**	0.1773 ±0.3798	0.642	0.9567 ±0.4283	0.824
SWT	Hybrid	c. −512C>T	548.4273 ±7.6437	541.8096 ±5.1482	542.9651 ±5.7449	−1.540 ±3.768	0.677	2.731 ±4.055	0.503	−3.887 ±4.907	0.431
		c.47807T>C	543.0757 ±4.7860	549.6418 ±10.0726	--	−6.566 ±9.391	0.480	--	--	--	--
	Angus	c. −512C>T	561.7755 ±4.7414	566.8402 ±3.9781	566.3548 ±5.7223	2.733 ±3.082	0.603	−2.290 ±3.151	0.469	2.775 ±3.880	0.476

		c.47807T>C	565.5030 ±3.4366	553.1399 ±11.6405	--	12.36 ±11.53	**0.009***	--	--	--	--
	Charolais	c. −512C>T	566.5822 ±7.0095	567.4065 ±4.7495	561.5180 ±5.6036	−3.161 ±3.878	0.361	2.532 ±3.973	0.525	3.356 ±5.012	0.505
		c.47807T>C	564.9797 ±4.0949	571.1108 ±9.4681	552.3621 ±32.4572	−3.299 ±8.171	0.769	−6.309 ±16.19	0.698	12.44 ±18.18	0.496
CWT	Hybrid	c. −512C>T	318.1534 ±4.5503	312.1593 ±3.0704	313.6565 ±3.4242	−1.109 ±2.243	0.616	2.248 ±2.410	0.354	−3.746 ±2.917	0.200
		c.47807T>C	313.6844 ±2.7955	313.9673 ±5.9775	--	−0.2830 ±5.599	0.949	--	--	--	--
	Angus	c. −512C>T	327.7389 ±3.0014	330.4248 ±2.4680	328.6938 ±3.6535	0.8163 ±2.022	0.975	−0.4775 ±2.065	0.818	2.208 ±2.579	0.394
		c.47807T>C	329.6357 ±2.0476	318.0187 ±7.4687	--	11.62 ±7.451	**0.002***	--	--	--	--
	Charolais	c. −512C>T	331.9311 ±4.6136	336.0236 ±2.7942	333.6158 ±3.4682	0.2964 ±2.721	0.922	−0.8423 ±2.764	0.762	3.250 ±3.669	0.378
		c.47807T>C	334.3281 ±2.2621	336.6227 ±6.3628	338.6085 ±23.9428	−2.260 ±5.707	0.699	2.140 ±11.97	0.859	0.1544 ±13.49	0.991
AVBF	Hybrid	c. −512C>T	11.5566 ±0.5775	12.1207 ±0.2987	12.0899 ±0.3584	0.1797 ±0.3168	0.604	−0.2667 ±0.3398	0.435	0.2974 ±0.4265	0.488

		c.47807T>C	12.0545 ±0.2287	11.5685 ±0.8064	--	0.4860 ±0.8236	0.586	--	--	--	--
	Angus	c. −512C>T	18.2582 ±0.6106	16.9072 ±0.4913	16.0640 ±0.7600	−1.133 ±0.4343	**0.011***	1.097 ±0.4430	**0.015***	−0.2539 ±0.5677	0.656
		c.47807T>C	17.1962 ±0.4530	16.9843 ±1.6687	--	0.2118 ±1.667	0.923	--	--	--	--
	Charolais	c. −512C>T	7.1692 ±0.6431	8.1788 ±0.3926	7.6128 ±0.4853	0.9559 ±0.3816	0.861	−0.2218 ±0.3840	0.565	0.7878 ±0.5076	0.123
		c.47807T>C	7.8010 ±0.3408	8.2118 ±0.9045	4.1126 ±3.3155	0.1080 ±0.8085	0.821	−1.844 ±1.657	0.267	2.255 ±1.866	0.229
LMY	Hybrid	c. −512C>T	58.4502 ±0.5539	57.9772 ±0.3198	57.9331 ±0.3741	−0.1944 ±0.2960	0.535	0.2586 ±0.3181	0.419	−0.2144 ±0.3917	0.586
		c.47807T>C	58.0295 ±0.2682	58.0787 ±0.7593	--	−0.4928 ±0.7545	0.976	--	--	--	--
	Angus	c. −512C>T	52.8394 ±0.5252	53.9145 ±0.4147	54.6649 ±0.6630	0.9345 ±0.3871	**0.017***	−0.9128 ±0.3945	**0.022***	0.1624 ±0.5182	0.755
		c.47807T>C	53.7136 ±0.3692	53.7067 ±1.4574	--	0.6881 ±1.464	0.988	--	--	--	--
	Charolais	c. −512C>T	62.4750 ±0.6304	62.1731 ±0.3692	62.5816 ±0.4668	0.1055 ±0.3771	0.706	−0.5329 ±0.3827	0.890	−0.3552 ±0.5176	0.494

		c.47807T>C	62.3450 ±0.2913	62.2477 ±0.8733	66.0502 ±3.3763	−0.3382 ±0.7977	0.583	1.853 ±1.688	0.274	−1.950 ±1.904	0.307
CREA	Hybrid	c. −512C>T	85.1524 ±1.2275	83.8593 ±0.7515	83.6145 ±0.8642	−0.6127 ±0.6406	0.341	0.7689 ±0.6889	0.265	−0.5241 ±0.8418	0.536
		c.47807T>C	84.0642 ±0.6650	82.5021 ±1.6575	--	1.562 ±1.611	0.336	--	--	--	--
	Angus	c. −512C>T	81.3229 ±1.0112	82.4774 ±0.7859	83.1490 ±1.2947	0.9437 ±0.7693	0.257	−0.9131 ±0.7829	0.247	0.2414 ±1.063	0.821
		c.47807T>C	82.3655 ±0.6290	79.5685 ±2.7594	--	2.797 ±2.794	0.158	--	--	--	--
	Charolais	c. −512C>T	92.0392 ±1.8254	94.7278 ±1.1634	94.3857 ±1.4087	0.9234 ±1.049	0.325	−1.173 ±1.069	0.275	1.515 ±1.384	0.275
		c.47807T>C	94.0185 ±0.9719	95.5022 ±2.4966	99.2984 ±9.0128	−1.734 ±2.205	0.363	2.640 ±4.502	0.559	−1.156 ±5.069	0.820
CMAR	Hybrid	c. −512C>T	4.5444 ±0.0159	4.5482 ±0.0639	4.5779 ±0.0738	0.2068 ±0.5555	0.719	−0.1675 ±0.5978	0.781	−0.1294 ±0.7318	0.860
		c.47807T>C	4.5585 ±0.0552	4.5324 ±0.1436	--	0.2618 ±0.1407	0.861	--	--	--	--
	Angus	c. −512C>T	6.3266 ±0.2139	6.1663 ±0.1807	6.4076 ±0.2568	0.7670 ±0.1371	0.918	−0.4099 ±0.1340	0.760	−0.1911 ±0.1644	0.247

	c.47807T>C	6.2234	6.4549	--	−0.2315	0.501	--	--	--	--
		±0.1561	±0.5030		±0.4951					
Charolais	c. −512C>T	4.4819	4.4995	4.5532	0.3907	0.693	−0.3570	0.695	−0.1806	0.873
		±0.1661	±0.1189	±0.1374	±0.8814		±0.9080		±0.1123	
	c.47807T>C	4.4839	4.8389	3.8100	−0.1957	0.313	−0.3370	0.340	0.6920	**0.080†**
		±0.1124	±0.2232	±0.7054	±0.1832		±0.3503		±0.3912	

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

Figure 3.13. Haplotype block for IGF1 SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Figure 3.14. Haplotype block for IGF1 SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Figure 3.15. Haplotype block for IGF1 SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.20. IGF1 haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype name[a]	Allele arrangement[b,c]	Frequency[c]
Hybrid	HIGF1_01	T-T	0.606
	HIGF1_02	C-T	0.359
	HIGF1_03	T-C	0.017
	HIGF1_04	C-C	0.017
Angus	AIGF1_01	C-T	0.541
	AIGF1_02	T-T	0.439
	AIGF1_03	C-C	0.017
	AIGF1_04	T-C	0.002
Charolais	CIGF1_01	T-T	0.537
	CIGF1_02	C-T	0.412
	CIGF1_03	T-C	0.027
	CIGF1_04	C-C	0.024

[a] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[b] SNPs c. −512C>T, c.47807T>C were used chronologically to set the allele arrangement for hybrid, Angus and Charolais animal populations.

[c] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.21. Log likelihood ratio (LR) test result for IGF1 haplotypes in the hybrid, Angus and Charolais cattle populations.

Cattle population	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	UBF	−566.678	−568.994	10.67	0.0011
	UREA	−913.253	−915.633	10.96	0.0009
	AUBF	1376.37	1379.58	14.78	0.0001
	AUREA	954.734	957.85	14.35	0.0002
	SWT	−1605.84	−1611.51	26.11	<0.0001
	CWT	−1413.82	−1421.29	34.4	<0.0001
	AVBF	−699.202	−701.414	10.19	0.0014
	LMY	−667.365	−669.456	9.63	0.0019
	CREA	−951.766	−954.045	10.49	0.0012
	CMAR	−47.4918	−47.1706	1.48	0.2238
Angus	UBF	−286.845	−287.372	2.428	0.1192
	UREA	−458.054	−458.054	0	1.0
	AUBF	602.504	602.504	0	1.0
	AUREA	381.786	381.786	0	1.0
	SWT	−761.750	−761.750	0	1.0
	CWT	−677.133	−677.133	0	1.0
	AVBF	−385.520	−386.267	3.442	0.0636
	LMY	−365.153	−365.816	3.052	0.0806
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.703	−142.703	0	1.0
Charolais	UBF	−225.126	−225.126	0	1.0
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.664	599.664	0	1.0
	AUREA	354.899	354.899	0	1.0
	SWT	−722.287	−722.287	0	1.0
	CWT	−668.033	−668.033	0	1.0
	AVBF	−316.704	−316.704	0	1.0

LMY	−319.990	−319.990	0	1.0
CREA	−494.255	−494.255	0	1.0
CMAR	−42.7920	−42.7920	0	1.0

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait.

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.22. Least square means of fat deposition and carcass merit traits and estimated effects of IGF1 haplotypes in the hybrid and Angus beef cattle populations.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HIGF1_01	8.9445 ±0.2901	9.2680 ±0.2446	9.0689 ±0.4143	0.1351 ±0.2233	0.482	−0.6218 ±0.2380	0.795	0.2613 ±0.2923	0.374
		HIGF1_02	9.1191 ±0.4384	9.1465 ±0.2466	9.1210 ±0.2768	−0.8021 ±0.2230	0.906	−0.9836 ±0.2459	0.997	0.2647 ±0.3022	0.931
UREA	Hybrid	HIGF1_01	83.6271 ±0.6483	82.6531 ±0.5263	84.0257 ±1.0046	−0.1203 ±0.5626	0.885	−0.1993 ±0.5961	0.739	−1.173 ±0.7454	0.117
		HIGF1_02	84.0471 ±1.0742	82.8853 ±0.5399	83.2657 ±0.6158	−0.1323 ±0.5615	0.772	0.3907 ±0.6171	0.529	−0.7712 ±0.7710	0.318
AUBF	Hybrid	HIGF1_01	0.0324 ±0.0015	0.0344 ±0.0012	0.0330 ±0.0021	0.7594 ±0.1165	0.470	−0.2880 ±0.1241	0.817	0.1689 ±0.1532	0.271
		HIGF1_02	0.0333 ±0.0023	0.0340 ±0.0012	0.0331 ±0.0014	−0.3585 ±0.1164	0.714	0.9324 ±0.1282	0.942	0.7803 ±0.1583	0.624
AURE-A	Hybrid	HIGF1_01	0.1632 ±0.0039	0.1623 ±0.0032	0.1659 ±0.0064	0.7505 ±0.3575	0.941	−0.1342 ±0.3800	0.725	−0.2220 ±0.4798	0.645
		HIGF1_02	0.1631	0.1628	0.1635	0.3419	0.839	−0.1947	0.961	−0.4469	0.928

			±0.0068	±0.0032	±0.0037	±0.3568		±0.3929		±0.4958	
SWT	Hybrid	HIGF1_01	542.0856	542.2670	548.9302	2.482	0.453	−3.422	0.394	−3.241	0.504
			±5.7638	±5.1113	±7.5215	±3.732		±3.988		±4.822	
		HIGF1_02	547.1355	542.6529	542.5867	−1.488	0.634	2.274	0.583	−2.208	0.660
			±7.8877	±5.1526	±5.5953	±3.730		±4.123		±4.991	
CWT	Hybrid	HIGF1_01	313.0789	312.3998	317.9765	1.545	0.436	−2.449	0.303	−3.128	0.276
			±3.3974	±3.0061	±4.4503	±2.221		±2.371		±2.868	
		HIGF1_02	317.8439	312.6403	312.9244	−1.499	0.455	2.460	0.316	−2.744	0.358
			±4.6638	±3.0239	±3.2895	±2.219		±2.450		±2.967	
AVBF	Hybrid	HIGF1_01	11.8784	12.2234	11.5767	−0.1569	0.962	0.1509	0.655	0.4959	0.237
			±0.3728	±0.3047	±0.5686	±0.3161		±0.3360		±0.4186	
		HIGF1_02	11.9776	12.0778	11.9421	−0.5789	0.795	0.1776	0.959	0.1180	0.786
			±0.6069	±0.3116	±0.3548	±0.3157		±0.3476		±0.4328	
LMY	Hybrid	HIGF1_01	58.1229	57.8705	58.3779	0.1982	0.983	−0.1275	0.684	−0.3799	0.326
			±0.3759	±0.3156	±0.5409	±0.2932		±0.3121		±0.3839	
		HIGF1_02	58.1584	57.9827	58.0501	−0.1237	0.976	0.5415	0.867	−0.1216	0.760
			±0.5747	±0.3223	±0.3620	±0.2927		±0.3227		±0.3967	
CREA	Hybrid	HIGF1_01	83.8001	83.7582	84.7788	0.3391	0.593	−0.4894	0.472	−0.5313	0.523
			±0.8603	±0.7352	±1.1983	±0.6347		±0.6770		±0.8274	
		HIGF1_02	85.1887	83.7997	83.6164	−0.5793	0.362	0.7861	0.261	−0.6029	0.483

			±1.2645	±0.7440	±0.8275	±0.6332		±0.6981		±0.8535	
CMAR	Hybrid	HIGF1_01	4.5740	4.5493	4.5315	−0.2220	0.713	0.2124	0.719	−0.3429	0.962
			±0.0735	±0.0624	±0.1033	±0.5504		±0.5873		±0.7191	
		HIGF1_02	4.5541	4.5400	4.5739	0.1816	0.763	−0.9898	0.871	−0.2396	0.748
			±0.1093	±0.0634	±0.0708	±0.5495		±0.6062		±0.7423	

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b]Least square means and SE for haplotype homozygous (animal contains same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c]Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d]Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10.

Table 3.23. Least square means of fat deposition and carcass merit traits and estimated effects of INS SNPs in the hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Dominance effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c. −526T>C	9.2033 ±0.2612	9.3256 ±0.2586	8.0980 ±0.5328	−0.2267 ±0.2347	0.383	0.5526 ±0.2864	**0.056†**	0.6750 ±0.3430	**0.051†**
		c. −397T>C	9.2449 ±0.2595	9.2642 ±0.2564	8.0958 ±0.5371	0.2847 ±0.2327	0.243	−0.5745 ±0.2870	**0.047***	0.5938 ±0.3459	**0.088†**
	Charolais	c. −526T>C	8.0394 ±0.3642	8.0454 ±0.3575	8.6200 ±0.5953	0.1763 ±0.2621	0.379	−0.2903 ±0.2972	0.331	−0.2843 ±0.3498	0.418
		c. −397T>C	8.0255 ±0.3672	8.0919 ±0.3584	8.3832 ±0.6415	−0.1267 ±0.2724	0.520	0.1788 ±0.3219	0.580	−0.1124 ±0.3644	0.758
UREA	Hybrid	c. −526T>C	83.2193 ±0.5761	83.5394 ±0.5734	82.0890 ±1.2992	−0.1547 ±0.5902	0.828	0.5652 ±0.7145	0.431	0.8852 ±0.8658	0.308
		c. −397T>C	83.2265 ±0.5798	83.7234 ±0.5760	81.5181 ±1.3203	0.2145 ±0.5879	0.739	−0.8542 ±0.7201	0.237	1.351 ±0.8759	0.125
	Charolais	c. −526T>C	83.2559 ±0.9146	84.1555 ±0.8993	82.8082 ±1.7221	0.2262 ±0.7867	0.914	0.2238 ±0.9025	0.804	1.123 ±1.093	0.306

		c. −397T>C	83.2973	84.2275	81.6612	−0.9169	0.732	−0.8181	0.408	1.748	0.129
			±0.9156	±0.8929	±1.8845	±0.8211		±0.9850		±1.145	
AUBF	Hybrid	c. −526T>C	0.0344	0.0340	0.0286	−0.1750	0.172	0.2919	**0.052†**	0.2460	0.172
			±0.0013	±0.0013	±0.0028	±0.1224		±0.1492		±0.1794	
		c. −397T>C	0.0349	0.0336	0.0282	0.2350	**0.060***	−0.3334	**0.028***	0.2043	0.261
			±0.0013	±0.0013	±0.0028	±0.1216		±0.1499		±0.1813	
	Charolais	c. −526T>C	83.2559	84.1555	82.8082	0.3020	0.246	−0.5413	**0.054†**	−0.5899	**0.087†**
			±0.9146	±0.8993	±1.7221	±0.2424		±0.2786		±0.3423	
		c. −397T>C	0.0313	0.0320	0.0376	−0.1978	0.487	0.3139	0.312	−0.2418	0.508
			±0.0026	±0.0025	±0.0058	±0.2538		±0.3093		±0.3640	
AURE	Hybrid	c. −526T>C	0.1638	0.1636	0.1613	−0.7455	0.780	0.1258	0.781	0.1130	0.838
-A			±0.0034	±0.0034	±0.0081	±0.3743		±0.4514		±0.5505	
		c. −397T>C	0.1643	0.1648	0.1589	0.1211	0.707	−0.2707	0.556	0.3237	0.565
			±0.0035	±0.0035	±0.0084	±0.3737		±0.4580		±0.5593	
	Charolais	c. −526T>C	0.2114	0.2254	0.2097	0.5468	0.986	0.8428	0.939	0.1483	0.279
			±0.0087	±0.0086	±0.0202	±0.9257		±0.1092		±0.1364	
		c. −397T>C	0.2118	0.2258	0.1952	−0.2851	0.811	−0.8310	0.492	0.2227	0.124
			±0.0086	±0.0085	±0.0225	±0.961		±0.1205		±0.1439	
SWT	Hybrid	c. −526T>C	542.7275	548.8860	522.2724	−1.879	0.746	10.23	**0.036***	16.39	**0.005***
			±5.4187	±5.3396	±9.5377	±3.911		±4.844		±5.714	

		c. −397T>C	43.5621 ±5.4014	548.1908 ±5.3151	520.0694 ±9.5747	0.3427 ±3.879	0.427	−11.75 ±4.832	**0.016***	16.38 ±5.767	**0.005***
	Charolais	c. −526T>C	562.8662 ±5.0200	567.9663 ±4.9334	564.4943 ±9.2123	2.545 ±4.185	0.454	−0.8140 ±4.796	0.866	4.286 ±5.781	0.460
		c. −397T>C	562.9248 ±5.0309	568.7022 ±4.9060	558.2833 ±10.0667	−1.532 ±4.379	0.631	−2.321 ±5.235	0.659	8.098 ±6.058	0.183
CWT	Hybrid	c. −526T>C	312.4971 ±3.2234	316.7150 ±3.1764	305.4344 ±5.6919	0.4096 ±2.329	0.750	3.531 ±2.896	0.224	7.749 ±3.417	0.025
		c. −397T>C	313.0920 ±3.2116	316.0589 ±3.1602	305.0328 ±5.7176	0.4761 ±2.310	0.899	−4.030 ±2.892	0.165	6.997 ±3.451	0.044
	Charolais	c. −526T>C	332.6972 ±3.0533	336.2653 ±3.0127	334.2613 ±6.4786	1.936 ±2.973	0.516	−0.7820 ±3.470	0.822	2.786 ±4.286	0.517
		c. −397T>C	333.0458 ±2.9895	335.8286 ±2.9198	331.5999 ±7.0209	−0.9854 ±3.034	0.709	−0.7229 ±3.730	0.847	3.506 ±4.409	0.428
AVBF	Hybrid	c. −526T>C	11.8528 ±0.3258	12.3574 ±0.3243	11.2860 ±0.7313	0.8287 ±0.3324	0.755	0.2834 ±0.4018	0.483	0.7880 ±0.4866	0.107
		c. −397T>C	11.8930 ±0.3188	12.2704 ±0.3169	11.6733 ±0.7380	−0.1213 ±0.3296	0.684	−0.1099 ±0.4036	0.787	0.4872 ±0.4918	0.325
	Charolais	c. −526T>C	7.7780 ±0.4413	7.7622 ±0.4350	8.3653 ±0.9086	0.1673 ±4178	0.599	−0.2936 ±0.4846	0.546	−0.3095 ±0.5959	0.605

		c. −397T>C	7.7926	7.7897	8.1460	−0.9006	0.737	0.1767	0.741	−0.1796	0.776
			±0.4406	±0.4301	±1.0074	±0.4366		±0.5339		±0.6291	
LMY	Hybrid	c. −526T>C	58.1441	57.7338	58.9280	0.6547	0.955	−0.3919	0.299	−0.8023	0.077
			±0.3440	±0.3406	±0.7012	±0.3083		±0.3768		±0.4512	
		c. −397T>C	58.0980	57.8535	58.4403	0.3109	0.884	0.1711	0.653	−0.4156	0.365
			±0.3441	±0.3399	±0.7096	±0.3061		±0.3787		±0.4563	
	Charolais	c. −526T>C	62.4633	62.3496	61.6640	−0.2795	0.402	0.3996	0.414	0.2860	0.638
			±0.4011	±0.3966	±0.9041	±0.4146		±0.4874		±0.6066	
		c. −397T>C	62.4632	62.3271	61.8399	0.2248	0.493	−0.3117	0.565	0.1755	0.786
			±0.4048	±0.3958	±1.0129	±0.4352		±0.5404		±0.6429	
CREA	Hybrid	c. −526T>C	83.7662	84.0504	84.7439	0.3886	0.558	−0.4888	0.553	−0.2046	0.835
			±0.7916	±0.7821	±1.5451	±0.6639		±0.8191		±0.9764	
		c. −397T>C	83.7191	84.2110	83.7071	−0.2405	0.713	−0.6025	0.994	0.4980	0.616
			±0.7915	±0.7802	±1.5618	±0.6615		±0.8226		±0.9878	
	Charolais	c. −526T>C	94.3614	94.2374	92.7854	−0.5195	0.529	0.7880	0.553	0.6640	0.682
			±1.2712	±1.2513	±2.4993	±1.145		±1.322		±1.614	
		c. −397T>C	94.4093	94.1324	92.4370	0.6471	0.488	−0.9861	0.498	0.7092	0.677
			±1.2562	±1.2257	±2.7462	±1.191		±1.448		±1.697	
CMAR	Hybrid	c. −526T>C	4.5049	4.6327	4.4552	0.4951	0.377	0.2484	0.727	0.1527	**0.072†**
			±0.0677	±0.0669	±0.1332	±0.5770		±0.7082		±0.8449	

	c. −397T>C	4.5056 ±0.0681	4.6291 ±0.0672	4.5015 ±0.1350	−0.5985 ±0.5745	0.291	−0.2048 ±0.7123	0.977	0.1256 ±0.8556	0.144
Charolais	c. −526T>C	4.5162 ±0.1220	4.5260 ±0.1198	4.3904 ±0.2090	−0.3387 ±0.9351	0.773	0.6292 ±0.1064	0.556	0.7275 ±0.1265	0.567
	c. −397T>C	4.5262 ±0.1256	4.5276 ±0.1226	4.3189 ±0.2299	0.5414 ±0.9861	0.637	−0.1037 ±0.1170	0.378	0.1050 ±0.1335	0.434

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

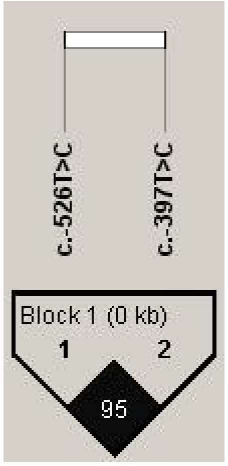

Figure 3.16. Haplotype block for INS SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

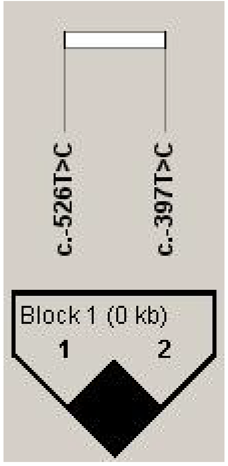

Figure 3.17. Haplotype block for INS SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.24. INS haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Animal	Haplotype block[a]	Haplotype name[b]	Allele arrangement[c,d]	Frequency[d]
Hybrid	HINSB1	HINS_01	T-T	0.524
		HINS_02	T-C	0.176
		HINS_03	C-T	0.175
		HINS_04	C-C	0.124
Charolais	CINSB1	CINS_01	T-T	0.545
		CINS_02	C-T	0.158
		CINS_03	C-C	0.149
		CINS_04	T-C	0.147

[a] Haplotype block is obtained from HAPLOVIEW analyses of SNP genotypes. Name is given by the Author, while last two digit indicate block no. i.e., B1 is block one.

[b] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[c] SNPs c. −526T>C, c. −397T>C were used chronologically to set the allele arrangement for hybrid and Charolais.

[d] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.25. Log likelihood (LR) ratio test result for INS haplotypes in the hybrid, Angus and Charolais cattle populations.

Animal	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	UBF	−566.678	−568.994	10.67	0.0011
	UREA	−913.253	−915.633	10.96	0.0009
	AUBF	1376.54	1379.58	14.00	0.0002
	AUREA	954.734	957.85	14.35	0.0002
	SWT	−1605.84	−1611.51	26.11	<0.0001
	CWT	−1413.82	−1421.29	34.4	<0.0001
	AVBF	−699.202	−701.414	10.19	0.0014
	LMY	−667.365	−669.456	9.63	0.0019
	CREA	−951.766	−954.045	10.49	0.0012
	CMAR	−47.4155	−47.1706	1.13	0.2878
Charolais	UBF	−225.126	−225.126	0	1.0
	UREA	−425.644	−425.644	0	1.0
	AUBF	599.664	599.664	0	1.0
	AUREA	354.899	354.899	0	1.0
	SWT	−722.287	−722.287	0	1.0
	CWT	−668.033	−668.033	0	1.0
	AVBF	−316.704	−316.704	0	1.0
	LMY	−319.990	−319.990	0	1.0
	CREA	−494.255	−494.255	0	1.0
	CMAR	−42.7920	−42.7920	0	1.0

[a] UBF = Ultrasound backfat; UREA = Ultrasound rib eye area; AUBF = Average daily gain of ultrasound backfat; AUREA = Average daily gain of ultrasound rib eye area; SWT = Slaughter weight; CWT = Carcass weight; AVBF = Average backfat; LMY = Lean meat yield; CREA= Carcass rib eye area; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait.

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.26. Least square means of fat deposition and carcass merit traits and estimated effects of INS haplotypes in the hybrid beef cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	Hybrid	HINS_01	9.1200 ±0.2571	9.2433 ±0.4435	9.1181 ±0.2621	0.2224 ±0.1524	0.914	0.9432 ±0.1529	0.995	0.1242 ±0.4483	0.783
		HINS_02	--	9.3225 ±0.2814	9.0242 ±0.2330	−0.2983 ±0.3010	0.314	--	--	--	--
		HINS_03	--	9.3783 ±0.2818	8.9906 ±0.2337	−0.3877 ±0.3040	0.181	--	--	--	--
		HINS_04	7.9397 ±0.5664	9.1306 ±0.5342	9.2611 ±0.2207	0.5765 ±0.2781	**0.050***	−0.6607 ±0.2936	**0.026***	0.5302 ±0.5733	0.358
UREA	Hybrid	HINS_01	82.7890 ±0.5935	84.8448 ±1.0794	83.1009 ±0.6154	0.1993 ±0.3884	0.578	−0.1560 ±0.3885	0.690	1.900 ±1.130	**0.095†**
		HINS_02	--	83.5474 ±0.6454	82.9786 ±0.4896	−0.5689 ±0.7649	0.457	--	--	--	--
		HINS_03	--	83.6752 ±0.6434	82.9050 ±0.4886	−0.7701 ±0.7688	0.306	--	--	--	--
		HINS_04	81.4476	84.7500	83.1673	0.4452	0.554	−0.8599	0.245	2.443	**0.093†**

			±1.4027	±1.2961	±0.4845	±0.6848		±0.7370		±1.445	
AUBF	Hybrid	HINS_01	0.0342 ±0.0013	0.0343 ±0.0023	0.0327 ±0.0013	−0.7379 ±0.7974	0.391	0.7595 ±0.8002	0.346	0.8740 ±0.2338	0.710
		HINS_02	--	0.0335 ±0.0014	0.0336 ±0.0011	0.1174 ±0.1577	0.949	--	--	--	--
		HINS_03	--	0.0340 ±0.0014	0.0333 ±0.0012	−0.7896 ±0.1592	0.593	--	--	--	--
		HINS_04	0.0274 ±0.0029	0.0335 ±0.0027	0.0342 ±0.0011	0.2959 ±0.1440	**0.049***	−0.3409 ±0.1526	**0.027***	0.2695 ±0.2991	0.371
AURE-A	Hybrid	HINS_01	0.1628 ±0.0065	0.1630 ±0.0034	0.1634 ±0.0037	0.1984 ±0.2492	1.000	−0.2071 ±0.2501	0.934	−0.3807 ±0.7101	0.957
		HINS_02	--	0.1637 ±0.0040	0.1628 ±0.0028	−0.9477 ±0.4895	0.849	--	--	--	--
		HINS_03	--	0.1643 ±0.0040	0.1625 ±0.0029	−0.1855 ±0.4907	0.732	--	--	--	--
		HINS_04	0.1578 ±0.0088	0.1665 ±0.0077	0.1632 ±0.0027	0.1557 ±0.4289	0.641	−0.2679 ±0.4662	0.567	0.5973 ±0.9004	0.508
SWT	Hybrid	HINS_01	541.7563 ±5.3871	549.1700 ±8.0877	543.4965 ±5.3744	1.044 ±2.517	0.574	−0.8701 ±2.525	0.732	6.544 ±7.396	0.379
		HINS_02	--	547.3861	540.8602	−6.526	0.182	--	--	--	--

				±5.5681	±5.0046	±4.982					
		HINS_03	--	549.6168	539.4496	−10.17	**0.034***	--	--	--	--
				±5.5690	±4.9998	±5.053					
		HINS_04	516.7650	550.1384	545.7315	11.30	**0.027***	−14.48	**0.004***	18.89	**0.047***
			±10.1221	±9.5243	±4.9031	±4.761		±5.006		±9.438	
CWT	Hybrid	HINS_01	311.7217	316.8899	314.4849	1.481	0.260	−1.382	0.361	3.787	0.392
			±3.1572	±4.7796	±3.1521	±1.497		±1.502		±4.401	
		HINS_02	--	316.1370	311.9615	−4.175	0.153	--	--	--	--
				±3.2746	±2.9319	±2.965					
		HINS_03	--	317.4428	311.1483	−6.294	**0.029***	--	--	--	--
				±3.2834	±2.9392	±3.006					
		HINS_04	303.2121	317.6584	314.3395	4.076	0.195	−5.564	**0.065†**	8.883	0.118
			±6.0310	±5.6808	±2.8833	±2.841		±2.994		±5.661	
AVBF	Hybrid	HINS_01	11.8013	11.8435	12.2720	0.2292	0.263	−0.2353	0.282	−0.1931	0.762
			±0.3358	±0.6087	±0.3477	±0.2176		±0.2184		±0.6359	
		HINS_02	--	12.3669	11.8126	−0.5542	0.195	--	--	--	--
				±0.3729	±0.2915	±0.4291					
		HINS_03	--	12.2855	11.8561	−0.4293	0.302	--	--	--	--
				±0.3728	±0.2920	±0.4327					
		HINS_04	11.3478	13.0068	11.9579	0.6307	0.933	−0.3050	0.460	1.354	**0.095†**

			±0.7795	±0.7110	±0.2584	±0.3875		±0.4109		±0.8037	
LMY	Hybrid	HINS_01	58.1359	58.5705	57.7894	0.2505	0.561	0.1732	0.390	0.6079	0.302
			±0.3443	±0.5863	±0.3499	±0.4311		±0.2003		±0.5877	
		HINS_02	--	57.7072	58.2211	0.5139	0.189	--	--	--	--
				±0.3715	±0.3088	±0.3948					
		HINS_03	--	57.7949	58.1707	0.3758	0.321	--	--	--	--
				±0.3703	±0.3070	±0.3995					
		HINS_04	58.8159	57.4044	58.0207	−0.2275	0.592	0.3976	0.305	−1.014	0.181
			±0.7449	±0.7021	±0.2883	±0.3654		±0.3865		±0.7552	
CREA	Hybrid	HINS_01	83.4705	86.1428	83.8370	−0.1566	0.389	−0.1833	0.672	2.489	**0.051†**
			±0.7858	±1.2915	±0.7930	±0.1999		±0.4305		±1.264	
		HINS_02	--	83.9774	83.9137	−0.6368	0.940	--	--	--	--
				±0.8348	±0.7098	±0.8540					
		HINS_03	--	84.3262	83.7073	−0.6189	0.475	--	--	--	--
				±0.8362	±0.7112	±0.8642					
		HINS_04	84.2450	84.4900	83.8450	−0.2734	0.731	0.2000	0.814	0.4450	0.787
			±1.6458	±1.5572	±0.6809	±0.7988		±0.8448		±1.639	
CMAR	Hybrid	HINS_01	4.4929	4.5055	4.6257	0.6503	**0.077†**	−0.6638	**0.078†**	−0.5379	0.626
			±0.0667	±0.1112	±0.0675	±0.3729		±0.3743		±0.1099	
		HINS_02	--	4.6529	4.4957	−0.1572	**0.034***	--	--	--	--

		±0.0715	±0.0605	±0.7368					
HINS_03	--	4.6407	4.5024	−0.1384	**0.062†**	--	--	--	--
		±0.0717	±0.0607	±0.7470					
HINS_04	4.4394	4.6519	4.5554	0.3239	0.665	−0.5801	0.429	0.1545	0.278
	±0.1416	±0.1339	±0.0573	±0.6903		±0.7297		±0.1419	

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b] Least square means and SE for haplotype homozygous (animal contain same haplotype at both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c] Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d] Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10.

Table 3.27. Least square means of fat deposition and carcass merit traits and estimated effects of LIPE SNPs in the hybrid, Angus and Charolais beef cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Domina-nce effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.−11470G>A	9.1188	9.2089	9.0612	−0.4478	0.960	0.2882	0.895	0.1189	0.682
			±0.2806	±0.2535	±0.3808	±0.2102		±0.2177		±0.2884	
		c. −9627G>A	9.1712	9.1872	9.0375	0.4830	0.933	-0.6684	0.764	0.8285	0.777
			±0.2775	±0.2527	±0.3906	±0.2127		±0.2217		±0.2918	
		c.276A>G	9.1651	9.2009	8.9809	−0.6560	0.864	0.9207	0.674	0.1279	0.660
			±0.2771	±0.2531	±0.3818	±0.2103		±0.2180		±0.2894	
		c.2692C>T	9.2689	9.2572	9.0081	−0.1213	0.501	0.1304	0.487	0.1187	0.710
			±0.2738	±0.3009	±0.3118	±0.1852		±0.1865		±0.3172	
		c.5332G>A	9.0621	9.3189	8.8079	0.1724	0.857	-0.2080	0.653	0.2823	0.356
			±0.2752	±0.2473	±0.4175	±0.2219		±0.4610		±0.3042	
		c.7195C>T	9.0741	9.2744	8.9563	−0.1261	0.925	0.1472	0.726	0.3473	0.368
			±0.2864	±0.2487	±0.3715	±0.2117		±0.4176		±0.3835	
		c.7324G>A	9.1102	9.3169	8.7823	0.8340	0.793	-0.2823	0.512	0.2344	0.449
			±0.2744	±0.2493	±0.3826	±0.2116		±0.4288		±0.3081	

	c.8549A>G	9.1284	9.0645	9.3393	0.1083	0.718	-0.1054	0.636	-0.1694	0.556
		±0.3470	±0.2556	±0.3483	±0.2215		±0.2218		±0.2863	
	c.8560C>T	9.1387	9.1748	9.1706	0.2213	0.807	-0.1594	0.947	0.2014	0.949
		±0.2789	±0.2687	±0.4431	±0.2203		±0.2397		±0.3111	
	c.8563C>T	9.1804	8.9422	8.0025	−0.4024	0.585	0.5889	0.453	0.3507	0.743
		±0.2186	±0.7385	±1.5616	±0.5359		±0.7813		±1.066	
	c.8689A>G	9.1288	9.1056	9.6501	0.1055	0.684	-0.2607	0.437	-0.2838	0.470
		±0.2440	±0.2755	±0.6478	±0.2516		±0.3332		±0.3911	
	c.8731G>A	9.0625	9.2043	9.4179	−0.1650	0.405	0.1777	0.492	-0.3596	0.912
		±0.2788	±0.2734	±0.4823	±0.2301		±0.2576		±0.3252	
	c.8782G>C	9.1164	9.5523	9.0976	−0.3889	0.397	-0.9401	0.994	0.4453	0.749
		±0.2201	±0.4920	±2.6547	±0.4763		±1.326		±1.383	
	c.8893G>A	9.1107	9.2423	8.7324	0.2327	0.814	-0.1891	0.549	0.3207	0.379
		±0.2607	±0.2613	0.5950	±0.2525		±0.3142		±0.3622	
	c.9937A>T	8.9593	9.0683	10.1449	0.3104	0.253	-0.5928	0.121	-0.4838	0.274
		0.2322	±0.2864	0.7425	±0.2704		±0.3801		±0.4412	
Angus	c.−11470G>	15.4278	15.7039	15.7850	0.1623	0.460	-0.1786	0.511	0.9753	0.779
	A	±0.4866	±0.3439	±0.3926	±0.2641		±0.2708		±0.3468	
	c. −9627G>A	15.3645	15.6857	15.8259	−0.2128	0.340	0.2307	0.407	0.9047	0.798
		±0.5057	±0.3550	0.3989	±0.2673		±0.2767		±0.3532	

c.276A>G	15.3578	15.7198	15.8261	0.2095	0.344	-0.2342	0.397	0.1279	0.717
	±0.4980	0.3476	0.3929	±0.2664		±0.2751		±0.3516	
c.2692C>T	15.4124	15.5876	15.8487	0.2271	0.301	-0.2182	0.404	-0.4301	0.909
	±0.5012	±0.3800	0.3653	±0.2480		±0.2603		±0.3733	
c.5332G>A	15.6589	15.6583	15.7320	−0.3881	0.812	0.3655	0.899	-0.3712	0.917
	±0.4833	±0.3214	±0.4580	±0.2869		±0.2883		±0.3549	
c.7195C>T	15.3083	15.7036	15.8130	0.2268	0.330	-0.2524	0.372	0.1430	0.688
	±0.5028	±0.3427	±0.4001	±0.2735		±0.2811		±0.3551	
c.7324G>A	15.3769	15.6996	15.7835	−0.1823	0.404	0.2033	0.458	0.1194	0.734
	±0.4934	±0.3444	±0.3931	±0.2651		±0.2724		±0.3504	
c.8549A>G	15.7718	15.7002	15.3892	−0.1686	0.435	0.1913	0.491	0.1197	0.734
	±0.3865	±0.3470	±0.4997	±0.2675		±0.2763		±0.3517	
c.8560C>T	15.3194	15.6113	15.8420	0.2559	0.254	-0.2613	0.338	0.3056	0.931
	±0.4962	±0.3517	±0.3850	±0.2627		±0.2712		±0.3537	
c.8563C>T	15.6124	15.9032	17.6975	0.6189	0.305	-1.043	0.220	-0.7518	0.499
	±0.2926	±0.7482	±1.7036	±0.5626		±0.8463		±1.108	
c.8689A>G	15.9338	15.5678	15.1652	−0.3792	0.110	0.3843	0.187	0.1831	0.961
	±0.3556	±0.3602	0.5460	±0.2694		±0.2896		±0.3734	
c.8731G>A	15.4167	15.6533	15.7465	−0.1532	0.465	0.1649	0.544	0.7171	0.839
	±0.4872	±0.3443	±0.3939	±0.2639		±0.2706		±0.3523	

	c.8893G>A	15.6087 ±0.2970	16.1053 ±0.5501	17.3634 2.4247	−0.5463 ±0.5094	0.259	0.8774 ±1.214	0.472	-0.3808 ±1.272	0.765
	c.9937A>T	15.9283 0.3555	15.5548 0.3646	15.3073 0.5314	−0.3266 ±0.2673	0.158	0.3105 ±0.2844	0.277	-0.6304 ±0.3755	0.867
Charolais	c.−11470G>A	7.9545 ±0.3737	8.2222 ±0.3415	8.0011 ±0.4656	0.8134 ±0.2250	0.754	-0.2327 ±0.2354	0.922	0.2444 ±0.2999	0.417
	c. −9627G>A	7.8472 ±0.3801	8.2698 ±0.3414	8.0310 ±0.4497	−0.1570 ±0.2220	0.496	0.9191 ±0.2285	0.688	0.3306 ±0.2915	0.259
	c.276A>G	7.8689 ±0.3731	8.3095 ±0.3304	7.7959 ±0.4862	0.9748 ±0.2347	0.710	0.3651 ±0.2487	0.884	0.4771 ±0.3053	0.120
	c.2692C>T	7.9981 ±0.3859	8.2360 ±0.4127	8.1649 ±0.3746	0.8656 0.1986	0.715	-0.8337 ±0.1992	0.676	0.1544 ±0.3651	0.673
	c.5332G>A	7.9848 ±0.3659	8.1341 ±0.3400	8.3320 ±0.6307	−0.1614 ±0.2495	0.607	0.1736 ±0.3106	0.578	-0.2424 ±0.3606	0.947
	c.7195C>T	7.7786 ±0.3793	8.3592 ±0.3311	7.7234 ±0.4815	0.1337 ±0.2363	0.682	0.2762 ±0.2468	0.911	0.6082 ±0.2971	**0.043***
	c.7324G>A	7.9922 ±0.3732	8.2351 ±0.3367	7.8029 ±0.4964	−0.1053 ±0.2351	0.965	-0.9467 ±0.2502	0.706	0.3376 ±0.3086	0.276
	c.8549A>G	8.1908 ±0.3785	8.0890 ±0.3562	7.8965 ±0.4380	−0.1428 ±0.2108	0.552	0.1471 ±0.2135	0.492	0.4538 ±0.3004	0.880

		c.8560C>T	7.8156 ±0.3502	8.4969 ±0.3511	7.6853 ±0.5340	0.2258 ±0.2366	0.299	0.6514 ±0.2665	0.807	0.7464 ±0.3390	**0.029***
		c.8563C>T	8.1368 ±0.3316	7.9936 ±0.4746	7.8267 ±0.8202	−0.1495 ±0.3025	0.576	0.1550 ±0.3967	0.697	0.1189 ±0.5423	0.983
		c.8689A>G	7.9812 ±0.3467	8.3421 ±0.3656	7.0292 ±0.6698	−0.6830 ±0.2692	0.643	0.4760 ±0.3243	0.144	0.8370 ±0.3838	**0.031***
		c.8731G>A	7.9565 ±0.3358	8.5775 ±0.3571	7.6295 ±0.5968	−0.1614 ±0.2479	0.513	-0.1635 ±0.2924	0.577	0.7845 ±0.3819	**0.042***
		c.8782G>C	8.1029 ±0.3106	8.2899 ±0.5166	--	−0.1870 ±0.4729	0.723	--	--	--	--
		c.8893G>A	8.0602 ±0.3411	8.2909 ±0.3800	7.6721 ±0.5687	0.2661 ±0.2348	0.976	-0.1941 ±0.2751	0.482	0.4248 ±0.3622	0.243
		c.9937A>T	8.0870 ±0.3349	8.5485 ±0.3789	6.9256 ±0.7296	−0.9958 ±0.3005	0.620	0.5807 ±0.3610	0.110	1.042 ±0.4386	**0.019***
UREA	Hybrid	c.−11470G>A	83.2702 ±0.6287	83.1499 ±0.5616	83.4337 ±0.9065	0.4617 ±0.5207	0.903	-0.8178 ±0.5389	0.880	-0.2020 ±0.7353	0.784
		c. −9627G>A	83.2150 ±0.6260	83.1352 ±0.5676	83.4590 ±0.9368	−0.8267 ±0.5276	0.822	0.1220 ±0.5499	0.825	-0.2018 ±0.7419	0.787
		c.276A>G	83.2005 ±0.6227	83.3193 ±0.5670	83.2723 ±0.9097	0.5063 ±0.5193	0.872	-0.3591 ±0.5387	0.947	0.8287 ±0.7356	0.911

c.2692C>T	83.0674	83.5723	83.0168	−0.1549	0.988	0.2531	0.957	0.5302	0.516
	±0.6135	±0.6948	±0.7364	±0.4617		±0.4662		±0.8117	
c.5332G>A	83.1568	83.3211	83.1490	−0.3957	0.837	0.1527	0.989	0.1784	0.818
	±0.6266	±0.5579	±1.0131	±0.5495		±1.148		±0.7705	
c.7195C>T	83.0188	83.3545	83.3436	0.1883	0.661	-0.2802	0.789	0.4929	0.960
	±0.6561	±0.5632	±0.8928	±0.5246		±1.042		±0.9712	
c.7324G>A	83.1540	83.3195	83.1818	−0.4281	0.883	0.4713	0.965	0.1791	0.820
	±0.6292	±0.5687	±0.9232	±0.5242		±1.068		±0.7824	
c.8549A>G	83.2491	83.2274	83.0248	−0.1122	0.799	0.1121	0.838	0.9046	0.902
	±0.7893	±0.5413	±0.7961	±0.5454		±0.5462		±0.7321	
c.8560C>T	82.8758	83.2191	84.0821	0.5264	0.311	-0.6031	0.315	-0.2598	0.745
	±0.6056	±0.5848	±1.0708	±0.5488		±0.5993		±0.7941	
c.8563C>T	83.2047	84.1520	77.6022	−0.8057	0.611	2.801	0.163	3.749	0.170
	±0.4199	±1.8606	±3.9767	±1.382		±2.000		±2.723	
c.8689A>G	83.2907	83.1307	83.7456	0.1105	0.987	-0.2275	0.788	-0.3874	0.698
	±0.5196	±0.6150	±1.6108	±0.6254		±0.8400		±0.9949	
c.8731G>A	82.8093	83.2527	84.6148	−0.7408	0.182	0.9028	0.163	-0.4594	0.580
	±0.5991	±0.5962	±1.1709	±0.5711		±0.6437		±0.8263	
c.8782G>C	83.1829	83.3606	78.3078	0.9275	0.954	-2.438	0.483	2.615	0.470
	±0.4590	±1.2217	±6.9014	±1.237		±3.454		±3.601	

	c.8893G>A	83.5700	82.9846	82.8841	0.4640	0.423	-0.3429	0.667	-0.2425	0.794
		±0.5889	±0.5883	±1.4730	±0.6348		±0.7941		±0.9221	
	c.9937A>T	83.0701	83.4799	83.7943	0.3907	0.564	-0.3621	0.709	0.4772	0.966
		±0.5354	±0.6801	±1.8737	±0.6784		±0.9648		±1.122	
Angus	c.−11470G>A	81.2437	81.1297	80.6327	−0.3374	0.681	0.3055	0.638	0.1915	0.818
		±1.1562	±0.8128	±0.9299	±0.6307		±0.6468		±0.8293	
	c. −9627G>A	81.2571	80.6980	80.5729	0.2997	0.741	-0.3421	0.597	-0.2170	0.795
		±1.1354	±0.7627	±0.8715	±0.6231		±0.6449		±0.8323	
	c.276A>G	81.3867	80.7881	80.5885	−0.3609	0.670	0.3991	0.538	-0.1995	0.811
		±1.1420	±0.7765	±0.8868	±0.6248		±0.6453		±0.8304	
	c.2692C>T	81.9751	81.3928	80.5268	−0.7536	0.259	0.7242	0.247	0.1419	0.874
		±1.1958	±0.9047	±0.8692	±0.5932		±0.6230		±0.8938	
	c.5332G>A	80.7246	81.0692	80.8339	−0.3777	0.881	0.5466	0.937	0.2899	0.732
		±1.1567	±0.7733	±1.0963	±0.6839		±0.6868		±0.8453	
	c.7195C>T	81.1420	81.1649	80.5057	−0.3783	0.663	0.3181	0.636	0.3411	0.688
		±1.1914	±0.8058	±0.9443	±0.6520		±0.6701		±0.8478	
	c.7324G>A	80.7573	81.2260	80.6598	0.1386	0.939	-0.4874	0.940	0.5174	0.538
		±1.1716	±0.8146	±0.9314	±0.6322		±0.6493		±0.8359	
	c.8549A>G	80.6742	80.9162	81.7531	0.4815	0.555	-0.5394	0.418	-0.2974	0.726
		±0.9201	±0.8248	±1.1940	±0.6423		±0.6632		±0.8460	

	c.8560C>T	81.3265	80.9359	80.8280	−0.2217	0.861	0.2492	0.704	-0.1414	0.869
		±1.1837	±0.8312	±0.9127	±0.6326		±0.6530		±0.8541	
	c.8563C>T	81.0053	80.3764	82.5766	−0.2010	0.932	-0.7857	0.701	-1.415	0.598
		±0.7181	±1.8094	±4.1086	±1.355		±2.040		±2.672	
	c.8689A>G	81.2903	80.6455	81.0577	−0.2680	0.544	0.1163	0.868	-0.5285	0.556
		±0.8556	±0.8667	±1.3113	±0.6473		±0.6947		±0.8950	
	c.8731G>A	81.4883	81.1488	80.2561	0.6613	0.369	-0.6161	0.345	0.2766	0.745
		±1.1571	±0.8093	±0.9302	±0.6333		±0.6492		±0.8470	
	c.8893G>A	80.7615	82.0925	87.8994	−1.625	0.166	3.569	0.219	-2.238	0.462
		±0.7066	±1.3100	±5.7762	±1.216		±2.893		±3.031	
	c.9937A>T	81.1955	80.2035	82.1816	0.9816	0.968	-0.4930	0.468	-1.485	0.100
		±0.8346	±0.8566	±1.2569	±0.6420		±0.6766		±0.8958	
Charolais	c.−11470G>A	84.0915	83.5387	83.0004	−0.5475	0.481	0.5456	0.448	-0.7220	0.995
		±0.9643	±0.8569	±1.3042	±0.6808		±0.7158		±0.9395	
	c. −9627G>A	84.4074	83.3560	83.1609	0.6973	0.326	-0.6233	0.368	-0.4281	0.640
		±0.9776	±0.8474	±1.2309	±0.6681		±0.6894		±0.9127	
	c.276A>G	84.4262	83.3765	82.8100	−0.8719	0.254	0.8081	0.289	-0.2416	0.802
		±0.9959	±0.8515	±1.3906	±0.7127		±0.7594		±0.9582	
	c.2692C>T	84.1060	82.7949	84.3763	0.1024	0.746	-0.1352	0.818	-1.446	0.186
		±1.0657	±1.1535	±1.0358	0.5826		±0.5849		±1.087	

c.5332G>A	84.0960	83.3921	83.0203	0.6239	0.549	-0.5379	0.572	-0.1660	0.882
	±0.9279	±0.8412	±1.8389	±0.7604		±0.9486		±1.120	
c.7195C>T	84.3693	83.3942	83.0554	−0.7387	0.442	0.6569	0.390	-0.3182	0.737
	±1.0023	±0.8309	±1.3722	±0.7187		±0.7609		±0.9405	
c.7324G>A	84.0590	83.6125	82.6553	0.6316	0.424	-0.7019	0.359	0.2553	0.793
	±0.9614	±0.8402	±1.4084	±0.7089		±0.7613		±0.9714	
c.8549A>G	82.6921	83.2097	86.4253	1.723	**0.011***	-1.867	**0.004***	-1.349	0.139
	±0.9847	±0.9032	±1.1781	±0.6290		±0.6343		±0.9067	
c.8560C>T	84.5800	82.9156	82.7840	−1.175	**0.074†**	0.8980	0.267	-0.7664	0.472
	±0.8809	±0.8973	±1.5301	±0.7055		±0.8055		±1.062	
c.8563C>T	84.1307	81.6361	80.9181	−2.026	**0.042***	1.606	0.182	-0.8883	0.590
	±0.7485	±1.2717	±2.3899	±0.9214		±1.198		±1.641	
c.8689A>G	0.0302	0.0345	0.0332	0.6018	0.279	-0.3727	0.713	0.4586	0.704
	±0.0023	±0.0025	±0.0061	±0.8099		±1.011		±1.205	
c.8731G>A	84.1577	83.3025	82.6384	0.7986	0.281	-0.7597	0.397	-0.9554	0.937
	±0.8775	±0.9738	±1.7622	±0.7457		±0.8929		±1.195	
c.8782G>C	83.4912	84.2662	--	−0.7749	0.546	--	--	--	--
	±0.7925	±1.5030		±1.462					
c.8893G>A	83.0687	84.0728	85.2680	−1.063	0.191	1.100	0.194	-0.9560	0.932
	±0.8575	±0.9857	±1.6458	±0.7129		±0.8427		±1.123	

		c.9937A>T	83.6347	83.4268	84.7254	0.1881	0.637	0.5807	0.629	1.042	0.586
			±0.8884	±1.0240	±2.2151	±0.9005		±0.3610		±0.4386	
AUBF	Hybrid	c.−11470G>A	0.0339	0.0336	0.0333	−0.3263	0.800	0.3231	0.776	-0.1764	0.991
			±0.0014	±0.0013	±0.0019	±0.1091		±0.1131		±0.1514	
		c. −9627G>A	0.0343	0.0332	0.0335	0.5545	0.682	-0.4034	0.727	-0.6790	0.659
			±0.0014	±0.0013	±0.0020	±0.1105		±0.1153		±0.1530	
		c.276A>G	0.0343	0.0333	0.0330	−0.7087	0.576	0.6382	0.574	-0.3446	0.821
			±0.0014	±0.0013	±0.0019	±0.1089		±0.1131		±0.1517	
		c.2692C>T	0.0347	0.0341	0.0322	−0.1224	0.194	0.1271	0.186	0.6528	0.691
			±0.0014	±0.0015	±0.0016	±0.9496		±0.9566		±0.1634	
		c.5332G>A	0.0338	0.0338	0.0326	0.4305	0.841	-0.1097	0.649	0.1630	0.992
			±0.0014	±0.0012	±0.0021	±0.1151		±0.2401		±0.1594	
		c.7195C>T	0.0339	0.0337	0.0330	−0.4331	0.772	0.9185	0.674	0.6850	0.734
			±0.0014	±0.0012	±0.0019	±0.1097		±0.2173		±0.2008	
		c.7324G>A	0.0340	0.0339	0.0320	0.8193	0.510	-0.1888	0.399	-0.1030	0.949
			±0.0014	±0.0012	±0.0020	±0.1096		±0.2229		±0.1615	
		c.8549A>G	0.0339	0.0332	0.0342	0.1830	0.940	-0.1679	0.884	-0.8710	0.562
			±0.0017	±0.0013	±0.0018	±0.1145		±0.1147		±0.1494	
		c.8560C>T	0.0336	0.0337	0.0340	0.1986	0.787	-0.2196	0.860	-0.7400	0.964
			±0.0014	±0.0013	±0.0023	±0.1140		±0.1242		±0.1623	

	c.8563C>T	0.0339	0.0313	0.0240	−0.3681	0.239	0.4951	0.226	0.2382	0.670
		±0.0010	±0.0038	±0.0081	±0.2800		±0.4075		±0.5555	
	c.8689A>G	0.0338	0.0331	0.0355	−0.5955	0.960	-0.8385	0.632	-0.1620	0.432
		±0.0012	±0.0014	±0.0034	±0.1311		±0.1743		±0.2052	
	c.8731G>A	0.0333	0.0337	0.0348	−0.6191	0.552	0.7503	0.576	-0.3754	0.826
		±0.0014	±0.0013	±0.0025	±0.1190		±0.1335		±0.1695	
	c.8782G>C	0.0333	0.0363	0.0370	−0.2880	0.237	0.1874	0.787	0.1124	0.876
		±0.0011	±0.0025	±0.0138	±0.2473		±0.6898		±0.7193	
	c.8893G>A	0.0334	0.0343	0.0306	0.1487	0.835	-0.1359	0.411	0.2332	0.221
		±0.0013	±0.0013	±0.0031	±0.1320		±0.1644		±0.1900	
	c.9937A>T	0.0329	0.0331	0.0384	0.1264	0.371	-0.2752	0.168	-0.2471	0.286
		±0.0012	±0.0015	±0.0039	±0.1408		±0.1988		±0.2309	
Angus	c.−11470G>A	0.0702	0.0670	0.0689	−0.2290	0.955	0.6313	0.825	-0.2517	0.502
		±0.0048	±0.0032	±0.0037	±0.2786		±0.2850		±0.3731	
	c. −9627G>A	0.0700	0.0674	0.0692	0.1229	0.973	-0.4354	0.883	-0.2190	0.567
		±0.0051	±0.0034	±0.0039	±0.2837		±0.2931		±0.3803	
	c.276A>G	0.0693	0.0676	0.0692	0.2472	0.899	0.6284	0.983	-0.1662	0.661
		±0.0050	±0.0033	±0.0038	±0.2818		±0.2906		±0.3772	
	c.2692C>T	0.0707	0.0663	0.0688	−0.2301	0.944	0.9390	0.733	-0.3429	0.392
		±0.0049	±0.0035	±0.0034	±0.2616		±0.2739		±0.3984	

c.5332G>A	0.0726 ±0.0048	0.0670 ±0.0029	0.0680 ±0.0046	0.2170 ±0.3066	0.494	-0.2315 ±0.3072	0.453	-0.3349 ±0.3795	0.380
c.7195C>T	0.0697 ±0.0050	0.0665 ±0.0031	0.0701 ±0.0038	0.7571 ±0.2891	0.772	-0.1677 ±0.2962	0.955	-0.3404 ±0.3821	0.375
c.7324G>A	0.0692 ±0.0049	0.0673 ±0.0032	0.0689 ±0.0038	−0.1708 ±0.2799	0.928	-0.1250 ±0.2871	0.965	-0.1786 ±0.3769	0.637
c.8549A>G	0.0701 ±0.0037	0.0675 ±0.0032	0.0689 ±0.0049	−0.9638 ±0.2776	0.703	0.5803 ±0.2869	0.840	-0.1999 ±0.3760	0.596
c.8560C>T	0.0694 ±0.0050	0.0676 ±0.0033	0.0680 ±0.0037	−0.4932 ±0.2796	0.888	0.6866 ±0.2885	0.812	-0.1080 ±0.3850	0.780
c.8563C>T	0.0672 ±0.0025	0.0749 ±0.0078	0.0875 ±0.0183	0.8734 ±0.6048	0.153	-0.1014 ±0.9140	0.269	-0.2467 ±0.1190	0.836
c.8689A>G	0.0688 ±0.0033	0.0668 ±0.0034	0.0704 ±0.0055	0.3326 ±0.2823	0.975	-0.8059 ±0.3046	0.792	-0.2721 ±0.4036	0.502
c.8731G>A	0.0693 ±0.0048	0.0672 ±0.0031	0.0679 ±0.0037	0.5174 ±0.2785	0.877	-0.7387 ±0.2850	0.796	-0.1430 ±0.3788	0.707
c.8893G>A	0.0684 ±0.0027	0.0652 ±0.0056	0.1045 ±0.0258	0.2400 ±0.5319	0.974	0.1804 ±0.1294	0.165	-0.2123 ±0.1370	0.123
c.9937A>T	0.0690 ±0.0033	0.0672 ±0.0034	0.0688 ±0.0053	−0.5170 ±0.2780	0.821	0.6810 ±0.2965	0.982	-0.1752 ±0.4045	0.666

Charolais	c.−11470G>A	0.0321	0.0318	0.0326	0.1297	0.939	-0.2596	0.908	-0.5524	0.853
		±0.0028	±0.0024	±0.0039	±0.2118		±0.2229		±0.2980	
	c. −9627G>A	0.0309	0.0321	0.0338	−0.1393	0.501	0.1437	0.507	-0.2579	0.929
		±0.0029	±0.0024	±0.0037	±0.2091		±0.2156		±0.2906	
	c.276A>G	0.0310	0.0327	0.0311	0.4720	0.817	-0.5579	0.981	0.1619	0.586
		±0.0027	±0.0023	±0.0040	±0.2159		±0.2295		±0.2964	
	c.2692C>T	0.0338	0.0324	0.0321	-0.8983	0.615	0.8890	0.610	-0.5628	0.868
		±0.0027	±0.0031	±0.0027	0.1733		±0.1739		±0.3387	
	c.5332G>A	0.0316	0.0321	0.0336	−0.7518	0.728	0.9880	0.740	-0.4841	0.891
		±0.0026	±0.0024	±0.0056	±0.2374		±0.2963		±0.3534	
	c.7195C>T	0.0306	0.0342	0.0268	−0.4412	0.875	0.1891	0.423	0.5545	**0.064†**
		±0.0028	±0.0022	±0.0041	±0.2247		±0.2350		±0.2963	
	c.7324G>A	0.0325	0.0323	0.0299	0.1020	0.653	-0.1330	0.575	0.1078	0.728
		±0.0027	±0.0023	±0.0043	±0.2196		±0.2368		±0.3089	
	c.8549A>G	0.0305	0.0328	0.0328	0.1286	0.548	-0.1143	0.577	0.1195	0.689
		±0.0028	±0.0025	±0.0034	±0.2066		±0.2039		±0.2976	
	c.8560C>T	0.0310	0.0338	0.0287	0.2689	0.915	0.1138	0.651	0.3923	0.247
		±0.0025	±0.0026	±0.0047	±0.2209		±0.2509		±0.3378	
	c.8563C>T	0.0328	0.0294	0.0271	−0.3066	0.308	0.2834	0.460	-0.5041	0.924
		±0.0022	±0.0039	±0.0076	±0.2944		±0.3824		±0.5240	

		c.8689A>G	0.0302 ±0.0023	0.0345 ±0.0025	0.0332 ±0.0061	0.2967 ±0.2480	0.216	-0.1534 ±0.3148	0.627	0.2792 ±0.3772	0.461
		c.8731G>A	0.0318 ±0.0022	0.0355 ±0.0026	0.0292 ±0.0051	−0.6869 ±0.2225	0.760	-0.1312 ±0.2663	0.623	0.5044 ±0.3665	0.171
		c.8782G>C	0.0316 ±0.0017	0.0408 ±0.0043	--	−0.9177 ±0.4491	**0.041***	--	--	--	--
		c.8893G>A	0.0334 ±0.0023	0.0303 ±0.0027	0.0305 ±0.0050	0.2116 ±0.2219	0.328	-0.1481 ±0.2630	0.575	-0.1590 ±0.3540	0.654
		c.9937A>T	0.0293 ±0.0023	0.0367 ±0.0026	0.0329 ±0.0067	0.4549 ±0.2724	**0.097†**	-0.1776 ±0.3471	0.610	0.5565 ±0.4299	0.198
AURE-A	Hybrid	c.−11470G>A	0.1666 ±0.0038	0.1613 ±0.0033	0.1622 ±0.0056	−0.2742 ±0.3258	0.373	0.2178 ±0.3373	0.521	-0.3067 ±0.4684	0.515
		c. −9627G>A	0.1670 ±0.0037	0.1602 ±0.0034	0.1634 ±0.0058	0.2821 ±0.3304	0.331	-0.1806 ±0.3442	0.602	-0.4958 ±0.4732	0.296
		c.276A>G	0.1670 ±0.0037	0.1609 ±0.0034	0.1623 ±0.0056	−0.3052 ±0.3255	0.289	0.2343 ±0.3374	0.490	-0.3788 ±0.4694	0.422
		c.2692C>T	0.1660 ±0.0037	0.1628 ±0.0043	0.1595 ±0.0046	−0.3240 ±0.2936	0.282	0.3242 ±0.2958	0.274	0.3346 ±0.5199	0.995
		c.5332G>A	0.1664 ±0.0037	0.1615 ±0.0033	0.1613 ±0.0062	0.3180 ±0.3424	0.250	-0.3437 ±0.7171	0.633	-0.3989 ±0.4877	0.416

c.7195C>T	0.1650	0.1618	0.1644	−0.7835	0.704	0.2186	0.738	-0.1173	0.849
	±0.0039	±0.0033	±0.0055	±0.3281		±0.6515		±0.6159	
c.7324G>A	0.1664	0.1613	0.1618	0.2842	0.330	-0.3087	0.645	-0.4197	0.400
	±0.0037	±0.0034	±0.0057	±0.3269		±0.6668		±0.4961	
c.8549A>G	0.1632	0.1635	0.1629	−0.1504	0.937	0.1519	0.965	0.5056	0.914
	±0.0049	±0.0033	±0.0049	±0.3430		±0.3435		±0.4670	
c.8560C>T	0.1611	0.1654	0.1647	0.2518	0.566	-0.1797	0.638	0.2492	0.625
	±0.0037	±0.0035	±0.0067	±0.3467		±0.3802		±0.5081	
c.8563C>T	0.1633	0.1809	0.1186	−0.1100	0.768	0.2233	0.082	0.3998	0.022
	±0.0024	±0.0118	±0.0253	±0.8872		±0.1274		±0.1733	
c.8689A>G	0.1625	0.1651	0.1623	0.1369	0.732	0.1222	0.982	0.2638	0.679
	±0.0031	±0.0037	±0.0102	±0.3934		±0.5341		±0.6349	
c.8731G>A	0.1621	0.1640	0.1692	−0.3010	0.472	0.3588	0.382	-0.1657	0.755
	±0.0036	±0.0036	±0.0074	±0.3598		±0.4083		±0.5285	
c.8782G>C	0.1660	0.1487	0.1088	0.1849	**0.018***	-0.2863	0.195	0.1133	0.623
	±0.0026	±0.0077	±0.0439	±0.7875		±0.2199		±0.2292	
c.8893G>A	0.1663	0.1605	0.1647	0.3355	0.490	-0.8178	0.871	-0.4990	0.398
	±0.0035	±0.0035	±0.0092	±0.4012		±0.5029		±0.5875	
c.9937A>T	0.1614	0.1678	0.1645	0.4517	0.299	-0.1557	0.801	0.4866	0.499
	±0.0034	±0.0043	±0.0119	±0.4318		±0.6157		±0.7160	

Angus	c.−11470G>A	0.2035 ±0.0139	0.2098 ±0.0088	0.1911 ±0.0106	−0.8197 ±0.8363	0.295	0.6216 ±0.8543	0.469	0.1252 ±0.1149	0.277
	c. −9627G>A	0.2068 ±0.0140	0.2079 ±0.0085	0.1878 ±0.0102	0.1141 ±0.8301	0.143	-0.9541 ±0.8549	0.266	0.1063 ±0.1156	0.360
	c.276A>G	0.2105 ±0.0139	0.2087 ±0.0085	0.1874 ±0.0103	−0.1322 ±0.8303	**0.092†**	0.1158 ±0.8534	0.177	0.9773 ±0.1156	0.400
	c.2692C>T	0.2103 ±0.0144	0.2134 ±0.0100	0.1907 ±0.0094	−0.1245 ±0.7933	0.100	0.9795 ±0.8323	0.241	0.1289 ±0.1228	0.296
	c.5332G>A	0.1963 ±0.0139	0.2067 ±0.0079	0.1986 ±0.0134	−0.6825 ±0.9271	0.984	0.1152 ±0.9297	0.901	0.9246 ±0.1154	0.425
	c.7195C>T	0.2056 ±0.0141	0.2102 ±0.0083	0.1903 ±0.0106	−0.9711 ±0.8521	0.227	0.7681 ±0.8732	0.381	0.1228 ±0.1158	0.291
	c.7324G>A	0.2031 ±0.0136	0.2116 ±0.0085	0.1907 ±0.0103	0.8434 ±0.8229	0.275	-0.6211 ±0.8395	0.461	0.1467 ±0.1140	0.200
	c.8549A>G	0.1914 ±0.0099	0.2066 ±0.0086	0.2127 ±0.0137	0.1147 ±0.8035	0.133	-0.1064 ±0.8319	0.203	0.4551 ±0.1148	0.693
	c.8560C>T	0.2101 ±0.0138	0.2099 ±0.0087	0.1891 ±0.0100	−0.1221 ±0.8151	0.113	0.1048 ±0.8385	0.213	0.1030 ±0.1163	0.378
	c.8563C>T	0.2013 ±0.0067	0.2324 ±0.0231	0.2485 ±0.0552	0.2782 ±0.1827	0.124	-0.2363 ±0.2764	0.395	0.7485 ±0.3583	0.835

	c.8689A>G	0.1951	0.2083	0.2090	0.8807	0.243	-0.6970	0.447	0.6212	0.620
		±0.0093	±0.0095	±0.0161	±0.8368		±0.9135		±0.1248	
	c.8731G>A	0.2119	0.2094	0.1876	0.1355	**0.090†**	-0.1217	0.153	0.9652	0.406
		±0.0136	±0.0085	±0.0105	±0.8307		±0.8476		±0.1156	
	c.8893G>A	0.2026	0.2000	0.2744	−0.2865	0.886	0.3586	0.373	-0.3852	0.371
		±0.0071	±0.0167	±0.0799	±0.1602		±0.4002		±0.4280	
	c.9937A>T	0.1949	0.2030	0.2205	0.1150	0.132	-0.1277	0.150	-0.4683	0.707
		±0.0093	±0.0096	±0.0154	±0.8219		±0.8820		±0.1242	
Charolais	c.−11470G>A	0.2147	0.2154	0.2329	0.7217	0.317	-0.9085	0.293	-0.8394	0.479
		±0.0095	±0.0082	±0.0147	±0.8180		±0.8602		±0.1180	
	c. −9627G>A	0.2177	0.2122	0.2348	−0.6247	0.407	0.8542	0.304	-0.1403	0.224
		±0.0098	±0.0082	±0.0137	±0.8073		±0.8278		±0.1150	
	c.276A>G	0.2178	0.2136	0.2304	0.3691	0.616	-0.6313	0.489	-0.1046	0.385
		±0.0099	±0.0080	±0.0156	±0.8571		±0.9089		±0.1200	
	c.2692C>T	0.2128	0.2224	0.2194	0.3297	0.573	-0.3257	0.639	0.6290	0.648
		±0.0101	±0.0118	±0.0101	0.6911		±0.6928		±0.1375	
	c.5332G>A	0.2151	0.2193	0.2217	−0.3734	0.508	0.3277	0.777	0.9258	0.947
		±0.0090	±0.0080	±0.0215	±0.9231		±0.1152		±0.1390	
	c.7195C>T	0.2149	0.2158	0.2326	0.6859	0.287	-0.8815	0.341	-0.7932	0.505
		±0.0102	±0.0078	±0.0156	±0.8734		±0.9222		±0.1184	

		c.7324G>A	0.2141 ±0.0096	0.2177 ±0.0080	0.2291 ±0.0162	−0.6402 ±0.8493	0.397	0.7518 ±0.9193	0.415	-0.3950 ±0.1227	0.748
		c.8549A>G	0.2212 ±0.0097	0.2094 ±0.0084	0.2381 ±0.0122	0.6105 ±0.7579	0.551	-0.8452 ±0.7644	0.271	-0.2022 ±0.1132	0.076
		c.8560C>T	0.2231 ±0.0085	0.2102 ±0.0091	0.2309 ±0.0177	−0.1916 ±0.8468	0.694	-0.3897 ±0.9629	0.687	-0.1685 ±0.1336	0.209
		c.8563C>T	0.2236 ±0.0067	0.2024 ±0.0145	0.1720 ±0.0289	−0.2372 ±0.1146	**0.064†**	0.2582 ±0.1482	**0.084†**	0.4570 ±0.2031	0.822
		c.8689A>G	0.2206 ±0.0080	0.2110 ±0.0090	0.2437 ±0.0235	0.4618 ±0.9640	0.600	-0.1150 ±0.1234	0.354	-0.2117 ±0.1484	0.156
		c.8731G>A	0.2206 ±0.0078	0.2183 ±0.0099	0.2223 ±0.0203	0.4310 ±0.8813	0.936	0.8307 ±0.1062	0.938	-0.3182 ±0.1483	0.831
		c.8782G>C	0.2159 ±0.0064	0.2386 ±0.0169	--	−0.2264 ±0.1779	0.178	--	--	--	--
		c.8893G>A	0.2229 ±0.0077	0.2014 ±0.0095	0.2462 ±0.0186	0.1611 ±0.8611	0.610	0.1165 ±0.1011	0.251	-0.3319 ±0.1374	**0.017***
		c.9937A>T	0.2179 ±0.0087	0.2033 ±0.0102	0.2480 ±0.0260	0.1145 ±0.1065	0.746	-0.1507 ±0.1356	0.268	-0.2961 ±0.1680	**0.080†**
SWT	Hybrid	c.−11470G>A	541.3812 ±5.6736	544.7476 ±5.2502	542.8802 ±7.0727	1.281 ±3.545	0.628	-0.7495 ±3.675	0.839	2.617 ±4.703	0.580

c. −9627G>A	541.6309	543.5592	546.2164	−2.214	0.396	2.293	0.542	-0.3645	0.939
	±5.7320	±5.3318	±7.2845	±3.585		±3.736		±4.757	
c.276A>G	541.6861	544.3157	543.9492	1.441	0.523	-1.132	0.761	1.498	0.752
	±5.6628	±5.2660	±7.1310	±3.561		±3.696		±4.726	
c.2692C>T	542.4351	542.9862	546.8593	2.087	0.507	-2.212	0.477	-1.661	0.745
	±5.4064	±5.7331	±5.8369	±3.064		±3.090		±5.089	
c.5332G>A	541.0728	545.1137	542.8979	−1.809	0.372	1.494	0.849	3.895	0.443
	±5.6593	±5.2188	±7.6662	±3.749		±7.795		±5.045	
c.7195C>T	540.3669	544.9053	544.3406	2.424	0.366	-3.904	0.582	0.5999	0.925
	±5.4072	±5.2182	±6.9821	±3.586		±7.048		±6.332	
c.7324G>A	540.9990	545.0869	543.3305	−1.807	0.473	2.009	0.784	3.934	0.443
	±5.6698	±5.2610	±7.1905	±3.585		±7.286		±5.096	
c.8549A>G	543.7455	541.1709	547.2040	1.815	0.765	-1.729	0.637	-4.304	0.347
	±6.5915	±5.3435	±6.6181	±3.644		±3.647		±4.552	
c.8560C>T	543.3978	541.6971	546.6948	0.6382	0.700	-1.648	0.671	-3.349	0.496
	±5.6702	±5.4986	±7.8320	±3.564		±3.861		±4.892	
c.8563C>T	543.1119	544.7482	533.5742	−1.353	0.861	4.769	0.697	6.405	0.702
	±4.9189	±12.0233	±24.6335	±8.318		±12.18		±16.66	
c.8689A>G	544.2451	539.9381	559.3931	0.9941	0.850	-7.574	0.172	-11.88	**0.065†**
	±5.2172	±5.5950	±11.1423	±4.246		±5.521		±6.386	

	c.8731G>A	541.1778	942.9344	549.1545	−3.200	0.290	3.988	0.345	-2.232	0.669
		±5.6923	±5.5614	±8.4671	±3.763		±4.194		±5.200	
	c.8782G>C	542.6741	545.0543	538.4247	−1.908	0.779	-2.125	0.919	4.505	0.837
		±5.0325	±8.7151	±41.8209	±7.596		±20.80		±21.74	
	c.8893G>A	544.7478	541.1745	547.1319	1.235	0.618	1.192	0.818	-4.765	0.421
		±5.3049	±5.3306	±10.2550	±4.184		±5.154		±5.890	
	c.9937A>T	542.6400	539.3215	568.3877	3.311	0.503	-12.87	**0.046***	-16.19	**0.030***
		5.1540	±5.9017	±12.8688	±4.684		±6.397		±7.380	
Angus	c.−11470G>A	567.7484	565.6077	562.8438	−2.505	0.686	2.452	0.423	0.3116	0.936
		±5.5513	±3.9773	±4.5153	±2.972		±3.048		±3.890	
	c. −9627G>A	568.2886	564.7962	562.4879	2.784	0.709	-2.900	0.353	-0.5920	0.882
		±5.6609	±3.9551	±4.4517	±3.005		±3.111		±3.975	
	c.276A>G	568.6901	564.8441	562.4657	−2.973	0.666	3.112	0.314	-0.7338	0.852
		±5.6230	±3.9600	±4.4606	±2.983		±3.082		±3.931	
	c.2692C>T	571.3293	565.6226	563.1078	−3.777	0.381	4.111	0.164	-1.596	0.705
		±5.6935	±4.3412	±4.1784	±2.798		±2.937		±4.207	
	c.5332G>A	564.7658	564.9492	565.9002	−0.5851	0.593	0.5672	0.862	-0.3838	0.924
		±5.5262	±3.7421	±5.2394	±3.229		±3.244		±3.992	
	c.7195C>T	569.1173	566.1719	561.2736	−4.100	0.430	3.922	0.217	0.9765	0.807
		±5.7440	±3.9845	±4.6156	±3.078		±3.163		±3.981	

	c.7324G>A	567.7310	565.6823	562.8698	2.499	0.767	-2.431	0.431	0.3819	0.923
		±5.6367	±3.9837	±4.5240	±2.989		±3.072		±3.940	
	c.8549A>G	564.0949	565.3439	568.0575	1.845	0.974	-1.981	0.530	-0.7323	0.854
		±4.4749	±4.0296	±5.7384	±3.043		±3.141		±3.980	
	c.8560C>T	568.5925	565.3181	562.9186	−2.758	0.788	2.837	0.360	-0.4375	0.913
		±5.6983	±4.0814	±4.4536	±2.985		±3.082		±4.008	
	c.8563C>T	564.2672	576.9844	580.2459	10.67	0.158	-7.989	0.402	4.728	0.705
		±3.4188	±8.4628	±19.1495	±6.311		±9.501		±12.45	
	c.8689A>G	565.0828	562.9558	571.4201	1.695	0.880	-3.169	0.334	-5.296	0.208
		±4.1160	±4.1661	±6.2218	±3.055		±3.265		±4.191	
	c.8731G>A	568.7768	565.3009	562.0801	3.329	0.561	-3.348	0.275	-0.1275	0.974
		±5.5744	±3.9855	±4.5366	±2.984		±3.059		±3.976	
	c.8893G>A	564.6503	567.9686	565.9019	−2.976	0.468	0.6258	0.964	2.692	0.850
		±3.5978	±6.3502	±27.2740	±5.800		±13.66		±14.24	
	c.9937A>T	565.2773	561.5441	573.0661	1.957	0.962	-3.894	0.221	-7.628	**0.069†**
		±4.0684	±4.1665	±5.9852	±3.005		±3.165		±4.155	
Charolais	c.−11470G>A	463.2818	563.9112	574.0659	4.294	0.252	-5.392	0.157	-4.763	0.337
		±5.2969	±4.7387	±7.0188	±3.611		±3.788		±4.936	
	c. −9627G>A	564.3256	564.4290	570.0759	−2.369	0.521	2.875	0.436	-2.772	0.567
		±5.3855	±4.7051	±6.6813	±3.560		±3.672		±4.822	

c.276A>G	564.4949	564.8604	569.3366	1.855	0.645	-2.421	0.547	-2.055	0.684
	±5.3309	±4.5780	±7.3786	±3.755		±4.002		±5.033	
c.2692C>T	563.8293	569.2353	564.9045	0.6115	0.873	-0.5376	0.864	4.868	0.403
	±5.6753	±6.1446	±5.5161	3.116		±3.119		±5.798	
c.5332G>A	565.1521	564.7695	571.1049	−1.279	0.819	2.976	0.556	-3.359	0.573
	±5.0916	±4.6367	±9.8355	±4.041		±5.038		±5.932	
c.7195C>T	563.4686	564.6476	572.0817	3.484	0.422	-4.307	0.288	-3.128	0.530
	±5.5100	±4.6286	±7.4057	±3.821		±4.041		±4.963	
c.7324G>A	563.5131	564.6513	573.0680	−3.742	0.341	4.777	0.239	-3.639	0.478
	±5.3353	±4.7049	±7.6033	±3.771		±4.044		±5.111	
c.8549A>G	567.6560	560.1946	573.1496	1.684	0.594	-2.747	0.427	-10.21	**0.040***
	±5.2598	±4.8068	±6.3194	±3.437		±3.442		±4.931	
c.8560C>T	563.4213	565.9981	570.3051	3.128	0.388	-3.442	0.429	-0.8651	0.879
	±4.9655	±5.0295	±8.3258	±3.796		±4.335		±5.660	
c.8563C>T	568.3945	552.1118	557.7265	−10.44	**0.032***	5.334	0.404	-10.95	0.212
	±4.1739	±6.8735	±12.7618	±4.910		±6.367		±8.721	
c.8689A>G	564.5498	565.6197	572.8459	2.614	0.647	-4.148	0.441	-3.078	0.631
	±4.7943	±5.1440	±10.6553	±4.322		±5.361		±6.379	
c.8731G>A	561.7816	570.7942	561.1236	−3.474	0.384	-0.3290	0.945	9.342	0.146
	±4.5222	±5.0731	±9.3284	±3.993		±4.753		±6.393	

		c.8782G>C	566.7858 ±4.0143	554.8251 ±7.8412	--	1196 ±7.710	0.115	--	--	--	--
		c.8893G>A	566.2563 ±4.6712	565.1224 ±5.3478	561.2374 ±8.8180	1.955 ±3.798	0.657	-2.509 ±4.490	0.578	1.376 ±5.972	0.819
		c.9937A>T	566.2722 ±5.0537	565.2670 ±5.7960	566.3245 ±12.1372	−0.4710 ±4.934	0.861	-0.2615 ±6.130	0.997	-1.031 ±7.490	0.891
CWT	Hybrid	c.−11470G>A	311.9131 ±3.3791	315.0596 ±3.1271	313.1637 ±4.2117	1.136 ±2.112	0.514	-0.6253 ±2.188	0.776	2.521 ±2.800	0.371
		c. −9627G>A	311.9525 ±3.3774	314.2270 ±3.1389	314.7640 ±4.3067	−1.595 ±2.129	0.336	1.406 ±2.219	0.529	0.8687 ±2.828	0.760
		c.276A>G	311.9781 ±3.3582	314.7819 ±3.1219	314.0761 ±4.2338	1.410 ±2.118	0.378	-1.049 ±2.198	0.635	1.755 ±2.812	0.535
		c.2692C>T	312.5128 ±3.2711	314.5482 ±3.4636	315.8545 ±3.5243	1.698 ±1.836	0.365	-1.671 ±1.852	0.370	0.3645 ±3.045	0.905
		c.5332G>A	311.8720 ±3.3658	315.1001 ±3.1036	313.1966 ±4.5605	−1.397 ±2.232	0.311	0.7143 ±4.639	0.878	2.921 ±3.002	0.334
		c.7195C>T	311.3987 ±3.4584	315.0302 ±3.1081	313.9753 ±4.1569	1.688 ±2.135	0.314	-2.938 ±4.194	0.486	0.7246 ±3.767	0.848
		c.7324G>A	311.5878 ±3.3735	315.1929 ±3.1303	313.7333 ±4.2779	−1.627 ±2.134	0.337	1.556 ±4.335	0.721	3.282 ±3.032	0.280

	c.8549A>G	315.1478 ±3.8831	312.1476 ±3.0956	315.9805 ±3.8980	0.4835 ±2.215	0.964	-0.4163 ±2.214	0.851	-3.417 ±2.779	0.220
	c.8560C>T	313.6872 ±3.2935	312.4842 ±3.1875	317.7560 ±4.6639	1.057 ±2.170	0.504	-2.034 ±2.350	0.389	-3.237 ±2.990	0.280
	c.8563C>T	313.6579 ±2.8179	317.1070 ±7.2911	305.0451 ±15.0652	−0.1641 ±5.107	0.797	4.306 ±7.472	0.566	7.755 ±10.21	0.450
	c.8689A>G	314.0583 ±3.0836	312.3416 ±3.3122	319.0852 ±6.6404	0.1689 ±2.528	0.979	-2.513 ±3.297	0.448	-4.230 ±3.816	0.269
	c.8731G>A	312.9081 ±3.2947	312.8460 ±3.2171	318.7685 ±5.0471	−1.872 ±2.288	0.318	2.930 ±2.549	0.251	-2.992 ±3.170	0.348
	c.8782G>C	313.4739 ±2.8973	313.9127 ±5.2327	318.0538 ±25.7645	−0.6470 ±4.6630	0.864	2.290 ±12.83	0.859	-1.851 ±13.40	0.891
	c.8893G>A	314.9170 ±3.1381	311.5901 ±3.1533	318.2341 ±6.0883	0.8841 ±2.491	0.586	1.659 ±3.064	0.590	-4.985 ±3.502	0.156
	c.9937A>T	312.7086 ±3.0120	311.9101 ±3.4675	320.6061 ±7.6698	1.134 ±2.785	0.707	-3.949 ±3.825	0.303	-4.747 ±4.415	0.283
Angus	c.−11470G>A	330.7059 ±3.5161	330.1951 ±2.4495	326.9934 ±2.7984	−2.073 ±1.954	0.544	1.856 ±2.002	0.356	1.345 ±2.602	0.606
	c. −9627G>A	330.4849 ±3.5988	329.7098 ±2.4511	326.9456 ±2.7703	1.965 ±1.970	0.680	-1.770 ±2.037	0.387	0.9945 ±2.645	0.708

c.276A>G	330.9657 ±3.6038	329.6729 ±2.4900	326.9078 ±2.8105	−2.168 ±1.961	0.612	2.029 ±2.024	0.318	0.7361 ±2.620	0.779
c.2692C>T	332.2434 ±3.6136	331.1140 ±2.6946	326.9363 ±2.5520	−2.977 ±1.847	0.261	2.654 ±1.937	0.173	1.524 ±2.813	0.589
c.5332G>A	330.1536 ±3.5292	329.5636 ±2.3069	327.0722 ±3.3468	1.592 ±2.136	0.711	-1.541 ±2.146	0.475	0.9507 ±2.647	0.720
c.7195C>T	330.4367 ±3.6363	330.6035 ±2.4302	326.3487 ±2.8512	−2.438 ±2.0228	0.521	2.044 ±2.079	0.328	2.211 ±2.662	0.408
c.7324G>A	329.7587 ±3.5614	330.4853 ±2.4465	327.0375 ±2.7977	1.713 ±1.967	0.751	-1.361 ±2.016	0.501	2.087 ±2.630	0.430
c.8549A>G	327.8178 ±2.7940	329.6170 ±2.5136	330.8707 ±3.6655	1.578 ±1.997	0.843	-1.526 ±2.064	0.461	0.2728 ±2.668	0.919
c.8560C>T	330.9144 ±3.6094	330.4704 ±2.5157	326.6923 ±2.7523	−2.413 ±1.964	0.585	2.111 ±2.024	0.298	1.667 ±2.683	0.536
c.8563C>T	328.7613 ±2.0680	336.5528 ±5.7176	334.6910 ±12.7480	5.640 ±4.275	0.292	-2.965 ±6.344	0.641	4.827 ±8.389	0.567
c.8689A>G	328.7254 ±2.5606	329.0326 ±2.6172	331.3415 ±4.0096	1.028 ±2.001	0.828	-1.308 ±2.155	0.545	-1.001 ±2.810	0.723
c.8731G>A	330.6905 ±3.5449	330.3832 ±2.4648	326.3952 ±2.8266	2.438 ±1.974	0.496	-2.148 ±2.019	0.289	1.840 ±2.665	0.492

	c.8893G>A	329.0980 ±2.1628	329.5881 ±4.0714	337.7398 18.0801	−1.012 ±3.782	0.631	4.321 ±9.055	0.634	-3.831 ±9.504	0.688
	c.9937A>T	328.8599 ±2.5518	328.0910 ±2.6419	333.0499 3.8653	1.370 ±1.966	0.979	-2.095 ±2.090	0.318	-2.864 ±2.792	0.307
Charolais	c.−11470G>A	335.8260 ±3.1909	334.9517 ±2.7658	330.3967 ±4.7151	−2.277 ±2.593	0.382	2.715 ±2.726	0.322	1.840 ±3.691	0.619
	c. −9627G>A	336.8290 ±3.1748	335.0258 ±2.6639	329.7954 ±4.3346	3.211 ±2.529	0.207	-3.517 ±2.601	0.179	1.714 ±3.586	0.634
	c.276A>G	336.6079 ±3.3584	334.0159 ±2.7738	331.3035 ±5.0595	−2.634 ±2.717	0.334	2.652 ±2.890	0.361	0.6026 ±3.750	0.987
	c.2692C>T	336.1894 ±3.4075	338.1929 ±3.8671	331.1288 ±3.3669	-2.487 2.198	0.263	2.530 ±2.197	0.252	4.534 ±4.274	0.291
	c.5332G>A	335.4601 ±3.0876	333.8472 ±2.7504	334.1865 ±6.8931	1.126 ±2.923	0.699	-0.6368 ±3.649	0.862	-0.9760 ±4.371	0.824
	c.7195C>T	336.3455 ±3.4040	334.0374 ±2.6721	332.5051 ±5.0175	−2.022 ±2.763	0.466	1.920 ±2.924	0.513	-0.3879 ±3.706	0.917
	c.7324G>A	335.7759 ±3.2230	334.3138 ±2.7394	332.0540 ±5.1862	1.740 ±2.698	0.520	-1.861 ±2.915	0.525	0.3988 ±3.834	0.917
	c.8549A>G	332.3203 ±3.3690	333.0723 ±2.9718	340.6785 ±4.1769	3.792 ±2.452	0.135	-4.179 ±2.487	**0.095†**	-3.427 ±3.635	0.348

		c.8560C>T	335.2729	336.5592	324.3341	−3.055	0.254	5.469	**0.073†**	6.756	0.107
			±2.7639	±2.9230	±5.5893	±2.679		±3.026		±4.163	
		c.8563C>T	335.9517	329.9732	324.7379	−5.779	0.115	5.607	0.235	-0.3716	0.954
			±2.4245	±4.7256	±9.2471	±3.629		±4.705		±6.448	
		c.8689A>G	333.2369	335.7829	337.5311	2.352	0.456	-2.147	0.585	0.3989	0.933
			2.8239	±3.1105	±7.5313	±3.078		±3.914		±4.690	
		c.8731G>A	333.0439	339.2314	321.2302	1.033	0.718	-5.907	**0.085†**	12.09	**0.011***
			±2.7359	±3.2954	±6.5493	±2.893		±3.406		±4.699	
		c.8782G>C	335.5776	325.5130	--	10.07	**0.081†**	--	--	--	--
			±2.4925	±5.5569		±5.679					
		c.8893G>A	333.4163	335.2244	337.8452	−2.052	0.454	2.214	0.498	-0.4064	0.927
			±2.7557	±3.2933	±6.1030	±2.737		±3.254		±4.389	
		c.9937A>T	334.7710	333.0193	334.7359	−0.8400	0.792	0.1755	0.997	-1.734	0.743
			±3.2367	±3.7489	±8.3938	±3.414		±4.294		±5.271	
AVBF	Hybrid	c.−11470G>A	12.2589	11.8816	11.8748	−0.2301	0.458	0.1920	0.527	-0.1853	0.654
			±0.3510	±0.3133	±0.5073	±0.2906		±0.3020		±0.4126	
		c. −9627G>A	12.2344	11.9424	11.9372	0.1803	0.613	-0.1486	0.631	-0.1434	0.731
			±0.3483	±0.3158	±0.5238	±0.2948		±0.3081		±0.4167	
		c.276A>G	12.2339	11.9834	11.7132	−0.2584	0.433	0.2604	0.392	0.9863	0.982
			±0.3454	±0.3145	±0.5084	±0.2914		±0.3021		±0.4142	

c.2692C>T	12.3389	11.8651	12.0453	−0.1692	0.506	0.1468	0.577	-0.3270	0.478
	±0.3338	±0.3815	±0.4084	±0.2595		±0.2619		±0.4595	
c.5332G>A	12.1013	12.0663	11.6823	0.1605	0.742	-0.2703	0.676	0.4594	0.916
	±0.3428	±0.3046	±0.5623	±0.3072		±0.6411		±0.4318	
c.7195C>T	12.1845	12.0457	11.6751	−0.2341	0.496	0.6140	0.291	0.4732	0.387
	±0.3544	±0.3034	±0.4912	±0.2920		±0.5784		±0.5430	
c.7324G>A	12.2053	12.0703	11.5153	0.3013	0.350	-0.5495	0.357	-0.4819	0.912
	±0.3393	±0.3062	±0.5073	±0.2919		±0.5929		±0.4378	
c.8549A>G	11.7001	11.9439	12.5793	0.4415	0.179	-0.4396	0.153	-0.1958	0.635
	±0.4402	±0.3008	±0.4443	±0.3048		±0.3058		±0.4109	
c.8560C>T	12.3380	11.7606	12.1023	−0.2553	0.484	0.1179	0.729	-0.4595	0.306
	±0.3434	±0.3316	±0.6047	±0.3102		±0.3381		±0.4477	
c.8563C>T	12.0641	12.1877	9.5713	−0.5181	0.608	1.246	0.271	1.370	0.376
	±0.2580	±1.0543	±2.2475	±0.7781		±1.129		±1.538	
c.8689A>G	11.7325	12.4479	12.6707	0.6090	**0.079†**	-0.4691	0.318	0.2463	0.660
	±0.2685	±0.3253	±0.8953	±0.3453		±0.4688		±0.5574	
c.8731G>A	12.2734	11.6985	12.5909	0.9789	0.835	0.1588	0.662	-0.7337	0.117
	±0.3356	±0.3343	±0.6595	±0.3237		±0.3628		±0.4662	
c.8782G>C	12.0012	12.3259	11.3593	−0.2573	0.691	-0.3209	0.868	0.6457	0.748
	±0.2391	±0.6741	±3.8507	±0.6905		±1.928		±2.010	

	c.8893G>A	12.1568 ±0.3267	11.9492 ±0.3262	11.6098 ±0.8265	0.2393 ±0.3567	0.437	-0.2735 ±0.4465	0.542	0.6591 ±0.5191	0.899
	c.9937A>T	11.5466 ±0.2605	12.3342 ±0.3417	12.9526 ±1.0111	0.7555 ±0.3609	**0.037***	-0.7030 ±0.5230	0.180	0.8456 ±0.6089	0.890
Angus	c.−11470G>A	16.7087 ±0.7764	17.7030 ±0.5337	16.6860 ±0.6165	−0.1890 ±4353	0.662	0.1138 ±0.4437	0.980	1.006 ±0.5725	**0.081†**
	c. −9627G>A	16.4713 ±0.8103	17.6354 ±0.5524	16.8205 ±0.6275	0.2521 ±0.4420	0.945	0.1746 ±0.4547	0.702	0.9895 ±0.5845	**0.093†**
	c.276A>G	16.4508 ±0.7957	17.6825 ±0.5394	16.8119 ±0.6168	−0.2905 ±0.4393	0.940	-0.1806 ±0.4508	0.690	1.051 ±0.5805	**0.072†**
	c.2692C>T	16.5664 ±0.8201	17.6934 ±0.6103	16.9670 ±0.5842	0.1380 ±0.4167	0.989	-0.2003 ±0.4358	0.647	0.9267 ±0.6276	0.142
	c.5332G>A	17.0309 ±0.7741	17.3825 ±0.4996	16.5087 ±0.7336	0.3006 ±0.4725	0.519	-0.2611 ±0.4733	0.583	0.6126 ±0.5831	0.294
	c.7195C>T	16.3472 ±0.7983	17.7198 ±0.5278	16.6762 ±0.6253	−0.5773 ±0.4486	0.883	-0.1645 ±0.4569	0.719	1.208 ±0.5811	**0.040†**
	c.7324G>A	16.4759 ±0.7829	17.0773 ±0.5330	16.6863 ±0.6151	0.1035 ±0.4344	0.799	0.1052 ±0.4430	0.813	1.126 ±0.5734	**0.052†**
	c.8549A>G	16.8883 ±0.5884	17.5207 ±0.5241	16.6383 ±0.7760	0.3197 ±0.4259	0.914	0.1250 ±0.4395	0.776	0.7574 ±0.5664	0.183

	c.8560C>T	16.3387	17.5751	16.8234	0.4505	0.952	-0.2424	0.581	0.9941	**0.085†**
		±0.7855	±0.5472	±0.6025	±0.4256		±0.4367		±0.5726	
	c.8563C>T	17.1873	15.8610	19.2673	−0.2957	0.756	-1.040	0.442	-2.366	0.182
		±0.4594	±1.1877	±2.7099	±0.8988		±1.347		±1.763	
	c.8689A>G	17.2538	17.4491	16.2052	−0.3179	0.486	0.5243	0.274	0.7196	0.248
		±0.5629	±0.5710	0.8864	±0.4442		±0.4778		±0.6206	
	c.8731G>A	16.4430	17.6959	16.6103	0.1166	0.775	0.8369	0.850	1.169	**0.044***
		±0.7742	±0.5347	±0.6182	±0.4331		±0.4397		±0.5752	
	c.8893G>A	17.0350	18.3743	14.8612	−1.015	0.226	-1.087	0.590	2.426	0.253
		±0.4564	±0.8882	±4.0049	±0.8327		±2.006		±2.112	
	c.9937A>T	17.2402	17.4117	16.5083	−0.2263	0.618	0.3660	0.437	0.5375	0.391
		±0.5657	±0.5813	±0.8633	±0.4403		±0.4691		±0.6246	
Charolais	c.−11470G>A	7.6002	8.0536	7.5489	0.8847	0.834	0.2563	0.947	0.4790	0.351
		±0.4733	±0.4141	±0.6741	±0.3651		±0.3827		±0.5117	
	c. −9627G>A	7.5082	8.1338	7.5313	−0.1277	0.738	0.1157	0.975	0.6141	0.220
		±0.4837	±0.4118	±0.6333	±0.3602		±0.3690		±0.4986	
	c.276A>G	7.4651	8.0216	7.6448	0.2223	0.581	-0.8986	0.825	0.4666	0.372
		±0.4984	±0.4182	±0.7241	±0.3829		±0.4060		±0.5200	
	c.2692C>T	7.5611	8.4412	7.6969	0.9903	0.781	-0.6786	0.829	0.8122	0.183
		±0.4981	±0.5606	±0.4902	0.3173		±0.3141		±0.6067	

c.5332G>A	7.6478 ±0.4598	7.8395 ±0.4124	8.3815 ±0.9741	−0.2778 ±0.4088	0.546	0.3669 ±0.5104	0.474	-0.1752 ±0.6077	0.774
c.7195C>T	7.3883 ±0.5074	7.9846 ±0.4100	7.9331 ±0.7194	0.3614 ±0.3876	0.401	-0.2724 ±0.4095	0.507	0.3239 ±0.5122	0.529
c.7324G>A	7.4674 ±0.4835	8.0017 ±0.4168	7.8764 ±0.7406	−0.3034 ±0.3803	0.444	0.2045 ±0.4089	0.618	0.3298 ±0.5295	0.535
c.8549A>G	8.1990 ±0.4725	7.7450 ±0.4249	7.1140 ±0.5768	−0.5330 ±0.3233	0.104	0.5425 ±0.3285	0.101	0.8845 ±0.4750	0.853
c.8560C>T	7.5224 ±0.4294	8.3578 ±0.4442	7.1140 ±0.8035	0.1801 ±0.3822	0.611	0.2042 ±0.4304	0.636	1.040 ±0.5797	**0.075†**
c.8563C>T	7.8927 ±0.3667	7.5111 ±0.6768	7.8034 ±1.3064	−0.2011 ±0.5097	0.662	0.4469 ±0.6614	0.946	-0.3369 ±0.9062	0.711
c.8689A>G	7.8583 ±0.4227	7.8170 ±0.4613	6.9974 ±1.0607	−0.2299 ±0.4328	0.523	0.4305 ±0.5461	0.432	0.3891 ±0.6529	0.553
c.8731G>A	7.7258 ±0.4301	8.0230 ±0.4853	7.3978 ±0.8996	−0.2467 ±0.3841	0.949	-0.1640 ±0.4595	0.722	0.4612 ±0.6197	0.458
c.8782G>C	7.7265 ±0.3594	8.3968 ±0.7440	--	−0.6703 ±0.7453	0.369	--	--	--	--
c.8893G>A	7.7577 ±0.4053	8.2541 ±0.4778	6.5707 ±0.8564	0.1656 ±0.3827	0.716	-0.5935 ±0.4512	0.191	1.090 ±0.6060	**0.074†**

		c.9937A>T	8.1816 ±0.4262	8.1687 ±0.4973	6.9200 ±1.1823	−0.3213 ±0.4813	0.429	0.6308 ±0.6105	0.303	0.6179 ±0.7527	0.414
LMY	Hybrid	c.−11470G>A	57.9519 ±0.3689	58.1536 ±0.3334	57.9199 ±0.5002	0.2731 ±0.2755	0.971	0.1603 ±0.2857	0.955	0.2177 ±0.3784	0.567
		c. −9627G>A	57.9361 ±0.3670	58.1437 ±0.3345	57.8457 ±0.5141	−0.9169 ±0.2788	0.924	-0.4518 ±0.2907	0.877	0.2528 ±0.3819	0.510
		c.276A>G	57.9351 ±0.3661	58.1299 ±0.3346	58.0187 ±0.5030	0.7239 ±0.2762	0.892	-0.4183 ±0.2866	0.884	0.1530 ±0.3800	0.689
		c.2692C>T	57.8348 ±0.3489	58.2670 ±0.3864	57.7060 ±0.4024	−0.2941 ±0.2430	0.920	0.6440 ±0.2449	0.793	0.4965 ±0.4191	0.237
		c.5332G>A	58.0850 ±0.3653	57.9943 ±0.3285	58.0572 ±0.5513	0.3555 ±0.2912	0.728	-0.1448 ±0.6071	0.812	-0.1564 ±0.4002	0.697
		c.7195C>T	58.0185 ±0.3788	58.0589 ±0.3292	58.0154 ±0.4899	0.5542 ±0.2777	0.908	-0.1234 ±0.5492	0.823	-0.7041 ±0.5039	0.889
		c.7324G>A	57.9969 ±0.3655	58.0197 ±0.3324	58.1732 ±0.5067	−0.7435 ±0.2778	0.879	0.6233 ±0.5653	0.913	-0.4761 ±0.4054	0.907
		c.8549A>G	58.0852 ±0.4551	58.1831 ±0.3352	57.5780 ±0.4568	−0.2584 ±0.2908	0.445	0.2536 ±0.2908	0.386	0.3515 ±0.3753	0.352
		c.8560C>T	57.8542 ±0.3658	58.1540 ±0.3523	57.9402 ±0.5814	0.1177 ±0.2895	0.789	-0.4300 ±0.3146	0.892	0.2568 ±0.4082	0.532

	c.8563C>T	57.9883 ±0.2942	57.9717 ±0.9711	59.3976 ±2.0506	0.3202 ±0.7033	0.793	-0.7046 ±1.025	0.494	-0.7212 ±1.398	0.608
	c.8689A>G	58.3153 ±0.3011	57.6117 ±0.3450	58.0666 ±0.8409	−0.4399 ±0.3287	0.185	0.1244 ±0.4349	0.776	-0.5793 ±0.5120	0.259
	c.8731G>A	57.8825 ±0.3549	58.2865 ±0.3486	57.3346 ±0.6267	0.4296 ±0.3029	0.797	-0.2740 ±0.3370	0.419	0.6780 ±0.4265	0.114
	c.8782G>C	58.0155 ±0.2827	58.0328 ±0.6428	58.5443 ±3.4870	−0.4359 ±0.6253	0.970	0.2644 ±1.743	0.880	-0.2471 ±1.817	0.892
	c.8893G>A	57.8198 ±0.3383	58.2065 ±0.3389	58.4634 ±0.7786	−0.3553 ±0.3308	0.232	0.3218 ±0.4121	0.437	0.6494 ±0.4753	0.892
	c.9937A>T	58.4747 ±0.2837	57.7009 ±0.3549	57.9943 ±0.9474	−0.5541 ±0.3460	0.111	0.2402 ±0.4865	0.623	-0.5336 ±0.5652	0.348
Angus	c.−11470G>A	53.8497 ±0.6736	53.3967 ±0.4465	54.1076 ±0.5251	0.2289 ±0.3886	0.562	-0.1289 ±0.3978	0.747	-0.5820 ±0.5200	0.265
	c. −9627G>A	53.9566 ±0.7042	53.4177 ±0.4594	54.0313 ±0.5317	−0.1513 ±0.3962	0.709	0.3732 ±0.4092	0.926	-0.5763 ±0.5332	0.282
	c.276A>G	53.9720 ±0.6916	53.3943 ±0.4510	54.0324 ±0.5250	0.1485 ±0.3921	0.713	-0.3024 ±0.4041	0.941	-0.6079 ±0.5273	0.251
	c.2692C>T	53.9200 ±0.7099	53.4095 ±0.5102	53.9240 ±0.4851	0.1118 ±0.3732	0.764	-0.2003 ±0.3921	0.995	-0.5125 ±0.5699	0.371

c.5332G>A	53.5189	53.5710	54.4755	−0.5036	0.240	0.4783	0.265	-0.4262	0.422
	±0.6734	±0.4128	±0.6399	±0.4266		±0.4279		±0.5282	
c.7195C>T	54.0779	53.3750	54.1230	0.1542	0.704	-0.2255	0.957	-0.7254	0.174
	±0.7008	±0.4448	±0.5384	±0.4029		±0.4130		±0.5310	
c.7324G>A	53.8475	53.4323	54.1135	−0.2317	0.555	0.1330	0.740	-0.5483	0.297
	±0.6820	±0.4476	±0.5261	±0.3896		±0.3997		±0.5240	
c.8549A>G	53.9393	53.4920	53.7832	−0.1543	0.677	0.7804	0.841	-0.3692	0.473
	±0.4875	±0.4284	±0.6670	±0.3740		±0.3876		±0.5126	
c.8560C>T	54.0534	53.5359	54.0237	0.8252	0.814	0.1486	0.971	-0.5027	0.339
	±0.6852	±0.4608	±0.5140	±0.3815		±0.3934		±0.5227	
c.8563C>T	53.6947	55.1958	51.1897	0.3076	0.714	1.253	0.308	2.754	0.088†
	±0.3850	±1.0662	±2.4622	±0.8199		±1.227		±1.603	
c.8689A>G	53.7202	53.5871	54.0685	0.8492	0.825	-0.1741	0.685	-0.3073	0.587
	±0.4733	±0.4809	±0.7751	±0.3948		±0.4275		±0.5639	
c.8731G>A	53.9601	53.4378	54.1764	−0.2125	0.588	0.1081	0.785	-0.6305	0.232
	±0.6795	±0.4538	±0.5339	±0.3896		±0.3980		±0.5254	
c.8893G>A	53.8102	52.9365	54.6475	0.6959	0.348	0.4186	0.818	-1.292	0.503
	±0.3727	±0.7811	±3.6232	±0.7400		±1.815		±1.923	
c.9937A>T	53.7406	53.5756	54.0114	0.5732	0.879	-0.1354	0.746	-0.3003	0.596
	±0.4762	±0.4906	±0.7511	±0.3903		±0.4174		±0.5651	

Charolais	c.−11470G>A	62.4736	62.2129	62.5304	−0.3854	0.948	-0.2835	0.941	-0.2891	0.582
		±0.4401	±0.3801	±0.6610	±0.3659		±0.3847		±0.5239	
	c. −9627G>A	62.5758	62.1260	62.5848	0.7738	0.847	0.4498	0.990	-0.4543	0.376
		±0.4541	±0.3812	±0.6189	±0.3615		±0.3710		±0.5110	
	c.276A>G	62.5747	62.1514	62.5615	−0.1207	0.775	0.6581	0.987	-0.4167	0.437
		±0.4553	±0.3722	±0.7053	±0.3845		±0.4074		±0.5338	
	c.2692C>T	62.4677	61.8334	62.6213	0.5856	0.826	-0.7681	0.808	-0.7111	0.255
		±0.4662	±0.5394	±0.4658	0.3171		±0.3151		±0.6222	
	c.5332G>A	62.4502	62.2701	62.4809	0.8276	0.909	0.1539	0.976	-0.1954	0.752
		±0.4161	±0.3693	±0.9639	±0.4116		±0.5136		±0.6176	
	c.7195C>T	62.7168	62.2010	62.3445	−0.2703	0.558	0.1861	0.653	-0.3296	0.531
		±0.4771	±0.3732	±0.7067	±0.3908		±0.4128		±0.5243	
	c.7324G>A	62.6243	62.1814	62.4393	0.1950	0.634	-0.9247	0.822	-0.3504	0.520
		±0.4474	±0.3790	±0.7287	±0.3809		±0.4110		±0.5427	
	c.8549A>G	62.0638	62.4713	63.1079	0.5087	0.126	-0.5220	0.116	-0.1146	0.812
		±0.4590	±0.4085	±0.5652	±0.3244		±0.3299		±0.4798	
	c.8560C>T	62.5703	61.8201	63.2969	−0.3339	0.890	-0.3633	0.398	-1.114	**0.062†**
		±0.3860	±0.4098	±0.7899	±0.3799		±0.4282		±0.5909	
	c.8563C>T	62.2908	62.3944	62.6587	0.1470	0.733	-0.1840	0.784	-0.8043	0.930
		±0.3170	±0.6594	±1.3075	±0.5165		±0.6687		±0.9165	

		c.8689A>G	62.3390 ±0.3811	62.3629 ±0.4225	62.6927 ±1.0579	0.9439 ±0.4317	0.713	-0.1769 ±0.5528	0.750	-0.1530 ±0.6634	0.818
		c.8731G>A	62.4098 ±0.3984	62.3680 ±0.4633	63.0422 ±0.8901	−0.1751 ±0.3827	0.651	0.3162 ±0.4593	0.493	-0.3580 ±0.6266	0.569
		c.8782G>C	62.4790 ±0.3372	62.1916 ±0.7395	--	0.2874 ±0.7526	0.710	--	--	--	--
		c.8893G>A	62.3527 ±0.3698	62.1237 ±0.4470	63.2651 ±0.8497	−0.1855 ±0.3836	0.703	0.4562 ±0.4570	0.320	-0.6853 ±0.6183	0.270
		c.9937A>T	62.0538 ±0.3985	62.0126 ±0.4678	62.7003 ±1.1882	0.1392 ±0.4815	0.652	-0.3233 ±0.6189	0.603	-0.3644 ±0.7668	0.636
CREA	Hybrid	c.−11470G>A	84.1521 ±0.8575	84.1873 ±0.7816	83.0136 ±1.1239	−0.4489 ±0.6003	0.460	0.5692 ±0.6221	0.363	0.6044 ±0.8122	0.459
		c. −9627G>A	84.0167 ±0.8420	84.2253 ±0.7717	83.0919 ±1.1412	0.3181 ±0.6034	0.601	-0.4624 ±0.6286	0.464	0.6710 ±0.8164	0.414
		c.276A>G	84.0034 ±0.8425	84.3629 ±0.7738	83.0608 ±1.1203	−0.3040 ±0.5981	0.615	0.4713 ±0.6200	0.450	0.8308 ±0.8105	0.306
		c.2692C>T	83.9614 ±0.8306	84.5026 ±0.8994	82.9417 ±0.9245	−0.4363 ±0.5275	0.412	0.5098 ±0.5312	0.340	1.051 ±0.8922	0.240
		c.5332G>A	84.2488 ±0.8452	84.0546 ±0.7662	83.0070 ±1.2270	0.5003 ±0.6338	0.446	-1.317 ±1.320	0.322	-0.2435 ±0.8633	0.779

c.7195C>T	84.1062 ±0.8728	84.2857 ±0.7668	82.9068 ±1.0983	−0.4682 ±0.6048	0.449	0.9613 ±1.194	0.423	1.183 ±1.086	0.277
c.7324G>A	84.1542 ±0.8464	84.1611 ±0.7743	83.0764 ±1.1357	0.4224 ±0.6052	0.494	-1.151 ±1.230	0.353	-0.4540 ±0.8736	0.959
c.8549A>G	83.4370 ±1.0126	84.1812 ±0.7616	83.8520 ±1.0163	0.1999 ±0.6301	0.745	-0.2075 ±0.6304	0.743	0.5367 ±0.8071	0.508
c.8560C>T	84.1125 ±0.8351	84.5417 ±0.8049	84.4896 ±1.2756	−0.3832 ±0.6229	0.914	-0.1886 ±0.6767	0.781	-0.7593 ±0.8719	0.387
c.8563C>T	83.8978 ±0.6683	84.6801 ±2.0852	81.4194 ±4.3877	−0.1591 ±1.501	0.902	1.239 ±2.191	0.574	2.022 ±2.988	0.501
c.8689A>G	84.4411 ±0.7251	82.9485 ±0.8072	86.8874 ±1.8265	−0.2811 ±0.7153	0.695	-1.223 ±0.9331	0.191	-2.716 ±1.092	**0.014***
c.8731G>A	83.9354 ±0.8208	84.0294 ±0.8031	83.3407 ±1.3779	0.1598 ±0.6514	0.799	-0.2974 ±0.7281	0.684	0.3914 ±0.9155	0.670
c.8782G>C	83.7961 ±0.6907	85.0709 ±1.4259	84.4075 ±7.4792	−1.173 ±1.344	0.386	0.3057 ±3.733	0.935	0.9691 ±3.895	0.804
c.8893G>A	83.5358 ±0.7822	84.3166 ±0.7849	85.1316 ±1.6967	−0.7890 ±0.7118	0.272	0.7979 ±0.8842	0.370	-0.1710 ±1.016	0.987
c.9937A>T	84.4627 ±0.7318	83.0471 ±0.8747	87.8984 ±2.1188	−0.1495 ±0.7822	0.848	-1.718 ±1.075	0.112	-3.133 ±1.245	**0.013***

Angus	c.−11470G>A	82.0021 ±1.2837	82.1601 ±0.8164	82.5530 ±0.9860	0.2945 ±0.7702	0.631	-0.2754 ±0.7888	0.728	-0.1175 ±1.057	0.912
	c. −9627G>A	81.4722 ±1.2902	81.9599 ±0.7868	82.6411 ±0.9470	−0.6014 ±0.7653	0.364	0.5844 ±0.7899	0.461	-0.9680 ±1.068	0.928
	c.276A>G	81.6593 ±1.2850	82.0416 ±0.7931	82.6209 ±0.9550	0.4994 ±0.7625	0.434	-0.4808 ±0.7857	0.542	-0.9851 ±1.060	0.926
	c.2692C>T	81.8394 ±1.3180	82.1488 ±0.8994	82.3749 ±0.8516	0.2593 ±0.7323	0.645	-0.2678 ±0.7703	0.729	0.4162 ±1.144	0.971
	c.5332G>A	81.4973 ±1.2632	81.9737 ±0.7027	83.6668 ±1.2217	−1.109 ±0.8540	0.172	1.085 ±0.8566	0.208	-0.6083 ±1.065	0.569
	c.7195C>T	81.6685 ±1.3346	82.1962 ±0.7951	82.5489 ±1.0022	0.4248 ±0.7971	0.516	-0.4402 ±0.8193	0.593	0.8755 ±1.080	0.936
	c.7324G>A	81.0376 ±1.2691	82.3890 ±0.7937	82.5553 ±0.9653	−0.6609 ±0.7668	0.334	0.7589 ±0.7837	0.335	0.5926 ±1.062	0.578
	c.8549A>G	82.4381 ±0.9114	81.9819 ±0.7903	81.7176 ±1.2570	−3.784 ±0.7345	0.521	0.3602 ±0.7610	0.639	-0.9594 ±1.047	0.927
	c.8560C>T	81.7719 ±1.3159	82.4045 ±0.8423	82.5127 ±0.9629	0.3217 ±0.7659	0.559	-0.3704 ±0.7894	0.640	0.2622 ±1.079	0.809
	c.8563C>T	82.2659 ±0.6663	83.0746 ±2.1783	77.5722 ±5.1617	−0.5256 ±1.712	0.726	2.347 ±2.582	0.366	3.156 ±3.356	0.349

	c.8689A>G	82.7375 ±0.8538	82.0286 ±0.8691	81.3999 ±1.4763	−0.6801 ±0.7681	0.296	0.6688 ±0.8383	0.427	-0.4011 ±1.144	0.972
	c.8731G>A	81.6503 ±1.3110	82.3879 ±0.8370	82.5149 ±1.0140	−0.3843 ±0.7827	0.538	0.4323 ±0.8005	0.590	0.3054 ±1.077	0.778
	c.8893G>A	82.2391 ±0.6573	82.5981 ±1.5319	80.5281 ±7.3373	−0.1876 ±1.466	0.860	-0.8555 ±3.673	0.817	1.214 ±3.928	0.758
	c.9937A>T	82.8424 ±0.8442	81.6448 ±0.8728	82.3639 ±1.3994	−0.4822 ±0.7487	0.419	0.2393 ±0.8027	0.767	-0.9583 ±1.133	0.400
Charolais	c.−11470G>A	94.4098 ±1.3625	94.3310 ±1.2030	93.2471 ±1.8812	−0.4677 ±0.9970	0.673	0.5814 ±1.048	0.580	0.5025 ±1.386	0.718
	c. −9627G>A	94.7876 ±1.3876	94.1718 ±1.1936	93.2142 ±1.7743	0.7581 ±0.9803	0.457	-0.7867 ±1.011	0.438	0.1710 ±1.350	0.899
	c.276A>G	94.8848 ±1.4507	93.9542 ±1.2394	93.5501 ±2.0287	−0.7387 ±1.041	0.502	0.6673 ±1.109	0.549	-0.2633 ±1.400	0.851
	c.2692C>T	94.3010 ±1.4097	94.3705 ±1.5698	94.2865 ±1.3810	-0.6401 0.8584	0.958	0.7268 ±0.8613	0.993	0.7678 ±1.647	0.963
	c.5332G>A	94.4065 ±1.2827	93.7579 ±1.1544	96.1046 ±2.6590	−0.9353 ±1.115	0.856	0.8490 ±1.387	0.542	-1.498 ±1.647	0.365
	c.7195C>T	94.9932 ±1.4307	93.8374 ±1.1728	93.9122 ±1.9895	−0.6966 ±1.055	0.588	0.5405 ±1.117	0.630	-0.6153 ±1.388	0.659

		c.7324G>A	94.6928	93.8918	94.0578	0.4541	0.692	-0.3175	0.777	-0.4835	0.737
			±1.3684	±1.1884	±2.0449	±1.038		±1.117		±1.434	
		c.8549A>G	93.5217	93.9392	96.2147	1.239	0.201	-1.347	0.155	-0.9289	0.493
			±1.4368	±1.3123	±1.7273	±0.9293		±0.9424		±1.351	
		c.8560C>T	94.6285	93.6140	94.6688	−0.3479	0.696	-0.2018	0.987	-1.035	0.514
			±1.2771	±1.3048	±2.2560	±1.045		±1.193		±1.581	
		c.8563C>T	94.3910	92.7261	94.2937	−0.8033	0.606	0.4866	0.978	-1.616	0.512
			±1.0662	±1.8721	±3.5590	±1.380		±1.792		±2.455	
		c.8689A>G	94.0172	94.4014	94.2550	0.2538	0.710	-0.1189	0.936	0.2653	0.881
			±1.2067	±1.3091	±2.9074	±1.186		±1.487		±1.774	
		c.8731G>A	93.6692	95.1636	93.9283	−0.6727	0.542	0.1295	0.921	1.365	0.440
			±1.1934	±1.3565	±2.5382	±1.089		±1.300		±1.759	
		c.8782G>C	94.3160	93.6276	--	0.6884	0.766	--	--	--	--
			±1.1127	±2.1647		±2.126					
		c.8893G>A	93.8321	94.5832	94.9077	−0.6222	0.615	0.5378	0.666	0.2133	0.898
			±1.1844	±1.3782	±2.3859	±1.047		±1.240		±1.659	
		c.9937A>T	93.9125	93.6488	93.8793	−0.1373	0.976	0.1661	0.992	-0.2471	0.905
			±1.3360	±1.5374	±3.2921	±1.339		±1.670		±2.044	
CMAR	Hybrid	c.−11470G>	4.5146	4.5654	4.6263	0.5485	0.279	-0.5585	0.299	-0.5014	0.943
		A	±0.0730	±0.0664	±0.0964	±0.5185		±0.5376		±0.7041	

c. −9627G>A	4.5050	4.5700	4.6541	−0.7250	0.156	0.7459	0.174	-0.9540	0.894
	±0.0733	±0.0671	±0.0993	±0.5246		±0.5471		±0.7106	
c.276A>G	4.5091	4.5719	4.6175	0.5596	0.260	-0.5416	0.316	0.8580	0.904
	±0.0726	±0.0666	±0.0970	±0.5198		±0.5394		±0.7068	
c.2692C>T	4.5290	4.5738	4.5976	0.3511	0.450	-0.3430	0.461	0.1054	0.893
	±0.0695	±0.0759	±0.0784	±0.4587		±0.4624		±0.7826	
c.5332G>A	4.4986	4.5965	4.5760	−0.5623	0.268	0.7719	0.500	0.9867	0.188
	±0.0717	±0.0649	±0.1052	±0.5482		±0.1140		±0.7471	
c.7195C>T	4.5190	4.5701	4.5920	0.3904	0.427	-0.6304	0.543	-0.1367	0.885
	±0.0745	±0.0653	±0.0943	±0.5231		±0.1033		±0.9420	
c.7324G>A	4.5047	4.5853	4.5926	−0.5196	0.300	0.8731	0.414	0.8118	0.284
	±0.0722	±0.0659	±0.0975	±0.5232		±0.1064		±0.7568	
c.8549A>G	4.6416	4.5244	4.5483	−0.4521	0.397	0.4666	0.396	-0.7050	0.313
	±0.0883	±0.0668	±0.0887	±0.5459		±0.5462		±0.6981	
c.8560C>T	4.5551	4.5196	4.6977	0.3863	0.459	-0.7129	0.224	-0.1068	0.158
	±0.0722	±0.0696	±0.1102	±0.5388		±0.5841		±0.7525	
c.8563C>T	4.5541	4.6891	4.5448	0.6981	0.566	0.4618	0.981	0.1396	0.591
	±0.0580	±0.1804	±0.3796	±0.1299		±0.1895		±0.2585	
c.8689A>G	4.5629	4.5662	4.4460	−0.2450	0.691	0.5849	0.477	0.6178	0.520
	±0.0629	±0.0702	±0.1600	±0.6211		±0.8182		±0.9578	

	c.8731G>A	4.5624	4.5168	4.7072	−0.3033	0.573	0.7238	0.251	-0.1180	0.137
		±0.709	±0.0694	±0.1190	±0.5638		±0.6288		±0.7906	
	c.8782G>C	4.5824	4.3203	6.0372	0.1594	0.171	0.7274	**0.024***	-0.9895	**0.003***
		±0.0548	±0.1191	±0.6365	±0.1156		±0.3179		±0.3316	
	c.8893G>A	4.6046	4.5192	4.4745	0.7560	0.207	-0.6501	0.400	-0.2038	0.819
		±0.0674	±0.0676	±0.1473	±0.6191		±0.7693		±0.8846	
	c.9937A>T	4.5299	4.5559	4.5409	0.1762	0.799	-0.5504	0.954	0.2051	0.851
		±0.0661	±0.0783	±0.1864	±0.6805		±0.9427		±0.1091	
Angus	c.−11470G>A	6.1645	6.3176	6.2235	0.1018	0.980	-0.2656	0.838	0.1242	0.453
		±0.2526	±0.1854	±0.2085	±0.1320		±0.1297		±0.1648	
	c. −9627G>A	6.1173	6.2584	6.1996	−0.2212	0.930	0.4110	0.756	0.9992	0.552
		±0.2422	±0.1714	±0.1921	±0.1272		±0.1315		±0.1676	
	c.276A>G	6.1290	6.2467	6.1951	0.1756	0.959	-0.3305	0.801	0.8468	0.611
		±0.2416	±0.1727	±0.1935	±0.1264		±0.1305		±0.1659	
	c.2692C>T	6.1641	6.3538	6.1738	−0.3126	0.750	-0.4817	0.970	0.1849	0.314
		±0.2471	±0.1881	±0.1810	±0.1218		±0.1277		±0.1829	
	c.5332G>A	6.2299	6.3026	6.1137	0.6458	0.619	-0.5994	0.663	0.1240	0.463
		±0.2520	±0.1771	±0.2393	±0.1423		±0.1369		±0.1684	
	c.7195C>T	6.1218	6.3315	6.1984	0.1005	0.996	-0.3684	0.785	0.1740	0.304
		±0.2606	±0.1853	±0.2124	±0.1369		±0.1345		±0.1687	

	c.7324G>A	6.1434 ±0.2560	6.3131 ±0.1852	6.2223 ±0.2084	−0.1820 ±0.1325	0.946	0.3760 ±0.1304	0.774	0.1321 ±0.1667	0.430
	c.8549A>G	6.2986 ±0.2072	6.2902 ±0.1880	6.1627 ±0.2599	−0.5735 ±0.1342	0.727	0.6751 ±0.1324	0.612	0.5783 ±0.1663	0.729
	c.8560C>T	6.1388 ±0.2548	6.2881 ±0.1843	6.2725 ±0.2006	0.5303 ±0.1321	0.759	-0.6586 ±0.1307	0.616	0.8131 ±0.1697	0.633
	c.8563C>T	6.3075 ±0.1638	5.6101 ±0.3774	5.5387 ±0.8407	−0.5629 ±0.2771	**0.049***	0.3770 ±0.3986	0.347	-0.3061 ±0.5231	0.560
	c.8689A>G	6.2602 ±0.1822	6.2369 ±0.1842	6.1177 ±0.2699	−0.5801 ±0.1303	0.733	0.7123 ±0.1396	0.611	0.4794 ±0.1783	0.789
	c.8731G>A	6.2168 ±0.2525	6.3270 ±0.1841	6.1719 ±0.2079	0.4287 ±0.1325	0.695	-0.1845 ±0.1301	0.888	0.1361 ±0.1686	0.422
	c.8893G>A	6.2268 ±0.1589	6.2179 ±0.2733	7.1153 ±1.1557	−0.5227 ±0.2480	0.858	0.4443 ±0.5785	0.444	-0.4531 ±0.6016	0.453
	c.9937A>T	6.2479 ±0.1805	6.2240 ±0.1846	6.1873 ±0.2618	−0.2865 ±0.1288	0.902	0.3030 ±0.1369	0.825	0.6351 ±0.1789	0.972
Charolais	c.−11470G>A	4.5183 ±0.1263	4.5596 ±0.1141	4.3764 ±0.1625	−0.4390 ±0.8151	0.582	0.7095 ±0.8525	0.406	0.1122 ±0.1099	0.309
	c. −9627G>A	4.4790 ±0.1267	4.5663 ±0.1121	4.4264 ±0.1537	0.3459 ±0.7947	0.958	-0.2631 ±0.8166	0.747	0.1136 ±0.1058	0.285

c.276A>G	4.4819	4.5691	4.3908	−0.7750	0.915	0.4557	0.609	0.1328	0.232
	±0.1250	±0.1089	±0.1681	±0.8387		±0.8895		±0.1106	
c.2692C>T	4.5092	4.4803	4.5219	0.5405	0.958	-0.6391	0.930	-0.3529	0.787
	±0.1348	±0.1445	±0.1308	0.7028		±0.7055		±0.1297	
c.5332G>A	4.4850	4.5450	4.4172	−0.1491	0.898	-0.3388	0.764	0.9392	0.478
	±0.1249	±0.1151	±0.2253	±0.9080		±0.1130		±0.1319	
c.7195C>T	4.4770	4.5709	4.3695	−0.1415	0.838	0.5378	0.553	0.1477	0.181
	±0.1315	±0.1129	±0.1712	±0.8593		±0.9040		±0.1098	
c.7324G>A	4.5022	4.5526	4.3900	0.2526	0.757	-0.5606	0.538	0.1065	0.350
	±0.1281	±0.1144	±0.1756	±0.8518		±0.9090		±0.1133	
c.8549A>G	4.4865	4.5260	4.6023	0.5578	0.469	-0.5790	0.454	-0.1840	0.866
	±0.1314	±0.1228	±0.1535	±0.7612		±0.7713		±0.1090	
c.8560C>T	4.5111	4.6256	4.2188	−0.4702	0.601	0.1461	0.133	0.2607	**0.038***
	±0.1205	±0.1212	±0.1905	±0.8594		±0.9686		±0.1244	
c.8563C>T	4.5485	4.4117	4.3342	−0.1211	0.267	0.1072	0.460	-0.2967	0.881
	±0.1143	±0.1686	±0.2965	±0.1105		±0.1446		±0.1978	
c.8689A>G	4.4988	4.4990	4.8302	0.8391	0.425	-0.1657	0.160	-0.1655	0.237
	±0.1123	±0.1196	±0.2364	±0.9576		±0.1174		±0.1394	
c.8731G>A	4.5230	4.5826	4.4266	0.2834	0.972	-0.4821	0.654	0.1079	0.442
	±0.1250	±0.1325	±0.2198	±0.9006		±0.1073		±0.1398	

c.8782G>C	4.5167 ±0.1084	4.6109 ±0.1849	--	−0.9419 ±0.1716	0.580	--	--	--	--
c.8893G>A	4.5248 ±0.1177	4.5428 ±0.1318	4.3091 ±0.2016	0.5694 ±0.8407	0.518	-0.1078 ±0.9877	0.277	0.1259 ±0.1303	0.337
c.9937A>T	4.5604 ±0.1265	4.5521 ±0.1426	4.9195 ±0.2686	0.9005 ±0.1087	0.454	-0.1796 ±0.1320	0.176	-0.1879 ±0.1602	0.243

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

Figure 3.18. Haplotype block for LIPE SNPs in the hybrid cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

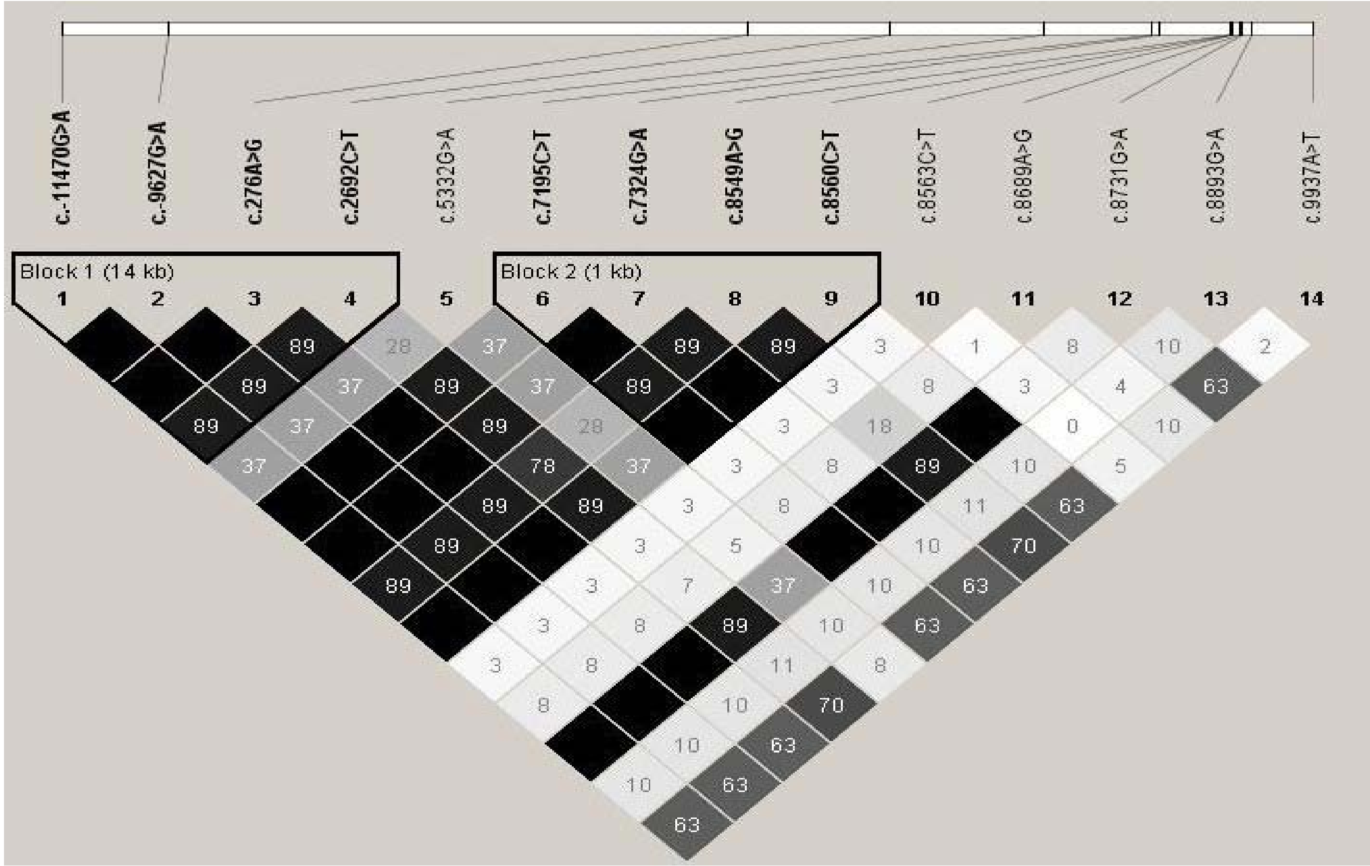

Figure 3.19. Haplotype blocks for LIPE SNPs in the Angus cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

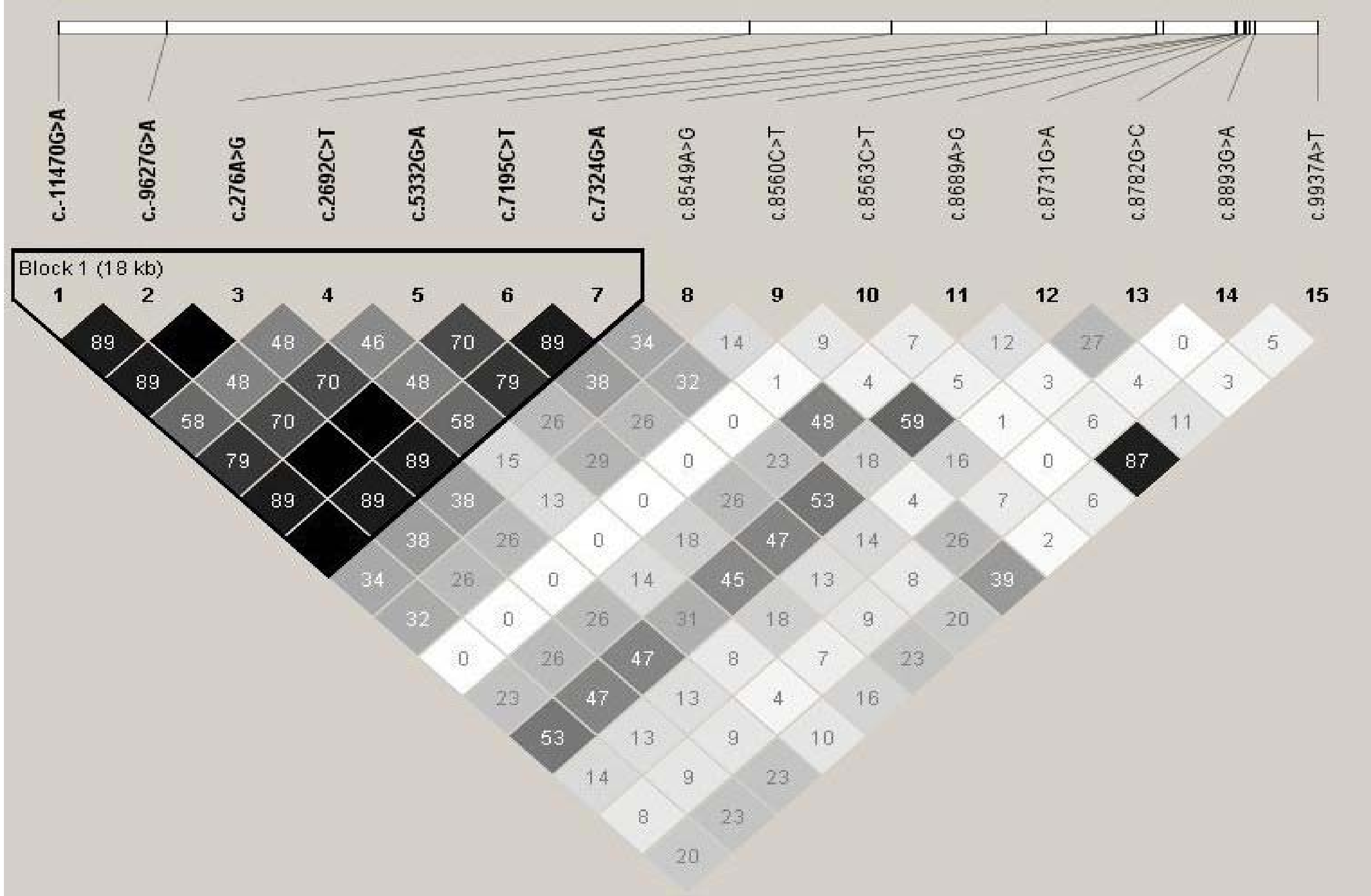

Figure 3.20. Haplotype block for LIPE SNPs in the Charolais cattle population. Complete black box indicates r-square value is 1. In other cases, r-square value is mentioned within the boxes ranges from 0 to 0.99.

Table 3.28. LIPE haplotypes in the hybrid, Angus and Charolais beef cattle populations.

Cattle population	Haplotype block name[a]	Haplotype name[b]	Allele arrangement[c,d]	Frequency[d]
Hybrid	HLIPEB1	HLIPEB1_01	G-G-A-C-G-C-G-G	0.346
		HLIPEB1_02	A-A-G-T-A-T-A-A	0.245
		HLIPEB1_03	G-G-A-C-G-C-G-A	0.099
		HLIPEB1_04	A-A-A-C-A-C-A-A	0.037
		HLIPEB1_05	G-G-G-T-G-T-G-G	0.032
		Others 59 types	---	0.241
	HLIPEB2	HLIPEB2_01	T-C-A-A-G-G-A	0.218
		HLIPEB2_02	C-C-A-G-G-G-A	0.199
		HLIPEB2_03	C-C-G-G-G-G-T	0.156
		HLIPEB2_04	C-C-A-G-G-A-A	0.151
		HLIPEB2_05	T-C-A-A-G-A-A	0.036
		HLIPEB2_06	T-C-A-G-G-G-A	0.030
		Others 45 types	---	0.209
Angus	ALIPEB1	ALIPEB1_01	A-A-G-T	0.417
		ALIPEB1_02	G-G-A-C	0.228
		ALIPEB1_03	A-G-G-T	0.121
		ALIPEB1_04	G-A-A-C	0.119
		ALIPEB1_05	G-G-A-T	0.044
		Other 6 types	---	0.070
	ALIPEB2	ALIPEB2_01	T-A-A-T	0.391
		ALIPEB2_02	C-G-G-C	0.255
		ALIPEB2_03	C-A-A-C	0.131
		ALIPEB2_04	T-G-G-T	0.129
		Other 8 types	---	0.089
	ALIPEB3	ALIPEB3_01	C-A-A-G-A	0.279
		ALIPEB3_02	C-A-G-G-T	0.239
		ALIPEB3_03	C-G-A-G-A	0.227
		ALIPEB3_04	C-G-G-G-T	0.076

		ALIPEB3_05	C-A-G-G-A	0.047
		ALIPEB3_06	C-G-G-G-A	0.039
		ALIPEB3_07	C-A-A-A-A	0.031
		Other 10 types	---	0.063
	ALIPEB4	ALIPEB4_01	G-T-A-T-A	0.30
		ALIPEB4_02	A-C-G-C-G	0.177
		ALIPEB4_03	A-T-G-T-G	0.101
		ALIPEB4_04	G-T-G-T-A	0.084
		ALIPEB4_05	G-C-A-C-A	0.084
		ALIPEB4_06	A-T-G-C-G	0.032
		Other 19 types	---	0.222
Charolais	CLIPEB1	CLIPEB1_01	G-G-A-C-G-C-G	0.387
		CLIPEB1_02	A-A-G-T-A-T-A	0.143
		CLIPEB1_03	A-A-G-T-G-T-A	0.077
		CLIPEB1_04	A-A-A-T-G-T-G	0.049
		CLIPEB1_05	G-G-G-T-A-C-A	0.047
		CLIPEB1_06	A-G-G-T-G-T-G	0.033
		CLIPEB1_07	G-A-A-C-A-C-A	0.033
		Other 23 types	---	0.230
	CLIPEB2	CLIPEB2_01	A-C-C-A-G-G-G-A	0.149
		CLIPEB2_02	G-C-C-G-G-G-G-T	0.126
		CLIPEB2_03	A-T-C-A-A-G-G-A	0.120
		CLIPEB2_04	G-C-C-A-G-G-A-A	0.108
		CLIPEB2_05	G-C-C-A-G-G-G-A	0.082
		CLIPEB2_06	A-C-T-A-G-G-G-A	0.032
		Other 55 types	---	0.383

[a] Haplotype blocks HLIPEB1, ALIPEB1, ALIPEB2, CLIPEB1 were obtained from HAPLOVIEW analyses of SNP genotypes. Name is given by the Author, while last two digit indicate block no. i.e., B1 is block one. In hybrid, SNPs c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T were considered as HLIPEB2 (block 2). In Angus, SNPs c.8563C>T, c.8689A>G, c.8731G>A, c.8893G>A, c.9937A>T were considered as ALIPEB3 (block 3) and SNPs c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A were considered as ALIPEB4 (block 4). In

Charolais, SNPs c.8549A>G, c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T were considered as CLIPEB2 (block 2).

[b] Haplotype names were given by the Author. Last two digits were assigned based on the frequency, i.e., H_01 is equal or more frequent than H_02.

[c] Allele arrangement for HLIPEB1 obtained from SNPs c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A, c.8549A>G. Allele arrangement for HLIPEB2 obtained from SNPs c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T. Allele arrangement for ALIPEB1 obtained from SNPs c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T. Allele arrangement for ALIPEB2 obtained from SNPs c.7195C>T, c.7324G>A, c.8549A>G, c.8560C>T. Allele arrangement for ALIPEB3 obtained from SNPs c.8563C>T, c.8689A>G, c.8731G>A, c.8893G>A, c.9937A>T. Allele arrangement for ALIPEB4 obtained from SNPs c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A. Allele arrangement for CLIPEB1 obtained from SNPs c.−11470G>A, c. −9627G>A, c.276A>G, c.2692C>T, c.5332G>A, c.7195C>T, c.7324G>A. Allele arrangement for CLIPEB2 obtained from SNPs c.8549A>G, c.8560C>T, c.8563C>T, c.8689A>G, c.8731G>A, c.8782G>C, c.8893G>A, c.9937A>T. All SNPs alleles were placed in chronological order within the block.

[d] Allele arrangement and frequency of haplotypes deduced by the software HAPLORE analyses of SNP genotypes.

Table 3.29. Log likelihood ratio (LR) test result for LIPE haplotypes in hybrid, Angus and Charolais cattle populations.

Animal	Haplotype Block	Trait[a]	Log likelihood value of full model[b]	Log likelihood value of reduced model[c]	Chi-square test value	Chi-square test P-value[d]
Hybrid	HLIPEB1	UBF	−551.151	−568.994	71.51	<0.00001
		UREA	−894.156	−915.633	87.94	<0.00001
		AUBF	1357.05	1379.58	89.76	<0.00001
		AUREA	937.726	957.85	78.33	<0.00001
		SWT	−1573.25	−1611.51	150.08	<0.00001
		CWT	−1385.60	−1421.29	129.96	<0.00001
		AVBF	−678.656	−701.414	94.62	<0.00001
		LMY	−649.144	−669.456	83.91	<0.00001
		CREA	−936.342	−954.045	71.03	<0.00001
		CMAR	−48.4436	−47.1706	4.74	0.0295
	HLIPEB2	UBF	−546.065	−568.994	94.93	<0.00001
		UREA	−883.310	−915.633	137.89	<0.00001
		AUBF	1326.77	1379.58	229.2	<0.00001
		AUREA	918.401	957.85	167.32	<0.00001
		SWT	−1553.40	−1611.51	241.49	<0.00001
		CWT	−1367.52	−1421.29	213.22	<0.00001
		AVBF	−674.985	−701.414	111.53	<0.00001
		LMY	−644.252	−669.456	106.44	<0.00001
		CREA	−920.358	−954.045	144.64	<0.00001
		CMAR	−44.9655	−47.1706	11.28	0.0008
Angus	ALIPEB1	UBF	−287.372	−287.372	0	1.0
		UREA	−458.052	−458.054	0.01	0.9203
		AUBF	602.504	602.504	0	1.0
		AUREA	382.108	381.786	1.48	0.2238
		SWT	−761.750	−761.750	0	1.0
		CWT	−677.108	−677.133	0.12	0.729

	AVBF	−386.267	−386.267	0	1.0
	LMY	−365.816	−365.816	0	1.0
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.703	−142.703	0	1.0
ALIPEB2	UBF	−287.372	−287.372	0	1.0
	UREA	−458.054	−458.054	0	1.0
	AUBF	602.503	602.504	0.006	0.9383
	AUREA	381.944	381.786	0.728	0.3935
	SWT	−761.750	−761.750	0	1.0
	CWT	−677.130	−677.133	0.016	0.8993
	AVBF	−386.265	−386.267	0.01	0.9203
	LMY	−365.816	−365.816	0	1.0
	CREA	−503.640	−503.640	0	1.0
	CMAR	−142.703	−142.703	0	1.0
ALIPEB3	UBF	−270.644	−287.372	77.04	<0.00001
	UREA	−424.419	−458.054	154.89	<0.00001
	AUBF	555.403	602.504	216.91	<0.00001
	AUREA	353.749	381.786	129.12	<0.00001
	SWT	−711.039	−761.750	233.53	<0.00001
	CWT	−634.547	−677.133	196.12	<0.00001
	AVBF	−363.455	−386.267	105.05	<0.00001
	LMY	−344.327	−365.816	98.96	<0.00001
	CREA	−471.309	−503.640	148.89	<0.00001
	CMAR	−136.302	−142.703	29.48	<0.00001
ALIPEB4	UBF	−283.128	−287.372	19.54	0.00001
	UREA	−449.537	−458.054	39.22	<0.00001
	AUBF	592.188	602.504	47.51	<0.00001
	AUREA	376.439	381.786	24.62	<0.00001
	SWT	−751.682	−761.750	46.37	<0.00001
	CWT	−668.356	−677.133	40.42	<0.00001
	AVBF	−379.498	−386.267	31.17	<0.00001
	LMY	−358.752	−365.816	32.53	<0.00001
	CREA	−495.801	−503.640	36.10	<0.00001

		CMAR	−141.540	−142.703	5.36	0.0206
Charolais	CLIPEB1	UBF	−220.450	−225.126	21.53	<0.00001
		UREA	−414.377	−425.644	51.89	<0.00001
		AUBF	586.235	599.664	61.84	<0.00001
		AUREA	345.113	354.899	45.07	<0.00001
		SWT	−702.400	−722.287	91.58	<0.00001
		CWT	−651.154	−668.033	77.73	<0.00001
		AVBF	−308.523	−316.704	37.67	<0.00001
		LMY	−312.205	−319.990	35.85	<0.00001
		CREA	−482.568	−494.255	53.82	<0.00001
		CMAR	−44.2776	−42.7920	6.84	0.0089
	CLIPEB2	UBF	−202.766	−225.126	102.97	<0.00001
		UREA	−390.157	−425.644	163.43	<0.00001
		AUBF	546.599	599.664	244.38	<0.00001
		AUREA	321.952	354.899	151.73	<0.00001
		SWT	−656.889	−722.287	301.17	<0.00001
		CWT	−609.552	−668.033	269.32	<0.00001
		AVBF	−293.860	−316.704	105.20	<0.00001
		LMY	−298.005	−319.990	101.25	<0.00001
		CREA	−451.756	−494.255	195.72	<0.00001
		CMAR	−44.2768	−42.7920	6.83	0.009

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Full model include haplotypes random effect for univariate analysis of a single trait.

[c] Reduced model exclude haplotypes random effect.

[d] Chi-square test value and P-value obtained from LR ratio test statistic (Kendall and Stuart, 1979).

Table 3.30. Least square means of fat deposition and carcass merit traits and estimated effects of LIPE haplotypes in the hybrid cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygo-us[b]	Haplotype heterozygo-us[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Domina-nce effect[e]	P value
UBF	HLIPEB1	HLIPEB1_01	9.0157 ±0.3581	9.1924 ±0.3086	9.0516 ±0.2476	−0.2893 ±0.1868	0.997	−0.1798 ±0.1917	0.926	0.1587 ±0.3220	0.624
		HLIPEB1_02	8.6236 ±0.4244	9.3816 ±0.3346	9.0763 ±0.2315	0.1197 ±0.2142	0.820	−0.2263 ±0.2248	0.315	0.5317 ±0.3630	0.145
		HLIPEB1_03	9.7210 ±1.1916	9.1450 ±0.3293	9.0530 ±0.2215	−0.1429 ±0.2980	0.544	0.3340 ±0.5976	0.578	−0.2420 ±0.6560	0.714
		HLIPEB1_04	--	8.8570 ±0.5798	9.1045 ±0.2130	0.2475 ±0.5918	0.751	--	--	--	--
		HLIPEB1_05	--	9.1070 ±0.5908	9.0815 ±0.2124	−0.2552 ±0.6007	0.994	--	--	--	--
	HLIPEB2	HLIPEB2_01	9.8509 ±0.5547	9.3183 ±0.3050	8.9466 ±0.2337	−0.4181 ±0.2393	**0.072†**	0.4521 ±0.2876	0.118	−0.8051 ±0.3794	0.833
		HLIPEB2_02	9.8399 ±1.2100	8.9464 ±0.2793	9.2152 ±0.2278	0.1725 ±0.2925	0.671	0.3123 ±0.6108	0.611	−0.5812 ±0.6431	0.369
		HLIPEB2_03	10.1154	9.2550	9.0541	−0.3323	0.223	0.5307	0.207	−0.3298	0.506

			±0.8267	±0.3267	±0.2105	±0.2886		±0.4189		±0.4934	
		HLIPEB2_04	8.7380	9.1004	9.1567	0.1388	0.518	−0.2094	0.569	0.1531	0.740
			±0.7107	±0.3596	±0.2222	±0.2984		±0.3656		±0.4596	
		HLIPEB2_05	--	9.5232	9.0860	−0.4372	0.355	--	--	--	--
				±0.5232	±0.2063	±0.5317					
		HLIPEB2_06	--	7.3222	9.2386	1.916	**0.001***	--	--	--	--
				±0.6031	±0.1815	±0.6089					
UREA	HLIPEB1	HLIPEB1_01	82.7730	82.5113	83.5029	0.4565	0.333	−0.3649	0.449	−0.6266	0.447
			±0.8395	±0.7075	±0.5475	±0.4690		±0.4802		±0.8203	
		HLIPEB1_02	83.5449	82.4320	83.2167	0.2008	0.896	0.1641	0.772	−0.9489	0.304
			±1.0347	±0.7797	±0.4937	±0.5317		±0.5636		±0.9207	
		HLIPEB1_03	86.1804	82.8148	83.0961	−0.1009	0.842	1.542	0.315	−1.823	0.281
			±3.0401	±0.7672	±0.4657	±0.7562		±1.533		±1.688	
		HLIPEB1_04	--	83.6025	83.0333	−0.5691	0.667	--	--	--	--
				±1.4511	±0.4365	±1.509					
		HLIPEB1_05	--	85.3442	82.9019	−2.442	0.114	--	--	--	--
				±1.4723	±0.4300	±1.522					
	HLIPEB2	HLIPEB2_01	85.3834	83.1430	82.9402	−0.7812	0.173	1.222	**0.093†**	−1.019	0.295
			±1.3710	±0.6657	±0.4551	±0.5873		±0.7228		±0.9718	
		HLIPEB2_02	78.8090	82.9084	83.4261	0.8029	0.285	−2.309	0.139	1.791	0.277

			±3.0647	±0.5962	±0.4659	±0.7101		±1.555		±1.645	
		HLIPEB2_03	83.7847	83.4552	83.0519	−0.3894	0.561	0.3664	0.735	0.3685	0.977
			±2.1041	±0.7518	±0.4260	±0.7192		±1.076		±1.278	
		HLIPEB2_04	83.8552	82.6965	83.2755	0.1130	0.820	0.2899	0.756	−0.8688	0.467
			±1.7751	±0.8241	±0.4498	±0.7490		±0.9300		±1.187	
		HLIPEB2_05	--	83.6389	83.1253	−0.5136	0.668	--	--	--	--
				±1.2901	±0.3806	±1.345					
		HLIPEB2_06	--	81.5033	83.2580	1.755	0.238	--	--	--	--
				±1.5340	±0.3736	±1.572					
AUBF	HLIPEB1	HLIPEB1_01	0.0329	0.0343	0.0331	−0.5428	0.962	−0.1189	0.905	0.1302	0.440
			±0.0018	±0.0015	±0.0012	±0.9663		±0.9920		±0.1675	
		HLIPEB1_02	0.0317	0.0341	0.0335	0.5777	0.766	−0.8816	0.452	0.1515	0.425
			±0.0022	±0.0017	±0.0011	±0.1103		±0.1167		±0.1891	
		HLIPEB1_03	0.0363	0.0345	0.0330	−0.1531	0.282	0.1671	0.593	−0.1767	0.959
			±0.0062	±0.0017	±0.0011	±0.1546		±0.3111		±0.3418	
		HLIPEB1_04	--	0.0344	0.0333	−0.1119	0.667	--	--	--	--
				±0.0030	±0.0010	±0.3074					
		HLIPEB1_05	--	0.0350	0.0332	−0.1717	0.599	--	--	--	--
				±0.0030	±0.0010	±0.3117					
	HLIPEB2	HLIPEB2_01	0.0369	0.0344	0.0327	−0.1918	0.113	0.2093	0.166	−0.4154	0.836

			±0.0029	±0.0015	±0.0011	±0.1242		±0.1504		±0.2003	
		HLIPEB2_02	0.0359	0.0322	0.0342	0.1460	0.384	0.8733	0.786	−0.2800	0.411
			±0.0063	±0.0013	±0.0011	±0.1500		±0.3205		±0.3382	
		HLIPEB2_03	0.0316	0.0349	0.0332	−0.3826	0.899	−0.7863	0.683	0.2528	0.299
			±0.0037	±0.0018	±0.0010	±0.1557		±0.1918		±0.2428	
		HLIPEB2_04	0.0316	0.0349	0.0332	−0.3826	0.899	−0.7863	0.683	0.2528	0.299
			±0.0037	±0.0018	±0.0010	±0.1557		±0.1918		±0.2428	
		HLIPEB2_05	--	0.0335	0.0335	0.4131	0.954	--	--	--	--
				±0.0027	±0.0009	±0.2784					
		HLIPEB2_06	--	0.0268	0.0339	0.7087	**0.023***	--	--	--	--
				±0.0032	±0.0008	±0.3216					
AURE-A	HLIPEB1	HLIPEB1_01	0.1623	0.1619	0.1628	0.3451	0.899	−0.2552	0.933	−0.6663	0.899
			±0.0052	±0.0043	±0.0033	±0.2948		±0.3035		±0.5239	
		HLIPEB1_02	0.1636	0.1578	0.1640	0.1563	0.474	−0.2037	0.955	−0.5998	0.305
			±0.0065	±0.0048	±0.0029	±0.3309		±0.3563		±0.5840	
		HLIPEB1_03	0.1709	0.1669	0.1609	−0.5844	0.262	0.5021	0.611	0.1041	0.924
			±0.0195	±0.0047	±0.0027	±0.4791		±0.9833		±0.1086	
		HLIPEB1_04	--	0.1713	0.1617	−0.9561	0.369	--	--	--	--
				±0.0092	±0.0024	±0.9652					
		HLIPEB1_05	--	0.1762	0.1614	−0.1475	0.126	--	--	--	--

				±0.0094	±0.0024	±0.9744					
	HLIPEB2	HLIPEB2_01	0.1756	0.1654	0.1614	−0.5766	0.145	0.7132	0.127	−0.3145	0.617
			±0.0088	±0.0043	±0.0029	±0.3769		±0.4649		±0.6251	
		HLIPEB2_02	0.1197	0.1625	0.1652	0.5851	0.171	−0.2272	**0.024***	0.2006	0.059†
			±0.0196	±0.0038	±0.0030	±0.4563		±0.9956		±0.1054	
		HLIPEB2_03	0.1617	0.1662	0.1627	−0.1942	0.727	−0.5087	0.942	0.3919	0.635
			±0.0135	±0.0048	±0.0027	±0.4625		±0.6917		±0.8218	
		HLIPEB2_04	0.1669	0.1646	0.1629	−0.1827	0.615	0.1973	0.743	−0.3136	0.967
			±0.0114	±0.0053	±0.0029	±0.4815		±0.5983		±0.7639	
		HLIPEB2_05	--	0.1587	0.1639	0.5229	0.496	--	--	--	--
				±0.0083	±0.0024	±0.8646					
		HLIPEB2_06	--	0.1544	0.1640	0.9610	0.404	--	--	--	--
				±0.0099	±0.0024	±0.1011					
SWT	HLIPEB1	HLIPEB1_01	539.4869	539.5955	545.2688	3.264	0.273	−2.891	0.377	−2.782	0.605
			±6.8218	±6.0677	±5.1645	±3.170		±3.253		±5.360	
		HLIPEB1_02	544.3655	545.0639	541.5415	−1.799	0.341	1.412	0.714	2.110	0.729
			±7.8218	±6.5100	±5.0749	±3.670		±3.840		±6.067	
		HLIPEB1_03	548.2656	544.9275	542.0245	−2.950	0.434	3.121	0.755	−0.2175	0.984
			±20.0742	±6.3743	±4.8381	±5.007		±9.941		±10.90	
		HLIPEB1_04	--	538.0962	543.1810	5.085	0.715	--	--	--	--

				±10.2057	±4.7299	±10.02					
		HLIPEB1_05	--	546.7807	542.3449	−4.436	0.701	--	--	--	--
				±10.4095	±4.7652	±10.20					
	HLIPEB2	HLIPEB2_01	551.4881	543.0127	542.1927	−3.054	0.414	4.648	0.344	−3.828	0.547
			±9.8205	±6.0119	±5.0496	±4.098		±4.884		±6.319	
		HLIPEB2_02	551.3779	539.7650	544.9571	3.746	0.621	3.210	0.755	−8.402	0.438
			±20.5495	±5.8243	±5.0571	±5.057		±10.26		±10.78	
		HLIPEB2_03	571.5154	541.4983	542.7581	−4.886	0.295	14.38	**0.041***	−15.64	**0.057†**
			±14.1891	±6.5241	±4.9151	±4.955		±6.994		±8.144	
		HLIPEB2_04	555.2017	537.4808	543.9987	−0.8843	0.812	5.602	0.359	−12.12	0.110
			±12.2378	±6.8818	±4.8518	±5.012		±6.065		±7.547	
		HLIPEB2_05	--	544.0860	543.1270	−0.9589	0.800	--	--	--	--
				±9.3572	±4.7367	±9.016					
		HLIPEB2_06	--	518.3927	544.6275	26.23	**0.007***	--	--	--	--
				±10.7792	±4.6380	±10.30					
CWT	HLIPEB1	HLIPEB1_01	311.4013	309.3963	315.6990	2.707	0.136	−2.149	0.267	−4.154	0.194
			±4.0319	±3.5817	±3.0414	±1.887		±1.933		±3.187	
		HLIPEB1_02	313.9195	313.2317	313.1144	−0.3499	0.554	0.4026	0.861	−0.2852	0.938
			±4.6448	±3.8568	±2.9924	±2.188		±2.290		±3.622	
		HLIPEB1_03	310.8256	313.9368	313.1094	−0.4094	0.751	−1.142	0.848	1.969	0.763

			±11.9708	±3.7673	±2.8408	±2.987		±5.934		±6.506	
		HLIPEB1_04	--	314.9289	313.0921	−1.837	0.663	--	--	--	--
				±6.0821	±2.8101	±5.978					
		HLIPEB1_05	--	320.3694	312.5939	−7.775	0.218	--	--	--	--
				±6.1889	±2.8229	±6.067					
	HLIPEB2	HLIPEB2_01	321.5726	312.0986	312.9979	−2.129	0.346	4.287	0.140	−5.187	0.168
			±5.7940	±3.5145	±2.9328	±2.433		±2.894		±3.751	
		HLIPEB2_02	324.8526	311.3420	314.4404	1.673	0.747	5.206	0.395	−8.305	0.196
			±12.1883	±3.4227	±2.9637	±3.004		±6.087		±6.396	
		HLIPEB2_03	320.6891	313.6032	313.2135	−1.704	0.525	3.738	0.374	−3.348	0.494
			±8.4577	±3.8472	±2.8713	±2.946		±4.179		±4.871	
		HLIPEB2_04	322.5595	309.1056	314.1054	−0.2738	0.813	4.227	0.241	−9.227	**0.041***
			±7.2456	±4.0546	±2.8427	±2.980		±3.598		±4.479	
		HLIPEB2_05	--	314.9798	313.3339	−1.646	0.654	--	--	--	--
				±5.5415	±2.7778	±5.355					
		HLIPEB2_06	--	302.0590	314.1134	12.05	**0.033***	--	--	--	--
				±6.3995	±2.6940	±6.145					
AVBF	HLIPEB1	HLIPEB1_01	12.2310	11.8201	11.8637	−0.1569	0.548	0.1837	0.495	−0.2272	0.619
			±0.4747	±0.4023	±0.3137	±0.2599		±0.2675		±0.4549	
		HLIPEB1_02	11.4319	11.7769	12.0663	0.3114	0.434	−0.3172	0.316	0.2780	0.958

			±0.5851	±0.4506	±0.2964	±0.2971		±0.3156		±0.5131	
		HLIPEB1_03	12.8259	11.8267	11.9265	−0.1429	0.893	0.4497	0.597	−0.5495	0.557
			±1.6853	±0.4385	±0.2762	±0.4198		±0.8485		±0.9328	
		HLIPEB1_04	--	11.7445	11.9352	0.1907	0.884	--	--	--	--
				±0.8072	±0.2578	±0.8353					
		HLIPEB1_05	--	12.0044	11.9128	−0.9160	0.934	--	--	--	--
				±0.8225	±0.2569	±0.8465					
	HLIPEB2	HLIPEB2_01	12.7144	11.8740	12.0137	−0.1419	0.638	0.3504	0.396	−0.4901	0.373
			±0.7828	±0.4082	±0.2959	±0.3388		±0.4104		±0.5469	
		HLIPEB2_02	13.3687	11.8887	12.0796	0.5501	0.979	0.6446	0.464	−0.8355	0.368
			±1.7299	±0.3706	±0.2961	±0.4113		±0.8755		±0.9233	
		HLIPEB2_03	13.4340	12.7254	11.7931	−0.8881	**0.024***	0.8204	0.171	0.1118	0.876
			±1.1683	±0.4199	±0.2398	±0.4004		±0.5972		±0.7092	
		HLIPEB2_04	11.4731	12.0154	12.0629	0.1790	0.585	−0.2949	0.575	0.2475	0.710
			±1.0084	±0.4913	±0.2881	±0.4251		±0.5237		±0.6622	
		HLIPEB2_05	--	12.4635	11.9830	−0.4804	0.479	--	--	--	--
				±0.7374	±0.2600	±0.7594					
		HLIPEB2_06	--	9.5906	12.1930	2.603	**0.002***	--	--	--	--
				±0.8488	±0.2095	±0.8692					
LMY	HLIPEB1	HLIPEB1_01	57.8644	58.2407	58.1078	0.8937	0.725	−0.1217	0.628	0.2546	0.548

		±0.4619	±0.3966	±0.3161	±0.2436		±0.2502		±0.4213	
	HLIPEB1_02	58.2378	58.0074	58.1027	−0.3544	0.869	0.6757	0.820	−0.1628	0.734
		±0.5562	±0.4377	±0.3017	±0.2797		±0.2952		±0.4768	
	HLIPEB1_03	57.5931	58.2693	58.0599	−0.1170	0.855	−0.2334	0.767	0.4428	0.608
		±1.5593	±0.4250	±0.2819	±0.3897		±0.7828		±0.8594	
	HLIPEB1_04	--	58.5488	58.0577	−0.4911	0.587	--	--	--	--
			±0.7555	±0.2693	±0.7737					
	HLIPEB1_05	--	58.3493	58.0780	−0.2713	0.708	--	--	--	--
			±0.7701	±0.2688	±0.7853					
HLIPEB2	HLIPEB2_01	57.0804	58.1189	58.0902	0.2881	0.338	−0.5049	0.185	0.5336	0.287
		±0.7309	±0.4010	±0.3066	±0.3164		±0.3792		±0.5005	
	HLIPEB2_02	56.5410	58.1681	57.9656	−0.4711	0.994	−0.7123	0.379	0.9148	0.281
		±1.5950	±0.3755	±0.3080	±0.3863		±0.8046		±0.8468	
	HLIPEB2_03	57.8374	57.4942	58.1805	0.4859	0.185	−0.1716	0.757	−0.5147	0.430
		±1.0884	±0.4319	±0.2795	±0.3811		±0.5512		±0.6491	
	HLIPEB2_04	58.7256	58.1401	57.9418	−0.3024	0.363	0.3919	0.418	−0.1936	0.750
		±0.9368	±0.4763	±0.2962	±0.3929		±0.4811		±0.6045	
	HLIPEB2_05	--	57.7243	58.0475	0.3232	0.586	--	--	--	--
			±0.6899	±0.2731	±0.7007					
	HLIPEB2_06	--	59.8354	57.9088	−1.927	**0.014***	--	--	--	--

				±0.8026	±0.2514	±0.8071					
CREA	HLIPEB1	HLIPEB1_01	83.5916	83.7185	84.1480	0.2981	0.585	−0.2782	0.619	−0.1513	0.872
			±1.0621	±0.9210	±0.7474	±0.5427		±0.5571		±0.9318	
		HLIPEB1_02	82.9721	82.9117	84.4897	0.9160	0.144	−0.7588	0.248	−0.8192	0.439
			±1.2573	±1.0068	±0.7218	±0.6231		±0.6551		±1.052	
		HLIPEB1_03	84.4239	84.5400	83.7446	−0.6996	0.422	0.3397	0.845	0.4558	0.811
			±3.4511	±0.9776	±0.6742	±0.8632		±1.727		±1.895	
		HLIPEB1_04	--	85.6694	83.7675	−1.902	0.270	--	--	--	--
				±1.6941	±0.6627	±1.715					
		HLIPEB1_05	--	86.3370	83.7213	−2.616	0.134	--	--	--	--
				±1.7239	±0.6618	±1.739					
	HLIPEB2	HLIPEB2_01	82.8591	83.5616	84.2169	0.6696	0.337	−0.6789	0.414	0.2359	0.983
			±1.6107	±0.9163	±0.7255	±0.6897		±0.8263		±1.083	
		HLIPEB2_02	83.0348	84.0128	83.8797	−0.3702	0.954	−0.4224	0.810	0.5556	0.763
			±3.4709	±0.8626	±0.7195	±0.8466		±1.747		±1.837	
		HLIPEB2_03	88.4980	83.2930	83.9278	−0.5037	0.545	2.285	**0.057†**	−2.920	**0.038***
			±2.3676	±0.9876	±0.6765	±0.8343		±1.190		±1.396	
		HLIPEB2_04	86.5206	83.8243	83.7890	−0.7642	0.383	1.366	0.191	−1.331	0.308
			±2.0431	±1.0696	±0.6912	±0.8532		±1.040		±1.302	
		HLIPEB2_05	--	84.5014	83.8519	−0.6495	0.665	--	--	--	--

				±1.5187	±0.6496	±1.523					
		HLIPEB2_06	--	83.0385	83.9650	0.9265	0.594	--	--	--	--
				±1.7878	±0.6445	±1.766					
CMAR	HLIPEB1	HLIPEB1_01	4.5630	4.4788	4.5997	0.3144	0.500	−0.1834	0.704	−0.1025	0.204
			±0.0910	±0.0787	±0.0637	±0.4687		±0.4804		±0.8045	
		HLIPEB1_02	4.5637	4.5731	4.5561	−0.6425	0.827	0.3779	0.948	0.1318	0.885
			±0.1080	±0.0858	±0.0605	±0.5384		±0.5672		±0.9131	
		HLIPEB1_03	4.5380	4.5864	4.5541	−0.2388	0.720	−0.8023	0.957	0.4040	0.807
			±0.2986	±0.0831	±0.0564	±0.7467		±0.1497		±0.1642	
		HLIPEB1_04	--	4.7545	4.5430	−0.2115	0.146	--	--	--	--
				±0.1452	±0.0542	±0.1479					
		HLIPEB1_05	--	4.7184	4.5474	−0.1710	0.261	--	--	--	--
				±0.1481	±0.0542	±0.1503					
	HLIPEB2	HLIPEB2_01	4.7484	4.5762	4.5175	−0.9191	0.115	0.1154	0.105	−0.5674	0.545
			±0.1369	±0.0760	±0.0587	±0.5900		±0.7079		±0.9323	
		HLIPEB2_02	5.1398	4.5483	4.5459	−0.5246	0.428	0.2970	**0.049***	−0.2946	**0.063†**
			±0.2963	±0.0693	±0.0567	±0.7185		±0.1495		±0.1574	
		HLIPEB2_03	4.5207	4.6087	4.5408	−0.3756	0.580	−0.1007	0.923	0.7796	0.523
			±0.2036	±0.0812	±0.0528	±0.7128		±0.1031		±0.1213	
		HLIPEB2_04	4.6197	4.6331	4.5298	−0.7199	0.368	0.4498	0.618	0.5833	0.607

	±0.1741	±0.0875	±0.0536	±0.7317		±0.8970		±0.1129	
HLIPEB2_05	--	4.4984	4.5609	0.6257	0.666	--	--	--	--
		±0.1284	±0.0502	±0.1307					
HLIPEB2_06	--	4.3245	4.5695	0.2450	**0.096†**	--	--	--	--
		±0.1508	±0.0483	±0.1513					

[a]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b]Least square means and SE for haplotype homozygous (animal contains same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c]Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d]Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10

Table 3.31. Least square means of fat deposition and carcass merit traits and estimated effects of LIPE haplotypes in the Angus cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygo-us[b]	Haplotype heterozygo-us[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Domina-nce effect[e]	P value
UBF	ALIPEB3	ALIPEB3_01	16.5033 ±0.6197	15.0010 0.4972	15.7631 ±0.3166	−0.9865 ±0.2804	0.714	0.3701 ±0.3068	0.230	−1.132 ±0.5414	**0.038***
		ALIPEB3_02	14.6107 ±0.8198	15.4646 ±0.3750	15.9413 ±0.3392	0.5626 ±0.3125	**0.063†**	−0.6653 ±0.4112	0.108	0.1886 ±0.4889	0.701
		ALIPEB3_03	16.8010 ±0.8950	15.4426 ±0.3808	15.7776 ±0.3346	−0.1029 ±0.3274	0.961	0.5117 ±0.4520	0.260	−0.8467 ±0.5251	0.109
		ALIPEB3_04	15.7011 ±1.2994	15.6328 ±0.5818	15.7059 ±0.3089	0.4334 ±0.4498	0.961	−0.2410 ±0.6489	0.997	−0.7070 ±0.8075	0.930
		ALIPEB3_05	--	15.8256 ±0.6466	15.6857 ±0.3029	−0.1399 ±0.6280	0.800	--	--	--	--
		ALIPEB3_06	17.4569 ±2.4561	16.7226 ±0.7463	15.6224 ±0.2942	−1.055 ±0.6505	**0.099†**	0.9173 ±1.228	0.457	0.1830 ±1.375	0.894
		ALIPEB3_07	--	15.9924 ±0.7631	15.6785 ±0.3004	−0.3140 ±0.7496	0.633	--	--	--	--
	ALIPEB4	ALIPEB4_01	15.8691	16.0359	15.3874	−0.3039	0.226	0.2409	0.330	0.4076	0.331

			±0.4841	±0.4117	±0.3296	±0.2374		±0.2460		±0.4173	
		ALIPEB4_02	15.5474	15.6545	15.6570	0.5005	0.607	−0.5480	0.840	0.5227	0.931
			±0.5436	±0.6055	±0.3143	±0.2643		±0.2710		±0.6007	
		ALIPEB4_03	--	15.2039	15.7601	0.5562	0.360	--	--	--	--
				±0.4735	±0.3061	±0.4761					
		ALIPEB4_04	--	15.3705	15.7003	0.3298	0.586	--	--	--	--
				±0.4967	±0.3000	±0.4916					
		ALIPEB4_05	--	15.3059	15.7193	0.4133	0.608	--	--	--	--
				±0.5163	±0.3062	±0.5252					
		ALIPEB4_06	--	16.7096	15.5757	−1.134	0.110	--	--	--	--
				±0.7126	±0.2811	±0.6977					
UREA	ALIPEB3	ALIPEB3_01	79.6408	80.5368	81.1666	0.7308	0.265	−0.7629	0.291	0.1331	0.917
			±1.4671	±1.1839	±0.7695	±0.6507		±0.7199		±1.270	
		ALIPEB3_02	79.8329	80.5676	81.2566	0.7000	0.331	−0.7119	0.461	0.2287	0.984
			±1.9356	±0.9187	±0.8384	±0.7347		±0.9628		±1.141	
		ALIPEB3_03	80.3870	81.6663	80.4988	−0.6712	0.396		0.958	1.223	0.317
			±2.0978	±0.9294	±0.8260	±0.7622		−0.5589		±1.218	
								±1.051			
		ALIPEB3_04	82.8149	80.2270	80.9614	0.3421	0.987	0.9267	0.540	−1.661	0.376
			±3.0284	±1.3697	±0.7542	±1.050		±1.507		±1.869	

		ALIPEB3_05	--	84.2310 ±1.4913	80.5848 ±0.7205	−3.646 ±1.436	**0.012***	--	--	--	--
		ALIPEB3_06	86.9998 ±5.7282	81.0523 ±1.7636	80.8518 ±0.7298	−0.8889 ±1.533	0.555	3.074 ±2.863	0.285	−2.874 ±3.195	0.371
		ALIPEB3_07	--	79.2963 ±1.7867	81.0265 ±0.7446	1.730 ±1.736	0.332	--	--	--	--
	ALIPEB4	ALIPEB4_01	79.8666 ±1.1685	81.3033 ±0.9993	81.1670 ±0.8082	0.5311 ±0.5662	0.325	−0.6502 ±0.5866	0.269	0.7865 ±0.9955	0.431
		ALIPEB4_02	81.6066 ±1.2981	80.9707 ±1.4441	80.8783 ±0.7574	−0.3386 ±0.6290	0.809	0.3642 ±0.6445	0.573	−0.2718 ±1.427	0.849
		ALIPEB4_03	--	79.4551 ±1.0971	81.3204 ±0.6954	1.865 ±1.122	0.153	--	--	--	--
		ALIPEB4_04	--	80.3816 ±1.1983	81.1141 ±0.7371	0.7325 ±1.173	0.608	--	--	--	--
		ALIPEB4_05	--	79.2692 ±1.1933	81.2970 ±0.6892	2.028 ±1.233	0.164	--	--	--	--
		ALIPEB4_06	--	81.4603 ±1.7289	80.9579 ±0.7177	−0.5025 ±1.677	0.774	--	--	--	--
AUBF	ALIPEB3	ALIPEB3_01	0.0742 ±0.0065	0.0657 ±0.0051	0.0678 ±0.0031	−0.1906 ±0.2991	0.521	0.3197 ±0.3309	0.336	−0.5321 ±0.5849	0.365

	ALIPEB3_02	0.0602 ±0.0087	0.0672 ±0.0038	0.0693 ±0.0034	0.3186 ±0.3332	0.328	−0.4519 ±0.4421	0.308	0.2412 ±0.5286	0.649
	ALIPEB3_03	0.0718 ±0.0095	0.0653 ±0.0038	0.0695 ±0.0032	0.2053 ±0.3458	0.535	0.1162 ±0.4860	0.812	−0.5374 ±0.5686	0.347
	ALIPEB3_04	0.0586 ±0.0137	0.0732 ±0.0060	0.0676 ±0.0029	−0.1367 ±0.4768	0.762	−0.4485 ±0.6889	0.517	0.1010 ±0.8654	0.245
	ALIPEB3_05	--	0.0676 ±0.0068	0.0681 ±0.0029	0.5160 ±0.6705	0.948	--	--	--	--
	ALIPEB3_06	0.1051 ±0.0263	0.0714 ±0.0079	0.0676 ±0.0029	−0.7457 ±0.6916	0.278	0.1876 ±0.1317	0.156	−0.1496 ±0.1482	0.315
	ALIPEB3_07	--	0.0721 ±0.0080	0.0678 ±0.0028	−0.4347 ±0.8037	0.575	--	--	--	--
ALIPEB4	ALIPEB4_01	0.0717 ±0.0049	0.0695 ±0.0040	0.0666 ±0.0030	−0.2646 ±0.2535	0.308	0.2581 ±0.2646	0.332	0.3740 ±0.4469	0.934
	ALIPEB4_02	0.0719 ±0.0055	0.0671 ±0.0062	0.0677 ±0.0028	−0.1808 ±0.2777	0.570	0.2091 ±0.2866	0.467	−0.2658 ±0.6481	0.683
	ALIPEB4_03	--	0.0637 ±0.0046	0.0694 ±0.0027	0.5707 ±0.4908	0.278	--	--	--	--
	ALIPEB4_04	--	0.0683 ±0.0050	0.0682 ±0.0028	−0.1673 ±0.5187	0.956	--	--	--	--

		ALIPEB4_05	--	0.0663 ±0.0051	0.0686 ±0.0028	0.2325 ±0.5432	0.718	--	--	--	--
		ALIPEB4_06	--	0.0712 ±0.0074	0.0680 ±0.0026	−0.3201 ±0.7418	0.670	--	--	--	--
AUR--EA	ALIPEB3	ALIPEB3_01	0.1685 ±0.0189	0.2021 ±0.0146	0.2059 ±0.0076	0.1509 ±0.8895	**0.086†**	−0.1870 ±0.9876	**0.060†**	0.1482 ±0.1754	0.400
		ALIPEB3_02	0.2085 ±0.0259	0.2021 ±0.0101	0.2009 ±0.0088	−0.2334 ±0.9832	0.702	0.3823 ±0.1330	0.775	−0.2633 ±0.1619	0.871
		ALIPEB3_03	0.1838 ±0.0286	0.2058 ±0.0105	0.2004 ±0.0087	0.5628 ±0.1023	0.881	−0.8307 ±0.1469	0.573	0.1375 ±0.1738	0.431
		ALIPEB3_04	0.2938 ±0.0398	0.1915 ±0.0171	0.1999 ±0.0070	−0.1521 ±0.1395	0.325	0.4698 ±0.2025	**0.022***	−0.5531 ±0.2604	**0.036***
		ALIPEB3_05	--	0.2057 ±0.0198	0.2013 ±0.0073	−0.4405 ±0.2017	0.878	--	--	--	--
		ALIPEB3_06	0.2737 ±0.0800	0.2035 ±0.0232	0.2013 ±0.0072	−0.1053 ±0.2050	0.635	0.3621 ±0.4002	0.368	−0.3400 ±0.4565	0.458
		ALIPEB3_07	--	0.2161 ±0.0239	0.2008 ±0.0072	−0.1533 ±0.2434	0.608	--	--	--	--
	ALIPEB4	ALIPEB4_01	0.1877	0.1957	0.2091	0.1115	0.177	−0.1068	0.186	−0.2728	0.840

			±0.0145	±0.0115	±0.0081	±0.7671		±0.8043		±0.1348	
		ALIPEB4_02	0.1952	0.2086	0.2031	0.2907	0.909	−0.3943	0.650	0.9442	0.637
			±0.0163	±0.0187	±0.0077	±0.8347		±0.8659		±0.1993	
		ALIPEB4_03	--	0.2025	0.2025	0.1279	0.831	--	--	--	--
				±0.0134	±0.0077	±0.1475					
		ALIPEB4_04	--	0.1828	0.2064	0.2360	0.114	--	--	--	--
				±0.0143	±0.0071	±0.1539					
		ALIPEB4_05	--	0.2074	0.2014	−0.6026	0.875	--	--	--	--
				±0.0148	±0.0077	±0.1615					
		ALIPEB4_06	--	0.2244	0.2011	−0.2329	0.288	--	--	--	--
				±0.0220	±0.0069	±0.2222					
SWT	ALIPEB3	ALIPEB3_01	562.6954	561.5409	566.0066	2.334	0.493	−1.656	0.636	−2.810	0.649
			±7.0298	±5.6340	±3.5756	±3.149		±3.485		±6.151	
		ALIPEB3_02	574.3770	562.8509	565.5221	−0.5602	0.932	4.427	0.343	−7.099	0.201
			±9.2537	±4.2182	±3.8124	±3.543		±4.645		±5.524	
		ALIPEB3_03	561.1834	566.4763	564.1140	−0.8096	0.972	−1.465	0.775	3.828	0.521
			±10.1160	±4.2804	±3.7549	±3.677		±5.114		±5.943	
		ALIPEB3_04	600.2269	558.2027	564.8531	−3.625	0.389	17.69	0.015	−24.34	**0.007***
			±14.2726	±6.3662	±3.3286	±5.046		±7.137		±8.895	
		ALIPEB3_05	--	577.9419	563.6288	−14.31	**0.034***	--	--	--	--

				±7.1976	±3.3906	±6.981					
		ALIPEB3_06	560.9529	554.0337	565.5865	9.309	0.252	−2.317	0.867	−9.236	0.552
			±27.6522	±8.4267	±3.3598	±7.342		±13.83		±15.46	
		ALIPEB3_07	--	551.6684	565.7403	14.07	0.139	--	--	--	--
				±8.5298	±3.3929	±8.363					
	ALIPEB4	ALIPEB4_01	562.7834	561.5268	567.1489	2.703	0.239	−2.183	0.437	−3.439	0.470
			±5.5925	±4.7931	±3.8923	±2.696		±2.794		±4.741	
		ALIPEB4_02	563.0887	569.7772	564.5533	0.1693	0.274	−0.7323	0.812	5.956	0.382
			±6.2191	±6.9049	±3.6798	±3.002		±3.068		±6.783	
		ALIPEB4_03	--	565.1210	564.8583	−0.2627	0.445	--	--	--	--
				±5.5446	±3.6735	±5.453					
		ALIPEB4_04	--	557.0247	566.5789	9.554	0.191	--	--	--	--
				±5.7122	±3.5476	±5.557					
		ALIPEB4_05	--	564.0267	565.1150	1.088	0.528	--	--	--	--
				±6.0062	±3.6609	±6.009					
		ALIPEB4_06	--	569.2509	564.6389	−4.612	0.591	--	--	--	--
				±8.2915	±3.5413	±7.997					
CWT	ALIPEB3	ALIPEB3_01	328.6678	326.8051	330.1512	1.378	0.557	−0.7417	0.752	−2.604	0.529
			±4.6350	±3.6748	±2.2523	±2.112		±2.337		±4.124	
		ALIPEB3_02	333.4860	328.0948	329.9306	0.1952	0.720	1.778	0.570	−3.613	0.335

		±6.1518	±2.7005	±2.3926	±2.361		±3.115		±3.731	
	ALIPEB3_03	323.0066	330.4496	329.1834	0.4734	0.636	−3.088	0.370	4.355	0.277
		±6.7251	±2.7303	±2.3765	±2.452		±3.426		±3.993	
	ALIPEB3_04	354.9613	324.9377	329.2818	−2.885	0.307	12.84	**0.008***	−17.18	**0.005***
		±9.4401	±4.1388	±2.0134	±3.362		±4.756		±5.973	
	ALIPEB3_05	--	338.1310	328.5573	−9.574	**0.033***	--	--	--	--
			±4.7598	±2.1194	±4.673					
	ALIPEB3_06	336.1258	323.2848	329.7257	4.092	0.475	3.200	0.731	−9.641	0.358
		±18.5666	±5.5777	±2.0996	±4.891		±9.285		±10.43	
	ALIPEB3_07	--	323.7125	329.7428	6.030	0.396	--	--	--	--
			±5.6865	±2.1222	±5.640					
ALIPEB4	ALIPEB4_01	326.4712	326.3169	331.2986	2.792	**0.072†**	−2.414	0.192	−2.568	0.413
		±3.5391	±2.9711	±2.3417	±1.776		±1.842		±3.124	
	ALIPEB4_02	329.7639	332.5206	328.5257	−0.9294	0.516	0.6191	0.761	3.376	0.455
		±4.0237	±4.4972	±2.2937	±1.979		±2.029		±4.499	
	ALIPEB4_03	--	329.3354	329.0657	−0.2697	0.372	--	--	--	--
			±3.5049	±2.2361	±3.562					
	ALIPEB4_04	--	325.4477	329.9421	4.494	0.412	--	--	--	--
			±3.6378	±2.1520	±3.668					
	ALIPEB4_05	--	330.5557	328.7957	−1.760	0.181	--	--	--	--

				±3.8196	±2.2262	±3.916					
		ALIPEB4_06	--	329.8614	329.0760	−0.7853	0.924	--	--	--	--
				±5.3738	±2.1270	±5.260					
AVBF	ALIPEB3	ALIPEB3_01	15.7706	15.9588	17.8033	1.214	**0.009***	−1.016	**0.047***	−0.8282	0.357
			±0.9999	±0.7892	±0.4706	±0.4579		±0.5066		±0.8954	
		ALIPEB3_02	16.4529	16.9971	17.5115	0.5214	0.326	−0.5293	0.445	0.1491	0.986
			±1.3641	±0.6013	±0.5390	±0.5210		±0.6893		±0.8226	
		ALIPEB3_03	19.6604	17.3163	17.0576	−0.6829	0.205	1.301	**0.086†**	−1.043	0.237
			±1.4829	±0.6090	±0.5291	±0.5406		±0.7532		±0.8776	
		ALIPEB3_04	19.1085	17.0336	17.2462	−0.2714	0.722	0.9312	0.389	−1.144	0.398
			±2.1453	±0.9476	±0.4749	±0.7449		±1.077		±1.348	
		ALIPEB3_05	--	18.9827	17.1049	−1.878	**0.073†**	--	--	--	--
				±1.0496	±0.4594	±1.036					
		ALIPEB3_06	14.8679	18.5599	17.1954	−0.7580	0.488	−1.164	0.572	2.528	0.275
			±4.1053	±1.2337	±0.4644	±1.082		±2.053		±2.306	
		ALIPEB3_07	--	18.6989	17.1708	−1.528	0.226	--	--	--	--
				±1.2533	±0.4552	±1.247					
	ALIPEB4	ALIPEB4_01	16.4936	17.5844	17.0778	0.1667	0.672	−0.2921	0.475	0.7987	0.249
			±0.7868	±0.6632	±0.5219	±0.3928		±0.4070		±0.6901	
		ALIPEB4_02	16.5267	18.5650	17.0297	0.7447	0.866	−0.2515	0.570	1.787	**0.072†**

			±0.8691	±0.9750	±0.4789	±0.4335		±0.4419		±0.9861	
		ALIPEB4_03	--	16.7541	17.2168	0.4627	0.558	--	--	--	--
				±0.7552	±0.4737	±0.7791					
		ALIPEB4_04	--	16.1389	17.3225	1.184	0.142	--	--	--	--
				±0.7798	±0.4412	±0.7982					
		ALIPEB4_05	--	16.8377	17.1820	0.3444	0.693	--	--	--	--
				±0.8246	±0.4716	±0.8563					
		ALIPEB4_06	--	18.8875	17.0055	−1.882	0.103	--	--	--	--
				±1.1625	±0.4399	±1.146					
LMY	ALIPEB3	ALIPEB3_01	54.9030	54.7011	53.2426	−0.9809±	**0.019***	0.8302	**0.072†**	0.6283	0.439
			±0.8898	±0.6950	±0.3932	±0.4125		±0.4572		±0.8093	
		ALIPEB3_02	53.5274	53.9386	53.5128	−0.2375	0.600	0.7288	0.991	0.4184	0.576
			±1.2162	±0.5080	±0.4493	±0.4650		±0.6199		±0.7450	
		ALIPEB3_03	51.5300	53.8019	53.7616	0.4284	0.387	−1.116	0.102	1.156	0.148
			±1.3272	±0.5172	±0.4407	±0.4832		±0.6785		±0.7953	
		ALIPEB3_04	52.2494	53.7358	53.7119	0.2958	0.650	−0.7312	0.451	0.7551	0.537
			±1.9138	±0.8338	±0.3884	±0.6641		±0.9661		±1.219	
		ALIPEB3_05	--	52.8143	53.7589	0.9446	0.312	--	--	--	--
				±0.9357	±0.3816	±0.9366					
		ALIPEB3_06	54.5696	52.5902	53.7399	0.7680	0.423	0.4148	0.823	−1.565	0.457

			±3.7037	±1.0927	±0.3761	±0.9631		±1.853		±2.096	
		ALIPEB3_07	--	52.3337 ±1.1164	53.7622 ±0.3715	1.429 ±1.124	0.201	--	--	--	--
	ALIPEB4	ALIPEB4_01	54.5102 ±0.6871	53.1656 ±0.5710	53.8706 ±0.4371	−0.1536 ±0.3519	0.658	0.3198 ±0.3642	0.382	−1.025 ±0.6164	0.099
		ALIPEB4_02	54.0116 ±0.7605	52.5615 ±0.8617	53.9019 ±0.3942	0.9414 ±0.3850	0.835	0.5483 ±0.3950	0.891	−1.395 ±0.8907	0.120
		ALIPEB4_03	--	54.0469 ±0.6498	53.7095 ±0.3939	−0.3374 ±0.6889	0.647	--	--	--	--
		ALIPEB4_04	--	54.3787 ±0.6817	53.6465 ±0.3679	−0.7321 ±0.7116	0.312	--	--	--	--
		ALIPEB4_05	--	54.0339 ±0.7117	53.7243 ±0.3907	−0.3096 ±0.7552	0.705	--	--	--	--
		ALIPEB4_06	--	51.8647 ±1.0184	53.8960 ±0.3556	2.031 ±1.015	**0.048***	--	--	--	--
CREA	ALIPEB3	ALIPEB3_01	83.3453 ±1.8021	82.8109 ±1.4018	82.0590 ±0.7734	−0.6695 ±0.838	0.423	0.6432 ±0.9312	0.491	0.1088 ±1.650	0.948
		ALIPEB3_02	79.8152 ±2.4180	82.1549 ±0.9710	82.6476 ±0.8507	0.9086 ±0.9202	0.311	−1.416 ±1.238	0.255	0.9235 ±1.498	0.539
		ALIPEB3_03	79.9650	83.3550	81.8143	−0.5624	0.580	−0.9246	0.498	2.465	0.127

		±2.6484	±0.9781	±0.8121	±0.9544		±1.360		±1.608	
	ALIPEB3_04	85.8895	81.5752	82.3375	−0.3022	0.805	1.776	0.360	−2.538	0.302
		±3.8202	±1.6562	±0.7481	±1.326		±1.933		±2.450	
	ALIPEB3_05	--	85.1190	82.0479	−3.071	**0.099***	--	--	--	--
			±1.8370	±0.6865	±1.865					
	ALIPEB3_06	80.4069	80.8377	82.4132	1.432	0.463	−1.003	0.789	−0.5723	0.893
		±7.4517	±2.1727	±0.6991	±1.917		±3.728		±4.239	
	ALIPEB3_07	--	80.5759	82.4394	1.863	0.427	--	--	--	--
			±2.2357	±0.7080	±2.265					
ALIPEB4	ALIPEB4_01	83.5959	80.7000	82.5691	−0.1035	0.966	0.5134	0.487	−2.382	**0.056†**
		±1.3351	±1.0777	±0.7771	±0.7100		±0.7353		±1.237	
	ALIPEB4_02	81.9233	81.7162	82.3654	0.2662	0.524	−0.2210	0.781	−0.4281	0.815
		±1.4866	±1.7147	±0.7020	±0.7632		±0.7925		±1.826	
	ALIPEB4_03	--	82.1207	82.3002	0.1796	0.886	--	--	--	--
			±1.2361	±0.7145	±1.357					
	ALIPEB4_04	--	81.6611	82.4120	0.7509	0.667	--	--	--	--
			±1.3589	±0.7091	±1.436					
	ALIPEB4_05	--	82.2184	82.2738	0.5547	0.813	--	--	--	--
			±1.3642	±0.7091	±1.485					
	ALIPEB4_06	--	79.0314	82.4019	3.370	**0.093†**	--	--	--	--

				±1.9979	±0.6166	±2.017					
CMAR	ALIPEB3	ALIPEB3_01	6.0793	5.9731	6.3395	0.1865	0.163	−0.1301	0.378	−0.2363	0.364
			±0.3023	±0.2453	±0.1625	±0.1333		±0.1471		±0.2594	
		ALIPEB3_02	6.4232	6.2054	6.2610	−0.7493	0.950	0.8107	0.683	−0.1366	0.562
			±0.3981	±0.1890	±0.1725	±0.1512		±0.1980		±0.2346	
		ALIPEB3_03	7.3008	6.3220	6.1281	−0.3559	**0.022***	0.5864	**0.007***	−0.3924	0.116
			±0.4220	±0.1784	±0.1565	±0.1541		±0.2133		±0.2479	
		ALIPEB3_04	6.6191	5.5796	6.3271	0.3708	**0.084†**	0.1460	0.631	−0.8934	**0.019***
			±0.6089	±0.2757	±0.1525	±0.2137		±0.3028		±0.3755	
		ALIPEB3_05	--	6.2321	6.2482	0.1615	0.953	--	--	--	--
				±0.3131	±0.1538	±0.3001					
		ALIPEB3_06	7.2591	6.5933	6.2162	−0.4136	0.193	0.5214	0.375	−0.1444	0.825
			±1.1715	±0.3647	±0.1566	±0.3143		±0.5852		±0.6516	
		ALIPEB3_07	--	6.0775	6.2583	0.1808	0.607	--	--	--	--
				±0.3674	±0.1523	±0.3574					
	ALIPEB4	ALIPEB4_01	6.0344	6.3308	6.2600	0.8622	0.467	−0.1128	0.342	0.1836	0.363
			±0.2436	±0.2112	±0.1751	±0.1144		±0.1182		±0.2007	
		ALIPEB4_02	6.1577	6.3593	6.2410	0.2750	0.950	−0.4167	0.750	0.1599	0.578
			±0.2687	±0.2968	±0.1648	±0.1274		±0.1302		±0.2867	
		ALIPEB4_03	--	6.4966	6.1747	−0.3219	0.201	--	--	--	--

		±0.2413	±0.1642	±0.2312					
ALIPEB4_04	--	6.3629	6.2173	−0.1456	0.582	--	--	--	--
		±0.2498	±0.1601	±0.2379					
ALIPEB4_05	--	6.5894	6.1603	−0.4291	0.123	--	--	--	--
		±0.2633	±0.1680	±0.2555					
ALIPEB4_06	--	6.4391	6.2295	−0.2096	0.535	--	--	--	--
		±0.3547	±0.1572	±0.3393					

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b] Least square means and SE for haplotype homozygous (animal contains same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c] Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d] Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10

Table 3.32. Least square means of fat deposition and carcass merit traits and estimated effects of LIPE haplotypes in the Charolais cattle population.

Trait[a]	Animal	Haplotype name	Haplotype homozygous[b]	Haplotype heterozygous[b]	Other haplotypes[b]	Haplotype substitution effect[c]	P value	Additive effect[d]	P value	Dominance effect[e]	P value
UBF	CLIPEB1	CLIPEB1_01	7.7475 ±0.3924	8.2786 ±0.4713	8.1869 ±0.3330	0.2030 ±0.1699	0.272	−0.2197 ±0.1717	0.203	0.3114 ±0.4219	0.462
		CLIPEB1_02	8.6049 ±0.7235	7.7270 ±0.4736	8.1197 ±0.3210	−0.1044 ±0.3047	0.997	0.2426 ±0.3546	0.495	−0.6353 ±0.4985	0.205
		CLIPEB1_03	3.8205 ±1.9302	8.7598 ±0.5252	7.9681 ±0.3387	−0.2870 ±0.4678	0.463	−2.074 ±0.9634	**0.033***	2.865 ±0.9999	0.005
		CLIPEB1_04	--	7.7608 ±0.5451	8.1244 ±0.3152	0.3636 ±0.5071	0.427	--	--	--	--
		CLIPEB1_05	--	7.6873 ±0.5586	8.1279 ±0.3157	0.4406 ±0.5189	0.350	--	--	--	--
		CLIPEB1_06	--	7.9106 ±0.6846	8.0957 ±0.3092	0.1851 ±0.6499	0.876	--	--	--	--
		CLIPEB1_07	--	7.9106 ±0.6846	8.0957 ±0.3092	0.1851 ±0.6499	0.876	--	--	--	--
	CLIPEB2	CLIPEB2_01	8.0427	8.0379	8.2150	0.1097	0.694	−0.8618	0.771	−0.9101	0.832

			±0.6109	±0.4307	±0.3219	±0.2724		±0.2955		±0.4284	
		CLIPEB2_02	5.7175	8.5947	8.1533	0.2005	0.452	−1.218	**0.012***	1.659	**0.003***
			±0.9565	±0.4273	±0.2991	±0.3374		±0.4750		±0.5552	
		CLIPEB2_03	9.2491	8.6206	7.9569	−0.6575	**0.051†**	0.6461	0.189	0.1762	0.976
			±0.9920	±0.4151	±0.3195	±0.3124		±0.4891		±0.5863	
		CLIPEB2_04	8.2091	7.8723	8.2143	0.1560	0.695	−0.2643	0.995	−0.3394	0.542
			±0.8639	±0.4829	±0.3041	±0.3389		±0.4261		±0.5550	
		CLIPEB2_05	--	8.1565	8.1609	0.4352	0.932	--	--	--	--
				±0.5125	±0.3111	±0.4836					
		CLIPEB2_06	6.6611	7.4715	8.2150	0.7552	0.202	−0.7770	0.429	0.3347	0.976
			±1.9604	±0.7385	±0.3099	±0.6226		±0.9785		±1.110	
UREA	CLIPEB1	CLIPEB1_01	84.5067	81.5293	83.9626	−0.1231	0.950	0.2720	0.603	−2.705	**0.038***
			±1.0756	±1.3418	±0.8816	±0.5215		±0.5215		±1.292	
		CLIPEB1_02	82.7029	81.6607	84.2694	1.492	0.124	−0.7832	0.466	−1.825	0.228
			±2.1413	±1.3250	±0.8413	±0.9058		±1.069		±1.506	
		CLIPEB1_03	79.9484	83.7502	83.7799	0.3073	0.651	−1.916	0.536	1.886	0.563
			±6.1672	±1.4530	±0.7896	±1.387		±3.092		±3.248	
		CLIPEB1_04	--	85.9667	83.4778	−2.489	**0.084†**	--	--	--	--
				±1.5738	±0.7792	±1.545					
		CLIPEB1_05	--	85.6266	83.5371	−2.090	0.146	--	--	--	--

				±1.6187	±0.7792	±1.588					
		CLIPEB1_06	--	83.4471	83.7658	0.3188	0.663	--	--	--	--
				±2.0173	±0.7827	±1.987					
		CLIPEB1_07	--	83.4471	83.7658	0.3188	0.663	--	--	--	--
				±2.0173	±0.7827	±1.987					
	CLIPEB2	CLIPEB2_01	79.7428	82.0534	84.6095	2.467	**0.003***	−2.433	**0.009***	−0.1228	0.928
			±1.8233	±1.2126	±0.8287	±0.8257		±0.9141		±1.339	
		CLIPEB2_02	83.8176	84.6486	83.5396	−0.7209	0.367	0.1390	0.927	0.9700	0.591
			±2.9902	±1.2041	±0.7107	±1.050		±1.516		±1.800	
		CLIPEB2_03	85.7922	83.4332	83.7717	−0.1470	0.781	1.010	0.525	−1.349	0.482
			±3.1470	±1.1700	±0.7403	±1.003		±1.583		±1.913	
		CLIPEB2_04	85.6633	83.1457	83.7753	−0.2270	0.895	0.9440	0.491	−1.574	0.387
			±2.6799	±1.3706	±0.7102	±1.060		±1.365		±1.809	
		CLIPEB2_05	--	85.4668	83.4189	−2.048	0.205	--	--	--	--
				±1.4284	±0.7605	±1.453					
		CLIPEB2_06	87.5179	84.8613	83.6703	−1.423	0.385	1.924	0.542	−0.7328	0.842
			±6.2800	±2.2067	±0.6819	±1.891		±3.146		±3.677	
AUBF	CLIPEB1	CLIPEB1_01	0.0307	0.0327	0.0320	0.6012	0.695	−0.6781	0.674	0.1318	0.743
			±0.0028	±0.0038	±0.0022	±0.1587		±0.1605		±0.4009	
		CLIPEB1_02	0.0345	0.0248	0.0333	0.3245	0.218	0.5667	0.858	−0.9115	**0.044***

		±0.0062	±0.0034	±0.0018	±0.2583		±0.3161		±0.4477	
	CLIPEB1_03	0.0096	0.0408	0.0301	−0.5523	0.191	−0.1984	**0.034***	0.3057	**0.002***
		±0.0184	±0.0042	±0.0022	±0.411		±0.9242		±0.9741	
	CLIPEB1_04	--	0.0342	0.0316	−0.2648	0.570	--	--	--	--
			±0.0046	±0.0018	±0.4712					
	CLIPEB1_05	--	0.0334	0.0317	−0.1734	0.714	--	--	--	--
			±0.0047	±0.0018	±0.4841					
	CLIPEB1_06	--	0.0280	0.0320	0.3994	0.485	--	--	--	--
			±0.0058	±0.0018	±0.5909					
	CLIPEB1_07	--	0.0280	0.0320	0.3994	0.485	--	--	--	--
			±0.0058	±0.0018	±0.5909					
CLIPEB2	CLIPEB2_01	0.0330	0.0303	0.0332	0.8871	0.723	−0.6329	0.982	−0.2760	0.513
		±0.0055	±0.0035	±0.0022	±0.2526		±0.2844		±0.4203	
	CLIPEB2_02	0.0254	0.0368	0.0317	−0.1851	0.527	−0.3130	0.498	0.8273	0.134
		±0.0091	±0.0036	±0.0021	±0.3214		±0.4604		±0.5481	
	CLIPEB2_03	0.0410	0.0381	0.0305	−0.6742	**0.026***	0.5236	0.276	0.2351	0.685
		±0.0095	±0.0035	±0.0022	±0.3031		±0.4791		±0.5787	
	CLIPEB2_04	0.0341	0.0294	0.0331	0.1342	0.662	0.5327	0.899	−0.4213	0.450
		±0.0082	±0.0041	±0.0020	±0.3230		±0.4180		±0.5562	
	CLIPEB2_05	--	0.0285	0.0332	0.4701	0.274	--	--	--	--

				±0.0043	±0.0022	±0.4390					
		CLIPEB2_06	0.0349	0.0248	0.0329	0.5171	0.393	0.1017	0.916	−0.9079	0.421
			±0.0192	±0.0068	±0.0021	±0.5791		±0.9625		±0.1125	
AUR-	CLIPEB1	CLIPEB1_01	0.2140	0.2069	0.2220	0.4551	0.385	−0.3993	0.534	−0.1111	0.490
-EA			±0.0106	±0.0146	±0.0079	±0.6344		±0.6405		±0.1604	
		CLIPEB1_02	0.1929	0.2170	0.2187	0.8133	0.520	−0.1291	0.315	0.1119	0.539
			±0.0249	±0.0133	±0.0067	±0.1018		±0.1280		±0.1815	
		CLIPEB1_03	0.1791	0.2229	0.2165	−0.2716	0.945	0.2512	0.628	0.2512	0.543
			±0.0766	±0.0158	±0.0065	±0.1588		±0.4110		±0.4110	
		CLIPEB1_04	--	0.2195	0.2170	−0.2518	0.836	--	--	--	--
				±0.0181	±0.0063	±0.1887					
		CLIPEB1_05	--	0.2160	0.2173	0.1257	0.981	--	--	--	--
				±0.0186	±0.0063	±0.1937					
		CLIPEB1_06	--	0.2295	0.2161	−0.1338	0.830	--	--	--	--
				±0.0221	±0.0063	±0.2314					
		CLIPEB1_07	--	0.2295	0.2161	−0.1338	0.830	--	--	--	--
				±0.0221	±0.0063	±0.2314					
	CLIPEB2	CLIPEB2_01	0.1935	0.2238	0.2179	0.6109	0.518	−0.1218	0.279	0.1814	0.279
			±0.0214	±0.0130	±0.0073	±0.9712		±0.1120		±0.1668	
		CLIPEB2_02	0.2074	0.2091	0.2199	0.8998	0.748	−0.6280	0.731	−0.4513	0.837

			±0.0357	±0.0137	±0.0070	±0.1251		±0.1820		±0.2188	
		CLIPEB2_03	0.2218	0.2165	0.2176	0.5634	0.860	0.2081	0.915	−0.3259	0.890
			±0.0382	±0.0134	±0.0070	±0.1211		±0.1935		±0.2352	
		CLIPEB2_04	0.2541	0.1940	0.2197	0.3652	0.673	0.1717	0.299	−0.4290	**0.054†**
			±0.0318	±0.0156	±0.0069	±0.1263		±0.1647		±0.2203	
		CLIPEB2_05	--	0.2229	0.2164	−0.6456	0.885	--	--	--	--
				±0.0147	±0.0068	±0.1602					
		CLIPEB2_06	0.1379	0.2263	0.2175	0.6456	0.953	−0.3979	0.303	0.4860	0.290
			±0.0767	±0.0259	±0.0064	±0.2229		±0.3848		±0.4575	
SWT	CLIPEB1	CLIPEB1_01	553.7321	563.4705	569.2638	3.563	0.223	−2.897	0.296	−12.64	**0.067†**
			±7.0123	±5.5729	±4.5322	±2.757		±2.761		±6.847	
		CLIPEB1_02	557.2087	550.8358	569.0531	10.68	**0.023***	−5.922	0.292	−12.30	0.122
			±11.1709	±6.8032	±4.2355	±4.700		±5.602		±7.896	
		CLIPEB1_03	620.1397	577.8443	562.5755	−17.34	**0.015***	28.78	**0.077†**	−13.51	0.426
			±32.1681	±7.6951	±4.2741	±7.303		±16.12		±16.91	
		CLIPEB1_04	--	562.3480	565.6342	3.286	0.656	--	--	--	--
				±8.4404	±4.2194	±8.265					
		CLIPEB1_05	--	561.3724	565.7159	4.343	0.572	--	--	--	--
				±8.6605	±4.2161	±8.471					
		CLIPEB1_06	--	569.3394	565.0082	−4.331	0.610	--	--	--	--

				±10.7225	±4.1800	±10.55					
		CLIPEB1_07	--	569.3394	565.0082	−4.331	0.610	--	--	--	--
				±10.7225	±4.1800	±10.55					
	CLIPEB2	CLIPEB2_01	548.5100	572.8312	563.1597	2.650	0.555	−7.325	0.126	17.00	**0.016***
			±9.4608	±6.2605	±4.2421	±4.393		±4.756		±6.974	
		CLIPEB2_02	565.6461	572.2922	562.4534	−6.550	0.303	1.596	0.840	8.242	0.378
			±15.6218	±6.4671	±4.0455	±5.472		±7.881		±9.309	
		CLIPEB2_03	556.6545	577.0604	560.9542	−9.640	**0.081†**	−2.150	0.791	18.26	**0.062†**
			±16.0146	±6.0835	±4.0432	±5.158		±8.033		±9.687	
		CLIPEB2_04	569.2967	558.9903	565.2405	1.886	0.778	2.028	0.775	−8.278	0.375
			±14.0340	±7.4305	±4.2035	±5.532		±7.063		±9.297	
		CLIPEB2_05	--	553.1933	566.4545	13.26	**0.096†**	--	--	--	--
				±7.2707	±3.8270	±7.439					
		CLIPEB2_06	505.1850	556.1997	565.3371	15.82	**0.097†**	−30.08	**0.064†**	20.94	0.264
			±32.1740	±11.5482	±3.9378	±9.903		±16.10		±18.65	
CWT	CLIPEB1	CLIPEB1_01	336.8813	329.6250	334.7244	−0.7785	0.704	1.078	0.599	−6.178	0.228
			±3.6316	±4.8373	±2.8092	±2.029		±2.044		±5.103	
		CLIPEB1_02	325.8367	327.6401	336.7789	7.010	**0.035***	−5.471	0.180	−3.668	0.525
			±7.9467	±4.3901	±2.3725	±3.268		±4.061		±5.749	
		CLIPEB1_03	275.4917	335.3550	334.8400	3.968	0.444	−29.67	**0.015***	30.19	**0.019***

		±23.9016	±5.1325	±2.3662	±5.173		±12.00		±12.74	
	CLIPEB1_04	--	337.2744	334.2181	−3.056	0.613	--	--	--	--
			±5.9133	±2.3946	±6.043					
	CLIPEB1_05	--	336.5885	334.3092	−2.279	0.713	--	--	--	--
			±6.0747	±2.3884	±6.204					
	CLIPEB1_06	--	335.9378	334.4071	−1.531	0.845	--	--	--	--
			±7.4294	±2.3917	±7.589					
	CLIPEB1_07	--	335.9378	334.4071	−1.531	0.845	--	--	--	--
			±7.4294	±2.3917	±7.589					
CLIPEB2	CLIPEB2_01	331.1773	338.2601	333.4548	−0.7452	0.812	−1.139	0.750	5.944	0.263
		±6.9276	±4.3442	±2.6453	±3.155		±3.571		±5.287	
	CLIPEB2_02	339.9562	339.0640	333.0751	−4.959	0.234	3.441	0.553	2.548	0.713
		±11.3669	±4.4595	±2.4589	±3.996		±5.784		±6.914	
	CLIPEB2_03	328.8837	339.2225	333.2438	−3.102	0.437	−2.180	0.722	8.159	0.271
		±12.0650	±4.3576	±2.5353	±3.856		±6.092		±7.381	
	CLIPEB2_04	343.7493	332.7277	334.1976	−1.768	0.654	4.776	0.367	−6.246	0.375
		±10.2673	±5.1421	±2.4969	±4.052		±5.268		±7.014	
	CLIPEB2_05	--	331.7673	334.8878	3.120	0.577	--	--	--	--
			±5.0223	±2.4506	±5.321					
	CLIPEB2_06	302.1454	323.1538	335.2583	13.51	**0.057†**	−16.56	0.172	4.452	0.755

			±24.0534	±8.2485	±2.2436	±7.076		±12.06		±14.24	
AVBF	CLIPEB1	CLIPEB1_01	7.3757	8.1724	7.9305	0.2535	0.393	−0.2774	0.329	0.5193	0.464
			±0.5156	±0.6785	±0.4028	±0.2803		±0.2830		±0.7057	
		CLIPEB1_02	7.9254	7.8176	7.8201	−0.2990	0.975	0.5263	0.927	−0.5521	0.946
			±1.1245	±0.6357	±0.3568	±0.4653		±0.5726		±0.8098	
		CLIPEB1_03	7.2843	7.8904	7.8215	−0.2064	0.932	−0.2686	0.874	0.3375	0.851
			±3.3570	±0.7306	±0.3466	±0.7216		±1.685		±1.787	
		CLIPEB1_04	--	6.8072	7.9503	1.143	0.164	--	--	--	--
				±0.8119	±0.3284	±0.8299					
		CLIPEB1_05	--	6.8438	7.9389	1.095	0.192	--	--	--	--
				±0.8350	±0.3289	±0.8524					
		CLIPEB1_06	--	7.7847	7.8338	0.4912	0.975	--	--	--	--
				±1.0269	±0.3319	±1.048					
		CLIPEB1_07	--	7.7847	7.8338	0.4912	0.975	--	--	--	--
				±1.0269	±0.3319	±1.048					
	CLIPEB2	CLIPEB2_01	9.4836	8.5440	7.4508	−1.039	**0.021***	1.016	**0.045***	0.7681	0.918
			±0.9828	±0.6270	±0.3965	±0.4458		±0.5027		±0.7421	
		CLIPEB2_02	5.9865	8.5131	7.7331	−0.1298	0.900	−0.8733	0.292	1.653	**0.094†**
			±1.6257	±0.6501	±0.3773	±0.5745		±0.8249		±0.9814	
		CLIPEB2_03	8.8293	8.4011	7.6191	−0.7194	0.213	0.6051	0.486	0.1769	0.866

			±1.7202	±0.6343	±0.3929	±0.5474		±0.8665		±1.047	
		CLIPEB2_04	7.5820	7.6098	7.8974	0.2203	0.731	−0.1577	0.834	−0.1299	0.897
			±1.4685	±0.7433	±0.3735	±0.5778		±0.7507		±0.9973	
		CLIPEB2_05	--	7.1750	7.9694	0.7944	0.335	--	--	--	--
				±0.7314	±0.3652	±0.7671					
		CLIPEB2_06	4.1421	7.0802	7.8829	1.145	0.249	−1.870	0.280	1.068	0.598
			±3.4414	±1.2067	±0.3691	±1.035		±1.724		±2.017	
LMY	CLIPEB1	CLIPEB1_01	62.6993	62.0799	62.2957	−0.1811	0.565	0.2018	0.484	−0.4176	0.563
			±0.4901	±0.6668	±0.3728	±0.2847		±0.2875		±0.7192	
		CLIPEB1_02	62.9335	62.1663	62.3449	−0.9043	0.805	0.2943	0.609	−0.4729	0.562
			±1.1173	±0.5975	±0.3037	±0.4590		±0.5735		±0.8129	
		CLIPEB1_03	60.8192	61.9895	62.4621	0.5265	0.418	−0.8214	0.634	0.3489	0.849
			±3.4244	±0.7214	±0.3181	±0.7210		±1.719		±1.831	
		CLIPEB1_04	--	64.0832	62.1561	−1.927	**0.021***	--	--	--	--
				±0.7975	±0.2758	±0.8301					
		CLIPEB1_05	--	63.9498	62.1764	−1.773	**0.037***	--	--	--	--
				±0.8218	±0.2765	±0.8550					
		CLIPEB1_06	--	62.2713	62.3630	0.9177	0.836	--	--	--	--
				±1.0015	±0.2912	±1.042					
		CLIPEB1_07	--	62.2713	62.3630	0.9177	0.836	--	--	--	--

				±1.0015	±0.2912	±1.042					
	CLIPEB2	CLIPEB2_01	60.9791	61.2930	62.8059	1.100	**0.015***	−0.9134	**0.076†**	−0.5995	0.430
			±0.9852	±0.6119	±0.3641	±0.4432		±0.5099		±0.7563	
		CLIPEB2_02	62.3600	61.9030	62.4507	0.3525	0.631	−0.4533	0.957	−0.5023	0.619
			±1.6544	±0.6456	±0.3503	±0.5797		±0.8425		±1.008	
		CLIPEB2_03	62.3178	61.8386	62.5040	0.4640	0.449	−0.9308	0.917	−0.5723	0.597
			±1.7593	±0.6321	±0.3610	±0.5598		±0.8889		±1.078	
		CLIPEB2_04	62.3500	62.4446	62.3194	−0.6907	0.941	0.1529	0.984	0.1098	0.915
			±1.4905	±0.7388	±0.3458	±0.5857		±0.7677		±1.024	
		CLIPEB2_05	--	62.9919	62.2118	−0.7801	0.349	--	--	--	--
				±0.7065	±0.3363	±0.7568					
		CLIPEB2_06	66.5217	63.4052	62.2824	−1.440	0.149	2.120	0.232	−0.9969	0.633
			±3.5195	±1.2111	±0.3359	±1.040		±1.764		±2.080	
CREA	CLIPEB1	CLIPEB1_01	95.0263	93.4469	94.1210	−0.3911	0.670	0.4527	0.563	−1.127	0.562
			±1.5120	±1.9343	±1.2112	±0.7710		±0.7793		±1.937	
		CLIPEB1_02	95.3299	92.6015	94.5443	0.5504	0.716	0.3928	0.804	−2.336	0.296
			±3.1222	±1.8352	±1.0906	±1.316		±1.579		±2.228	
		CLIPEB1_03	76.0442	92.3549	94.7077	3.401	**0.074†**	−9.332	**0.042***	6.979	0.147
			±9.0421	±2.0513	±1.0503	±1.997		±4.536		±4.786	
		CLIPEB1_04	--	99.4375	93.6280	−5.810	**0.010***	--	--	--	--

				±2.2459	±1.0093	±2.255					
		CLIPEB1_05	--	98.8663	93.7345	−5.132	**0.025***	--	--	--	--
				±2.3204	±1.0187	±2.325					
		CLIPEB1_06	--	94.1498	94.2657	0.1159	0.862	--	--	--	--
				±2.9238	±1.0541	±2.923					
		CLIPEB1_07	--	94.1498	94.2657	0.1159	0.862	--	--	--	--
				±2.9238	±1.0541	±2.923					
	CLIPEB2	CLIPEB2_01	92.8686	91.3948	95.1192	1.866	0.126	−1.125	0.406	−2.599	0.191
			±2.6928	±1.7915	±1.2252	±1.217		±1.350		±1.978	
		CLIPEB2_02	89.3783	94.6977	94.0519	0.5209	0.818	−2.337	0.293	2.983	0.258
			±4.3775	±1.7852	±1.0838	±1.545		±2.214		±2.623	
		CLIPEB2_03	95.8144	93.9226	94.0787	−0.2118	0.834	0.8679	0.708	−1.024	0.714
			±4.6045	±1.7463	±1.1566	±1.465		±2.310		±2.786	
		CLIPEB2_04	95.0346	93.8169	94.0957	−0.1247	0.967	0.4695	0.814	−0.7483	0.777
			±3.9463	±2.0643	±1.1349	±1.553		1.994		±2.632	
		CLIPEB2_05	--	94.8549	93.9679	−0.8870	0.726	--	--	--	--
				±2.1175	±1.1406	±2.142					
		CLIPEB2_06	98.6321	95.7772	93.9721	−1.976	0.451	2.330	0.612	−0.5249	0.922
			±9.1546	±3.2792	±1.1080	±2.804		4.582		±5.312	
CMAR	CLIPEB1	CLIPEB1_01	4.4805	4.4098	4.5526	0.4110	0.524	−0.3603	0.564	−0.1068	0.488

		±0.1386	±0.1679	±0.1166	±0.6152		±0.6218		±0.1531	
	CLIPEB1_02	4.3946	4.3988	4.5467	0.1026	0.340	−0.7606	0.553	−0.7190	0.692
		±0.2589	±0.1659	±0.1098	±0.1085		±0.1279		±0.1799	
	CLIPEB1_03	4.2970	4.7013	4.4822	−0.1732	0.286	−0.9260	0.797	0.3117	0.409
		±0.7197	±0.1798	±0.1057	±0.1668		±0.3603		±0.3763	
	CLIPEB1_04	--	4.4277	4.5271	0.9934	0.574	--	--	--	--
			±0.1912	±0.1021	±0.1835					
	CLIPEB1_05	--	4.4389	4.5246	0.8557	0.632	--	--	--	--
			±0.1963	±0.1024	±0.1880					
	CLIPEB1_06	--	4.5542	4.5123	−0.4191	0.827	--	--	--	--
			±0.2434	±0.1031	±0.2349					
	CLIPEB1_07	--	4.5542	4.5123	−0.4191	0.827	--	--	--	--
			±0.2434	±0.1031	±0.2349					
CLIPEB2	CLIPEB2_01	4.7642	4.5567	4.4980	−0.1136	0.264	0.1331	0.231	−0.7444	0.644
		±0.2255	±0.1559	±0.1132	±0.1015		±0.1105		±0.1608	
	CLIPEB2_02	4.9952	4.5397	4.5160	−0.1047	0.437	0.2396	0.188	−0.2159	0.312
		±0.3614	±0.1543	±0.1017	±0.1260		±0.1812		±0.2130	
	CLIPEB2_03	4.3007	4.7344	4.4737	−0.1376	0.263	−0.8653	0.640	0.3472	0.120
		±0.3711	±0.1481	±0.1073	±0.1186		±0.1846		±0.2219	
	CLIPEB2_04	4.4865	4.4497	4.5446	0.6008	0.650	−0.2904	0.857	−0.6578	0.755

	±0.3235	±0.1774	±0.1079	±0.1270		±0.1607		±0.2101	
CLIPEB2_05	--	4.7025	4.4958	−0.2068	0.243	--	--	--	--
		±0.1869	±0.1104	±0.1796					
CLIPEB2_06	3.5760	4.3455	4.5464	0.2920	0.203	−0.4852	0.190	0.2843	0.501
	±0.7364	±0.2725	±0.1061	±0.2315		±0.3680		±0.4206	

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

.[b] Least square means and SE for haplotype homozygous (animal contains same haplotype at the both strand of the chromosome), haplotype heterozygous (one chromosomal strand contain the haplotype under test and the other chromosomal strand contain any other haplotype), other haplotypes (both strand of the chromosome contain any other haplotype except the haplotype under test).

[c] Substitution of one haplotype in the population with the other haplotype. It is like allele substation effect of a SNP (Falconer and Mackay, 1996).

[d] Additive effect was estimated by subtracting the solution for the “haplotype homozygous” genotype from that for the “other haplotypes”. It is like additive effect of a SNP (Falconer and Mackay, 1996).

[e] Estimated by subtracting the average of solutions for “haplotype homozygous and other haplotypes” from that for haplotype heterozygous. It is similar to dominance effect of a SNP (Falconer and Mackay, 1996).

*P<0.05, †P<0.10.

Table 3.33. Least square means of fat deposition and carcass merit traits and estimated effects of OLR1 c.10463C>A SNP in the hybrid, Angus and Charolais cattle populations.

Trait[a]	Animal	SNP name	LS mean values for genotypes[b,c]			Allele substitution effect[d]	P value	Additive effect[e]	P value	Dominance effect[f]	P value
			AA	AB	BB						
UBF	Hybrid	c.10463C>A	9.0624	9.2327	10.1219	−0.3046	0.326	0.5298	0.191	−0.3595	0.455
			±0.2279	±0.3104	±0.7979	±0.2703		±0.4043		±0.4789	
	Angus	c.10463C>A	15.6403	16.0016	14.2892	−0.9880	0.769	−0.6755	0.429	1.037	0.280
			±0.3052	±0.5385	±1.7112	±0.4602		±0.8500		±0.9572	
	Charolais	c.10463C>A	8.0215	8.2749	8.0897	−0.2024	0.429	0.3409	0.954	0.2193	0.737
			±0.3268	±0.3939	±1.1799	±0.3010		±0.5836		±0.6515	
UREA	Hybrid	c.10463C>A	83.2742	83.4198	80.9321	0.3443	0.564	−1.171	0.254	1.317	0.283
			±0.4833	±0.7240	±2.0059	±0.6772		±1.024		±1.223	
	Angus	c.10463C>A	80.7877	82.1802	79.5025	−0.8681	0.389	−0.6426	0.753	2.035	0.377
			±0.7018	±1.2728	±4.0911	±1.097		±2.034		±2.294	
	Charolais	c.10463C>A	83.4013	84.0366	87.4466	−0.9510	0.404	2.023	0.264	−1.387	0.491
			±0.7786	±1.0380	±3.6091	±0.9209		±1.804		±2.006	
AUBF	Hybrid	c.10463C>A	0.0330	0.0346	0.0382	−0.1988	0.187	0.2581	0.223	−0.9482	0.707
			±0.0011	±0.0015	±0.0041	±0.1402		±0.2111		±0.2514	

	Angus	c.10463C>A	0.0687 ±0.0027	0.0660 ±0.0055	0.0459 ±0.0183	0.4915 ±0.4860	0.323	−0.1141 ±0.9135	0.214	0.8703 ±0.1036	0.403
	Charolais	c.10463C>A	0.0318 ±0.0021	0.0322 0.0030	0.0410 ±0.0114	−0.1285 ±0.2886	0.678	0.4580 ±0.5701	0.424	−0.4214 ±0.6320	0.507
AURE-A	Hybrid	c.10463C>A	0.1618 ±0.0028	0.1681 ±0.0044	0.1578 ±0.0127	−0.3284 ±0.4268	0.376	−0.1975 ±0.6507	0.762	0.8349 ±0.7818	0.286
	Angus	c.10463C>A	0.2003 ±0.0070	0.2188 ±0.0163	0.1984 ±0.0564	−0.1352 ±0.1477	0.393	−0.9463 ±0.2825	0.973	0.1936 ±0.3228	0.550
	Charolais	c.10463C>A	0.2140 ±0.0069	0.2260 ±0.0108	0.2529 ±0..0446	−0.1366 ±0.1123	0.310	0.1945 ±0.2246	0.388	−0.7399 ±0.2482	0.766
SWT	Hybrid	c.10463C>A	544.0681 ±4.9329	540.7028 ±6.0385	547.8839 ±13.5631	1.403 ±4.550	0.620	1.908 ±6.715	0.777	−5.273 ±7.864	0.505
	Angus	c.10463C>A	564.2809 ±3.6240	571.8181 ±6.0984	526.3981 ±18.9514	−0.8035 ±5.181	0.673	−18.94 ±9.391	**0.046***	26.48 ±10.55	**0.013***
	Charolais	c.10463C>A	563.8645 ±4.2573	567.3540 ±5.5880	594.5573 ±19.0496	−6.183 ±4.878	0.182	15.35 ±9.509	0.109	−11.86 ±10.58	0.264
CWT	Hybrid	c.10463C>A	314.3510 ±2.9452	312.5297 ±3.6019	308.6918 ±8.0777	2.196 ±2.707	0.326	−2.830 ±3.998	0.482	1.008 ±4.682	0.830
	Angus	c.10463C>A	328.6992 ±2.1998	333.3752 ±3.9358	305.0147 ±12.5937	−0.5144 ±3.428	0.667	−11.84 ±6.262	**0.061†**	16.52 ±7.059	**0.021***

	Charolais	c.10463C>A	333.3449 ±2.3994	336.6487 ±3.5683	355.6595 ±13.9492	−5.020 ±3.546	0.159	11.16 ±7.013	0.114	−7.854 ±7.766	0.314
AVBF	Hybrid	c.10463C>A	11.9731 ±0.2705	11.8469 ±0.4050	14.3626 ±1.1218	−0.3731 ±0.3785	0.380	1.195 ±0.5725	**0.039***	−1.321 ±0.6839	**0.055†**
	Angus	c.10463C>A	17.0549 ±0.4550	18.1658 ±0.8660	15.2034 ±2.8341	−0.5925 ±0.7589	0.440	−0.9257 ±1.412	0.514	2.037 ±1.596	0.204
	Charolais	c.10463C>A	7.8035 ±0.3771	7.8716 ±0.5301	6.6615 ±1.9585	0.7141 ±0.4976	0.931	−0.5710 ±0.9820	0.562	0.6391 ±1.090	0.559
LMY	Hybrid	c.10463C>A	58.1465 ±0.2983	58.0583 ±0.4060	55.8247 ±1.0428	0.4886 ±0.3543	0.210	−1.161 ±0.5283	**0.030***	1.073 ±0.6258	**0.088†**
	Angus	c.10463C>A	53.8170 ±0.3732	52.9429 ±0.7643	54.4542 ±2.5612	0.5706 ±0.6800	0.402	0.3186 ±1.279	0.804	−1.193 ±1.451	0.413
	Charolais	c.10463C>A	62.3700 ±0.3381	62.2862 ±0.5050	64.7473 ±1.9824	−0.1867 ±0.5020	0.761	1.189 ±0.9969	0.235	−1.272 ±1.104	0.251
CREA	Hybrid	c.10463C>A	84.4971 ±0.7193	83.1586 ±0.9326	80.5432 ±2.2721	1.576 ±0.7683	**0.041***	−1.977 ±1.142	**0.085†**	0.6384 ±1.346	0.637
	Angus	c.10463C>A	82.1727 ±0.6611	83.3089 ±1.4995	76.7157 ±5.1658	−0.1533 ±1.360	0.851	−2.729 ±2.584	0.293	3.865 ±2.948	0.192
	Charolais	c.10463C>A	93.9096 ±1.0742	94.2427 ±1.4675	105.4099 ±5.2523	−1.563 ±1.351	0.288	5.750 ±2.629	**0.031***	−5.417 ±2.921	**0.066†**

CMAR	Hybrid	c.10463C>A	4.5402	4.5927	4.6183	−0.4744	0.509	0.3904	0.696	0.1341	0.909
			±0.0595	±0.0788	±0.1970	±0.6668		±0.9942		±0.1174	
	Angus	c.10463C>A	6.1937	6.6231	7.2429	−0.4542	**0.052†**	0.4757	0.237	−0.7954	0.860
			±0.1683	±0.2752	±0.8421	±0.2272		±0.4006		±0.4495	
	Charolais	c.10463C>A	4.5114	4.5244	4.3751	0.6165	0.982	−0.6813	0.750	0.8114	0.734
			±0.1122	±0.1382	±0.4298	±0.1097		0.2132		0.2379	

[a] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score.

[b] Least square means and SE for genotypes AA, AB and BB.

[c] AA genotype means the animal is homozygous for first allele. First allele is the allele which appear first in the SNP name or the preferred allele of the locus, i.e., if the SNP name c.100A>B, then A is the first allele. The other allele is considered as second allele and it is denoted by BB. Heterozygous animals were denoted by AB.

[d] Substitution of one allele in the population with the other allele (Falconer and Mackay, 1996).

[e] Additive effect was estimated by subtracting the solution for the “AA” genotype from that for the “BB” genotype (Falconer and Mackay, 1996).

[f] Estimated by subtracting the average of solutions for homozygous genotypes from that for heterozygous genotype (Falconer and Mackay, 1996).

*P < 0.05. †P<0.10.

Table 3.34. Summary of candidate genes associations with fat deposition and carcass merit traits in beef cattle populations.

Gene name[a]	Hybrid cattle population trait[b]	Angus cattle population trait[b]	Charolais cattle population trait[b]
ACS	UREA*, CREA**, CMAR*	----	----
FABP3	UREA**	UREA*, SWT**, CWT**	CMAR**
FASN	SWT**, CREA**	CWT*, AVBF*, LMY*, CMAR*	UBF**, UREA*, AUBF*, AUREA*, SWT**
GPAM	UBF**, AUBF**, SWT**, CWT**, CREA**, CMAR**	AURA**, SWT**, CWT**, CMAR*	UBF*
IDH1	UBF**, SWT**, CWT**, AVBF**, LMY**, CMAR**	CMAR**	----
IGF1	----	UBF**, SWT**, CWT**, AVBF**, LMY**	UBF**, UREA**, AUREA*
INS	UBF**, AUBF*, SWT**	----	----
LIPE	AUREA**, SWT**, AVBF**, CREA**, CMAR**	AUREA*, AVBF**, CMAR**	UBF**, UREA**, AUBF**, AUREA*, SWT**, CWT*, CMAR**
OLR1	AVBF**, LMY**, CREA**	SWT**, CWT**, CMAR*	CREA**

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b]UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score. *P<0.10, **P<0.05.

Table 3.35. FDR of P-values from gene specific SNPs significant allele substitution effects for fat deposition and carcass merit traits.

Trait[a]	Animal	Gene[b]	SNP	P-value[c]	FDR[d]
UBF	Hybrid	GPAM	c.−1564G>A	0.026	0.130
		IDH1	c.9970A>G	0.043	0.129
	Angus	IGF1	c. −512C>T	0.027	0.054†
	Charolais	GPAM	c.35863A>C	0.053	0.159
UREA	Hybrid	FABP3	c.21T>C	0.047	0.094†
			c.4593C>G	0.090	0.090†
	Angus	FABP3	c.21T>C	0.073	0.146
			c.4593C>G	0.078	0.078†
	Charolais	FASN	c.12865G>A	0.055	0.220
		IGF1	c.47807T>C	0.014	0.028*
		LIPE	c.8549A>G	0.011	0.165
			c.8560C>T	0.074	0.370
			c.8563C>T	0.042	0.315
AUBF	Hybrid	GPAM	c.35863A>C	0.016	0.080†
		INS	c. −397T>C	0.06	0.120
	Charolais	FASN	c.12865G>A	0.099	0.395
		LIPE	c.8782G>C	0.041	0.615
			c.9937A>T	0.097	0.727
AUREA	Hybrid	LIPE	c.8782G>C	0.018	0.270
	Angus	GPAM	c. −345C>T	0.044	0.088†
		LIPE	c.276A>G	0.092	0.644
			c.8731G>A	0.09	1.00
	Charolais	FASN	c.12865G>A	0.08	0.320
		IGF1	c.47807T>C	0.067	0.134
		LIPE	c.8563C>T	0.064	0.960

SWT	Hybrid	GPAM	c.26006A>G	0.009	0.045*
		IDH1	c.9970A>G	0.033	0.099
	Angus	FABP3	c.21T>C	0.017	0.034
			c.4593C>G	0.017	0.034*
		IGF1	c.47807T>C	0.009	0.018*
	Charolais	FASN	c.12794A>C	0.083	0.166
			c.12865G>A	0.035	0.140
		LIPE	c.8563C>T	0.032	0.480
CWT	Hybrid	GPAM	c.26006A>G	0.019	0.095†
		IDH1	c.9970A>G	0.043	0.129
	Angus	FABP3	c.21T>C	0.008	0.008*
			c.4593C>G	0.007	0.014*
		FASN	c.14169T>C	0.072	0.288
		IGF1	c.47807T>C	0.002	0.004*
	Charolais	LIPE	c.8782G>C	0.081	1.00
AVBF	Hybrid	LIPE	c.8689A>G	0.079	0.592
			c.9937A>T	0.037	0.555
	Angus	FASN	c.10388C>T	0.058	0.232
			c.12865G>A	0.077	0.154
		IGF1	c. −512C>T	0.011	0.022*
LMY	Angus	FASN	c.10388C>T	0.079	0.316
			c.12865G>A	0.088	0.176
		IGF1	c. −512C>T	0.017	0.034*
CREA	Hybrid	FASN	c.14169T>C	0.042	0.210
		GPAM	c.18088G>C	0.026	0.130
CMAR	Hybrid	GPAM	c.−1564G>A	0.015	0.075†
	Angus	FASN	c.10388C>T	0.081	0.108
			c.12865G>A	0.063	0.252
			c.14169T>C	0.080	0.160
		GAPM	c. −345C>T	0.082	0.164
		LIPE	c.8563C>T	0.049	0.686
	Charolais	FABP3	c.7627T>C	0.023	0.069†

[a] UBF = Ultrasound backfat; UREA = Ultrasound rib eye area; AUBF = Average daily gain of ultrasound backfat; AUREA = Average daily gain of ultrasound rib eye area; SWT = Slaughter weight; CWT = Carcass weight; AVBF = Average backfat; LMY = Lean meat yield; CREA= Carcass rib eye area ; CMAR = Carcass marbling score.

[b] FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM=mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive.

[c] P-value we obtained from allele substitution effect.

[d] FDR=False discovery rate. It is calculated as $FDR=mP_{(i)} / I$, where m is the total number of tests, $P_{(i)}$ is the SNP P-value at rank i when the P-values are ranked from lowest to highest and I is the rank of the SNP under test ((Benjamini and Hochberg, 1995; Weller et al., 1998;). *P<0.05, †P<0.10.

Table 3.36. Summary of haplotype based candidate genes associations with fat deposition and carcass merit traits in beef cattle populations.

Gene name[a]	Hybrid cattle population trait[b]	Angus cattle population trait[b]	Charolais cattle population trait[b]
FABP3	UREA**, AUREA*, SWT**, CWT**	----	----
FASN	AUREA*, CREA*	----	----
GPAM	UBF**, AUBF*, SWT**, CWT**, AVBF**, LMY** CREA**, CMAR**	UREA**, AURA**, CWT*, AVBF**, LMY**, CREA**, CMAR**	----
IDH1	UBF**, SWT**, CWT**,	----	----
IGF1	UBF**, AUBF**, AVBF**, LMY**, CREA**	---	----
INS	UBF**, AUBF**, SWT**, CWT**, CMAR**	----	----
LIPE	UBF**, AUBF**, SWT**, CWT**, AVBF**, LMY**, CREA**, CMAR**	UBF*, UREA**, AUREA*, SWT**, CWT**, AVBF*, LMY*, CREA*, CMAR**	UBF*, UREA**, AUBF**, SWT**, CWT*, AVBF**, LMY**, CREA**

[a] ACSF3=acyl-CoA synthetase family member 3; FABP3= fatty acid binding protein-3; FASN= fatty acid synthase; GPAM= mitochondrial glycerol 3-phosphate acyltransferase; IDH1= isocitrate dehydrogenase 1 (NADP+), soluble; IGF1= insulin-like growth factor 1; INS= Insulin; LIPE= lipase, hormone-sensitive; OLR1= oxidized low density lipoprotein (lectin-like) receptor 1.

[b] UBF = Ultrasound backfat, mm; UREA = Ultrasound rib eye area, cm^2; AUBF = Average daily gain of ultrasound backfat, mm; AUREA = Average daily gain of ultrasound rib eye area, cm^2; SWT = Slaughter weight, kg; CWT = Carcass weight, kg; AVBF = Average backfat, mm; LMY = Lean meat yield, %; CREA= Carcass rib eye area, cm^2 ; CMAR = Carcass marbling score. *$P<0.10$, **$P\leq0.05$.

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