Genomic selection for pork quality and carcass traits in both cross- and pure-bred populations

by

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ABSTRACT

Pork quality and carcass characteristics are now being integrated into swine breeding objectives because of their economic value. Understanding the genetic basis for these traits is necessary for this to be accomplished. The main objective of this study was to improve pork quality traits in two Canadian swine populations. Data from 6,408 commercial crossbred pigs with performance traits recorded in production systems with 2,100 of them having meat quality and carcass measurements. These pigs were progeny from 139 Duroc boars bred to 429 F1 hybrid Landrace × Large White sows. In the first study, phenotypic and genetic parameters for meat quality and carcass traits were estimated. Heritability estimates (± SE) for carcass traits were moderate to high and ranged from 0.22 ± 0.08 for *longissimus dorsi* muscle area to 0.63 ± 0.04 for trimmed ham weight, except for firmness that was low. Heritability estimates (± SE) for meat quality traits varied from 0.10 ± 0.04 to 0.39 ± 0.06, for the Minolta b* of ham *quadriceps femoris* muscle and shear force, respectively. There were high negative genetic correlations between drip loss with pH and shear force and a positive correlation with cooking loss. Genetic correlation between carcass weight with carcass marbling was highly positive. It was concluded that selection for increasing primal and subprimal cut weights with better pork quality may be possible. Furthermore, the use of pH is confirmed as an indicator for pork water-holding capacity and cooking loss. In the second study, heritability, phenotypic, and genetic correlations between performance traits (n=9) with meat quality (n=25) and carcass (n=19) traits were estimated. Performance traits had low-to-moderate heritabilities (±SE), ranged from 0.07±0.13 to 0.45±0.07 for weaning weight, and ultrasound backfat depth, respectively. The results indicate that: (a) selection for birth weight may increase drip loss, lightness of *longissimus dorsi*, and *gluteus*

medius muscles but may reduce fat depth; (b) selection for nursery weight can be valuable for increasing both quantity and quality traits; (c) selection for increased daily gain may increase the carcass weight and most of the primal cuts. These findings suggest that deterioration of pork quality may have occurred over many generations through the selection for less backfat thickness, and feed efficiency, but selection for growth had no adverse effects on pork quality. The heritabilities of carcass and pork quality traits indicated that they can be improved through traditional selection and genomic selection, respectively. The estimated genetic parameters for performance, carcass and meat quality traits can be incorporated into the breeding programs that emphasize product quality in these Canadian swine populations. In the third study, a genomic selection was performed for meat quality and carcass traits in 2,100 commercial pigs and 107 Duroc purebred pigs using Illumina's PorcineSNP60 BeadChip and single-step BLUP (ssBLUP). It was concluded that genomic predictions models developed using ssBLUP could predict the parental purebreds without substantial loss of prediction accuracy compared to their crossbred progenies to improve carcass and pork quality traits. The prediction accuracies for the purebred parental resulted from the ssBLUP evaluation were also compared with the accuracies from the traditional parental average. The results showed that the prediction accuracies resulted from the ssBLUP had average improvements of 17% and 16% for pork quality and carcass, respectively. In conclusion, this study confirmed that genomics could improve pork quality through genomic selection from commercial crossbred pigs to meet the demands by consumers, packers and processors.

Allah says in his glorious book:

"We desired to bestow a favor upon those who were deemed weak in the land, and to make them the leaders, and to make them the heirs"

Quran, Al-Qasas, Verse 5

To

This work is dedicated to my Parents, Rahmangholi Miar and Talat Miarabbaskiani who always believed in me and supported me in whatever I pursued. It is also dedicated to my beloved wife, Shima Borzouie, for her support in every single moment of my life.

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This thesis is only a beginning of my journey…

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List of Abbreviations

ADG	Average daily gain
BFW	Backfat thickness weight
BLUP	Best linear unbiased prediction
BOW	Bone/Neural weight
BUTT	Butt shoulder weight
BW	Birth weight
CCW	Cold carcass weight
CL	Cooking loss
CLEN	Carcass length
CMAR	Carcass marbling score
DL	Drip loss
ENDW	End body weight
FCR	Feed conversion ratio
FD	Backfat depth
GBLUP	Genomic best linear unbiased prediction
GEBV	Genomic estimated breeding value
GLM	General linear model
GS	Genomic selection
HCW	Hot carcass weight
HGMA	Minolta a* ham gluteus medius
HGMB	Minolta b* ham gluteus medius

HGML Minolta L* ham gluteus medius

HILA Minolta a* ham iliopsoas

HILB Minolta b* ham iliopsoas

HILL Minolta L* ham iliopsoas

HQFA Minolta a* ham quadriceps femoris

HQFB Minolta b* ham quadriceps femoris

HQFL Minolta L* ham quadriceps femoris

IBS Identical by state

IGF2 Insulin-like growth factor 2

LD Loin depth

LEA *Longissimus dorsi* muscle

LOINA Minolta a* loin

LOINB Minolta b* loin

LOINL Minolta L* loin

MAS Marker-assisted selection

NSIF National Swine Improvement Federation

NURW Nursery weight

PHU pH ultimate

PICN Trimmed picnic shoulder weight

PSE Pale, soft and exudative

QTL Quantitative trait loci

REAA Minolta a* rib eye area

REAB Minolta b* rib eye area

REAL Minolta L* rib eye area

REAW Rib eye weight

RIBS Ribs weight

RTW Rib trim weight

SHF Shear force

SNP Single nucleotide polymorphism

ssBLUP Single-step BLUP

TBEL Trimmed belly weight

TEXS Texture score

THAM Trimmed ham

TLOIN Trimmed loin weight

UBEL Untrimmed belly weight

UFD Ultrasound backfat depth

UHAM Untrimmed ham weight

UIMF Ultrasound intramuscular fat

ULD Ultrasound loin depth

ULOIN Untrimmed loin weight

USH Untrimmed shoulder weight

USW Untrimmed side weight

WLW Whole loin weight

WNW Weaning weight

CHAPTER 1. General Introduction

1.1. INTRODUCTION

The major focus of traditional swine breeding programs has been production efficiency with traits of interest such as reproductive, growth, backfat thickness and feed efficiency performance. More recently, the swine industry has focused on pork quality due to the processors', packers' and consumers' demands for food with better quality (Martinez and Zering, 2004; van Wijk et al., 2005). Consequently, many researchers have focused on the genetics underlying pork quality traits during the last 20 years (Cameron, 1993; Hovenier et al., 1993a; Hovenier et al., 1993b; Sellier, 1998; De Vries et al., 1998; Verbeke et al., 1999; Knap et al., 2002; Rosenvold and Anderson, 2003; van Wijk et al., 2005). Meat quality traits are recognized as quantitative traits, which are affected by genetic and environmental factors, including muscle physiology and characteristics, environmental conditions (nutrition, growth rate, age, pre-slaughter conditions, slaughter practices and post mortem conditions), chilling, storage conditions and the genetics of the pigs (Schafer et al., 2002; Rosenvold and Anderson, 2003).

Meat quality traits are low-to-moderately heritable while carcass composition traits are highly heritable (Ciobanu et al., 2011). Various factors may influence the variance component estimates including the end-point adjustment, population size, sampling and available pedigree (Miar et al., 2014a). Genetic improvement of meat and carcass quality in swine breeding programs requires estimating the genetic and phenotypic parameters of these traits. Estimates of heritabilities for meat quality and carcass characteristics and genetic correlations between these economically important traits are limited but have received attention recently (Newcom et al.,

2002; van Wijk et al., 2005). However, to the best of my knowledge, there is no comprehensive parameter estimation for most of pork and carcass quality traits. Therefore, in the first study of this thesis, the genetic parameters including heritabilities, genetic and phenotypic correlations among pork quality and carcass traits were investigated in commercial crossbred pigs. Moreover, the second study of this thesis was a further investigation focusing on genetic and phenotypic correlations between performance traits with pork and carcass quality traits. These studies are needed for Canadian swine populations in order to implement selection programs that emphasize product quality.

Increased understanding of the genes affecting pork quality could better satisfy consumer demands for excellent eating quality by applying genetic selection for pork quality with better eating quality. Traditional breeding approaches apply sophisticated statistical methods such as best linear unbiased prediction (BLUP) to evaluate the genetic potential of animals for economically important traits using phenotype and pedigree information observed on the animal. However, the genetic gain achieved is relatively slow for traits of low-to-moderate heritability (Miar et al., 2014b), or expensive to measure, such as those determined post-mortem e.g. pork quality. Therefore, selection of purebreds based on crossbred progeny performance for these traits would be useful in improving pure line parents to produce improved pork quality for their crossbred progenies. Recently, the Illumina PorcineSNP60 BeadChip was developed (Ramos et al., 2009) and has been used in genome-wide association studies to identify genes that explain variation in meat quality traits. Nowadays, the availability of dense panels of DNA markers covering the whole genome along with powerful new statistical tools have made genomic selection (GS) feasible in pigs. The large number of single nucleotide polymorphisms (SNPs) generated by high throughput technologies can be used in GS to select superior animals with

better meat quality. Many quantitative trait loci (QTL) affecting meat quality traits have been detected in pigs, demonstrating the potential for this improvement. Genomic selection uses the linkage disequilibrium between DNA markers and QTL affecting economically important traits in livestock (Toosi et al., 2010). Genomic selection sums the effects of markers covering the whole genome so that potentially all of the genetic variance associated with the traits and explained by the markers are considered. The effect of all markers associated with the trait in the whole genome is used to predict the genomic estimated breeding value (GEBV) of each animal.

Various statistical methods have been developed to predict GEBV such as ridge regression, various Bayesian approaches, Genomic BLUP (GBLUP), selection index and single-step BLUP (Meuwissen et al., 2001; Gianola et al., 2006; Habier et al., 2007; VanRaden et al., 2009; Misztal et al., 2009; Legarra et al., 2009; Calus, 2010; Habier et al., 2011; Erbe et al., 2012; Brondum et al., 2012). Single-step methodology can be simpler, faster, more accurate and applicable to complicated models compared to multi-step methods such as GBLUP (Aguilar et al., 2010) and also can predict genomic breeding values for either with genotypes or without genotypes. This approach has been successfully implemented for pigs (Forni et al., 2011; Christensen et al., 2012), chickens (Chen et al., 2011) and dairy cattle (Aguilar et al., 2011; Tsuruta et al., 2011; VanRaden, 2012).

By implementing GS, prediction of the genetic potential of animals becomes possible at an early stage of their life before their phenotypic records are available. It will increase the rate of genetic gain by reducing generation interval. Although generation interval in swine is not as long as in cattle it can still play a role for meat quality traits that are measured post-mortem. However, the largest benefit of GS will be from an increase in the accuracy of selection for pork quality by selecting animals based on their genomic potential rather than phenotypic information

from their relatives using traditional BLUP (Meuwissen et al., 2001; Hayes et al., 2009). This can greatly improve selection accuracy to accelerate genetic gain for pork quality traits.

Meuwissen et al. (2001) showed that genomic selection could lead to increases in the rate of genetic gain especially for traits that are not easy to measure and have low heritability such as meat quality. Christensen et al. (2012) showed that GS produces more accurate predictions for feed conversion ratio compared to traditional breeding resulting in extra genetic gain in pigs. Improved reliability of genomic prediction has resulted in an increased rate of genetic gain in pigs and dairy cattle (VanRaden et al., 2009; Forni et al., 2011; Christensen et al., 2012). Therefore, the third study in this thesis was performed to improve pork quality and carcass traits from a Duroc parental pure-line using their commercial crossbreds and single-step methodology.

1.2. OBJECTIVES

The major objective of this study was to improve meat quality and carcass traits from Duroc parental purebreds using their commercial crossbreds resulting from understanding genetic parameters for these traits, their correlations with performance traits, and improving selection accuracy to accelerate genetic gain in pigs.

The specific objectives included:

a) Estimating phenotypic and genetic parameters including heritabilities, phenotypic and genetic correlations among pork quality, among carcass traits and between them in commercial crossbred pigs.
b) Estimating phenotypic and genetic parameters including heritabilities for various growth, and performance traits, phenotypic and genetic correlations between

performance traits with pork quality and carcass traits in commercial crossbred pigs.

c) Applying genomic selection for various pork quality and carcass traits using single-step BLUP using commercial crossbred animals and their pure parental lines for genomic selection of the parental Duroc purebreds.

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CHAPTER 2. Literature Review[1]

2.1. INTRODUCTION

Pig breeders have become increasingly aware of meat quality to meet the demands of processors, packers, and consumers for better pork quality (Dransfield et al., 2005). However, measurement of meat quality traits on a routine basis is expensive and relatively difficult. Ultrasound technology has been used very effectively to reduce the fat content of pork and is now being used to predict marbling, an important aspect of quality, on live animals with relatively low cost. However, many meat quality traits (e.g. pork water holding capacity) need to be measured post-mortem, which make them difficult and expensive to measure. Therefore, genetic improvement of pork quality requires an understanding of the genetic basis of these traits to implement selection programs that emphasize product quality.

Most of the economically important traits including pork quality in livestock are quantitative, meaning they are regulated by multiple genes and part of their variation is influenced by the environment. Two models, the infinitesimal model and the finite loci model, have been used to explain the genetic variations observed in quantitative traits. The infinitesimal model assumes that traits are determined by an infinite number of unlinked additive loci, each with an infinitesimally small effect (Fischer, 1918). On the other hand, the finite loci model assumes the genome has a finite numbers of genes, after all there are around 20,000 loci in the human genome (Ewing and Green, 2000), with only a few associated with variation in each trait.

[1] A version of this Chapter has been submitted to Journal of Springer Science Reviews. Miar et al., 2014. Genomic selection, a new era for pork quality improvement.

Based on the latter model, it has been predicted that 50 to 100 genes, each with an unequal effect, determine genetic variation in quantitative traits that are called quantitative trait loci, or QTL (Hayes and Goddard, 2001). Of course the behavior of even 100 genes, taking into account the potential interactions among them, may be indistinguishable from the infinitesimal model.

Genetic maps of livestock based on DNA markers provide new tools for detection and mapping of genes for economically important traits in livestock (Rohrer et al., 1996; Groenen et al., 2000; Maddox et al., 2001). Rohrer et al. (1996) reported a comprehensive map for the porcine genome, which was used very effectively to search for loci affecting traits of interest (Hu et al., 2007). Detection of QTL and their use in selection to increase accuracy of selection and improve the rate of genetic gain in livestock has occurred (Weller, 2001) although the impact has been relatively small (Dekkers, 2004). Over the past 30 years, two approaches have been used to uncover the polymorphisms underlying variation in economically important traits. One approach is that genes (QTL) affecting a trait of interest are mapped to a chromosomal location using genetic markers (Andersson and Georges, 2004), the other is to use candidate genes based on their role in the biology of the trait (Goddard and Hayes, 2009). These two methods have been used to detect genetic markers suitable for marker-assisted selection (MAS) in domestic animals (Rothschild et al., 2007).

Meuwissen et al. (2001) conducted a simulation study and showed that it is theoretically possible to predict breeding values of animals more accurately than traditional methods if a high-density of markers was used. Today, this method is called "genomic selection". Recently, the availability of dense panels of DNA markers covering the whole genomes of major domestic animal species including the pig (Ramos et al., 2009) and using appropriate statistical tools have

made genomic selection (GS) feasible in pigs (Nejati-Javaremi et al., 1997; Meuwissen et al., 2001; Fernando et al., 2007).

Genomic selection uses the linkage disequilibrium between DNA markers and QTL affecting economically important traits in livestock (Toosi et al., 2010). The effect of all markers associated with the trait in the whole genome is used to predict the genomic estimated breeding value (GEBV) of each animal. This approach, also termed genomic prediction or genomic evaluation, is used to improve selection accuracy for economically important traits (Meuwissen et al., 2001; Hayes et al., 2009). Meuwissen et al. (2001) showed that genomic selection could lead to increases in the rate of genetic gain especially for traits that are not easy to measure and have low heritability such as meat quality. Christensen et al. (2012) showed that GS produce more accurate predictions for feed conversion ratio compared to traditional breeding resulting in extra genetic gain. Various statistical methods have been developed to predict GEBV such as ridge regression, Bayesian approaches and GBLUP (Meuwissen et al., 2001; Gianola et al., 2006; Habier et al., 2007; Calus, 2010; Habier et al., 2011; Erbe et al., 2012; Brondum et al., 2012).

The objective of this Chapter is to provide a summary of the successful approaches for genomic prediction in pigs to improve pork quality traits and present recent highlights of their applications in swine breeding programs.

2.2. NOVEL BREEDING OBJECTIVES

Until recently pig breeders have mainly focused on production traits to increase the leanness of the carcass and reduce cost. More recently, the importance of meat quality is growing

for meat processors, packers and consumers because of its high economic value (Dransfield et al., 2005). Therefore, many pork producers are integrating marbling and quality grade as well as leanness to their breeding programs to meet these demands. This has led to the development of breeding objectives that include pork quality traits where increasing muscle tissue and decreasing backfat are two major objectives of swine breeding programs.

Pork quality is affected by a large number of factors including breed, genotype, feeding, stunning, pre-slaughter handling, slaughter method, storage and chilling conditions (Rosenvold and Andersen, 2003). These factors are classified into two groups: genetic and non-genetic factors (de Vries et al., 2000). Sellier and Monin (1994) showed that the genetic factors affecting pork quality are important components of the variation because they are traits with low-to-moderate heritability. It should be noted that the effect of genetics on pork quality include between breed and within breed differences resulting from major genes as well as polygenic effects.

2.3. BREED DIFFERENCES

Pork from different breeds shows variation in water holding capacity, colour, intramuscular fat and tenderness (Sellier and Monin, 1994). Pork from Chinese purebred or crossbred pigs was more tender than that from American and European breeds when assessed by a taste panel (Touraille et al., 1989; Suzuki et al., 1991). Hampshire pork was found to have decreased water holding capacity and increased cooking loss due to lower ultimate pH (Monin and Sellier, 1985). Meat from Hampshire was also determined to have increased tenderness

(Sellier and Monin, 1994). However, this breed effect can probably be completely explained through the high frequency of one single gene, called the RN gene (Milan et al., 1996).

Some breeds such as Belgian Landrace and Pietrain had a high frequency of a single locus called Halothane (Fujii et al., 1991). This locus is likely responsible for developing pale, soft and exudative meat, which is less tender. Therefore, meat from other breeds such as Large White or French Landrace are of better quality in comparison with Belgian Landrace and Pietrain breeds (Touraille and Monin, 1989; Monin et al., 1986). On the other hand, Halothane positive pigs had a higher yield of processed ham. Thus, the mutations underlying the Halothane (Fujii et al., 1991) and RN (Milan et al., 1996) genes were used to remove these defects from pigs through marker assisted selection (Van der Steen et al., 2000). Consequently, the Landrace breed can produce high quality pork if the Halothane gene has been removed. Large White and Landrace pigs typically have half the amount of intramuscular fat of that found in Duroc meat (Armero et al., 1998), which contributes to the better eating quality of Duroc pork (de Vries et al., 2000). Therefore, there is high genetic variation for pork quality resulting from breed differences.

2.4. GENOTYPE

The effects of genetics on pork quality include both between and within breed differences. This within breed variation is explained by genetics and environmental factors. The genetics' portion of this variation is described by the degree of heritability. Higher heritability shows the stronger influence of genetics factors. Miar et al. (2014c) provided a comprehensive report of heritabilities for most pork quality traits indicating that they are low-to-moderately (10-

39%) heritable. These quality traits are expected to be controlled by a large number of genes with small effect called polygenic effects and by some single genes with large effects called major genes (Rosenvold and Andersen, 2003). There are a small number of major genes affecting pork quality such as Halothane and RN (mentioned above), Calpastatin (Ciobanu et al., 2004) and Insulin-like growth factor 2 (IGF2). As an example, it was estimated that 15-30% of phenotypic variation in lean mass and 10-20% in backfat thickness was explained by IGF2 (Jeon et al., 1999; Nezer et al. 1999).

These traits are hard and expensive to measure in a simple and unique manner (Cameron, 1993) and are often measured post-mortem. Therefore, identifying and understanding the QTL underlying pork quality traits is necessary to implement a successful swine breeding program that emphasizes product quality.

2.5. APPLICATION OF MOLECULAR GENETICS FOR PORK QUALITY IMPROVEMENT

Recent progress in molecular genetic technology enabled the genotyping of tens of thousands of single nucleotide polymorphisms (SNPs) covering the whole genomes of major species of livestock. SNPs are the most commonly used DNA markers in animal genetics studies due to their amenability for high throughput platforms and their abundance in the genome (Vignal et al., 2002). Single nucleotide polymorphisms are a single base change in the DNA sequence. This single base pair change can occur within coding or non-coding sequences. Those residing in coding sequences may change the amino acid sequence of the protein and result in a

change in phenotype. Those in non-coding regions may still change the phenotype through affecting gene expression level.

Today, high throughput technologies have been used to generate dense panels of SNPs (Weller, 2010). Major species of livestock have high density SNP chips such as the Illumina porcine SNP60 Beadchip for pigs (Ramos et al., 2009), Illumina Bovine SNP50 BeadChip for cattle (Matukumalli et al., 2009) and Illumina Ovine SNP50 BeadChip for sheep (Cockett et al., 2009). Advancement of molecular genetics has led to identification of many QTL for economically important traits in livestock. As of October 2014, more than 6,621 QTL relevant to meat and carcass quality traits have been deposited in the pig QTLdb (http://www.animalgenome.org/cgi-bin/QTLdb/SS/index). These QTLs can be used to select superior animals with better pork quality.

2.6. MARKER-ASSISTED SELECTION

Marker-assisted selection (MAS) is the selection of animals or plants based on the combined information of traditional genetics and marker information. There are two types of MAS: One is the candidate gene approach which uses causative mutations with a major effect on a particular trait such as the halothane gene in pigs that controls muscle growth (Goddard and Hayes, 2009). Another uses linkage disequilibrium between markers with QTL. The breeding value will be predicted based on the combined information of polygenic effects and significant markers (Meuwissen and Goddard, 1996). However, the genetic gain from this method of selection was small (Dekkers, 2004) because genetic gain using MAS depends on the percentage of genetic variance of the trait that was explained by the markers (Meuwissen and Goddard,

1996). Marker-assisted selection relies on using a relatively small number of markers in the breeding value prediction models. As many genes determine most of the quantitative traits, MAS will therefore capture only a small proportion of genetic variance in the trait because of the low number of markers (Goddard and Hayes, 2007; Goddard and Hayes, 2009).

2.7. GENOMIC SELECTION

The limitations of MAS can be overcome by using a high-density of markers across the genome to capture a larger percentage of the genetic variance of the trait of interest (Meuwissen et al., 2001). This alternative method is called genome-wide selection or genomic selection (GS). Genomic selection uses high marker density and assumes each QTL is in linkage disequilibrium with at least one closely linked marker. The assumption underlying GS is that the effects of chromosome segments will be the same within the population because the markers are in linkage disequilibrium with the QTL. Therefore, the density of markers must be high enough to ensure that all QTL are in linkage disequilibrium with at least one marker.

Genomic selection needs a reference population that is a sample of individuals with genotypic and phenotypic records to develop a GEBV prediction equation (Goddard and Hayes, 2009). The effect of each marker is estimated using appropriate statistical analysis, and hence a prediction equation can be developed that combines all the estimated effects of marker genotypes to predict the GEBV for each animal. Subsequently this prediction equation is applied to the candidate population with genotypic records but without phenotypic information (selection population) to predict GEBV for each individual and this can be used to select the best animals for breeding in the selection population (Meuwissen et al., 2001; Goddard and Hayes, 2009) as

indicated in Figure 2.1. Using GS would be beneficial especially for the traits where traditional genetic selection was not very effective in breeding programs. For example, meat quality traits can only be recorded post mortem, they are expensive and hard to measure and have low-to-moderate heritability (Goddard and Hayes, 2009; Miar et al., 2014b; Miar et al., 2014c).

By implementing GS, prediction of the genetic potential of animals becomes possible at an early stage of their life when they do not have phenotypic records. It will increase the rate of genetic gain by reducing the generation interval especially in species with a long generation interval such as bovine and equine. Although the generation interval in swine is not as large as in cattle it can still be applicant for meat quality traits that are measured post-mortem. However, the largest benefit of GS will be from an increase in the accuracy of selection for pork quality by selecting animals based on their genomic potential rather than phenotypic information from their relatives using traditional BLUP (Meuwissen et al., 2001; Hayes et al., 2009).

2.8. STATISTICAL METHODS FOR GENOMIC EVALUATION

The main challenge for prediction of GEBV of each individual using high density markers is that in most situations the number of SNPs (usually approximately 50,000 to 60,000) is larger than the number of animals, which is normally a few thousands (Calus, 2010). Several statistical approaches have been developed to solve the problems of multicollinearity between markers and over-parameterization when using high-density markers as in the least squares model. The statistical methods developed for prediction of GEBV include ridge regression, GBLUP, and various Bayesian approaches (Hoerl and Kennard, 1970; Nejati-Javaremi et al., 1997; Meuwissen et al., 2001; Xu, 2003; Gianola et al., 2006; Fernando et al., 2007; Habier et

al., 2007; Hayes et al., 2009; VanRaden et al., 2009; Friedman et al., 2010; Zhang et al., 2010; Habier et al., 2011; Erbe et al., 2012; Brondum et al., 2012). These methods consider different assumptions about the distribution of QTL effects that affect the accuracy of genomic evaluation.

Generally, the prediction model for GEBV is defined as a linear mixed model for the analysis of bi-allelic genotypes that can be obtained as shown in Equation 1.

$$y_i = \mu + \Sigma_j x_{ij}\beta_j\delta_j + e_i, \qquad \textit{(Equation 1),}$$

where y_i is the phenotypic observation of the i^{th} animal, μ is the overall mean, x_{ij} can be 0, 1, or 2 depending on the SNP genotype at the j^{th} marker locus of the i^{th} individual, β_j is the allele substitution effect of j^{th} marker, δ_j is an indicator variable which is equal to 1 or 0 for the inclusion or exclusion of j^{th} marker, and e_i is a random residual.

In this Chapter, some of the statistical methods that have been used widely for genomic prediction in livestock breeding programs such as ridge regression, GBLUP and Bayesian approaches are discussed briefly.

2.8.1. GBLUP method

The genomic best linear unbiased prediction (GBLUP) method was first proposed by Nejati-Javaremi et al. (1997). They compared two methods of using total allelic relationship and pedigree-derived genetic relationship in mixed model equations to derive best linear unbiased prediction (BLUP) of breeding values. They concluded that using the total allelic relationship gives more accurate breeding values than a pedigree-derived genetic relationship because it

accounts for variation in average measures of relationship and identity by state alleles. Habier et al. (2007) modified the method for implementing genomic selection using the genomic relationship matrix (G) instead of the allelic relationship matrix (Habier et al., 2007; Goddard, 2009). Genetic markers could estimate the proportion of chromosome segments shared by individuals including identical by state (IBS) loci. Therefore, GS can capture the Mendelian segregation during gamete formation and hence selection based on a genomic relationship matrix can be more accurate than an additive relationship matrix (Goddard and Hayes, 2007).

The statistical model for GBLUP sums the individual marker effects to predict GEBV with the assumption of normality for the marker effects as shown in Equation 2 (Hayes and Goddard, 2010):

$$\boldsymbol{y = 1_n\mu + Zg + e}\,, \qquad \textit{(Equation 2),}$$

where $\boldsymbol{y}$ is a phenotypic observation vector for $\boldsymbol{n}$ individuals, $\boldsymbol{\mu}$ is the overall mean, $\mathbf{1_n}$ is a vector of ones, $\boldsymbol{Z}$ is the design matrix for the breeding values, $\boldsymbol{g}$ is a vector of breeding values and $\boldsymbol{e}$ is the residual error vector with an assumed $\boldsymbol{N(0,\sigma_e^2)}$ distribution. In this model, $\boldsymbol{g = Wu_j}$ where $\boldsymbol{u_j}$ is the effect of $\boldsymbol{j}^{\text{th}}$ marker and variance V(**g**) = $\boldsymbol{WW'\sigma_u^2}$. $\boldsymbol{W}$ matrix contains $\boldsymbol{w_{ij}}$ elements for $\boldsymbol{i}^{\text{th}}$ animal which shows the deviation of the number of alleles at the $\boldsymbol{j}^{\text{th}}$ marker from the $2\boldsymbol{p_j}$ so that is equal to $0 - 2p_j$ for the homozygous AA, $1 - 2p_j$ for the heterozygous Aa and $2 - 2p_j$ for the homozygous aa. The diagonal elements of *WW'* for $\boldsymbol{m}$ markers would be equal to $\sum_{\boldsymbol{j=1}}^{\boldsymbol{m}} \mathbf{2}\boldsymbol{p_j}\left(\mathbf{1} - \boldsymbol{p_j}\right)$. In GBLUP, the breeding values will be predicted as shown in Equation 3.

$$[\hat{\boldsymbol{g}}] = \left[\boldsymbol{Z'Z} + \boldsymbol{G^{-1}}\frac{\boldsymbol{\sigma_e^2}}{\boldsymbol{\sigma_g^2}}\right]^{-\mathbf{1}} [\boldsymbol{Z'y}] \qquad \textit{(Equation 3)}$$

This method has good properties to capture the genomic relationships between individuals. VanRaden et al. (2009) showed that this method is at least as good as other methods for many traits in dairy cattle.

2.8.2. Ridge regression

Ridge regression was first proposed by Hoerl and Kennard (1970). They used ridge regression instead of the least squares method to estimate the coefficients of the linear model. Meuwissen et al. (2001) modified the method for implementation in the analysis of genetic markers. Ridge regression assumes that all marker effects are normally distributed with equal variance. One of the best properties of this method is that it can overcome multicollinearity between markers because the regression coefficients are shrunk towards zero using a shrinkage parameter (λ). El-Dereny and Rashwan (2011) showed that ridge regression is more accurate than the ordinary least squares method when multicollinearity exists. It uses the same linear model as the least squares method, but the only difference is that it includes a shrinkage parameter (λ) to the diagonal elements of least squares equation as shown in Equation 4.

$$\begin{bmatrix} \boldsymbol{X'R^{-1}X} & \boldsymbol{X'R^{-1}Z} \\ \boldsymbol{Z'R^{-1}X} & \boldsymbol{Z'R^{-1}Z + I\lambda} \end{bmatrix} \begin{bmatrix} \widehat{\boldsymbol{\beta}} \\ \widehat{\boldsymbol{\gamma}} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X'R^{-1}y} \\ \boldsymbol{Z'R^{-1}y} \end{bmatrix} \quad (\textit{Equation 4}),$$

where $\boldsymbol{y}$ is a phenotypic observation vector for $\boldsymbol{n}$ individuals, $\boldsymbol{X}$ is the design matrix of the fixed effects, $\boldsymbol{Z}$ is the design matrix for the random effects and $\boldsymbol{R}$ is an $\mathbf{n} \times \mathbf{n}$ covariance matrix for the residual errors and $\boldsymbol{I}$ is an identity matrix with the same dimension as $\boldsymbol{Z'R^{-1}Z}$.

The shrinkage parameter controls the amount of shrinkage on the regression coefficients. The level of shrinkage increases as λ increases which shrinks all the regression coefficients to zero (Xu and Hu, 2010). Ridge regression can fit a large number of markers into the model but this is not the optimal shrinkage because all the regression coefficients become so small leading to the assumption of equality of variance of markers effects that is not a desirable property. Desirable shrinkage should not shrink the markers with large effects and should penalize the markers with small or no effects. More desirable methods can select the markers based on their effects, and these methods will be discussed in subsequent sections.

In comparison to other methods, ridge regression is a simple and fast method to predict GEBV. Sargolzaei et al. (2009) introduced free software, GEBV, a genomic breeding value estimator for livestock, to implement ridge regression for genomic evaluation that can deal with large datasets.

2.8.3. Bayesian methods

There are three methods of Bayesian approach that have been used frequently in animal genetic evaluations. Two of them, BayesA and BayesB, were proposed by Meuwissen et al. (2001) and BayesC was proposed by Kizilkaya et al. (2010). Recently, new Bayesian approaches are emerging with different letters including BayesCπ, BayesDπ, BayesD (Habier et al., 2011), BayesR (Erbe et al., 2012) and BayesRS (Brondum et al., 2012). In Bayesian statistics, the data

are modeled at two levels; first is the data level and second is the variances of genomic segments. The difference between Bayesian and ridge regression at the data level is the variance of the markers. In Bayesian statistics, it is assumed that the variance for each marker loci comes from a prior distribution and the data, whereas in ridge regression it is assumed that the variance of all the markers is equal. It seems that the Bayesian approach is more realistic than the methods that assume equal variance for each locus due to the assumption that not all markers contribute to the genetic variation.

Meuwissen et al. (2001) described the BayesA approach such that the markers are assumed to have different variances as they follow the scaled inverse chi-square distribution, χ^{-2} (v, S), where S is a scale parameter and v is the degrees of freedom. Furthermore, the BayesA approach considers all markers in the model. Therefore, it needs more computations than other Bayesian approaches because large numbers of effects are included simultaneously in the model and no marker effect was assumed with zero variance.

Another variation, BayesB, was also proposed by Meuwissen et al. (2001). This method assumes that there are many markers with zero genetic variance and a few with non-zero genetic variance. It considers a high density, π, for those loci with zero genetic variance and an inverted chi-square distribution for loci with genetic variance larger than zero. This method can exclude those loci with no effect on the quantitative trait of interest. Therefore, BayesB needs less computational time than BayesA because many loci have no effect and thus do not enter the equations.

Another Bayesian method is called BayesC, which was proposed by Kizilkaya et al. (2010). BayesC uses common variance for all markers that is estimated from the marker data so that it is not influenced by the prior as much as BayesB. Onteru et al. (2011; 2012) mentioned

that BayesB is more sensitive to the prior than BayesC. Bayesian methods such as BayesB and BayesC that use a prior distribution of the markers variance increase the accuracy of genomic selection in comparison with the ridge regression method (Meuwissen et al., 2001; Smaragdov, 2009). A further approach is BayesD where the estimated scale parameter of the scaled inverse chi-square distribution is used instead of specified scale parameter. BayesCπ and BayesDπ (Habier et al., 2011) are modifications of BayesC and BayesD where the probability of having a zero SNP π is estimated. Other Bayesian approaches, BayesR (Erbe et al., 2012) and BayesRC (Brondum et al., 2012) have emerged even more recently. BayesR uses a mixture of normal distributions as the prior for SNP effects, including a distribution that sets SNP effects to zero. BayesRC was developed for multi-population genomic prediction and uses a location genetic variance achieved from one population that will be then used as priors for another population.

These various statistical methods can be applied to predict GEBV of pigs and consequently select superior animals with better pork quality based on their GEBV.

2.9. ALTERNATIVE METHODS FOR GENOMIC SELECTION

Combining the genomic information and polygenic information seems to be a necessity for accurate selection of superior animals for breeding. One of the first proposed methods for combining both sources of information was a selection index bending approach, which was proposed by VanRaden et al. (2009). The selection index prediction includes genomic breeding value and EBV estimated using a subset of the population used for genomic prediction and traditional BLUP from the whole population. Consequently, these alternative methods would

utilize genomic information from genotyped animals and their relatives, which are not genotyped; phenotypic information of relatives could also enrich the genomic prediction of young boars; these methods can reduce the bias in either genomic prediction or classical evaluations. One of the most used alternative methods for combining genomic and classical information is single-step BLUP (ssBLUP) proposed by Misztal et al. (2009).

2.10. SINGLE- VERSUS MULTI-STEP BLUP FOR GS

Combining genomic and traditional information can improve the accuracy of predictions. Single-step BLUP is a modification of BLUP and integrates the pedigree relationship matrix and genomic relationship matrix into a single matrix, called the H matrix. This method was proposed by Misztal et al. (2009) and Legarra et al. (2009). The inverse of the H matrix is a simple form and can substitute for the inverse of the additive relationship matrix in existing software (Aguilar et al., 2010).

Multi-step prediction methods involve 1) estimating EBV of each individual based on its pedigree using BLUP; 2) adjusting the phenotype (calculating de-regressed EBV); 3) estimating the allelic effects for each SNP; and 4) combining genomic prediction (GEBV) and BLUP evaluations (EBV) (VanRaden, 2008). However, ssBLUP utilizes just phenotypic records, which are not dependent on other estimated effects and accuracy of EBV (Misztal et al., 2013). Using approximations for adjusting phenotype can inflate the GEBV and reduce the accuracy in multi-step approaches. Furthermore, the multi-step approach is more prone to errors because of its complexity.

Single-step methodology can be simpler, faster, more accurate and applicable to complicated models compared to multi-step methods such as GBLUP (Aguilar et al., 2010). This approach has been successfully implemented for pigs (Forni et al., 2011; Christensen et al., 2012), chickens (Chen et al., 2011) and dairy cattle (Aguilar et al., 2011; Tsuruta et al., 2011; VanRaden, 2012). These studies showed that single-step is generally at least as accurate as multi-step methods, the process is simpler, and the inflation of GEBV is smaller than multi-steps.

2.11. ACCURACIES OF GEBVs

Accuracy of prediction of GEBV is the correlation between true breeding values and estimated breeding values. The accuracy of prediction has been investigated by using both simulation studies and real data. Different accuracies have been achieved by using different statistical methods for different heritabilities. The accuracies of genomic evaluations ranged from 0.46-0.88, 0.59-0.96 and 0.56-0.98 for ridge regression, GBLUP and Bayesian approaches in simulation studies, respectively. (Meuwissen et al., 2001; Habier et al., 2007; Fernando et al., 2007; VanRaden, 2008; Habier et al., 2009; Christensen and Lund, 2010; Kizilkaya et al., 2010).

In real data, the accuracies of genomic prediction have different ranges using different statistical methods (Table 2.1). These studies showed that different methods are similar in their expected accuracy of genomic prediction. In addition to the statistical methods of genomic prediction, there are several factors affecting the accuracy of genomic breeding value prediction such as reference population size, number of SNPs, heritability of the trait, effective population size (N_e) and number of loci affecting the traits (Muir, 2007; Daetwyler et al., 2008; Goddard and Hayes, 2009).

One of the most important factors affecting accuracy of GEBV is the number of SNPs to be analyzed (Hayes and Goddard, 2010). This depends on the extent of linkage disequilibrium in the species of interest. If there is not sufficient linkage disequilibrium between SNPs and QTL, more SNPs are needed in the genotyping panel to increase the power of QTL detection. The accuracy of genomic predictions is high if the mean linkage disequilibrium between two adjacent markers is greater than 0.2 (Calus et al., 2008). Sved et al. (1971) showed that the expected linkage disequilibrium depends on the effective population size and distance between markers. Meuwissen et al. (2001) demonstrated that 1 cM of inter-marker spacing is needed to have a high accuracy of prediction given an N_e=100. The effective population size for Holstein-Friesian cattle is approximately 100. Therefore it is estimated that Holstein-Friesian cattle needs approximately 30,000 markers based on the 30 Morgan length of genome (Hayes and Goddard, 2010) and hence GS can increase the accuracy using a density of 30,000 SNPs in dairy cattle. In a similar manner, the effective population for Duroc breed in USA was estimated to be 113 (Welsh et al., 2010). Therefore, it is estimated that Duroc pig needs approximately 26,000 markers based on the 23 Morgan length of genome (Rohrer et al., 1996) and hence GS needs a density of 26,000 SNPs in pigs to improve the accuracy.

The other factor affecting the genomic prediction is the size of reference population. It is suggested that large reference population size is needed to predict GEBV accurately for low heritability traits (pork quality traits). The number of animals needed in the reference population increases as the heritability declines or N_e of the population increases (Goddard and Hayes, 2009).

Another factor affecting the accuracy is the number of loci affecting the trait. Although the number of QTLs affecting pork quality traits has not been defined yet, Goddard (2009)

showed that the number of QTLs affecting any trait can be calculated as $q = 2N_eL$, where q is the number of QTLs affecting the trait and L is the length of the genome in Morgans. Then, the accuracy of GEBV can be calculated as shown by Equation 5:

$$\boldsymbol{r = [1 - \lambda/(2N\sqrt{a}) \times ln(1 + a + 2\sqrt{a})/(1 + a - 2\sqrt{a})]^{\frac{1}{2}}} \qquad (\textit{Equation 5}),$$

where a = 1+2λ/N, and λ=qK/h^2, with K=1/log(2N_e), where h^2 is the heritability of the trait and N is the number of individuals with phenotypic record in the reference population (Goddard, 2009).

2.12. APPLICATION OF GS IN PORK QUALITY

The ability to select animals based on their GEBV or GS would allow the opportunity to redesign livestock breeding programs to select animals at an early stage of their life and increase the accuracy of prediction. Consequently, this would increase the genetic gain by decreasing generation interval, increasing the selection accuracy, and the frequency of favorable alleles (Falconer and Mackay, 1996; Goddard and Hayes, 2009). In dairy cattle, reducing the generation interval using GS was predicted to increase the genetic gain by twice compared to traditional evaluation and this results in reducing costs for proving bulls by more than 90% (Schaeffer, 2006). In practice genomic selection was successful in increasing the accuracy in young dairy bulls, averaging 23% across traits with a range from 8 to 43% (VanRaden et al., 2009). Genomic selection explains a greater proportion of genetic variance than MAS and it is not limited to within families.

The commercial production system in pig breeding is pyramidal. Nucleus herds supply genetics to multipliers and later to commercial crossbreds. The main limitation of this system is that purebred performance can be a poor indicator of crossbred performance (Dekkers, 2007). Using GS for some traits such as lowly heritable traits, difficult and expensive to measure traits, sex limited traits, traits that are expressed late in life and after slaughter traits, would enable the rate of genetic gain to be greatest. Measurement of carcass and meat quality traits is difficult, expensive, and can only be performed post-mortem. Therefore, genomic selection of purebred pigs based on crossbred performance for these traits would be useful to help improve pure lines to produce superior commercial crossbred animals without the need for measurements on pure lines. Miar et al. (2014a) showed the potential of genomic selection for pork pH in the pure parental lines using the prediction models developed from their crossbred progeny. Different models were proposed to select purebreds for crossbred performance. Although most studies used additive gene action, the dominance model is the likely genetic basis of heterosis. In a simulation study, Zeng et al. (2013) suggested that GS with a dominance model is superior when dominance effects are present allowing the opportunity to maximize the crossbred performance through purebred selection.

Development of composite lines and introgression of valuable alleles between populations are the other potential applications of GS in livestock breeding programs. Genomic selection increases the efficiency of introgression of favourable QTL alleles from a donor line to a recipient line (Ødegård et al., 2009). Therefore, GS can improve composite lines, which are often used in the pig industry (Piyasatian et al., 2006). Genomic selection has introduced a new paradigm for pig breeding and hence can be successfully applied to livestock breeding programs in optimizing mating strategies and herd management.

2.13. CHALLENGES IN GENOMIC SELECTION FOR PORK QUALITY

Although GS is revolutionizing animal breeding, it also faces some challenges including the need for large reference populations, and further investigation is required to understand the impact for long-term genetic gain, non-additive genetic effects, and selection involving multiple breeds. One of the major challenges is the requirement of large reference population size to predict GEBV accurately. In most cases to date, small reference populations have been used for genomic prediction while it is known that larger reference populations result in higher accuracy of genomic prediction (Dalton, 2009; Goddard and Hayes, 2009). Another major challenge is that long-term genetic gain could be less than phenotypic selection (Muir, 2007; Goddard, 2008). There are two reasons for this issue including the effect of selection on the pattern of linkage disequilibrium between marker and QTL resulting in changing the linkage disequilibrium which is the criteria for genomic selection, and the genomic selection uses only the markers that have been detected to affect the trait while phenotypic selection uses all QTL automatically (Goddard, 2008; Hayes et al., 2009). Even so, improvement is required over the short-term and we are confident that increased understanding and use of different populations will help address the risk of a long-term decrease in gain.

Another major challenge in GS is the involvement of multiple breeds in livestock industries. De Roos et al. (2008) showed that large reference population sizes and more than 300,000 SNPs are needed for divergent breeds. Another challenge in using genomic selection is using non-additive genetic effects. It might be beneficial to improve the accuracy of selection by including non-additive genetic effects such as dominance and epistatic effects. There are some methods for genomic prediction which allow us to estimate non-additive genetic effects e.g.

estimation of interactions between high density of markers has been developed by Gianola et al. (2006) and estimation of both dominance and epistatic effects by using single-marker Bayesian approach (Xu and Jia, 2007), and the dominance model developed by Zeng et al. (2013).

2.14. CONCLUSIONS

The objective of this Chapter was to provide a summary of strategies for implementing genomic selection in swine breeding programs to improve pork quality. In the last decade, traditional BLUP and using indirect selection with correlated traits was used to predict the genetic potential of animals for pork quality. Although it was successful, the process was slow for pork quality as it is hard and expensive to measure, low-to-moderately heritable and must be measured post-mortem. Recently, identification of genetic markers underlying pork quality became possible, which were used in MAS programs. The effect of each QTL on the trait of interest is small, limiting the value of MAS and confirming the need for dense markers to capture more genetic variation in that trait (Hayes and Goddard, 2010). This has led to the development of GS.

Genomic selection is one of the ultimate applications of genetic markers in animal genetic improvement. Genomic selection uses a dense panel of markers covering the whole genome assuming all QTL are in linkage disequilibrium with at least one of the markers. Genomic prediction can be applied based on multi-step approaches using various statistical methods including Bayesian approaches, GBLUP and ridge regression or ssBLUP into the reference population with known genotypes and phenotypes. The results of genomic prediction are implemented to select animals in the selection population with known

genotypes and unknown phenotypes to completely redesign livestock breeding programs. Genomic selection enables prediction of breeding values of young selection candidates, results in reducing the generation interval and increasing accuracy of selection. The accuracy of genomic selection strongly relies on a number of factors such as size of the reference population, number of SNPs, heritability of the trait, effective population size (N_e) and number of loci affecting the traits (Muir, 2007; Daetwyler et al., 2008; Goddard and Hayes, 2009). In conclusion, GS opens the possibility of using high density of markers covering the whole genome to increase the rate of genetic gain for pork quality traits to help ensure that demand for high quality and affordable pork is satisfied.

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Table 2.1: Ranges of genomic prediction accuracies using real data with different statistical methods

Statistical methods	Accuracy	References
Ridge regression	0.15-0.73	Moser et al., 2009; Hayes et al., 2009; Moser et al., 2010
GBLUP	0.13-0.82	Harris et al., 2008; Berry et al., 2009; Schenkel et al., 2009; VanRaden et al., 2009; Hayes et al., 2009; Luan et al., 2009
BayesA	0.37-0.82	Moser et al., 2009; Hayes et al., 2009; de Roos et al., 2009; Cleveland et al., 2010
BayesB	0.13-0.70	Luan et al., 2009; Hayes et al., 2009
BayesC	0.33-0.6	Cleveland et al., 2010

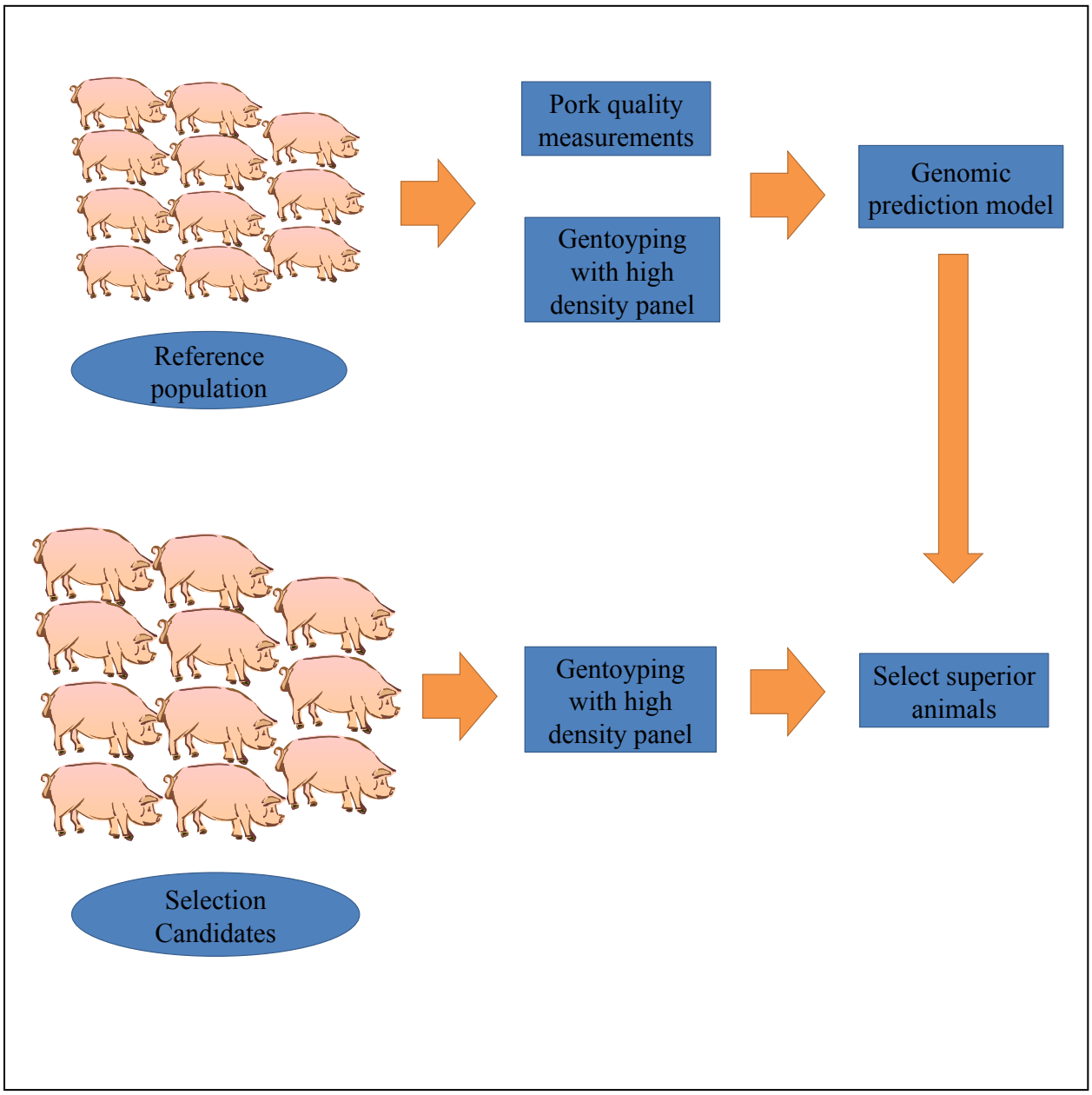

Figure 2.1: Genomic selection for pork quality

CHAPTER 3. Genetic and Phenotypic Parameters for Carcass and Meat Quality Traits in Commercial Crossbred Pigs[1]

3.1. INTRODUCTION

Meat quality and carcass yield are growing in importance for meat processors, packers and consumers because of their high economic value. Processors are normally paid for the weight of the carcass, and not for the weight of each primal cut. More recently, the pork industry is moving towards using a grading system meeting the demands of processors, packers, and consumers based on different primal cut weights (van Wijk et al., 2005). Specific goals of breeding strategies are changed because of alterations in the price of each component of the carcass. However, assessing meat quality on a routine basis is difficult and expensive for processors.

Anecdotally, many pork producers have been particularly attentive to lean meat content as well as to marbling and quality grade to better meet consumer demands. Consequently, carcass and meat quality traits are of increasing relevance for the pig industry. This has led to the development of breeding objectives that include pork quality traits where increasing muscle tissue and decreasing fat are two major objectives of swine breeding programs. Meat quality traits are low-to-moderately heritable while carcass composition traits are highly heritable (Ciobanu et al., 2011).

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Genetic improvement of meat and carcass quality in swine breeding program requires estimating the genetic and phenotypic parameters of these traits. In order to estimates of heritabilities for meat quality and carcass characteristics and genetic correlations between these economically important traits are limited but have received attention recently (Newcom et al., 2002; van Wijk et al., 2005). Study of genetic parameters for pork quality and carcass characteristics is required for Canadian swine populations to implement selection programs that emphasize product quality. The objectives of this study were 1) to estimate heritabilities for various carcass and pork quality traits and 2) to estimate phenotypic and genetic correlations between them in commercial crossbred pigs.

3.2. MATERIALS AND METHODS

The hogs used in this study were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines.

3.2.1. Animals and Management

The commercial crossbred pigs used in this study were a combination of full and half sib progeny groups representing a multi-generation family structure drawn from breeding populations (Hypor Inc., and Genesus Genetics, Canada). These pigs were progeny from 139 Duroc boars bred to 429 F1 hybrid Landrace × Large White sows. These breeds are representative of a large proportion of the Canadian pork production herd. Duroc is being increasingly used for its increased marbling, pH and darker colour (redness) of the meat as a

result of retailer demand for improved meat quality (Plastow et al., 2005). Pedigree information of 15 ancestral generations comprising 9,439 individuals was available.

3.2.2. Slaughter and Carcass Evaluation

Approximately half of the pigs were born and raised in a farm managed by Hypor in Regina, SK, Canada and rest of them in a farm managed by Genesus Genetics in Oakville, MB, Canada. Piglets were born and raised under commercial finishing conditions with *ad libitum* access to a canola, wheat, barley, soybean diet and water. Males were castrated at 3 to 5 d after birth. The pigs were grown to a final test weight of 115 kg. All pigs were shipped to a provincial abattoir near Brandon, Manitoba, on the Wednesday of each week after they completed their test period. Average slaughter weight was 124 kg live weight, and the average age at slaughter was 160 days. Animals were shipped to the slaughter plant on a weekly basis with the Hypor slaughter groups ranging from 20 to 35 pigs and the Genesus slaughter groups ranging from 20 to 25 pigs. Pigs were housed overnight at the abattoir with *ad libitum* access to water. All animals in a batch were slaughtered the following morning and the carcass traits were collected within 24 h post mortem. Slaughter date was recorded for all animals, and this was used to assign a slaughter batch (n = 88).

Hot carcass weight (**HCW**), which was defined as the weight of the carcass including the head, leaf fat and kidneys on the carcass, was recorded on the kill floor immediately after animals were stunned, exsanguinated, scalded, de-haired, dressed and the carcass was split. Following an 18 to 24 h chill, the cold carcass weight (**CCW**), defined as the weight of the carcass with the head, leaf fat, kidneys, and front feet, and the carcass length (**CLEN**), defined as

the distance from the anterior edge of the first rib at its junction with the vertebral column to the anterior edge of the pubic symphysis (Figure 3.1) were recorded. At this point, the carcasses were broken into the primal cuts (ham, shoulder, belly, and loin). The loin was further broken into the front (anterior portion), a 3-rib sample, a 1-inch chop, a 4-rib sample, and a back (posterior portion). The 3-rib and 4-rib segments were frozen in preparation for shipping to the University of Alberta's Meat Science Laboratory. The chop was removed at the level of the 3rd and 4th last rib (which corresponded to the Canadian grading site) and was used to determine: (a) the area of the *longissimus dorsi* muscle (**LEA**) – determined by using a grid calibrated in 1 square centimeter squares (Figure 3.2); (b) subcutaneous fat (**FD**) and loin depth (**LD**) – measured by a ruler 50 mm off the midline, perpendicular to the skin and measured in millimeters (Figure 3.3); (c) texture score (**TEXS**) measured as a tactile rating that assessed the degree of firmness and exudation or weeping of the *longissimus dorsi* muscle on a subjective 5-point scale (1= extremely soft and weeping; 5 = very firm and dry; a score of 3 being normal) to determine if the loin was pale, soft and exudative (PSE); and (d) subjective marbling score (**CMAR**; 1 to 6, with 0 = devoid, 1 = practically devoid, 2 = trace amount of marbling, 3 = slight, 4 = small, 5 = moderate, 6 = abundant) as determined by the National Swine Improvement Federation (NSIF) marbling charts (NSIF, 1997).

Primal cuts of ham, loin, shoulder and belly were weighed and further dissected into trimmed subprimal cuts. The weights of the untrimmed ham, subdivisions of the loin (front, 3-rib sample, chop, 4-rib sample, and back), shoulder, and belly were combined to determine the untrimmed side weight (**USW**). Hams with foot attached or untrimmed (**UHAM**), and untrimmed shoulders (**USH**) were removed from the side weight (Figures 3.4 and 3.5). Belly (**UBEL**) and loin (**ULOIN**) were separated from each other and weighed (Figure 3.6).

Untrimmed loin weight was recorded as the sum of the weights of the front, chop, 3-rib sample, and 4-rib sample, and back of the loin. After the loin chop was evaluated as previously described, it was defatted and deboned in preparation for drip loss determination. Hams were processed to a bone-in ham without fat cover, and with the foot, tail bone (**THAM**). The commercial fat trim of the loin was obtained by a commercial trim of the front and back portions and using that percentage to estimate the trimmed weight on the chop and the 3-rib and 4-rib samples, these were then combined with the trimmed weights of the front and back to obtain the trimmed weight of the entire loin (**TLOIN**). It should be noted that the 3-rib and 4-rib samples had to be untrimmed when they arrived at the Meat Science Laboratory. The neck bones and jowl were removed from the shoulder and the picnic (**PICN**) and butt (**BUTT**) were separated by a cut made at right angles to the long axis of the shoulder at a distance approximately 2.54 cm below the exposed surface of the blade (scapula) bone (Figure 3.7). The square cut bellies were trimmed (**TBEL**) and the ribs (**RIBS**) were removed (Figure 3.8).

3.2.3. Meat Quality Measurements

Meat quality measurements were taken in both the slaughterhouse and University of Alberta's Meat Science Laboratory and measurements were performed on both loin and ham. At the slaughterhouse, the front or anterior portion of the loin (*longissimus dorsi* muscle) was used in determining Minolta colour and ultimate or 24 h pH (**PHU**). Loin Minolta L*, a*, and b* (**LOINL**, **LOINA**, and **LOINB**) were taken on four sites on the fresh cut surface of a loin chop from the boneless center cut loin using a Minolta CR 310 colorimeter set at C illuminant (Minolta camera, Osaka, Japan – Figure 3.9). An ultimate pH measurement was taken in the loin

muscle at two locations at 24 h postmortem. Meat quality measurements taken on the ham included Minolta L*, a*, and b* values on the fresh cut surface of the inside ham muscle on the *gluteus medius* (**HGML**, **HGMA**, and **HGMB**), *quadriceps femoris* (**HQFL**, **HQFA**, and **HQFB**), and *iliopsoas* muscles (**HILL**, **HILA**, and **HILB –** Figure 3.10). Drip loss (**DL**) determination at the abattoir involved weighing the 1-inch defatted and deboned loin chop and placing it on a stainless steel grid within a container for 48 h at 4°C. At the end of the 48 h, the meat samples were lightly blotted dry with a soaker pad and weighed. The difference in weight was expressed as a percentage of the initial weight to determine drip loss.

At 4 days postmortem, frozen 3-Rib and 4-Rib samples of the loin of each carcass were packed in coolers and transported by overnight courier to Meat Science Laboratory at the University of Alberta for further meat quality analyses. Prior to analysis, the pork loin was removed from frozen storage and allowed to thaw at 4 °C for 61 h. Each thawed pork loin was removed from the vacuum package bag and was weighed and recorded as whole loin weight, (**WLW**), defined as the weight of 3-Rib and 4-Rib of the loin received at University of Alberta containing meat, fat and bone. The thick backfat was taken from the loin, was weighed and recorded as backfat weight (**BFW**). Then, rib eye was removed from the loin and its weight was recorded as rib eye weight (**REAW**), and it was used for the meat quality assays. A 1-inch chop was removed from the tail end of the loin section and refrigerated at 4 °C for 1 h. Rib eye Minolta L*, a*, and b* values (**REAL**, **REAA**, and **REAB**), were taken on three sites of the chop using a commercial color meter (CR400, Konica-Minolta, Osaka, Japan) on a D 65 light setting which mimics daylight. To measure cooking loss (**CL**), a 200 g roast was cooked in a 71^{o}C water-bath and weighed before and after cooking and cooking loss was recorded as the percentage of weight change divided by the initial weight multiplied by 100. Shear force (**SHF**)

was the mean of six 1 cm^2 cores cut from the roast that had been cooked and then refrigerated overnight at 4 °C. The remainder of the pork loin section was physically dissected into muscle and fat, recorded as rib trim weight (**RTW**), and bone, recorded as bone weight (**BOW**).

3.2.4. Statistical and Genetic Analyses

There were 2,100 pigs with meat quality and carcass data. The significance of the fixed effects and covariates for each trait was determined using the REML procedure of ASREML 3.0 software (Gilmour et al., 2012), and different significant ($P < 0.1$) fixed factors for each trait were remained in the subsequent mixed model analyses. The significance of different random terms in the model was determined by likelihood ratio test using ASREML 3.0 software (Gilmour et al., 2012). It was confirmed that the effects of common litter were not significant ($P > 0.05$) for meat quality and carcass traits, except for HCW, CCW, LEA, PHU and DL. Maternal genetic effects were tested in a similar manner and were shown not to be significant ($P > 0.05$).

Genetic and phenotypic (co)variances were estimated for commercial crossbred populations using a pairwise bivariate animal model using ASREML 3.0 software (Gilmour et al., 2012). The animal model included random additive polygenic effects in the final model for all traits, and random litter effect for some traits as presented in Table 3.2. Birth weight, whole loin weight received at Meat Science Laboratory, cold carcass weight, and slaughter age were included in the model as linear covariates if they were significant ($P < 0.05$) as presented in Table 3.2. Company, sex, and slaughter batch were included in the model as fixed effects as presented in Table 3.2. The model is given by:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_3 & 0 \\ 0 & Z_4 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where $\boldsymbol{y_1}$ and $\boldsymbol{y_2}$ are the vectors of phenotypic measurements for traits 1 and 2, respectively; $\boldsymbol{X_1}$ and $\boldsymbol{X_2}$ are the incidence matrices relating the fixed effects to vectors $\boldsymbol{y_1}$ and $\boldsymbol{y_2}$, respectively; $\boldsymbol{b_1}$and $\boldsymbol{b_2}$ are the vectors of fixed effects for traits 1 and 2, respectively; $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$ are the incidence matrices relating the phenotypic observations to the vector of polygenic ($\mathbf{a}$) effects for traits 1 and 2, respectively; $\boldsymbol{Z_3}$ and $\boldsymbol{Z_4}$ are the incidence matrices relating the phenotypic observations to the vector of common litter ($\boldsymbol{c}$) effects for traits 1 and 2, respectively; and $\boldsymbol{e_1}$ and $\boldsymbol{e_2}$ are the vectors of random residuals for the traits 1 and 2, respectively.

It was assumed that random effects were independent. In particular, the variances were assumed to be $V(a) = A\sigma_a^2$, $V(c) = I\sigma_c^2$, *and* $V(e) = I\sigma_e^2$; where $\boldsymbol{A}$ is the numerator relationship matrix, $\boldsymbol{I}$ is the identity matrix, σ_a^2 is a direct additive genetic variance, σ_c^2 is a common litter effect variance, and σ_e^2 is a residual variance. Heritability was estimated using variance components obtained from the bivariate analyses, and the average estimates of corresponding pairwise bivariate analyses were reported as the heritabilities:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

A preliminary univariate animal model for each trait was performed to obtain initial values of variance parameters that were then used in subsequent bivariate analyses. The initial values of covariance parameters between traits were obtained by multiplying their standard deviations by their phenotypic or genetic correlations. Pairwise bivariate analyses were performed separately for carcass and meat quality traits. The 2-trait animal model used to estimate (co)variance components, phenotypic and genetic correlations as well as the heritabilities was implemented in ASREML 3.0 (Gilmour et al., 2012).

3.3. RESULTS AND DISCUSSION

3.3.1. Means and standard deviations

Most of the traits were recorded on all individuals within group. Means, standard deviations, number of measurements per trait, minimum and maximum for each carcass and meat quality trait are given in Table 3.1. There are a total of 19 carcass and 24 meat quality traits analyzed in this study. Most of the carcass traits had 2,084 observations except for TBEL with 1,663, HCW and CCW with 2,086 observations. Most of the meat quality traits had 2,067 to 2,084 observations except for DL with 1,418 observations available for the analysis (Table 3.1). Furthermore, relevant fixed and random effects fitted in the mixed model analysis for carcass and meat quality traits are presented in Table 3.2.

3.3.2. Heritability estimates

Heritability estimates with their standard errors are presented in Tables 3.3 and 3.4 (diagonal elements). Several factors influence the heritability estimates which may include the end-point adjustment such as age or weight adjustment, sampling, population size, effect of heterosis on crossbred populations and the completeness of pedigree (Miar et al., 2014). Although a total of 44 heritabilities for Carcass (n=19) and meat quality (n=25) traits were presented in Tables 3.3 and 3.4 for completeness, we will mainly focus here on those new and rarely reported traits. Heritabilities for some traits reported extensively elsewhere will not be discussed unless it is useful to compare them with the present study.

Heritability estimates (± SE) for carcass traits were moderate to high except for firmness that was low, and ranged from 0.22 ± 0.08 for LEA to 0.63 ± 0.04, and 0.63 ± 0.06 for THAM, and ULOIN, respectively. Carcass traits generally have been reported as moderate to high heritable traits in previous studies (Stewart and Schinckel, 1991; Lo et al., 1992; Ducos, 1994; Gibson et al., 1998; Sonesson et al., 1998; Newcom et al., 2002; van Wijk et al., 2005). Primal and subprimal cuts weights were more heritable (0.51 on average) than subjective marbling score (0.23 ± 0.05). Heritability estimates for UBEL (0.49 ± 0.06) and TBEL (0.53 ± 0.06) were nearly identical. Heritability estimate for ULOIN was more heritable (0.63 ± 0.06) than TLOIN (0.52 ± 0.07). This was different for the UHAM that was less heritable (0.46 ± 0.06) compared to THAM (0.63 ± 0.04). The heritability estimates obtained for carcass traits are among the highest heritabilities estimated in this study. The high values of heritability for the carcass traits would indicate the significant potential for improving carcass merit traits in commercial crossbred pigs.

The heritability estimates for HCW and CCW were 0.28 ± 0.08, and 0.29 ± 0.08, respectively. Zumbach et al. (2008) reported low to moderate heritability of 0.14 and 0.28 for carcass weight in environments without and with heat stress, respectively, and this is the only literature available at the present. The moderate heritabilities for HCW and CCW indicate that genetic improvement for these traits is achievable through selection. Heritability estimates for basic carcass yield component traits were 0.31 ± 0.06, 0.41 ± 0.06, and 0.51 ± 0.07 for FD, LD, and CLEN, respectively. Backfat depth is the most studied trait among all carcass merit traits as it is related to overall carcass yield (Marcoux et al., 2007). For FD, the estimate in this study (0.31 ± 0.06) was lower than the average heritability (0.43) of many previous studies reported by Ciobanu et al. (2011). Heritability estimate of LD in the present study (0.41 ± 0.06) was close to the average (0.47) of many previous studies reported by Stewart and Schinckel (1991). For

CLEN, the estimate of heritability in this study (0.51 ± 0.07) was in agreement with the average (0.56 and 0.57) of all studies reviewed by Stewart and Schinckel (1991), and Ducos (1994), respectively. These moderate-to-high heritabilities would be expected because pig breeders have known that these carcass traits are easy to change by selection.

For LEA, the heritability estimate in the present study (0.22 ± 0.08) was lower than estimates by Suzuki et al. (2005) for ultrasound measurements of LEA in Duroc (0.41), and average estimate (0.47) of previous studies by Stewart and Schinckel (1991). The differences with previous studies may be due to using carcass measurement in the current study compared to ultrasound measurements in the previous studies. In addition to differences in measurement techniques, sample size and statistical models used for (co)variance estimation were also different from previous studies. Marbling is an estimate of intramuscular fat, which has been associated with increased sensory acceptance in cooked pork (Brewer et al., 2001). The moderate heritability of CMAR in this study (0.23 ± 0.05) suggested that genetic improvement of marbling might be possible. Intramuscular fat content can also influence sensory quality. Generally, as intramuscular fat content increases, the sensory chewiness score decreases, especially in pork with normal pH values (Lonergan et al., 2007). It appears that the estimate of CMAR in this study is within the range of previous reports. Most studies (Lo et al., 1992; Gibson et al., 1998; Sonesson et al., 1998; van Wijk et al., 2005) estimated a low to moderate (0.13 – 0.31) heritability for CMAR. The estimated heritability of TEXS in this study was 0.09 ± 0.04, indicating the presence of a small additive genetic effect on TEXS. The difference (0.09 vs. 0.20) between this study and van Wijk et al. (2005) may be due to the existence of heterosis in this crossbred population, different subjective measurement of firmness, and different statistical models used for (co)variance estimation.

Heritability estimates for primal and subprimal cuts weight were 0.55 ± 0.06, 0.46 ± 0.06, 0.63 ± 0.06, 0.55 ± 0.06, 0.49 ± 0.06, 0.63 ± 0.04, 0.52 ± 0.07, 0.53 ± 0.06, 0.44 ± 0.06, 0.29 ± 0.05, and 0.32 ± 0.06, for USW, UHAM, ULOIN, USH, UBEL, THAM, TLOIN, TBEL, PICN, BUTT, and RIBS, respectively. These heritabilities are among the highest in this study and were within the range of previous reports (Newcom et al., 2002; van Wijk et al. 2005), which presented a range of 0.40 to 0.57 for UHAM, 0.29 to 0.51 for ULOIN, 0.39 to 0.76 for THAM, 0.51 to 0.72 for TLOIN, and 0.51 for UBEL. However, limited studies on heritability estimation of primal and subprimal traits especially for USW, USH, UBEL, TBEL, PICN, BUTT, and RIBS, make it difficult to compare these results with literature values. The estimated heritabilities of these traits were moderate or high indicating great opportunities to improve these traits in swine breeding programs.

Heritability estimates (± SE) for meat quality traits varied from 0.10 ± 0.04 for HQFB to 0.39 ± 0.06 for SHF. The heritability estimates for the traits related to water holding capacity were low to moderate including DL, PHU, and CL (0.21 ± 0.09, 0.15 ± 0.09, and 0.20 ± 0.05, respectively). Different measurements of rib eye weight had a moderate heritability, and ranged from 0.22 ± 0.06 for RTW to 0.38 ± 0.06 for BFW except for the bone weight of rib eye that was low (0.12 ± 0.05).

Ultimate pH is the most studied trait among all meat quality traits because it is associated with pork colour, drip loss and water-holding capacity and so it is a significant economic indicator (Bendall and Swatland, 1988). The estimated heritability of PHU in this study (0.15 ± 0.09) was within the range (0.07 – 0.39) reported previously (Cameron et al., 1990; De Vries et al., 1994; Hermesch et al., 2000a; Andersen and Pedersen, 2000; van Wijk et al., 2005; Ciobanu et al., 2011). This was close to the average estimate (0.21) of 33 studies reviewed by Ciobanu et

al. (2011). Ultimate pH in this study and van Wijk et al. (2005) were corrected for common litter environmental effects in contrast to the other studies. The heritability estimate for DL (0.21 ± 0.09) was within the range (0.01 to 0.31) of literature reports (De Vries et al., 1994; Sonesson et al., 1998; Hermesch et al., 2000a; van Wijk et al. 2005; Ciobanu et al., 2011), and it is close to the average estimate (0.16) of 10 studies reviewed by Ciobanu et al. (2011). For CL, the estimate in this study (0.20 ± 0.05) was in agreement with the average (0.16) of all studies reviewed by Ciobanu et al. (2011). Shear force, which evaluates the degrees of tenderness, had the highest heritability estimate (0.39 ± 0.06) among meat quality traits. Although the current estimate was higher than estimates (0.17 and 0.20) reported by Lo et al. (1992) and de Vries et al. (1994), respectively, it is close to the average (0.30) of all studies reviewed by Ciobanu et al. (2011).

Among the technological meat quality traits, color had the highest heritability, and ranged from 0.10 ± 0.05 to 0.38 ± 0.06 (average=0.25). Generally, the estimated heritabilities for the lightness of loin (0.31 ± 0.06) and rib eye area (0.28 ± 0.06) were in agreement with the average estimate (0.28) found in previous studies (Cameron, 1990; Hermesch et al., 2000a; van Wijk et al., 2005; Ciobanu et al., 2011). The estimated heritabilities for the redness of loin (0.36 ± 0.06) and rib eye area (0.26 ± 0.09) were lower than the range of published estimates (0.52 and 0.57) by Sonesson et al. (1998) and Andersen and Pedersen (2000), respectively. This might be due to different population structure and statistical models used for variance component estimations. For LOINB and REAB, the estimated heritabilities in this study (0.20±0.06, and 0.31±0.06, respectively) were higher than the estimate of redness of loin (0.15) published by van Wijk et al. (2005). It might be due to their adjustment for cold carcass weight, which was not significant in the current study. Furthermore, the estimate of heritability for REAB was higher than the estimate of heritability for LOINB in this study. This can be explained by the differences in the

average measurement of REAB, which was smaller than the average measurement of LOINB (2.81 *vs.* 15.07). This might be due to measuring of LOINB before freezing and early post-mortem and measuring of REAB after freezing and late post-mortem. The average estimated heritabilities for the lightness of ham (0.20) were close but higher than the estimate (0.11) by van Wijk et al. (2005). The average estimated heritabilities (0.27) for the redness of ham were in agreement with the estimate (0.26) published by van Wijk et al. (2005). For yellowness of ham, the average (0.12) estimate in this study was the same as reported by van Wijk et al. (2005). Heritability estimates for Minolta color traits measured on different muscles of ham were 0.22 ± 0.05, 0.38 ± 0.06, 0.12 ± 0.05, 0.19 ± 0.05, 0.27 ± 0.06, 0.10 ± 0.04, 0.32 ± 0.06, 0.16 ± 0.05, and 0.26 ± 0.06 for HGML, HGMA, HGMB, HQFL, HQFA, HQFB, HILL, HILA, and HILB, respectively. To our knowledge, no heritability estimates for Minolta color traits measured on the *gluteus medius*, *quadriceps femoris*, and *iliopsoas* muscles were previously available for comparison and would be worth further investigation. Heritability estimates for different weights of rib eye area were 0.28 ± 0.06, 0.31 ± 0.06, 0.38 ± 0.06, 0.22 ± 0.06, and 0.12 ± 0.05, for WLW, REAW, BFW, RTW, and BOW, respectively. Again, these estimates are new in the present study, and no estimates were available in literature, and warrant further investigation. Low-to-moderate heritabilities of pork quality indicate opportunities to improve these traits through genomic selection.

3.3.3. Correlations among Traits

The phenotypic and genetic correlations and their standard errors are reported in Tables 3.3, 3.4, 3.5 and 3.6. Generally, almost all of the phenotypic correlations and most of the genetic

correlations were significant ($P < 0.05$). Although presented for completeness, phenotypic correlations will not be discussed because they are of little interpretive value.

3.3.3.1. Correlations among Carcass Traits

The phenotypic and genetic correlations among carcass traits are presented in Table 3.3. Almost all of the phenotypic and most of the genetic correlations among carcass traits were significant ($P < 0.05$). Generally, high genetic correlations were found between HCW and primal and sub-primal weights, and other carcass traits except for FD (0.39 ± 0.15) and TBEL (0.42 ± 0.17), which were moderate. A strong negative genetic correlation was observed between HCW and TEXS (-0.61 ± 0.27). Cold carcass weight had high average (0.81) genetic correlations with primal, sub-primal and carcass traits. Cold carcass weight had negative genetic correlation only with TEXS (-0.63 ± 0.26), which was similar to that of HCW. Unfortunately, no genetic correlations were available for comparisons in the literature for HCW and CCW and suggest a need for further validation.

Backfat depth was moderately correlated with LD (-0.34 ± 0.12), CMAR (0.33 ± 0.14), USW (0.28 ± 0.11), USH (0.28 ± 0.11), and UBEL (0.30 ± 0.11). Loin depth was highly correlated with LEA (0.78 ± 0.05), and ULOIN (0.53 ± 0.16) but moderately correlated with TLOIN (0.44 ± 0.10). Moderate genetic correlations were found between LD with TEXS (-0.40 ± 0.20), USW (0.37 ± 0.10), UHAM (0.49 ± 0.09), and BUTT (0.31 ± 0.12), but the correlations between LD with USH (0.29 ± 0.10), and THAM (0.24 ± 0.09) were in a low range. Carcass length was moderately to highly correlated with LEA (0.47 ± 0.14), USW (0.80 ± 0.05), UHAM (0.71 ± 0.06), ULOIN (0.56 ± 0.09), USH (0.69 ± 0.06), UBEL (0.69 ± 0.06), THAM (0.31 ±

0.07), TLOIN (0.56 ± 0.08), BUTT (0.36 ± 0.11), and RIBS (0.52 ± 0.11). A negative genetic correlation was found between LEA and TEXS (-0.56 ± 0.28) indicating the adverse effect of selection for LEA on pork quality. Moderate to high genetic correlations were estimated between LEA with USW (0.72 ± 0.12), UHAM (0.75 ± 0.12), ULOIN (0.66 ± 0.13), USH (0.57 ± 0.13), UBEL (0.50 ± 0.17), THAM (0.42 ± 0.13), TLOIN (0.79 ± 0.12), BUTT (0.69 ± 0.16), and RIBS (0.56 ± 0.19).

TEXS is used to assess the degree of firmness and exudation or weeping of the *longissimus dorsi* muscle and was negatively correlated with most of the primal and sub-primal cut weights including HCW (-0.61 ± 0.27), CCW (-0.63 ± 0.26), LD (-0.40 ± 0.20), LEA (-0.56 ± 0.28), USW (-0.48 ± 0.18), UHAM (-0.56 ± 0.17), USH (-0.47 ± 0.17), THAM (-0.38 ± 0.17), BUTT (-0.61 ± 0.21), and RIBS (-0.49 ± 0.23). These results showed that deterioration of pork quality may have occurred over many generations through the selection for increasing carcass weight. In addition, unfavorable genetic correlations between TBEL and PICN subprimal cuts with DL indicated adverse effect on water holding capacity. Carcass marbling, which is associated with eating quality and consumer demand (Brewer et al., 2001), was correlated with HCW (0.63 ± 0.22), CCW (0.59 ± 0.21), FD (0.33 ± 0.14), USW (0.35 ± 0.13), USH (0.42 ± 0.12), and THAM (0.29 ± 0.11) but there was no correlation with LD (0.01 ± 0.15), CLEN (0.03 ± 0.14), LEA (0.05 ± 0.20), TEXS (0.04 ± 0.24), and the remainder of the sub-primal weights (0.14 on average).

The primal and subprimal cut weights were moderately to highly correlated with each other and ranged from (0.32 ± 0.11) for THAM-RIBS to (0.96 ± 0.01) for TLOIN-ULOIN, with a few correlations being exceptions with low and non-significant ($P > 0.05$) correlations. Untrimmed side weight had a moderate to high correlation with all of the primal and subprimal

cuts except with TBEL, which was low (0.22 ± 0.09). Both primal cuts for loin and ham were highly correlated with their subprimal cuts, although the correlation between ULOIN and TLOIN was higher (0.96 ± 0.01) than correlation between UHAM and THAM (0.59 ± 0.05) which might be due to differences in fat deposition in hams and loins. These results were in agreement with van Wijk et al. (2005) who reported the genetic correlations of 0.60 for ULOIN-TLOIN and 0.61 for UHAM-THAM. Newcom et al. (2002) showed high genetic correlations for UHAM-THAM (0.89) and ULOIN-TLOIN (0.90). In contrast, UBEL had a low (0.21 ± 0.09) genetic correlation with trimmed belly (TBEL), which might be due to more fat deposition in belly. Untrimmed ham weight had moderate to high genetic correlations with all of the subprimal cuts (0.64 on average), excepting with TBEL that had a low correlation (0.21 ± 0.10). A few reports presented genetic correlations between ham and loin primal and subprimal cuts but no genetic correlations were available in the literature for others (Newcom et al., 2002; van Wijk et al., 2005).

The valuable sub-primal cuts of the carcass are the hams and loins and so their weights are most important to overall carcass value. A high genetic correlation was found between UHAM and ULOIN (0.77 ± 0.12), and it was higher than the correlation observed between THAM and TLOIN (0.18 ± 0.07). This result showed that selection for high ham yield (UHAM) would lead to high loin yield (ULOIN). However, selection for high trimmed ham (THAM) may not necessarily increase high trimmed loin (TLOIN) due to their low genetic correlation. In addition, ULOIN was correlated with UBEL (0.83 ± 0.03), BUTT (0.33 ± 0.10), and RIBS (0.43 ± 0.11). The high genetic correlation between ULOIN and UBEL confirmed that selection for loin weight would increase belly yield. There were moderate to high genetic correlations between USH with UBEL (0.44 ± 0.08), THAM (0.57 ± 0.04), PICN (0.36 ± 0.09), BUTT (0.47 ± 0.09), and RIBS (0.49 ± 0.11) and a low genetic correlation was found with TBEL (0.18 ±

0.09). A high genetic correlation was observed between UBEL and TLOIN (0.87 ± 0.03). Genetic correlation between TBEL and PICN was high (0.91 ± 0.07). Ribs weight and BUTT had moderate to high genetic correlations with those primal and subprimal weights. Genetic correlations among primal and subprimal cuts were limited in the literature, most likely because these traits are difficult and expensive to measure.

3.3.3.2. Correlations among Meat Quality Traits

The phenotypic and genetic correlations among meat quality traits are presented in Table 3.4. Most of the phenotypic and genetic correlations among meat quality traits were significant ($P < 0.05$). Strong negative genetic correlations were found between PHU with CL (-0.62 ± 0.26), and DL (-0.99 ± 0.49). Ciobanu et al. (2011) reported the genetic correlations of -0.68 for PHU-CL and -0.71 for PHU-DL as the average correlations of many previous studies, which were in good agreement with our estimates. These high genetic correlations were in the range of -0.82 to -0.45 for PHU-CL and -0.99 to -0.50 for PHU-DL (De Vries et al., 1994; Sellier, 1998; Gibson et al., 1998; Hermesch et al., 2000b). This substantiates evidence of the value of muscle pH as an indicator trait for drip loss and cooking loss in crossbred pig genetic improvement programs to improve pork quality traits and reduce the cost of DL and CL measurement.

Estimated genetic correlations between DL with LOINL (0.55 ± 0.24), and LOINA (0.42 ± 0.19) were moderate to high, whereas corresponding correlations between DL and Minolta L* and a* measurements of ham muscles were not significant (0.27 and 0.08, respectively on average). Sellier (1998) and van Wijk et al. (2005) reported moderate genetic correlations between DL and LOINL (0.49 and 0.38, respectively), which were in agreement with this study.

No genetic correlation between DL and color of ham was found, which might be due to the measurement of DL on loin. DL had positive high correlation with CL (0.52 ± 0.20) but negative correlation with SHF (-0.38 ± 0.18). A high genetic correlation between DL and CL was reported by Sellier (1998) that was in agreement with this study (0.66).

Shear force assesses the degree of toughness and was highly correlated with CL (0.58 ± 0.13). This result suggested that genetic improvement for CL by selecting for reduced cooking loss may result in more tender meat. SHF was positively correlated with the Minolta A* measurements of ham including HGMA (0.35 ± 0.13) and HQFA (0.45 ± 0.14), and was negatively correlated with the Minolta measurements of rib eye area including REAL (-0.33 ± 0.14) and REAB (-0.35 ± 0.13). No information was found for Minolta color traits measured on the *gluteus medius*, *quadriceps femoris*, and *iliopsoas* muscles in literature. The Minolta color measurements on the loin were moderately to highly correlated with the corresponding measurements on the ham (*gluteus medius, quadriceps femoris, and iliopsoas*) muscles except for the Minolta b* between LOINB and HGMB. No literature values were found for these traits and to our awareness; this is the first report for these traits. Minolta L* were negatively correlated with the Minolta a* measurements for both ham and loin, and ranged from (-0.36 ± 0.16) for REAL-REAA to (-0.46 ± 0.17) for HQFL-HQFA. The Minolta L* for both ham and loin were highly correlated with Minolta b* values, and ranged from (0.51 ± 0.12) for LOINL-LOINB to (0.92 ± 0.03) for HILL-HILB and were in good agreement with the average estimate of 0.81 reported by van Wijk et al. (2005).

Minolta a* of ham muscle on the *gluteus medius* was negatively correlated with LOINL (-0.30 ± 0.14); however, HQFA and HILA were not correlated with LOINL. The correlations between PHU and the color measurements showed a moderate to high negative genetic

correlations, ranged from (-0.37 ± 0.16), with LOINA to (-0.98 ± 0.35) with HQFB. This substantiates evidence of the value of PHU as an indicator trait for color measurements on either loin or ham.

3.3.3.3. Correlations between Carcass and Meat Quality Traits

The phenotypic and genetic correlations between carcass and pork quality traits are presented in Tables 3.5 and 3.6, respectively. Generally, some of the phenotypic and genetic correlations were significant ($P < 0.05$). Low negative genetic correlations were estimated for HCW and CCW with meat redness of loin and ham *gluteus medius*. No correlation was found for FD with either drip loss or PHU. The estimated correlations for FD with pork lightness of loin and ham *gluteus medius* were of favorable low to moderate magnitude (-0.25 ± 0.12, and -0.39 ± 0.14, respectively). These indicated that pork quality was not negatively affected by selection against backfat depth. There was a low correlation between LD and SHF (-0.24 ± 0.12). In addition, LD and LEA were similarly and highly negatively correlated with PHU (-0.66 ± 0.17, -0.78 ± 0.28, respectively). Moderate correlations were observed between LD and LEA with lightness of loin (0.36 ± 0.12, 0.42 ± 0.12) and ham (0.31, 0.22 on average, respectively). This indicates that single-trait selection on loin depth and loin eye area may lead to undesirable low pH pork with pale color.

Favorable low to moderate negative genetic correlations were obtained for CLEN with both lightness of loin and ham (-0.29 ± 0.11, -0.12 on average) and PHU (0.38 ± 0.17). Firmness was moderately to highly correlated with lightness of loin and ham (-0.38 ± 0.19, and -0.42 on average) and DL (-0.72 ± 0.26). This indicates the value of subjective texture score as an

indicator trait for meat water-holding capacity. Carcass marbling was lowly correlated with all of the meat quality traits. Low-to-moderate correlations were estimated for PHU and DL for most of the primal and subprimal cuts except for TLOIN that was highly correlated with PHU (-0.68 ± 0.23). In addition, the correlations of the color traits for most of the primal and subprimal cuts were of favorable moderate to high magnitude. Untrimmed loin weight and TLOIN were lowly to moderately correlated with LOINL (0.25 ± 0.11 and 0.34 ± 0.12), respectively, which were higher than correlations of UHAM and THAM with lightness of ham (both averaging on 0.21). The Minolta color measurements were also lowly to moderately and favorably correlated with most of the primal and subprimal cut weight, except for HQFB, which was found to be unfavorably correlated with TLOIN. Primal and subprimal weights were favorably and lowly correlated with DL, except for TBEL and PICN, which were found to be unfavorably correlated with DL (-0.46 ± 0.14, and -0.36 ± 0.15, respectively).

To our knowledge, no literature exists that presents correlations of primal and subprimal cuts except for loin and somewhat ham with pork quality traits. This study showed that pork quality traits had favorable genetic relationships with the primal and subprimal weights. This indicated that selection for primal and subprimal cut weight would not negatively affect pork quality. van Wijk et al. (2005) is the only literature that presented genetic relationships between loin and ham primal and subprimal cuts with pork quality traits which were similar to this study. Our study confirmed the results by van Wijk et al. (2005) that favorable correlations between cut weight and meat quality traits are in contrast to the general perception, which is indicating the negative relationship between cut weights and pork quality traits.

3.4. IMPLICATIONS

Measurement of carcass and meat quality traits is difficult, expensive, can only be performed post-mortem, and is destructive to the sample. Therefore, selection of purebreds based on crossbred performance for these traits would be useful to help improving pure lines of pigs to produce improved pork quality from commercial crossbred pigs without the need for measurements on pure lines. Estimates of genetic parameters for carcass, and meat quality traits in crossbred pigs will provide not only insight into the biological basis of these traits but also a valuable reference to develop efficient genetic improvement programs for these traits. Genetic parameters obtained herein are valuable for the design of a breeding program emphasizing product quality in Canadian swine populations, especially with the new parameters for traits that have not previously been studied. Furthermore, the use of pH is suggested as an effective indicator for DL and CL of meat. It was concluded that selection for increasing primal and subprimal cut weights with better pork quality may be possible. In addition, moderate to high heritability of carcass traits would indicate a potential opportunity for improving carcass merit traits in commercial crossbred pigs. In addition, the high cost of data collection and low-to-moderate heritability of meat quality traits provide the opportunities to improve them through genomic efforts.

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Table 3.1: The descriptive statistics for carcass and meat quality traits: abbreviations, number of animals per trait (n), means, SD, minimum (Min.) and maximum (Max.) values

Trait	Abbreviation	n	Mean	SD	Min.	Max.
		Carcass traits				
Hot carcass weight, kg	HCW	2086	93.12	9.13	64.60	130.00
Cold carcass weight, kg	CCW	2086	80.58	8.02	55.50	115.30
Backfat depth, mm	FD	2084	14.42	4.00	6.00	32.00
Loin depth, mm	LD	2084	68.46	5.50	52.00	88.00
Carcass length, cm	CLEN	2084	83.43	2.78	52.30	92.40
***Longissimus dorsi* muscle area, cm^2**	LEA	2084	53.20	5.91	35.00	74.50
Texture score	TEXS	2084	3.02	0.37	1.00	4.00
Carcass marbling score	CMAR	2084	2.91	1.03	1.00	6.00
Untrimmed side weight, kg	USW	2084	39.85	3.98	27.25	57.01
Untrimmed ham weight, kg	UHAM	2084	11.04	0.97	8.41	15.09
Untrimmed loin weight, kg	ULOIN	2084	14.56	5.07	7.12	29.37
Untrimmed shoulder weight, kg	USH	2084	9.49	1.82	5.23	15.98
Untrimmed belly weight, kg	UBEL	2084	8.29	1.38	4.39	12.71
Trimmed ham weight, kg	THAM	2084	8.29	1.38	4.39	12.71
Trimmed loin weight, kg	TLOIN	2084	7.53	3.70	1.52	13.51
Trimmed belly weight, kg	TBEL	1663	11.33	2.92	6.24	18.76
Trimmed picnic shoulder weight, kg	PICN	2084	7.02	2.53	1.76	14.40
Butt shoulder weight, kg	BUTT	2084	4.30	0.51	2.77	6.53
Ribs weight, kg	RIBS	2084	3.04	1.10	1.05	5.84
		Meat quality traits				
Whole loin weight [a], kg	WLW	2067	1.53	0.24	0.94	2.61
Rib eye weight [a], kg	REAW	2077	0.60	0.10	0.25	0.99
Backfat weight [a], kg	BFW	2074	0.35	0.11	0.105	1.41
Rib trim weight [a], kg	RTW	2071	0.35	0.07	0.17	0.87
Bone weight [a], kg	BOW	2077	0.17	0.03	0.08	0.36
Cooking loss [a], %	CL	2073	26.69	3.26	11.65	53.74
Minolta L* rib eye area [a]	REAL	2075	44.45	2.84	30.55	56.85
Minolta a* rib eye area [a]	REAA	2075	7.81	1.21	3.39	11.94
Minolta b* rib eye area [a]	REAB	2075	2.81	1.21	-1.54	7.48
Shear force, newton [a]	SHF	2074	49.02	1.29	21.62	118.00
Minolta L* loin	LOINL	2084	48.42	2.84	39.83	60.50
Minolta a* loin	LOINA	2084	6.18	1.60	2.00	12.43
Minolta b* loin	LOINB	2084	15.07	2.03	9.10	22.35
pH ultimate	PHU	2084	5.73	0.18	5.28	6.36
Minolta L* ham *gluteus medius*	HGML	2084	45.35	2.40	37.80	54.20
Minolta a* ham *gluteus medius*	HGMA	2084	6.75	1.24	2.40	10.90
Minolta b* ham *gluteus medius*	HGMB	2084	13.78	1.20	9.60	17.70
Minolta L* ham *quadriceps femoris*	HQFL	2084	50.06	3.38	36.30	62.30
Minolta a* ham *quadriceps femoris*	HQFA	2084	4.69	1.59	0	17.70

Minolta b* ham *quadriceps femoris*	HQFB	2084	13.91	1.60	9.20	19.50
Minolta L* ham *iliopsoas*	HILL	2084	42.79	2.80	32.60	54.90
Minolta a* ham *iliopsoas*	HILA	2084	19.72	1.80	12.00	25.80
Minolta b* ham *iliopsoas*	HILB	2084	16.99	1.70	11.30	22.20
Drip loss, %	DL	1418	1.49	0.19	0.72	2.14

[a] *All information is from the rib eye muscle received at the University of Alberta's Meat Science Laboratory.*

Table 3.2: Significance of the fixed and random effects included in the models for the analysis of carcass and meat quality traits

Trait	Fixed Effects						Random Effects		
	Company	Sex	Batch	Age	WLW[1]	CCW[2]	Dam	Litter	Animal
				Carcass traits					
Hot carcass weight	**	**	**	**	-	-	NS	**	✓
Cold carcass weight	**	**	**	**	-	-	NS	**	✓
Backfat depth	NS	**	*	NS	-	-	NS	NS	✓
Loin depth	**	**	**	NS	-	-	NS	NS	✓
Carcass length	**	**	**	**	-	-	NS	NS	✓
***Longissimus dorsi* muscle area**	**	**	**	**	-	-	NS	**	✓
Texture score	**	NS	**	-	-	-	NS	NS	✓
Carcass marbling score	NS	**	**	-	-	-	NS	NS	✓
Untrimmed side weight	**	**	**	**	-	-	NS	NS	✓
Untrimmed ham weight	**	NS	**	**	-	-	NS	NS	✓
Untrimmed loin weight	**	**	**	**	-	-	NS	NS	✓
Untrimmed shoulder weight	**	**	**	**	-	-	NS	NS	✓
Untrimmed belly weight	**	**	**	**	-	-	NS	NS	✓
Trimmed ham weight	**	NS	**	**	-	-	NS	NS	✓
Trimmed loin weight	**	NS	**	**	-	-	NS	NS	✓
Trimmed belly weight	**	**	**	**	-	-	NS	NS	✓
Trimmed picnic shoulder weight	**	**	**	**	-	-	NS	NS	✓
Butt shoulder weight	**	**	**	**	-	-	NS	NS	✓
Ribs weight	*	*	**	**	-	-	NS	NS	✓
				Meat quality traits					
Whole loin weight	**	**	**	-	-	**	NS	NS	✓
Diaphragm weight	**	*	**	-	**	-	NS	NS	✓
Rib eye weight	NS	**	**	-	**	-	NS	NS	✓
Backfat weight	**	**	**	-	**	-	NS	NS	✓
Rib trim weight	**	**	**	-	**	-	NS	NS	✓
Bone weight	**	**	**	-	**	-	NS	NS	✓
Cooking loss	**	**	**	-	-	-	NS	NS	✓
Minolta L* rib eye area	*	**	**	-	-	-	NS	NS	✓
Minolta a* rib eye area	**	**	**	-	-	-	NS	NS	✓
Minolta b* rib eye area	**	**	**	-	-	-	NS	NS	✓
Shear force	NS	**	**	-	-	-	NS	NS	✓
Minolta L* loin	NS	*	**	-	-	-	NS	NS	✓
Minolta a* loin	*	**	**	-	-	-	NS	NS	✓
Minolta b* loin	**	**	**	-	-	-	NS	NS	✓
pH ultimate	**	NS	**	-	-	-	NS	**	✓
Minolta L* ham *gluteus medius*	NS	NS	**	-	-	-	NS	NS	✓
Minolta a* ham *gluteus medius*	NS	**	**	-	-	-	NS	NS	✓
Minolta b* ham *gluteus medius*	**	**	**	-	-	-	NS	NS	✓
Minolta L* ham *quadriceps femoris*	**	NS	**	-	-	-	NS	NS	✓

Minolta a* ham *quadriceps femoris*	**	NS	**	-	-	-	NS	NS	✓
Minolta b* ham *quadriceps femoris*	**	NS	**	-	-	-	NS	NS	✓
Minolta L* ham *iliopsoas*	**	**	**	-	-	-	NS	NS	✓
Minolta a* ham *iliopsoas*	**	NS	**	-	-	-	NS	NS	✓
Minolta b* ham *iliopsoas*	**	**	**	-	-	-	NS	NS	✓
Drip loss	**	NS	**	-	-	-	NS	**	✓

***P < 0.05; * P < 0.1; NS: Non-significant.*

Table 3.3: Estimates of genetic (below diagonal), phenotypic (above diagonal) correlations, heritabilities (diagonal) and their standard error of estimates among carcass traits

Trait[1]	HCW	CCW	FD	LD	CLEN	LEA	TEXS	CMAR	USW
HCW	***0.28±0.08*** [a]	**0.32±0.02**	**0.50±0.04**	**0.37±0.04**	**0.63±0.02**	**0.30±0.02**	**0.38±0.05**	**0.44±0.04**	**0.98±0.00**
CCW	**0.64±0.22**	***0.29±0.08***	**0.47±0.04**	**0.39±0.04**	**0.59±0.02**	**0.32±0.02**	**0.37±0.05**	**0.44±0.05**	**0.99±0.00**
FD	**0.39±0.15**	**0.35±0.16**	***0.31±0.06***	**-0.37±0.02**	0.01±0.03	**-0.38±0.02**	**-0.14±0.02**	**0.33±0.02**	**0.33±0.03**
LD	**0.77±0.24**	**0.78±0.21**	**-0.34±0.12**	***0.41±0.06***	**0.11±0.03**	**0.70±0.01**	-0.04±0.03	**-0.22±0.03**	**0.22±0.03**
CLEN	**0.89±0.06**	**0.77±0.15**	0.19±0.12	0.14±0.11	***0.51±0.07***	**0.35±0.05**	-0.01±0.03	-0.00±0.03	**0.61±0.02**
LEA	**0.70±0.26**	**0.63±0.26**	-0.24±0.13	**0.78±0.05**	**0.47±0.14**	***0.22±0.08***	**0.30±0.06**	0.13±0.08	**0.43±0.04**
TEXS	**-0.61±0.27**	**-0.63±0.26**	0.15±0.23	**-0.40±0.20**	-0.09±0.19	**-0.56±0.28**	***0.09±0.04***	**-0.11±0.02**	**-0.18±0.03**
CMAR	**0.63±0.22**	**0.59±0.21**	**0.33±0.14**	0.01±0.15	0.03±0.14	0.05±0.20	0.04±0.24	***0.23±0.05***	**0.16±0.03**
USW	**0.99±0.00**	**0.99±0.00**	**0.28±0.11**	**0.37±0.10**	**0.80±0.05**	**0.72±0.12**	**-0.48±0.18**	**0.35±0.13**	***0.55±0.06***
UHAM	**0.99±0.02**	**0.99±0.01**	0.07±0.13	**0.49±0.09**	**0.71±0.06**	**0.75±0.12**	**-0.56±0.17**	0.22±0.14	**0.93±0.02**
ULOIN	**0.70±0.07**	**0.73±0.07**	0.16±0.19	**0.53±0.16**	**0.56±0.09**	**0.66±0.13**	-0.32±0.27	0.02±0.14	**0.62±0.04**
USH	**0.99±0.01**	**0.98±0.02**	**0.28±0.11**	**0.29±0.10**	**0.69±0.06**	**0.57±0.13**	**-0.47±0.17**	**0.42±0.12**	**0.90±0.02**
UBEL	**0.96±0.0**	**0.96±0.03**	**0.30±0.11**	0.17±0.11	**0.69±0.06**	**0.50±0.17**	-0.25±0.19	0.19±0.13	**0.78±0.04**
THAM	**0.92±0.12**	**0.91±0.11**	0.10±0.09	**0.24±0.09**	**0.31±0.07**	**0.42±0.13**	**-0.38±0.17**	**0.29±0.11**	**0.52±0.06**
TLOIN	**0.88±0.08**	**0.88±0.08**	0.00±0.13	**0.44±0.10**	**0.56±0.08**	**0.79±0.12**	-0.28±0.19	-0.06±0.14	**0.57±0.06**
TBEL	**0.42±0.17**	**0.41±0.17**	0.15±0.11	-0.10±0.11	0.12±0.10	-0.01±0.16	-0.13±0.19	0.11±0.13	**0.22±0.09**
PICN	**0.70±0.16**	**0.70±0.16**	0.02±0.12	0.06±0.11	0.17±0.10	0.27±0.16	-0.23±0.19	0.18±0.13	**0.39±0.09**
BUTT	**0.78±0.13**	**0.82±0.13**	-0.15±0.14	**0.31±0.12**	**0.36±0.11**	**0.69±0.16**	**-0.61±0.21**	0.22±0.15	**0.60±0.08**
RIBS	**0.71±0.13**	0.17±0.38	-0.23±0.16	0.27±0.15	**0.52±0.11**	**0.56±0.19**	**-0.49±0.23**	0.15±0.17	**0.61±0.09**

Continued

Table 3.3. Continued

Traits[1]	UHAM	ULOIN	USH	UBEL	THAM	TLOIN	TBEL	PICN	BUTT	RIBS
HCW	**0.63±0.02**	**0.67±0.01**	**0.63±0.01**	**0.58±0.01**	**0.56±0.02**	**0.60±0.01**	**0.46±0.04**	**0.45±0.04**	**0.40±0.04**	**0.35±0.05**
CCW	**0.67±0.02**	**0.70±0.01**	**0.66±0.02**	**0.61±0.01**	**0.58±0.02**	**0.63±0.01**	**0.47±0.04**	**0.46±0.04**	**0.41±0.04**	**0.43±0.03**
FD	**0.12±0.03**	**0.38±0.05**	**0.32±0.03**	**0.31±0.03**	**0.09±0.03**	0.03±0.03	**0.14±0.03**	0.03±0.03	-0.01±0.03	0.01±0.03
LD	**0.32±0.03**	**0.41±0.05**	**0.11±0.03**	**0.12±0.03**	**0.22±0.03**	**0.35±0.03**	0.01±0.03	**0.13±0.03**	**0.19±0.03**	**0.17±0.03**
CLEN	**0.52±0.02**	**0.53±0.04**	**0.50±0.02**	**0.51±0.02**	**0.36±0.03**	**0.52±0.03**	**0.16±0.03**	**0.24±0.03**	**0.29±0.03**	**0.39±0.03**
LEA	**0.46±0.03**	**0.45±0.04**	**0.35±0.05**	**0.39±0.05**	**0.40±0.04**	**0.51±0.03**	**0.31±0.06**	**0.35±0.05**	**0.35±0.04**	**0.33±0.05**
TEXS	**-0.13±0.03**	**-0.17±0.03**	**-0.14±0.03**	**-0.15±0.03**	**-0.07±0.03**	**-0.15±0.03**	**-0.07±0.02**	**-0.07±0.02**	**-0.07±0.02**	**-0.11±0.03**
CMAR	0.04±0.03	**0.08±0.04**	**0.22±0.03**	**0.12±0.03**	**0.07±0.03**	-0.04±0.03	**0.06±0.02**	0.02±0.02	0.03±0.02	**0.08±0.03**
USW	**0.88±0.01**	**0.75±0.01**	**0.86±0.01**	**0.83±0.01**	**0.62±0.02**	**0.70±0.02**	**0.29±0.03**	**0.42±0.03**	**0.47±0.02**	**0.48±0.03**
UHAM	***0.46±0.06***	**0.66±0.03**	**0.70±0.02**	**0.74±0.01**	**0.70±0.01**	**0.63±0.02**	**0.24±0.03**	**0.39±0.03**	**0.43±0.02**	**0.43±0.03**
ULOIN	**0.77±0.12**	***0.63±0.06***	**0.44±0.03**	**0.74±0.01**	**0.07±0.02**	**0.91±0.01**	**0.13±0.03**	**0.22±0.03**	**0.26±0.03**	**0.42±0.03**
USH	**0.83±0.04**	0.15±0.11	***0.55±0.06***	**0.56±0.02**	**0.60±0.02**	**0.36±0.03**	**0.21±0.03**	**0.42±0.03**	**0.49±0.02**	**0.39±0.03**
UBEL	**0.71±0.05**	**0.83±0.03**	**0.44±0.08**	***0.49±0.06***	**0.29±0.03**	**0.72±0.02**	**0.33±0.03**	**0.33±0.03**	**0.36±0.03**	**0.47±0.03**
THAM	**0.59±0.05**	**-0.26±0.08**	**0.57±0.04**	0.02±0.08	***0.63±0.04***	**0.21±0.03**	**0.21±0.03**	**0.31±0.03**	**0.34±0.03**	**0.32±0.04**
TLOIN	**0.53±0.08**	**0.96±0.01**	0.15±0.10	**0.87±0.03**	**0.18±0.07**	***0.52±0.07***	**0.09±0.03**	**0.21±0.03**	**0.28±0.03**	**0.44±0.03**
TBEL	**0.21±0.10**	-0.02±0.09	**0.18±0.09**	**0.21±0.09**	**0.18±0.07**	-0.06±0.10	***0.53±0.06***	**0.67±0.02**	**0.40±0.02**	**0.50±0.03**
PICN	**0.38±0.09**	0.15±0.10	**0.36±0.09**	**0.28±0.10**	**0.21±0.06**	0.09±0.10	**0.91±0.07**	***0.44±0.06***	**0.49±0.02**	**0.51±0.03**
BUTT	**0.66±0.08**	**0.33±0.10**	**0.47±0.09**	**0.48±0.10**	**0.28±0.09**	**0.42±0.11**	**0.63±0.08**	**0.75±0.06**	***0.29±0.05***	**0.42±0.02**
RIBS	**0.61±0.10**	**0.43±0.11**	**0.49±0.11**	**0.56±0.10**	**0.32±0.11**	**0.58±0.12**	**0.82±0.06**	**0.75±0.07**	**0.80±0.08**	***0.32±0.06***

[1] ***HCW*** *= Hot carcass weight (kg);* ***CCW*** *= Cold carcass weight (kg);* ***FD*** *= Backfat depth (mm);* ***LD*** *= Loin depth (mm);* ***CLEN*** *= Carcass length (cm);* ***LEA*** *= Longissimus dorsi muscle area (cm^2);* ***TEXS*** *= Texture score;* ***CMAR*** *= Carcass marbling score;* ***USW*** *= Untrimmed side weight (kg);* ***UHAM*** *= Untrimmed ham weight (kg);* ***ULOIN*** *= Untrimmed loin weight (kg);* ***USH*** *= Untrimmed shoulder weight (kg);* ***UBEL*** *= Untrimmed belly weight (kg);* ***THAM*** *= Trimmed ham weight (kg);* ***TLOIN*** *= Trimmed loin weight (kg);* ***TBEL*** *= Trimmed belly weight (kg);* ***PICN*** *= Trimmed picnic shoulder weight (kg);* ***BUTT*** *= Butt shoulder weight (kg);* ***RIBS*** *= Ribs weight (kg).*

[a] *The significant correlations are bolded ($P < 0.05$).*

Table 3.4: Estimates of genetic (below diagonal), phenotypic (above diagonal) correlations, heritabilities (diagonal) and their standard error of estimates among meat quality traits

Traits[1]	WLW	REAW	BFW	RTW	BOW	CL	REAL	REAA
WLW	***0.28±0.08***	**-0.14±0.03**[a]	**-0.24±0.03**	**0.12±0.03**	**0.17±0.03**	**0.10±0.03**	-0.03±0.03	**0.04±0.02**
REAW	0.16±0.16	***0.31±0.06***	**-0.46±0.02**	**0.09±0.03**	-0.02±0.03	**0.12±0.03**	**-0.10±0.02**	**0.23±0.08**
BFW	-0.19±0.14	**-0.88±0.07**	***0.38±0.06***	**-0.27±0.03**	**-0.22±0.03**	**-0.15±0.03**	**0.06±0.03**	**0.29±0.07**
RTW	0.17±0.18	0.29±0.17	**-0.69±0.12**	***0.22±0.06***	**0.16±0.03**	**0.07±0.03**	**-0.04±0.02**	**0.26±0.08**
BOW	0.23±0.20	0.17±0.21	**-0.48±0.18**	**0.97±0.21**	***0.12±0.05***	0.03±0.03	-0.03±0.03	**0.27±0.07**
CL	-0.02±0.18	**0.49±0.15**	**-0.43±0.15**	**0.41±0.19**	0.16±0.24	***0.20±0.05***	**0.13±0.03**	-0.00±0.03
REAL	-0.01±0.16	0.09±0.16	0.12±0.14	0.08±0.18	-0.37±0.20	0.10±0.18	***0.28±0.06***	**-0.19±0.03**
REAA	-0.11±0.14	-0.27±0.16	0.07±0.16	-0.26±0.19	0.24±0.23	-0.14±0.19	**-0.36±0.16**	***0.26±0.09***
REAB	-0.02±0.16	-0.01±0.15	0.14±0.14	-0.10±0.17	-0.15±0.21	-0.03±0.18	**0.60±0.10**	**0.59±0.16**
SHF	0.11±0.15	0.00±0.15	0.38±0.35	0.09±0.17	0.12±0.20	**0.58±0.13**	**-0.33±0.14**	-0.15±0.16
LOINL	0.13±0.16	0.15±0.16	-0.13±0.15	0.20±0.18	-0.03±0.22	0.27±0.18	0.20±0.16	-0.21±0.17
LOINA	-0.08±0.15	-0.16±0.15	-0.14±0.14	0.28±0.16	0.14±0.21	0.14±0.53	**-0.30±0.15**	**0.76±0.16**
LOINB	0.25±0.18	0.07±0.18	-0.16±0.17	0.34±0.20	-0.02±0.26	**0.38±0.19**	-0.10±0.18	0.32±0.19
PHU	-0.15±0.22	-0.38±0.23	0.04±0.21	0.14±0.24	0.50±0.27	**-0.62±0.26**	-0.02±0.21	0.33±0.31
HGML	-0.16±0.18	**0.35±0.17**	-0.28±0.16	**0.40±0.19**	0.04±0.24	0.32±0.20	**0.35±0.17**	-0.29±0.18
HGMA	-0.24±0.14	0.05±0.14	0.06±0.13	-0.17±0.17	-0.02±0.20	0.14±0.17	-0.19±0.14	**0.43±0.16**
HGMB	-0.21±0.21	**0.40±0.20**	-0.14±0.20	0.29±0.23	-0.03±0.28	**0.46±0.22**	0.23±0.21	0.13±0.23
HQFL	-0.21±0.18	0.28±0.17	-0.03±0.17	0.09±0.20	0.10±0.24	**0.38±0.19**	**0.40±0.17**	-0.28±0.20
HQFA	-0.08±0.16	-0.21±0.16	0.13±0.15	-0.24±0.18	0.18±0.22	-0.05±0.18	**-0.40±0.15**	**0.69±0.18**
HQFB	-0.14±0.23	0.10±0.23	0.13±0.21	0.01±0.26	0.38±0.29	0.43±0.25	0.04±0.23	0.19±0.23
HILL	-0.01±0.16	0.02±0.15	0.21±0.14	-0.09±0.18	-0.18±0.22	0.11±0.18	0.16±0.16	0.03±0.17
HILA	-0.20±0.19	-0.01±0.19	0.08±0.18	-0.17±0.21	0.03±0.26	-0.09±0.22	-0.21±0.19	0.16±0.20
HILB	-0.02±0.17	-0.01±0.16	**0.35±0.15**	-0.20±0.19	-0.13±0.23	0.08±0.19	0.12±0.17	0.03±0.18
DL	-0.31±0.19	**0.39±0.18**	**-0.44±0.16**	0.09±0.22	-0.18±0.26	**0.52±0.20**	**0.57±0.21**	0.04±0.30

Continued

Table 3.4. Continued

Traits	REAB	SHF	LOINL	LOINA	LOINB	PHU	HGML	HGMA	HGMB
WLW	0.02±0.02	-0.03±0.03	0.01±0.03	-0.02±0.03	0.02±0.03	**0.09±0.04**	-0.00±0.03	**-0.07±0.03**	0.01±0.03
REAW	**-0.16±0.03**	**0.08±0.03**	-0.02±0.03	**-0.09±0.03**	**-0.06±0.03**	**0.12±0.06**	0.01±0.03	-0.03±0.03	-0.01±0.03
BFW	**0.10±0.03**	**-0.13±0.03**	0.03±0.03	0.04±0.03	**0.06±0.03**	**0.13±0.06**	-0.04±0.03	**0.04±0.02**	0.00±0.03
RTW	-0.02±0.03	0.04±0.03	-0.01±0.03	-0.00±0.03	-0.02±0.03	**0.20±0.07**	**0.04±0.02**	-0.04±0.03	0.00±0.03
BOW	-0.02±0.03	**0.08±0.03**	-0.03±0.03	0.05±0.03	0.01±0.03	**0.20±0.08**	-0.02±0.03	-0.00±0.03	-0.02±0.02
CL	**0.09±0.03**	**0.29±0.03**	**0.14±0.03**	**0.07±0.03**	**0.12±0.03**	**-0.16±0.03**	**0.08±0.03**	**0.07±0.03**	**0.09±0.03**
REAL	**0.65±0.02**	**-0.18±0.03**	**0.23±0.03**	0.03±0.03	**0.15±0.03**	**-0.12±0.03**	**0.22±0.03**	0.02±0.03	**0.18±0.03**
REAA	**0.43±0.04**	**-0.09±0.03**	0.01±0.03	**0.37±0.03**	**0.19±0.04**	**-0.06±0.03**	-0.02±0.03	**0.25±0.04**	**0.10±0.05**
REAB	***0.31±0.06***	**-0.19±0.03**	**0.17±0.03**	**0.19±0.03**	**0.21±0.03**	**-0.13±0.03**	**0.16±0.03**	**0.13±0.03**	**0.18±0.03**
SHF	**-0.35±0.13**	***0.39±0.06***	**-0.06±0.03**	0.00±0.03	-0.03±0.03	-0.05±0.03	**-0.07±0.03**	0.05±0.03	-0.05±0.03
LOINL	-0.03±0.16	-0.12±0.15	***0.31±0.06***	**0.23±0.03**	**0.77±0.01**	**-0.37±0.02**	**0.34±0.02**	0.04±0.03	**0.30±0.02**
LOINA	0.19±0.14	0.22±0.14	**-0.40±0.15**	***0.36±0.06***	**0.72±0.01**	**-0.30±0.03**	0.02±0.03	**0.42±0.02**	**0.18±0.03**
LOINB	0.11±0.18	-0.01±0.17	**0.51±0.12**	**0.46±0.13**	***0.20±0.06***	**-0.44±0.02**	**0.22±0.03**	**0.24±0.03**	**0.31±0.02**
PHU	0.14±0.19	0.20±0.21	**-0.65±0.21**	**-0.37±0.16**	**-0.64±0.16**	*0.15±0.09*	**-0.23±0.03**	**-0.14±0.03**	**-0.22±0.02**
HGML	0.03±0.17	-0.20±0.16	**0.45±0.15**	**-0.42±0.16**	-0.06±0.20	**-0.49±0.23**	***0.22±0.05***	0.04±0.03	**0.80±0.01**
HGMA	0.14±0.14	**0.35±0.13**	**-0.30±0.14**	**0.55±0.11**	0.13±0.17	0.01±0.20	**-0.42±0.15**	***0.38±0.06***	**0.48±0.02**
HGMB	0.32±0.21	0.09±0.20	0.33±0.19	0.03±0.21	0.39±0.21	**-0.65±0.33**	**0.56±0.14**	**0.34±0.17**	***0.12±0.05***
HQFL	0.06±0.29	-0.30±0.17	**0.66±0.14**	-0.18±0.18	0.28±0.20	**-0.60±0.26**	**0.74±0.15**	-0.20±0.17	0.36±0.22
HQFA	0.09±0.16	**0.45±0.14**	-0.16±0.16	**0.53±0.13**	0.19±0.18	-0.11±0.22	-0.18±0.18	**0.52±0.12**	0.24±0.21
HQFB	0.27±0.21	-0.05±0.21	**0.67±0.17**	0.19±0.21	**0.71±0.19**	**-0.98±0.35**	**0.70±0.22**	0.05±0.21	**0.87±0.25**
HILL	0.03±0.15	-0.00±0.15	**0.39±0.14**	-0.15±0.15	0.30±0.17	-0.17±0.21	0.24±0.16	-0.06±0.14	**0.36±0.18**
HILA	-0.13±0.19	0.07±0.17	0.06±0.19	**0.43±0.16**	**0.44±0.19**	-0.39±0.27	-0.34±0.20	**0.58±0.15**	0.11±0.25
HILB	-0.01±0.16	0.01±0.16	**0.31±0.15**	-0.00±0.16	**0.48±0.17**	**-0.48±0.23**	0.13±0.18	0.04±0.15	**0.46±0.18**
DL	0.23±0.19	**-0.38±0.18**	**0.55±0.24**	**0.42±0.19**	0.40±0.24	**-0.99±0.49**	0.30±0.21	0.06±0.18	0.26±0.24

Continued

Table 3.4. Continued

Traits	HQFL	HQFA	HQFB	HILL	HILA	HILB	DL
WLW	**-0.06±0.03**	0.00±0.03	-0.02±0.03	-0.03±0.03	-0.03±0.03	-0.04±0.03	**0.16±0.08**
REAW	0.03±0.03	-0.03±0.03	0.00±0.03	**-0.05±0.02**	0.00±0.03	-0.04±0.03	**0.25±0.08**
BFW	-0.00±0.03	0.02±0.03	0.02±0.03	0.02±0.03	**-0.05±0.02**	0.03±0.03	**0.20±0.10**
RTW	-0.01±0.03	-0.01±0.03	0.00±0.03	-0.01±0.03	0.02±0.03	-0.00±0.03	**0.27±0.08**
BOW	0.02±0.03	0.04±0.03	0.03±0.02	-0.02±0.03	0.01±0.03	-0.02±0.03	**0.28±0.08**
CL	**0.12±0.03**	0.05±0.03	**0.12±0.02**	**0.07±0.03**	0.03±0.03	**0.06±0.03**	**0.14±0.03**
REAL	**0.18±0.03**	-0.00±0.03	**0.14±0.03**	**0.12±0.03**	-0.01±0.03	**0.10±0.03**	**0.27±0.03**
REAA	0.00±0.03	**0.23±0.03**	**0.11±0.04**	0.02±0.03	**0.11±0.03**	0.06±0.04	**0.06±0.03**
REAB	**0.15±0.03**	**0.11±0.03**	**0.17±0.03**	**0.08±0.03**	0.02±0.03	**0.08±0.03**	**0.25±0.03**
SHF	-0.05±0.03	**0.06±0.03**	-0.00±0.03	-0.00±0.03	0.05±0.03	-0.00±0.03	**-0.10±0.03**
LOINL	**0.30±0.02**	-0.01±0.03	**0.24±0.02**	**0.24±0.03**	**0.06±0.03**	**0.23±0.03**	**0.26±0.03**
LOINA	**0.08±0.03**	**0.29±0.03**	**0.17±0.03**	0.04±0.03	**0.19±0.03**	**0.11±0.03**	**0.24±0.03**
LOINB	**0.24±0.02**	**0.13±0.03**	**0.26±0.02**	**0.20±0.03**	**0.14±0.03**	**0.24±0.03**	**0.30±0.03**
PHU	**-0.17±0.03**	**-0.08±0.03**	**-0.18±0.02**	**-0.17±0.03**	**-0.12±0.03**	**-0.19±0.03**	**-0.16±0.03**
HGML	**0.31±0.02**	-0.01±0.03	**0.24±0.02**	**0.24±0.03**	-0.04±0.03	**0.18±0.03**	**0.16±0.03**
HGMA	**0.09±0.03**	**0.32±0.03**	**0.19±0.03**	**0.12±0.03**	**0.26±0.02**	**0.21±0.03**	**0.14±0.03**
HGMB	**0.25±0.02**	**0.13±0.03**	**0.29±0.02**	**0.26±0.02**	**0.10±0.02**	**0.30±0.02**	**0.19±0.03**
HQFL	***0.19±0.05***	-0.03±0.03	**0.74±0.01**	**0.24±0.03**	0.03±0.03	**0.19±0.03**	**0.16±0.03**
HQFA	**-0.46±0.17**	***0.27±0.06***	**0.53±0.02**	**-0.06±0.03**	**0.23±0.02**	**0.06±0.03**	**0.10±0.03**
HQFB	**0.67±0.13**	0.20±0.21	***0.10±0.04***	**0.13±0.03**	**0.12±0.02**	**0.18±0.02**	**0.16±0.03**
HILL	0.09±0.18	-0.18±0.16	0.10±0.22	***0.32±0.06***	**0.17±0.03**	**0.83±0.01**	**0.13±0.03**
HILA	0.01±0.22	**0.38±0.17**	0.21±0.26	-0.29±0.19	***0.16±0.05***	**0.52±0.02**	**0.08±0.03**
HILB	0.04±0.19	-0.11±0.17	0.31±0.39	**0.92±0.03**	0.00±0.21	***0.26±0.06***	**0.15±0.03**
DL	0.36±0.22	0.08±0.19	0.41±0.26	0.16±0.20	0.09±0.23	0.24±0.21	***0.21±0.09***

[1] ***WLW*** *= Whole loin weight (kg);* ***REAW*** *= Rib eye weight (kg);* ***BFW*** *= Backfat thickness weight (kg);* ***RTW*** *= Rib trim weight (kg);* ***BOW*** *= Bone/Neural weight (kg);* ***CL*** *= Cooking loss (%);* ***REAL*** *= Minolta L* rib eye area;* ***REAA*** *= Minolta a* rib eye area;* ***REAB*** *= Minolta b* rib eye area;* ***SHF*** *= Shear force (newton);* ***LOINL*** *= Minolta L* loin;* ***LOINA*** *= Minolta a* loin;* ***LOINB*** *= Minolta b* loin;* ***PHU*** *= pH ultimate;* ***HGML*** *= Minolta L* ham gluteus medius;* ***HGMA*** *= Minolta a* ham gluteus medius;* ***HGMB*** *= Minolta b* ham gluteus medius;* ***HQFL*** *= Minolta L* ham quadriceps femoris;* ***HQFA*** *= Minolta a* ham quadriceps femoris;* ***HQFB*** *= Minolta b* ham quadriceps femoris;* ***HILL*** *= Minolta L* ham iliopsoas;* ***HILA*** *= Minolta a* ham*

iliopsoas; ***HILB*** *= Minolta b* ham iliopsoas;* ***DL*** *= Drip loss (%).*
[a] *The significant correlations are bolded (P < 0.05).*

Table 3.5: Estimates of phenotypic correlations and their standard error of estimates between meat quality and carcass traits

Traits[1]	HCW	CCW	FD	LD	CLEN	LEA	TEXS	CMAR	USW	UHAM
WLW	**0.39±0.05**	**0.35±0.05**	0.02±0.03	0.04±0.03	-0.01±0.03	**0.32±0.06**	**-0.04±0.02**	-0.03± 0.03	**-0.11± 0.04**	**-0.14±0.03**
REAW	**0.40±0.05**	**0.40±0.05**	**-0.22±0.03**	**0.21±0.03**	**0.10±0.03**	**0.31± 0.05**	0.03±0.02	**-0.08±0.03**	**0.08±0.03**	**0.13±0.03**
BFW	**0.40±0.05**	**0.40±0.05**	**0.42±0.02**	**-0.17±0.03**	**-0.07±0.03**	**0.30±0.06**	-0.04±0.03	**0.11±0.03**	**0.09±0.03**	-0.02±0.03
RTW	**0.40±0.05**	**0.41±0.05**	**-0.20±0.03**	**0.10±0.03**	0.03±0.03	**0.31±0.06**	-0.02±0.03	-0.04±0.03	-0.02±0.03	0.01±0.03
BOW	**0.40±0.05**	**0.41±0.05**	**-0.11±0.03**	0.01±0.03	**0.09±0.03**	**0.32±0.06**	**-0.07±0.02**	-0.03±0.03	0.02±0.03	0.03±0.03
CL	**0.28±0.06**	**0.27±0.06**	**-0.07±0.03**	0.03±0.03	-0.01±0.03	**0.22±0.05**	-0.05±0.02	-0.05±0.03	-0.01±0.02	0.00±0.03
REAL	**0.29±0.06**	**0.28±0.06**	-0.03±0.03	0.03±0.03	**-0.06±0.03**	**0.21±0.06**	**-0.13±0.02**	-0.01±0.03	-0.02±0.03	-0.01±0.03
REAA	0.00±0.03	0.00±0.03	**0.08±0.03**	-0.03±0.03	0.01±0.03	**-0.06±0.03**	0.08±0.07	**0.17±0.04**	0.02±0.03	0.04±0.05
REAB	0.02±0.03	0.01±0.03	0.00±0.03	0.01±0.03	-0.03±0.03	-0.01±0.03	**-0.13±0.02**	**0.07±0.03**	0.02±0.03	0.02±0.03
SHF	-0.05±0.03	-0.04±0.03	-0.02±0.03	-0.03±0.03	0.01±0.03	-0.01±0.03	**0.08±0.03**	-0.04±0.03	-0.04±0.03	-0.05±0.03
LOINL	**0.12±0.03**	**0.11±0.03**	**0.12±0.03**	**0.07±0.03**	**-0.11±0.03**	**0.07±0.03**	**-0.39±0.02**	**0.09±0.03**	**0.11±0.03**	**0.07±0.03**
LOINA	0.04±0.03	0.04±0.03	**0.19±0.03**	**-0.07±0.03**	-0.05±0.03	**-0.12±0.03**	**-0.30±0.02**	**0.17±0.03**	0.04±0.03	-0.03±0.03
LOINB	**0.12±0.03**	**0.11±0.03**	**0.18±0.03**	0.03±0.03	**-0.09±0.03**	-0.00±0.03	**-0.44±0.02**	**0.15±0.03**	**0.11±0.03**	0.05±0.03
PHU	0.02±0.03	0.02±0.03	0.00±0.03	**-0.10±0.03**	**0.12±0.03**	**-0.05±0.02**	**0.19±0.03**	**0.06±0.03**	0.03±0.03	0.04±0.03
HGML	0.03±0.03	0.04±0.03	**-0.10±0.03**	**0.15±0.03**	-0.01±0.03	**0.12±0.03**	**-0.18±0.02**	-0.03±0.03	0.03±0.03	**0.08±0.03**
HGMA	-0.04±0.03	-0.05±0.03	**0.09±0.03**	-0.04±0.03	-0.05±0.03	-0.05±0.03	**-0.12±0.02**	0.05±0.03	-0.05±0.03	-0.04±0.03
HGMB	0.03±0.03	0.03±0.03	-0.01±0.03	**0.09±0.03**	-0.04±0.03	**0.07±0.03**	**-0.22±0.02**	0.03±0.02	0.02±0.03	**0.06±0.03**
HQFL	0.05±0.03	**0.06±0.03**	0.02±0.03	0.03±0.03	-0.01±0.03	0.02±0.03	**-0.20±0.02**	0.05±0.03	**0.06±0.03**	**0.12±0.03**
HQFA	-0.01±0.03	-0.00±0.03	0.02±0.03	0.02±0.03	0.01±0.03	0.00±0.03	**-0.09±0.02**	-0.00±0.03	-0.00±0.03	**-0.10±0.03**
HQFB	**0.08±0.03**	**0.09±0.03**	0.01±0.03	**0.05±0.02**	0.03±0.03	0.05±0.03	**-0.20±0.02**	**0.04±0.02**	**0.08±0.03**	**0.07±0.03**
HILL	-0.01±0.03	-0.01±0.03	0.00±0.03	0.03±0.03	-0.02±0.03	0.01±0.03	**-0.11±0.02**	-0.02±0.03	-0.00±0.03	**0.07±0.03**
HILA	-0.02±0.03	-0.02±0.03	-0.01±0.03	0.01±0.03	-0.02±0.03	0.00±0.03	**-0.07±0.02**	-0.03±0.03	-0.0±0.03	-0.02±0.03
HILB	0.02±0.03	0.02±0.03	0.03±0.03	0.03±0.03	-0.02±0.03	-0.01±0.03	**-0.14±0.02**	-0.00±0.03	0.02±0.03	**0.06±0.03**
DL	0.01±0.03	0.01±0.03	0.01±0.03	0.02±0.03	-0.03±0.03	0.01±0.03	**-0.23±0.06**	**0.07±0.03**	0.03±0.03	**0.06±0.04**

Continued

Table 3.5. Continued.

Traits	ULOIN	USH	UBEL	THAM	TLOIN	TBEL	PICN	BUTT	RIBS
WLW	-0.03±0.03	-0.03±0.03	-0.01±0.03	0.01±0.03	**-0.07±0.03**	**0.40±0.02**	**0.37±0.03**	**0.33±0.03**	**0.20±0.03**
REAW	0.03±0.03	**0.08±0.03**	-0.01±0.03	**0.12±0.03**	**0.10±0.03**	**-0.06±0.03**	**0.11±0.03**	**0.20±0.03**	**0.14± 0.03**
BFW	**0.09±0.03**	0.03±0.03	**0.16±0.03**	-0.04±0.03	-0.02±0.03	**0.25±0.03**	0.04±0.03	**-0.12±0.03**	**-0.11±0.03**
RTW	0.00±0.03	0.01±0.02	**-0.08±0.03**	0.01±0.03	0.04±0.03	-0.05±0.03	0.02±0.03	**0.11±0.03**	**0.06±0.03**
BOW	-0.01±0.03	**0.07±0.03**	-0.03±0.03	0.03±0.03	0.03±0.03	**-0.08±0.03**	0.03±0.03	**0.09±0.03**	**0.08±0.03**
CL	**0.06±0.03**	-0.04±0.03	0.00±0.03	**-0.06±0.03**	**0.07±0.03**	**-0.06±0.03**	-0.03±0.03	0.03±0.03	0.01±0.03
REAL	0.02±0.03	-0.02±0.03	-0.01±0.03	-0.03±0.03	0.02±0.03	0.01±0.03	-0.00±0.03	-0.02±0.03	-0.03±0.03
REAA	0.04±0.04	0.05±0.05	**0.10±0.05**	0.04±0.05	0.05±0.05	**0.14±0.05**	**0.13±0.07**	**0.15±0.07**	**0.23±0.07**
REAB	0.05±0.03	0.00±0.03	0.04±0.03	-0.02±0.03	0.04±0.03	**0.08±0.03**	0.04±0.03	0.01±0.03	0.04±0.03
SHF	-0.02±0.03	-0.03±0.03	-0.04±0.03	-0.03±0.03	-0.01±0.03	**-0.12±0.03**	**-0.09±0.03**	-0.04±0.03	-0.03±0.03
LOINL	**0.19±0.03**	**0.07±0.03**	**0.13±0.03**	**-0.07±0.03**	**0.17±0.03**	0.01±0.03	0.03±0.03	0.05±0.03	-0.01±0.03
LOINA	**0.18±0.03**	-0.01±0.03	**0.08±0.03**	**-0.13±0.03**	**0.12±0.03**	-0.02±0.03	-0.01±0.03	-0.00±0.03	**0.07±0.03**
LOINB	**0.28±0.03**	0.03±0.03	**0.16±0.03**	**-0.14±0.03**	**0.24±0.03**	0.02±0.03	0.04±0.03	0.05±0.03	**0.06±0.03**
PHU	**-0.07±0.03**	**0.08±0.03**	0.03±0.03	**0.08±0.03**	**-0.09±0.03**	**0.08±0.03**	0.05±0.03	**0.07±0.03**	0.06±0.04
HGML	-0.02±0.03	0.03±0.03	0.00±0.03	**0.09±0.03**	0.05±0.03	-0.00±0.03	0.00±0.03	0.02±0.03	0.03±0.03
HGMA	0.00±0.03	**-0.09±0.03**	-0.01±0.03	-0.05±0.03	-0.04±0.03	**-0.06±0.03**	**-0.07±0.03**	**-0.10±0.03**	0.01±0.03
HGMB	**0.06±0.03**	-0.02±0.03	0.04±0.03	0.00±0.03	**0.08±0.03**	-0.02±0.03	-0.01±0.03	-0.02±0.03	0.04±0.03
HQFL	0.02±0.03	0.04±0.03	0.05±0.03	**0.06±0.03**	0.02±0.03	0.01±0.03	0.01±0.03	-0.00±0.03	0.02±0.03
HQFA	**0.06±0.03**	-0.01±0.03	0.01±0.03	**-0.08±0.03**	0.05±0.03	0.01±0.03	-0.02±0.03	-0.04±0.03	0.00±0.03
HQFB	**0.13±0.03**	0.05±0.03	**0.10±0.03**	-0.01±0.03	**0.12±0.03**	0.03±0.03	0.03±0.03	0.02±0.03	0.04±0.03
HILL	-0.03±0.03	-0.03±0.03	0.01±0.03	0.04±0.03	-0.04±0.03	-0.00±0.03	-0.02±0.03	**-0.06±0.03**	-0.01±0.03
HILA	0.05±0.03	**-0.07±0.03**	0.03±0.03	-0.05±0.03	**0.07±0.03**	-0.02±0.03	-0.04±0.03	-0.05±0.03	0.01±0.03
HILB	**0.06±0.03**	-0.03±0.03	**0.06±0.03**	-0.01±0.03	0.05±0.03	-0.00±0.03	-0.02±0.03	**-0.06±0.03**	-0.00±0.03
DL	0.03±0.03	0.06±0.04	0.04±0.04	0.07±0.04	0.04±0.04	-0.05±0.04	0.03±0.05	**0.12±0.06**	**0.19±0.07**

[1] ***WLW*** *= Whole loin weight (kg);* ***REAW*** *= Rib eye weight (kg);* ***BFW*** *= Backfat thickness weight (kg);* ***RTW*** *= Rib trim weight (kg);* ***BOW*** *= Bone/Neural weight (kg);* ***CL*** *= Cooking loss (%);* ***REAL*** *= Minolta L* rib eye area;* ***REAA*** *= Minolta a* rib eye area;* ***REAB*** *= Minolta b* rib eye area;* ***SHF*** *= Shear force (newton);* ***LOINL*** *= Minolta L* loin;* ***LOINA*** *= Minolta a* loin;* ***LOINB*** *= Minolta b* loin;* ***PHU*** *= pH ultimate;* ***HGML*** *= Minolta L* ham gluteus medius;* ***HGMA*** *= Minolta a* ham gluteus medius;* ***HGMB*** *= Minolta b* ham gluteus medius;* ***HQFL*** *= Minolta L* ham quadriceps femoris;* ***HQFA*** *= Minolta a* ham quadriceps femoris;* ***HQFB*** *= Minolta b* ham quadriceps femoris;* ***HILL*** *= Minolta L* ham iliopsoas;* ***HILA*** *= Minolta a* ham iliopsoas;* ***HILB*** *= Minolta b* ham iliopsoas;* ***DL***

*= Drip loss (%);**HCW** = Hot carcass weight (kg); **CCW** = Cold carcass weight (kg); **FD** = Backfat depth (mm); **LD** = Loin depth (mm); **CLEN** = Carcass length (cm); **LEA** = Longissimus dorsi muscle area (cm^2); **TEXS** = Texture score; **CMAR** = Carcass marbling score; **USW** = Untrimmed side weight (kg); **UHAM** = Untrimmed ham weight (kg); **ULOIN** = Untrimmed loin weight (kg); **USH** = Untrimmed shoulder weight (kg); **UBEL** = Untrimmed belly weight (kg); **THAM** = Trimmed ham weight (kg); **TLOIN** = Trimmed loin weight (kg); **TBEL** = Trimmed belly weight (kg); **PICN** = Trimmed picnic shoulder weight (kg); **BUTT** = Butt shoulder weight (kg); **RIBS** = Ribs weight (kg).*

[a] *The significant correlations are bolded ($P < 0.05$).*

Table 3.6: Estimates of genetic correlations and their standard error of estimates between meat quality and carcass traits

Traits[1]	HCW	CCW	FD	LD	CLEN	LEA	TEXS	CMAR	USW	UHAM
WLW	-0.32±0.21	**-0.54±0.16**	-0.00±0.15	0.01±0.14	0.02±0.13	0.15±0.19	-0.06±0.23	-0.07±0.16	-0.08±0.13	-0.13±0.13
REAW	**0.40±0.19**	**0.39±0.19**	**-0.31±0.13**	**0.40±0.12**	0.06±0.13	**0.57±0.17**	-0.18±0.23	0.12±0.16	**0.24±0.12**	**0.33±0.12**
BFW	0.13±0.18	0.07±0.18	**0.60±0.10**	**-0.22±0.10**	-0.03±0.12	**-0.35±0.17**	-0.18±0.21	-0.00±0.15	0.07±0.12	-0.05±0.12
RTW	0.11±0.22	0.19±0.21	**-0.41±0.14**	**0.26±0.12**	0.09±0.13	0.22±0.19	**-0.39±0.19**	-0.10±0.16	0.09±0.13	0.11±0.13
BOW	**0.60±0.27**	**0.63±0.27**	-0.24±0.17	-0.04±0.16	**0.30±0.15**	0.16±0.24	-0.24±0.27	0.22±0.19	**0.31±0.15**	**0.35±0.16**
CL	-0.06±0.24	-0.05±0.22	-0.10±0.16	-0.10±0.15	-0.01±0.14	0.07±0.21	-0.35±0.24	-0.03±0.18	-0.01±0.14	0.02±0.15
REAL	-0.04±0.21	-0.08±0.20	-0.04±0.14	0.05±0.13	-0.12±0.12	0.17±0.19	-0.20±0.22	-0.12±0.16	-0.02±0.12	0.05±0.12
REAA	-0.02±0.29	-0.02±0.28	-0.04±0.15	0.02±0.14	-0.06±0.13	0.10±0.26	-0.08±0.22	0.14±0.16	-0.03±0.13	-0.06±0.13
REAB	0.08±0.12	0.07± 0.12	-0.12±0.14	0.17±0.13	-0.07±0.12	0.20±0.13	-0.26±0.21	-0.03±0.16	0.09±0.12	0.14±0.12
SHF	-0.09±0.12	-0.07±0.11	0.17±0.13	**-0.24±0.12**	-0.07±0.11	-0.12±0.13	0.08±0.22	**0.30±0.14**	-0.07±0.12	-0.16±0.12
LOINL	0.01±0.12	0.03±0.12	**-0.25±0.12**	**0.36±0.12**	**-0.29±0.11**	**0.42±0.12**	**-0.38±0.19**	-0.12±0.16	0.01±0.12	0.09±0.13
LOINA	**-0.21±0.10**	-0.17±0.12	0.02±0.14	0.08±0.13	**-0.24±0.12**	-0.02±0.13	0.09±0.22	-0.03±0.15	-0.17±0.12	**-0.24±0.12**
LOINB	-0.10±0.14	-0.08±0.14	-0.27±0.16	**0.38±0.14**	**-0.32±0.13**	**0.35±0.15**	-0.37±0.21	-0.13±0.17	-0.08±0.14	-0.05±0.14
PHU	-0.35±0.40	-0.37±0.38	0.21±0.21	**-0.66±0.17**	**0.38±0.17**	**-0.78±0.28**	0.05±0.31	0.22±0.21	0.22±0.18	0.18±0.18
HGML	0.14±0.14	0.15±0.13	**-0.39±0.14**	**0.37±0.13**	-0.04±0.13	**0.30±0.13**	-0.36±0.22	0.11±0.17	0.10±0.14	**0.26±0.13**
HGMA	**-0.21±0.10**	**-0.21±0.10**	0.06±0.13	0.06±0.12	**-0.26±0.11**	0.05±0.13	0.10±0.20	0.11±0.15	**-0.22±0.11**	**-0.22±0.10**
HGMB	0.01±0.18	0.01± 0.18	-0.33±0.19	**0.41±0.17**	-0.27±0.17	**0.37±0.18**	-0.21±0.28	0.12±0.21	-0.04±0.18	0.09±0.17
HQFL	0.06±0.14	0.07±0.13	-0.16±0.16	**0.28±0.14**	**-0.26±0.12**	0.16±0.15	**-0.61±0.19**	0.01±0.17	0.08±0.14	**0.24±0.12**
HQFA	0.02±0.13	0.02±0.13	0.24±0.14	0.06±0.13	-0.10±0.12	0.08±0.13	0.16±0.23	0.15±0.16	0.01±0.13	-0.12±0.12
HQFB	0.17±0.17	0.19±0.17	-0.07±0.19	**0.39±0.16**	-0.21±0.17	**0.34±0.17**	**-0.55±0.23**	0.10±0.21	0.18±0.16	0.26±0.16
HILL	0.06±0.12	0.05±0.12	-0.17±0.13	**0.27±0.12**	-0.07±0.12	0.19±0.12	-0.27±0.21	-0.17±0.15	0.04±0.12	0.12±0.12
HILA	-0.15±0.14	-0.15±0.14	-0.05±0.15	0.03±0.15	**-0.26±0.13**	-0.01±0.15	-0.14±0.23	-0.15±0.17	-0.15±0.14	-0.12±0.14
HILB	0.07±0.13	0.06±0.13	-0.07±0.15	**0.27±0.13**	-0.13±0.13	0.17±0.14	-0.22±0.23	-0.18±0.16	0.06±0.13	0.12±0.13
DL	0.27±0.32	0.22±0.31	0.01±0.17	0.15±0.16	-0.25±0.16	0.30±0.31	**-0.72±0.26**	-0.06±0.19	0.02±0.15	0.05±0.15

Continued

Table 3.6. Continued.

Traits	ULOIN	USH	UBEL	THAM	TLOIN	TBEL	PICN	BUTT	RIBS
WLW	0.15±0.12	-0.03±0.13	0.12±0.13	-0.04±0.10	0.01±0.13	**0.74±0.07**	**0.80±0.07**	**0.74±0.08**	**0.57±0.13**
REAW	0.08±0.12	**0.26±0.12**	0.04±0.13	**0.23±0.09**	0.18±0.13	-0.16±0.12	0.15±0.13	**0.34±0.13**	**0.34±0.16**
BFW	0.14±0.11	-0.07±0.11	**0.26±0.11**	-0.08±0.09	-0.00±0.12	**0.38±0.09**	0.10±0.11	**-0.32±0.13**	-0.24±0.15
RTW	0.14±0.12	0.11±0.12	-0.01±0.13	0.03±0.10	0.15±0.14	-0.10±0.13	0.07±0.13	**0.39±0.14**	**0.38±0.16**
BOW	-0.01±0.15	**0.44±0.15**	0.13±0.16	0.22±0.13	0.16±0.17	-0.10±0.15	**0.32±0.16**	**0.57±0.16**	**0.74±0.16**
CL	0.13±0.13	-0.05±0.14	0.09±0.14	-0.12±0.12	0.19±0.15	**-0.26±0.13**	-0.18±0.14	0.02±0.15	0.28±0.18
REAL	0.16±0.11	-0.06±0.12	-0.03±0.13	-0.07±0.09	0.10±0.12	0.04±0.12	-0.03±0.13	-0.00±0.13	-0.05±0.16
REAA	-0.06±0.12	-0.03±0.12	0.08±0.13	-0.07±0.10	-0.03±0.13	0.14±0.12	0.04±0.13	0.01±0.14	**0.35±0.15**
REAB	**0.20±0.10**	0.00±0.12	0.09±0.12	-0.05±0.10	0.16±0.12	**0.20±0.10**	0.15±0.12	0.14±0.14	**0.31±0.15**
SHF	-0.07±0.11	0.01±0.12	-0.01±0.11	-0.07±0.09	-0.13±0.12	-0.11±0.11	-0.16±0.12	-0.06±0.13	0.05±0.16
LOINL	**0.25±0.11**	-0.07±0.12	0.09±0.12	**-0.20±0.10**	**0.34±0.12**	-0.15±0.12	-0.05±0.12	0.15±0.14	-0.24±0.15
LOINA	**0.22±0.10**	**-0.25±0.11**	0.07±0.12	**-0.36±0.09**	**0.23±0.11**	-0.15±0.12	-0.02±0.12	0.15±0.13	0.16±0.15
LOINB	**0.55±0.10**	**-0.29±0.13**	**0.28±0.13**	**-0.52±0.10**	**0.67±0.11**	-0.11±0.14	0.08±0.14	**0.34±0.15**	0.05±0.18
PHU	**-0.42±0.19**	**0.44±0.16**	-0.03±0.19	**0.45±0.15**	**-0.68±0.23**	0.28±0.19	0.12±0.19	0.05±0.20	0.05±0.24
HGML	-0.17±0.12	0.22±0.13	-0.12±0.14	**0.32±0.11**	-0.00±0.15	-0.09±0.14	-0.01±0.14	0.22±0.15	-0.01±0.17
HGMA	-0.06±0.11	**-0.29±0.11**	-0.11±0.11	-0.13±0.09	-0.15±0.12	-0.11±0.11	**-0.25±0.12**	-0.13±0.13	0.08±0.15
HGMB	0.10±0.17	-0.15±0.17	0.06±0.18	-0.04±0.15	0.20±0.19	-0.12±0.18	-0.13±0.17	0.13±0.18	0.08±0.22
HQFL	-0.01±0.13	0.05±0.13	-0.03±0.14	**0.21±0.10**	0.12±0.15	-0.14±0.14	-0.12±0.14	-0.05±0.15	-0.15±0.17
HQFA	0.05±0.12	0.04±0.12	-0.01±0.13	-0.07±0.10	-0.01±0.13	0.03±0.13	-0.03±0.13	0.02±0.14	0.24±0.16
HQFB	**0.33±0.15**	0.03±0.16	0.21±0.17	-0.02±0.15	**0.42±0.17**	-0.08±0.17	-0.09±0.17	0.10±0.18	0.14±0.21
HILL	-0.00±0.11	-0.03±0.12	0.01±0.12	0.10±0.09	0.02±0.13	0.09±0.12	0.09±0.12	-0.10±0.13	-0.04±0.15
HILA	0.09±0.12	**-0.28±0.13**	0.00±0.14	-0.17±0.11	0.20±0.14	-0.13±0.13	**-0.24±0.12**	-0.16±0.15	-0.13±0.18
HILB	**0.25±0.12**	-0.15±0.13	0.19±0.13	-0.07±0.11	**0.29±0.13**	0.08±0.13	0.00±0.14	-0.16±0.15	-0.10±0.18
DL	-0.07±0.14	0.09±0.14	-0.09±0.15	0.08±0.12	-0.07±0.16	**-0.46±0.14**	**-0.36±0.15**	-0.09±0.16	0.03±0.19

[1] ***WLW*** *= Whole loin weight (kg);* ***REAW*** *= Rib eye weight (kg);* ***BFW*** *= Backfat thickness weight (kg);* ***RTW*** *= Rib trim weight (kg);* ***BOW*** *= Bone/Neural weight (kg);* ***CL*** *= Cooking loss (%);* ***REAL*** *= Minolta L* rib eye area;* ***REAA*** *= Minolta a* rib eye area;* ***REAB*** *= Minolta b* rib eye area;* ***SHF*** *= Shear force (newton);* ***LOINL*** *= Minolta L* loin;* ***LOINA*** *= Minolta a* loin;* ***LOINB*** *= Minolta b* loin;* ***PHU*** *= pH ultimate;* ***HGML*** *= Minolta L* ham gluteus medius;* ***HGMA*** *= Minolta a* ham gluteus medius;* ***HGMB*** *= Minolta b* ham gluteus medius;* ***HQFL*** *= Minolta L* ham quadriceps femoris;* ***HQFA*** *= Minolta a* ham quadriceps femoris;* ***HQFB*** *= Minolta b* ham quadriceps femoris;* ***HILL*** *= Minolta L* ham iliopsoas;* ***HILA*** *= Minolta a* ham iliopsoas;* ***HILB*** *= Minolta b* ham iliopsoas;* ***DL*** *= Drip loss (%);****HCW =*** *Hot carcass weight (kg);* ***CCW =*** *Cold carcass weight (kg);* ***FD =*** *Backfat depth (mm);* ***LD =*** *Loin depth (mm);* ***CLEN =*** *Carcass length (cm);* ***LEA =*** *Longissimus dorsi muscle area (cm^2);* ***TEXS =*** *Texture score;* ***CMAR =*** *Carcass marbling score;* ***USW =*** *Untrimmed side weight (kg);* ***UHAM =*** *Untrimmed ham weight (kg);* ***ULOIN =*** *Untrimmed loin weight (kg);* ***USH =*** *Untrimmed shoulder weight (kg);* ***UBEL =*** *Untrimmed belly weight (kg);* ***THAM =*** *Trimmed ham weight (kg);* ***TLOIN =*** *Trimmed loin weight (kg);* ***TBEL =*** *Trimmed belly weight (kg);* ***PICN =*** *Trimmed picnic shoulder weight (kg);* ***BUTT =*** *Butt shoulder weight (kg);* ***RIBS =*** *Ribs weight (kg).*

[a] *The significant correlations are bolded ($P < 0.05$).*

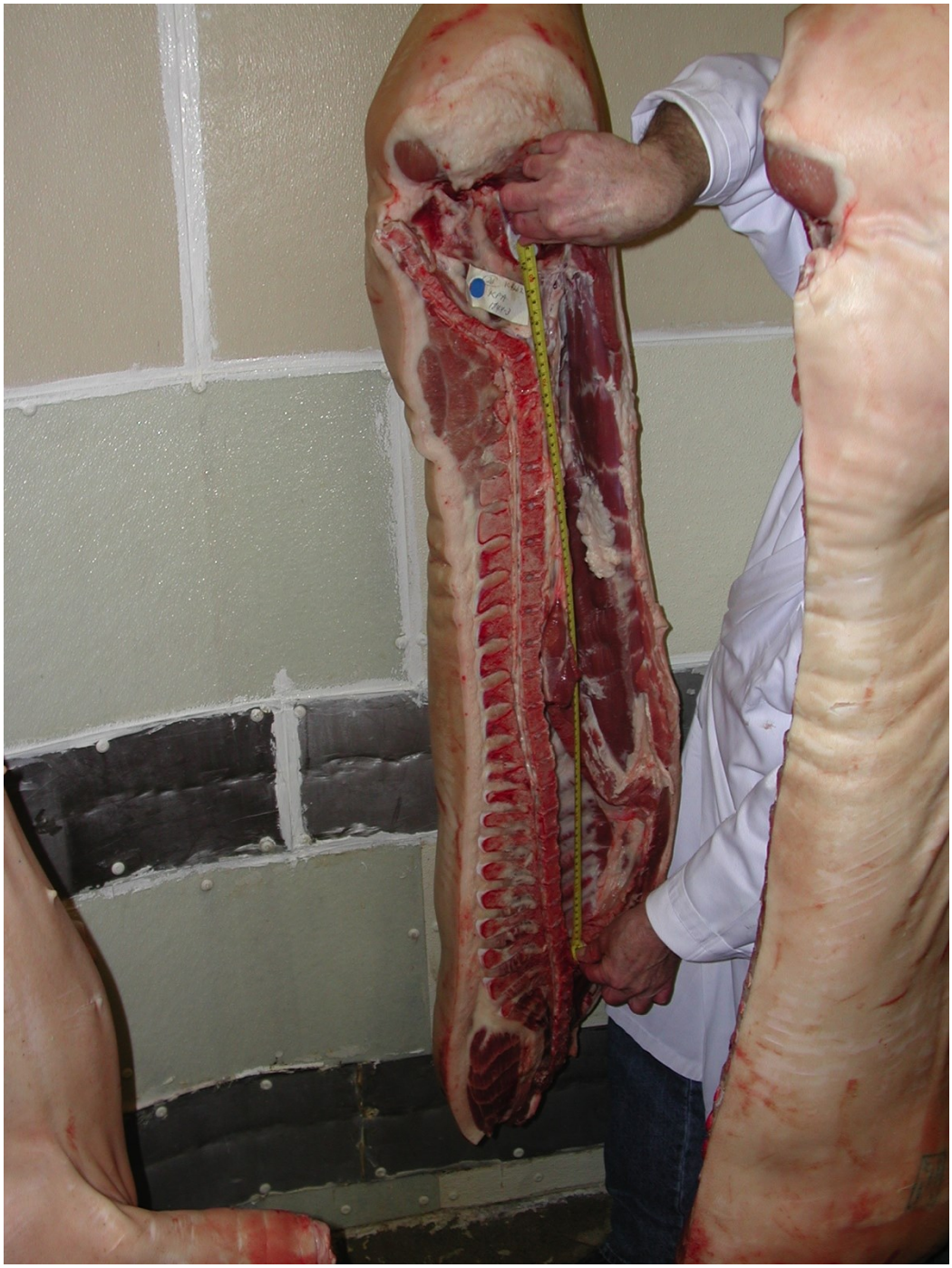

Figure 3.1: Measurement of carcass length

(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

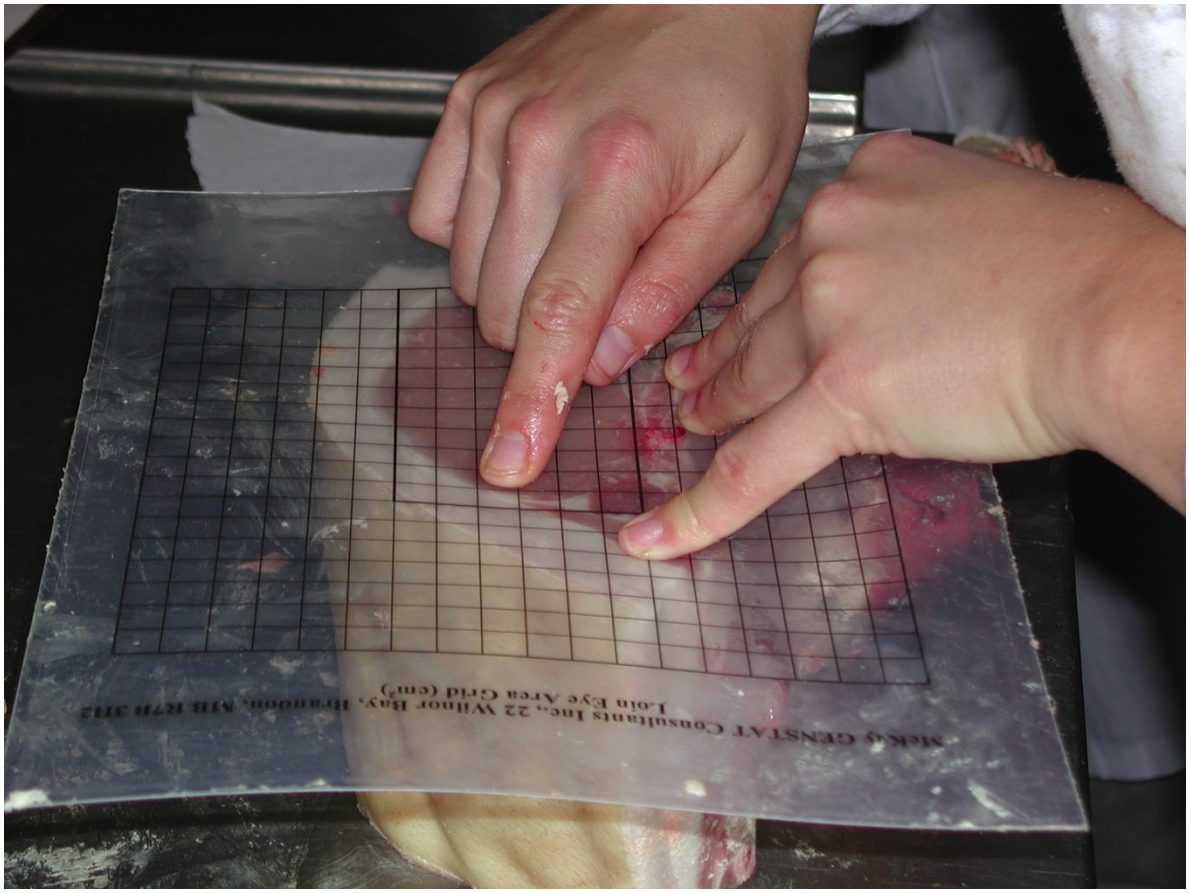

Figure 3.2: Measurement of loin eye area

(Courtesy of Dr. Bob Mc Kay, McKay GENSTAT Consultants Inc.)

Figure 3.3: Measurement of loin depth
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

Figure 3.4: Removal of the ham

(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

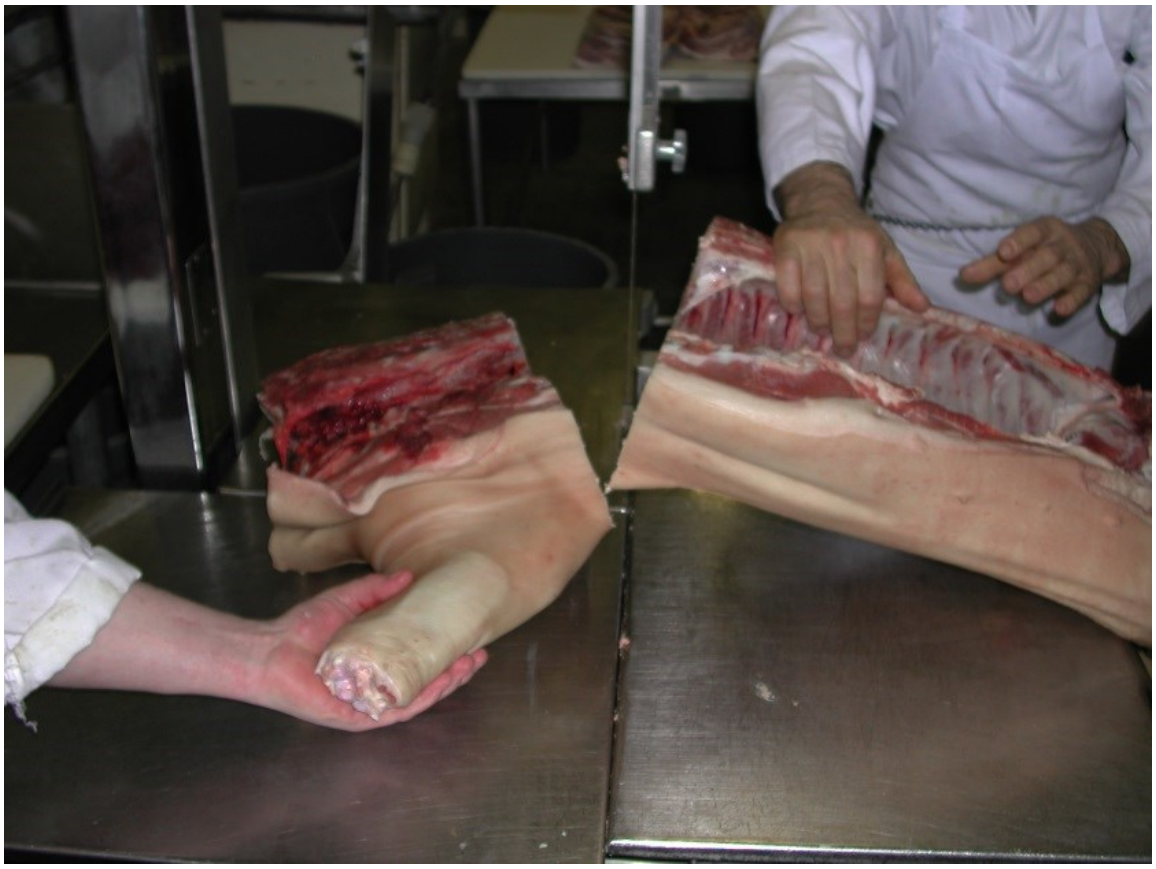

Figure 3.5: Removal of the Shoulder from the side
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

Figure 3.6: Loin and Belly Separated from each other
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

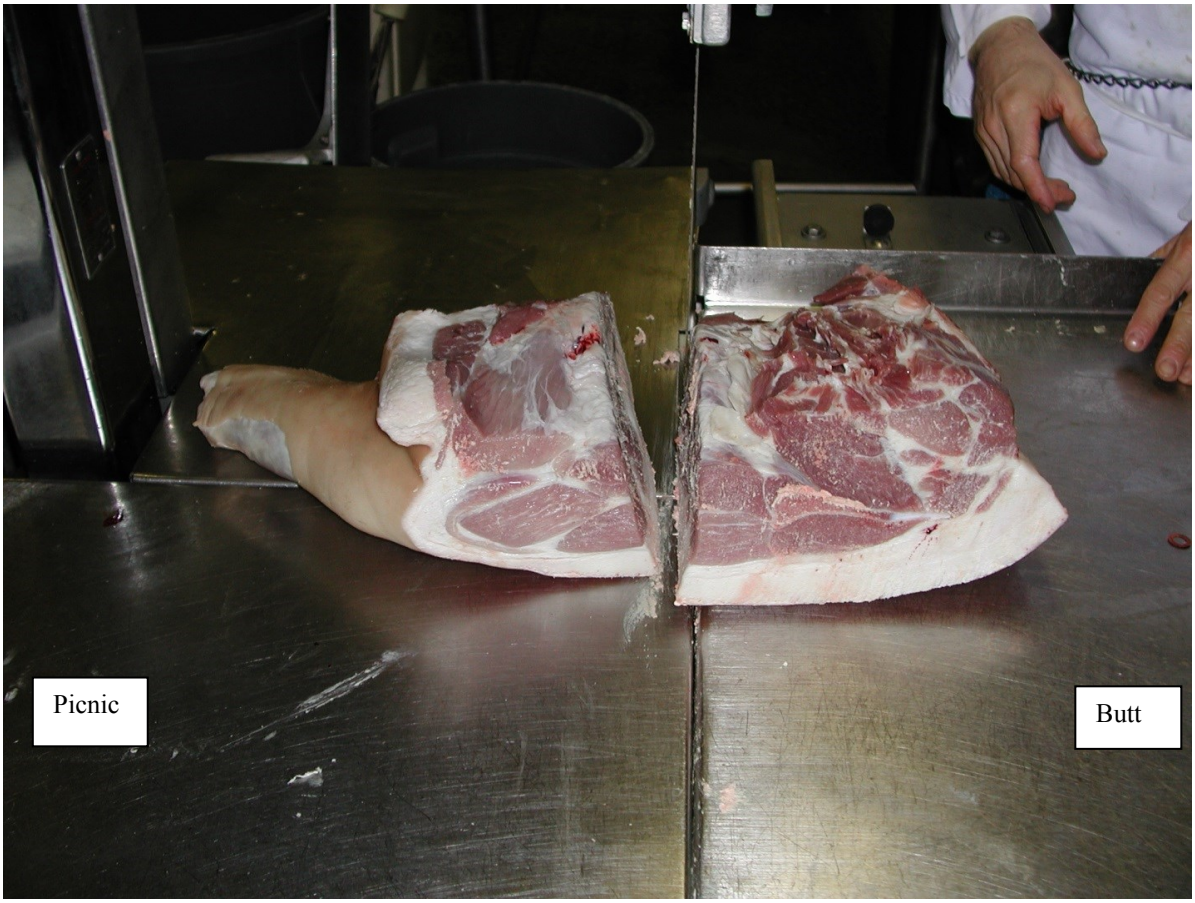

Figure 3.7: The separation of the shoulder into the Picnic and the Butt
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

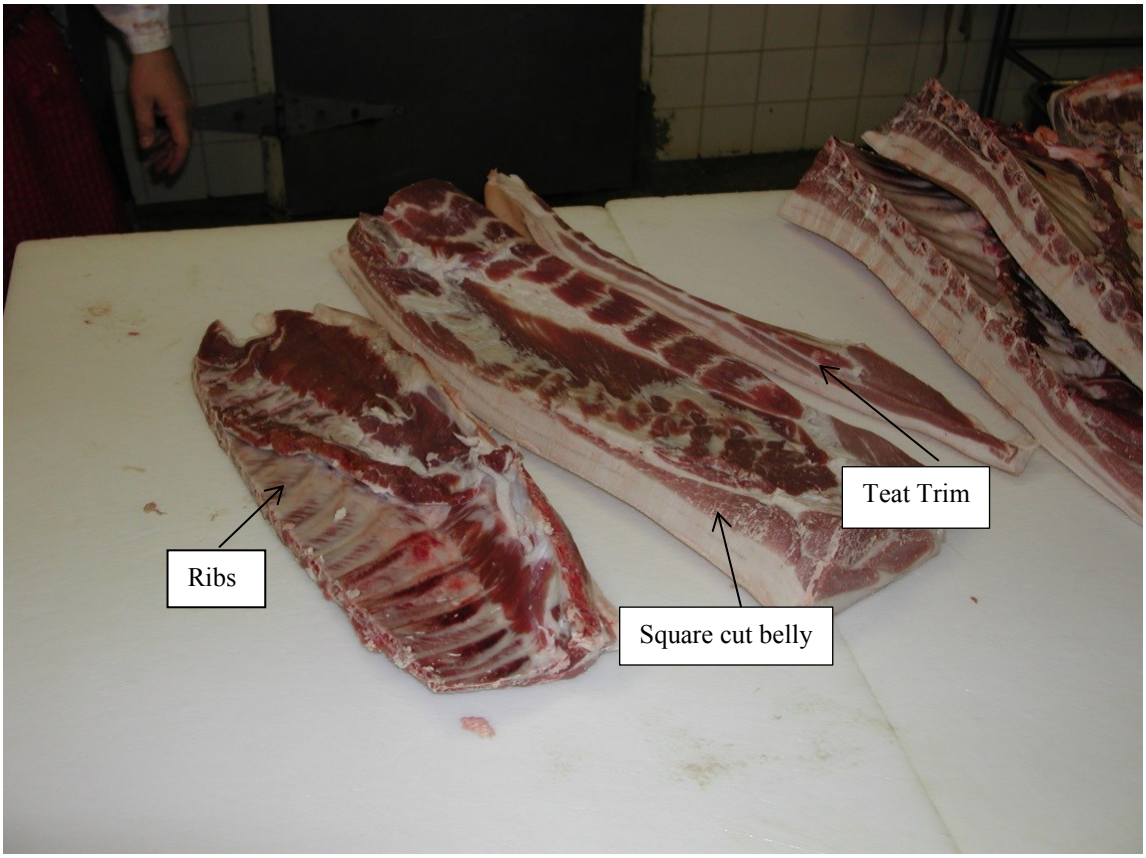

Figure 3.8: Square cut belly after removal of the ribs and treat trim
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

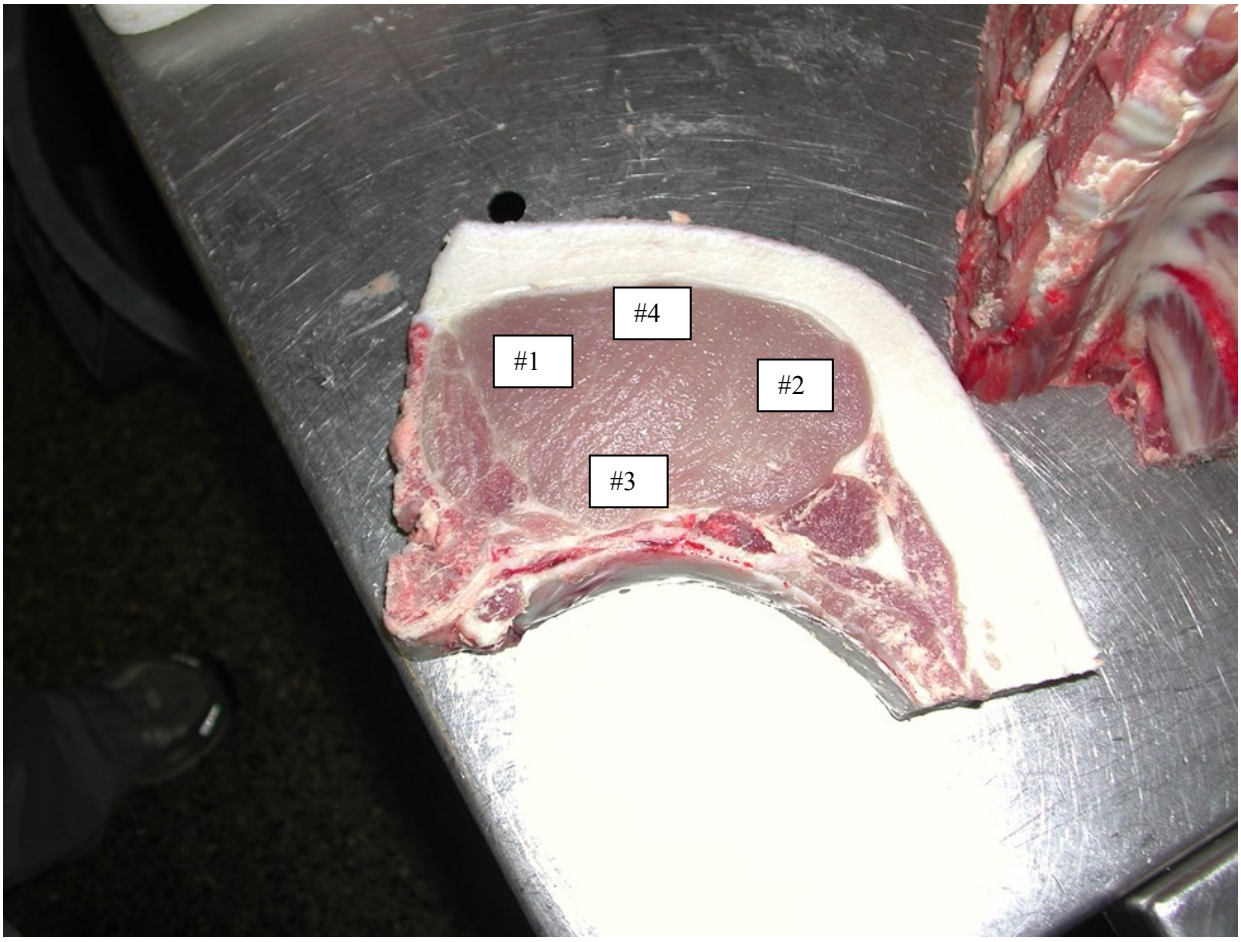

Figure 3.9: Four sites on a loin chop were used to measure Minolta L*, a*, and b*. Site#1 and #2 were used to take final pH
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

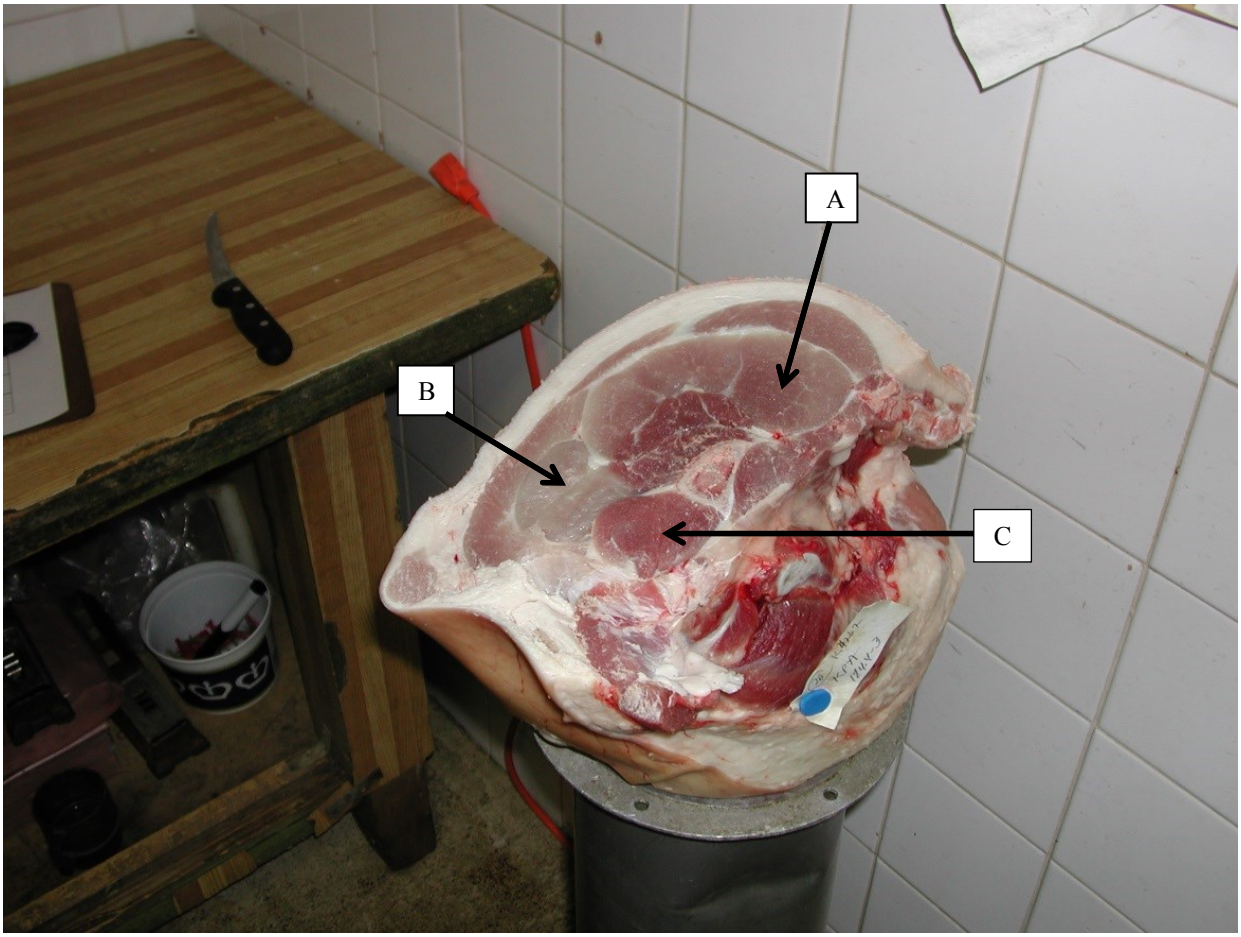

Figure 3.2: The Ham Face prior to Minolta Evaluation: A=Gluteus medius; B=Quadriceps femoris; C=Iliopsoas
(Courtesy of Dr. Bob McKay, McKay GENSTAT Consultants Inc.)

CHAPTER 4. Genetic and Phenotypic Correlations between Performance Traits with Meat Quality and Carcass Characteristics in Commercial Crossbred Pigs[1]

4.1. INTRODUCTION

Swine breeding programs have mainly focused on production efficiency to increase the leanness of the carcasses in previous decades. This has led to dramatic improvement in production efficiency including leanness and feed efficiency owing to relatively moderate-to-high heritabilities. However, the importance of meat and carcass quality is growing for pig breeders to meet processor's, packer's, and consumer's demands for better pork quality (Dransfield et al., 2005). Genetic correlations between pork quality and carcass characteristics and other economic important traits are, however, limited. Understanding of the genetic control of pork quality traits and their correlations with growth and performance traits are needed for Canadian swine populations to implement a successful breeding program that emphasizes product quality.

Meat quality traits are low-to-moderately heritable while carcass composition traits are moderate-to-highly heritable (Miar et al. 2014b). Latorre et al. (2008) stated that the relationships between meat quality traits and growth traits are contradictory. Cameron (1990) showed that selection for increased leanness reduced eating quality. Furthermore, weak negative genetic correlations between performance and meat quality traits have been reported and their magnitudes depend on breed (De Vries et al., 1994). Medium weight pigs at birth had better

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tenderness and water holding capacity than light weight piglets but the intramuscular fat was higher in light piglets (Rehfeldt et al., 2008). van Wijk et al. (2005) stated that average daily gain was unfavorably correlated with subprimal cuts and with most meat quality traits. Jiang et al. (2012) reported that different breeds in the Chinese swine industry had different meat quality and carcass characteristics. Various factors may influence the variance component estimates including the end-point adjustment, population size, sampling and available pedigree (Miar et al., 2014a). Phenotypic and genetic correlations between meat and carcass quality traits have been reported in the previous Chapter (Miar et al., 2014b). This study is a further investigation focusing on genetic and phenotypic correlations between performance traits with pork and carcass quality traits.

The objectives of this study were 1) to estimate heritabilities for various growth, and performance traits; and 2) to estimate phenotypic and genetic correlations between performance traits with pork quality and carcass traits in commercial crossbred pigs.

4.2. MATERIALS AND METHODS

The hogs used in this study were cared for according to the Canadian Council on Animal Care (CCAC, 1993) guidelines.

4.2.1. Animals and Management

The commercial crossbred pigs used in this study were progeny from a total of 139 sires of the Duroc boars bred to 429 F1 hybrid Landrace × Large White sows. These breeds were

chosen because they are representative of a large percentage of the Canadian swine industry. They were a combination of full and half sib families representing a multi-generation family structure drawn from two breeding populations (Genesus Genetics, and Hypor Inc., Canada). Pedigree information of 15 ancestral generations comprising 9,439 individuals was available (Miar et al., 2014b).

4.2.2. Performance Evaluation and Housing

Piglets were born over a 2-year period from 2010 to 2012. All piglets were individually tagged and weighed at birth (birth weight, **BW**), weaned at an average age of 21 days (7.5 kg), raised in a nursery for 5 to 6 weeks, and then moved to pre-grower barn for 4 weeks. During this time, both weaning weight (**WNW**) and nursery weight (**NURW**) were recorded. Pigs were then randomly allocated to finishing sites for 9 weeks under commercial finishing conditions with *ad libitum* access to a canola, wheat, barley, soybean diet and water (Miar et al., 2014b). Male piglets were castrated at 3 to 5 days after birth. The end body weight (**ENDW**), ultrasound backfat depth (**UFD**), ultrasound loin depth (**ULD**), and ultrasound intramuscular fat (**UIMF**) were measured at the end of finishing test with an average body weight of 115 kg. The live body weights recorded at the birth and end of finishing were used to calculate the average daily gain (**ADG**) using the following equation: ADG = (ENDW – start test weight)/Days. Feed conversion ratio (**FCR**) was calculated based on the daily feed intake recorded by electronic feeders for some animals.

4.2.3. Carcass and Meat Quality Measurements

Carcass and meat quality measurements have been described in the previous Chapter (Miar et al., 2014b). Briefly, pigs were housed overnight at the abattoir (East 40 Packers, Brandon, Manitoba, Canada) with *ad libitum* access to water. Animals were slaughtered on a federally-provincially inspected kill floor and handling of the animals upon arrival and before slaughter. Moreover, the slaughter process adhered to Government of Canada and Manitoba Guidelines. The average slaughter weight and age were 124 kg and 160 days, respectively. Hot carcass weight (**HCW**), cold carcass weight (**CCW**), and the carcass length (**CLEN**) were recorded according to Miar et al. (2014b). Then, the carcasses were broken into the primal cuts and the loin was further broken into the front, back, 3-rib sample, 1-inch chop, and 4-rib sample. The chop removed at 3rd and 4th last rib was used to determine: (a) *longissimus dorsi* muscle area (**LEA**); (b) subcutaneous backfat depth (**FD**); (c) loin depth (**LD**); (d) texture score (**TEXS**) measured on a subjective 5-point scale (1= extremely soft and weeping; 5 = very firm and dry; a score of 3 being normal) to determine if the loin was pale, soft and exudative (PSE); (e) subjective marbling score (**CMAR**; 1 to 6, with 0 = devoid, 1 = practically devoid, 2 = trace amount of marbling, 3 = slight, 4 = small, 5 = moderate, 6 = abundant) as determined by the National Swine Improvement Federation (NSIF) marbling charts (NSIF, 1997) as described in the previous Chapter (Miar et al., 2014b).

Primal cuts of loin, ham, shoulder and belly were dissected into subprimal cuts. Untrimmed side weight (**USW**) was determined as the sum of the weights of untrimmed ham, loin, shoulder, and belly. Untrimmed shoulder (**USH**), untrimmed ham (**UHAM**) were removed from the side weight. Untrimmed loin (**ULOIN**) and belly (**UBEL**) were separated from each other. Then, subprimal cuts of ham (**THAM**), loin (**TLOIN**), picnic shoulder (**PICN**), butt

(**BUTT**), belly (**TBEL**) and ribs (**RIBS**) were recorded as described in the previous Chapter (Miar et al., 2014b).

At the slaughterhouse, meat quality measurements were taken on *longissimus dorsi* muscle of the loin. Ultimate or 24 h pH (**PHU**), drip loss (**DL**), Minolta L*, a*, and b* (**LOINL**, **LOINA**, and **LOINB**) were taken on loin as described in the previous Chapter (Miar et al., 2014b). Minolta L*, a*, and b* measurements were taken on different muscles of ham including *gluteus medius* (**HGML**, **HGMA**, and **HGMB**), *quadriceps femoris* (**HQFL**, **HQFA**, and **HQFB**), and *iliopsoas* muscles (**HILL**, **HILA**, and **HILB**).

At the Meat Science Laboratory of University of Alberta, frozen 3-Rib and 4-Rib samples of the loin of each carcass were used to record whole loin weight (**WLW**), backfat weight (**BFW**), and rib eye weight (**REAW**) as described in the previous Chapter (Miar et al., 2014b). Rib eye area was used for subsequent pork quality assays. Rib eye Minolta L*, a*, and b* values (**REAL**, **REAA**, and **REAB**) were taken using a commercial color meter (CR400, Konica-Minolta, Osaka, Japan) on a D 65 light setting which mimics daylight (Miar et al., 2014b). Cooking loss (**CL**) and shear force (**SHF**) were measured as described in the previous Chapter (Miar et al., 2014b). The remainder of the loin was dissected into the muscle and fat (**RTW**), bone (**BOW**) and diaphragm.

4.2.4. Statistical Analyses

There were 6,408 pigs with growth and performance records with 2,100 of them having meat quality and carcass data. The significance of the fixed effects and covariates for each trait was determined using the REML procedure of ASREML 3.0 software (Gilmour et al., 2012).

The significance of different random terms in the model was determined by likelihood ratio test using ASREML 3.0 software (Gilmour et al., 2012). The full animal model included random direct, maternal additive genetic and common environment (litter of birth) effects. Maternal genetic and common environment effects were tested separately by comparing −2 residual log likelihoods of full and reduced (excluding the random effect of interest) models having degrees of freedom equal to the number of parameters tested. The model, which best fit the data was selected. Common litter effects were significant ($P<0.05$) for BW, WNW, NURW, ENDW, ADG, UFD, ULD, HCW, CCW, LEA, PH, and DL and were not significant ($P>0.05$) for most meat quality, and carcass composition traits (Miar et al., 2014b). The maternal effect was only significant ($P<0.05$) for WNW.

Genetic and phenotypic (co)variances were estimated using a pairwise bivariate animal model by ASREML 3.0 (Gilmour et al., 2012). Relevant fixed and random effects for carcass and meat quality traits were described in the previous Chapter (Miar et al., 2014b), and for performance traits are presented in Table 4.1. The final animal model included linear covariates of birth weight, whole loin weight received at the Meat Science Laboratory, cold carcass weight and slaughter age. Fixed effects including company, sex, and batch (test or slaughter batch) were fitted in the final model. In addition, additive polygenic effects for all traits, random litter effect, and maternal effect for some traits were included in the final model. The model is given by:

$$y = Xb + Z_1a + Z_2m + Z_3c + e,$$

where $\boldsymbol{y}$ is the vector of phenotypic measurements, $\boldsymbol{X}$ is the incidence matrix relating the fixed effects to vector $\boldsymbol{y}$, $\boldsymbol{b}$ is the vector of fixed effects, Z_1 is the incidence matrix relating the

phenotypic observations to the vector of polygenic (**a**) effects, Z_2 is the incidence matrix relating the phenotypic observations to the vector of maternal genetic (**m**) effects, Z_3 is the incidence matrix relating the phenotypic observations to the vector of common litter (**c**) effects, and **e** is the vector of random residuals.

It was assumed that random effects were independent except for the covariance between the direct and the maternal additive genetic effects. In particular, the (co)variances of random variables were as follows:

$$V\begin{bmatrix} a_1 \\ a_2 \\ m_1 \\ m_2 \\ c_1 \\ c_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a1} & A\sigma_{a12} & A\sigma_{a1m1} & A\sigma_{a1m2} & 0 & 0 & 0 & 0 \\ . & A\sigma^2_{a2} & A\sigma_{a2m1} & A\sigma_{a2m2} & 0 & 0 & 0 & 0 \\ . & . & A\sigma^2_{m1} & A\sigma_{m1m2} & 0 & 0 & 0 & 0 \\ . & . & . & A\sigma^2_{m2} & 0 & 0 & 0 & 0 \\ . & . & . & . & I\sigma^2_{c1} & I\sigma_{c1c2} & 0 & 0 \\ . & . & . & . & . & I\sigma^2_{c2} & 0 & 0 \\ . & . & . & . & . & . & I\sigma^2_{e1} & I\sigma_{e12} \\ . & . & . & . & . & . & . & I\sigma^2_{e2} \end{bmatrix},$$

where ***A*** is the numerator relationship matrix, ***I*** is the identity matrix, σ^2_{a1}, σ^2_{a2}, σ^2_{m1}, σ^2_{m2}, σ^2_{c1}, σ^2_{c2}, σ^2_{e1} and σ^2_{e2} are direct additive genetic variances, maternal genetic variances, common litter effect variances and residual variance for traits 1 and 2, respectively, and σ_{am} is the covariance between the direct and the maternal additive genetic effects. Variance components obtained from the bivariate analyses used to estimated heritability for each performance trait and the average estimates of corresponding pairwise bivariate analyses were reported as the heritabilities:

$$h^2 = \frac{\sigma^2_a}{\sigma^2_p}$$

A preliminary univariate animal model for each trait was performed to obtain initial values of variance parameters that were then used in subsequent bivariate analyses. Initial values of covariance parameters were obtained by multiplying their standard deviations by their phenotypic or genetic correlations. Pairwise bivariate analyses were performed between performance traits with carcass and pork quality traits. The 2-trait individual animal model used to estimate (co)variance components, were used to calculate the phenotypic and genetic correlations as well as the heritability as implemented in ASREML 3.0 (Gilmour et al., 2012).

4.3. RESULTS AND DISCUSSION

4.3.1. Means and standard deviations

Most of the performance, carcass and pork quality traits were recorded for all individuals within group. Means, standard deviations, number of measurements per trait, minimum and maximum for each performance trait are given in Table 4.2. The descriptive statistics for meat quality and carcass traits were previously reported in Chapter 3 (Miar et al., 2014b).

4.3.2. Heritabilities

Heritability estimates for performance traits with their standard errors are presented in Table 4.3 (diagonal elements). Univariate estimates of heritability for all traits were similar to the bivariate estimates. Moderate heritability was obtained for most of the performance traits with

the estimates of 0.26, 0.24, 0.38, 0.30, 0.45, 0.38, 0.26, and 0.20 for BW, NURW, ENDW, ADG, UFD, ULD, UIMF, and FCR (Table 4.3). Weaning weight had a lower heritability of 0.07 in this study. These estimates were within the range (0.00 – 0.74) of the heritability values previously reported for growth and performance traits (Cassady et al., 2002; Clutter, 2011). Several factors influence the heritability estimates, which may include the end-point adjustment such as age or weight adjustment, sampling, population size, effect of heterosis on crossbred populations and the completeness of pedigree (Miar et al., 2014a), which may result in the various estimates among the different literature. The low-to-moderate heritability estimated from this study revealed that genomic technology can play an important role for improvement of these economically important traits.

The estimated heritability for BW (0.26±0.08) in this study was higher than the estimates from many other works (Roehe, 1999; Cassady et al., 2002; Knol et al., 2002; Arango et al., 2006), but lower than the report (0.36) by Roehe et al. (2010), who used two-generations of outdoor reared piglets and suggested that direct heritability estimates were substantially larger under outdoor conditions. However, the estimate from the first generation of outdoor piglets also reported by Roehe et al. (2009) was lower (0.20), which is close to our estimate from the crossbred population. Another difference is that Roehe et al (2009; 2010) used a Bayesian method while we used an animal model. These results revealed that the breed, population structure and statistical method have an important effect on the genetic parameter estimate. The estimated heritability of WNW in this study (0.07±0.07) was in agreement with literature values (Kaufmann et al., 2008). The estimated maternal heritability for WNW was 0.10±0.03, which was similar to 0.17 reported by Cassady et al. (2002). Cassady et al. (2002) estimated the heritability as 0.00 to 0.10 in two different genetic types. According to these studies, the

maternal effect was a more important component of the genetic variation of weaning weight than the direct additive genetic effect. This may be due to effects of milk production, uterine capacity and nutrition to weaning (Kaufmann et al., 2008). The reports for genetic parameter estimates for NURW and ENDW are very limited, although they are important indicators to determine the production efficiency in the swine industry. The average ENDW was 110 (SD = 10) kg and this off test weight was not considered for heritability estimations in the literature. The NURW and ENDW heritability estimates were 0.24±0.16, and 0.38±0.18, respectively. The heritability for weight increased (0.07 to 0.38) from weaning to 160 days of age showing that the maternal genetic variance decreased as the pigs grew. This result is expected due to the separation of pigs from their dams. The common litter environment effect was fitted in the animal models for all performance traits except for UIMF and FCR.

ADG has been reported as a moderately heritable trait. The heritability estimate in this study is 0.30±0.08, which is in agreement with many other reports (Kaufmann et al., 2008; Clutter, 2011). However, van Wijk et al. (2005) reported a lower heritability of 0.19, which may be due to the different evaluation of ADG. van Wijk et al. (2005) calculated the ADG based on the carcass weight and the assumption of the same birth weight of 1.36 kg for all animals, which could narrow down the sample variance and result in the low heritability estimation. Genetic parameters for ADG were widely studied and the reported estimates vary considerably, ranging from 0.03 to 0.49 (Cameron et al., 1988; Lo et al., 1992; Gilbert et al., 2007; Hoque et al., 2007; Cai et al., 2008). The heritability of UFD in this study (0.45±0.07) was in good agreement with the previous report of 0.44-0.54 (Clutter and Brascamp, 1998; van Wijk et al., 2005). Stewart and Schinckel (1991) reviewed many papers and reported a weighted average heritability of 0.41 for backfat. The heritability estimate of ULD in the present study (0.38±0.07) was the same as

the report (0.38) by Maignel et al. (2010) who used a similar typical Canadian three-way cross population and sample size as in the current study. However, the present estimate was slightly lower than the estimates of 0.47 and 0.48 reported by Stewart and Schinckel (1991) and Ducos (1994), respectively.

Marbling is one of the most important appearance factors used by consumers to perceive quality because it affects purchase decisions and perceived satisfaction of consumption (Brewer et al., 2001). The amount of marbling depends on implementation of different pig breeding and management techniques (Lo et al., 1992), which may be one of the reasons for the variation observed in the estimation of UIMF. The heritability of UIMF was moderate in the present study (0.26±0.06). UIMF has previously been reported to be a moderately heritable trait, ranging from 0.13 to 0.31, which was in agreement with the current result (Lo et al., 1992; Gibson et al., 1998; Sonesson et al., 1998; Schwab et al., 2009). The estimated heritability of FCR in this study was 0.20±0.06, which was lower than the average of 0.30 reviewed by Clutter (2011), which may be due to using different statistical models, breeds and sample size.

Generally, meat quality traits had low-to-moderate (0.10±0.04 to 0.39±0.06) heritabilities while carcass composition traits had moderate-to-high (0.22±0.08 to 0.63±0.04) heritabilities. The details can be found in the previous Chapter, which was conducted on the same population (Miar et al., 2014b).

4.3.3. Correlations among Traits

The phenotypic and genetic correlations and their standard errors are presented in Tables 4.3-4.7. Generally, almost all of the phenotypic correlations and some of the genetic correlations

were significant ($P<0.05$). Although presented for completeness, phenotypic correlations will not be discussed because they are of little interpretive value.

4.3.3.1. Correlations among Growth and Performance Traits

The phenotypic and genetic correlations among growth and performance traits are presented in Table 4.3. Almost all of the phenotypic correlations between performance traits were significant ($P<0.05$). Genetic correlations indicated that selection for increased growth rate could increase ULD (0.31±0.13), UIMF (0.69±0.25), and UFD (0.26±0.12). Growth is in general lowly and negatively correlated with backfat thickness but favourably correlated with marbling and loin depth. The ADG and FD are the most important traits of performance testing, and the genetic correlation between them (0.01±0.14) is in the range of estimates (-0.26 to 0.55) reviewed by Clutter (2011). The wide range of genetic correlations between ADG and UFD reported by Clutter (2011) may be due to the method of measurement, technician effect, breed differences, and sampling errors (Koots and Gibson, 1994). These results suggested that breeding programs aimed at improving intramuscular fat should expect improvement (higher marbling) through the selection for growth. Suzuki et al. (2005) reported a low genetic correlation of 0.06 between UIMF and ADG that is lower than this study, which may be due to using the smaller samples size and purebred Duroc in their study. We highlight that the genetic correlation between ADG and ULD is a new contribution to our knowledge.

Birth weight had strong genetic correlations with ENDW (0.79±0.40) and ULD (0.75±0.36). Generally, genetic correlations of ENDW with performance traits were significant ($P<0.05$) except for the correlations with NURW and FCR. ENDW had high genetic correlations

with BW (0.79±0.40), WNW (0.93±0.45), ADG (0.87±0.04), and UIMF (0.60±0.27). None of these genetic correlations were previously reported and it seems that selection for BW, WNW, and ADG will lead to increased ENDW and UIMF. Low-to-moderate correlations were found between ENDW with UFD (0.28±0.13), and ULD (0.37±0.12). Genetic correlations of ENDW with these traits were not reported in the literature. UFD had moderate genetic correlation with ULD (-0.33±0.14). This result was similar to the average value of -0.35 reported by Clutter and Brascamp (1998) and -0.45 by Newcom et al. (2002).

In addition, UIMF was moderately to highly correlated with NURW (0.75±0.35), ENDW (0.60±0.27), ADG (0.69±0.25), UFD (0.48±0.19), and ULD (-0.47±0.20). However, no genetic correlations were found for NURW and ENDW (-0.01±0.44) but these results confirmed that selection based on NURW would increase UIMF. These results also imply that increased backfat and decreased loin depth may be expected when selection is directed toward increased marbling. FCR was also moderately correlated with UFD (0.39±0.17), indicating that selection for decreased FCR may result in decreased backfat depth. Although the genetic correlation between ADG and FCR was not significant in the present study, a moderate to high and negative genetic correlation was reported by Clutter (2011). This difference may result from differences in sample size, breeds, and the feeding type. The nature of this discrepancy was not investigated further within the present study, but it warrants further examination.

4.3.3.2. Correlations between Performance and Carcass Traits

The phenotypic and genetic correlations between performance and carcass traits are presented in Tables 4.4-4.5. Almost all of the phenotypic correlations between performance and carcass traits were significant ($P<0.05$). Although pork quality importance is increasing, pig

breeders are only paid for carcass yield. Results of genetic correlations indicated that selection for BW would reduce the amount of backfat depth (-0.69±0.30), which was different from the report by Fix et al. (2010) who demonstrated no significant (*P>0.05*) genetic correlation between BW and FD. The differences may be due to different statistical models.

However, selection for WNW and NURW would increase loin depth because of their moderate to high genetic correlations (0.39±0.14 and 0.69±0.27), respectively. To our knowledge, these estimates in the present study are a new contribution to the literature. Weaning weight had low genetic correlations with THAM, TBEL, and PICN (0.17±0.08, 0.19±0.05, and 0.27±0.13, respectively). Nursery weight was highly correlated with subprimal cuts including TBEL (0.91±0.11), PICN (0.94±0.13), BUTT (0.94±0.17), and RIBS (0.94±0.32). This implies that selection for high nursery weight will also lead to increased belly, picnic shoulder, and butt muscle yield. This study also indicates that the NURW should be recorded in pig breeding programs as an indicator trait for subprimal cuts selection. However, no genetic correlations for WNW and NURW with carcass traits were found in the literature.

Average daily gain is one of the most important traits of selection in the pig breeding programs. Based on the estimates of this study, genetic correlations between ADG and carcass yield were moderate to high, and selection on ADG would have favorable effects on carcass yield. In general, growth is moderately to highly correlated (averaging 0.47) with primal and subprimal cut weights. These results indicated that selection for higher growth could have an increasing effect on the most valuable primal and subprimal weights. However, our results were not in agreement with van Wijk et al. (2005) who reported adverse effects (on an average of -0.29) of growth on some primal and subprimal weights. The discrepancy might be due to the different genetic background, less pedigree information, and smaller sample size in their study.

In addition, growth is highly correlated to HCW (0.75±0.28) and CCW (0.78±0.27), which were not reported previously.

This study revealed that ultrasound measurements of backfat thickness, marbling score, and loin depth have moderate to strong genetic correlations with their corresponding measurements of carcass merit. The weakest genetic correlation (0.39±0.12) between ultrasound measures and their corresponding carcass measurements was observed between ULD and LD. This may be due to the difficulty of ultrasonic measurement of loin depth compared to backfat depth and marbling. Ultrasound backfat depth was correlated with UBEL (0.29±0.13), TBEL (0.29±0.13), and PICN (0.29±0.14). Again, to our knowledge, these estimates are new and imply that selection against ultrasound backfat depth would not necessarily reduce belly and picnic shoulder weights.

Low genetic correlations were estimated for ULD with HCW (0.20±0.10), USW (0.26±0.13), UHAM (0.29±0.13), ULOIN (0.26±0.13), PICN (0.23±0.11), and BUTT (0.34±0.13). These new results indicated that selection for high ultrasound loin depth may result in higher carcass, primal and subprimal yield including ham, loin, picnic shoulder and butt weight. High genetic correlations were also found between UIMF with TBEL (0.75±0.22), PICN (0.77±0.25), and BUTT (0.82±0.22). These imply that selection for high UIMF results in high trimmed belly, picnic shoulder and butt weight. This may be due to a similar pattern of intramuscular fat deposition in these subprimal cuts. Feed conversion ratio was only correlated with TLOIN, indicating that selection for low FCR has no significant effect on carcass traits except of TLOIN (0.44±0.26). However, these results need to be further confirmed in a larger sample with FCR records.

4.3.3.3. Correlations between Performance and Meat Quality Traits

The phenotypic and genetic correlations between performance and meat quality traits are presented in Tables 4.6-4.7. Almost all of the phenotypic correlations between performance and meat quality traits were significant ($P<0.05$). However, a few significant ($P<0.05$) genetic correlations were found that can explain the hypothesis of negative effect of selection for performance traits on pork quality.

Several novel aspects were derived from this study in terms of the genetic correlation of birth weight, weaning weight, and nursery weight with pork quality. High genetic correlations were observed between BW with LOINL (0.76±0.37), LOINB (0.86±0.43), HGML (0.80±0.31), and DL (0.93±0.42). These results imply that selection for birth weight may increase drip loss, which could result in lighter color of loin *longissimus dorsi*, and ham *gluteus medius* muscles. No genetic correlations between BW and meat quality traits were found in the published literature. However, selection for high WNW does not affect pork quality but may increase the REAW (0.20±0.07), RTW (0.34±0.14), and BOW (0.46±0.17). These results indicate that selection for WNW will have no negative effects on pork quality. Moderate to high genetic antagonism was observed between NURW with CL (-0.51±0.24), and HGML (-0.69±0.35), which were also novel in this study. These results indicate that selection for high nursery weight will result in low cooking loss and lighter color of ham *gluteus medius.* However, NURW had low-to-moderate and favorable genetic correlations with other pork quality traits, indicating that selection for NURW does not have adverse effects on pork quality according to our study. The high genetic correlation found between NURW and BFW, indicating that selection for NURW will increase the backfat weight of rib eye area muscle.

Average daily gain, which is one of the main selection criteria in swine breeding, had no genetic correlations with any of the pork quality traits except for BOW and RTW, indicating that deterioration of pork quality was not occurring through selection for increasing ADG in these two populations. This is different to the report by van Wijk et al. (2005) who showed unfavorable strong genetic correlations between growth rate and pork quality traits. However, De Vries et al. (1994) and Hermesch et al. (2000) reported no genetic correlation between growth and pork quality traits, which are similar to our results. In addition, ADG was correlated with RTW (0.32±0.16), and BOW (0.43±0.19) of rib eye area, which are also novel in this study. Ultrasound backfat depth was negatively correlated to REAW (-0.75±0.11), RTW (-0.66±0.11), BOW (-0.45±0.17), and CL (-0.41±0.13) but positively correlated to BFW (0.89±0.05). Low to moderate genetic correlations were also found between UFD with REAL (0.24±0.12), REAB (0.24±0.12), HILL (0.34±0.13), and HILB (0.33±0.14). These results indicate that selection for leaner carcass will not affect pork quality traits except for cooking loss and rib eye weight (Table 4.7). Most of the color traits were favorably correlated with UFD except for the lightness and yellowness of *iliopsoas* muscle of ham.

Unfavorable moderate genetic correlation was observed between ULD and PHU (-0.49±0.24). This was also different to the genetic correlation between carcass loin depth and pH observed by van Wijk et al. (2005). This might be due to the different method of loin depth measurement, genetic background, less pedigree information, and smaller sample size in their study. This indicates that single-trait selection on ultrasound loin depth may lead to undesirable lower pH pork. However, this result was similar to the genetic correlation between carcass loin depth and pH in this population (Miar et al., 2014b). Ultrasound loin depth was also correlated to REAW (0.66±0.10) and BOW (-0.36±0.18), which were not reported before. Unfavorable strong

genetic correlations were obtained between UIMF with PHU (0.73±0.37), REAB (0.77±0.18), and HGMB (0.73±0.36). This indicates that selection on ultrasound intramuscular fat may lead to undesirable higher pH of meat with darker color. However, cooking loss was negatively correlated to UIMF (-0.67±0.26), indicating that increased UIMF will result in decreased cooking loss. Feed conversion ratio was only correlated with LOINL, indicating that selection for low FCR does not change pork quality except of lightness of loin (0.43±0.19). Genetic correlations between FCR and pork quality traits obtained in this study may be biased due to the small dataset available for FCR.

4.4. IMPLICATIONS

Meat quality and carcass yield are important traits for the pork industry with consumers paying more attention to quality as well as value. Measurements of carcass and pork quality traits are difficult and expensive and can only be performed post-mortem. Genetic improvement of these traits is possible through indirect selection on performance traits, which requires knowledge of genetic parameters for these traits. However, the estimates of genetic correlations between carcass and pork quality with performance traits are limited despite its importance because the lack of measurement records of carcass and pork quality traits. In addition, segregation of the alleles from major loci is affecting the variation of pork quality traits in certain populations (Ciobanu et al., 2011). Therefore, understanding of genetic parameters for performance, pork quality, and carcass traits is essential for Canadian swine populations to implement efficient selection programs that emphasize product quality.

Genetic parameters obtained herein are valuable for the design of a breeding program emphasizing product quality in Canadian swine population. The low-to-moderate heritabilities of performance traits indicated that they could be improved using traditional breeding methods or genomic selection. Selection for high birth weight would have unfavorable consequences on pork quality traits including undesirable higher drip loss pork with paler color. It was concluded that selection for nursery weight would increase both quantity and quality traits. Furthermore, selection for ADG is also favorable for increasing carcass weight, primal and subprimal cuts weights with no adverse effects on pork quality. However, selection for intramuscular fat may affect pork quality traits but selection for FCR may reduce the lightness of loin. These results imply that selection for leaner carcass may affect cooking loss and lightness of ham. Although these results indicated that deterioration of pork quality may have occurred over many generations through the selection for lower backfat thickness and increased feed efficiency, selection for growth had no adverse effects on pork quality traits. The genetic parameters identified here are valuable for understanding the biology of these traits making it possible to improve them simultaneously resulting in high quality product produced efficiently and at decreased cost.

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Table 4.1. Significance of the fixed and random effects included in the models for the analysis of Performance Traits

Traits	Fixed Effects				Random Effects		
	Company	Sex	Batch	BW[1]	Dam	Litter	Animal
Birth weight	**	**	**	-	NS	**	✓
Weaning weight	**	*	**	**	**	**	✓
Nursery weight	NS	**	**	**	NS	**	✓
End weight	*	**	**	-	NS	**	✓
ADG	**	**	**	-	NS	**	✓
Ultrasound backfat	*	**	**	-	NS	**	✓
Ultrasound loin	**	*	**	-	NS	**	✓
Ultrasound IMF	**	**	**	-	NS	NS	✓
Feed conversion ratio	NS	**	**	-	NS	NS	✓

***P<0.05; * P<0.1; NS: Non-significant.*

[1] *Birth weight.*

Table 4.2. Descriptive statistics for performance traits: number of animals per trait (n), means, SD, minimum (Min.) and maximum (Max.) values

Traits	n	Mean	SD	Min.	Max.
Birth weight, kg	6408	1.53	0.35	0.50	2.90
Weaning weight, kg	5918	6.9	1.41	1.24	12.20
Nursery weight, kg	2262	37.58	7.70	10.00	60.00
End weight, kg	5004	109.88	10.24	67.40	147.00
ADG, g/d	4436	976.60	145.32	351.00	1492.00
Ultrasound backfat depth, mm	4810	13.73	3.17	5.20	28.70
Ultrasound loin depth, mm	4811	63.15	5.62	40.90	82.20
Ultrasound IMF	1807	1.26	0.83	0	6.60
Feed conversion ratio	708	2.64	0.30	1.55	4.06

Table 4.3. Estimates of genetic (below diagonal), phenotypic (above diagonal) correlations, heritabilities (diagonal) and their standard error of estimates among performance traits

Traits[1]	BW	WNW	NURW	ENDW	ADG	UFD	ULD	UIMF	FCR
BW	***0.26±0.08***	**0.69±0.06**[2]	**0.47±0.03**	**0.25±0.04**	**0.42±0.04**	-0.05±0.04	**0.10±0.04**	**0.13±0.05**	-
WNW	-0.00±0.74	*0.07±0.07*	**0.19±0.03**	**0.31±0.02**	**0.22±0.08**	**0.26±0.02**	**0.16±0.02**	**0.25±0.06**	-
NURW	-0.05±0.74	0.02±0.83	*0.24±0.16*	**0.50±0.03**	**0.52±0.03**	**0.26±0.02**	**0.18±0.04**	**0.47±0.06**	-
ENDW	**0.79±0.40**	**0.93±0.45**	-0.01±0.44	***0.38±0.08***	**0.80±0.01**	**0.31±0.02**	**0.41±0.02**	**0.36±0.04**	**0.33±0.04**
ADG	-0.68±0.70	0.06±0.67	-0.03±0.45	**0.87±0.04**	***0.30±0.08***	**0.27±0.02**	**0.31±0.02**	**0.32±0.03**	**0.31±0.04**
UFD	-0.36±0.40	0.03±0.83	-0.47±0.86	**0.28±0.13**	**0.26±0.12**	***0.45±0.07***	**0.08±0.02**	**0.34±0.04**	**0.28±0.04**
ULD	**0.75±0.36**	0.04±0.79	-0.48±0.49	**0.37±0.12**	**0.31±0.13**	**-0.33±0.14**	***0.38±0.07***	0.10±0.07	**0.21±0.05**
UIMF	0.33±0.39	0.00±0.72	**0.75±0.35**	**0.60±0.27**	**0.69±0.25**	**0.48± 0.19**	**-0.47±0.20**	***0.26±0.06***	-
FCR	-	-	-	0.04±0.21	-0.19±0.20	**0.39±0.17**	0.05±0.21	-	***0.20±0.06***

[1] ***BW*** *= Birth weight (kg);* ***WNW*** *= Weaning weigh (kg);* ***NURW*** *= Nursery weight (kg);* ***ENDW*** *= End weight (kg);* ***ADG*** *= Average daily gain (g/d);* ***UFD*** *= Ultrasound backfat depth (mm);* ***ULD*** *= Ultrasound loin depth (mm);* ***UIMF*** *=Ultrasound IMF;* ***FCR*** *= Feed conversion ratio.*

[2] *The significant correlations are bolded (P<0.05).*

Table 4.4. Estimates of phenotypic correlations and their standard error of estimates between carcass and performance traits

Traits[1]	BW	WNW	NURW	ADG	UFD	ULD	UIMF	FCR
HCW	0.02±0.05	0.04±0.05	-0.03±0.04	**0.37±0.02**[2]	**0.14±0.03**	**0.16±0.03**	**0.40±0.05**	**0.41±0.05**
CCW	0.02±0.05	0.04±0.05	-0.03±0.05	**0.37±0.02**	**0.13±0.03**	**0.16±0.03**	**0.40±0.05**	**0.41±0.05**
FD	-0.06±0.05	-0.07±0.04	**0.28±0.06**	**0.34±0.03**	**0.37±0.03**	**0.16±0.04**	-0.05±0.04	**0.32±0.05**
LD	0.07±0.04	**-0.09±0.04**	0.06±0.06	**0.32±0.03**	**-0.06±0.03**	**0.15±0.03**	0.03±0.04	-0.09±0.06
CLEN	0.00±0.05	0.01±0.05	**0.19±0.08**	**0.36±0.05**	**0.09±0.04**	**0.15±0.07**	0.04±0.05	-0.09±0.07
LEA	-0.01±0.05	-0.02±0.04	-0.00±0.04	**0.07±0.03**	**-0.10±0.03**	**0.12±0.03**	**0.32±0.06**	**0.27±0.07**
TEXS	**0.18±0.07**	-0.05±0.04	**0.41±0.08**	**0.32±0.03**	**0.17±0.05**	**0.19±0.05**	0.04±0.04	0.04±0.05
CMAR	0.05±0.05	-0.03±0.06	**0.36±0.09**	**0.33±0.03**	**0.15±0.05**	**0.17±0.05**	0.00±0.04	**0.12±0.05**
USW	0.02±0.05	0.04±0.05	**0.19±0.08**	**0.39±0.04**	**0.19±0.05**	**0.26±0.06**	0.04±0.04	0.09±0.07
UHAM	0.10±0.06	0.03±0.05	**0.37±0.09**	**0.34±0.05**	**0.26±0.07**	**0.31±0.07**	0.05±0.04	0.02±0.07
ULOIN	0.01±0.05	-0.01±0.05	**0.27±0.09**	**0.35±0.05**	**0.22±0.06**	**0.28±0.07**	0.02±0.04	0.14±0.08
USH	**0.12±0.06**	**0.09±0.04**	**0.36±0.10**	**0.36±0.05**	**0.24±0.08**	**0.29±0.07**	0.01±0.04	0.09±0.07
UBEL	0.07±0.06	-0.02±0.05	**0.37±0.10**	**0.35±0.05**	**0.33±0.07**	**0.30±0.07**	0.03±0.04	**0.18±0.07**
THAM	**0.17±0.05**	**0.17±0.04**	**0.35±0.10**	**0.35±0.05**	**0.23±0.08**	**0.28±0.08**	0.00±0.04	0.02±0.09
TLOIN	0.03±0.06	-0.01±0.05	**0.33±0.10**	**0.34±0.05**	**0.19±0.08**	**0.28±0.08**	0.04±0.04	0.03±0.10
TBEL	**0.24±0.05**	**0.14±0.04**	**0.53±0.04**	**0.29±0.04**	**0.33±0.07**	**0.32±0.07**	**0.18±0.04**	**0.26±0.08**
PICN	**0.35±0.06**	**0.12±0.05**	**0.42±0.06**	**0.28±0.04**	**0.33±0.07**	**0.29±0.07**	**0.11±0.04**	0.06±0.07
BUTT	**0.39±0.07**	**0.11±0.04**	**0.43±0.06**	**0.31±0.05**	**0.30±0.07**	**0.28±0.07**	**0.11±0.04**	-0.02±0.06
RIBS	**0.54±0.09**	**0.16±0.07**	**0.40±0.09**	**0.32±0.05**	**0.32±0.07**	**0.29±0.07**	**0.22±0.07**	0.06±0.07

[1] ***BW*** *= Birth weight (kg);* ***WNW*** *= Weaning weigh (kg);* ***NURW*** *= Nursery weight (kg);* ***ENDW*** *= End weight (kg);* ***ADG*** *= Average daily gain (g/d);* ***UFD*** *= Ultrasound backfat depth (mm);* ***ULD*** *= Ultrasound loin depth (mm);* ***UIMF*** *=Ultrasound IMF;* ***FCR*** *= Feed conversion ratio;* ***HCW*** *= Hot carcass weight (kg);* ***CCW*** *= Cold carcass weight (kg);* ***FD*** *= Backfat depth (mm);* ***LD*** *= Loin depth (mm);* ***CLEN*** *= Carcass length (cm);* ***LEA*** *= Longissimus dorsi muscle area (cm^2);* ***TEXS*** *= Texture score;* ***CMAR*** *= Carcass marbling score;* ***USW*** *= Untrimmed side weight (kg);* ***UHAM*** *= Untrimmed ham weight (kg);* ***ULOIN*** *= Untrimmed loin weight (kg);* ***USH*** *= Untrimmed shoulder weight (kg);* ***UBEL*** *= Untrimmed belly weight (kg);* ***THAM*** *= Trimmed ham weight (kg);* ***TLOIN*** *= Trimmed loin weight (kg);* ***TBEL*** *= Trimmed belly weight (kg);* ***PICN*** *= Trimmed picnic shoulder weight (kg);* ***BUTT*** *= Butt shoulder weight (kg);* ***RIBS*** *= Ribs weight (kg).*

[2] *The significant correlations are bolded ($P<0.05$).*

Table 4.5. Estimates of genetic correlations and their standard error of estimates between carcass and performance traits

Traits[1]	BW	WNW	NURW	ADG	UFD	ULD	UIMF	FCR
HCW	0.19±0.84	-0.06±0.13	-0.94±0.89	**0.75±0.28**[2]	0.11±0.34	**0.20±0.10**	0.47±0.41	0.15±0.28
CCW	0.40±0.74	-0.07±0.12	-0.93±0.89	**0.78±0.27**	0.05±0.33	0.39±0.30	0.54±0.40	0.15±0.27
FD	**-0.69±0.30**	-0.85±0.68	-0.18±0.40	0.01±0.14	**0.53±0.12**	0.10±0.13	-0.22±0.28	0.20±0.20
LD	0.32±0.26	**0.39±0.14**	**0.69±0.27**	-0.10±0.13	-0.02±0.12	**0.39±0.12**	0.16±0.24	0.30±0.20
CLEN	0.18±0.59	-0.07±0.13	-0.18±0.33	**0.44±0.14**	0.05±0.14	0.10±0.13	0.15±0.23	-0.21±0.18
LEA	-0.25±0.73	-0.08±0.14	0.80±0.71	0.10±0.27	0.12 ±0.30	0.47±0.27	0.57±0.38	0.33±0.24
TEXS	-0.34±0.48	0.11±0.26	-0.29±0.42	-0.36±0.20	0.09±0.20	-0.24±0.20	-0.64±0.48	-0.03±0.33
CMAR	-0.38±0.34	-0.09±0.12	-0.32±0.31	0.05±0.15	-0.16±0.14	-0.09±0.14	**0.59±0.28**	0.38±0.23
USW	-0.19±0.26	-0.08±0.13	-0.10±0.33	**0.43±0.14**	0.09±0.14	**0.26±0.13**	0.24±0.24	0.18±0.17
UHAM	-0.18±0.26	-0.06±0.13	0.01±0.31	**0.34±0.14**	0.11±0.14	**0.29±0.13**	0.30±0.24	0.15±0.18
ULOIN	-0.25±0.19	-0.11±0.11	-0.01±0.26	0.13±0.13	0.14±0.13	**0.26±0.13**	0.17±0.19	0.34±0.18
USH	0.01±0.25	0.16±0.12	0.01±0.27	**0.35±0.14**	-0.09±0.14	0.17±0.13	-0.06±0.22	0.17±0.18
UBEL	-0.25±0.24	-0.17±0.12	0.10±0.28	**0.48±0.14**	**0.29±0.13**	0.21±0.13	0.18±0.23	0.21±0.18
THAM	0.22±0.18	**0.17±0.08**	0.12±0.21	**0.25±0.12**	-0.04±0.11	0.13±0.10	0.05±0.15	0.09±0.20
TLOIN	-0.24±0.22	-0.12±0.12	-0.01±0.27	0.18±0.16	0.06±0.15	0.14±0.14	0.22±0.21	**0.44±0.26**
TBEL	0.16±0.22	**0.19±0.05**	**0.91±0.11**	**0.77±0.07**	**0.29±0.13**	0.19±0.13	**0.75±0.22**	0.32±0.20
PICN	0.40±0.25	**0.27±0.13**	**0.94±0.13**	**0.79±0.08**	**0.29±0.14**	**0.23±0.11**	**0.77±0.25**	0.17±0.19
BUTT	0.50±0.30	0.26±0.16	**0.94±0.17**	**0.74±0.10**	-0.15±0.16	**0.34±0.13**	**0.82±0.22**	0.07±0.18
RIBS	0.45±0.47	0.29±0.22	**0.94±0.32**	**0.73±0.12**	-0.22±0.20	0.23±0.17	0.62±0.41	0.00±0.21

[1] ***BW*** *= Birth weight (kg);* ***WNW*** *= Weaning weigh (kg);* ***NURW*** *= Nursery weight (kg);* ***ENDW*** *= End weight (kg);* ***ADG*** *= Average daily gain (g/d);* ***UFD*** *= Ultrasound backfat depth (mm);* ***ULD*** *= Ultrasound loin depth (mm);* ***UIMF*** *=Ultrasound IMF;* ***FCR*** *= Feed conversion ratio;* ***HCW*** *= Hot carcass weight (kg);* ***CCW*** *= Cold carcass weight (kg);* ***FD*** *= Backfat depth (mm);* ***LD*** *= Loin depth (mm);* ***CLEN*** *= Carcass length (cm);* ***LEA*** *= Longissimus dorsi muscle area (cm^2);* ***TEXS*** *= Texture score;* ***CMAR*** *= Carcass marbling score;* ***USW*** *= Untrimmed side weight (kg);* ***UHAM*** *= Untrimmed ham weight (kg);* ***ULOIN*** *= Untrimmed loin weight (kg);* ***USH*** *= Untrimmed shoulder weight (kg);* ***UBEL*** *= Untrimmed belly weight (kg);* ***THAM*** *= Trimmed ham weight (kg);* ***TLOIN*** *= Trimmed loin weight (kg);* ***TBEL*** *= Trimmed belly weight (kg);* ***PICN*** *= Trimmed picnic shoulder weight (kg);* ***BUTT*** *= Butt shoulder weight (kg);* ***RIBS*** *= Ribs weight (kg).*

[2] *The significant correlations are bolded (P<0.05).*

Table 4.6. Estimates of phenotypic correlations and their standard error of estimates between meat quality and performance traits

Traits[1]	BW	WNW	NURW	ADG	UFD	ULD	UIMF	FCR
WLW	**0.48±0.08**[2]	**0.11±0.04**	**0.36±0.08**	**0.33±0.05**	**0.32±0.07**	**0.28±0.06**	**0.06±0.03**	0.09±0.07
REAW	**0.53±0.09**	**0.26±0.04**	**0.41±0.09**	**0.33±0.05**	**0.21±0.08**	**0.24±0.07**	**-0.16±0.04**	-0.10±0.06
BFW	**0.40±0.11**	**0.12±0.05**	**0.41±0.08**	**0.34±0.05**	0.31±0.54	**0.26±0.08**	**0.19±0.04**	**0.38±0.06**
RTW	**0.51±0.10**	**0.24±0.04**	**0.42±0.09**	**0.34±0.05**	**0.20±0.09**	**0.27±0.08**	0.00±0.04	**-0.19±0.06**
BOW	**0.50±0.10**	**0.18±0.04**	**0.41±0.09**	**0.33±0.05**	**0.26±0.08**	**0.27±0.08**	-0.07±0.04	**-0.18±0.06**
CL	0.04±0.04	-0.07±0.04	0.15±0.09	**0.33±0.03**	**-0.06±0.03**	**0.12±0.04**	-0.06±0.04	-0.01±0.06
REAL	-0.08±0.05	**-0.14±0.04**	**0.23±0.09**	**0.32±0.03**	**0.12±0.04**	0.06±0.05	**0.21±0.04**	0.07±0.06
REAA	**0.15±0.05**	**0.14±0.04**	**0.18±0.04**	0.02±0.03	**0.11±0.03**	**-0.06±0.03**	**0.22±0.05**	**0.21±0.08**
REAB	**0.13±0.05**	-0.03±0.04	**0.43±0.08**	**0.33±0.03**	**0.19±0.04**	0.11±0.06	**0.29±0.04**	**0.14±0.06**
SHF	-0.06±0.04	-0.03±0.04	-0.02±0.05	**0.30±0.04**	**-0.11±0.03**	-0.02±0.03	**-0.15±0.04**	-0.06±0.06
LOINL	**0.16±0.05**	0.00±0.04	**0.26±0.08**	**0.33±0.03**	**0.15±0.03**	**0.13±0.04**	-0.03±0.04	**0.12±0.06**
LOINA	**0.15±0.05**	0.03±0.04	**0.37±0.08**	**0.33±0.03**	**0.11±0.04**	**0.13±0.05**	-0.06±0.04	0.06±0.06
LOINB	**0.18±0.04**	0.03±0.04	**0.36±0.08**	**0.33±0.03**	**0.18±0.04**	**0.17±0.05**	-0.03±0.04	**0.14±0.06**
PHU	-0.03±0.04	-0.01±0.04	0.01±0.04	0.03±0.03	-0.02±0.03	-0.04±0.03	0.05±0.04	-0.01±0.06
HGML	**0.15±0.04**	0.01±0.04	**0.25±0.09**	**0.32±0.03**	0.00±0.04	0.07±0.04	0.04±0.04	0.03±0.06
HGMA	**0.15±0.05**	0.01±0.04	**0.30±0.10**	**0.32±0.03**	**0.11±0.05**	**0.13±0.05**	-0.06±0.04	0.02±0.06
HGMB	**0.10±0.05**	0.03±0.04	**0.41±0.08**	**0.33±0.03**	**0.10±0.04**	**0.15±0.05**	0.02±0.04	0.00±0.06
HQFL	0.04±0.05	-0.02±0.04	**0.25±0.07**	**0.33±0.03**	**0.06±0.03**	**0.08±0.04**	-0.03±0.04	0.06±0.06
HQFA	0.04±0.04	0.02±0.04	**0.34±0.08**	**0.33±0.03**	**0.10±0.04**	0.09±0.05	0.05±0.04	-0.08±0.05
HQFB	0.08±0.05	0.00±0.04	**0.42±0.06**	**0.33±0.03**	**0.12±0.04**	**0.13±0.05**	0.06±0.04	-0.00±0.06
HILL	**0.11±0.04**	0.01±0.04	**0.18±0.08**	**0.33±0.03**	**0.13±0.03**	**0.10±0.04**	0.03±0.04	0.03±0.06
HILA	0.07±0.04	0.03±0.04	**0.36±0.08**	**0.33±0.03**	0.05±0.04	**0.11±0.05**	0.01±0.04	0.04±0.06
HILB	**0.11±0.05**	-0.01±0.04	**0.30±0.09**	**0.32±0.03**	**0.14±0.04**	**0.13±0.05**	0.03±0.04	0.04±0.06
DL	**0.14±0.04**	0.02±0.04	-0.07±0.04	-0.02±0.03	**-0.06±0.03**	0.01±0.03	0.02±0.05	0.11±0.08

[1] ***BW*** *= Birth weight (kg);* ***WNW*** *= Weaning weigh (kg);* ***NURW*** *= Nursery weight (kg);* ***ADG*** *= Average daily gain (g/d);* ***UFD*** *= Ultrasound backfat depth (mm);* ***ULD*** *= Ultrasound loin depth (mm);* ***UIMF*** *=Ultrasound IMF;* ***FCR*** *= Feed conversion ratio;* ***WLW*** *= Whole loin weight (kg);* ***REAW*** *= Rib eye weight (kg);* ***BFW*** *= Backfat thickness weight (kg);* ***RTW*** *= Rib trim weight (kg);* ***BOW*** *= Bone/Neural weight (kg);* ***CL*** *= Cooking loss (%);* ***REAL*** *= Minolta L* rib eye area;* ***REAA*** *= Minolta a* rib eye area;* ***REAB*** *= Minolta b* rib eye area;* ***SHF*** *= Shear force (newton);* ***LOINL*** *= Minolta L**

loin; ***LOINA*** *= Minolta a* loin;* ***LOINB*** *= Minolta b* loin;* ***PHU*** *= pH ultimate;* ***HGML*** *= Minolta L* ham gluteus medius;* ***HGMA*** *= Minolta a* ham gluteus medius;* ***HGMB*** *= Minolta b* ham gluteus medius;* ***HQFL*** *= Minolta L* ham quadriceps femoris;* ***HQFA*** *= Minolta a* ham quadriceps femoris;* ***HQFB*** *= Minolta b* ham quadriceps femoris;* ***HILL*** *= Minolta L* ham iliopsoas;* ***HILA*** *= Minolta a* ham iliopsoas;* ***HILB*** *= Minolta b* ham iliopsoas;* ***DL*** *= Drip loss (%).*

[2] *The significant correlations are bolded (P<0.05).*

Table 4.7. Estimates of genetic correlations and their standard error of estimates between meat quality and performance traits

Traits[1]	BW	WNW	NURW	ADG	UFD	ULD	UIMF	FCR
WLW	0.41±0.25	**0.20±0.07**[2]	**0.80±0.18**	**0.52±0.13**	0.19±0.15	**0.42±0.13**	0.21±0.25	-0.05±0.24
REAW	0.43±0.31	**0.33±0.12**	-0.24±0.29	0.17±0.16	**-0.75±0.11**	**0.66±0.10**	-0.39±0.25	0.13±0.23
BFW	-0.33±0.27	0.08±0.14	**0.67±0.31**	-0.15±0.16	**0.89±0.05**	-0.17±0.14	0.36±0.23	0.24±0.19
RTW	-0.02±0.28	**0.34±0.14**	-0.09±0.40	**0.32±0.16**	**-0.66±0.11**	0.24±0.15	0.02±0.28	-0.28±0.22
BOW	0.09±0.34	**0.46±0.17**	-0.66±0.49	**0.43±0.19**	**-0.45±0.17**	**-0.36±0.18**	0.28±0.38	-0.33±0.26
CL	0.05±0.31	-0.02±0.18	**-0.51±0.24**	0.25±0.15	**-0.41±0.13**	0.11±0.15	**-0.67±0.26**	0.08±0.25
REAL	-0.11±0.25	-0.14±0.14	-0.10±0.22	0.02±0.14	**0.24±0.12**	0.04±0.13	**0.63±0.22**	0.29±0.20
REAA	0.63±0.44	0.22±0.13	-0.22±0.73	-0.14±0.18	0.05±0.17	-0.07±0.17	0.36±0.27	-0.07±0.22
REAB	0.36±0.34	0.03±0.15	0.23±0.23	-0.01±0.14	**0.24±0.12**	-0.14±0.12	**0.77±0.18**	0.18±0.22
SHF	-0.14±0.26	-0.04±0.13	-0.17±0.20	0.10±0.14	-0.14±0.12	-0.15±0.12	-0.30±0.23	-0.09±0.23
LOINL	**0.76±0.37**	-0.22±0.15	-0.06±0.41	0.08±0.14	0.12±0.13	0.20±0.13	-0.43±0.26	**0.43±0.19**
LOINA	0.50±0.34	-0.02±0.15	0.29±0.25	-0.00±0.14	-0.12±0.12	-0.12±0.12	-0.35±0.25	-0.18±0.21
LOINB	**0.86±0.43**	-0.17±0.17	0.41±0.26	0.11±0.16	0.05±0.14	0.11±0.15	-0.33±0.28	0.32±0.24
PHU	0.11±0.71	0.06±0.14	0.40±0.90	0.19±0.24	-0.43±0.25	**-0.49±0.24**	**0.73±0.37**	-0.30±0.30
HGML	**0.80±0.31**	-0.12±0.17	**-0.69±0.35**	0.00±0.16	-0.25±0.14	-0.13±0.14	0.42±0.29	0.30±0.23
HGMA	0.44±0.32	-0.00±0.15	-0.40±0.26	-0.20±0.13	0.05±0.12	-0.10±0.12	-0.23±0.26	-0.29±0.19
HGMB	0.79±0.49	-0.24±0.24	-0.11±0.65	-0.13±0.20	-0.18±0.19	-0.15±0.18	**0.73±0.36**	0.22±0.29
HQFL	0.02±0.33	-0.18±0.18	0.06±0.39	-0.07±0.16	-0.05±0.14	0.19±0.14	-0.24±0.31	0.15±0.23
HQFA	-0.40±0.30	-0.10±0.16	0.53±0.46	0.03±0.15	0.15±0.13	-0.09±0.13	0.14±0.29	-0.25±0.21
HQFB	-0.24±0.40	-0.30±0.24	-0.19±0.23	0.03±0.19	0.15±0.17	0.12±0.18	0.45±0.39	-0.03±0.28
HILL	0.41±0.28	-0.07±0.14	-0.01±0.25	0.22±0.14	**0.34±0.13**	0.10±0.13	0.28±0.24	0.20±0.22
HILA	0.37±0.29	0.28±0.17	0.21±0.35	-0.15±0.16	-0.01±0.14	0.01±0.14	-0.19±0.30	-0.29±0.22
HILB	0.45±0.30	-0.06±0.16	-0.11±0.26	0.16±0.15	**0.33±0.14**	0.08±0.14	0.34±0.26	-0.08±0.24
DL	**0.93±0.42**	0.07±0.13	-0.92±0.91	0.07±0.22	-0.15±0.21	-0.09±0.21	-0.25±0.34	0.13±0.27

[1] ***BW*** *= Birth weight (kg);* ***WNW*** *= Weaning weigh (kg);* ***NURW*** *= Nursery weight (kg);* ***ADG*** *= Average daily gain (g/d);* ***UFD*** *= Ultrasound backfat depth (mm);* ***ULD*** *= Ultrasound loin depth (mm);* ***UIMF*** *=Ultrasound IMF;* ***FCR*** *= Feed conversion ratio;* ***WLW*** *= Whole loin weight (kg);* ***REAW*** *= Rib eye weight (kg);* ***BFW*** *= Backfat thickness weight (kg);* ***RTW*** *= Rib trim weight (kg);* ***BOW*** *= Bone/Neural weight (kg);* ***CL*** *= Cooking loss (%);* ***REAL*** *= Minolta L* rib eye area;* ***REAA*** *= Minolta a* rib eye area;* ***REAB*** *= Minolta b* rib eye area;* ***SHF*** *=*

Shear force (newton); ***LOINL*** *= Minolta L* loin;* ***LOINA*** *= Minolta a* loin;* ***LOINB*** *= Minolta b* loin;* ***PHU*** *= pH ultimate;* ***HGML*** *= Minolta L* ham gluteus medius;* ***HGMA*** *= Minolta a* ham gluteus medius;* ***HGMB*** *= Minolta b* ham gluteus medius;* ***HQFL*** *= Minolta L* ham quadriceps femoris;* ***HQFA*** *= Minolta a* ham quadriceps femoris;* ***HQFB*** *= Minolta b* ham quadriceps femoris;* ***HILL*** *= Minolta L* ham iliopsoas;* ***HILA*** *= Minolta a* ham iliopsoas;* ***HILB*** *= Minolta b* ham iliopsoas;* ***DL*** *= Drip loss (%).*

[2] *The significant correlations are bolded (P<0.05).*

CHAPTER 5. Genomic Selection of Pork Quality and Carcass Traits in Purebred Pigs for Crossbred Performance[1]

5.1. INTRODCUTION

Many pig breeders select on purebred nucleus lines that are grown in high-health environmental conditions. However, the main objective of this selection is to improve crossbred performance under commercial field conditions. Therefore, performance of purebreds could be a poor predictor of their crossbred progenies due to the differences in their genetics and environmental conditions for some traits (Dekkers, 2007). Genetic improvement for meat quality through traditional quantitative selection has not been very effective not only because these traits have a low-to-moderate heritability, but also because these traits are very difficult and expensive to measure and often require the harvest of the animal so that they cannot be measured in purebreds. Researchers have addressed this through selecting purebred animals based on crossbred performance using combined crossbred and purebred selection (Wei and Steen, 1991; Wei, 1992, Lo et al., 1993; Lo et al., 1995; Lo et al., 1997). Although this method of selection could increase the response to selection, it was not applied extensively in the pig industry because of the expense of phenotypic measurements in the crossbred field (Dekkers, 2007). Dekkers (2007) proposed an alternative method to select purebreds for commercial crossbred performance using genomic selection.

[1] A version of this Chapter has been published in 10th World Congress on Genetics Applied to Livestock Production (WCGALP). Miar et al. 2014. Genomic Selection of Pork pH in Purebred Pigs for Crossbred Performance
AND another version will be submitted in BMC Genomics. Miar et al. 2014. Genomic Selection of Pork Quality and Carcass Traits in Purebred Pigs for Crossbred Performance.

Recently, the Illumina PorcineSNP60 BeadChip was developed (Ramos et al., 2009) and has been used in genome-wide association studies to identify genes that explain variation in meat quality traits (Zhang et al., 2014). Availability of a high-density SNP panel and new statistical methods, such as multiple-step methods including Bayesian statistics and GBLUP, and single-step BLUP (ssBLUP) have made genomic selection feasible in pigs (Nejati-Javaremi et al., 1997; Meuwissen et al., 2001; Gianola et al., 2006; Habier et al., 2007; VanRaden et al., 2009; Misztal et al., 2009; Legarra et al., 2009; Calus, 2010; Habier et al., 2011; Erbe et al., 2012; Brondum et al., 2012). Among these statistical methods, ssBLUP can incorporate marker genotypes into a traditional animal model by using H matrix in which A matrix and G matrix are combined (Misztal et al., 2009; Legarra et al., 2009). Aguilar et al. (2010) showed that this method could be simpler, faster, more accurate and applicable to complicated models than multi-step methods. This method has been successfully implemented for different species including pigs (Forni et al., 2011; Christensen et al., 2012), chickens (Chen et al., 2011) and dairy cattle (Aguilar et al., 2011; Tsuruta et al., 2011; VanRaden, 2012; Liu et al 2014).

A few studies showed that GS could be applied successfully in purebred populations compared to traditional methods because it can account for genetic differences between crossbred and purebred animals, non-additive gene action and genotype by environment effects (Daetwyler et al., 2007; Dekkers, 2007; Ibanez-Escriche et al., 2009). Genomic selection can reduce generation interval and improve selection accuracy to accelerate genetic improvement of economically important traits in livestock (Hayes et al., 2009) if used properly. Therefore, selection of purebreds based on crossbred progeny performance for these traits would be useful in improving pure line parents to produce improved pork quality for their crossbred progenies. The objective of this study was therefore to develop GEBV prediction equations using single-

step method for pork quality and carcass traits using commercial crossbred animals for selection in their pure parental lines.

5.2. MATERIALS AND METHODS

5.2.1. Animals and Management

The composition of this population has been previously described in Chapter three (Miar et al., 2014). Briefly, the commercial crossbred pigs used in this study were progeny from 139 sires of Duroc purebreds to 429 F1 hybrid Landrace × Large White sows from two breeding companies (Genesus Genetics, and Hypor Inc., Canada). They were a combination of full and half sib families representing a multi-generation family structure drawn from the breeding populations.

5.2.2. Carcass and Meat Quality Measurements

Carcass and meat quality measurements have been described in Chapter 3 (Miar et al., 2014). Briefly, carcass traits including hot carcass weight (**HCW**), cold carcass weight (**CCW**), carcass length (**CLEN**), *longissimus dorsi* muscle area (**LEA**), subcutaneous backfat depth (**FD**), loin depth (**LD**), texture score (**TEXS**), subjective marbling score (**CMAR),** untrimmed side weight (**USW**), untrimmed shoulder weight (**USH**), untrimmed ham weight (**UHAM**) untrimmed loin weight (**ULOIN**), untrimmed belly weight (**UBEL**), trimmed ham weight (**THAM**), trimmed loin weight (**TLOIN**), picnic shoulder weight (**PICN**), butt weight (**BUTT**), belly weight (**TBEL**) and ribs weight (**RIBS**) were recorded at slaughterhouse according to Miar et al. (2014) in Chapter three.

Briefly, pork quality traits including ultimate or 24 h pH (**PHU**), drip loss (**DL**), Minolta L*, a*, and b* on loin (**LOINL**, **LOINA**, and **LOINB**), Minolta L*, a*, and b* measurements on different muscles of ham including *gluteus medius* (**HGML**, **HGMA**, and **HGMB**), *quadriceps femoris* (**HQFL**, **HQFA**, and **HQFB**), and *iliopsoas* muscles (**HILL**, **HILA**, and **HILB**), rib eye Minolta L*, a*, and b* values (**REAL**, **REAA**, and **REAB**), cooking loss (**CL**) and shear force (**SHF**) were measured as described by Miar et al. (2014) in Chapter three.

5.2.3. Genotyping and Quality Control

Genomic DNA was extracted from ear tissues using a standard phenol/chloroform method. A total of 2,384 individuals were genotyped using the PorcineSNP60 Beadchip containing 64,232 SNPs following the manufacturer's protocol (Illumina Inc., San Diego, USA). SNPs were removed from the genotyping data for call rate < 95%, minor allele frequency < 0.05, and Chi-square > 600 of Hardy-Weinberg equilibrium test. A total of 44,507 SNP were retained in the analysis after the filtering.

5.2.4. Statistical and Genetic analysis

The significance of the fixed effects and covariates for each trait was determined using the animal model implemented using the ASREML 3.0 software (Gilmour et al., 2012), and different significant ($P < 0.1$) fixed factors for each trait remained in the subsequent analyses. The significance of different random terms in the model was determined by likelihood ratio test using ASREML 3.0 software (Gilmour et al., 2012). It was confirmed that the effects of common

litter were not significant ($P > 0.05$) for meat quality and carcass traits, except for HCW, CCW, LEA, PHU, and DL. Maternal genetic effects were tested in a similar manner and were shown to be not significant ($P > 0.05$). The animal model included random additive polygenic effects in the final model for all traits, and random litter effect for some traits. Birth weight, whole loin weight received at Meat Science Laboratory, cold carcass weight, and slaughter age were included in the model as linear covariates. Sex, and slaughter batch were included in the model as fixed effects.

In this study, ssBLUP was used to predict GEBVs of individual animals using commercial crossbred pigs (n = 2,100, with both genotype and phenotype information) and their parental purebreds (with only genotype, without phenotype). Their parental purebreds were investigated to explore the model predictability in the selection population. A matrix combined the genomic relationship matrix with pedigree-based relationship matrix was constructed in the population using 2,100 commercial crossbred and 107 Duroc purebred pigs followed the method described by Christensen and Lund (2010). The prediction model was then developed using ssBLUP for each trait as follows:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Za} + \boldsymbol{e}\,,$$

where $\boldsymbol{y}$ is a phenotypic observation vector for $\boldsymbol{n}$ individuals, $\boldsymbol{X}$ is the design matrix for the fixed effects, $\boldsymbol{b}$ is a vector of fixed effects, $\boldsymbol{Z}$ is the design matrix for the breeding values, $\boldsymbol{a}$ is a vector of additive genetic effects, which are the sum of the all marker on the genome and the remained polygenic effects and $\boldsymbol{e}$ is the residual error. It was assumed that $\boldsymbol{a} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{H}\sigma_A^2)$, where matrix $\boldsymbol{H}$ is

the modified genomic relationship matrix that combines pedigree-based relationship information as follows (Legarra et al., 2009; Christensen and Lund, 2010):

$$H = \begin{bmatrix} G_w & G_w A_{11}^{-1} A_{12} \\ A_{21} A_{11}^{-1} G_w & A_{21} A_{11}^{-1} G_w A_{11}^{-1} A_{12} + A_{22} - A_{21} A_{11}^{-1} A_{12} \end{bmatrix},$$

where $\mathbf{A}_{11}$ is the sub-matrix of the pedigree-based relationship matrix (**A**) for genotyped animals, $\mathbf{A}_{22}$ is the sub-matrix of **A** for non-genotyped animals, $\mathbf{A}_{12}$ (or $\mathbf{A}_{21}$) is the sub-matrix of **A** for relationships between genotyped and non-genotyped animals, and $G_w = (1-w)G + wA_{11}$, where $\boldsymbol{w}$ is the fraction of the genetic variance not captured by markers (Christensen et al., 2012). This fraction was between 0.05 to 0.40 for different traits. The inverse of **H** was calculated as follows (Christensen and Lund, 2010; Aguilar et al., 2010):

$$H^{-1} = \begin{bmatrix} G_w^{-1} - A_{11}^{-1} & 0 \\ 0 & 0 \end{bmatrix} - A^{-1}$$

where G_w^{-1} is the inverse of the G_w genomic relationship matrix and A^{-1} is the inverse of the pedigree-based relationship matrix for all animals. The **G** matrix used in the single-step blending was the same as in the GBLUP method.

5.2.5. Predictability and Accuracy

The predictability of genomic predictions were measured as correlations between the predicted breeding values using ssBLUP and adjusted phenotype for crossbreds, divided by the

square root of the heritability (Calus et al., 2014). However, the accuracies of genomic predictions were measured as correlations between the predicted breeding values using ssBLUP and most up-to-date EBV using traditional animal model for Duroc boars in the selection population. The most up-to-date EBVs used in this study were obtained using animal models unless our industry partners (Hypor Inc. and Genesus Genetics) provided them.

We have also calculated the gain of the accuracy using genomic selection in the purebreds than traditional parental average of purebreds. The accuracy of traditional parental average of purebreds was calculated as follows:

$$r = \frac{1}{2}\sqrt{r_{Sire}^2 + r_{Dam}^2},$$

where $\boldsymbol{r}$ is the accuracy of traditional parental average of purebreds, $\boldsymbol{r_{Sire}^2}$ and $\boldsymbol{r_{Dam}^2}$ are the reliabilities of EBV for sire and dam, respectively.

5.3. RESULTS AND DISCUSSION

Using single-step methodology can be simpler, faster, more accurate and applicable to complicated models more so than multi-step methods such as GBLUP (Aguilar et al., 2010). This approach has been successfully implemented for pigs (Forni et al., 2011; Christensen et al., 2012), chickens (Chen et al., 2011) and dairy cattle (Aguilar et al., 2011; Tsuruta et al., 2011; VanRaden, 2012; Liu et al., 2014). In this study, we used ssBLUP and the average accuracies of predictions in the crossbreds were 0.32 and 0.30 for carcass and pork quality traits, respectively

(Tables 5.1-5.2). The accuracies in the crossbreds for pork quality traits ranged from 0.17 to 0.42 for lightness of *quadriceps* muscle of ham and shear force, respectively. The accuracies in the crossbreds for carcass traits ranged from 0.10 to 0.45 for butt shoulder weight and both untrimmed loin weight and carcass length, respectively.

For the pure Duroc paternal lines, however, the accuracy of prediction was calculated by using the correlation between EBV and GEBV for the meat quality and carcass traits, which was varied across traits. The accuracies in the Duroc purebreds for pork quality traits were between 0.16 to 0.38 for lightness of *quadriceps* muscle of ham and shear force, respectively. The accuracies in the Duroc purebreds for carcass traits were from 0.09 to 0.39 for butt shoulder weight and carcass length, respectively.

The GEBV results showed that sufficient variation in GEBV existed in both commercial crossbred animals and pure lines for each trait. Figures 5.1-5.2 demonstrate the variation in GEBV for pork pH in commercial crossbred animals and purebreds, respectively. This confirms that selecting animals with known genotypes and unknown phenotypes may be possible so as to completely redesign livestock breeding programs.

Average accuracy across pork quality traits was 0.30 in commercial crossbreds, which dropped to 0.26 in purebreds. Moreover, average accuracy across carcass traits was 0.32 in commercial crossbreds, and dropped to 0.28 in purebreds. This showed that prediction models developed using ssBLUP for pork quality and carcass traits can predict the parental purebred lines without substantial loss of prediction accuracy compared to their crossbred progenies (Figures 5.3-5.4). Figures 5.3 and 5.4 show that prediction accuracies were reduced slowly in the purebred animals compared to their crossbred progenies. All of the accuracies in purebreds were less than those from crossbreds for both meat quality and carcass traits and might be due to the

unavailability of the phenotypic information in purebred population, and genotype by environment interactions between the purebred and crossbred populations.

The average accuracy across carcass traits is higher than those for pork quality traits and that may be due to the increased heritability of the carcass traits (Tables 5.1-5.2). The results showed that GS was successful in increasing the accuracy for carcass traits compared to traditional parental average, averaged 16% across traits with a range from 6 to 33%. In addition, the accuracy for pork quality traits using GS compared to traditional parental average were increased, and averaged 17% across traits with a range from 7 to 38%. The accuracy of GEBV prediction was affected by size of reference population, trait, and breed and to a lesser extent, by the statistical methods (Bolormaa et al., 2013) e.g. ssBLUP vs. others. Therefore, traits that had a large reference population size with a high heritability tended to give higher accuracies than average (Goddard, 2009). Our results confirmed this because the highest accuracy was estimated for ULOIN, which had the highest heritability (0.63) among pork quality traits.

The accuracies of prediction reported here were less than those typically found in literature (Hayes et al., 2009; VanRaden et al., 2009; Forni et al., 2011; Erbe et al., 2012). This is probably because the reference population size (T) in the literature was much higher than our study. For example, we had 1,948 crossbred measured for pork quality with an average heritability (h^2) of 0.25 (Th^2 = 487) whereas VanRaden et al. (2009) studied 10,000 Holsteins with daughter average for milk yield (h^2 = 0.8; Th^2 = 8,000). Therefore, it is not surprisingly that the prediction accuracy in the Holstein is 0.7 compared with 0.26 for our Duroc purebreds. Interestingly, Pryce et al. (2012) reported an average accuracy of 0.42 for residual feed intake in growing Holstein heifers that might be due to using heifers that had their own phenotypes. The low prediction accuracies of GEBV limit the genomic selection benefits in swine industry.

However, GS can still be valuable for traits that are difficult to be improved upon by traditional BLUP such as pork quality. These results suggest that increasing the reference sample size can increase the accuracy of predictions, which was similar to the results reported by Cleveland et al. (2010).

Although there are many reports of genomic predictions accuracy in other species (Kizilkaya et al., 2010; Toosi et al., 2010; Garrick, 2011; Weber et al., 2012; Gao et al., 2012; Pryce et al., 2012), little research has been done in pigs especially in relation to predictions in purebreds based on their crossbred performance (e.g. Cleveland et al., 2010; Christensen et al., 2012; Badke et al., 2014). The first implementation of genomic selection in pigs was for total number of born in a litter and stillborn percentage (Cleveland et al., 2010). They indicated that prediction accuracies could be comparable with those in dairy cattle if a larger reference population size is used.

Different models have been used for selection of purebreds for crossbred performance (Dekkers, 2007; Kinghorn et al., 2010). However, the model used in this study was an additive genetic model, but it included both genomic and additive relationship information and may have captured only the additive gene actions and not the dominant gene actions. Su et al. (2012) showed that incorporation of a dominance model might improve accuracies of predictions of breeding values of purebred pigs. Zeng et al. (2013) in a simulation study on crossbred animals indicated that a dominance model could increase the response to selection because dominance is the likely genetic basis of heterosis (Falconer and Mackay, 1996; Charlesworth and Willis, 2009). Extending the model of ssBLUP to include dominance genetic effects would be an interesting topic for future research.

When the most of the pedigreed animals are genotyped, estimates of additive genetic variance depend on the choices of genomic relationship matrix. In livestock species, a whole genotyped population can rarely be found and hence the pedigree and genomic information need to be combined. Several reports have demonstrated an increased accuracy with inclusion of genomic information in the genetic evaluations (Villanueva et al., 2005; VanRaden et al., 2009; Hayes et al., 2009). However, several studies have shown that GEBV and reliabilities may be inflated be due to incorrect weighting of genomic and polygenic information (VanRaden et al., 2009; Aguilar et al., 2010). Therefore, ssBLUP provides a natural way to weight both components based on the data for optimal predictions and eliminates several assumptions required in multi-step methods, and may result in more accurate evaluations for young animals (Forni et al., 2011). In addition, ssBLUP can be easily extended for analysis of multiple traits and can handle large amounts of genomic data.

The accuracies of the prediction models in this study showed that genomic prediction equations generated from commercial crossbred animals could be used to select animals in their parental pure lines for pork quality and carcass traits with known genotypes and unknown phenotypes. This enables pig breeders to predict breeding values of young selection candidates that will result in reducing generation interval with reasonable prediction accuracy and hence, accelerates the rate of genetic gain. This finding is supported by previous reports indicating that application of genomic predictions would be most beneficial for young animals with little information on their own resulting in low accuracy of traditional EBV (VanRaden, 2008). However, future investigations on including dominance effects in the genomic prediction models of ssBLUP should be explored using the data from the commercial animals in an attempt to further improve genomic prediction accuracies in the pure parental populations.

5.4. CONCLUSIONS

It is apparent that GS has great potential for the improvement of difficult to measure phenotypes and low heritability traits such as pork quality. The results showed the potential of genomic selection in the pure parental lines using ssBLUP without substantial loss of prediction accuracy compared to their crossbred progenies. The results of this study showed that a large number of phenotypic and genotypic data with high heritability gave more accuracy of predictions.

Results from this study show the potential for genomic selection of purebreds for commercial crossbred performance. This would enable genetic improvement of purebreds for performance of their crossbred descendants in the field, without the need to track pedigrees through the system.

5.5. LITERATURE CITED

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Table 5.1. Average of accuracies of genomic breeding values for carcass traits in purebred lines based on crossbred performance: number of animals per trait (n)

Traits	n	h^2	Accuracy GEBV of Crossbreds	Accuracy GEBV of Purebreds	Accuracy Parental Average Purebreds	Increase
HCW	1948	0.28	0.32	0.29	0.22	32%
CCW	1948	0.29	0.34	0.30	0.23	30%
FD	1948	0.31	0.29	0.24	0.20	20%
LD	1948	0.41	0.42	0.35	0.27	30%
CLEN	1948	0.51	0.45	0.39	0.32	22%
LEA	1948	0.22	0.24	0.18	0.16	13%
TEXS	1948	0.09	0.29	0.24	0.18	33%
CMAR	1948	0.23	0.32	0.28	0.23	22%
USW	1948	0.55	0.38	0.36	0.32	13%
UHAM	1948	0.46	0.35	0.33	0.29	14%
ULOIN	1948	0.63	0.45	0.35	0.32	9%
USH	1948	0.55	0.33	0.27	0.24	13%
UBEL	1948	0.49	0.28	0.22	0.20	10%
THAM	1948	0.63	0.38	0.35	0.33	6%
TLOIN	1948	0.52	0.39	0.38	0.35	9%
TBEL	1948	0.53	0.36	0.33	0.31	6%
PICN	1948	0.44	0.28	0.19	0.18	6%
BUTT	1948	0.29	0.10	0.09	0.08	13%
RIBS	1948	0.32	0.14	0.12	0.10	20%
Average	1948	0.41	0.32	0.28	0.24	17%

Table 5.2. Average of accuracies of genomic breeding values for pork quality traits in purebred lines based on crossbred performance: number of animals per trait (n)

Traits	n	h^2	Accuracy GEBV of Crossbreds	Accuracy GEBV of Purebreds	Accuracy Parental Average of Purebreds	Increase
CL	1948	0.20	0.35	0.33	0.28	18%
REAL	1948	0.28	0.28	0.23	0.21	10%
REAA	1948	0.26	0.22	0.19	0.16	19%
REAB	1948	0.31	0.35	0.25	0.23	9%
SHF	1948	0.39	0.42	0.38	0.35	9%
LOINL	1948	0.31	0.23	0.18	0.13	38%
LOINA	1948	0.36	0.29	0.25	0.22	14%
LOINB	1948	0.20	0.33	0.28	0.25	12%
PHU	1948	0.15	0.30	0.28	0.24	17%
HGML	1948	0.22	0.28	0.26	0.23	13%
HGMA	1948	0.38	0.26	0.26	0.22	18%
HGMB	1948	0.12	0.24	0.20	0.17	18%
HQFL	1948	0.19	0.17	0.16	0.15	7%
HQFA	1948	0.27	0.33	0.27	0.23	13%
HQFB	1948	0.10	0.35	0.33	0.29	14%
HILL	1948	0.32	0.25	0.22	0.19	16%
HILA	1948	0.16	0.33	0.28	0.24	17%
HILB	1948	0.26	0.36	0.30	0.25	20%
DL	1948	0.21	0.26	0.24	0.19	26%
Average	1948	0.25	0.30	0.26	0.22	16%

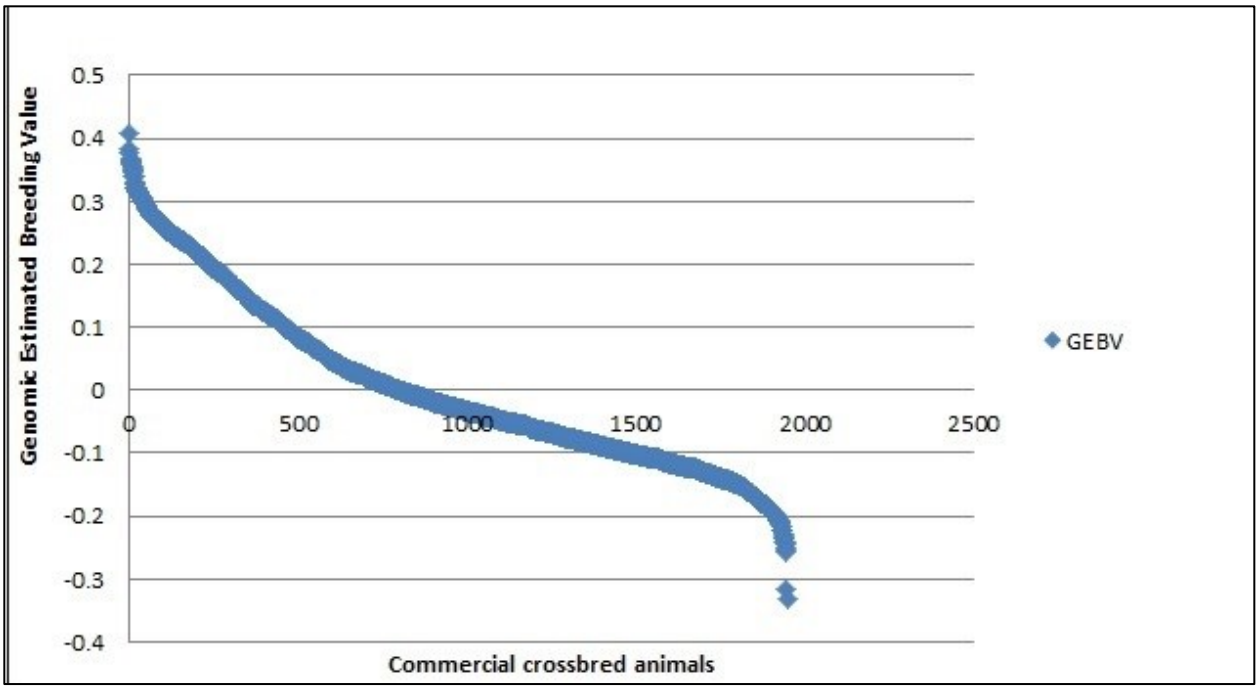

Figure 5.1. An example of variation of genomic estimated breeding values for pork pH in commercial crossbred pigs.

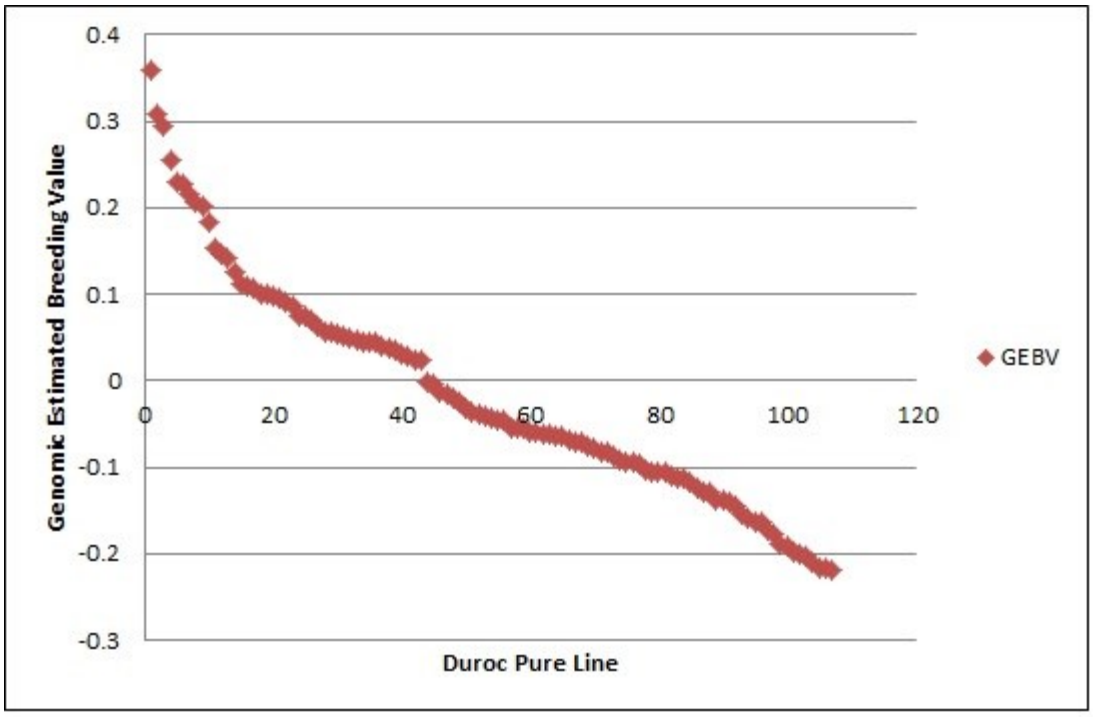

Figure 5.2. An example of variation of genomic estimated breeding values for pork pH in Duroc pure line.

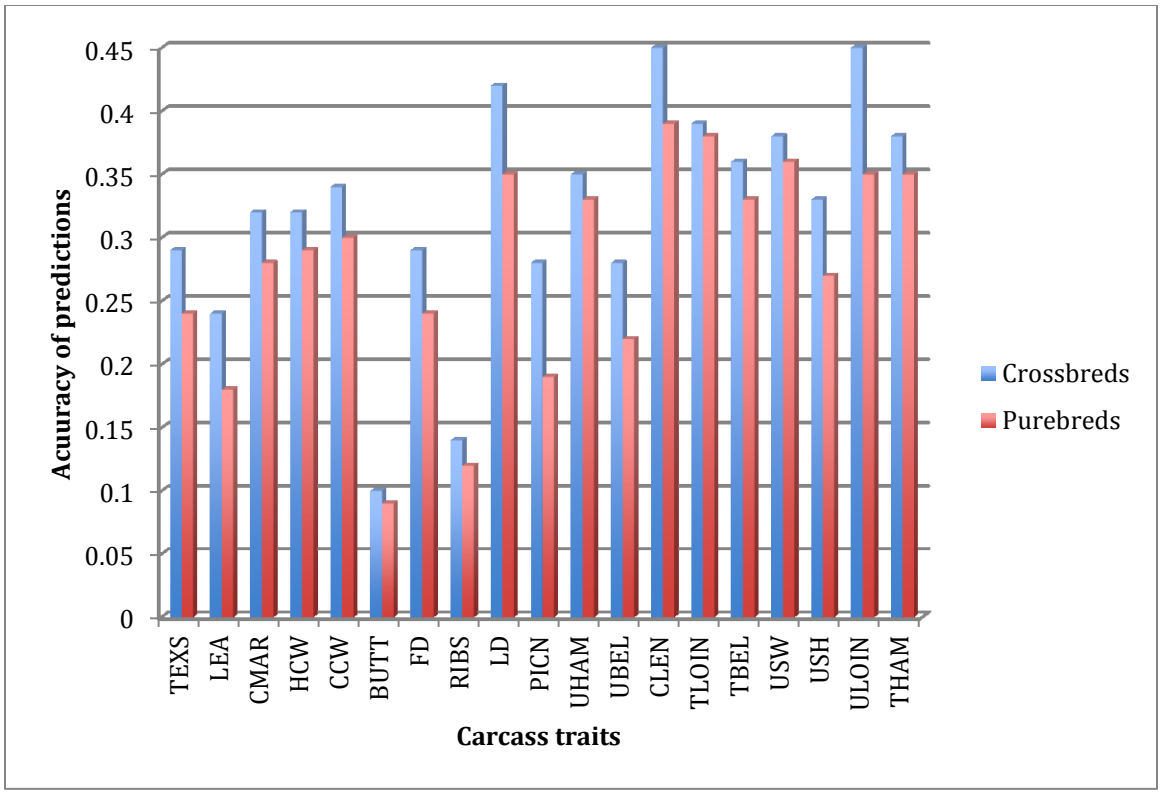

Figure 5.3. Predictions accuracies in purebreds using developed prediction models in their crossbred descendants for various carcass traits.

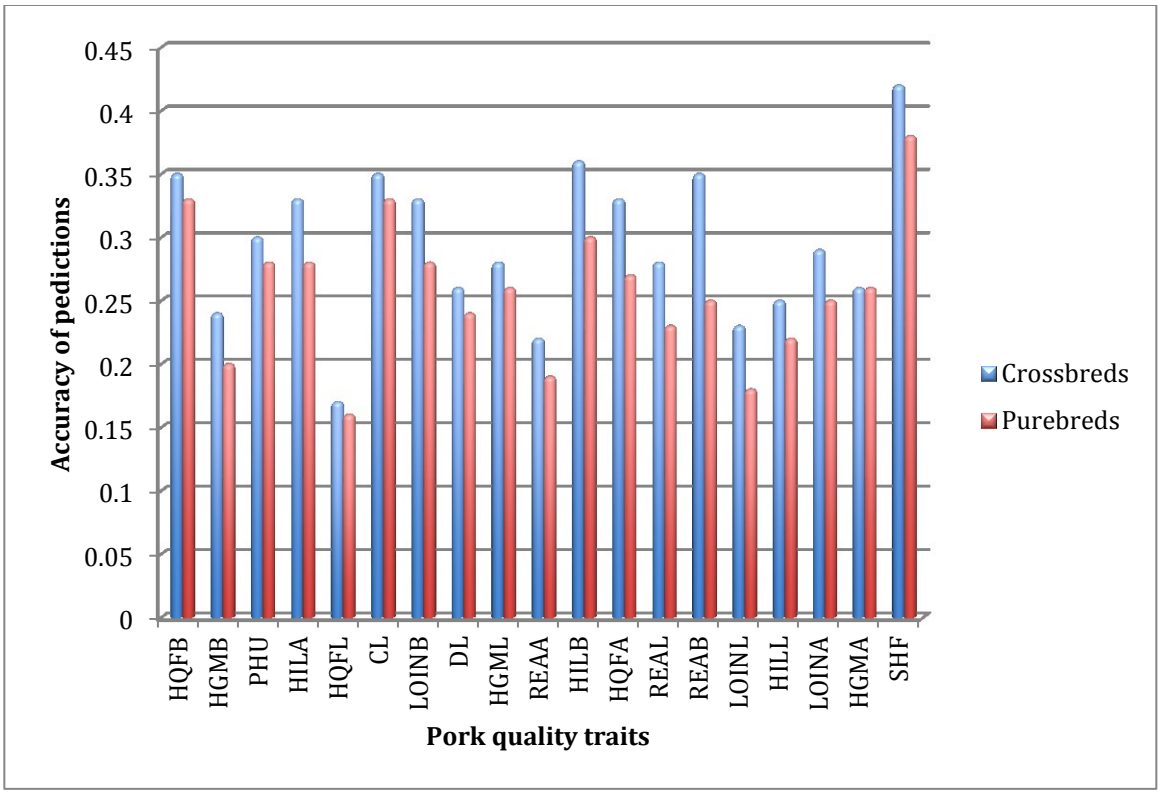

Figure 5.4. Predictions accuracies in purebreds using developed prediction models in their crossbred descendants for various pork quality traits.

CHAPTER 6. GENERAL DISCUSSION AND CONCLUSION

6.1. SUMMARY AND GENERAL DISCUSSION

Increased understanding of the underlying genetics affecting pork quality could better satisfy consumer demands for excellent eating quality. As a result, the pig industry has focused on improving pork quality using genetic technologies to meet the demands of processors, packers, and consumers (Dransfield et al., 2005). In the past decades, traditional BLUP was used to select superior animals with better pork quality. Traditional selection has applied indirect selection with correlated traits to predict genetic potential of animals for pork quality (Muir, 2007). Consequently, understanding of genetic and phenotypic correlations between pork quality, performance and carcass traits can be used to implement a successful breeding program to improve pork quality traits (van Wijk et al., 2005). Therefore, the objectives of this thesis were to provide a comprehensive study of genetic and phenotypic correlations between pork quality traits (n=25), performance traits (n=9), and carcass traits (n=19) in commercial crossbred pigs. Additionally, genetic variation underlying pork quality, carcass and performance traits was investigated that can be implemented in the Canadian swine breeding programs.

The objectives of the first study in Chapter 3 were to estimate 1) heritabilities for various carcass and pork quality traits and 2) phenotypic and genetic correlations among pork quality, carcass traits and between them in commercial crossbred pigs. Several estimates in this study were new contributions to the genetic parameters for carcass and pork quality traits especially on ham traits. Novel results of this study showed the significance of genetic selection for various

carcass weight traits including hot carcass, cold carcass, rib eye, primal, and subprimal cuts weights in the swine breeding programs due to their moderate to high heritabilities. For example, heritability estimates for primal and subprimal cuts weight were 0.55 ± 0.06, 0.46 ± 0.06, 0.63 ± 0.06, 0.55 ± 0.06, 0.49 ± 0.06, 0.63 ± 0.04, 0.52 ± 0.07, 0.53 ± 0.06, 0.44 ± 0.06, 0.29 ± 0.05, and 0.32 ± 0.06, for USW, UHAM, ULOIN, USH, UBEL, THAM, TLOIN, TBEL, PICN, BUTT, and RIBS, respectively. However, firmness and color measurements of *gluteus medius*, *quadriceps femoris*, and *iliopsoas* muscles had low-to-moderate heritabilities indicating the opportunities for genomic selection to improve them. The genetic correlations between PHU and the color measurements showed moderate to high negative genetic correlations, ranging from (-0.37 ± 0.16), with LOINA to (-0.98 ± 0.35) with HQFB. Also, strong negative genetic correlations were found between PHU with CL (-0.62 ± 0.26), and DL (-0.99 ± 0.49). Therefore, these results confirmed the value of pH as an indicator trait for pork water-holding capacity, cooking loss and color.

The genetic correlations in this study indicated the value of carcass and ham weight as good indicator traits for indirect selection of primal, subprimal, and carcass traits. However, an unfavorable genetic correlation was found between both carcass weight and loin eye area with texture score while a favorable genetic relationship was found between ham weight and texture score. These results indicated that deterioration of pork quality may have occurred over many generations through the selection for increasing carcass weight and especially for loin weight. It was concluded that single-trait selection on loin traits might lead to increased belly weight and undesirable low pH pork with pale color. Therefore, selection for ham weight can be valuable for increasing both carcass weight, primal and subprimal cuts weights without adverse consequences on pork quality. In addition, color of ham muscles had moderate to high genetic correlations with

corresponding measurements on the loin indicating that selection can be made on ham. Lightness and yellowness reflectance of ham were highly positively correlated to each other and negatively to pH. Favorable correlation between backfat depth and pork lightness of ham showed that selection for leanness over many generations was not as adverse as selection for loin weight traits. Although novel genetic parameter estimates are valuable for the design of a breeding program in Canadian swine populations, the implications of genetic relationships between carcass and meat quality traits with growth and performance traits need for further investigation.

The objectives of the second study in Chapter 4 were to estimate 1) heritabilities for various growth, and performance traits; and 2) phenotypic and genetic correlations between performance traits with pork quality and carcass traits in commercial crossbred pigs. Several estimates in this study were new contributions to the genetic correlations between performance traits with carcass and pork quality traits. Novel results from this study showed that NURW is an important trait and selection for NURW will have significant effects on carcass and pork quality traits through indirect selection. Genetic correlation indicated that selection for birth weight, weaning weight, and growth may increase market weight, ultrasound loin depth, and ultrasound intramuscular fat. Favorable correlations were found between both weaning and NURW with LD. However, selection for NURW would lead to increased belly, picnic shoulder, and butt muscles yield, which were dissimilar with weaning weight. Birth weight had adverse effects on pork quality traits that may lead to undesirable increased drip loss pork with pale color but no adverse effect was found between weaning weight and pork quality. In addition, a favorable genetic correlation was observed between NURW and pork quality, showing that selection for NURW may lead to increased carcass yield, while with no adverse effect on pork quality except

for *gluteus medius* lightness. Therefore, selection for NURW can be valuable for increasing market weight and loin depth without adverse effects on pork quality traits.

Favorable genetic correlations were obtained between growth and the most valuable primal, subprimal, cold and hot carcass weights. These results indicated that selection for growth traits would increase carcass yield, which was dissimilar to selection for ultrasound loin depth. It can be concluded that single-trait selection on ultrasound loin depth might lead to undesirable lower pH pork. However, no genetic effect was observed on water holding capacity. Therefore, selection for ADG can be valuable for increasing both carcass weight, primal and subprimal cuts weights. Selection for intramuscular fat may increase belly, picnic shoulder, butt weights, backfat thickness and reduce ultrasound loin depth and cooking loss, and produce undesirable increased pH of meat with a dark color. In addition, novel results in this study showed that selection for decreased FCR may reduce backfat depth with no adverse consequences on pork quality traits except for paler loin, and selection for leaner carcass may affect pork quality traits including cooking loss and lightness of ham.

As has been discussed in the first part of this Chapter, traditionally, genetic potential for pork quality was selected using BLUP methods through indirect selection on correlated traits. Although it was successful the genetic progress was slow for pork quality traits. Recently, the availability of dense panels of DNA markers covering the whole genome of pigs (Ramos et al., 2009) and appropriate statistical methods have made genomic selection feasible in pigs (Nejati-Javaremi et al., 1997; Meuwissen et al., 2001; Xu, 2003; Gianola et al., 2006; Fernando et al., 2007; Habier et al., 2007; Hayes et al., 2009; VanRaden et al., 2009; Friedman et al., 2010; Zhang et al., 2010; Habier et al., 2011; Erbe et al., 2012; Brondum et al., 2012).

Genomic prediction can be developed in the reference population with known genotypes and phenotypes. The results of genomic prediction can be applied to select animals in the selection population with known genotypes and unknown phenotypes. Genomic selection enables prediction of breeding values of young selection candidates, results in reducing the generation interval and increasing accuracy of selection. Genomic selection of purebred pigs based on crossbred performance for pork quality traits can help improving pure lines to produce better pork quality from superior commercial crossbred animals without the need of measurements on pure lines. Therefore, the objective of the third study in Chapter 5 was to develop genomic prediction equations for various pork quality and carcass traits using ssBLUP and commercial crossbred animals to select the superior pure parental lines for breeding. Single-step methodology was used, as it was simpler, faster, more accurate and applicable to complicated models compared to multi-step methods such as GBLUP (Aguilar et al., 2010). Sufficient variation in genomic breeding values confirms that selecting animals with known genotypes and unknown phenotypes may be possible. Average accuracy across pork quality traits was 0.30 in commercial crossbreds, which dropped to 0.26 in their parental purebreds. Moreover, average accuracy across carcass traits was 0.32 in commercial crossbreds, and dropped to 0.28 in their parental purebreds. Therefore, it was concluded that genomic selection using ssBLUP could predict the parental purebred lines without substantial loss of prediction accuracy compared to their crossbreds. This study indicated that traits with high heritabilities tended to give higher accuracies than average (Goddard, 2009).

The relatively low prediction accuracies of GEBV in this study can still be valuable for pork quality traits as they are hard and expensive to measure and often measured post-mortem. These relatively low prediction accuracies might be due to lower reference population size in our

study compared to others. For instance, we had 1,948 crossbreds measured for pork quality with an average heritability of 0.25 (Th^2 = 487) whereas VanRaden et al. (2009) studied 10,000 Holsteins with daughter average for milk yield (h^2 = 0.8; Th^2 = 8,000). Therefore, comparing the results with literature suggested that increasing reference sample size could increase the accuracy of predictions, which was similar to the results reported by Cleveland et al. (2010). To the best of my knowledge, few reports have been published in pigs, especially in relation to predictions in purebreds based on their crossbreds performance (e.g. Cleveland et al., 2010; Christensen et al., 2012; Badke et al., 2014). The accuracies of the prediction models in this study showed that genomic prediction equations generated from commercial crossbred animals could be used to select animals in their parental pure lines for pork quality and carcass traits. In conclusion, GS opens the possibility of using high density of markers covering the whole genome to increase the rate of genetic gain for pork quality traits to ensure that demand for high quality and affordable pork is satisfied.

6.2. GENERAL CONCLUSIONS AND IMPLICATIONS IN SWINE INDUSTRY

Measurement of carcass and meat quality traits is difficult, expensive, can only be performed post-mortem, and is destructive to the sample. Therefore, selection of purebreds based on crossbred performance for these traits would be useful to help improving pure lines of pigs to produce improved pork quality from commercial crossbred pigs without the need of phenotypic measurements on pure lines. Estimates of genetic parameters for performance, carcass, and meat quality traits in crossbred pigs will provide not only insight into the biological basis of these

traits but also a valuable reference to develop efficient genetic improvement programs for these traits. Genetic parameters obtained in Chapters 3 and 4 are valuable for the design of a breeding program emphasizing product quality in Canadian swine populations, especially for new parameters in traits that have not previously been studied. Furthermore, the use of pH is recommended as an effective indicator for drip loss, cooking loss and color of meat. It was concluded that selection for increasing primal and subprimal cut weights with better pork quality may be possible. In addition, moderate to high heritability of carcass traits would suggest an opportunity for improving carcass merit traits in commercial crossbred pigs. In addition, the high cost of data collection and low-to-moderate heritability of meat quality traits provide opportunities to improve them through genomic efforts.

The low-to-moderate heritabilities of performance traits indicated that they could be improved through traditional breeding methods or through genomic selection. Selection for high birth weight would have unfavorable consequences on pork quality traits including undesirable higher drip loss pork with paler color. It was concluded that selection for nursery weight would increase both quantity and quality traits. Furthermore, selection for ADG was also favorable for increasing carcass weight, primal and subprimal cuts weights with no adverse effects on pork quality. However, selection for intramuscular fat may affect pork quality traits but selection for FCR may reduce the lightness of loin. These results implied that selection for a leaner carcass might affect cooking loss and lightness of ham but it would be worth further investigations to confirm these results. These results indicated that deterioration of pork quality may have occurred over many generations through the selection for lower backfat thickness and feed efficiency, which selection for growth appears to have no adverse effects on pork quality traits. The genetic parameters obtained here are valuable for understanding the biology of these traits

by estimating the variance components of each trait indicating the heritability of each traits, and phenotypic and genetic correlations between these traits. This makes it possible to improve them simultaneously resulting in high quality product produced more efficiently and at lower cost.

Genomic prediction equations developed using ssBLUP can be used to select the parental Duroc purebreds without substantial loss of prediction accuracies than their crossbred progenies. This provides an opportunity to predict breeding values of young parental pigs to further reduce generational interval with improved accuracy, which will lead to accelerate genetic gain in the swine breeding programs. This study showed that the amount of prediction accuracy depends on heritability of trait and size of reference population. Therefore, low-to-moderate heritability of pork quality traits led to relatively low accuracies. Although the accuracies are relatively low they still can be useful to increase the genetic gain for pork quality and carcass traits because the prediction accuracies were increased by an average of 17% and 16%, respectively. The results showed that GS was successful in increasing the accuracy for carcass traits compared to traditional parental average, averaged 16% across traits with a range from 6 to 33%. In addition, the accuracy for pork quality traits using GS compared to traditional parental average were increased, averaged 17% across traits with a range from 7 to 38%. In conclusion, genetic technologies such as "omics" can help pig breeders to improve pork quality from commercial crossbred pigs to meet the demands by consumers, packers and processors.

6.3. GENERAL RECOMMENDATIONS

a) Additive genetic models were used in a single-step method. Heterosis is a significant contributor to the profitability in a commercial swine operation,

extending the model of ssBLUP to include dominance genetics effects would be an interesting topic for future research.

b) Also, future investigations on including associated metabolites with pork quality traits including muscle fibre types or metabolomics studies should be explored using the data from the purebred animals in an attempt to further improve genomic prediction accuracies in the purebred populations.

c) In addition, genetic and phenotypic parameters obtained in this thesis were based on traditional BLUP animal models. The availability of high-density genotypes and new statistical methods such as GBLUP and Bayesian approaches provide opportunities to investigate the genetic and phenotypic parameters using these novel methods and compare the results with the previous traditional BLUP results determined in this thesis. This would enable the pig breeders to use new technologies to improve their breeding programs using more accurate method.

6.4. LITERATURE CITED

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APPENDIX 1. STATUS OF MANUSCRIPTS SUBMITTED FROM THE PhD THESIS (AS OF 30 October 2014)

1. Estimated of genetic and phenotypic parameters for beef carcass and ultrasound traits using animal models, which is **not included in this thesis** since it was related to **Canadian beef**:

   Miar Y, GS Plastow, HL Bruce, SS Moore, ON Durunna, JD Nkrumah, Z Wang (2014) Genetic and Phenotypic Parameters Estimation for Ultrasound and Carcass Merit traits in Crossbred Beef Cattle. **PUBLISHED in Canadian Journal of Animal Science,** 94(2): 273-280.

2. Based on **Chapter 3**:

   Miar Y, GS Plastow, SS Moore, G Manafiazar, P Charagu, RA Kemp, B Van Haandel, AE Huisman, CY Zhang, RB McKay, HL Bruce, Z Wang (2014) Genetic and Phenotypic Parameters for Carcass and Meat Quality Traits in Commercial Crossbred Pigs. **PUBLISHED in Journal of Animal Science**, 92(7): 2869-84.

3. Based on **Chapter 4**:

   Miar Y, GS Plastow, HL Bruce, SS Moore, G Manafiazar, P Charagu, RA Kemp, B Van Haandel, RB McKay, AE Huisman, CY Zhang, Z Wang (2014) Genetic Relationships between Performance Traits with Meat Quality and Carcass Characteristics in Commercial Crossbred Pigs. **PUBLISHED in PLOS ONE**, PLOS ONE 9(10):e110105.

4. Based on **Chapter 2**:

   Miar Y, GS Plastow, Z Wang (2014) Genomic Selection, a new era for improvement of meat quality. **SUBMITTED in Springer Science Reviews.**

5. Based on **Chapter 5:**

   Miar Y, GS Plastow, HL Bruce, RA Kemp, P Charagu, CY Zhang, AE Huisman, Z Wang (2014) Genomic Selection of Pork pH in Purebred Pigs for Crossbred Performance. 10th World Congress on Genetics Applied to Livestock Production (WCGALP), Vancouver, British Columbia, CANADA, Aug. 17-22, 2014.

   AND

   Miar Y, GS Plastow, HL Bruce, P Charagu, RA Kemp, AE Huisman, Z Wang (2014) Genomic Selection of Pork Quality and Carcass Traits in Purebred Pigs for Crossbred Performance. **WILL BE SUBMITTED** to **BMC Genomics**.

APPENDIX 2. Phenotypic measurements

A. Slaughter and Carcass Evaluation

All slaughter and carcass evaluation were performed in East 40 Packers in Brandon, Manitoba, Canada as described by the National Swine Improvement Federation guidelines (NSIF, 1997). Hot carcass weight (**HCW**), which was defined as the weight of the carcass including the head, leaf fat and kidneys on the carcass, was recorded on the kill floor immediately after animals were stunned, exsanguinated, scalded, de-haired, dressed and the carcass was split. Following an 18 to 24 h chill, the cold carcass weight (**CCW**), defined as the weight of the carcass with the head, leaf fat, kidneys, and front feet, and the carcass length (**CLEN**), defined as the distance from the anterior edge of the first rib at its junction with the vertebral column to the anterior edge of the pubic symphysis (Figure 3.1) were recorded. At this point, the carcasses were broken into the primal cuts (ham, shoulder, belly, and loin). The loin was further broken into the front (anterior portion), a 3-rib sample, a 1-inch chop, a 4-rib sample, and a back (posterior portion). The 3-rib and 4-rib segments were labelled and placed in bags corresponding to the kill order and frozen in preparation for shipping to the University of Alberta's Meat Science Laboratory. The chop was removed at the level of the 3rd and 4th last rib (which corresponded to the Canadian grading site) and was used to determine: (a) the area of the *longissimus dorsi* muscle (**LEA**) – determined by using a grid calibrated in 1 square centimeter squares (Figure 3.2); (b) subcutaneous fat (**FD**) and loin depth (**LD**) – measured by a ruler 50 mm off the midline, perpendicular to the skin and measured in millimeters (Figure 3.3); (c) texture score (**TEXS**) measured as a tactile rating that assessed the degree of firmness and

exudation or weeping of the *longissimus dorsi* muscle on a subjective 5-point scale (1= extremely soft and weeping; 5 = very firm and dry; a score of 3 being normal) to determine if the loin was pale, soft and exudative (PSE); and (d) subjective marbling score (**CMAR**; 1 to 6, with 0 = devoid, 1 = practically devoid, 2 = trace amount of marbling, 3 = slight, 4 = small, 5 = moderate, 6 = abundant) as determined by the National Swine Improvement Federation (NSIF) marbling charts (NSIF, 1997).

Primal cuts of ham, loin, shoulder and belly were weighed and further dissected into trimmed subprimal cuts. The weights of the untrimmed ham, subdivisions of the loin (front, 3-rib sample, chop, 4-rib sample, and back), shoulder, and belly were combined to determine the untrimmed side weight (**USW**). Hams with foot attached or untrimmed (**UHAM**), and untrimmed shoulders (**USH**) were removed from the side weight (Figures 3.4 and 3.5). Belly (**UBEL**) and loin (**ULOIN**) were separated from each other and weighed (Figure 3.6). Untrimmed loin weight was recorded as the sum of the weights of the front, chop, 3-rib sample, and 4-rib sample, and back of the loin. After the loin chop was evaluated as previously described, it was defatted and deboned in preparation for drip loss determination. Hams were processed to a bone-in ham without fat cover, and with the foot, tail bone (**THAM**). The commercial fat trim of the loin was obtained by a commercial trim of the front and back portions and using that percentage to estimate the trimmed weight on the chop and the 3-rib and 4-rib samples, these were then combined with the trimmed weights of the front and back to obtain the trimmed weight of the entire loin (**TLOIN**). It should be noted that the 3-rib and 4-rib samples had to be untrimmed when they arrived at the Meat Science Laboratory. The neck bones and jowl were removed from the shoulder and the picnic (**PICN**) and butt (**BUTT**) were separated by a cut made at right angles to the long axis of the shoulder at a distance approximately 2.54 cm

below the exposed surface of the blade (scapula) bone (Figure 3.7). The square cut bellies were trimmed (**TBEL**) and the ribs (**RIBS**) were removed (Figure 3.8).

B. Meat Quality Measurements

Meat quality measurements were taken in both the slaughterhouse (East 40 Packers in Brandon, Manitoba, Canada) and Meat Science Laboratory of University of Alberta. The measurements were performed on both loin and ham as described by the National Swine Improvement Federation guidelines (NSIF, 1997). At the slaughterhouse, the front or anterior portion of the loin (*longissimus dorsi* muscle) was used in determining Minolta colour and ultimate or 24 h pH (**PHU**). Loin Minolta L*, a*, and b* (**LOINL**, **LOINA**, and **LOINB**) were taken on four sites on the fresh cut surface of a loin chop from the boneless center cut loin using a Minolta CR 310 colorimeter set at C illuminant (Minolta camera, Osaka, Japan – Figure 3.9). An ultimate pH measurement was taken in the loin muscle at two locations at 24 h postmortem. Meat quality measurements taken on the ham included Minolta L*, a*, and b* values on the fresh cut surface of the inside ham muscle on the *gluteus medius* (**HGML**, **HGMA**, and **HGMB**), *quadriceps femoris* (**HQFL**, **HQFA**, and **HQFB**), and *iliopsoas* muscles (**HILL**, **HILA**, and **HILB –** Figure 3.10). Drip loss (**DL**) determination at the abattoir involved weighing the 1-inch defatted and deboned loin chop and placing it on a stainless steel grid within a container for 48 h at 4°C. At the end of the 48 h, the meat samples were lightly blotted dry with a soaker pad and weighed. The difference in weight was expressed as a percentage of the initial weight to determine drip loss.

At 4 days postmortem, frozen 3-Rib and 4-Rib samples of the loin of each carcass were

packed in coolers and transported by overnight courier to Meat Science Laboratory at the University of Alberta for further meat quality analyses. Prior to analysis, the pork loin was removed from frozen storage and allowed to thaw at 4 °C for 61 h. Each thawed pork loin was removed from the vacuum package bag and was weighed and recorded as whole loin weight, (**WLW**), defined as the weight of 3-Rib and 4-Rib of the loin received at University of Alberta containing meat, fat and bone. The thick backfat was taken from the loin, was weighed and recorded as backfat weight (**BFW**). Then, rib eye was removed from the loin and its weight was recorded as rib eye weight (**REAW**), and it was used for the meat quality assays. A 1-inch chop was removed from the tail end of the loin section and refrigerated at 4 °C for 1 h. Rib eye Minolta L*, a*, and b* values (**REAL**, **REAA**, and **REAB**), were taken on three sites of the chop using a commercial color meter (CR400, Konica-Minolta, Osaka, Japan) on a D 65 light setting which mimics daylight. To measure cooking loss (**CL**), a 200 g roast was cooked in a 71^{o}C water-bath and weighed before and after cooking and cooking loss was recorded as the percentage of weight change divided by the initial weight multiplied by 100. Shear force (**SHF**) was the mean of six 1 cm^2 cores cut from the roast that had been cooked and then refrigerated overnight at 4 °C. The remainder of the pork loin section was physically dissected into muscle and fat, recorded as rib trim weight (**RTW**), and bone, recorded as bone weight (**BOW**).