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Whole Genome Scan of QTL for Ultrasound and Carcass Merit Traits in Beef Cattle

by

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ABSTRACT

A whole genome scan was conducted to identify and fine map QTL regions for ultrasound and carcass merit traits in beef cattle. A total of 465 steers and bulls, genotyped for 4592 SNPs, were analysed for 16 ultrasound and carcass merit traits using interval mapping, single marker regression and Bayesian shrinkage approaches. Thirty QTL and 22 SNPs associated with traits were identified by interval mapping and single marker regression respectively. In Bayesian shrinkage estimation, 218 QTL were identified, wherein 11 of the 30 QTL identified by interval mapping were confirmed. The proportions of QTL variance on the trait variations estimated by Bayesian shrinkage analysis were relatively small. They ranged from 0.1 to 4.8% compared to 6.1 to 11.7% in interval mapping because the QTL in Bayesian approach were adjusted to remove effects of other QTL in the genome. These results are useful for detection of underlying causative QTN variants.

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TABLE OF CONTENTS

5. General Discussions and Future Research

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ADG_UREA	Average daily gain ultrasound ribeye area
ANOVA	Analysis of variance
AVE_BF	Average backfat
BC	Backcross
BLAST	Basic local alignment search tool
BTA	*Bos taurus* autosome
cM	Centimorgan
CMAR	Carcass marbling
CREA	Carcass ribeye area
CWT	Carcass weight
DNA	Deoxyribonucleic acid
EBV	Estimated breeding values
F2	Second filial generation
FAO	Food and agriculture organization
GRDFAT	Carcass grade fat
LD	Linkage disequilibrium
LMY	Lean meat yield
MAF	Minor allele frequency
MAS	Marker assisted selection
MEAN_UBF	Mean ultrasound backfat
MEAN_UMAR	Mean ultrasound marbling
MEAN_UREA	Mean ultrasound ribeye area

miRNAs	Micro RNAs
NCBI	National Center for Biotechnology Information
QTL	Quantitative trait loci
QTN	Quantitative trait nucleotide
RFLP	Restriction fragment length polymorphism
RH	Radiation hybrid mapping
SNP	Single nucleotide polymorphism
UBF	Ultrasound backfat
UMAR	Ultrasound marbling
UREA	Ultrasound ribeye area
YGRDAE	Carcass yield grade

1. General Introduction

1.1. Introduction

Cattle domestication started about 10 000 years ago and, to date, more than a billion cattle are being raised annually worldwide for beef and dairy products as well as hides and draft power (Hayes et al. 2008; Burt 2009; Tellam et al. 2009). Beef production plays an important role in economic development, in which bovine meat is one of the major sources of protein nutrition for a 6.6 billion human population (Tellam et al. 2009). Beef ranks third in the world meat market after pig and poultry meat, and beef production in 2009 was estimated at 65.1 million tons (FAO, 2009). Even though beef has been consumed by many people, however, the consumers' demand on beef, especially in developed countries, is shifting towards the quality products that are leaner, healthy, safe, and produced using acceptable procedures (Verbeke et al. 2010). Therefore, for the beef industry to remain profitable, breeders and producers should produce animals and meat products that meet consumer preferences.

Significant genetic improvements of carcass quality in beef cattle have been achieved through traditional selection methods based on observable phenotypes and pedigree information without knowledge of the genetic architecture of the selected trait (Gutierrez-Gil et al. 2008; Dekkers and Hospital 2002). Traditional selection is based on quantitative genetic theory derived from Fisher's infinitesimal model that assumes a trait under selection is influenced by an infinite number of genes and that each gene has an infinitesimally small effect

on the trait (Dekkers and Hospital 2002). Conventional quantitative analysis has been used to predict breeding values and animals with the best predicted genetic merit for the trait of interest are selected as parents (DeNise 2004). Despite the tremendous genetic improvements that have been achieved by the genetic merit prediction and selection, Dekkers and Hospital (2002) pointed out several factors that limit the effectiveness of quantitative genetic selection due to: 1) phenotype being an imperfect predictor of an animal's breeding value or the trait has a low heritability. 2) phenotype may not be observed on both sexes or prior to the time when selection decisions have to be made, 3) phenotype is not very effective in resolving negative associations between genes resulting from epistasis or linkage.

Characterization of beef cattle at the molecular level can facilitate the understanding of genetic makeup of animals and their effect on phenotypic traits. Use of molecular information in beef cattle also makes it possible to select and breed animals with specific allele genotypes that naturally improve the quality of carcass and efficiency of production (Wibowo et al. 2007). Carcass traits are among the quantitative traits whose variations are controlled by segregation of multiple genes with small to moderate effects, therefore, selection of superior individuals in a population for genetic improvement using exiting variations requires collection of phenotype measurements on a relatively larger sample of progeny in order to accurately estimate breeding values of selected candidates (Dekkers and Hospital 2002). However, carcass merit traits are measured at a late stage of an animal's production cycle and animals have to be sacrificed to obtain accurate measurements of carcass traits. Thus, mapping of QTL and identification

of DNA markers influencing carcass merit traits have a potential to enhance the rate of genetic improvement through incorporating these QTL in selection programs in comparison to selection based on breeding value obtained from phenotype alone (Davis and DeNise, 1998). The current advancement in molecular genetics technology has enabled sequencing the entire genome of an organism and a better understanding about genetic architecture and DNA variants. The discovery of DNA polymorphic markers such as single nucleotide polymorphisms (SNPs) or microsatellites have facilitated the detection of QTL in animals (Hocquette et al. 2007). Incorporation of QTL information on estimation of breeding values (EBV) in animals through marker-assisted selection (MAS) can also increase selection accuracy and thus the rate of genetic improvement, especially for traits that are difficult or expensive to measure, or which can only be measured late in life such as carcass merit traits. Since DNA information can be obtained at any stage of an animal's life to assess its genetic potential with no restriction to sex, as a result, some of the limitations associated with quantitative genetic prediction and selection based on phenotype can be alleviated (Dekkers and Hospital, 2002).

Although numerous QTL has been reported for various carcass traits in beef cattle, however, most of the QTL mapped previously are in larger intervals which can range from 20 to 40 cM that may contain possibly thousands of genes (Grapes et al. 2004). Therefore, further studies are still needed to fine map the previous detected QTL regions associated with traits in order to facilitate detection of DNA markers or potential candidate genes contributing to variations

of traits in beef populations in order to effectively implement the MAS. Furthermore, the detection of QTL for carcass merit traits is still a focus of research because traditional QTL mapping procedures have encountered several biological and statistical complications. Some of the challenges that have been encountered in QTL mapping include small genetic variances of individual loci (Lynch and Walsh 1998), pleiotropy or interaction of QTL with other genes and environmental factors (Glazier et al. 2002), incidence of false positives as a result of statistical method robustness or unsuitable experimental designs as well as the increase of the number of DNA markers analyzed (Xu 2003a; Wang et al. 2005; Takasuga et al. 2007), and small number of informative offspring per pedigree (Beavis 1998; Xu 2003b).

1.2. Research Hypothesis

Phenotypic variations in ultrasound and carcass merit traits which exist among beef cattle in the Kinsella beef hybrid population are determined by genetic variations of alternative alleles of segregating genes. Hence it is possible to use genetic markers to identify and fine map quantitative trait loci that segregate in the population and to use this genetic markers information to improve the accuracy of selecting beef cattle with superior genotypes for carcass merit traits. In addition, the QTL regions can be fine mapped and the accuracy of estimations on QTL effects can be improved through more advanced statistical and QTL analyses.

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2. Literature Review

2.1. Quantitative Trait Loci Mapping

Chromosome regions where the genes that affect quantitative traits are located are referred to as quantitative trait loci (QTL). The identification of such chromosome regions or QTL mapping is carried out using animal populations created to maximize phenotypic variance for the traits of interest. Individuals carrying the desired allelic variant of QTL can be identified through either linkage analysis, linkage-disequilibrium scanning or by a direct candidate gene study for the desired variant (Anderson, 2001). However, the linkage mapping approach usually identifies QTL in large confidence intervals which do not have sufficient resolution for effective identification of candidate genes to allow association tests (Ronin et al. 2003).

The QTL regions identified by linkage analyses via interval mapping approaches can be fine mapped up to a certain point to increase the mapping resolution using a high density of genetic markers (Darvas et al. 1993) and/or through association analyses that identify QTL by exploring historical linkage disequilibrium (LD) between genetic markers and causative mutations. Other alternatives for improving QTL mapping resolution include using enhanced statistical approaches such as composite interval mapping which fits selected markers in untested regions as cofactors in the model to absorb the effects of background QTL (Jansen 1993; Zeng 1994), multiple-interval mapping which estimates locations and effects of QTL simultaneously (Kao et al. 1999) and

Bayesian shrinkage approaches which can handle all model effects simultaneously (Xu 2003a; Wang et al. 2005). Subsequent to QTL mapping, further analysis is conducted to identify the underlying functional quantitative trait nucleotides (QTN) within the QTL regions, which give rise to phenotypic variations. Detection of QTL is an essential step for positional cloning of genes affecting the traits of interest (Imai et al. 2007).

2.2. QTL Mapping Population

The first step in the process of QTL mapping is to create a mapping population by making a cross using founder animals or by using an existing population. Different types of cross have been designed in livestock populations to establish linkage disequilibrium that allow co-segregation of QTL and markers within the mapping population to facilitate QTL detection (Kearsey 1998). Line crossing from divergent founder animals with large phenotypic differences is commonly used in swine and poultry to analyse the effects of two alternating QTL alleles segregating in a population through mean difference between the genotype groups (Kerje et al 2003; Knott et al. 1998). The power to detect QTL in line crossing is especially high if there are large differences in gene allele frequencies for the studied trait. In outbred animals, QTL mapping is more complicated than inbred line crosses because QTL are not segregating in all families and markers might not be fully informative, therefore large samples are needed to estimate the QTL effect on a trait.

Common mapping populations in outbred species such as bovine include full-sib, half-sib or daughter and granddaughter designs (Casas 2002; Weller et al. 1990). In addition, existing commercial herd populations consisting of multiple half-sib families can be utilized for QTL mapping. Using available commercial lines of beef or dairy cattle is less expensive than creating experimental populations, which is costly and time consuming (Grapes *et al*., 2006; Grapes *et al*., 2004). Paternal half-sib family or daughter design in beef and dairy cattle, respectively, are mostly used for QTL mapping where two progeny groups from the common heterozygous parent (sire) tend to have different means of a quantitative trait due to alternative alleles they received at a linked QTL (Mizoshita et al. 2004). On the other hand, divergent breeds of cattle such as *Bos taurus* and *Bos indicus* or beef and dairy breeds have also been commonly crossed to create second filial generation (F2) mapping populations, signifying that they may carry different alleles at loci controlling traits of interest, in which the statistical power of the experiment can be enhanced (Casas et al. 2003a, Guetierez-Gil et al. 2009).

2.3. Ultrasound and Carcass Merit Traits

Ultrasound measures have been used to predict carcass merit traits such as back fat thickness, longissimus muscle area, and marbling in live animals. The ultrasound measurements provide an early indication of carcass quality status of animals and they are non-destructive procedures to animals and body tissues, which allow monitoring changes in fat and muscle accretion and body

composition in the live animals during growth (Robeiro et al. 2008). However, the accuracies of ultrasound in predicting carcass traits are variable and depend on the cattle populations and the traits that are being measured. The correlations between ultrasound measurements and carcass traits in beef range from 0.45 to 0.96 for fat thickness; 0.2 to 0.94 for the area of *longissimus* muscle; and 0.2 to 0.91 for the marbling score (Houghton and Turlington 1992; Greiner et al. 2003). Although the ultimate measurement of carcass merit traits can only be made with high accuracy when animals are slaughtered, ultrasound measures provide a predictive or alternative measure to carcass merit traits, and data analyses on such ultrasound measures help in the understanding of the biological processes of animal development.

2.4. Genetic Markers

Genetic markers are any polymorphic loci that are in a pedigree. Most genetic markers are neutral and have no effect on the trait but are in linkage disequilibrium with the causative genes. However, some genetic markers are themselves part of causative genes, where their polymorphisms have direct effects on the trait variation (Montaldo and Meza-Herrera 1998). Major types of genetic markers that have been used for QTL mapping include random amplified polymorphic DNA (RAPDs), restriction fragment length polymorphisms (RFLPs), simple sequence repeats (SSRs) or microsatellites, and single nucleotide polymorphism (SNPs). The RAPDs, SSRs and RFLPs were commonly used in plant and animal populations for genetic and QTL mapping studies in the past,

before SNPs became available. SNP markers have become widely used as genetic markers in human, bovine and other species due to their high abundance in the genome, possible direct cause of the phenotype variation, relative high stability and suitability for high throughput genotyping compared to other genetic markers.

2.5. Methods of QTL Detection

Several statistical methods have been developed and applied in QTL mapping studies. The statistical methods can be categorized according to dimension of their QTL models such as one-dimensional search algorithms, such as single marker linkage disequilibrium QTL mapping and interval mapping, as well as multiple-QTL model approaches which includes various modified versions of interval mapping, and several Bayesian QTL mapping approaches.

2.5.1. Single marker linkage disequilibrium QTL mapping

Linkage disequilibrium (LD) QTL mapping, also referred to as association mapping, is an approach that tests associations between a single marker and a quantitative trait based on linkage disequilibrium using either *t*-test, analysis of variance (ANOVA) or simple regression (Doerge 2002). Individuals are divided into distinct genotype groups according to their marker genotype classes which are assumed to be in LD with the genotypes of the causative gene, and the analysis is performed to compare the observed trait means of marker genotype groups. Experimental populations such as back cross (BC) has only two marker genotype classes in which difference between trait means of marker genotype

classes can be tested using *t*-test. The analysis of variance (ANOVA) is statistical procedures that partition observed variance into components due to different sources of variation. The ANOVA is used to test the difference between trait means in populations that have three marker genotype classes, for example second filial generation (F2) and half-sib whereas the effects of marker genotype classes can be estimated by simple regression for a single marker. The *t* or *F*-statistic test above the threshold value is considered as evidence for significant association between a marker allele and the phenotype. A linear model for simple regression analysis for single marker can be described as

$$y = \mu + \beta x + e$$

where y is the phenotype, μ is the overall mean, β is the maker effect, x is the marker genotype, and e is residual error. The model can also include other fixed effects as cofactors such as breed, age or contemporary group, which may have effects on the association between markers and phenotype. Least squares linear regression methods are used to estimate the values of unknown model parameters of μ, β, and variance (σ^2) that minimize the mean squared residual errors obtained as the difference between phenotype and fitted value (Lynch and Walsh 1998). Single marker regression has less computational demand, however the position of a QTL is not precisely determined since this method cannot distinguish between large effect QTL far from the marker and small effects QTL close to the marker as both scenarios give the same likelihood ratio (Lander and Botstein (1989).

2.5.2. Interval Mapping

The interval mapping is a useful approach for detection of QTL within pairs of flanking markers and therefore gives an additional power for QTL detection and relatively accurate estimates of QTL effects as well as the QTL position in comparison to single marker analysis, particularly when the markers are widely spaced. Lander and Botstein (1989) pioneered the interval mapping using linear regression models where QTL are searched along the chromosomes at intervals of genetic markers at 1 or 2 cM apart. Each marker interval is subject to statistical estimates of model parameters and is therefore called a putative QTL. Estimates of model parameters can be carried out using either maximum likelihood ratio test or ANOVA in which the *F*-statistic test is used to indicate the significant presence of QTL. Classic models for interval mapping analysis can be described as

$$y = \mu + m\alpha + e$$

where y is the observed phenotype (normally corrected for fixed effects), μ is the overall mean, m is the genotype of putative QTL, α is the QTL effect, and e is a residual effect.

Interval mapping can be employed in either line-cross analysis, commonly used in pigs and poultry. It assumes founder lines are fixed for different QTL alleles (Haley et al. 1994) or the analysis is nested within half-sib families without making assumptions regarding the phase of common parents (sires) QTL alleles (Knott et al. 1996). The half-sib model described by Knott et al. (1996) is commonly used in beef and dairy cattle based on multiple-marker interval

mapping for half-sib families. In this approach, the probability of inheriting a sire's putative QTL allele is usually calculated for each animal at 1-cM intervals conditional on the information from the closest informative flanking markers. Regression analysis of QTL effects are nested within sire families because the linkage phase between a marker and a QTL could be different for each family (Ashwell et al. 2004). The test statistic to estimate the most likely position of a putative QTL can be calculated as *F*-statistic profiles or maximum likelihood (ML) estimations (Lander and Botstein 1989; Lynch and Walsh 1998). The *F*-ratio is calculated for every map position and the location with the largest *F*-statistic is considered as the most likely position of a putative QTL. Since the interval mapping method involves multiple testing along the genome, the significance thresholds of *F*-statistics are normally derived empirically by a permutation test which involve shuffling of the original phenotype data in a given number of times e.g. 10,000 permutations in order to control the chromosome-wise type-I error rate at a desired significance level as described by Churchill and Doerge (1994). The interval mapping approach infers missing genotypes of a marker using the nearest flanking markers. Nevertheless, interval mapping procedure analyze one position of the genome at a time and cannot handle models with multiple QTL. Therefore, it often results in problems of false significant tests and overestimation of QTL variance especially when a small sample size is used for QTL mapping. Therefore, a number of improved versions of interval mapping approaches have been developed to handle multiple-QTL models. These include

composite interval mapping (Jansen 1993; Zeng 1994) and multiple-interval mapping approaches (Kao et al. 1999).

Composite interval mapping is a multiple-QTL model approach, which estimates the effect for a target QTL in one interval while simultaneously including the effects of background QTL outside the testing interval as cofactors in order to adjust for the non-target QTL effects (Jansen 1993; Zeng 1994). The inclusion of cofactors as covariates improves the efficiency of QTL mapping. However, criteria for deleting and inserting a QTL can be arbitrary, which could obscure the significance of tested QTL (Xu 2003a).

The multiple-interval mapping method is a one-step multiple-QTL model approach developed to overcome the limitations of composite interval mapping. The multiple-interval mapping method is based on a variable selection to select optimal sets of putative QTL using approaches such as stepwise regression (Kao et al. 1999), Bayesian information criteria (BIC) (Ball 2001) or stochastic search variable selection (SSVS) (Yi et al. 2003) to determine whether the QTL should be included or dropped from the model. The multiple-interval mapping method has improved power and precision of QTL mapping compared to composite interval mapping.

2.5.3. Bayesian QTL mapping

Bayesian analysis is a statistical approach which makes inferences from data using probability models that link the data to the parameters (Yi and Shriner, 2008). Bayesian QTL mapping can evaluate associations of all genetic markers

simultaneously in a single model in which the number of QTL, their genomic positions and their genetic effects are inferred jointly, hence overcoming some of the limitations associated with the interval mapping genome scan and the single marker association analyses (Xu 2003a; Yi and Shriner, 2008). Bayesian statistics are based on probabilistic models and treats every variable and parameters as random variables. Every unknown parameter is assigned a prior probability distribution. Bayesian analysis generates a posterior probability distribution regarding unknown parameters of interest using the sample data expressed by likelihood and prior probability. In Bayesian QTL mapping, parameters are classified into observables which include phenotype and marker information, and unobservable parameters which include QTL position, QTL genotype, QTL effect and/or variance (Xu 2003a). Bayesian analysis infers the posterior distribution of the unobservable conditional on the observable. Combination of the prior information and the data can be achieved through Bayes' rule

$$p(b, v, x, \lambda|y, m) = \frac{p(y, m|b, v, x, \lambda)\, p(b, v, x, \lambda)}{p(y,m)}$$

where b is the QTL effect associated with markers, v is the QTL variance, x is QTL genotype, λ is the QTL position, y is the phenotype, and m is the marker genotype. The term $p(b, v, x, \lambda|y, m)$ represents posterior distribution of unknown parameters, the condition distribution of parameters given the data; $p(b, v, x, \lambda)$ represents the prior distribution, information based on previous experiments or theory; $p(y, m|b, v, x, \lambda)$ is the likelihood; $p(y,m)$ is the marginal posterior probability, a normalizing factor. Bayesian analysis can be implemented through the Markov chain Monte Carlo (MCMC) to draw a sample from the simulated

joint posterior distribution in order to make inferences on the unknown parameters (Xu 2003a; Wang et al. 2005). The MCMC sampling steps from posterior distribution of unknown parameters can be achieved using one of the main algorithm such as Gibbs sampling (Xu 2003a; Wang et al. 2005) or the Metropolis-Hastings algorithm. The mean values of the sample distributions represent the estimate for the respective unknown parameters.

Several Bayesian QTL mapping approaches have been developed including the Bayesian shrinkage estimation that forces marker intervals with no QTL to have estimated effects that shrink close to zero which increases the power to discriminate QTL effects from residual errors and generates clear signals of QTL effects (Xu 2003a; Wang et al. 2005). Other Bayesian QTL mapping approaches include genome-wide analysis of epistasis effects of QTL (Xu and Jia 2007; Xu 2007) and Bayesian QTL mapping for multiple traits (Benerjee et al. 2008). Generally, Bayesian approaches allow the incorporation of prior information for multiple unknown parameters into the observed data and it can estimate the effect of all putative QTLs in a genome simultaneously.

2.5.4. Positional Candidate Gene Analysis

The ultimate goal of QTL mapping is to identify causative mutations in genes responsible for the phenotype variation; therefore, candidate gene analysis can be carried out to identify polymorphic variants causing detectable phenotypic effects. The identified QTL regions could facilitate the identification of targeted candidate genes through positional candidate gene analysis. However the

candidate gene analysis needs a high resolution of the QTL region in order to increase the probability of selecting the potential candidate (Flint and Mott, 2001). Positional candidate gene analysis can be coupled with positional candidate cloning strategy for functional analysis to determine if the markers are true causative mutations (Anderson 2001; Marques et al. 2009). Examples of positional candidate gene analysis to determine associations between polymorphisms in genes and QTL with carcass merits in beef cattle include association analysis by Morsci et al. (2006) that confirmed the polymorphisms in the *somatostatin* (*SST*) and *adiponectin* (*ADIPOQ*) genes as the underlying effect to the ribeye muscle area QTL and the marbling score QTL on BTA 1, respectively. Buchanan et al. (2002) described associations between polymorphisms within the bovine *leptin* (*LEP*) with carcass fat levels in beef. Also, the SNPs in the leptin gene have shown significant associations with grade fat, ultrasound backfat thickness and lean meat yield (Nkrumah et al. 2004). Marques et al. (2009) reported the association between polymorphisms in the *2,4 dienoyl CoA reductase 1* (*DECR1*) and *core binding factor, runt domain, α subunit 2; translocated to 1 gene* (*CBFA2T1*) positional candidate genes on BTA 14 and 26 with ultrasound marbling score and ultrasound backfat in beef cattle, respectively. Additionally, the polymorphisms within the fibroblast growth factor 8 (*FGF8*) candidate gene on BTA 26 were reported to influence the carcass backfat and lean meat yield in beef cattle (Marques et al. 2009). The association test on the candidate gene by Barendse et al. (2004) found that the single nucleotide polymorphism on the thyroglobulin (*TG*) gene was contributing to the

variation of carcass marbling score in beef cattle. A study performed by Grobet et al. (1997) proved that the mutation in the myostatin gene was causative of the double muscle phenotype in the Belgian Blue cattle. The progress in searching for polymorphisms associated with carcass merit traits in candidate genes has enabled the development of commercially available DNA tests for cattle QTL (Hocquette et al. 2007). Examples of several candidate genes with polymorphisms associated with carcass traits in beef cattle are also summarized in Table 2.1.

2.6. QTL for Ultrasound and Carcass Merit traits

Chromosomal regions harbouring QTL for several ultrasound and carcass merit traits in beef cattle have been reported by many researchers and summarized in Table 2.2. Also, the allelic variants influencing carcass traits has been identified in a number of these QTL regions through association studies (Hocquette et al. 2007). The QTL for carcass traits in beef cattle that have been identified to date have also been summarized in an online QTL database (Cattle QTLdb 2003). These studies have used microsatellite or a combination of DNA markers to identify QTL for carcass merit traits such as carcass weight (Gutierrez-Gil et al. 2009; Takasuga et al. 2007; Mizoshita et al. 2004; Abe et al. 2008), and quality traits, such as carcass marbling (MacNeil and Grosz, 2002; Imai et al. 2007; Mizoguchi et al. 2005), carcass fatness (Kim et al. 2003), meat tenderness (Davis et al. 2007), carcass composition (Casas et al. 2003a; Casas et al. 2003b; Casas et al. 2001; Casas et al. 2000), meat quality (Gutierrez-Gil et al. 2008) and ultrasound traits (Li et al. 2006). Some of these QTL may not be sufficiently

informative for the development of marker assisted selection strategies or to identify the underlying causative quantitative trait nucleotides (QTN) because they are localized to large chromosomal regions due to the low density of markers maps used. Various strategies have been applied to fine map the identified QTL regions. These include the population-wide LD mapping which exploits historic LD and has been commonly used in dairy cattle where artificial insemination is widely used and bulls have larger families with phenotypic records. The Population-wide LD mapping has seldom been used in beef cattle because of the small number of offspring per family which do not have enough power to detect QTL effects. Nonetheless, commercial lines of beef cattle have been used for LD analysis to fine map the QTL for carcass traits (Li et al. 2002; Moore *et al*. 2003; Li et al. 2004; Kneeland et al. 2004). Beef cattle commercial lines are semi-closed populations in which individuals are related and share common haplotypes that are identical by descent. Use of greater density SNP markers is another useful strategy that has been used successfully for QTL fine-mapping in both beef and dairy cattle (Hirano et al. 2007; Druet et al. 2008; Daetwyler et al. 2008; Sherman et al. 2009, Snelling et al. 2010).

2.7. Scope of QTL Mapping Research

QTL mapping has been carried out to identify genetic markers that could be used to improve the quality of economically important traits in agricultural organisms such as beef cattle through marker-assisted selection. The current release of the cattle QTL database contains 2359 QTL that represent 212 traits for

beef and dairy (Cattle QTLdb 2003). Among the 2359 QTL on the cattle QTL databases there are 135 QTL for 6 important carcass traits of weight, fat thickness, marbling score, ribeye area, yield grade and subcutaneous fat (Table 2.2).

Despite the fact that many QTL for carcass merit traits have been identified in beef cattle, further studies are needed as previous studies, the QTL were analysed either using sparse marker density, few markers per chromosome, or the QTL were examined in only a few of the selected chromosomes and with less robust statistical methods. As a result, most of the reported QTLs are localized in larger chromosomal regions and thus have a weak confidence support. Therefore, a whole genome scan using a denser SNP marker set and with more robust QTL mapping methods will fine map and verify the previous identified QTL regions. Also, the SNP marker association analyses will be able to identify specific SNP markers influencing carcass merit traits which will facilitate marker-assisted selection.

Moreover, most of the QTL results in beef cattle may have their use for MAS limited to a mapping population because each individual beef population can have a different genetic background in which the identified genetic markers in one population are not necessarily useful for another population due to differences in linkage phase of a genetic marker and QTL (Dekkers and Hospital 2002). Therefore, more populations of beef cattle need to be genotyped to validate the QTL results. On the other hand, it is seldom possible to establish associations between genetic markers and all important carcass merit traits by focusing on a few restricted populations of beef cattle since each population can have a given

set of QTL which segregates for a proportion of all traits of interest. Therefore, QTL mapping in different populations should allow the capture of sufficient numbers of QTL for each trait of interest.

The objectives of this study is to conduct a whole genome scan to identify and fine map QTL regions for ultrasound and carcass merit traits in beef cattle using a denser SNP marker set through interval mapping, single marker regression and Bayesian shrinkage estimation approaches. The study also aims to identify SNP markers within genes that are associated with ultrasound and carcass merit traits as well as their possible gene locations and functions.

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Table 2.1: Examples of candidate genes with polymorphisms associated with carcass traits

BTA	Gene symbol	Gene name	Trait	Breed	Reference
3	*LEPR*	leptin receptor	Grade fat, intramuscular fat content, Subcutaneous fat content	Crossbreed	Schenkel et al. (2006)
4	*NPY*	neuropeptide Y	Carcass marbling, Ultrasound marbling	Crossbreed	Sherman et al. (2008)
7	*CAST*	calpastatin	Meat tenderness	-	Hocquette et al. (2007)
10	*CAPN3*	calpain 3, (p94)	Meat tenderness	-	Hocquette et al. (2007)
14	*CRH*	corticotropin releasing hormone	Carcass marbling, Ultrasound ribeye area	Crossbreed	Buchanan et al. 2005; Wibowo et al. (2007)
14	*TG*	thyroglobulin	Carcass marbling	-	Hocquette et al. (2007)
15	*UCP2*	uncoupling protein 2 (mitochondrial, proton carrier)	Average backfat, Lean meat yield, Yield grade	Crossbreed	Sherman et al. (2008)
15	*UCP3*	uncoupling protein 3 (mitochondrial, proton carrier)	Carcass marbling, Lean meat yield	Crossbreed	Sherman et al. (2008)
19	*GH1*	Growth hormone	Carcass marbling, Rump fat	Angus, Shorthorn	Barendse et al. (2006).
29	*IGF2*	insulin-like growth factor 2 (somatomedin A)	Carcass ribeye area, Ultrasound backfat, Ultrasound marbling,	Crossbreed	Goodall and Schmutz (2007); Sherman et al. (2008)
29	*CAPN1*	calpain 1, (mu/I) large subunit	Meat tenderness	-	Hocquette et al. (2007)

Table 2.2: Number of QTL reported for 6 carcass traits in beef cattle[z]

Trait	Number of QTL	Chromosomes
Carcass weight	28	1, 2, 4, 6, 7, 10, 13, 14, 15, 16, 18, 22, 24
Fat thickness	23	1, 2, 3, 5, 6, 7, 8, 14, 19, 20, 21, 23
Marbling score	50	2, 3, 4, 5, 6, 7, 8, 9, 10, 14, 16, 17, 18, 19, 20, 21, 22, 27
Ribeye area	3	2, 19, 26
Yield grade	9	1, 2, 5, 11, 14, 19, 20
Subcutaneous fat	22	1, 2, 6, 7, 10, 11, 12, 13, 14, 15, 19, 28

[z]This list includes only those QTL reported in the current release (December 2009) of the cattle QTL database (Cattle QTLdb 2003).

3. Whole Genome Fine Mapping of QTL for Ultrasound and Carcass Merit Traits in Beef Cattle

3.1. Introduction

Carcass merit traits in beef cattle are of particular interest to the beef industry as they are related to both the efficiency of beef production and consumer preferences for meat consumption, and as a result, they affect the profitability of the industry. A sustainable beef industry depends on efficient production and constant improvement of meat quality. Carcass merit traits are among the quantitative traits that are measured relatively late in an animal's production cycle. Incorporating the genes or DNA markers influencing carcass traits into the traditional genetic evaluation and selection programs using marker-assisted selection (MAS) holds great potential to accelerate the rate of genetic improvement by increasing the accuracy of genetic evaluation and shortening the generation interval (Dekkers and Hospital 2002). However, in order to implement marker-assisted selection effectively, closely linked DNA markers or gene alleles, or preferably functional quantitative trait nucleotides (QTN), influencing the quantitative traits of interest need be identified, characterized and validated.

In beef cattle, most of the early gene-discovery studies conducted to identify quantitative trait loci (QTL) of economic importance including carcass quality traits used microsatellite markers alone or in combination with single nucleotide polymorphism (SNP) markers (Beever et al. 1990; Stone et al. 1999; Keele et al. 1999; Casas et al. 2000; Li et al. 2006). Candidate gene and positional

candidate gene approaches have also been used to identify polymorphisms that affect carcass quality traits in beef cattle (Grobet et al. 1997; Moore et al. 2003; Nkrumah et al. 2004). In a previous study, a genome-wide scan for QTL affecting ultrasound and carcass backfat thickness was conducted in a hybrid beef steer population using a combination of 100 microsatellite and 355 SNP markers with 8 to 30 markers per chromosome (Li et al. 2006). However, the QTL were localized to large chromosomal regions (4 to 24 cM), which is likely due to the low density of markers used, thus limiting their usefulness in the development of marker-assisted selection strategies and as a tool for identifying causative quantitative trait nucleotide(s).

In cattle and other species, SNPs have become a widely used DNA marker type for QTL mapping and association analyses due to their high abundance in the genome, possible direct cause of phenotype variation, relatively high stability and suitability for high throughput genotyping in comparison to other DNA markers. The objective of this study was to conduct a whole genome scan to identify and fine map QTL regions for ultrasound and carcass merit traits in beef cattle by using a denser SNP marker set and to identify SNP markers within the QTL regions that are associated with the ultrasound and carcass merit traits through association analyses.

3.2. Materials and Methods

3.2.1. Animal Resources and Phenotypic Data

A total of 465 steers from 28 sire families from the University of Alberta's Kinsella Research station were used in this study. The animals were managed and cared for according to the guidelines of the Canadian Council of Animal Care (CCAC, 1993). The composition of this population has been previously described by Nkrumah et al. (2007a, b). Briefly, it was produced by crossing Angus, Charolais, or University of Alberta hybrid bulls and a hybrid dam line. The hybrid dam line was obtained by crossing among three composite cattle lines, namely beef synthetic 1, beef synthetic 2, and dairy x beef synthetic for more than 10 years. The beef synthetic 1 was composed of 33% Angus, 33% Charolais, and 20% Galloway with the reminder from other beef breeds. The beef synthetic 2 was composed of about 60% Hereford and 40% other beef breeds. The dairy x beef synthetic line was made up of approximately 60% dairy breeds (Holstein, Brown Swiss, or Simmental) and 40% beef breeds mainly Angus and Charolais (Goonewardene et al. 2003). Steers were produced over 3 years from a multiple-sire breeding program on pasture and the sire of each calf was later determined using a panel of microsatellite markers (Nkrumah et al. 2007a, b).

3.2.2. Traits Studied and Measurements

The measurements of ultrasound traits were obtained as part of the phenotypic data collection during the feedlot tests that were conducted at the University of Alberta's Kinsella Research Station in 2003, 2004 and 2005 with 2

batches of steers tested per year, and the carcass merit traits were collected in the abattoir, was described by Nkrumah et al. (2004; 2007a, b). Briefly, ultrasound measurements of rib eye area (UREA), backfat thickness (UBF) at the 12^{th} to 13^{th} ribs, and marbling score (UMAR) were recorded at 28-day intervals during the feeding tests for a period of approximately 100 days using an Aloka 500V real-time ultrasound with a 17-cm, 3.5-MHz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC). Average daily gain for ultrasound ribeye area (ADG_UREA), ultrasound backfat (ADG_UBF), and ultrasound marbling score (ADG_UMAR) were estimated using a linear regression analysis. Carcass weight (CWT) was measured as a summation of the left and right halves of each carcass. Carcass grade fat (GRDFAT) was measured at the 12^{th} – 13^{th} rib. Carcass marbling (CMAR) is a measure of the intramuscular fat with a score of 1 to <2 for trace marbling, 2 to <3 for slight marbling, 3 to <4 for small to moderate marbling, and ≥ 4 for slightly abundant or more marbling. Carcass average back fat (AVE_BF) is the fat thickness measured over the ribeye muscle at 12^{th} rib. Lean meat yield (LMY), an estimate of the saleable meat, was estimated using the following equation: lean meat yield, % = 57.96 + (0.202 × *L. thoracis* area, cm^2) – (0.027 × warm carcass weight, kg) – (0.703 × average backfat thickness, mm). Carcass ribeye area (CREA) was measured on the cross section of the *longissimus dorsi* muscle between the 12^{th} and 13^{th} ribs. Yield grade (YGRADE) refers to the proportion of lean meat and was classified as follows: 1 = ≥59%; 2 = 54 to 58%; and 3 = <54%. A total of 465 steers with phenotypic and genotype data were available for this study. However, only 370 steers from 16 sire families were used

for the interval QTL mapping analyses, with an average 23 progeny per sire and a half-sib family size that ranged between 9 and 56. Families where the number of offspring was less than 9 were excluded from the interval QTL mapping analyses. The average ages at start of test and at slaughter were 251 and 389 days, respectively. However, carcass merit data were available on 342 steers. The descriptive statistics of the ultrasound and carcass merit traits considered in the study are presented in Table 3.1.

3.2.3. DNA Isolation and SNP Genotyping

A 10-ml blood sample was collected by jugular venipuncture from each steer during the feedlot tests. Calf genomic DNA was extracted from blood samples using a standard saturated salt, phenol-chloroform method (Miller et al. 1988). Steers were genotyped for a total of 4592 SNP markers. The 4592 SNP markers were chosen based on their locations on a radiation hybrid map that was constructed based on marker loci across eight breeds of cattle (McKay et al. 2007). The 4592 SNP markers were distributed on all 29 bovine autosomes (BTA) spanning 2914.4 cM of the linkage maps with a range of number of SNPs per chromosome from 58 (BTA 27) to 334 (BTA5) and an average distance of 0.63 cM between SNP markers. The approximate locations of the 4592 SNP markers in cM were inferred based on a composite physical map of the bovine genome of Snelling et al. (2007).

3.2.4. Whole Genome QTL Fine Mapping

Phenotypes for ultrasound and carcass merit traits were pre-adjusted for the fixed effects of feedlot batch-year contemporary groups (6 levels for 2 feedlot batches over 3 years) and sire breeds as well as linear covariates of animal age at the start of the test for ultrasound traits and animal age at slaughter for carcass merit traits using PROC GLM (SAS 9.1.3 Institute Inc., NC), and the resulting residuals were used as phenotypes for the interval QTL mapping analyses. A whole genome QTL scan was first conducted using an across-family analysis through the multiple marker regression approach (Knott et al. 1996) as implemented in the *QTL Express* software (Seaton et al. 2002). The across-family QTL scan tests the QTL effects nested within sire families and provides evidence of the segregation of QTL in the overall experimental population. Subsequently, a within-family QTL analysis was carried out to further examine which sire family was potentially segregating for the putative QTL.

Both the across-family and within-family QTL scans were performed at a 1-cM marker interval and the *F*-statistic tests were plotted along the chromosome. The chromosome-wise significance thresholds of the *F*-statistic tests for both the across-family analyses and the within-family QTL analyses were obtained by 10,000 permutations (Churchill and Doerge 1994) also as implemented in the *QTL Express* software (Seaton et al. 2002). The genome-wide significance thresholds, P_{genome}, were determined for across-family analyses by applying a Bonferroni correction to the chromosome-wise thresholds, $P_{chromosome,}$ as described by de Koning et al. (1998):

$P_{genome} = 1 - (1 - P_{chromosome})^n$,

where *n* is the number of chromosomes used in the analysis.

The QTL search was first conducted using the one-QTL model. Background QTL effects were analyzed for chromosomes that showed multiple QTL peaks on *F*-statistic profiles. The most significant QTL were fitted as co-factors to determine the presence of another QTL on the same linkage group. Results showed no evidence of multiple QTL on chromosomes which showed multiple peaks on the *F*-statistics profiles for the traits under investigation.

3.2.5. Single SNP Association Analyses under Identified QTL Regions

SNPs in the significant QTL regions identified in across-family analyses were further assessed for their associations with the phenotypic traits using a single SNP marker association analysis**.** The association analysis was conducted using the Linear Mixed Model Procedure of SAS (SAS 9.1.3 Institute Inc., NC) and the unadjusted phenotypic values of the data set including 418 steers with 28 sires and 298 dams. The model included the fixed effects of breed of sire (Charolais, Angus, or hybrid), batch-year effect (six levels), SNP genotype effect and random effects of sire and dam of animal. Sires were considered to be unrelated and therefore the random effect of sire was included in the model to account for expected co-variances among paternal half-sibs as described in Nkrumah et al. (2007a). Animal age at the start of the test was included as a covariate for the analysis of ultrasound traits. Animal age at slaughter was included as a covariate for the association analyses of carcass merit traits. The

additive effect of a SNP marker was estimated as half the difference between genotypic values of the two homozygous genotypes. The dominance deviation was estimated as the deviation of heterozygote genotypic value from the mean of the two homozygous genotypic values (Falconer and Mackay 1996).

3.3. Results and Discussion

3.3.1. QTL for Ultrasound and Carcass Merit Traits

The whole genome across-family QTL scan identified 12 QTL that were significantly associated with 5 ultrasound measures on 9 *Bos taurus* autosomes (BTA) at a chromosome-wise significance level of 5% with 4 QTL exceeding the 1% chromosome-wide significance threshold (Table 3.2). For the carcass merit traits, a total of 18 significant QTL for 6 carcass merit traits were identified on 10 chromosomes at a chromosome-wise significance level of 5%, whereas 5 QTL exceeded the 1% chromosome-wise significance threshold (Table 3.3). However, none of the above QTL reached the genome-wide significance level of 5% (Table 3.2 and 3.3). Examples of QTL profiles for the across-family analyses are shown on Figure 3.1 to 3.5.

The within-family QTL analyses identified 53 QTL with significant effects for 9 ultrasound traits on 23 chromosomes in 14 sire families (Table 3.4) and 25 QTL regions for 7 carcass merit traits on 16 chromosomes in 11 families at the chromosome-wise threshold of 1% (Table 3.5). The within-family QTL analysis confirmed 4 QTL for ultrasound traits and 11 QTL for carcass merit traits that were identified by the across-family QTL analyses. For the remaining 15

across-families QTL identified, the within-family QTL analyses detected significant QTL nearby for 4 of them (Table 3.2 and 3.3).

The average QTL 95% confidence interval of the 30 QTL identified in the across-family QTL analyses was 2.9 cM with a range of 0.6 to 11 cM. Three of the 30 across-family QTL regions identified in this study were localized to similar chromosomal regions that were reported previously by other studies using different beef cattle populations (Casas et al. 2001; Casas et al. 2003; Takasuga et al. 2007), providing additional support for the findings. These include QTL for ADG_UREA, MEAN_UBF and UMAR on BTA 5, 8 and 21 respectively. The ADG_UREA QTL on BTA 5 within the interval of 43.9 to 45.3 cM is consistent with longissimus muscle area QTL at 53 (38 – 66 cM) reported by Casas et al. (2003). The QTL for MEAN_UBF identified on BTA 8 (7.0 to 8.1 cM) is consistent with a previous identified QTL for fat thickness located in an interval between 6 to 30 cM (Casas et al. 2001). On BTA 21, the chromosomal region of 37.9 to 40 cM for UMAR QTL is consistent with marbling score QTL detected at 40 cM by Takasuga et al. (2007) in Japanese Black Cattle..

Six of the remaining 27 across-family QTL regions were close to regions reported on the same chromosomes by other studies (Kim et al. 2003; Li et al. 2006; Takasuga et al. 2007). These comprised the QTL for CWT, UBF, GRDFAT, and AVE_BF on BTA 6, 13, 15 and 18 (Table 3.2 and 3.3). The CWT QTL on BTA 6 (18 to 20 cM) and 18 (53.9 to 55.6 cM) were closely located to carcass weight QTL reported at 38 cM (Takasuga et al. 2007) and between 33.4 to 40.2 cM (Kim et al. 2003), respectively. UBF QTL on BTA 13 at 34.1 to 36.7 cM

in this study is also close to the QTL location for subcutaneous fat at 28 cM reported by Takasuga et al. (2007) in Japanese Black cattle. The QTL for UBF, GRDFAT and AVE_BF detected on BTA 15 in this study were also reported in a previous study using the same beef cattle population (Li et al. 2006). However, the QTL locations were shifted by 11 to 25 cM, which is likely due to an updated version of the bovine composite map used in this study. It may also represent different QTL as a denser marker set was used in this study for QTL detection in comparison to the previous study (Li et al. 2006). However, further investigation is required to confirm these QTL regions. The remaining 21 QTL identified by the across-family analyses in this study were not reported previously. Although using a higher density of markers could increase the resolution of QTL detection (Meuwissen and Goddard 2000), further studies using a larger sample size are needed to verify these QTL regions.

In addition to the across-family analyses, we also performed a within-family QTL analyses to further investigate the sire families segregating the QTL. For the 30 QTLs identified in the across-family analyses, 15 were confirmed by the within-family QTL analyses at the significance level of 5% (Table 3.2 and 3.3). However, another 15 QTLs identified by the across family analysis were not confirmed by the within family QTL analyses at the significance level of 5%. Significant QTL effects that were obtained by pooling together several sire families with weak to moderate QTL effects may not be identified as a significant QTL within individual families, which was discussed in a previous QTL mapping study by Nkrumah et al. (2007a) for different traits. In addition, marker

heterozygosity differences between sires could be the cause of the shift of QTL locations between across-family and within family analyses (de Koning et al. 1999). It was noted that additional QTL were identified in the within-family analysis in comparison to the across family QTL analyses. It is likely that the effects of some of these QTL were overestimated due to a small number of informative offspring per sire half-sib family (Beavis 1998; Xu 2003) although half-sib families with less than 9 offspring were not included in the analyses.

It was observed that the ultrasound and carcass merit measurements made on similar traits do not share the same QTL. Possible explanation of the inconsistency between ultrasound and carcass merit traits QTL may be due to moderate correlations between ultrasound and carcass merit traits, which imply that matching evidence for both traits would not necessarily be expected (Johnson et al. 2005). It may also be due to the fact that different genes are involved at the various developmental stages.

3.3.2. SNPs Associated with Ultrasound and Carcass Merit Traits

Single SNP association analyses were performed for SNPs under or near the 30 significant QTL regions that were identified in the across-family study. The analysis detected 22 SNPs under 12 QTL regions that were significantly associated with 7 ultrasound and carcass merit traits. These include 8 SNPs that showed significant association ($P < 0.05$) with ultrasound traits of MEAN_UBF, UBF, and MEAN_UMAR on BTA 15 and 23; whereas for the carcass merit traits, a total of 14 SNPs had significant association ($P < 0.05$) with LMY, GRDFAT,

AVE_BF and CMAR on BTA 1, 5, 15, 18, and 29 (Table 3.6). Information regarding positions of the SNP on the chromosomes and their potential function of the above 22 SNPs were obtained from the databases of National Center for Biotechnology Information (NCBI) (Table 3.7).

SNP ss38334774 that is located at 14.1 cM on BTA 15 was found to have a significant additive effect on MEAN_UBF, in which genotype AA had a higher MEAN_UBF value. The SNP is located in an intron of the *Zinc finger and BTB domain-containing protein 16* (*ZBTB16*) gene (Table 3.7). In Human, the *ZBTB16* gene encodes a transcription factor that may play a role in myeloid maturation and in the development and maintenance of other differentiated tissues (Fischer et al. 2008). However, the role of the *ZBTB16* gene in regulating fat deposition in beef cattle needs further investigation.

Six SNPs were found to be significantly associated with UBF, of which three were located on BTA 15 in the region of 41.7 - 49.6 cM and three on BTA 23 in the region of 3.6 - 8.9 cM. The three SNP on BTA 15 had significant additive effects on UBF with the genotype GG of ss38325273 and TT of ss38323563 and ss38323565 SNPs having significant lower UBF. On BTA 23, ss38323823 SNP had a significant additive effect on UBF with the genotype GG having significantly lower UBF than genotype TT. The ss38323823 SNP also had a significant dominance effect on UBF. Both the ss38335355 and ss38335358 SNPs on BTA 23 have only two genotypes, i.e. AA and AG, detected in the population. The genotype AA of both SNPs has significantly higher UBF than AG. Of the 6 SNPs associated with UBF, SNP ss38325273 on BTA15 is located

in an intron of the *phosphodiesterase 3B, cGMP-inhibited* (*PDE3B*) gene, while SNPs ss38323563 and ss38323565 are located in the intronic region of the *RAB6A* gene. Among the three SNPs for UBF on BTA 23, the SNP ss38323823 is near the *BAK1* gene while SNPs ss38335355 and ss38335358 are close to *C23H6ORF142* gene. The product of the *PDE3B* gene is cGMP-inhibited 3',5'-cyclic phosphodiesterase B protein. Lobbert et al. (1996) reported that the human homologue *PDE3A* gene in rat is involved in fat metabolism. Furthermore, the *PDE3B* protein is the membrane component of adipose tissue microsomes, adipocytes and erythrocytes in human, rat and rabbit (Hanson et al. 2008; Kitamura et al. 1999), which suggests that the *PDE3B* gene may also play an important role on the deposition of body fat in beef cattle.

The ss38331825 SNP on BTA 15 had a significant association with MEAN_UMAR and exhibited a significant additive effect on MEAN_UMAR with genotype GG having a significantly low trait value. This SNP is a synonymous SNP located in the *USP2* (*ubiquitin specific peptidase 2*) gene. In human, the isopeptidase ubiquitin-specific protease-2a (USP2a) enzyme is the product of *USP2* gene that regulates the stability of fatty acid synthase in cancer cells. Inactivation of the *USP2a* function causes decreased fatty acid synthase protein levels and increased apoptosis (Graner et al. 2004), which warrants further investigation of the function of the gene in beef cattle.

For the carcass merit traits, four SNPs on BTA 5 and two SNPs on BTA 15 showed significant associations with LMY. On BTA 5, ss38324422 and ss38339138 SNPs have significant additive effects on LMY. Animals with

genotype CC of ss38324422 and GG of ss38339138 had significantly lower LMY than animals with the other two SNP genotypes. Likewise ss38334596 SNP had a significant dominance effect on LMY with genotype TC having lower LMY than the two homozygous SNP genotypes. However, further study is needed to confirm the dominance effect of ss38334596 SNP on the LMY. The ss61473002 SNP had two genotypes detected in the population and animals with AG genotype had higher LMY than those with GG genotype. On BTA 15, both the ss38332149 and ss38332148 SNP had significant additive effects on LMY whereby animals with CC genotypes for ss38332149 SNP and AA genotypes for ss38332148 SNP showed high amount of LMY than the other two SNP genotypes. Three of the four SNPs on BTA5 are located in the intronic regions of *LIN7A* gene while SNP ss38334596 is located in the intron of *SYT1* gene. Gene *LIN7A* encodes Lin-7 homolog A protein in bovine, and its molecular function based on thorough investigation has not been reported in cattle. The *SYT1* gene encodes synaptotagmin-1 protein. Molecular function of synaptotagmin-1 protein is not fully understood. However, a study on the phosphorylation of synaptotagmin-1by casein kinase II in bovine has shown that it is a Ca^{2+} binding and phospholipid binding protein whose functions may involve synaptic vesicle exocytosis (Davletov et al. 1993). SNP ss38332148 and ss38332149 on BTA15, which also have significant associations with AVE_BF, however, are located near gene and its function remains unclear.

Three SNPs on BTA 1, 18 and 27 were found to have significant associations with GRDFAT. The ss66538078 SNP on BTA 1 had a significant

additive effect on GRDFAT with genotype CC having low grade fat. The ss38322834 and ss38324558 SNPs on BTA 18 and 27 respectively showed both additive and dominance effects on GRDFAT. Animals with TC genotypes for the ss38322834 SNP and CC for the ss38324558 SNP had high grade fat values compared to those with alternative genotypes. SNP ss38322834 SNP on BTA 18 is located in the intron of *LOC506171* gene encoding a similar protein to phospholipase C, gamma 2 protein. The phospholipase C, gamma 2 enzyme plays important role on leptin signaling and leptin-mediated activation of human platelets (Dellas et al. 2007). Leptin is a hormone that involved in regulation of appetite, energy expenditure and body composition (Houseknecht et al. 1998). The SNPs on *leptin* gene have shown significant associations with several carcass traits in beef cattle including grade fat (backfat), ultrasound backfat thickness and lean meat yield (Nkrumah et al. 2004), which implies that the *LOC506171* gene may play an important role on regulation of GRDFAT through interaction with *leptin* gene.

The ss38339295 SNP on BTA 5 showed significant dominance effect and slightly significant additive effect on AVE_BF with GG genotype having higher trait values. The SNP is located close to *MYF6* gene which encodes myogenic factor 6 protein. In mice, the *MYF6* gene is homologous to bovine *MYF6* gene and plays a role in cell differentiation processes (Pin and Konieczny 2002). In cattle, the *MYF6* gene is considered to be involved in regulation of skeletal muscle development (Maak et al. 2006; Hudson et al. 2009), which may also affect fat deposition through energy partitioning, which needs further investigation.

Of the 30 significant QTL regions detected in the across-family analyses, 12 QTL regions for ultrasound and carcass merit traits were supported by SNPs in the proximate QTL locations with significant SNP associations whereas 18 QTL regions had no SNP that showed significant associations with traits (Table 3.6 and 3.7). Absence of significant association for SNPs under or near the significant QTL regions identified by the across-family QTL analyses could be a result of the single SNP marker association analysis having relatively low power of detecting QTL compared to the multiple marker interval QTL mapping method. Therefore, further increasing the sample size and the density of SNP markers under the QTL regions may lead to the identification of SNPs associated with the traits. Nevertheless, this study used both an interval mapping QTL genome scan and single SNP marker association to fine map QTL regions and to detect SNPs affecting ultrasound and carcass merit traits in beef cattle. Both methods analyze one position of the genome or one marker at a time, which could possibly result in high incidences of false positives due to multiple testing. However, 10000 permutations were carried out to set the significance threshold in order to combat false positives due to multiple testing in the whole genome QTL scan. Also, the QTL effects may be overestimated due to the fact that each QTL or SNP marker was analyzed independently, or due to a small number of animals in the genotype subclasses (Beavis 1998). Therefore, another study is underway to use a Bayesian approach to evaluate associations of all SNP markers simultaneously in a single model which will overcome some of the limitations associated with the interval mapping genome scan and the single SNP association analyses. Also, the use of

4592 SNPs in the current study may not capture all existing linkage disequilibrium between SNP markers and QTL on the bovine genome. Therefore, the use of the BovineSNP50 assay with a total of 58336 SNPs (Matukumalli et al. 2009) would be more powerful in narrowing down reported QTL and identifying SNPs influencing complex traits. Nevertheless, the fine mapped QTL regions and SNPs that were identified in this study will provide a reference for the identification of DNA markers for ultrasound and carcass merit traits for the implantation of MAS in beef cattle genetic improvement programs.

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Table 3.1: Descriptive statistics of ultrasound and carcass merit traits considered in the study

Variable	Steers, n	Mean	SD
Mean ultrasound marbling score	418	4.0183	0.5589
Average daily gain ultrasound marbling score	418	0.0071	0.0045
Mean ultrasound backfat, mm	418	3.8963	1.6719
Average daily gain ultrasound backfat, mm	418	0.0341	0.0193
Mean ultrasound ribeye area, cm^2	418	55.741	7.1370
Average daily ultrasound ribeye area, cm^2	418	0.1676	0.0717
Ultrasound marbling	418	5.1870	0.7849
Ultrasound backfat, mm	418	9.3168	3.5598
Ultrasound ribeye area, cm^2	418	83.545	10.572
Carcass weight, kg	342	312.3988	31.909
Grade fat, mm	342	10.7252	4.3051
Average backfat, mm	342	12.2133	4.2543
Carcass ribeye area, cm^2	342	84.0673	9.2881
Lean meat yield, %	342	57.9188	3.8099
Carcass marbling score	342	2.4975	0.5352
Yield grade	342	1.7193	0.7165

Table 3.2: Locations and QTL effects for ultrasound traits based on across-family analyses

Trait[z]	BTA	QTL peak cM)	QTL 95% interval (cM)	*F*-ratio	$P_{chromosome}$	P_{genome}	QTL%[y]
MEAN_UBF	8	8	7.0 – 8.1	2.63	0.0093**	0.2374	7.1[x,w]
	15	15	14.0 – 16.5	2.28	0.0477*	0.7577	5.7[x,w,v]
	27	58	57.7 – 59.0	2.39	0.0098**	0.2484	6.1
UBF	12	1	0.0 – 1.6	2.69	0.0496*	0.7713	7.8
	13	35	34.1 – 36.7	2.6	0.0497*	0.772	7.4[v]
	15	43	41.0 – 47.0	3.46	0.0090**	0.2306	11
	23	0	0.0 – 8.0	2.45	0.0425*	0.7162	6.1
MEAN_UMAR	15	14	11.5 – 17.2	2.74	0.0394*	0.6883	7.7[v]
UMAR	13	39	37.9 – 39.6	2.73	0.0365*	0.6598	7.2[w]
	21	39	37.9 – 40	2.53	0.0448*	0.7353	6.4[w]
ADG_UREA	5	45	43.9 – 45.3	2.96	0.0074**	0.1938	8.3[v]
	11	88	87.7 – 88.6	2.61	0.0384*	0.6786	8.3

[z]MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; MEAN_UMAR= mean ultrasound marbling; UMAR = ultrasound marbling; ADG_UREA = average daily gain ultrasound ribeye area.
[y]QTL contribution (%) = (residual mean square of reduced model – residual mean square of full model)/total phenotypic variance; *$P < 0.05$; **$P < 0.01$; [x]QTL confirmed at $P < 0.01$ in within-family analysis; [w]QTL confirmed at $P < 0.05$ in within-family analysis; [v]QTL detected at nearby region in within-family analysis

Table 3.3: Locations and QTL effects for carcass merit traits based on across-family analyses

Trait[z]	BTA	QTL peak (cM)	QTL 95% interval (cM)	*F*-ratio	$P_{chromosome}$	P_{genome}	QTL%[y]
CWT	6	19	18.0 – 20.0	3.01	0.0375*	0.6699	8.7
	15	84	82.0 – 86.0	3.13	0.0491*	0.7678	9.2
	18	54	53.9 – 55.6	3.21	0.0097**	0.2462	9.5[w]
	21	34	33.9 – 34.5	2.63	0.0418*	0.7101	7.2[w]
LMY	5	16	15.5 – 18.0	2.7	0.0466*	0.7494	8.5[w]
	15	16	14.5 – 17.0	2.8	0.0065**	0.1723	8.9[w]
GRDFAT	1	9	8.5 – 12.0	2.46	0.0389*	0.6836	7.3[w]
	15	15	12.5 – 17.5	3.33	0.0085**	0.2193	11.1[w,v]
	18	3	2.8 – 3.5	2.43	0.0428*	0.7186	7.2
	27	59	58.0 – 59.0	2.33	0.0495*	0.7706	6.7[w]
AVE_BF	5	8	0.0 – 11.0	2.74	0.0440*	0.7288	8.6
	15	16	13.0 – 17.5	3.45	0.0093**	0.2373	11.7[w]
CREA	1	6	4.0 – 6.1	2.69	0.0494*	0.7699	8.0[w]
	6	111	109.0 – 111.4	2.66	0.0434*	0.7238	7.9[x]
	10	16	15.9 – 16.5	2.34	0.0403*	0.6967	6.5
CMAR	1	4	0.0 – 5.2	2.66	0.0443*	0.7313	7.9[v]
	25	1	0.9 – 1.6	2.75	0.0092**	0.2351	8.3[w]
	29	20	19.0 – 20.7	2.56	0.0489*	0.7663	7.4

[z]CWT = carcass weight; LMY = lean meat yield; GRDFAT = carcass grade fat; AVE_BF = average backfat; CREA = carcass ribeye area; CMAR = carcass marbling.
[y]QTL contribution (%) = (residual mean square of reduced model – residual mean square of full model)/total phenotypic variance; *P < 0.05; **P < 0.01; [x]QTL confirmed at P < 0.01 in within-family analysis; [w]QTL confirmed at P < 0.05 in within-family analysis; [v]QTL detected at nearby region in within-family analysis.

Table 3.4: QTL locations and effects for ultrasound traits based on within-family analyses

Trait[z]	BTA	QTL location, cM	Family	Estimate	S.E.	*p*-value[y]
ADG_UBF	4	12	4	-0.022	0.005	0.0076
ADG_UBF	4	69	8	0.02	0.004	0.009
ADG_UBF	4	79	9	-0.003	0.002	0.007
ADG_UBF	8	51	6	-0.011	0.003	0.0096
ADG_UBF	12	30	6	0.014	0.004	0.0097
ADG_UBF	13	60	13	-0.026	0.007	0.008
ADG_UBF	29	44	1	0.89	0.209	0.0074
MEAN_UBF	2	110	12	3.873	0.098	0.0087
MEAN_UBF	8	126	10	-3.633	0.681	0.0083
MEAN_UBF	8	7	17	3.238	0.592	0.0097
MEAN_UBF	9	23	12	4.275	0.293	0.0063
MEAN_UBF	14	0	2	1.414	0.329	0.0097
MEAN_UBF	15	16	14	-2.129	0.452	0.0068
MEAN_UBF	15	31	17	-2.166	0.448	0.0086
MEAN_UBF	24	47	10	2.683	0.586	0.0092
MEAN_UBF	27	2	4	-1.552	0.372	0.0098
MEAN_UBF	29	18	17	-2.219	0.43	0.0086
UBF	17	83	2	4.711	1.188	0.0089
UBF	18	4	9	3.895	0.451	0.0068
UBF	21	29	4	-3.169	0.826	0.0079
UBF	21	48	8	-4.3731	0.844	0.0087
UBF	25	64	6	-2.501	0.696	0.0092
ADG_UMAR	2	9	18	0.008	0.001	0.0065
ADG_UMAR	4	60	3	0.004	0.001	0.0141
ADG_UMAR	20	61	18	-0.009	0.001	0.0083
MEAN_UMAR	1	32	4	0.754	0.158	0.0091
MEAN_UMAR	8	20	8	-0.781	0.176	0.0091
MEAN_UMAR	10	66	4	-0.398	0.095	0.009
MEAN_UMAR	12	89	6	-0.288	0.083	0.0086
MEAN_UMAR	13	1	14	-0.692	0.157	0.0095
MEAN_UMAR	14	18	17	-0.609	0.109	0.0096
UMAR	5	30	12	-15.904	1.053	0.0074
UMAR	9	1	7	1.044	0.253	0.0095
UMAR	10	110	3	-0.76	0.197	0.0078
UMAR	18	8	4	-0.799	3.763	0.0092
UMAR	19	71	4	-1.144	0.28	0.0084
ADG_UREA	3	91	8	-0.066	0.012	0.0096
ADG_UREA	9	59	18	0.106	0.013	0.0085
ADG_UREA	21	31	4	0.049	0.012	0.0083

ADG_UREA	21	19	10	-0.087	0.018	0.0088
ADG_UREA	27	40	4	0.043	0.012	0.0067
MEAN_UREA	2	33	2	-10.176	1.943	0.0089
MEAN_UREA	2	39	8	8.665	2.113	0.0083
MEAN_UREA	10	71	9	11.692	0.298	0.002
MEAN_UREA	12	61	10	-7.597	1.68	0.0088
MEAN_UREA	13	44	2	9.401	2.002	0.0095
MEAN_UREA	13	25	8	8.542	1.905	0.0081
MEAN_UREA	19	37	13	8.483	1.828	0.009
MEAN_UREA	23	19	3	4.545	1.181	0.0084
MEAN_UREA	27	53	17	-14.375	2.276	0.0094
UREA	9	63	18	19.073	1.947	0.007
UREA	12	77	9	-15.518	0.708	0.0092
UREA	20	12	1	-10.106	1.814	0.0096

[z]ADG_UBF = average daily gain ultrasound backfat; MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; ADG_UREA = average daily gain ultrasound ribeye area; MEAN_UREA = mean ultrasound ribeye area; UREA = ultrasound ribeye area; ADG_UMAR = average daily gain ultrasound marbling; MEAN_UMAR = mean ultrasound marbling; UMAR = ultrasound marbling; [y]Only 1% chromosome-wise significance level are reported for within-family QTL effects.

Table 3.5: QTL locations and effects for carcass merit traits based on within-family analyses

Trait[z]	BTA	QTL location, cM	Family	Estimate	S.E.	*p*-value[y]
CWT	9	39	8	60.984	11.268	0.0093
CWT	15	20	8	47.946	9.278	0.0096
CWT	15	37	10	-60.282	12.564	0.0019
CWT	28	36	13	-52.616	10.712	0.0083
CWT	29	41	13	56.33	10.715	0.0098
LMY	1	121	9	-13.238	1.071	0.0063
LMY	2	11	9	11.902	1.855	0.0033
LMY	9	0	14	-6.172	1.433	0.0091
LMY	13	98	18	11.873	2.412	0.0069
LMY	16	19	5	3.52	0.825	0.0085
LMY	16	84	14	6.626	1.601	0.0082
GRDFAT	9	51	9	10.264	0.549	0.0092
GRDFAT	15	77	5	-3.684	0.826	0.0083
GRDFAT	17	93	4	-4.213	1.062	0.0096
GRDFAT	25	52	7	7.737	2.059	0.0092
GRDFAT	29	0	4	-4.294	1.177	0.0085
AVE_BF	16	84	14	-6.578	1.699	0.0099
CREA	6	107	2	20.606	3.915	0.0099
CREA	25	28	5	9.06	2.267	0.0093
CREA	26	42	8	-19.21	4.454	0.0089
CMAR	4	43	10	0.992	0.226	0.0096
CMAR	20	52	9	-1.847	0.07	0.0099
CMAR	23	30	14	0.721	0.181	0.0078
YGRADE	10	90	6	0.589	0.155	0.0084
YGRADE	16	84	14	-1.182	0.272	0.0094

[z]CWT = carcass weight; LMY = lean meat yield; GRDFAT = carcass grade fat; AVE_BF = average backfat; CREA = carcass ribeye area; CMAR = carcass marbling; YGRDAE = carcass yield grade.

[y]Only 1% chromosome-wise significance level are reported for within-family QTL effects

Table 3.6: Location, genotype frequency and effects of SNPs significantly associated with ultrasound and carcass merit traits

Trait	BTA	SNP name	SNP genotypes (No. of animals)[x] and Estimate (± SE)			SNP location (cM)	a[w] ± SE	Prob[v].	d[u] ± SE	Prob[v].
MEAN_UBF	15	ss38334774	AA (97) 3.93 ± 0.17	AG (209) 3.73 ± 0.13	GG (106) 3.47 ± 0.16	14.1	0.228±0.10	0.0202	0.027 ±0.12	0.8235
UBF	15	ss38325273	CC (13) 10.63 ± 0.79	GC (142) 9.17 ± 0.27	GG (254) 8.64 ± 0.22	41.7	0.994 ± 0.41	0.0151	-0.462 ± 0.47	0.3235
		ss38323563	GG (169) 9.08 ± 0.26	TG (186) 8.96 ± 0.23	TT (59) 7.93 ± 0.40	41.7	0.572 ± 0.23	0.0164	0.458 ± 0.29	0.1253
		ss38323565	GG (172) 9.03 ± 0.27	TG (180) 9.01 ± 0.25	TT (60) 7.99 ± 0.41	49.6	0.516 ± 0.24	0.0301	0.502 ± 0.30	0.0963
UBF	23	ss38323823	GG (275) 8.86 ± 0.26	TG (132) 8.71 ± 0.31	TT (8) 11.21 ± 1.05	8.9	-1.177±0.53	0.0268	-1.329±0.57	0.0194
		ss38335355	AA (358) 8.99 ± 0.20	AG (55) 8.13 ± 0.40	-	3.6	0.859± 0.42	0.0398	-	-
		ss38335358	AA (359) 8.99 ± 0.20	AG (56) 8.12 ± 0.40	-	3.8	0.865±0.41	0.0366	-	-
MEAN_UMAR	15	ss38331825	AA (19) 4.13 ± 0.10	AG (153) 4.03 ± 0.05	GG (237) 3.91 ± 0.04	20.2	0.107 ± 0.05	0.0444	0.007± 0.06	0.9058
LMY	5	ss38324422	CC (29) 56.83 ± 0.0.76	TC (161) 57.75 ± 0.39	TT (227) 58.73 ± 0.37	16	-0.950 ± 0.39	0.0163	-0.027 ± 0.47	0.9541
		ss38334596	CC (294) 58.52 ± 0.35	TC (102) 56.95 ± 0.54	TT (6) 59.00 ± 1.62	17.3	-0.218 ± 0.81	0.7664	-1.809 ± 0.86	0.0353
		ss38339138	GG (39) 56.59 ± 0.72	TG (186) 58.09 ± 0.38	TT (186) 58.58 ± 0.39	14.8	-1.019 ± 0.38	0.0070	0.526 ± 0.45	0.2458
		ss61473002	AG (139) 58.91 ± 0.42	GG (270) 57.73 ± 0.35	-	16.6	1.177 ± 0.46	0.0111	-	-
LMY	15	ss38332149	CC (182) 58.64 ± 0.33	TC (176) 57.99 ± 0.37	TT (51) 57.08 ± 0.60	8.7	0.778 ± 0.32	0.0153	0.130± 0.42	0.7539
		ss38332148	AA (179) 58.57 ± 0.34	AG (173) 57.97 ± 0.39	GG (51) 57.11 ± 0.61	8.7	0.729 ±0.33	0.0266	0.125±0.43	0.7687
GRDFAT	1	ss66538078	CC (165) 10.08 ± 0.36	TC (195) 10.34 ± 0.36	TT (51) 11.74 ± 0.64	8.7	-0.830 ± 0.35	0.0197	-0.564 ± 0.46	0.2214
GRDFAT	18	ss38322834	CC (3) 16.69 ± 2.20	TC (76) 9.71 ± 0.57	TT (339) 10.42 ± 0.30	4.7	3.135 ± 1.10	0.0047	-3.843 ± 1.18	0.0013
GRDFAT	27	ss38324558	CC (334) 10.14 ± 0.33	TC (79) 10.50 ± 0.53	TT (3) 16.77 ± 2.21	58.8	-3.313 ± 1.12	0.0032	-2.952 ± 1.20	0.0141
AVE_BF	5	ss38339295	CC (354) 11.91 ± 0.31	CG (60) 11.17 ± 0.61	GG (3) 15.67 ± 2.19	10.4	-1.881 ± 1.10	0.0889	-2.627 ± 1.22	0.0331
AVE_BF	15	ss38332149	CC (182) 11.36 ± 0.32	TC (176) 11.97 ± 0.36	TT (51) 12.98 ± 0.63	8.7	-0.808 ± 0.35	0.0224	-0.195 ± 0.45	0.6678
		ss38332148	AA (179) 11.40 ± 0.34	AG (173) 12.03 ± 0.39	GG (51) 12.96 ± 0.65	8.7	-0.779 ±0.36	0.0311	-0.149±0.46	0.7489
CMAR	29	ss38322162	CC (6) 1.97 ± 0.20	TC (83) 2.44 ± 0.07	TT (327) 2.46 ± 0.05	21.6	-0.241 ± 0.10	0.0147	0.221 ± 0.11	0.0460
		ss38324688	AG (33) 2.22 ± 0.10	GG (380) 2.48 ± 0.04	-	18.8	-0.253 ± 0.10	0.0093	-	-

[x]Number of animals shown in brackets; a[w], additive genotypic value; d[u], dominance deviation; Prob[v], probability of additive or dominance genotypic value

Table 3.7: Summary of position and gene annotation for SNPs significantly associated with ultrasound and carcass traits

Trait	BTA	SNP name	SNP position (bp)	Function class	In Gene ID	In Gene name	In Gene description
MEAN_UBF	15	ss38334774	22919210	intron	534401	*ZBTB16; MGC127918*	zinc finger and BTB domain containing 16
UBF	15	ss38325273	36854388	intron	533323	*PDE3B*	phosphodiesterase 3B, cGMP-inhibited
		ss38323563	52710350	intron	616537	*RAB6A*	RAB6A, member RAS oncogene family
		ss38323565	52710098	intron	616537	*RAB6A*	RAB6A, member RAS oncogene family
UBF	23	ss38323823	8498505	nearest_gene	514090	*BAK1*	BCL2-antagonist/killer 1
		ss38335355	101039	nearest_gene	790110	*C23H6ORF142*	chromosome 6 open reading
		ss38335358	101057	nearest_gene	790110	*C23H6ORF142*	chromosome 6 open reading
MEAN_UMAR	15	ss38331825	28495153	synonymous contig reference	522980	*USP2; MGC137635*	ubiquitin specific peptidase 2
LMY	5	ss38324422	12423627	intron	528379	*LIN7A*	lin-7 homolog A (C. elegans)
		ss38334596	9087028	intron	281511	*SYT1*	synaptotagmin I
		ss38339138	12403425	intron	528379	*LIN7A*	lin-7 homolog A (C. elegans)
		ss61473002	12451776	intron	528379	*LIN7A*	lin-7 homolog A (C. elegans)
LMY	15	ss38332149	20509763	nearest_gene	538766	*MGC134087; MGC134087*	hypothetical LOC538766
		ss38332148	20509821	nearest_gene	538766	*MGC134087; MGC134087*	hypothetical LOC538766
GRDFAT	1	ss66538078	6350258	intron	540879	*C1H21ORF7*	chromosome 21 open reading frame 7 ortholog
GRDFAT	18	ss38322834	7459380	intron	506171	*LOC506171*	similar to phospholipase C, gamma 2
GRDFAT	27	ss38324558	42710278	nearest_gene	616397	*ZMAT4*	zinc finger, matrin type 4
AVE_BF	5	ss38339295	12323876	nearest_gene	281336	*MYF6*	myogenic factor 6 (herculin)
AVE_BF	15	ss38332149	20509763	nearest_gene	538766	*MGC134087; MGC134087*	hypothetical LOC538766
		ss38332148	20509821	nearest_gene	538766	*MGC134087; MGC134087*	hypothetical LOC538766
CMAR	29	ss38322162	16888647	nearest_gene	506046	*CCDC90B; MGC155307*	coiled-coil domain containing 90B
		ss38324688	15572469	nearest_gene	506046	*CCDC90B; MGC155307*	coiled-coil domain containing 90B

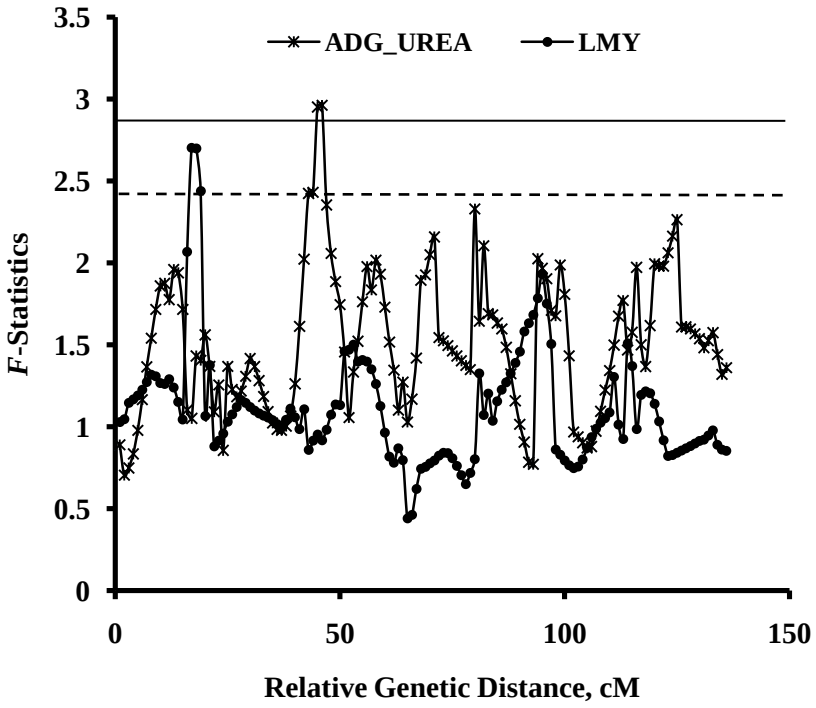

Figure 3.1: QTL profiles for across-family analyses on bovine chromosome 5. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10,000 permutations. ADG_UREA = average daily gain ultrasound ribeye area; LMY = lean meat yield.

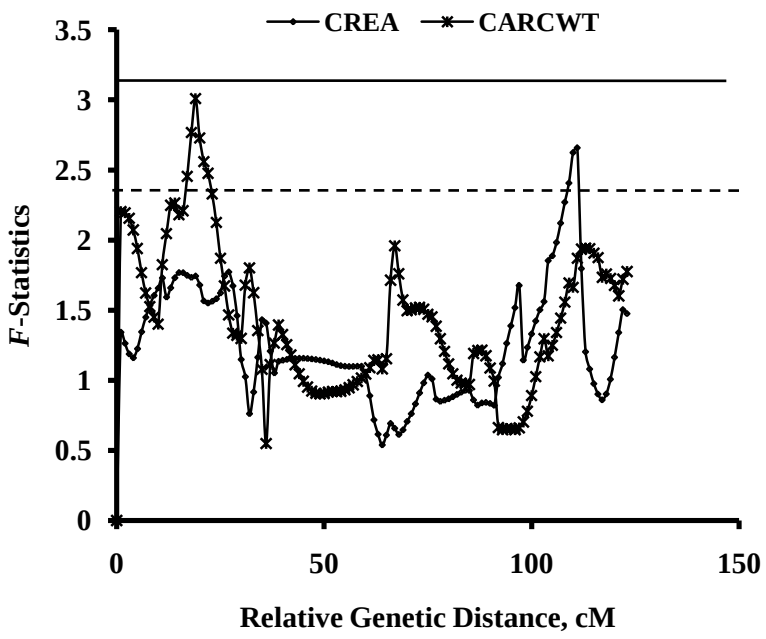

Figure 3.2 QTL profiles for across-family analyses on bovine chromosome 6. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10,000 permutations. CREA = carcass ribeye area; CARCTW = carcass weight.

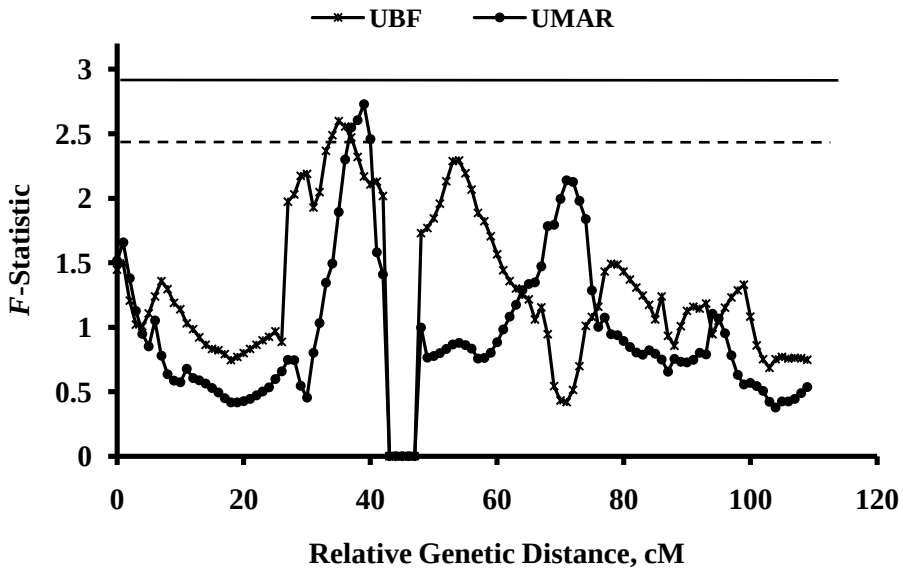

Figure 3.3: QTL profiles for across-family analyses on bovine chromosome 13. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10,000 permutations. UBF = ultrasound backfat; UMAR = ultrasound marbling.

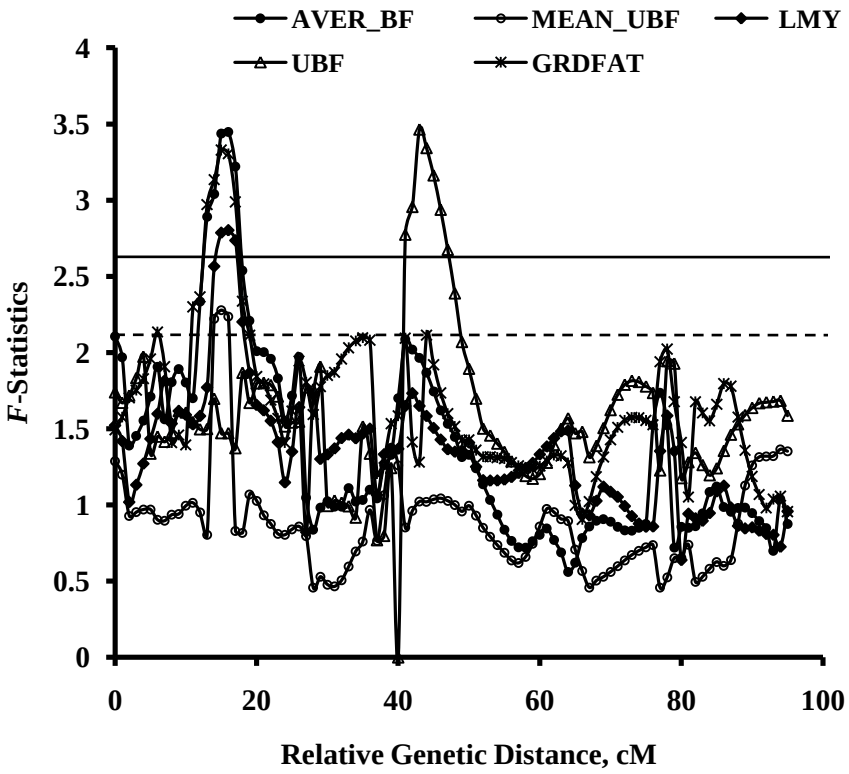

Figure 3.4: QTL profiles for across-family analyses on bovine chromosome 15. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold levels based on 10,000 permutations. MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; LMY = lean meat yield; GRDFAT = carcass grade fat; AVER_BF = average backfat.

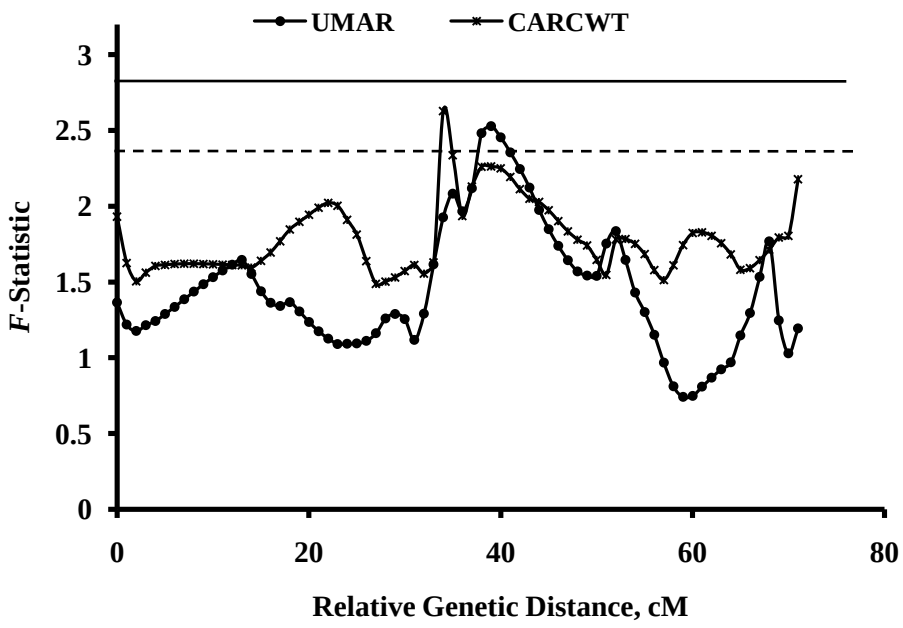

Figure 3.5: QTL profiles for across-family analyses on bovine chromosome 21. Horizontal lines represent the chromosome-wise 1% (solid line) and 5% (dashed line) threshold level based on 10,000 permutations. UMAR = ultrasound marbling; CWT = carcass weight.

4. Whole Genome QTL Fine Mapping for Ultrasound and Carcass Merit Traits in Beef Cattle using Bayesian Shrinkage Method

4.1. Introduction

Several statistical methods have been developed to identify quantitative trait loci (QTL) for economically important traits in agricultural organisms and complex traits in human (Lander and Botstein 1989; Knott et al. 1996; Jansen 1993; Zeng 1994; Kao et al. 1999; Xu 2003a, Wang et al. 2005). However, the statistical methods differ in terms of the power and accuracy of estimation of QTL effects and positions. Interval mapping with linear regression models for half-sib families has been commonly used for QTL analyses (Haley et al. 1994; Knott et al. 1996; Takasuga et al. 2007). However, the interval mapping approach and various modified versions of it may have limitations in evaluating the QTL effects of the entire genome with a dense marker map because it evaluates one interval at a time along the genome and requires multiple tests, which usually results in biased estimation of QTL effects and a higher false positive rate (Xu 2003a; Wang et al. 2005).

Bayesian shrinkage estimation is an alternative method to map QTL locations and to estimate QTL effects for quantitative traits. The method is able to evaluate all candidate markers on the entire genome in a single model simultaneously, thus overcoming at least some of the limitations of interval mapping approach and tends to have a more accurate estimation of QTL positions and effects in comparison to the interval mapping approach (Xu 2003a; Wang et

al. 2005). More importantly, the Bayesian shrinkage estimation method can handle oversaturated models in which marker intervals with negligible QTL effects are shrunk close to zero whereas the intervals with remarkable QTL effects are subject to virtually no shrinkage (Wang et al. 2005). The method has been applied previously in several species including the identification of QTL for wound-healing (Wang et al. 2005) in mice, detection of genetic markers associated with bristle number variations (Kopp et al. 2003) in fruit flies, and mapping of QTLs for several production traits (Xu 2003a) in barley. The results from these studies suggest that the Bayesian shrinkage approach provides a promising alternative to interval QTL search approaches.

In a previous study, we conducted a whole genome fine mapping of QTL for ultrasound and carcass merit traits based on 4592 SNPs in a composite beef cattle population using an interval mapping regression approach and single SNP marker association analyses (Nalaila et al. 2010). The objective of this study was to carry out fine mapping of QTL for the ultrasound and carcass merit traits in the composite beef cattle population using the Bayesian shrinkage estimation method, and to compare the QTL mapping results with those identified in our previous study (Nalaila et al. 2010). Use of different approaches for QTL analyses facilitates comparison and verification of QTL mapping results, which leads to the identification of reliable genetic markers for MAS and QTN search.

4.2. Materials and Methods

4.2.1. Animal Resources and Phenotypic Data

Information about animal resources and phenotypic data also traits studied and measurements are explained in Chapter 3.2.1 and 3.2.2 respectively. The statistics of the ultrasound and carcass merit traits are presented in Table 3.1.

4.2.3. DNA Isolation and SNP Genotyping

Information about DNA isolation and SNP genotyping are summarized in Chapter 3.2.3. The SNP markers with missing genotypes were imputed using *fastPHASE* (Scheet and Stephen 2006). The SNP markers with a minor allele frequency (MAF) less than 0.05 and Hardy-Weinberg equilibrium test $P < 0.0005$ were filtered out using *PLINK* (Purcell et al. 2007). In order to remove redundant marker information in the Bayesian shrinkage model, only SNP markers with pair-wise linkage disequilibrium (r^2) less than 0.2 were included in this analysis. Therefore, a total of 1207 SNP markers were selected for the Bayesian shrinkage analysis. The 1207 SNPs covered all 29 BTA with a range per chromosome of 4 SNPs (BTA 26) to 80 SNPs (BTA 28). The average distance between SNP markers was 2.3 cM with a range of 0.77 cM (BTA 28) to 11.06 cM (BTA 23) cM. The number of markers per BTA and average distance between SNP markers are presented in Table 4.1. All SNP markers were formatted into one data set representing the whole genome for the Bayesian shrinkage analysis with cumulative positions in cM from BTA1 to BTA29.

4.2.4. Statistical Analysis

Phenotypes of ultrasound and carcass merit traits were pre-adjusted for the fixed effects of year-batch contemporary groups, sire breeds, and as well as linear covariates of animal age at the start of the test for ultrasound traits and animal age at slaughter for carcass merit traits using *PROC GLM* (SAS 9.1.3 Institute Inc., NC), and the resulting residuals were used as phenotypes for the analyses. The Bayesian shrinkage QTL mapping was carried out using *PROC QTL*, which is a user-defined SAS procedure for QTL mapping software package that executes within the SAS platform (Hu and Xu 2009). The method allows fitting all of the 1207 SNP markers in a single model and estimates QTL of the entire genome simultaneously using a Bayesian Shrinkage approach. The method assumes that each marker interval has its own variance parameter and its own prior distribution so that the variance of each QTL can be estimated from the data (Xu 2003a). This assumption allows the obtaining of the shrinkage factors that vary across different QTL effects, in which chromosomal regions with no QTL are forced to shrink close to zero, whereas notable QTL effects are subject to less or virtually no shrinkage. The method also allows a dynamic estimation of the position of a QTL within a marker interval instead of being fixed at a marker (Wang et al., 2005). The statistical model used in this analysis was described by Xu (2003a) as follows:

$$y_i = b_0 + \sum_j^p x_{ij} b_j + \sum_j^p w_{ij} d_j + e_i$$

where y_i is the observed phenotypic value of individual *i*, b_0 is the population mean, *p* is the number of markers included in the model, x_{ij} and w_{ij} are dummy variables indicating the genotypes of the j^{th} maker of the i^{th} individual for the additive and dominant QTL allele effects of b_j and d_j associated with marker *j* respectively. The dummy variables of x_{ij} and w_{ij} are defined as A1A1 = 'A', A1A2 = 'H' and A2A2='B' indicating the three marker genotypes as the first homozygote, the heterozygote and the second homozygote, and x_{ij} and w_{ij} are defined as x_{ij} = 1, 0, -1 and w_{ij} = 0, 1, 0 for genotype A1A1, A1A2 and A2A2, respectively.

The analysis was implemented through the Markov chain Monte Carlo (MCMC), in which Markov chain length contained 22,000 sweeps. The burn-in period was 2000 sweeps (i.e. the first 2000 sweeps were deleted) then the chain was trimmed to reduce the series correlation by keeping one observation in every 20 sweeps and resulted in the posterior sample size of 1000 for the post-MCMC analysis. The MCMC sampling creates the empirical posterior distributions of parameters including QTL locations and effects, in which all the information about the QTL are inferred (Wang et al. 2005). The option of dynamic approach was specified, in which the QTL position is updated using the Metropolis-Hastings algorithm approach to select a new position in the neighbourhood of the old position (Wang et al., 2005). Empirical significant threshold values of α=0.05 and α=0.01 were determined for each QTL through a permutation procedure (Che and Xu 2010) in the *PROC QTL* with a static approach option specified based on 3500 randomly-shuffled datasets for each phenotypic trait to control the type I

error rates. The genetic variance attributed by each QTL was determined as $V_g = V_a + V_d$, where *g*, *a* and *d* are the genetic, additive and dominance effects for each QTL, respectively. The phenotypic variance (V_p) for each QTL was determined as $V_p = V_g + V_e$, where V_e is the residual variance for each QTL provided by *PROC QTL* within the MCMC sample data set for each QTL.

4.3. Results and Discussion

The whole genome analysis identified 218 QTL for 14 ultrasound and carcass merit traits, in which 105 QTL are for 7 ultrasound traits while 113 QTL are for 7 carcass merit traits. The detailed QTL positions, effects (additive and dominant), nearby markers and significant levels for the 14 ultrasound and carcass merit traits were summarized in Table 4.2. The percentile intervals and the QTL effect profiles that were plotted against the genome locations for each trait are shown in Figures 4.1 to 4.14. The distributions of the absolute QTL effects for each trait along the genome are shown in Figures 4.15 to 4.28. Although QTL effects for both additive and dominance were estimated in the present study, but most of the dominance effects are marginal. Therefore, the results and discussions were focused on the additive effects only. The dominance QTL effects and their variations are provided in Table 4.2 without explicitly discussing them due to limited results found in previous literatures.

Among the 218 QTL detected in this study, 176 of them were newly detected while 42 of them were in agreement with previous studies. Among the 42 QTL, 11 of them were similar to the QTL regions reported previously in the

current beef cattle population (Nalaila et al. 2010) and 31 of 218 are within the QTL regions reported from studies in other beef populations. The proportion of individual QTL variance accounted for phenotypic variance ranged from less than 1% for the majority of QTL to 4.8% for one QTL affecting CMAR on BTA 3. The proportion of phenotypic variance accounted jointly by all detected QTL ranged from 4.5% (CWT) to 23.9% (CMAR) (Table 4.2). In a previous interval QTL mapping study, the individual QTL effect ranged from 5.7% (MEAN_UBF) to 11.7% (AVE_BF) while the proportion of phenotypic variance accounted jointly by all significant QTL ranged the from 13.6% (UMAR) to 34.6% (CWT) (Nalaila et al. 2010). The QTL effects estimated by the current Bayesian shrinkage QTL analyses either individually or jointly are smaller than those estimated through the interval QTL method. Since the Bayesian shrinkage analysis fits all SNP markers in a single model simultaneously; therefore, it could reduce possible spurious QTL effects by adjusting all other QTL effects (Xu 2003a). Therefore, the method is able to reduce the number of spurious QTL effects and to avoid overestimation of QTL variances and to detect smaller QTL that were undetectable through interval mapping methods. Generally, the estimates of QTL effects for all traits showed similar patterns, such that many QTL had small effects close to zero and few QTL had moderate to large effects, which closely approximate to a gamma distribution (Figure 4.15 – Figure 4.28). Therefore, the Bayesian analysis is a viable tool for evaluating the polygenic effects of the entire genome (Xu 2003a).

4.3.1. Ultrasound measures of carcass traits

Sixteen QTL with significant effect on MEAN_UBF ($P < 0.05$) were identified on 15 different chromosomes and these QTL accounted for 5.4% of phenotypic variance. The individual QTL with highest variance for UBF was on BTA 4 (93.2 cM). The QTL for MEAN_UBF on BTA 2 (52.6 cM), 4 (93.2), 7 (70.1 cM), 8 (29.8 cM), 13 (48.7 cM), 14 (87.5 cM) and 27 (56.4 cM) were located within the QTL span for backfat thickness reported in other cattle populations (Casas et al. 2001; Casas et al. 2003; McClure et al. 2010). The MEAN_UBF QTL on BTA 27 was also similar to the QTL detected previously by interval mapping (Nalaila et al. 2010). Also, the MEAN_UBF QTL on BTA 8 (29.8 cM) was located at 22 cM apart from the previous QTL detected by interval mapping (Nalaila et al. 2010).

Twenty QTL identified on 13 different chromosomes were found to have a significant additive effect ($P < 0.05$) on UBF, which contributed to 20.7% of the phenotypic variation for the trait. The estimated proportion of UBF phenotypic variations accounted by a single QTL ranged from 0.2 to 3.6%. The individual QTL that accounted for 3.6% was the largest QTL mapped for the UBF and was located on BTA 1 (126.2 cM). The QTL on BTA 1 (126.2 cM) with other five QTL for UBF on BTA 4 (89.8 cM), 5 (53.6 cM), 6 (35.2 cM), 19 (94.7) and 21 (41.8 cM) were within the QTL regions reported for backfat thickness (Casas et al. 2000; Li et al. 2004; McClure et al. 2010). Furthermore, the UBF QTL region on BTA 13 (42 cM) was similar to the QTL detected by a previous study (Nalaila et al. 2010). However, the other QTL including those with a small effect were not

reported previously, which may suggest that they are the QTL segregating in the current beef cattle populations and the current Bayesian shrinkage method is capable of detecting QTL with smaller effects.

Fourteen QTL detected on 11 different chromosomes had significant ($P < 0.05$) effects on UMAR and they jointly accounted for 6.6% of the phenotypic variation for this trait with the individual QTL effect ranging from 0.17% to 0.90% (Table 4.2). Three QTL for UMAR on BTA 5 (69.4 cM), 10 (21.2 cM) and 27 (14.7 cM) were within the QTL confidence regions for marbling score found in the study by Casas et al. (2003), and one QTL on 13 (32 cM) was in agreement with the QTL region identified in the same beef cattle population using the interval QTL mapping method (Nalaila et al. 2010).

Twenty-two QTL with significant effect on MEAN_UMAR ($P < 0.05$) were identified on 16 different chromosomes and jointly explained 7.1% of phenotypic variance (Table 4.2). All individual QTL for MEAN_UMAR had less than 1% contribution on the phenotypic variance and the QTL with the highest variance for MEAN_UMAR was on BTA 2 (87.2 cM) accounting for 0.6% of phenotypic variance (Table 4.2). The MEAN_UMAR QTL on BTA 15 (35 cM) was located at 18 cM from the previous reported QTL (Nalaila et al. 2010).

Fourteen QTL on 14 different chromosomes have been found to have significant effects on UREA ($P < 0.05$). The 14 QTL jointly accounted for about 5.71% of phenotypic variation and the largest proportion accounted by a single QTL was 1.21% on BTA1 (28.3 cM) (Table 4.2). However, all of the 14 QTL regions were not reported in previous studies including the interval QTL mapping

study in the same beef cattle population (Nalaila et al. 2010). It is likely that the Bayesian shrinkage QTL mapping method is able to identify QTL with small effects in comparison to other QTL mapping methods. However, further studies are needed to validate these QTL regions.

A total of 10 QTL on 7 different chromosomes had significant effects on ADG_UREA, which jointly accounted for about 6.0% of phenotypic variance and the highest variance accounted by a single QTL was 3.1% on BTA 3 (87 cM) (Table 4.2). The QTL for ADG_UREA in the current study have not been reported in previous studies including the interval QTL mapping study in the same beef cattle population (Nalaila et al. 2010). However, the ADG_UREA QTL on BTA 5 (60.0 cM) was located at 14.7 cM from the previous QTL detected by interval mapping (Nalaila et al. 2010).

4.3.2. Carcass merit traits

The present study detected 11 QTL that have significant effects on CWT ($P < 0.05$) on 8 different chromosomes and they jointly accounted for 4.5% of the phenotypic variation (Table 4.2). The proportion of CWT phenotypic variance contributed by an individual QTL ranged from about 0.2 to 0.7% with the QTL on BTA 6 (26.2 cM) having a largest variance. Of the 11 QTL identified in this study, two QTL on BTA 2 (101.2 cM) and 6 (41.2 cM) were localized within the QTL regions that were identified previously (Takasuga et al. 2007; Setoguchi et al. 2009, McClure et al. 2010). The QTL on BTA 6 (26.2 cM) and 18 (63.5 cM)

were also detected in a previous interval QTL mapping study using the same beef cattle population (Nalaila et al. 2010).

Seventeen QTL identified on 11 different chromosomes had significant effects for GRDFAT ($P < 0.05$) with a collective contribution of 7.8% to the phenotypic variance. The highest additive variance accounted by an individual QTL was 1.6% by the QTL on BTA 4 at 44.4 cM (Table 4.2). The QTL for GRDFAT on BTA 1 (153.4 cM), 6 (29 cM) and 13 (47.6 cM) were similar to the QTL locations reported for fat thickness at 12^{th} rib in commercial American Angus population (McClure et al. 2010), whereas the QTL on BTA 21 (41.1 cM) was consistent with the location of fat thickness QTL reported in a commercial line of *Bos taurus* (Li et al. 2004). However, these QTL regions were not similar to those detected previously by interval mapping (Nalaila et al. 2010). The QTL on BTA 1 (8.7 cM) and 27 (53.2 cM) were consistent with previous QTL identified by interval mapping (Nalaila et al. 2010).

A total of 18 QTL on 12 different chromosomes were found to have significant ($P < 0.05$) effects on AVE_BF and these QTL jointly explained 7.24% of phenotypic variation with 0.72% being the largest proportion accounted by an individual QTL located on BTA 1 (9.7 cM) (Table 4.2). The 18 QTL for AVE_BF identified in this study were not reported previously. However, the AVE_BF QTL on BTA 5 (26.5 cM) was located about 15 cM apart from the QTL detected earlier by interval mapping (Nalaila et al. 2010) on the same population.

Twenty QTL were identified on 13 different chromosomes had significant additive effects on CREA ($P < 0.05$), and they jointly contributed to 11.5% of

phenotypic variations with 1.3% being the largest proportion of variance explained by a single QTL on BTA 5 (52.6 cM) (Table 4.2). Five QTL on BTA 5 (52.6 cM), 8 (114.9 cM), 11 (37.9 cM), 12 (59.7 cM) and 15 (101.6 cM) were consistent with the ribeye area QTL regions detected in a commercial American Angus populations (McClure et al. 2010). Two QTL positions for CREA on BTA 5 (52.6 cM) and 14 (23 cM) were also similar to a longissimus muscle area QTL reported in other beef cattle populations by Casas et al. (2003) and Takasuga et al. (2007). The QTL on BTA 1 (8.7 cM) was in agreement with one of the 3 QTL identified by interval mapping previously in the same beef cattle population (Nalaila et al. 2010).

Thirteen QTL on 11 chromosomes had significant additive effects on the LMY ($P < 0.05$), which jointly explained 16.5% of phenotypic variations (Table 4.2). The phenotypic variance accounted by an individual QTL ranged from 0.49% to 2.70%, in which the QTL on BTA 4 (89.8 cM) had the highest variance on LMY. The QTL on BTA 15 (24.3 cM) that accounted for 1.9% of the phenotypic variance was consistent with a previous identified QTL by interval mapping analysis (Nalaila et al. 2010).

Fifteen QTL with significant additive effects on CMAR ($P < 0.05$) were identified on 11 different chromosomes (Table 4.2) and they together explained 23.9% of the phenotypic variance. The phenotypic variance explained by an individual QTL ranged from 0.5 to 4.8 % with the CMAR QTL on BTA 3 (92.3 cM) having the highest proportion of variance (Table 4.2). The QTL on BTA 3 (6.8 cM) is within the span of the QTL region for marbling score reported by

Casas et al. (2003). Two QTL on BTA 1 (8.7 cM) and 29 (29.6 cM) were consistent with the QTL mapped by previous interval mapping (Nalaila et al. 2010).

4.3.3. QTL affecting more than one trait

Several QTL had significant effects on more than one trait. The QTL for CMAR on BTA 9 (106.2 cM) also had a significant ($P < 0.01$) effect on MEAN_UMAR (Tables 4.1). In addition, two QTL for MEAN_UMAR on BTA 3 (95.2 cM) and 27 (14.7 cM) also had significant ($P < 0.01$) effects on UMAR (Table 4.2). The UMAR QTL on BTA 28 (58.2 cM) also had significant ($P < 0.01$) effects on CMAR (Table 4.2). Both UMAR and CMAR traits are the measures of the amount of intramuscular fat in the animal's body or carcass, therefore, this result may imply that these traits might be affected by the same QTL. However, further study is needed to confirm these results.

The GRDFAT QTL located at 8.7 cM on BTA 1 also had a significant ($P < 0.05$) effect on CREA and CMAR (Table 4.2). The CREA and CMAR QTL regions on BTA 1 were also similar to the QTL detected by a previous study (Nalaila et al. 2010), which may imply that these traits are affected by the same QTL or different genes that are located very close to each other. The GRDFAT QTL on BTA 7 (128.9 cM) also had a significant effect on YGRADE (Table 4.2), and the AVE_BF QTL on BTA 15 (42.5 cM) also had a significant ($P < 0.05$) effect on MEAN_UBF (Tables 1). Both AVE_BF and MEAN_UBF are the measures of backfat thickness, which implies these traits could be sharing some of

the genes. In addition, the QTL for CWT on BTA 1 (46 cM) also showed a significant ($P < 0.05$) effect on CREA (Table 1). The QTL for CREA on BTA 4 (89.8 cM) also had a significant ($P < 0.01$) effect on LMY (Table 4.2).

4.3.4. Genes associated with SNPs that are located under or near the QTL regions

The genes associated with SNPs that are located under or near the QTL regions are summarized in Table 4.3. The SNPs under the 218 QTL were within or nearest to 173 genes. The current discussion focuses on genes that are potentially related to beef carcass traits.

SNP ss38333252 under the MEAN_UBF QTL on BTA 13 (48.7 cM) is located near *UCN3* gene. The *UCN3* is involved in regulation of insulin secretion in mice, particularly in the presence of nutrient excess (Li et al. 2007). However, the role of the *UCN3* gene in regulating deposition of backfat in cattle needs further investigations.

The ss38332167 SNP located under the UBF QTL on BTA 14 (50.3 cM) is close to *CRH* gene. The *CRH* regulates appetite and has been reported to be associated with post-natal growth in beef cattle (Buchanan et al. 2002). Other studies in beef cattle have shown that single nucleotide polymorphism in the corticotrophin-releasing hormone gene (*CRH*) was associated with end-of-test rib-eye area and hot carcass weight (Buchanan et al. 2005). However, further studies are needed to determine the role of *CRH* gene on variation of carcass backfat.

The UMAR QTL on BTA 10 (21.2 cM) was closer to ss38328787 SNP (20.7 cM). The ss38328787 SNP is close to the *MIR2290* gene, which plays a crucial role in the regulation of gene expression in eukaryotes (Glazov et al. 2009). Glazov et al. (2009) reported several distinct classes of bovine miRNA and miRNA-like small regulatory RNAs that were expressed upon viral infection. Studies on the regulatory role of *MIR2290* gene will improve our understanding of genes that affecting carcass marbling in beef.

The QTL for CWT on BTA 1 (7.1 cM) was located close to ss38323939 SNP (6.6 cM). The ss38323939 SNP is close to *SOD1* gene. The *SOD1* gene encodes superoxide dismutase 1 enzyme (SOD1), which binds copper and zinc ions and is one of the three superoxide dismutases that play crucial roles in structural stability in the body (Borges-Alvarez et al. 2010). Findings in mice showed that individuals who were lacking SOD1 have increased age-related muscle mass loss (sarcopenia) and shortened lifespan (Muller et al. 2007). In view of the fact that the *SOD1* gene plays an important role on muscle mass in mice, therefore it could also be a good candidate gene for further studies in beef cattle to determine its influence on the variations of carcass weight. SNP ss38331322 that is located at 40.2 cM on BTA 6 was closer to CWT QTL (41.2 cM). The ss38331322 SNP is close to *PPARGC1A* gene that controls muscle fibre type and brown adipocyte differentiation in beef cattle (Soria et al. 2009). Also the *PPARGC1A* gene has been reported to associate with a significant increase in milk protein percentage in Holstein cattle population (Khatib et al. 2007). Therefore, the *PPARGC1A* gene could also be good candidate for carcass weight.

The CREA QTL on BTA 1 (116.7 cM) was located close to ss64843848 SNP (114.7 cM). The ss64843848 SNP is close to *MIR551B* gene. Characterization of *MIR551B* gene in bovine through MicroRNAs sequencing showed five miRNAs (miR-23a, -23b, -99a, -125b and -126-5p) were very abundant across 11 bovine tissues including brain, subcutaneous fat, muscle, liver, kidney, spleen and thymus, accounting for 44.3% of all small RNA sequences (Jin et al. 2009). Furthermore, expression analysis of miRNAs showed that miR-133a is predominantly expressed in muscle (Jin et al. 2009), which implies that *MIR551B* could be involved on variation of CREA in beef cattle. The ss38340471 SNP shares the same location with CREA QTL on BTA 5 (85.9 cM). The ss38340471 SNP is close to *MIR135A-2* gene, which is a class of non-coding RNA gene that plays important roles in the regulation of target genes by binding to complementary regions of messenger transcripts to repress their translation or regulate degradation (Griffiths-Jones et al. 2006). The miRNAs have shown diverse cellular roles in different species as developmental timing in worms, cell death and fat metabolism in flies and haematopoiesis in mammals (Griffiths-Jones et al. 2006). Therefore, *MIR135A-2* gene warrants further studies in future to understand its regulatory roles on the development of carcass ribeye area. The CREA QTL on BTA 14 (23 cM) was at similar location with ss66538042 SNP, which is near to *MYC* gene. Conacci-Sorrell et al. (2010) reported the identification of Myc-nick, a cytoplasmically localized cleavage product of *MYC*, and provided an evidence for its role in cytoskeletal organization and cell

differentiation in humans. The *MYC* could have a significant role on the development of various tissues in bovine including muscle component of CREA.

The CMAR QTL on BTA 8 (29.3 cM) was clos to ss38323808 SNP, which is near to *MIR491* gene. The *MIR491* gene is in similar ontolog class with *MIR551B* gene, which is involved in post-transcriptional regulation of gene expression in multicellular organisms by affecting both the stability and translation of mRNAs (Jin et al. 2009). Although role of the *MIR491* gene related to CMAR is unknown, however this gene provided a basis for further studies on its effect on the carcass traits.

The QTL for CMAR on BTA 9 (106.2 cM) and 10 (54.5 cM) shared the same location with ss38335346 and ss38322538 SNPs respectively. The ss38335346 is near to *AGPAT4* gene, which its role on CMAR is not clear. However, the ss38322538 SNP was close to *CCNDBP1* gene, which is a synexpression group-restricted regulator of TGF-b signalling. Studies in mice suggested that the *CCNDBP1* appeared to regulate a subset of TGF-b target genes including the Olig1-Smad synexpression group (Ikushima et al. 2008). The growth factors have important functions in maintaining homoeostasis of multicellular organisms because they are proteins that mediate intercellular communication through regulation of cell growth and differentiation (Ikushima et al. 2008). However, the role of *CCNDBP1* on CMAR in cattle needs further investigation. Overall identification of comprehensive sets of genes affecting carcass merit traits is a crucial step toward gene-assisted selection (GAS) in beef cattle.

4.3.5. Comparison of QTL effects estimated by the interval regression and the Bayesian shrinkage methods

Generally, QTL with large effects can be detected by both the Bayesian shrinkage and interval regression mapping methods but the later is relatively incapable of detecting QTL with small effects. This was also noticed and explained by Xu (2003a). The additive variance of individual QTL estimated by the Bayesian shrinkage method in the current study explained, relatively, a small proportion of phenotypic variation compared to the interval mapping analysis although large numbers of QTL were identified using the same dataset. This is due to the fact that the Bayesian shrinkage method evaluates all QTLs in a single model simultaneously, which is more robust than the interval mapping regression method. In contrast, the interval mapping regression method models one QTL at a time without fully adjusting for other QTLs on the genome, which is more likely to result in an overestimation of QTL effect and variance in particular when sample size is relatively small (Beavis 1998; Xu 2003b). In this study, 12 QTL for 8 ultrasound and carcass merit traits detected earlier by the interval mapping approach (Nalaila, 2010) were not confirmed. It is likely that some QTL identified by the interval mapping approach were spurious QTL due to upward bias on estimation of their effects or higher false positive rate as the interval mapping method searches one QTL at a time (Zeng 1994; Goring et al. 2001). Therefore these QTL were not present in the current study following the adjustment of the effects of other QTL on the genome using this Bayesian shrinkage method.

Basically, the Bayesian shrinkage approach can provide estimates of QTL location and effects without a statistical threshold test. In this study, an empirical threshold was obtained using a permutation method under the framework of the Bayesian shrinkage method as developed by Che and Xu (2010). The application of a threshold in declaring a significant QTL region reduces the rate of false positives; thus increases the confidence of QTL detection. In addition, the consistency of QTL results obtained from the same data set using different statistical approaches as well as with the QTL regions identified in other studies in different beef cattle populations can provide more reliable genetic markers for MAS and hence speed up the QTN search and positional candidate gene studies. The genes associated with SNPs that are located under or near the QTL regions provide a foundation for further studies that aim at identifying gene SNP markers for ultrasound and carcass merit traits for the implementation of marker assisted selection in beef cattle and for the search of the causative QTN.

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Table 4.1: Number of markers per BTA and average distance between SNP markers

BTA	No. of SNPs	Sum of SNP intervals	SNPs average interval[1]	Std Dev[2]	Min.[3]	Max.[4]
1	61	150.2	2.4623	3.1965	0.1	15.8
2	66	119.2	1.8061	2.6939	0.1	15.7
3	63	133.5	2.1190	3.4870	0.1	19.5
4	45	102.5	2.2778	3.5347	0.1	19.9
5	70	137.3	1.9614	3.0307	0.1	17.5
6	47	123.4	2.6255	4.1442	0.1	21.8
7	47	130.4	2.7745	3.2841	0.1	15.8
8	44	131.7	2.9932	3.7842	0.1	13.9
9	42	100.6	2.3952	2.3533	0.1	8.4
10	53	112.9	2.1302	2.5688	0.1	10.6
11	50	126.7	2.5340	3.7853	0.1	18.0
12	34	108.0	3.1765	5.0246	0.1	26.4
13	32	100.7	3.1469	4.2958	0.1	15.3
14	34	101.6	2.9882	3.9388	0.1	14.0
15	48	94.8	1.9750	2.8393	0.1	13.4
16	47	94.3	2.0064	2.8392	0.1	15.6
17	34	89.9	2.6441	3.3973	0.1	11.6
18	40	87.6	2.1900	3.9730	0.1	18.3
19	26	103.9	3.9961	5.1178	0.1	18.3
20	43	68.0	1.5814	2.8442	0.1	14.2
21	24	51.3	2.1375	2.6686	0.1	8.2
22	28	78.8	2.8143	4.1128	0.1	15.9
23	5	55.3	11.0600	11.998	0.4	29.0
24	9	38.3	4.2555	7.2637	0.1	21.9
25	27	65.3	2.4185	2.5727	0.1	8.3
26	4	36.6	9.1500	7.2519	4.5	18.9
27	39	59.2	1.5179	2.8076	0.1	16.6
28	80	61.7	0.7712	1.8407	0.1	15.1
29	65	69.3	1.0661	1.8885	0.1	11.4

[1]SNPs average interval in chromosome (cM); [2]Standard deviation of SNP intervals; [3]Minimun SNP interval (cM); [4]Maximun SNP interval (cM).

Table 4.2: Estimates of QTL parameters for ultrasound and carcass merit traits

Trait	BTA	SNP[y]	SNP position[x], cM	QTL position, cM	Additive[w]	Variance[w]	Proportion[v]	Dominance	Variance[u]	Proportion[t]
MEAN_UBF	1	ss64321934	46	46	0.366122*	0.10554	0.089764	0.275341**	0.365909	0.311213
	2	ss38333790	52.6	52.6	-0.74028**	0.386908	0.329073	-0.0346	0.010491	0.008923
	3	-	87	87	-0.79171**	0.260958	0.22195	-0.00202	0.000792	0.000673
	3	ss38333713	96.3	96.3	2.150722**	0.297559	0.25308	0.005573	0.005359	0.004558
	4	ss38334500	92.1	93.2	1.716307**	1.17146	0.996352	0.015982	0.010036	0.008536
	5	ss38323069	89.7	90.2	0.895244**	0.55347	0.470738	0.131144*	0.075375	0.064108
	7	ss66538273	69.1	70.1	-1.00248**	0.219647	0.186814	-0.00341	0.001493	0.00127
	8	ss66538273	29.3	29.8	1.187541**	0.54058	0.459775	-0.02972	0.005425	0.004614
	9	ss66538150	69.1	69.6	-1.0092**	0.181073	0.154007	0.001274	0.000469	0.000399
	11	ss38326296	116.5	116.5	1.329661**	0.169408	0.144085	0.004747	0.001829	0.001556
	13	ss38333252	48.7	48.7	1.12253**	0.073483	0.062499	0.00606	0.001152	0.000979
	14	ss66537607	87.5	87.5	0.622084**	0.683435	0.581276	0.107932*	0.098808	0.084038
	15	ss38337040	42.5	42.5	-0.32033*	0.19536	0.166157	-0.35102**	0.098212	0.083532
	18	ss38337298	46.7	47.2	-1.06405**	0.477837	0.40641	-0.02804	0.008235	0.007004
	27	ss38323230	56.9	56.4	-1.54754**	0.606302	0.515673	-0.01849	0.004636	0.003943
	28	ss63187445	40.4	40.9	1.411095**	0.462503	0.393369	-0.00464	0.003815	0.003245
UBF	1	ss38322907	126.2	126.2	3.3433**	6.202805	3.622262	0.040994	0.370137	0.216149
	2	ss66538237	64.6	64.6	0.809575**	0.889158	0.519243	-0.82662**	2.893903	1.689957
	2	ss38322921	117.2	117.2	1.872115**	1.859609	1.085959	-0.08293	0.107526	0.062792
	3	ss38336741	3.8	7.4	1.59071**	2.37223	1.385315	0.414964**	0.294481	0.171969
	3	ss66537844	49.6	57.1	1.10124**	2.210567	1.290909	0.569734**	0.257627	0.150447
	3	ss38333136	95.2	95.2	3.787901**	0.768364	0.448703	0.073811	0.021302	0.01244
	4	ss38324841	89.8	89.8	1.710735**	2.644365	1.544234	-0.01097	0.044161	0.025789
	5	ss38324813	27.3	27.3	-1.48786**	0.89942	0.525236	0.00094	0.000155	9.03E-05
	5	ss38326905	53.6	53.6	0.826118*	0.458241	0.2676	0.001695	0.003364	0.001964
	5	ss38323313	86.4	86.4	1.575255**	1.435758	0.838442	0.03042	0.02498	0.014588
	6	ss38326151	35.2	35.2	-1.9783**	2.870818	1.676476	-0.08106	0.050114	0.029265
	6	ss38323786	139	139	-1.09867**	2.724338	1.590936	-0.05579	0.040257	0.023509
	7	ss38323611	88.8	88.8	1.968947**	1.614872	0.943039	0.102377	0.064753	0.037814
	13	ss38324702	34.1	42	1.291641**	1.989188	1.161629	0.056281	0.036705	0.021435
	14	ss38332167	50.3	50.3	2.03721**	2.290473	1.337571	0.050847	0.03712	0.021677
	19	ss66538043	20.2	20.2	0.815144**	1.09587	0.639957	0.008418	0.021615	0.012623
	19	ss66538209	94.7	94.7	-1.34209**	0.980687	0.572693	-0.00473	0.007642	0.004462
	20	ss38324135	42.7	51.7	1.522028**	0.426474	0.249049	-0.00079	0.00099	0.000578
	21	-	41.8	41.8	-1.22316**	1.179869	0.68901	-0.00511	0.004837	0.002824
	22	ss38329030	57.2	57.2	0.731556**	0.603123	0.352207	-0.54641**	0.362536	0.211711
MEAN_UMAR	1	ss38323846	40.6	39.6	0.275694**	0.012144	0.118878	-0.00105	8.96E-05	0.000877

	1	ss38334998	81.2	82.2	-0.54667**	0.023964	0.234597	-0.00053	2.40E-04	0.002344
	1	ss38324135	148.1	147.6	-0.18196**	0.024128	0.236198	0.04883*	4.02E-03	0.039374
	2	ss65205558	35.6	36.1	0.086591*	0.031826	0.311563	-0.13044**	8.40E-03	0.082269
	2	ss66538027	86.7	87.2	-0.43474**	0.062946	0.616204	-0.00061	8.33E-05	0.000816
	3	ss38333136	95.2	95.2	-0.11045*	0.019503	0.190924	0.26540**	4.23E-03	0.041415
	4	ss38327339	103.4	103.4	-0.21116**	0.037113	0.363318	-0.00122	3.47E-05	0.00034
	5	ss66538279	26	26.5	0.047413*	0.031782	0.311129	0.20786**	1.01E-02	0.099151
	5	ss38333117	120.7	120.7	0.472339**	0.060132	0.588661	0.00256	6.10E-04	0.00597
	6	ss66538247	43.8	45.3	-0.1841**	0.029045	0.284339	-0.00003	8.11E-05	0.000794
	7	ss66537587	91.1	91.1	0.056997*	0.012659	0.123922	-0.24462**	3.76E-03	0.036768
	8	ss38328464	118.4	118.9	-0.45127**	0.017594	0.17224	-0.00067	6.00E-05	0.000587
	9	ss38335346	106.2	107.2	0.157528**	0.034896	0.341613	-0.01994	8.92E-03	0.08731
	10	ss38324440	86	87.5	0.15624**	0.041256	0.403874	0.01291	1.23E-03	0.012073
	11	ss66537563	119.4	119.9	-0.27588**	0.02724	0.26666	-0.00684	5.65E-04	0.005526
	14	ss38323901	27.8	27.8	0.240492**	0.028129	0.275362	0.01066	1.57E-03	0.01535
	14	ss66537607	87.5	87.5	-0.26254**	0.054286	0.531432	-0.03512*	2.42E-03	0.02368
	15	ss66538055	35	35	0.234747**	0.051621	0.505337	-0.00098	1.30E-05	0.000128
	15	ss38328343	59.8	61.3	0.165583**	0.032726	0.320373	0.08085**	6.93E-03	0.067817
	19	ss38334236	58.5	62	-0.3166**	0.03125	0.305922	0.00128	7.90E-05	0.000773
	21	ss38324150	41.1	41.1	-0.31963**	0.033232	0.325319	-0.00106	8.98E-05	0.000879
	27	ss38335669	13.2	14.7	-0.34984**	0.025378	0.248437	0.00274	2.97E-04	0.002904
UMAR	1	ss38322512	72.7	73.7	0.513131**	0.284835	0.777868	0.064164*	0.091844	0.250821
	2	ss38333790	52.6	52.6	-0.62342**	0.212504	0.580335	-0.01577	0.007741	0.021139
	3	ss38333136	95.2	95.7	0.692361	0.264134	0.721334	-0.13963**	0.051224	0.139891
	3	ss66537544	120.8	121.3	1.111111**	0.208358	0.569014	-0.01671	0.00905	0.024715
	5	ss38340495	68.9	69.4	0.168595*	0.0844	0.230493	-0.33263**	0.02266	0.061883
	5	ss38323692	86.2	86.2	-0.32148**	0.082548	0.225434	-0.01176	0.001962	0.005358
	6	ss66537977	47	47	-0.64388**	0.329364	0.899475	0.000662	0.000178	0.000487
	10	ss38328787	20.7	21.2	0.380096**	0.098714	0.269584	-0.21757**	0.049972	0.136471
	11	ss66538251	52.3	52.3	0.332194**	0.207323	0.566187	-0.13917**	0.023888	0.065238
	11	ss38326296	116.5	116	-0.6611**	0.062517	0.170731	-0.00515	0.001085	0.002962
	13	ss66537669	32	32	0.52248**	0.13558	0.37026	0.001593	0.000408	0.001115
	15	ss38327992	55	55	0.485717**	0.140422	0.383485	-0.01059	0.026535	0.072466
	27	ss38335669	13.2	14.7	-0.40758**	0.166849	0.455656	-0.00654	0.010433	0.028491
	28	ss38323528	58.2	58.7	-0.40429**	0.149723	0.408885	-0.11727**	0.02185	0.059672
ADG_UREA	1	ss38322907	126.2	127.7	0.061151**	0.001992	0.823555	0.007337*	0.000175	0.072181
	1	ss38333732	155.1	155.1	-0.01702**	0.00143	0.591195	0.002568	6.46E-05	0.026713
	2	ss61484221	104.7	104.7	-0.06522**	0.000222	0.091595	0.000112	8.86E-07	0.000366
	3	ss38331439	3.8	5.3	-0.0805**	0.000301	0.124249	-0.00028	9.78E-06	0.004044
	3	-	87	87	0.145246**	0.007462	3.084134	-0.05179**	0.001118	0.462183

	5	ss38339200	58.5	60	0.06111**	0.001328	0.549068	-0.00144	2.74E-05	0.011333
	8	ss38325262	69.6	69.6	0.027765**	0.000512	0.211634	0.00443*	6.19E-05	0.025589
	8	ss38336907	129.8	129.8	0.06241**	0.000208	0.086088	-0.00012	1.11E-06	0.000459
	9	ss38322600	26.9	26.9	-0.03192**	0.001007	0.416075	0.005376	7.32E-05	0.030254
	10	ss38329478	115.6	115.6	-0.03671**	0.000417	0.172385	-0.00192	3.61E-05	0.014932
MEAN_UREA	1	ss38334998	81.2	81.2	2.835654**	10.01471	1.392706	0.008678	0.01324	0.001841
	2	ss38322523	11	11	3.306072**	6.325473	0.879658	-0.00384	0.017524	0.002437
	3	ss38331439	3.8	6.8	6.453504**	14.09327	1.959894	0.000203	1.027749	0.142925
	3	ss38322909	102.2	102.2	-1.50727**	3.440323	0.478432	1.950103**	2.091331	0.290833
	3	ss66537544	120.8	120.8	4.496742**	4.737407	0.658812	0.053052	0.093334	0.01298
	4	s66538094	19.7	22.7	-4.50287**	1.901598	0.264448	0.002804	0.003316	0.000461
	5	ss38339297	15.5	18.5	3.109329**	7.695158	1.070135	0.010177	0.012747	0.001773
	8	ss38326154	42.1	45.1	2.7183**	6.023006	0.837595	0.000598	0.006307	0.000877
	10	ss38334832	115.5	115.5	2.80134**	14.49225	2.015379	0.030088	0.053628	0.007458
UREA	1	ss66537759	24.8	28.3	3.495519**	43.99802	1.214988	-0.25302	14.77981	0.408138
	3	ss38324942	3.8	5.8	-3.9361**	10.96469	0.302785	4.913666**	5.638196	0.155696
	5	ss38323767	101.7	102.7	5.240364**	5.827349	0.16092	0.004218	0.001069	2.95E-05
	6	-	82.3	83.8	-9.51041**	30.88927	0.852995	-0.03528	0.034366	0.000949
	7	ss38335142	131.5	131.5	2.444313**	5.316752	0.14682	1.534077**	2.578992	0.071218
	9	ss38335346	106.2	107.2	-2.37492**	12.2008	0.33692	-2.07925**	3.200089	0.088369
	10	s38324682	97.7	97.7	1.727635*	5.932168	0.163814	-0.20809	0.146953	0.004058
	11	ss66537563	119.4	119.4	2.48161**	18.60755	0.51384	-0.67182*	0.695529	0.019207
	17	ss38336166	3.9	5.4	4.905766**	24.77541	0.684163	0.89785**	1.921397	0.053059
	18	ss28451881	47.8	48.8	5.968099**	9.440276	0.260689	-0.09725	0.177081	0.00489
	21	ss38324150	41.1	41.1	2.128162**	4.703248	0.129878	0.964664**	1.094409	0.030222
	27	ss38323377	52.7	53.2	7.042886**	16.91988	0.467235	0.087114	0.886824	0.024489
	28	ss63187445	40.4	40.9	-7.90167**	5.669515	0.156561	-0.13108	0.120681	0.003333
	29	ss38324305	50.9	50.9	1.842868**	11.48407	0.317128	-1.62852**	7.424599	0.205027
CWT	1	ss38323939	6.6	7.1	45.31756**	85.67125	0.406983	0.070339	0.289814	0.001377
	1	ss64321934	46	47.5	38.4511**	33.06813	0.157091	0.035153	0.136392	0.000648
	1	ss38322907	126.2	126.3	15.19338**	71.03872	0.337471	11.7534**	5.68023	0.026984
	2	ss38325754	100.2	101.2	33.87194**	93.28745	0.443163	-0.2665	1.004664	0.004773
	4	ss65316398	61.8	61.8	30.1484**	128.812	0.611924	-0.71237	4.791699	0.022763
	5	ss38329047	87.5	87.5	-26.4392**	58.0479	0.275757	-0.14379	0.678612	0.003224
	6	ss38324097	25.2	26.2	-15.248**	145.3761	0.690611	-2.23824*	13.67425	0.06496
	6	ss38331322	40.2	41.2	20.35768**	104.685	0.497308	0.124066	0.819323	0.003892
	15	ss38322121	65.2	65.4	8.958383**	119.4488	0.567443	-9.3519**	85.69356	0.407089
	18	ss38326834	54.4	63.5	-15.3892**	67.32804	0.319843	-0.02062	0.152405	0.000724
	20	ss62627427	23.1	23.1	-6.38117*	49.34899	0.234433	0.124831	0.359937	0.00171
AVE_BF	1	ss66538078	8.7	9.7	5.222085**	4.449362	0.724472	-0.10383	0.04791	0.007801

	2	-	3.8	6.3	3.780179**	3.558645	0.57944	-0.00778	0.002634	0.000429
	2	ss38329575	50.5	50.5	2.741385**	2.703839	0.440256	0.018891	0.031437	0.005119
	2	ss66538147	81.4	81.4	2.190087**	2.046697	0.333256	-2.34374**	0.537463	0.087513
	2	ss38328442	82	82	3.057647**	2.540139	0.413601	-2.33199**	1.415059	0.230408
	2	ss38326398	110.1	110.6	4.04706**	3.018803	0.49154	-0.07683	0.047106	0.00767
	3	ss38334140	75.5	75.5	-2.50142**	0.916666	0.149257	-0.00147	0.001988	0.000324
	4	ss65316398	61.8	61.8	-0.54325*	0.929354	0.151323	2.364506**	0.304369	0.049559
	5	ss66538279	26	26.5	3.093421**	3.810941	0.620521	0.20695*	0.378912	0.061697
	5	ss38324636	120	120.5	-2.1548**	1.427198	0.232385	-0.00808	0.003364	0.000548
	6	ss66537977	47	47.5	-2.57651**	3.101924	0.505074	0.307248*	0.643303	0.104747
	7	ss38322516	138	138.5	2.384511**	0.626151	0.101954	-2.11235**	0.274854	0.044753
	8	ss38324279	48	48	3.543809**	2.890571	0.47066	0.006534	0.003167	0.000516
	15	ss38337040	42.5	42.5	-2.13588**	2.926075	0.476441	0.042482	0.022859	0.003722
	15	ss38324125	101.6	101.6	-2.27799**	2.478188	0.403514	0.056499	0.092462	0.015055
	17	ss38324651	68.1	68.6	-2.71937**	3.83301	0.624114	-0.03072	0.057028	0.009286
	27	ss38323377	52.7	53.2	1.261289**	2.165834	0.352654	0.352041*	0.493387	0.080336
	29	ss38334851	39.7	40.2	1.623587**	1.068216	0.173933	0.033975	0.024043	0.003915
GRDFAT	1	ss66538078	8.7	8.7	2.199819**	3.482738	0.433617	-0.20826	0.161952	0.020164
	1	ss66537739	153.4	153.4	0.564805*	2.94132	0.366208	1.721013**	0.718082	0.089405
	3	ss38323208	55.1	55.1	-3.5904**	1.418022	0.17655	-0.03707	0.029972	0.003732
	3	ss66537665	74.8	74.8	2.269403**	5.366011	0.668093	-0.09762	0.108228	0.013475
	3	ss38322790	86.4	86.4	-4.16324**	3.175825	0.395405	-0.0239	0.025897	0.003224
	3	ss38322909	102.2	103.2	4.337599**	9.016525	1.122599	0.28758*	0.638947	0.079552
	4	ss38322669	43.9	44.4	2.265128**	12.87426	1.602905	1.302307**	1.167235	0.145326
	6	ss38324338	29	29	2.44325**	1.19653	0.148974	-0.00406	0.003711	0.000462
	7	ss38329588	8.5	8.5	-1.04526*	1.849271	0.230243	0.009685	0.00218	0.000271
	7	ss38322119	65.1	65.1	-1.32351*	2.997434	0.373194	-0.02513	0.008143	0.001014
	7	ss38322165	128.9	128.9	-1.03979*	1.891305	0.235476	-0.01508	0.003806	0.000474
	10	ss38324682	97.7	97.7	3.507917**	4.051382	0.504416	-0.00264	0.001594	0.000198
	12	ss38324078	97.6	97.6	-1.38412**	2.673927	0.332916	-0.02716	0.005591	0.000696
	13	ss38323604	47.6	47.6	1.55333**	2.748287	0.342174	0.050905	0.065861	0.0082
	15	ss38335183	62.7	63.7	1.410945**	1.572938	0.195838	-0.00784	0.002898	0.000361
	21	ss38324150	41.1	41.1	-1.48812*	3.310087	0.412121	-0.44969*	0.664785	0.082769
	27	ss38323377	52.7	53.2	2.15846**	2.274377	0.283171	0.127554	0.254926	0.031739
CREA	1	ss66538078	8.7	8.7	-3.52652*	11.33277	0.720463	-1.17313*	1.887775	0.120012
	1	ss64321934	46	46	2.012048*	9.365202	0.595378	-1.17741**	3.603705	0.2291
	1	ss64843848	114.7	116.7	8.901336**	10.34501	0.657668	-0.00559	0.047202	0.003001
	3	ss66537570	97.6	97.6	-2.4123**	8.665988	0.550927	2.032069**	4.022834	0.255745
	4	ss66538016	28.8	28.8	3.284013**	6.560794	0.417092	0.172037	0.211867	0.013469
	4	ss38324841	89.8	89.8	-4.50864**	7.715414	0.490495	-0.00682	0.020734	0.001318

	5	ss38339563	52.6	52.6	-5.14261**	21.20243	1.347912	0.098617	0.09602	0.006104
	5	ss38340495	68.9	68.9	-3.04184**	13.74748	0.873975	-1.50756**	1.814524	0.115356
	5	ss38340471	85.9	85.9	3.271999**	10.01697	0.636813	0.100229	0.128974	0.008199
	6	ss38322890	142.3	141.3	-3.85268**	7.817151	0.496963	-0.04051	0.052288	0.003324
	8	ss38322842	114.9	114.9	2.348765**	5.314423	0.337856	-0.09016	0.143262	0.009108
	10	ss65561641	98.3	98.3	1.704489*	4.031658	0.256306	-0.00691	0.004333	0.000275
	11	ss66537939	37.9	37.9	-4.96218**	11.56746	0.735383	-0.01717	0.012757	0.000811
	12	ss66537619	59.7	59.7	-1.48516*	5.992838	0.380985	-2.46262**	1.379781	0.087717
	14	ss66538042	23	23	-3.17905**	10.84976	0.689757	-0.0022	0.000139	8.82E-06
	14	ss66537607	87.5	87.5	1.184183*	8.089053	0.514249	2.529127**	2.050299	0.130345
	14	ss38328773	93.4	93.4	2.857982**	4.574746	0.290832	-3.23078**	1.912925	0.121611
	15	ss38324125	101.6	101.6	2.078857*	4.630056	0.294349	0.019566	0.014955	0.000951
	20	45114461	42.7	41.7	-2.63698**	10.39449	0.660814	-1.79065**	1.630074	0.103629
	22	11039315	14.2	13.2	5.152899**	8.788324	0.558704	0.034748	0.031981	0.002033
LMY	1	ss38324800	17.9	19.4	0.464921*	0.619015	0.307451	-0.52467*	5.386238	2.675221
	1	ss38322126	145.9	145.9	1.421462**	2.263531	1.124244	-0.03006	0.053656	0.02665
	2	-	3.8	5.8	-1.87755**	4.840333	2.404082	-0.02329	0.039935	0.019835
	3	ss38336860	99.6	99.6	-1.92641**	4.391512	2.181163	-0.05835	0.073366	0.036439
	4	ss38324841	89.8	89.8	-1.23756*	5.438191	2.701024	-1.04778**	1.046433	0.519739
	7	ss66537587	91.1	91.1	3.109444**	3.004424	1.492228	0.010252	0.004421	0.002196
	11	ss38322573	117.4	117.4	0.785062*	1.308198	0.649752	0.072359	0.071571	0.035548
	14	ss66537607	87.5	87.5	1.534523**	1.203715	0.597858	-0.00679	0.002888	0.001435
	15	ss38332148	24.3	24.3	-1.36446**	1.902147	0.944753	-0.02032	0.012025	0.005973
	20	ss61522292	17.8	17.8	-2.82367**	0.991966	0.492687	-0.00372	0.002271	0.001128
	20	ss38324910	53.7	53.7	0.949393*	2.227142	1.10617	0.441982**	0.372137	0.184832
	27	ss38323589	51.9	51.9	-1.36502**	2.531956	1.257564	-0.16677*	0.208361	0.103488
	28	ss63187445	40.4	40.4	-1.75018**	2.453928	1.21881	-0.0072	0.007124	0.003538
CMAR	1	ss66538078	8.7	8.7	0.071225*	0.016343	0.537535	-0.25315**	0.010144	0.333642
	1	-	151.1	151.1	-0.25041**	0.04163	1.369217	-0.03091	0.004195	0.13797
	2	ss66538017	53.5	53.5	-0.30755**	0.070423	2.316216	-0.00109	7.04E-05	0.002317
	2	ss38332354	57.1	57.1	-0.21453**	0.068693	2.259327	-0.00058	5.99E-05	0.00197
	2	ss38325760	73.7	73.7	0.198427**	0.03782	1.243892	0.005661	0.000556	0.018284
	3	ss38331439	3.8	6.8	0.092449*	0.027742	0.912425	0.038534*	0.005748	0.189063
	3	ss66538221	92.8	92.8	0.2887**	0.146932	4.832631	0.119731**	0.017705	0.582326
	4	ss66538094	19.7	22.7	0.520736**	0.016894	0.555655	0.002847	0.00029	0.009526
	6	ss38327022	29.7	29.7	0.282886**	0.065735	2.162022	0.001564	0.000281	0.009227
	8	ss38323808	29.3	29.3	0.310738**	0.05375	1.767849	0.012362	0.001469	0.048311
	9	ss38335346	106.2	106.2	0.134731*	0.02966	0.975519	-0.00332	0.000621	0.020415
	10	ss38322538	54.5	54.5	-0.25228**	0.059303	1.950476	-0.00157	0.000306	0.01006
	11	ss66538272	116.1	116.1	-0.18302**	0.032688	1.075117	0.000457	0.000109	0.003591

	28	ss38323528	58.2	58.2	-0.07634*	0.019424	0.638858	-0.0609*	0.006342	0.208606
	29	ss63270688	26.6	29.6	0.215406**	0.038872	1.278523	-0.00074	6.04E-05	0.001987
YGRADE	1	ss38335051	97.9	97.9	-0.19353*	0.064941	0.338743	-0.00087	4.90E-06	2.56E-05
	1	ss38323849	129	129	-0.6688**	0.354363	1.848427	0.13205**	0.037958	0.197995
	1	ss38333732	155.1	155.1	0.678434**	0.127495	0.665039	-0.02457	0.002203	0.01149
	2	s38322486	37	37	0.188445*	0.065858	0.343529	3.30E-05	1.76E-05	9.19E-05
	2	ss38322399	43.2	43.7	-0.65188**	0.074567	0.388958	-0.00269	0.000385	0.002008
	3	ss65658800	48.4	48.4	-0.24681**	0.059181	0.308702	0.324017**	0.005412	0.028232
	4	ss66538006	116.3	116.3	-0.61299**	0.139768	0.729059	0.001776	0.000153	0.000798
	5	ss38340496	70.2	70.2	0.592795**	0.086934	0.453465	0.00308	0.000641	0.003344
	7	ss38323732	9.6	9.6	-0.17664*	0.057559	0.300237	-0.0034	0.000793	0.004137
	7	ss38322165	128.9	128.9	-0.29835**	0.065775	0.343097	-0.01351	0.002879	0.015015
	9	ss38329347	14.8	14.8	-0.41236**	0.060944	0.317895	-0.00027	2.67E-05	0.000139
	9	ss38324745	90.7	90.7	0.213855**	0.053778	0.280518	0.000692	4.73E-05	0.000247
	11	ss28452549	15.5	15	0.66996**	0.195121	1.017792	0.004153	0.001633	0.008516
	16	ss38333246	67.3	66.3	0.459534**	0.050904	0.265524	0.000121	4.74E-06	2.47E-05
	19	ss38323711	102.5	102.5	0.283487**	0.075604	0.394363	0.007628	0.00084	0.004383
	20	ss38324607	55.5	55.5	-0.4435**	0.091127	0.475335	-0.02761	0.004991	0.026033
	25	ss61487242	5.2	5.2	-0.37003**	0.024726	0.128976	0.000185	1.28E-06	6.65E-06
	28	s38331569	2.7	2.7	-0.36143**	0.05452	0.284389	-0.05135*	0.004759	0.024824
	28	ss38335007	38.6	39.1	0.545905**	0.053694	0.280079	0.002913	0.000212	0.001107

[y]National Center for Biotechnology Information (NCBI) ID for SNP associated with putative QTL; [x]SNP location on the chromosome; [w]Additive variance; [v]Proportion of additive variance on the phenotypic variance (%); [u]Dominace variance; [t]Proportion of dominance variance on the phenotypic variance (%); MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; MEAN_UMAR = mean ultrasound marbling; UMAR = ultrasound marbling; ADG_UREA = average daily gain ultrasound ribeye area; MEAN_UREA = mean ultrasound ribeye area; UREA = ultrasound ribeye area. CWT = carcass weight; AVE_BF = average backfat; GRDFAT = carcass grade fat; CREA = carcass ribeye area; LMY = lean meat yield; CMAR = carcass marbling; YGRDAE = carcass yield grade; *P < 0.05; **P < 0.01

Table 4.3: Summary of genes associated with SNPs that are located under or near the QTL regions for ultrasound and carcass merit traits

Trait	BTA	SNP	Position (bp)	Function class	Gene name	Gene description
MEAN_UBF	1	ss64321934	41793196	nearest gene	*ARL6*	Bos taurus ADP-ribosylation factor-like 6 (ARL6), mRNA
	2	ss38333790	31773763	nearest gene	*CSRNP3*	Bos taurus cysteine-serine-rich nuclear protein 3 (CSRNP3), mRNA
	3	-	71628105	intron	*ZZZ3*	Bos taurus zinc finger, ZZ-type containing 3 (ZZZ3), mRNA
	3	ss38333713	93417390	nearest gene	*JUN*	Bos taurus jun oncogene (JUN), mRNA
	4	ss38334500	93149174	nearest gene	*GPR37*	Bos taurus G protein-coupled receptor 37 (endothelin receptor type B-like) (GPR37), mRNA
	5	ss38323069	88228164	nearest gene	*MRPS35*	Bos taurus mitochondrial ribosomal protein S35 (MRPS35), nuclear gene encoding mitochondrial protein, mRNA
	7	ss66538273	32070334	nearest gene	*HSD17B4*	Bos taurus hydroxysteroid (17-beta) dehydrogenase 4 (HSD17B4), mRNA
	8	ss66538273	23426537	nearest gene	*IFNT*	Bos taurus interferon-tau 3g (IFNT), mRNA
	9	ss66538150	223081	intron	*RNGTT*	Bos taurus RNA guanylyltransferase and 5'-phosphatase (RNGTT), mRNA
	11	ss38326296	94892677	nearest gene	*MGC151949*	Bos taurus similar to glycoprotein galactosyltransferase alpha 1, 3 (MGC151949), mRNA
	13	ss38333252	43470740	nearest gene	*UCN3*	Bos taurus urocortin 3 (stresscopin) (UCN3), mRNA
	14	ss66537607	62424259	nearest gene	*POLR2K*	Bos taurus polymerase (RNA) II (DNA directed) polypeptide K, 7.0kDa (POLR2K), mRNA
	15	ss38337040	32194742	intron	*C15H11orf63*	Bos taurus chromosome 11 open reading frame 63 ortholog (C15H11orf63), mRNA
	18	ss38337298	47861332	nearest gene	*MAP4K1*	Bos taurus mitogen-activated protein kinase 1 (MAP4K1), mRNA
	27	ss38323230	37434175	nearest gene	*IDO1*	Bos taurus indoleamine 2,3-dioxygenase 1 (IDO1), mRNA
	28	ss63187445	27699906	nearest gene	*C28H10orf104*	Bos taurus chromosome 10 open reading frame 104 ortholog (C28H10orf104), mRNA
UBF	1	ss38322907	110568327	exon	*MFSD1*	Bos taurus major facilitator superfamily domain containing 1 (MFSD1), mRNA
	2	ss66538237	49512651	intron	*KIF5C*	Bos taurus kinesin family member 5C (KIF5C), mRNA
	2	ss38322921	127508328	nearest gene	*MATN1*	Bos taurus matrilin 1, cartilage matrix protein (MATN1), mRNA
	3	ss38336741	9220807	exon	*NDUFS2*	Bos taurus NADH dehydrogenase (ubiquinone) Fe-S protein 2, 49kDa (NADH-coenzyme Q reductase) (NDUFS2), nuclear gene encoding mitochondrial protein, mRNA

	3	ss66537844	38549270	nearest gene	*MGC139448*	Bos taurus hypothetical protein LOC787473 (MGC139448), mRNA
	3	ss38333136	90945586	intron	*NFIA*	Bos taurus nuclear factor I/A (NFIA), mRNA
	4	ss38324841	91217499	nearest gene	*GPR85*	Bos taurus G protein-coupled receptor 85 (GPR85), mRNA
	5	ss38324813	17272101	nearest gene	*SLC6A15*	Bos taurus solute carrier family 6 (neutral amino acid transporter), member 15 (SLC6A15), mRNA
	5	ss38326905	37022996	nearest gene	*SLC38A2*	Bos taurus solute carrier family 38, member 2 (SLC38A2), mRNA
	5	ss38323313	67701052	intron	*ANKS1B*	Bos taurus ankyrin repeat and sterile alpha motif domain containing 1B (ANKS1B), mRNA
	6	ss38326151	40981871	nearest gene	*MIR218-1*	Bos taurus microRNA mir-218-1 (MIR218-1), microRNA
	6	ss38323786	59787612	intron	*CASP6*	Bos taurus caspase 6, apoptosis-related cysteine peptidase (CASP6), mRNA
	7	ss38323611	65978304	nearest gene	*MRPL22*	Bos taurus mitochondrial ribosomal protein L22 (MRPL22), nuclear gene encoding mitochondrial protein, mRNA
	13	ss38324702	25009332	nearest gene	*ENKUR*	Bos taurus enkurin, TRPC channel interacting protein (ENKUR), mRNA
	14	ss38332167	32510677	nearest gene	*CRH*	Bos taurus corticotropin releasing hormone (CRH), mRNA
	19	ss66538043	12005510	nearest gene	*CA4*	Bos taurus carbonic anhydrase IV (CA4), mRNA
	19	ss66538209	48639831	nearest gene	*METTL2B*	Bos taurus methyltransferase like 2B (METTL2B), mRNA
	20	ss38324910	51402608	nearest gene	*CDH10*	Bos taurus cadherin 10, type 2 (T2-cadherin) (CDH10), mRNA
	21	-	19103797	intron	*MRPL46*	Bos taurus mitochondrial ribosomal protein L46 (MRPL46), nuclear gene encoding mitochondrial protein, mRNA
	22	ss38329030	41649041	intron	*FHIT*	Bos taurus fragile histidine triad gene (FHIT), mRNA
MEAN_UMAR	1	ss38323846	35152843	nearest gene	*VGLL3*	Bos taurus vestigial like 3 (Drosophila) (VGLL3), mRNA
	1	ss38334998	68666549	intron	*SEC22A*	Bos taurus SEC22 vesicle trafficking protein homolog A (S. cerevisiae) (SEC22A), mRNA
	1	ss38324135	148863139	intron	*LSS*	Bos taurus lanosterol synthase (2,3-oxidosqualene-lanosterol cyclase) (LSS), mRNA
	2	ss65205558	18824550	nearest gene	*PLEKHA3*	Bos taurus pleckstrin homology domain containing, family A (phosphoinositide binding specific) member 3 (PLEKHA3), mRNA
	2	ss66538027	83412865	exon	*STAT1*	Bos taurus signal transducer and activator of transcription 1, 91kDa (STAT1), mRNA
	3	ss38333136	90945586	intron	*NFIA*	Bos taurus nuclear factor I/A (NFIA), mRNA

	4	ss38327339	104925374	nearest gene	*PTN*	Bos taurus pleiotrophin (PTN), mRNA
	5	ss66538279	14827654	nearest gene	*CCDC59*	Bos taurus coiled-coil domain containing 59 (CCDC59), mRNA
	5	ss38333117	118990366	nearest gene	*SGSM3*	Bos taurus small G protein signaling modulator 3 (SGSM3), mRNA
	6	ss66538247	46289361	nearest gene	*PI4K2B*	Bos taurus phosphatidylinositol 4-kinase type 2 beta (PI4K2B), mRNA
	7	ss66537587	70880939	nearest gene	*IL12B*	Bos taurus interleukin 12B (natural killer cell stimulatory factor 2, cytotoxic lymphocyte maturation factor 2, p40) (IL12B), mRNA
	8	ss38328464	107840541	intron	*PRPF4*	Bos taurus PRP4 pre-mRNA processing factor 4 homolog (yeast) (PRPF4), mRNA
	9	ss38335346	100858875	nearest gene	*AGPAT4*	Bos taurus 1-acylglycerol-3-phosphate O-acyltransferase 4 (lysophosphatidic acid acyltransferase, delta) (AGPAT4), mRNA.
	10	ss38324440	67485298	nearest gene	*DDHD1*	Bos taurus DDHD domain containing 1 (DDHD1), mRNA
	11	ss66537563	101475357	nearest gene	*GARNL3*	Bos taurus GTPase activating Rap/RanGAP domain-like 3 (GARNL3), mRNA.
	14	ss38323901	17289087	nearest gene	*HAS2*	Bos taurus hyaluronan synthase 2 (HAS2), mRNA
	14	ss66537607	62424259	nearest gene	*POLR2K*	Bos taurus polymerase (RNA) II (DNA directed) polypeptide K, 7.0kDa (POLR2K), mRNA
	15	ss66538055	28170828	exon	*VPS11*	Bos taurus vacuolar protein sorting 11 homolog (S. cerevisiae) (VPS11), mRNA
	15	ss38328343	43366680	intron	*LMO1*	Bos taurus LIM domain only 1 (rhombotin 1) (LMO1), mRNA
	19	ss38334236	32341595	nearest gene	*HS3ST3A1*	Bos taurus heparan sulfate (glucosamine) 3-O-sulfotransferase 3A1 (HS3ST3A1), mRNA
	21	ss38324150	18130029	nearest gene	*MRPL46*	Bos taurus mitochondrial ribosomal protein L46 (MRPL46), nuclear gene encoding mitochondrial protein, mRNA
	27	ss38335669	1051	nearest gene	*CLN8*	Bos taurus ceroid-lipofuscinosis, neuronal 8 (epilepsy, progressive with mental retardation) (CLN8), mRNA
UMAR	1	ss38322512	68338491	nearest gene	*DIRC2*	Bos taurus disrupted in renal carcinoma 2 (DIRC2), mRNA
	2	ss38333790	31773763	nearest gene	*CSRNP3*	Bos taurus cysteine-serine-rich nuclear protein 3 (CSRNP3), mRNA
	3	ss38333136	90945586	intron	*NFIA*	Bos taurus nuclear factor I/A (NFIA), mRNA
	3	ss66537544	116468662	nearest gene	*OSCP1*	Bos taurus organic solute carrier partner 1 (OSCP1), mRNA
	5	ss38340495	53242603	nearest gene	*GNS*	Bos taurus glucosamine (N-acetyl)-6-sulfatase (GNS), mRNA

	5	ss38323692	65557646	nearest gene	*NEDD1*	Bos taurus neural precursor cell expressed, developmentally down-regulated 1 (NEDD1), mRNA
	6	ss66537977	47210709	nearest gene	*RBPJ*	Bos taurus recombination signal binding protein for immunoglobulin kappa J region (RBPJ), mRNA
	10	ss38328787	12645355	nearest gene	*MIR2290*	Bos taurus microRNA mir-2290 (MIR2290), microRNA
	11	ss66538251	34760383	intron	*NRXN1*	Bos taurus neurexin 1 (NRXN1), mRNA
	11	ss38326296	94892677	nearest gene	*MGC151949*	Bos taurus similar to glycoprotein galactosyltransferase alpha 1, 3 (MGC151949), mRNA
	13	ss66537669	19145474	nearest gene	*ITGB1*	Bos taurus integrin, beta 1 (fibronectin receptor, beta polypeptide, antigen CD29 includes MDF2, MSK12) (ITGB1), mRNA
	15	ss38327992	65208287	exon	*PDHX*	Bos taurus pyruvate dehydrogenase complex, component X (PDHX), nuclear gene encoding mitochondrial protein, mRNA
	27	ss38335669	1051	nearest gene	*CLN8*	Bos taurus ceroid-lipofuscinosis, neuronal 8 (epilepsy, progressive with mental retardation) (CLN8), mRNA
	28	ss38323528	42698889	nearest gene	*LRRC18*	Bos taurus leucine rich repeat containing 18 (LRRC18), mRNA
ADG_UREA	1	ss38322907	110568327	exon	*MFSD1*	Bos taurus major facilitator superfamily domain containing 1 (MFSD1), mRNA.
	1	ss38333732	153517286	nearest gene	*KCNJ15*	Bos taurus potassium inwardly-rectifying channel, subfamily J, member 15 (KCNJ15), mRNA
	2	ss61484221	112999439	nearest gene	*EPHA4*	Bos taurus EPH receptor A4 (EPHA4), mRNA
	3	ss38331439	2653219	intron	*POGK*	Bos taurus pogo transposable element with KRAB domain (POGK), mRNA
	3	-	71628105	intron	*ZZZ3*	Bos taurus zinc finger, ZZ-type containing 3 (ZZZ3), mRNA
	5	ss38339200	33347924	nearest gene	*MCRS1*	Bos taurus microspherule protein 1 (MCRS1), mRNA
	8	ss38325262	65569795	intron	*TMOD1*	Bos taurus tropomodulin 1 (TMOD1), mRNA
	8	ss38336907	114064723	intron	*DBC1*	Bos taurus deleted in bladder cancer 1 (DBC1), mRNA
	9	ss38322600	19430616	nearest gene	*SH3BGRL2*	Bos taurus SH3 domain binding glutamic acid-rich protein like 2 (SH3BGRL2), mRNA
	10	ss38329478	100255297	nearest gene	*GPR65*	Bos taurus G protein-coupled receptor 65 (GPR65), mRNA
MEAN_UREA	1	ss38334998	68666549	intron	*SEC22A*	Bos taurus SEC22 vesicle trafficking protein homolog A (S. cerevisiae) (SEC22A), mRNA
	2	ss38322523	32909404	nearest gene	*GRB14*	Bos taurus growth factor receptor-bound protein 14 (GRB14), mRNA
	3	ss38331439	2653219	intron	*POGK*	Bos taurus pogo transposable element

						with KRAB domain (POGK), mRNA
	3	ss38322909	100811876	nearest gene	*ORC1L*	Bos taurus origin recognition complex, subunit 1-like (yeast) (ORC1L), mRNA
	3	ss66537544	116468662	nearest gene	*OSCP1*	Bos taurus organic solute carrier partner 1 (OSCP1), mRNA
	4	s66538094	5657544	nearest gene	*IKZF1*	Bos taurus IKAROS family zinc finger 1 (Ikaros) (IKZF1), mRNA
	5	ss38339297	12328921	nearest gene	*LIN7A*	Bos taurus lin-7 homolog A (C. elegans) (LIN7A), mRNA
	8	ss38326154	39821138	nearest gene	*GLDC*	Bos taurus glycine dehydrogenase (decarboxylating) (GLDC), nuclear gene encoding mitochondrial protein, mRNA
	10	ss38334832	96074573	nearest gene	*TSHR*	Bos taurus thyroid stimulating hormone receptor (TSHR), mRNA
UREA	1	ss66537759	24785995	nearest grne	*RBM11*	Bos taurus RNA binding motif protein 11 (RBM11), mRNA
	3	ss38324942	1071569	intron	*GPR161*	Bos taurus G protein-coupled receptor 161 (GPR161), mRNA
	5	ss38323767	93343336	nearest grne	*SOX5*	Bos taurus SRY (sex determining region Y)-box 5 (SOX5), mRNA
	6	-	92061352	exon	*CXCL2*	Bos taurus chemokine (C-X-C motif) ligand 2 (CXCL2), mRNA
	7	ss38335142	106483290	nearest grne	*LOC538782*	Bos taurus hypothetical LOC538782 (LOC538782), mRNA
	9	ss38335346	100858875	nearest grne	*AGPAT4*	Bos taurus 1-acylglycerol-3-phosphate O-acyltransferase 4 (lysophosphatidic acid acyltransferase, delta) (AGPAT4), mRNA
	10	s38324682	82562803	nearest grne	*CCDC127*	Bos taurus coiled-coil domain containing 127 (CCDC127), mRNA
	11	ss66537563	101475357	nearest grne	*GARNL3*	Bos taurus GTPase activating Rap/RanGAP domain-like 3 (GARNL3), mRNA
	17	ss38336166	4055580	nearest grne	*SFRP2*	Bos taurus secreted frizzled-related protein 2 (SFRP2), mRNA
	18	ss28451881	47966036	exon	*ACTN4*	Bos taurus actinin, alpha 4 (ACTN4), mRNA
	21	ss38324150	18130029	nearest grne	*MRPL46*	Bos taurus mitochondrial ribosomal protein L46 (MRPL46), nuclear gene encoding mitochondrial protein, mRNA
	27	ss38323377	33601535	nearest grne	*KCNU1*	Bos taurus potassium channel, subfamily U, member 1 (KCNU1), mRNA
	28	ss63187445	27699906	nearest grne	*C28H10orf104*	Bos taurus chromosome 10 open reading frame 104 ortholog (C28H10orf104), mRNA
	29	ss38324305	37418951	nearest grne	*TMEM45B*	Bos taurus transmembrane protein 45B (TMEM45B), mRNA
CWT	1	ss38323939	3083543	nearest gene	*SOD1*	Bos taurus superoxide dismutase 1, soluble (SOD1), mRNA
	1	ss64321934	41793196	nearest gene	*ARL6*	Bos taurus ADP-ribosylation factor-like 6 (ARL6), mRNA
	1	ss38322907	110568327	exon	*MFSD1*	Bos taurus major facilitator superfamily domain containing 1 (MFSD1), mRNA

	2	ss38325754	138454433	nearest gene	*ALDH4A1*	Bos taurus aldehyde dehydrogenase 4 family, member A1 (ALDH4A1), nuclear gene encoding mitochondrial protein, mRNA.
	4	ss65316398	63399865	intron	*EEPD1*	Bos taurus endonuclease/exonuclease/phosphatase family domain containing 1 (EEPD1), mRNA.
	5	ss38329047	79222461	intron	*RASD2*	Bos taurus RASD family, member 2 (RASD2), mRNA
	6	ss38324097	26486541	intron	*MAPKSP1*	Bos taurus MAPK scaffold protein 1 (MAPKSP1), mRNA
	6	ss38331322	43264686	nearest gene	*PPARGC1A*	Bos taurus peroxisome proliferator-activated receptor gamma, coactivator 1 alpha (PPARGC1A), mRNA
	15	ss38322121	51746916	nearest gene	*PDE2A*	Bos taurus phosphodiesterase 2A, cGMP-stimulated (PDE2A), transcript variant 2, non-coding RNA
	18	ss38326834	55488400	nearest gene	*HRC*	Bos taurus histidine rich calcium binding protein (HRC), mRNA
	20	ss62627427	19510164	nearest gene	*NDUFAF2*	Bos taurus NADH dehydrogenase (ubiquinone) 1 alpha subcomplex, assembly factor 2 (NDUFAF2), nuclear gene encoding mitochondrial protein, mRNA
AVE_BF	1	ss66538078	6350258	Nearest gene	*CCT8*	Bos taurus chaperonin containing TCP1, subunit 8 (theta) (CCT8), mRNA
	2	-	6420614	Intron	*MGC128040*	Bos taurus hypothetical protein MGC128040 (MGC128040), mRNA
	2	ss38329575	25285472	Nearest gene	*DLX1*	Bos taurus distal-less homeobox 1 (DLX1), mRNA
	2	ss66538147	78410203	Nearest gene	*MK167IP*	Bos taurus MKI67 (FHA domain) interacting nucleolar phosphoprotein (MKI67IP), mRNA
	2	ss38328442	80814630	Nearest gene	*GYPC*	Bos taurus glycophorin C (Gerbich blood group) (GYPC), mRNA
	2	ss38326398	90632	Exon	*PID1*	Bos taurus phosphotyrosine interaction domain containing 1 (PID1), mRNA
	3	ss38334140	68058861	Nearest gene	*LPHN2*	Bos taurus latrophilin 2 (LPHN2), mRNA
	4	ss65316398	63399865	Intron	*EEPD1*	Bos taurus endonuclease/exonuclease/phosphatase family domain containing 1 (EEPD1), mRNA
	5	ss66538279	14827654	Nearest gene	*CCDC*	Bos taurus coiled-coil domain containing 59 (CCDC59), mRNA
	5	ss38324636	118682287	Nearest gene	*PRR5*	Bos taurus proline rich 5 (renal) (PRR5), mRNA
	6	ss66537977	47210709	Nearest gene	*RBPJ*	Bos taurus recombination signal binding protein for immunoglobulin kappa J region (RBPJ), mRNA
	7	ss38322516	110964595	Nearest gene	*PJA2*	Bos taurus praja ring finger 2 (PJA2), mRNA

	8	ss38324279	45507466	Nearest gene	*DMRT1*	Bos taurus doublesex and mab-3 related transcription factor 1 (DMRT1), mRNA
	15	ss38337040	32194742	Intron	*C15H11orf63*	Bos taurus chromosome 11 open reading frame 63 ortholog (C15H11orf63), mRNA
	15	ss38324125	74993659	Intron	*TSPAN18*	Bos taurus tetraspanin 18 (TSPAN18), mRNA
	17	ss38324651	57681272	Nearest gene	*MYL2*	Bos taurus myosin, light chain 2, regulatory, cardiac, slow (MYL2), mRNA
	27	ss38323377	33601535	Nearest gene	*KCNU1*	Bos taurus potassium channel, subfamily U, member 1 (KCNU1), mRNA
	29	ss38334851	29741733	Nearest gene	*NRGN*	Bos taurus neurogranin (protein kinase C substrate, RC3) (NRGN), mRNA
GRDFAT	1	ss66538078	6350258	nearest gene	*CCT8*	Bos taurus chaperonin containing TCP1, subunit 8 (theta) (CCT8), mRNA
	1	ss66537739	152127697	nearest gene	*CHAF1B*	Bos taurus chromatin assembly factor 1, subunit B (p60) (CHAF1B), mRNA
	3	ss38323208	40201985	nearest gene	*PRMT6*	Bos taurus protein arginine methyltransferase 6 (PRMT6), mRNA
	3	ss66537665	68644513	nearest gene	*LPHN2*	Bos taurus latrophilin 2 (LPHN2), mRNA
	3	ss38322790	72583513	nearest gene	*PIGK*	Bos taurus phosphatidylinositol glycan anchor biosynthesis, class K (PIGK), mRNA
	3	ss38322909	100811876	nearest gene	*GPX7*	Bos taurus glutathione peroxidase 7 (GPX7), mRNA
	4	ss38322669	54568493	intron	*TFEC*	Bos taurus transcription factor EC (TFEC), mRNA
	6	ss38324338	31937563	intron	*PDLIM5*	Bos taurus PDZ and LIM domain 5 (PDLIM5), mRNA
	7	ss38329588	4820181	exon	*LSM4*	Bos taurus LSM4 homolog, U6 small nuclear RNA associated (S. cerevisiae) (LSM4), mRNA
	7	ss38322119	52832106	nearest gene	*SPRY4*	Bos taurus sprouty homolog 4 (Drosophila) (SPRY4), mRNA
	7	ss38322165	92996601	nearest gene	*ARRDC3*	Bos taurus arrestin domain containing 3 (ARRDC3), mRNA
	10	ss38324682	82562803	nearest gene	*ZFP36L1*	Bos taurus zinc finger protein 36, C3H type-like 1 (ZFP36L1), mRNA
	12	ss38324078	78069273	nearest gene	*LOC513822*	Bos taurus similar to RIKEN cDNA 4832428D23 (LOC513822), mRNA
	13	ss38323604	43109972	intron	*ABHD12*	Bos taurus abhydrolase domain containing 12 (ABHD12), mRNA
	15	ss38335183	45244386	nearest gene	*MRPL17*	Bos taurus mitochondrial ribosomal protein L17 (MRPL17), nuclear gene encoding mitochondrial protein, mRNA
	21	ss38324150	18130029	nearest gene	*MRPL46*	Bos taurus mitochondrial ribosomal protein L46 (MRPL46), nuclear gene encoding mitochondrial protein, mRNA
	27	ss38323377	33601535	nearest gene	*KCNU1*	Bos taurus potassium channel, subfamily U, member 1 (KCNU1), mRNA
CREA	1	ss66538078	6350258	nearest	*CCT8*	Bos taurus chaperonin containing TCP1,

				gene		subunit 8 (theta) (CCT8), mRNA
	1	ss64321934	41793196	nearest gene	*ARL6*	Bos taurus ADP-ribosylation factor-like 6 (ARL6), mRNA
	1	ss64843848	100876223	nearest gene	*MIR551B*	Bos taurus microRNA mir-551b (MIR551B), microRNA
	3	ss66537570	96195939	nearest gene	*PPAP2B*	Bos taurus phosphatidic acid phosphatase type 2B (PPAP2B), mRNA
	4	ss66538016	22890326	nearest gene	*ETV1*	Bos taurus ets variant 1 (ETV1), mRNA
	4	ss38324841	91217499	nearest gene	*SPAM1*	Bos taurus sperm adhesion molecule 1 (PH-20 hyaluronidase, zona pellucida binding) (SPAM1), mRNA
	5	ss38339563	37728419	nearest gene	*SLC38A2*	Bos taurus solute carrier family 38, member 2 (SLC38A2), mRNA
	5	ss38340495	53242603	nearest gene	*GNS*	Bos taurus glucosamine (N-acetyl)-6-sulfatase (GNS), mRNA
	5	ss38340471	66531514	nearest gene	*MIR135A-2*	Bos taurus microRNA mir-135a-2 (MIR135A-2), microRNA
	6	ss38322890	78854889	nearest gene	*LPHN3*	Bos taurus latrophilin 3 (LPHN3), mRNA
	8	ss38322842	103345581	nearest gene	*ACTL7B*	Bos taurus actin-like 7B (ACTL7B), mRNA
	10	ss65561641	39918066	intron	*STMN2*	Bos taurus stathmin-like 2 (STMN2), mRNA
	11	ss66537939	19734848	nearest gene	*CCDC75*	Bos taurus coiled-coil domain containing 75 (CCDC75), mRNA
	12	ss66537619	49365732	nearest gene	*KLF5*	Bos taurus Kruppel-like factor 5 (intestinal) (KLF5), mRNA
	14	ss66538042	11955276	nearest gene	*MYC*	Bos taurus v-myc myelocytomatosis viral oncogene homolog (avian) (MYC), mRNA
	14	ss66537607	62424259	nearest gene	*POLR2K*	Bos taurus polymerase (RNA) II (DNA directed) polypeptide K, 7.0kDa (POLR2K), mRNA
	14	ss38328773	65438173	intron	*PGCP*	Bos taurus plasma glutamate carboxypeptidase (PGCP), mRNA
	15	ss38324125	74993659	intron	*TSPAN18*	Bos taurus tetraspanin 18 (TSPAN18), mRNA
	20	ss38328796	45114461	nearest gene	*CDH6*	Bos taurus cadherin 6, type 2, K-cadherin (fetal kidney) (CDH6), mRNA
	22	ss38326759	11039315	intron	*ITGA9*	Bos taurus integrin, alpha 9 (ITGA9), mRNA
LMY	1	ss38324800	20870762	nearest gene	*MIRLET7C*	Bos taurus microRNA let-7c (MIRLET7C), microRNA
	1	ss38322126	145384804	nearest gene	*TFF3*	Bos taurus trefoil factor 3 (intestinal) (TFF3), mRNA
	2	-	6420614	intron	*MGC128040*	Bos taurus hypothetical protein MGC128040 (MGC128040), mRNA
	3	ss38336860	97403450	nearest gene	*DHCR24*	Bos taurus 24-dehydrocholesterol reductase (DHCR24), mRNA
	4	ss38324841	91217499	nearest gene	*SPAM1*	Bos taurus sperm adhesion molecule 1 (PH-20 hyaluronidase, zona pellucida binding) (SPAM1), mRNA

	7	ss66537587	70880939	nearest gene	*IL12B*	Bos taurus interleukin 12B (natural killer cell stimulatory factor 2, cytotoxic lymphocyte maturation factor 2, p40) (IL12B), mRNA
	11	ss38322573	97060575	nearest gene	*PDCL*	Bos taurus phosducin-like (PDCL), mRNA
	14	ss66537607	62424259	nearest gene	*POLR2K*	Bos taurus polymerase (RNA) II (DNA directed) polypeptide K, 7.0kDa (POLR2K), mRNA
	15	ss38332148	20509763	nearest gene	*HSPB2*	Bos taurus heat shock 27kDa protein 2 (HSPB2), mRNA
	20	ss61522292	13255633	nearest gene	*CD180*	Bos taurus CD180 molecule (CD180), mRNA
	20	ss38324910	51402608	nearest gene	*CDH10*	Bos taurus cadherin 10, type 2 (T2-cadherin) (CDH10), mRNA
	27	ss38323589	33170067	nearest gene	*KCNU1*	Bos taurus potassium channel, subfamily U, member 1 (KCNU1), mRNA
	28	ss63187445	27699906	nearest gene	*DDIT4*	Bos taurus DNA-damage-inducible transcript 4 (DDIT4), mRNA
CMAR	1	ss66538078	6350258	nearest gene	*CCT8*	Bos taurus chaperonin containing TCP1, subunit 8 (theta) (CCT8), mRNA
	1	-	150099856	nearest gene	*CBR1*	Bos taurus carbonyl reductase 1 (CBR1), mRNA
	2	ss66538017	35431781	intron	*FAP*	Bos taurus fibroblast activation protein, alpha (FAP), mRNA
	2	ss38332354	40439268	intron	*GALNT5*	Bos taurus UDP-N-acetyl-alpha-D-galactosamine:polypeptide N-acetylgalactosaminyltransferase 5 (GalNAc-T5) (GALNT5), mRNA
	2	ss38325760	68003253	nearest gene	*LYPD1*	Bos taurus LY6/PLAUR domain containing 1 (LYPD1), mRNA
	3	ss38331439	2653219	intron	*POGK*	Bos taurus pogo transposable element with KRAB domain (POGK), mRNA
	3	ss66538221	84018286	nearest gene	*SLC35D1*	Bos taurus solute carrier family 35 (UDP-glucuronic acid/UDP-N-acetylgalactosamine dual transporter), member D1 (SLC35D1), mRNA
	4	ss66538094	5657544	nearest gene	*IKZF1*	Bos taurus IKAROS family zinc finger 1 (Ikaros) (IKZF1), mRNA
	6	ss38327022	23882877	intron	*NFKB1*	Bos taurus nuclear factor of kappa light polypeptide gene enhancer in B-cells 1 (NFKB1), mRNA
	8	ss38323808	25568605	nearest gene	*MIR491*	Bos taurus microRNA mir-491 (MIR491), microRNA
	9	ss38335346	100858875	nearest gene	*AGPAT4*	Bos taurus 1-acylglycerol-3-phosphate O-acyltransferase 4 (lysophosphatidic acid acyltransferase, delta) (AGPAT4), mRNA
	10	ss38322538	38481568	nearest gene	*CCNDBP1*	Bos taurus cyclin D-type binding-protein 1 (CCNDBP1), mRNA
	11	ss66538272	95382206	nearest gene	*GGTA1*	Bos taurus alpha-galactosyltransferase 1 (glycoprotein) (GGTA1), mRNA
	28	ss38323528	42698889	nearest gene	*LRRC18*	Bos taurus leucine rich repeat containing 18 (LRRC18), mRNA

	29	ss63270688	21244296	intron	*MGC157332*	Bos taurus hypothetical protein LOC785165 (MGC157332), mRNA
YGRADE	1	ss38335051	84397541	nearest gene	*MAGEF1*	Bos taurus melanoma antigen family F, 1 (MAGEF1), mRNA
	1	ss38323849	35153193	nearest gene	*CHMP2B*	Bos taurus chromatin modifying protein 2B (CHMP2B), mRNA
	1	ss38333732	153517286	nearest gene	*KCNJ15*	Bos taurus potassium inwardly-rectifying channel, subfamily J, member 15 (KCNJ15), mRNA
	2	s38322486	17854127	intron	*ZNF385B*	Bos taurus zinc finger protein 385B (ZNF385B), mRNA
	2	ss38322399	21841024	nearest gene	*KIAA1715*	Bos taurus KIAA1715 (KIAA1715), mRNA
	3	ss65658800	36338392	exon	*GSTM3*	Bos taurus glutathione S-transferase mu 3 (brain) (GSTM3), mRNA
	4	ss66538006	115386317	nearest gene	*PDIA4*	Bos taurus protein disulfide isomerase family A, member 4 (PDIA4), mRNA
	5	ss38340496	52145848	nearest gene	*TMBIM4*	Bos taurus transmembrane BAX inhibitor motif containing 4 (TMBIM4), mRNA
	7	ss38323732	7215131	nearest gene	*AP1M1*	Bos taurus adaptor-related protein complex 1, mu 1 subunit (AP1M1), mRNA.
	7	ss38322165	92996601	nearest gene	*ARRDC3*	Bos taurus arrestin domain containing 3 (ARRDC3), mRNA
	9	ss38329347	11932336	nearest gene	*OOEP*	Bos taurus oocyte expressed protein homolog (dog) (OOEP), mRNA
	9	ss38324745	86636705	nearest gene	*EPM2A*	Bos taurus epilepsy, progressive myoclonus type 2A, Lafora disease (laforin) (EPM2A), mRNA
	11	ss28452549	2676384	nearest gene	*CIAO1*	Bos taurus cytosolic iron-sulfur protein assembly 1 (CIAO1), mRNA
	16	ss38333246	60858370	nearest gene	*GLUL*	Bos taurus glutamate-ammonia ligase (GLUL), mRNA
	19	ss38323711	56560923	nearest gene	*MGAT5B*	Bos taurus mannosyl (alpha-1,6-)-glycoprotein beta-1,6-N-acetyl-glucosaminyltransferase, isozyme B (MGAT5B), mRNA
	20	ss38324607	56587444	nearest gene	*CDH18*	Bos taurus cadherin 18, type 2 (CDH18), mRNA
	25	ss61487242	1413336	nearest gene	*TPSB1*	Bos taurus tryptase beta 1 (TPSB1), mRNA
	28	s38331569	4150241	nearest gene	*C28H1orf57*	Bos taurus chromosome 1 open reading frame 57 ortholog (C28H1orf57), mRNA
	28	ss38335007	27364335	exon	*PSAP*	Bos taurus prosaposin (PSAP), mRNA

MEAN_UBF = mean ultrasound backfat; UBF = ultrasound backfat; MEAN_UMAR = mean ultrasound marbling; UMAR = ultrasound marbling; ADG_UREA = average daily gain ultrasound ribeye area; MEAN_UREA = mean ultrasound ribeye area; UREA = ultrasound ribeye area. CWT = carcass weight; AVE_BF = average backfat; GRDFAT = carcass grade fat; CREA = carcass ribeye area; LMY = lean meat yield; CMAR = carcass marbling; YGRDAE = carcass yield grade.

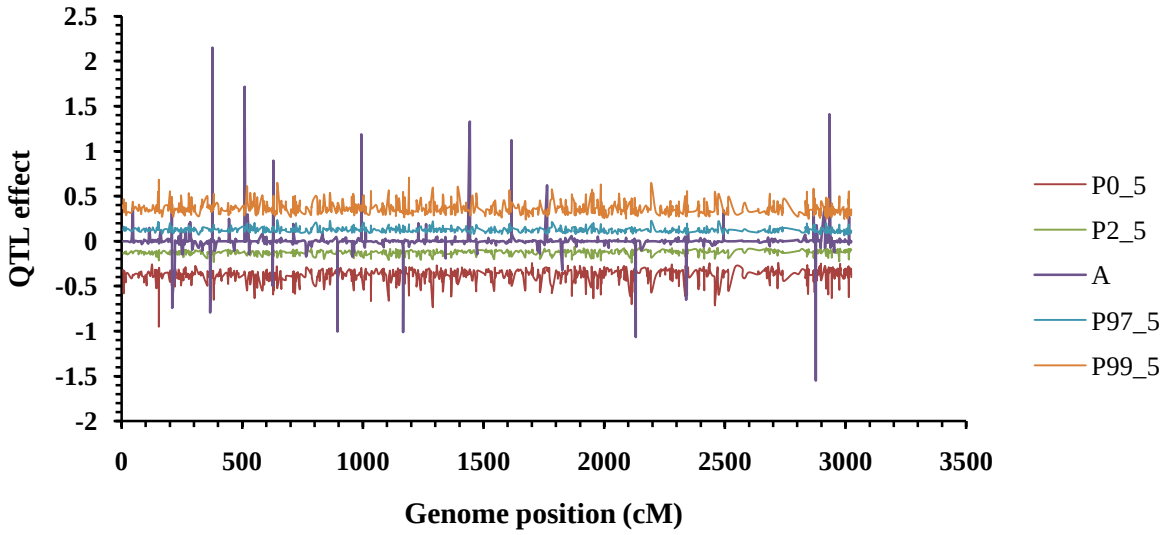

Figure 4.1: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for mean ultrasound backfat (MEAN_UBF) QTL.

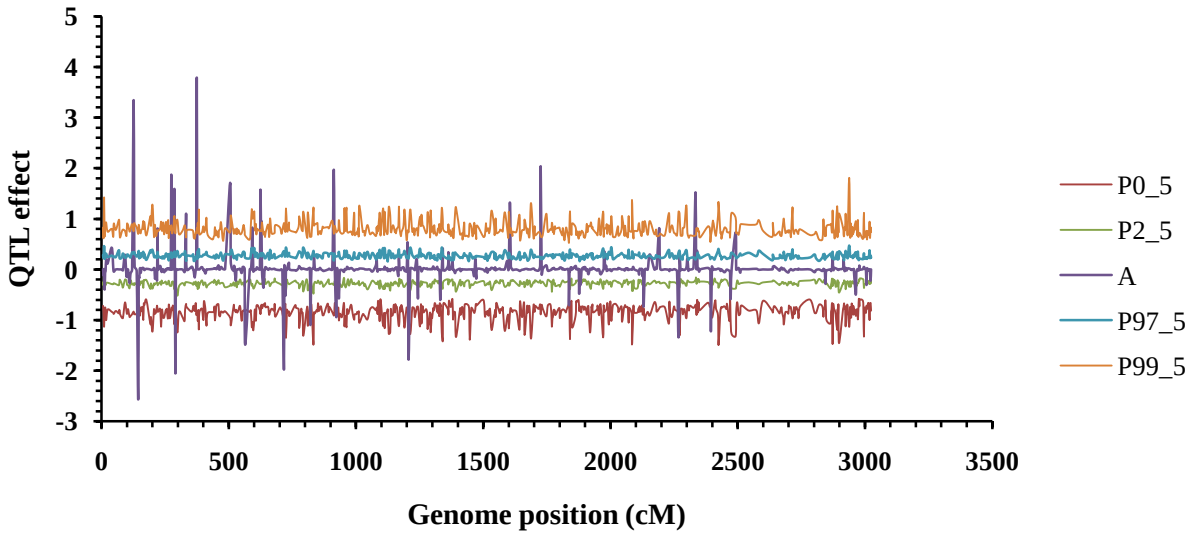

Figure 4.2: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for ultrasound backfat (UBF) QTL.

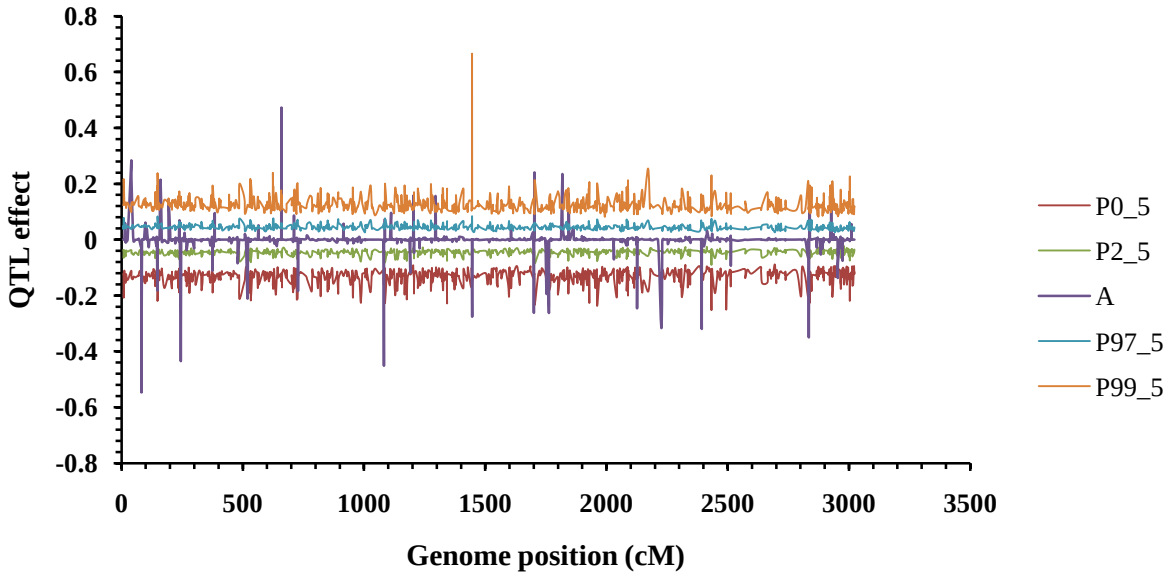

Figure 4.3: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for mean ultrasound marbling (MEAN_UMAR) QTL.

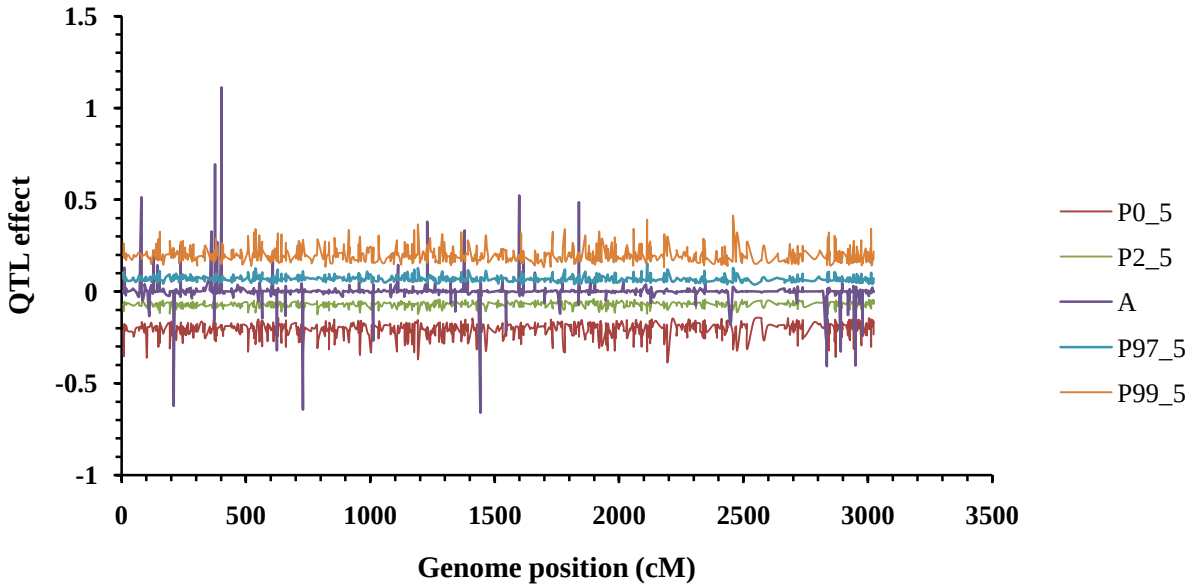

Figure 4.4: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for ultrasound marbling (UMAR) QTL.

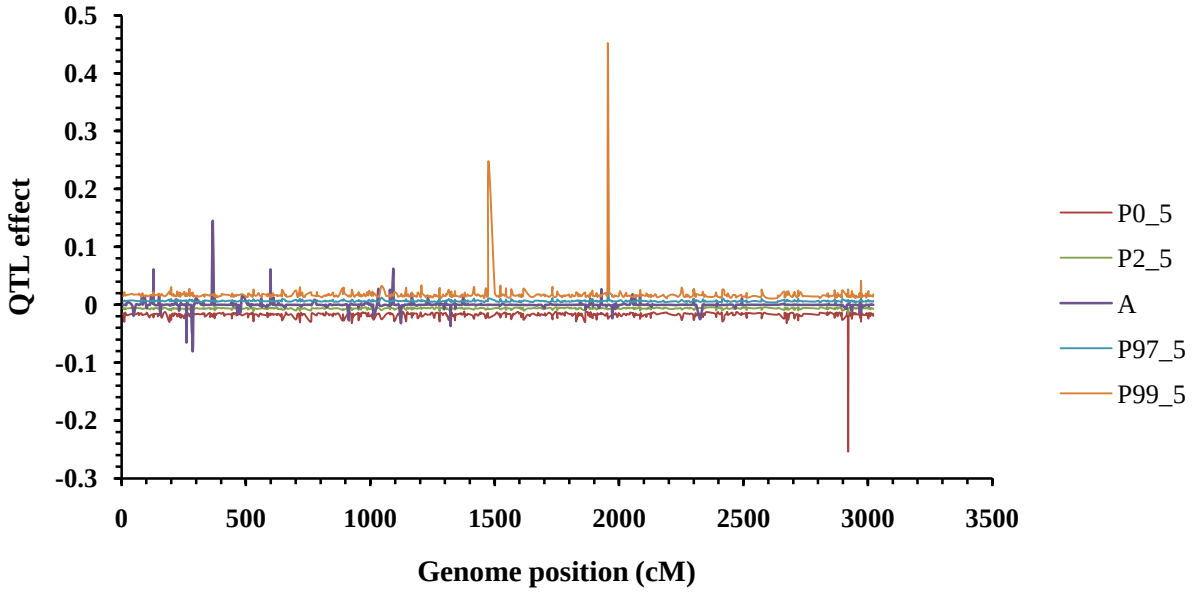

Figure 4.5: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for average daily gain ultrasound ribeye area (ADG_UREA) QTL.

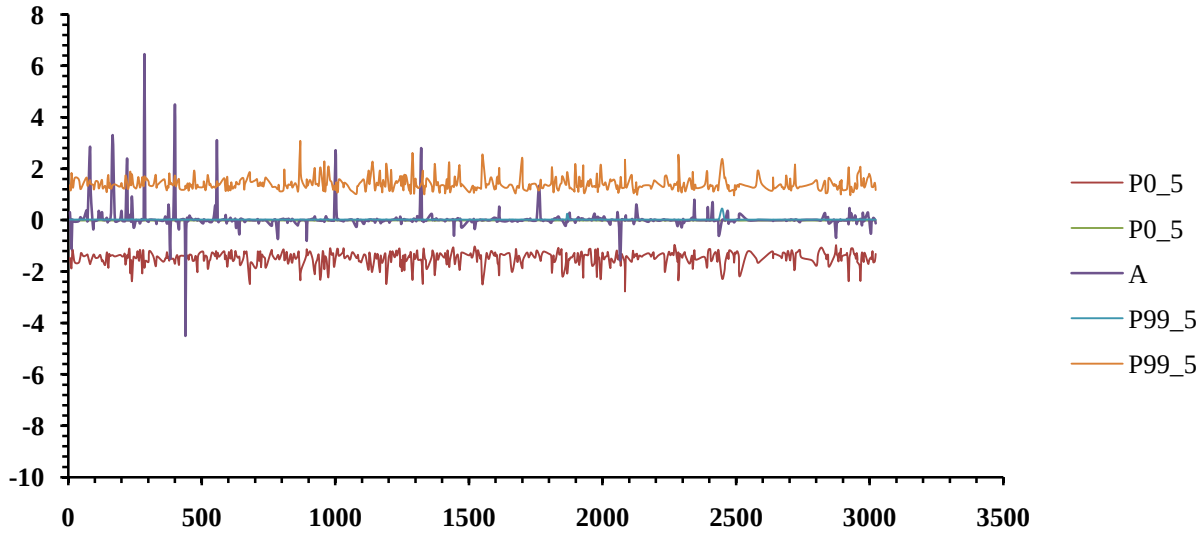

Figure 4.6: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for mean ultrasound ribeye area (MEAN_UREA) QTL.

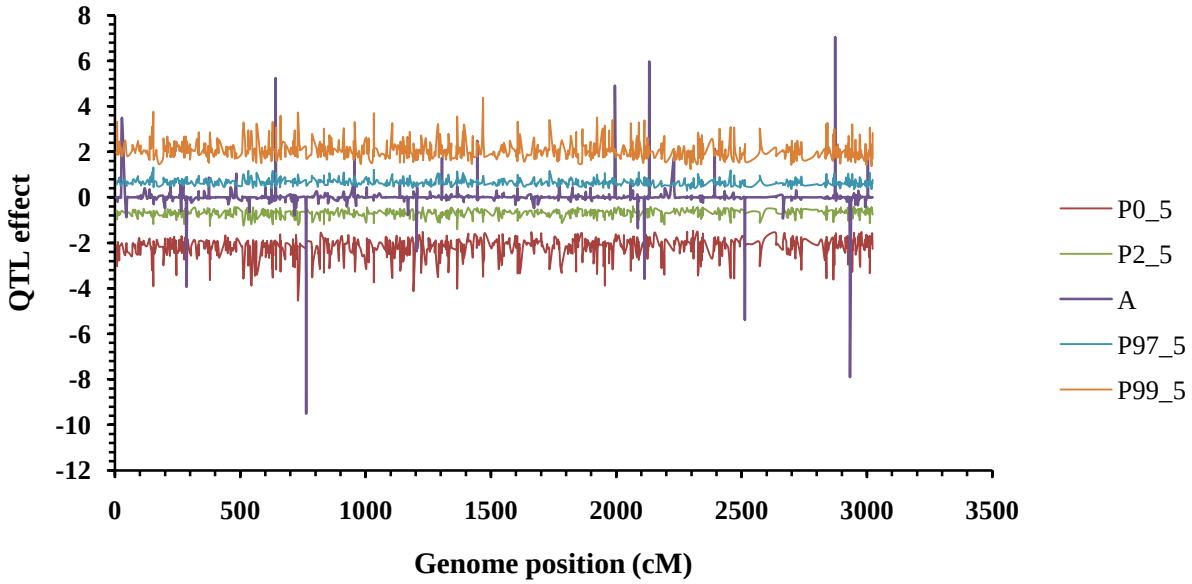

Figure 4.7: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for ultrasound ribeye area (UREA) QTL.

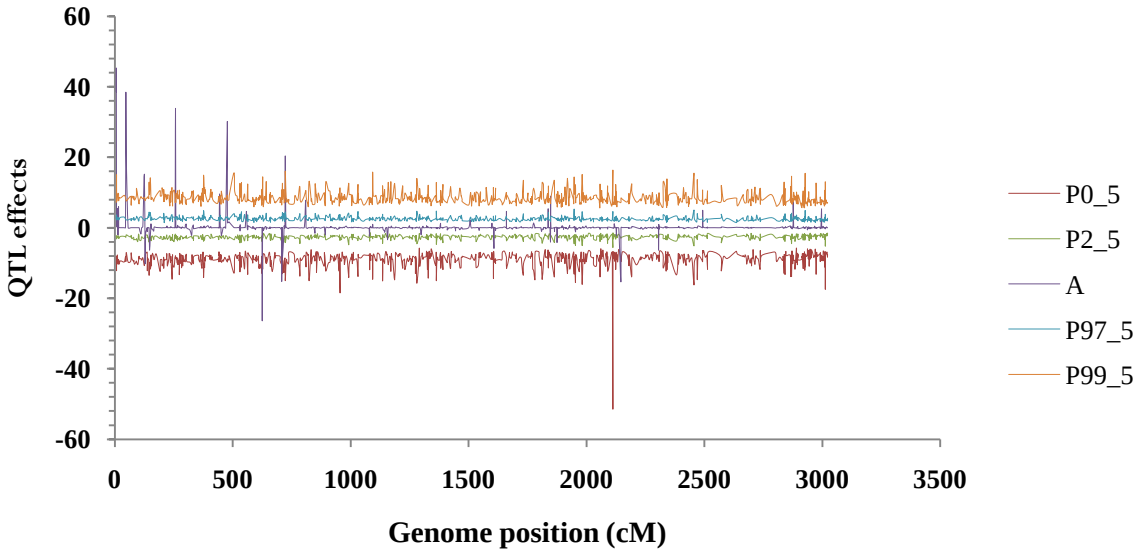

Figure 4.8: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for carcass weight (CWT) QTL.

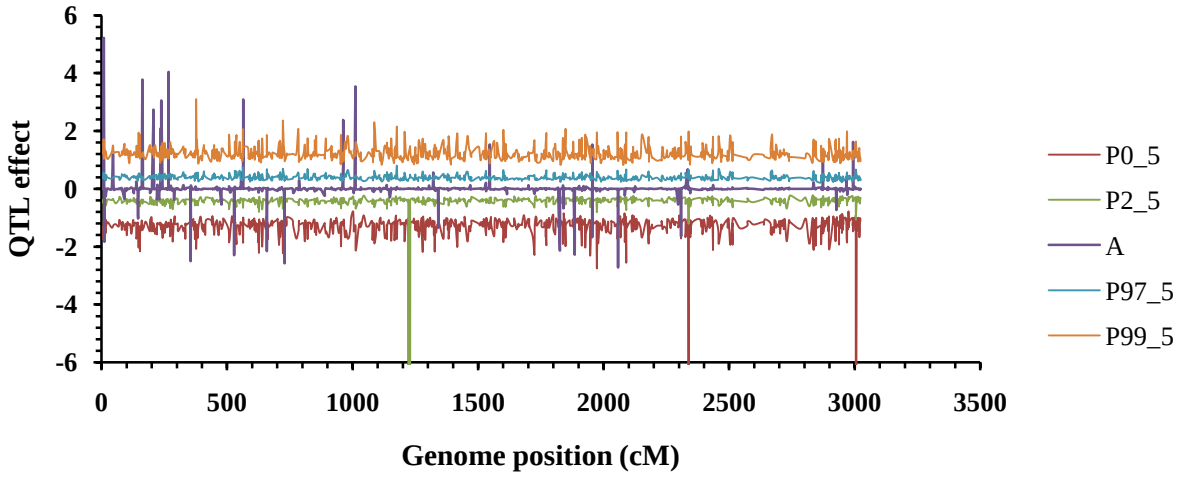

Figure 4.9: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for average backfat (AVE_BF) QTL.

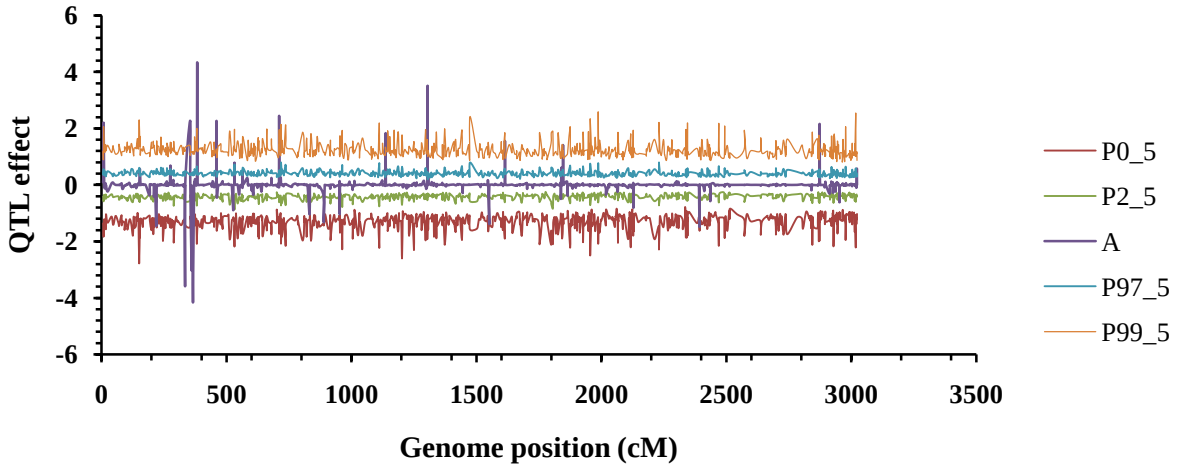

Figure 4.10: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for carcass grade fat (GRDFAT) QTL.

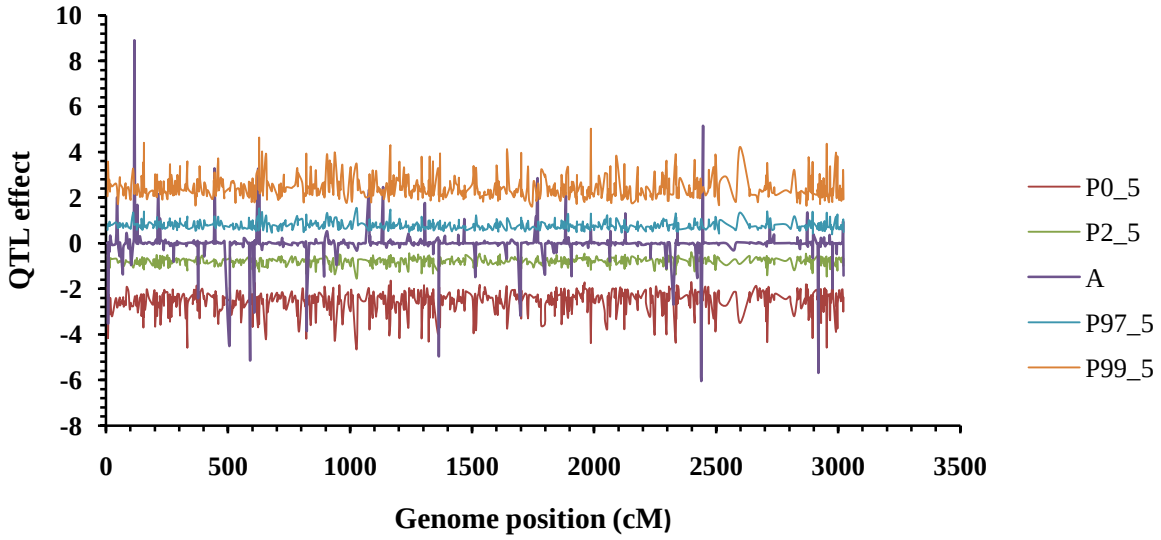

Figure 4.11: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for carcass ribeye area (CREA) QTL.

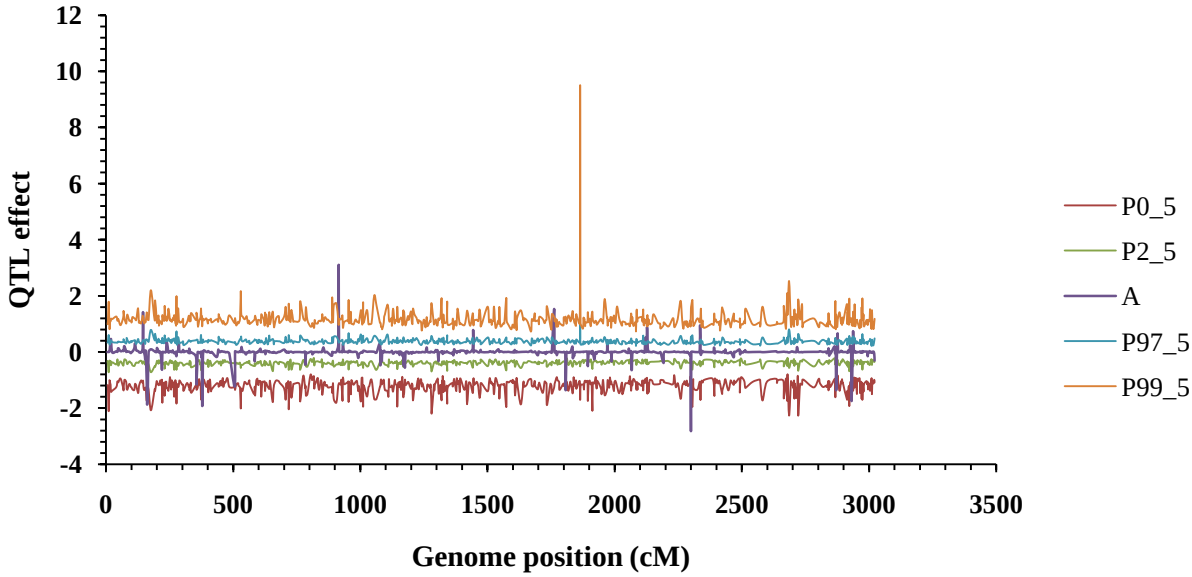

Figure 4.12: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for lean meat yield (LMY) QTL.

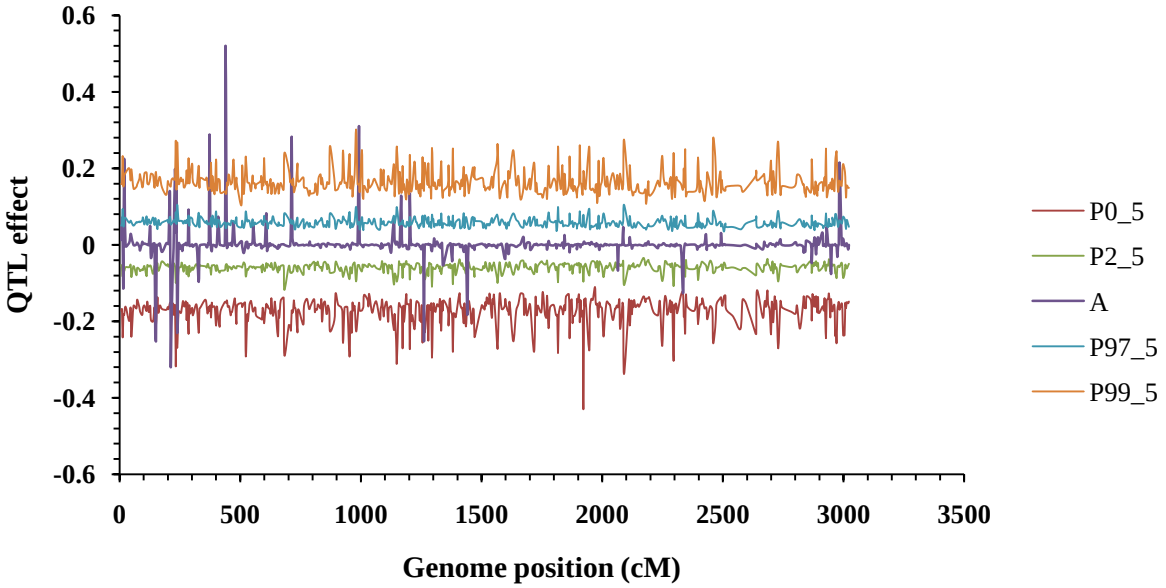

Figure 4.13: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for carcass marbling (CMAR) QTL.

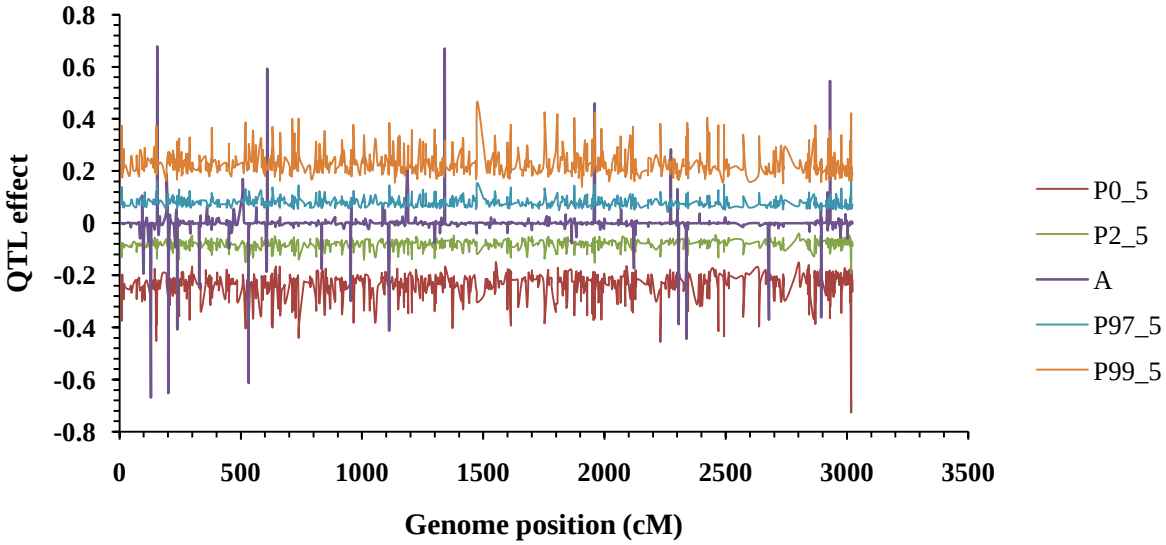

Figure 4.14: The percentiles intervals of 2.5% - 97.5% and 0.5% - 99.5% equivalent to α=0.05 and α=0.01 plotted against the genome location for carcass yield grade (YGRADE) QTL.

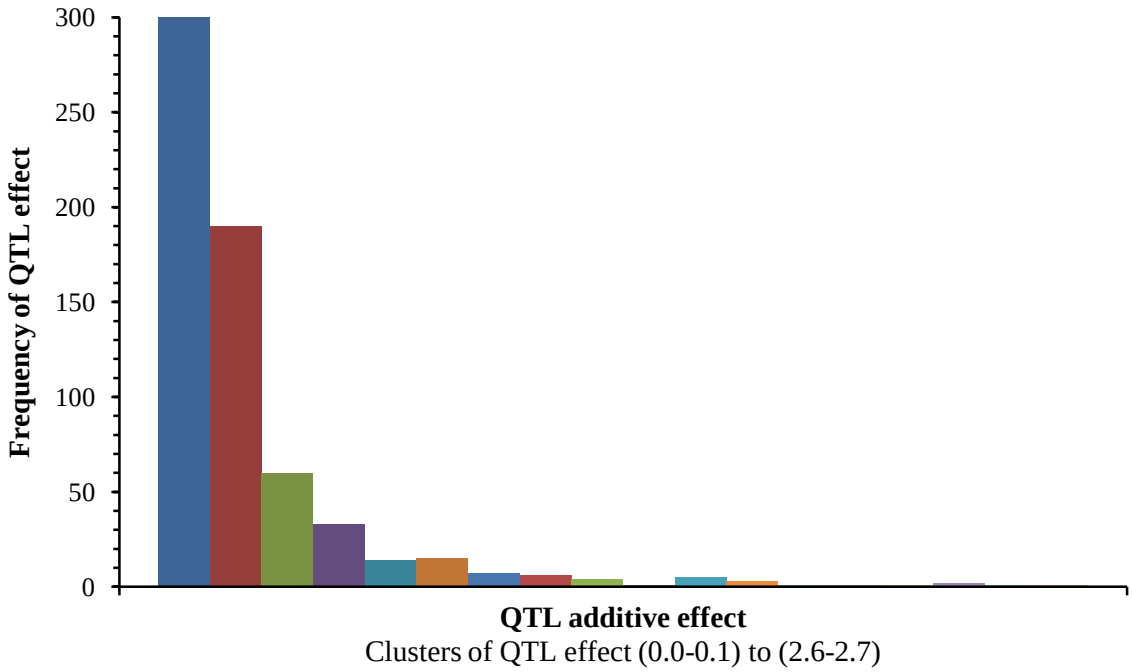

Figure 4.15: Genome-wide distribution of additive effect of QTL for mean ultrasound backfat (MEAN_UBF).

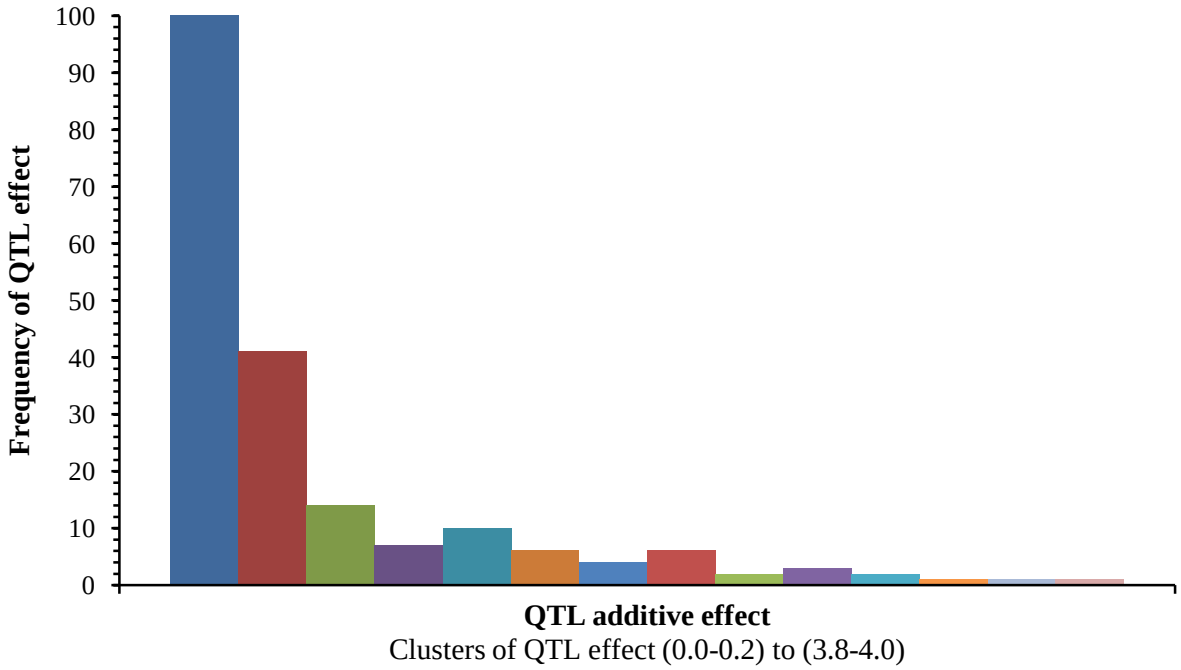

Figure 4.16: Genome-wide distribution of additive effect of QTL for ultrasound backfat (UBF).

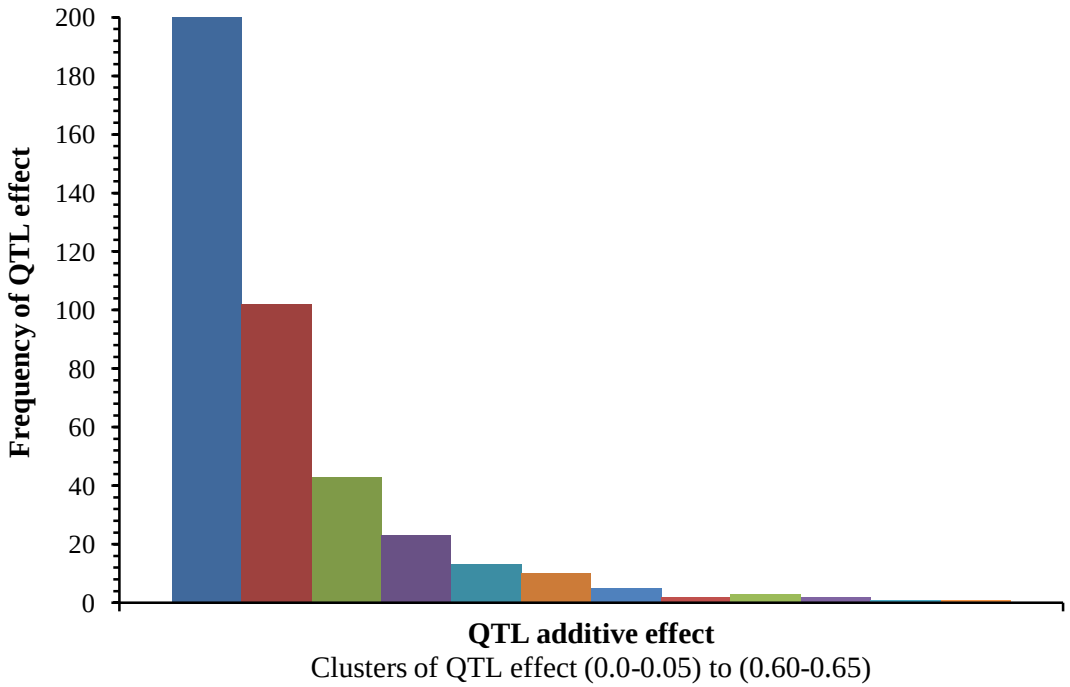

Figure 4.17: Genome-wide distribution of additive effect of QTL for mean ultrasound marbling (MEAN_UMAR).

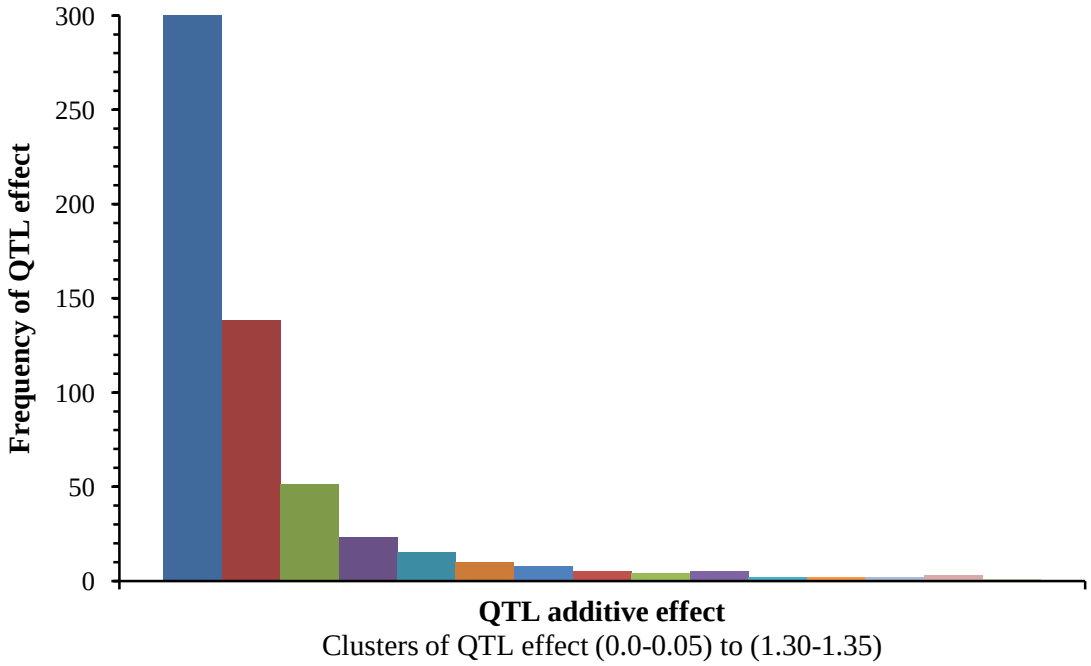

Figure 4.18: Genome-wide distribution of additive effect of QTL for ultrasound marbling (UMAR).

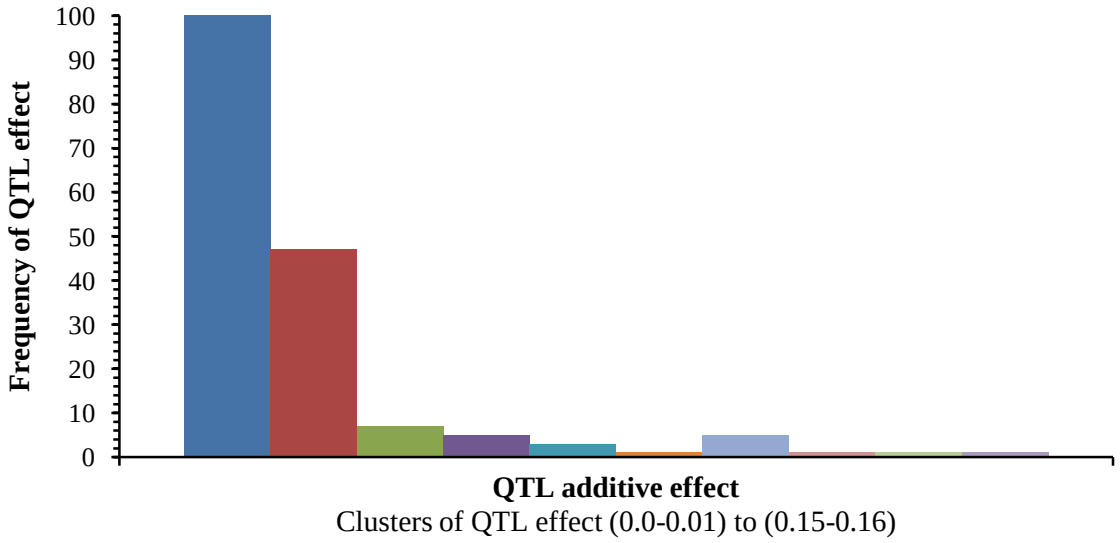

Figure 4.19: Genome-wide distribution of additive effect of QTL for average daily gain ultrasound ribeye area (ADG_UREA).

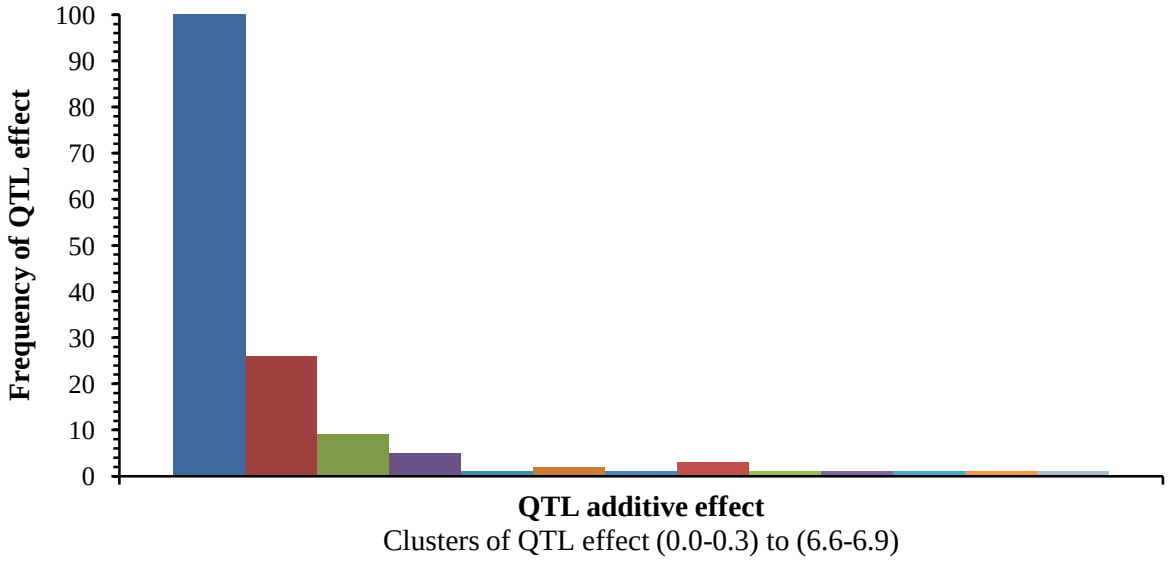

Figure 4.20: Genome-wide distribution of additive effect of QTL for mean ultrasound ribeye area (MEAN_UREA).

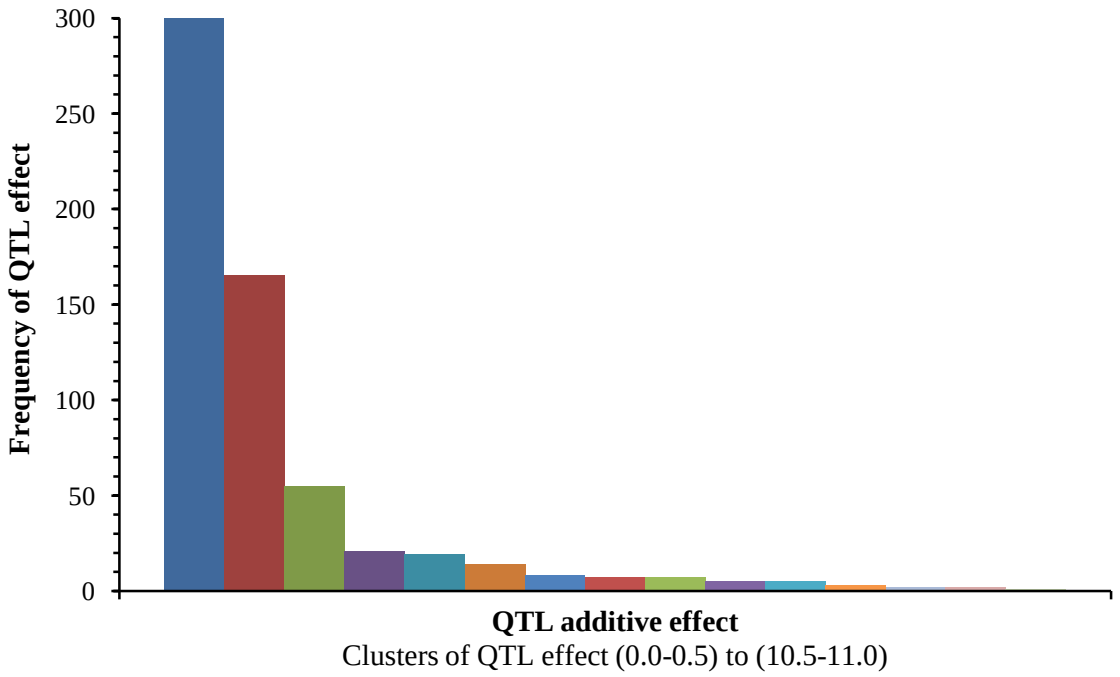

Figure 4.21: Genome-wide distribution of additive effect of QTL for ultrasound ribeye area (UREA).

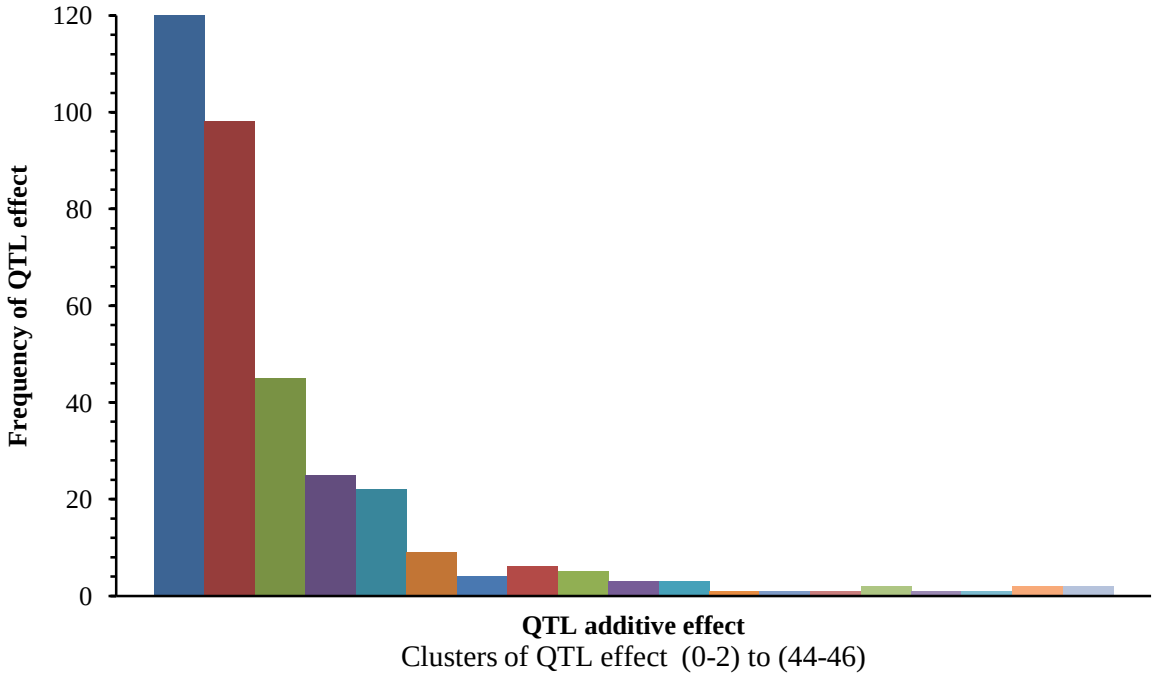

Figure 4.22: Genome-wide distribution of additive effect of QTL for carcass weight (CWT).

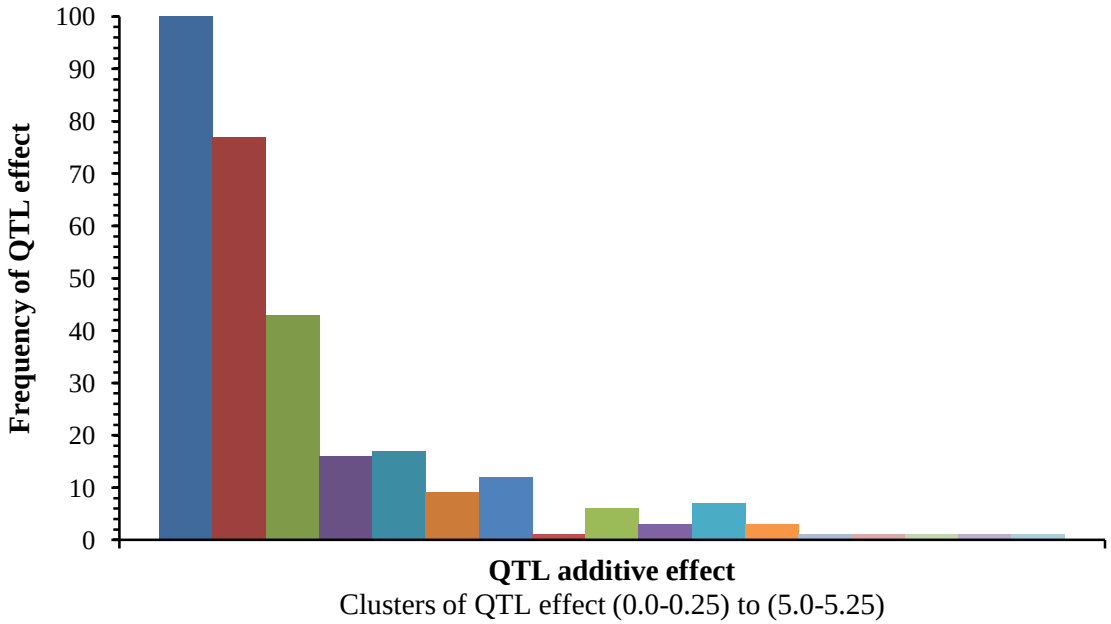

Figure 4.23: Genome-wide distribution of additive effect of QTL for carcass average backfat (AVE_BF).

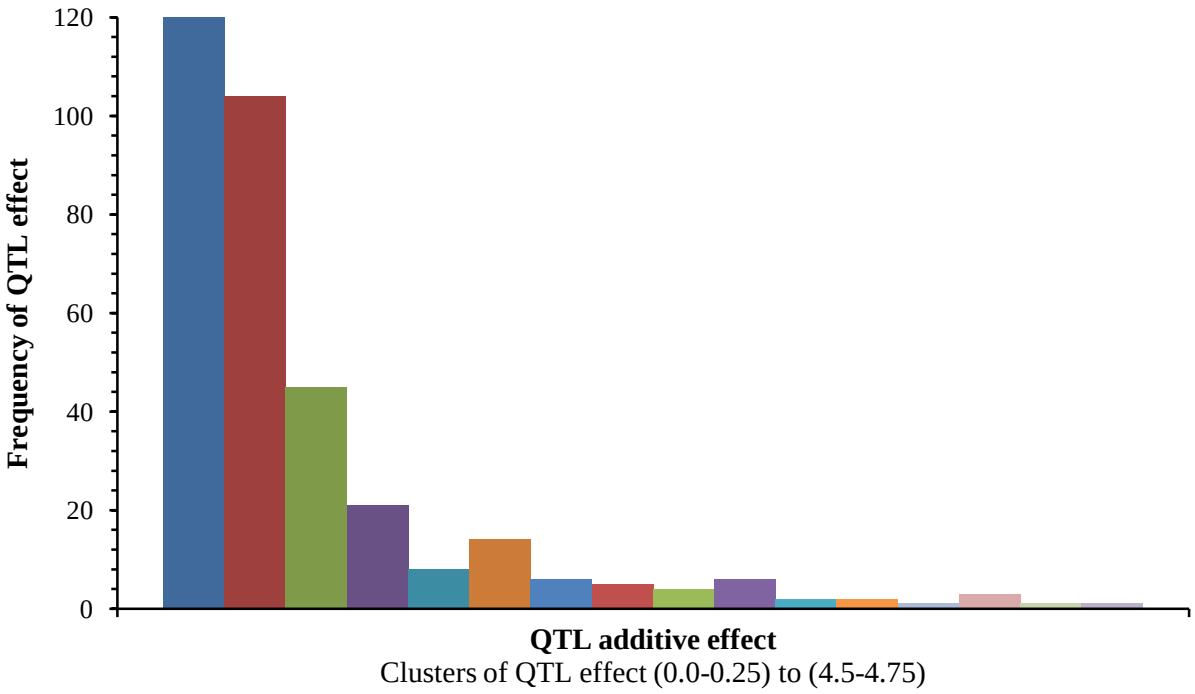

Figure 4.24: Genome-wide distribution of additive effect of QTL for carcass grade fat (GRDFAT).

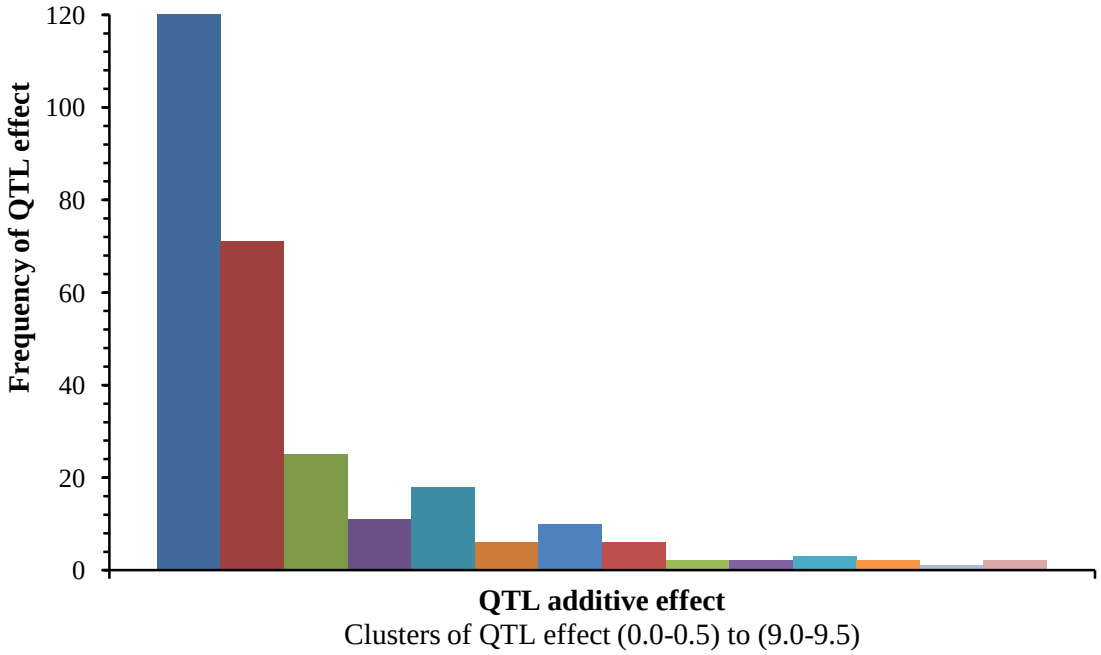

Figure 4.25: Genome-wide distribution of additive effect of QTL for carcass ribeye area (CREA).

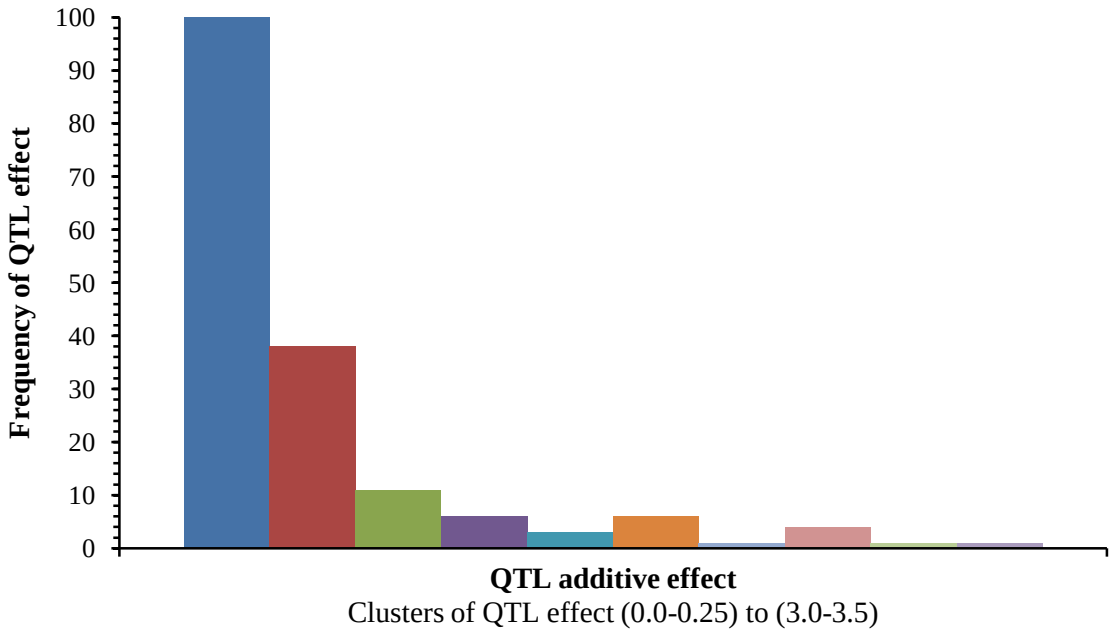

Figure 4.26: Genome-wide distribution of additive effect of QTL for lean meat yield (LMY).

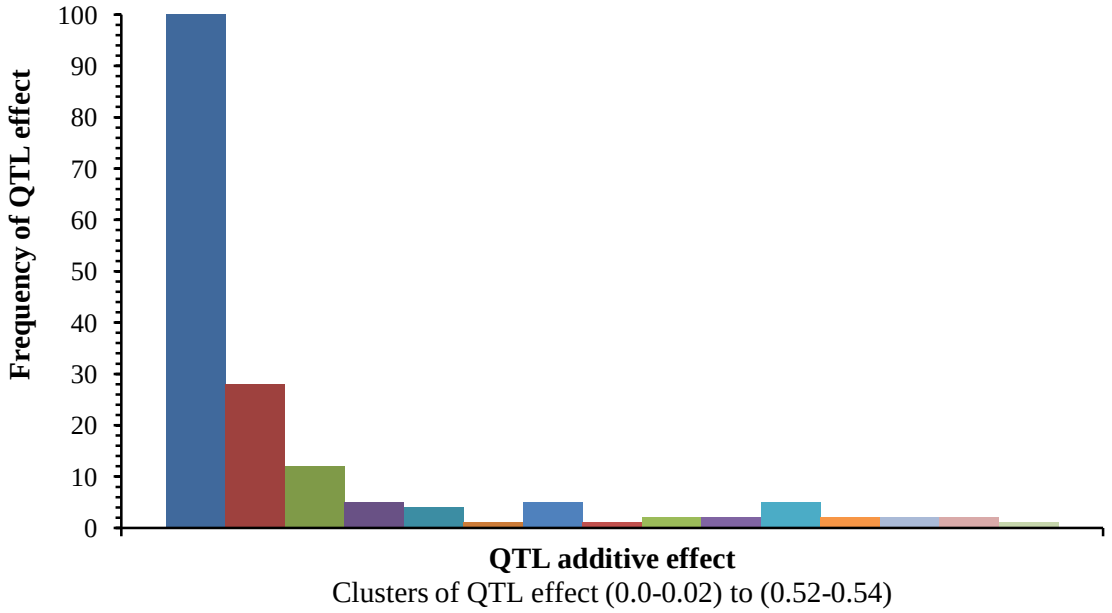

Figure 4.27: Genome-wide distribution of additive effect of QTL for carcass marbling (CMAR).

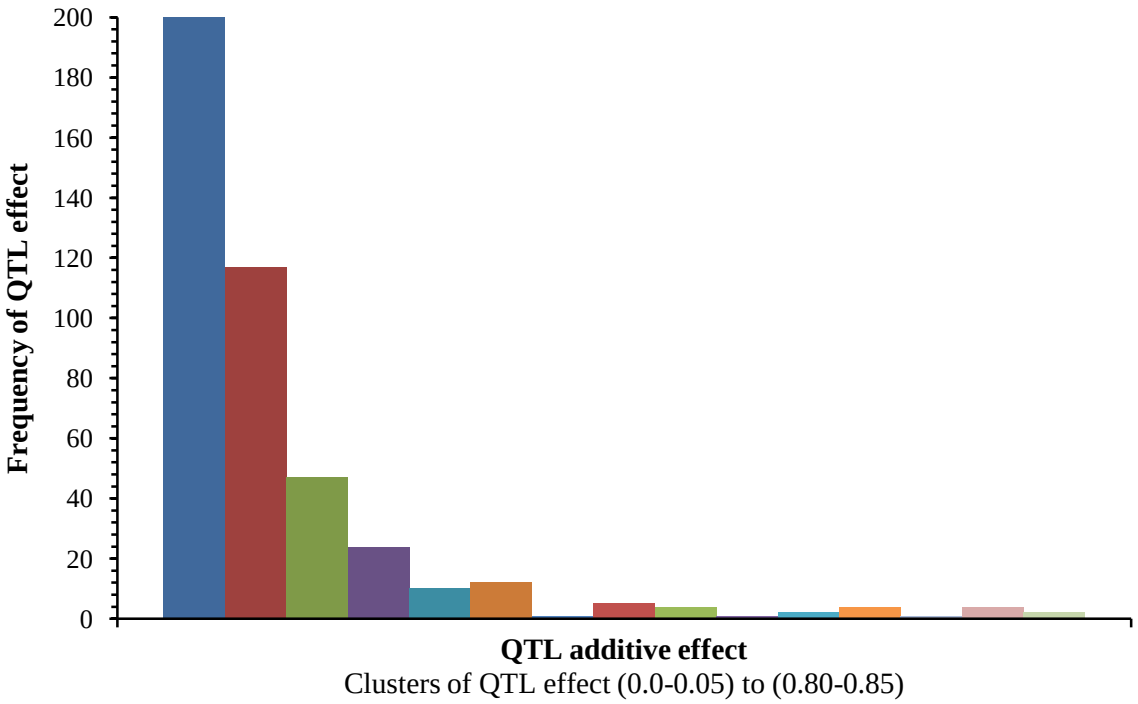

Figure 4.28: Genome-wide distribution of additive effect of QTL for carcass yield grade (YGRADE).

5. General Discussions and Future Research

5.1. General Discussions

Although significant genetic improvement in livestock has been achieved through selection of animals based on observable phenotypes without knowing the number and identities of genes affecting the trait, the phenotype-based selection has not been efficient for traits that have a low heritability, for traits that are difficult and expensive to measures, for traits that can only be measured at a later stage of animal reproduction cycle, and for traits that can only be observed in one sex (Dekkers and Hospital, 2002). Recent developments in molecular genetics and statistical methodologies have provided opportunities to make optimal use of molecular and phenotypic information in the selection process. The use of molecular genetics eliminates some of the limitations encountered in traditional phenotypic selection. The genetic markers will benefit the beef industry to improve the rate of genetic gain for traits that are mentioned above including carcass merit traits because MAS enables the evaluation of genetic merit values and selection for animals carrying beneficial alleles before the selection decision has to be made.

A considerable number of QTL has been reported in beef cattle (Cattle QTLdb 2003). However, most of the QTL mapping studies in beef cattle were carried out using a limited number of parental chromosomes sampled through selected sires, hence these QTL represent just a small proportion of the QTL that are contributing to the variation of carcass traits within a population (McClure et

al. 2010). Therefore, there are still large numbers of QTL for carcass traits that need to be identified in beef cattle. This study was conducted to fine map and detect QTL regions in the whole genome for ultrasound and carcass merit traits in beef cattle using a denser SNP marker set through three approaches, namely QTL interval regression mapping, single SNP association analyses under the identified QTL regions by the interval mapping, and Bayesian shrinkage QTL analyses. In a previous study the QTL were identified in large chromosome intervals ranged from 4 to 24 cM due to the relatively low density of genetic markers that was used in the analysis (Li et al. 2006). Fine mapping is required to increase the resolution of the identified QTL to be more useful for further practical applications of MAS and molecular procedures such as positional candidate gene research which requires a finer resolution within 1 to 2 cM (Darvasi et al. 1993; Kneeland et al. 2004). This study uses a denser panel of genetic markers of a total of 4592 SNP markers that are distributed on the whole bovine genome. In this thesis, the results of interval regression mapping was presented in Chapter 3 and the resolution of the identified QTL positions were fine mapped into small intervals ranged from 0.6 to 11 cM. The SNP markers within these QTL regions were further analysed through single marker regression and twenty two SNP markers were found to have significant associations with 3 ultrasound and 4 carcass merit traits. However, interval mapping and single marker regression approaches may result in high incidences of false positive due to multiple testing because they analyze one position of the genome or marker at a time. Also the effects of QTL could be

overestimated since each QTL or SNP marker was analyzed independently without fully adjusting of other QTL on the entire genome.

In order to verify the identified QTL regions using the interval regression mapping method, the Bayesian shrinkage estimation (Wang et al. 2005) was performed for the QTL detection with the same data set in Chapter 4. The Bayesian shrinkage estimation uses 1207 informative SNP markers with LD (r^2) <0.2 to avoid redundant marker information and to evaluate all QTL in the genome simultaneously in a single model that adjusts for the effects of other QTLs in the entire genome. As such, it overcomes major limitations associated with the interval mapping and single marker association analyses. It was found that the proportion of phenotypic variance accounted by total QTL variance estimated by Bayesian shrinkage analysis were relatively small and ranged from 0.1 to 4.8% in comparison to the interval mapping of 6.1 to 11.7%. In addition more QTL with smaller effects were detected by the Bayesian the shrinkage analysis. The distributions of QTL effects identified by Bayesian shrinkage approach have shown that a very small proportion of the identified QTL have moderate or large effects and the majority of the identified QTL have small effects. All the results indicate that Bayesian the shrinkage analysis is more robust to identify QTL with small effects and to provide a more reasonable estimation of QTL variance. The current results suggest further that the Bayesian shrinkage analysis should be considered to assess the QTL effects by fitting all markers on the entire genome in a single model simultaneously.

The use of 4592 SNPs in the interval mapping and 1207 SNPs in the Bayesian analysis could not capture all existing linkage disequilibrium that exist between SNP markers and the QTL on the bovine genome. Furthermore, not all QTL intervals were fine mapped into small enough intervals with the current number of SNP markers used. Therefore, more high density SNP markers are needed for further refining these QTL to be more useful for other studies aimed to identify causative mutations. Now that the BovineSNP50 chip has become available (Matukumali et al. 2009), it will provide a powerful tool for further identifying and fine mapping QTL regions for QTN search and for the application of MAS or/and genomic selection.

Nevertheless the current QTL and SNPs that associated with ultrasound and carcass traits provide good reference points for further analyses that could be used to identify polymorphic SNPs that regulate variations of carcass traits. Also, the genes that harbor SNPs associated with traits are useful candidates that could facilitate functional annotation of the bovine genome and promote further functional and comparative genomics studies of carcass merit traits genes in beef cattle. It is important that these QTL and SNP effects be confirmed and validated in other beef cattle populations with different genetic background before they can be applied to marker assisted selection.

5.2. Future Research

The QTL that have been mapped in the current study have led to the detection of SNPs that were associated with ultrasound and carcass merit traits as

well as the genes in which these SNPs were located. This information could be used to identify polymorphic SNP variants within the genes that regulate variation of carcass traits in beef cattle. This can be achieved through positional candidate gene analysis to identify causative mutations on the trait variations. Moreover, further research is encouraged to identify the QTL using higher denser SNP marker panels and to confirm the QTL using different cattle populations in different environments for the effective application of marker-assisted selection or genomic selection. Alternatively, the use of more advanced QTL mapping methods such as Bayesian-type methods, which can handle multiple markers of entire genome and provides more accurate estimates of QTL parameters should be emphasized for QTL detection.

5.4. Literature Cited

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