GENETIC AND BIOLOGICAL ARCHITECTURE OF PORK QUALITY, CARCASS, PRIMAL-CUT AND GROWTH TRAITS IN DUROC PIGS

by

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Dedicated to my wonderful and supportive parents and siblings, without whom I cannot have achieved as much as I have in life.

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"For you have not been given a Spirit of fear or timidity, but of power, love, and self-discipline."
2 Timothy 1:7

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LIST OF ABBREVIATIONS

ADG – average daily gain

AGE – age of the animal at the time of slaughter

AIREML – average information restricted maximum likelihood

BLFT – belly flop test

BL – belly length

BLUP – best linear unbiased prediction

BLW – boneless loin weight

BRW – back ribs weight

BW – belly width

BWR – belly width rear

DL – dam-litter (common environment effect)

DL1 – initial drip loss chop weight

DL2 – post drip loss chop weight

DLP – drip loss percentage

DP – dressing percentage

GBF – graded backfat depth

GBLUP – genomic best linear unbiased prediction

GI – grade index

GLD – graded loin depth

GWAS – genome-wide association study

HCW – hot carcass weight

LA – loin area

LC – loin circumference

LJPC – Japanese color scale score

LL – loin length

L* – Minolta L* on loin

a* – Minolta a* on loin

b* – Minolta b* on loin

LNC – NPPC color scale score

LNM – NPPC marbling scale score

LPHA – loin pH

LW – live weight

P1vP2up – grouping of parity one dams against parity two and up dams; parity effect

PCA – principal component analysis

PC – principal component

REML – restricted maximum likelihood

RMD – ruler muscle depth

SLDxST – slaughter date by slaughter technician effect

SRW – side ribs weight

ssGBLUP – single step genomic best linear unbiased prediction

ssGWAS – single step genome-wide association study

SW – sirloin weight

SY – season year effect

TBLW – trimmed belly weight

TBW – trimmed Boston butt weight

THW – trimmed ham weight

TPW – trimmed picnic shoulder weight

TW – tenderloin weight

UBLW – untrimmed belly weight

UBW – untrimmed Boston butt weight

UHW – untrimmed ham weight

ULW – untrimmed loin weight

USW – untrimmed shoulder weight

ABSTRACT

Within the last few decades, swine breeding programs have been refined to include pork quality and novel carcass traits alongside growth, feed efficiency, and carcass leanness in the selection programs for terminal sire lines with a goal to produce high quality and efficient pork product for consumers. In order to accurately select for multiple traits at once, it becomes imperative to explore their genetic and biological architecture. The genetic architecture of traits can be explored through the estimation of genetic parameters, genome-wide association studies (GWAS), gene networks and metabolic pathways. An alternative approach to explore the genetic and biological connection between traits is based on principal component analysis (PCA), which generates novel "pseudo-phenotypes" and biological types (biotypes). In this context, the main objective of this thesis was to understand the genetic and biological relationship between three growth, eight conventional carcass, 10 pork quality, and 18 novel carcass traits included in two studies. The phenotypic data set included 2,583 records from female Duroc pigs from a terminal sire line. The pedigree file contained 193,764 animals and the genotype file included 21,344 animals with 35,651 single nucleotide polymorphisms (SNPs). The results of the first study indicate that genetic progress can be achieved for all 39 traits. In general, the heritability estimates were moderate, while most genetic correlations were generally moderate to high and favorable. Some antagonisms were observed but those genetic correlations were low to moderate in nature. Thus, these relationships can be considered when developing selection indexes. The second study showed that there are strong links between traits through their principal components (PCs). The main PCs identified are linked to biotypes related to growth, muscle and fat deposition, pork color, and body composition. The PCs were also used as pseudo-phenotypes in the GWAS analysis, which identified important candidate genes and metabolic pathways linked to each biotype. All of this evidence links valuable variables such as belly, color, marbling, and leanness traits. Our findings greatly contribute to the optimization of genetic and genomic selection for the inclusion of valuable and novel traits to improve productive efficiency, novel carcass, and meat quality traits in terminal sire lines.

CHAPTER 1. LITERATURE REVIEW

1.1 The Evolution of Selection in the Pork Industry

Swine breeding objectives have undergone many changes and developments within the last century, evolving alongside consumer wants and utilizing technological advances in order to create a satisfactory product [1]. As the primary goal of pork producers is to create an end product that consumers will want to purchase, the breeding objectives of the industry should also progress towards selecting animals that can meet consumer demands [2]. However, an emphasis must also be placed on animal efficiency in order for the industry to continue to meet the global demand for pork products [3]. Additionally, selection for efficient pork production reduces the overall cost of inputs while reducing the environmental impact of the pork industry [4,5].

In order to assure the desired qualities are proliferated in a population, it is also important to consider the breeds included in breeding programs. Where maternal breeds are primarily relied upon to produce large litter sizes, sire lines are used to introduce improved production, carcass, and meat quality traits [1]. One predominant breed used as a terminal sire line in North America and around the world is the Duroc because of its rapid growth rate and desirable lean-to-fat ratio [6], as well as improved marbling [7]. According to the National Swine Registry, the Duroc breed was established in 1812 in New York and New Jersey. One of the founding sires was popular for his "*quick growth and maturity, deep body, broad ham and shoulder, and quiet disposition*," an impression that flourished as the breed's population grew. Since then, the Duroc breed has been distinguished for its efficiency, meat yield, and pork quality [8,9]. The crossbred progeny of the Duroc breed, which are the predominant meat animal in North America, have been shown to have increases in these valuable traits when compared with maternal breed sires [7,10–12] and higher meat quality when compared with other sire breeds [13–15].

Swine breeders have focused on selecting for traits such as average daily gain, feed efficiency, backfat depth, and lean mass in pigs for decades. The improvements made in those traits is tangible, evidenced recently by the increased average slaughter weight of 5.45 kilograms between the years 2009 and 2018 in the United States [16]. It has been well established that pigs can grow efficiently under well managed systems [17,18] and that growth traits tend to have higher heritabilities than meat quality traits [19,20]. However, faster growing animals also tend to have

poorer meat quality [18]. Additionally, meat quality and growth traits tend to have antagonistic genetic relationships [21]. This creates a problem, as consumers are looking for higher quality meat products now more than ever before [22]. Therefore, it is imperative for the swine industry to select for both meat quality and productive efficiency traits.

1.1.1 Defining Pork Quality

Meat quality is an infamously difficult term to define within the animal production industry, as consumer opinions can vary vastly depending upon personal preference and cultural background [23]. The challenge, then, for pork producers is finding where the largest overlap in preferences lie and translating them into actionable selection objectives. As consumer perception of a product starts when they enter the grocery store and look at the meat in the package [24], this is also where the industry should start.

In a study focused on the effect of pork loin color and consumer acceptance, it was found under a simulated retail display that 52.8% of the study's participants chose pork chops that were given a color score 5 and 6 on the National Pork Producers Council (NPPC) color standard (45.54 Minolta L* average value) [25]. Many other studies have also established that color has a substantial influence on the acceptance of pork products [24,26,27]. Additionally, several studies have shown that consumers tend to visually prefer pork with moderate to less fat content, both intramuscular (marbling) and subcutaneous (backfat) deposits [22,28,29]. However, producers should also consider the factors that can affect the palatability of the product. Studies have shown that consumers prefer tender meat with good pork flavor [30,31]. Based on these conclusions, the average consumer definition of pork quality is a cut that is pink-ish red in color with moderate marbling that is tender and tasty once cooked.

In a review of pork consumer preferences, Miller stated that the more technical influencers on pork quality are "pH, water holding capacity, color, and marbling [31]." Therefore, in order to satisfactorily meet consumer preferences, selection objectives should consider both the average consumer definition of quality and the technical factors. Now our overall selection goal has a clearer perspective: producers should consider consumer's preferred appearance and the biological influencers as well as classic production traits to maintain system efficiency.

In order to develop a selection index, the genetic parameters must be quantified to determine heritability and genetic relationship between desired traits. Recent literature has estimated genetic

parameters for meat quality and growth traits for the Duroc breed [32], three populations of commercial Duroc x (Large White x Landrace) pigs [33,34] and another population of Pietran x Large White crossbred pigs [35]. Across these studies, the same general trends were observed: lower heritability estimates for meat quality traits and higher heritabilities for growth and weight traits as well as inverse genetic relationships between the two. Each of these studies has shown that these traits are heritable and genetically correlated at ranging levels, providing a background and basis for the following studies. However, studies on meat quality and carcass traits are difficult to perform because of the nature of the traits, which must be collected postmortem and in slaughter facilities, which takes time and manpower. Additionally, data cannot be collected on the animals that are candidates for selection, so relatives or offspring must be used to gather phenotypes instead.

1.1.2 Defining Novel Traits

Another integral piece of the genetic puzzle is the process of defining novel traits, which requires the collection and analysis of data to describe desirable or undesirable phenotypes. Traits such as average daily gain, body weight, backfat depth, and loin-eye area have long been researched [36], but it has only been in recent decades that researchers began defining meat quality and carcass traits for the purpose of selection. In that time, carcass traits have only been researched in depth a handful of times [32–35]. However, not all carcass traits have been previously evaluated from a genetic parameter standpoint. An important series of traits that should be characterized are belly traits, as the belly is one of the most valuable cuts on the carcass. For example, the belly flop test has been linked to fat composition and belly length [37–39], which is a valuable piece of information for the quantity and quality of bacon that packers can market. Additionally, traits like belly width could be beneficial for breeders to select for to meet the preference of packers [21]. Defining novel traits supports the discovery and use of new economically valuable traits in selection indexes, which ultimately adds value to the production chain.

1.2 Genomic Approaches to Genetic Parameter and Breeding Value Estimation

Since the introduction of genotyping, animal breeders, researchers, and companies have sought to use genomics to more accurately perform selection on animals (especially for expensive or difficult-to-measure traits), to improve the accuracy of estimated breeding values (EBVs) and

to unravel biological mechanisms underlying the phenotypic expression of traits of interest [40]. As the cost of single nucleotide polymorphism (SNP) panels decreased and technologies and methodological approaches such as genotype imputation became more accurate and computationally feasible [41,42], the number of genotyped animals has increased substantially. With the increase in the number of available genotypes, new methods to estimate genetic parameters and breeding values had to be re-evaluated and defined.

Traditionally, EBVs were estimated using the Best Linear Unbiased Prediction (BLUP) method and an animal model. Traditional BLUP utilizes a pedigree-based relationship matrix (**A**) in order to estimate the breeding values, but as the use of genomics and single-nucleotide polymorphisms (SNPs) became more prevalent, a different method of estimating breeding values (genomic estimated breeding values; GEBVs) was introduced: Genomic Best Linear Unbiased Prediction (GBLUP). This method of estimation involved including the **G** (or genomic-based) matrix [43] instead of the **A** matrix. The use of the **G** matrix allowed each individual SNP's information to be accounted for, resulting in better estimates of the level of relatedness between individuals which might create more accurate estimates of the EBVs [44,45]. However, one downside of GBLUP is the density of the **G** matrix in the off-diagonal elements, which increases computational demands.

In 2009, the idea of a single-step process was introduced by Misztal et al. [46] and further expanded upon by Legarra et al. [47], Aguilar et al. [48], and Christensen and Lund [49]. The main idea behind the single-step GBLUP procedure was to combine pedigree and genomic information through the augmentation of the **A** matrix with the **G** matrix. This combination became known as the **H**, or 'hybrid', matrix [46–48]. Where BLUP uses the **A** matrix and GBLUP uses the **G** matrix, single-step Genomic Best Linear Unbiased Prediction (ssGBLUP; [50]) uses the **H** matrix, therefore accounting for genomic as well as pedigree relationship. The **H** matrix also creates a sparser matrix in the off-diagonals than the **G** matrix alone, which usually makes computation more efficient than GBLUP.

With the inclusion of genomic information, the estimation of the variance components had to adapt as well. Variance components have been estimated using the Restricted Maximum Likelihood (REML) approach [51–53], which is still commonly used today. The traditional REML method calculates variance components based on the **A**, **G**, or **H** matrixes, but as the computation became more complex and the matrixes denser, another form of REML was developed. The

average information REML (AIREML) algorithm [54,55] can utilize more complex mixed animal models to reduce computational time. Additionally, the use of genomic information lowers the standard errors for variance component estimation [56], indicating more accurate estimates. Heritabilities also tend to be lower when estimated with genomic information [57].

Genome-wide association analysis (GWAS) is a popular and efficient method to discover candidate genes and quantitative trait loci (QTLs) associated with phenotypes of interest [58]. GWAS has been used to wide acceptance and is now common practice in the animal breeding community, however, traditional GWAS also contained some flaws, namely a lack of statistical power to detect QTLs [59] and losses in accuracy when animals without genotypes are used [60]. After the development of the **H** matrix and the introduction of ssGBLUP, Wang et al. [59] proposed that a similar idea could be used in GWAS. By combining all phenotype, genotype, and pedigree information and considering it jointly, it allowed for the simultaneous consideration of all SNPs which resulted in increased accuracy of GEBVs, improved computational time and higher power in detecting important QTLs [58]. This concept became known as ssGWAS [59].

1.3 Principal Component Analysis

Principal component analysis (PCA) is frequently used as an exploratory analysis tool across a wide range of scientific disciplines because of its ability to be applied to vastly different data sets. The goals of PCA according to Abdi and Williams [61] are to extract the most important information from a data set while compressing the size, maintaining variability, and simplifying the amount of information contained within a data set in order to analyze the structure of the observations as newly created principal components (PCs). PCs are linear combinations of the original variables which explain proportions of variation and are given in descending order. The first PC has the largest proportion of the variance explained, or, in other words, it explains the largest proportion of the data set being analyzed [61]. The second PC is statistically independent of the first PC and explains the next largest proportion of the variation. For the third, fourth, and so on PCs, the concept is the same in descending order of the proportion of variance explained.

When applied to animal datasets PCs have a wide variety of applications. PCs can be used to facilitate the simultaneous selection of traits of interest by aiding in the detection of quantitative trait loci (QTL) [62,63], relating genomic regions to specific traits or biological types (biotypes) [64,65], evaluating the relationship between traits, measurements or estimated breeding values and

suggesting like-functions of traits [66,67], and more. The primary potential application for PCs in animal breeding is its ability to take a large number of variables, such as traits, and simplify them into fewer variables called "pseudo-phenotypes" while maintaining the genetic variation of the trait or traits needed for selection [68].

1.4 Summary and Hypothesis

In order to meet the goal of creating an improved product for meat consumers, animal breeders must apply the technology at hand and develop new tools to gather the information needed to develop an optimal selection goal. The estimation of genetic parameters is critical, as the heritability of each trait and their genetic correlations are needed to understand the relationship between traits on a genomic level and enable breeders to minimize the number of traits included in a selection objective. Alternative methods of quantifying phenotypes should also be considered where possible to maximize the efficiency of selection, such as through the use of principal component analysis.

Therefore, the overall objectives of this thesis were to describe the genetic relationship between and among pork quality, growth, and conventionally-measured and novel carcass traits by estimating their genetic parameters, performing a principal component analysis to develop pseudo-phenotypes, and using those pseudo-phenotypes (or new genetic traits) to identify candidate genes through a GWAS. The estimation of genetic parameters enables breeding companies to assess their selection index and adjust it based on current selection goals by studying the heritability and degree of genetic relationship between each trait. Additionally, comparing the estimates between the pedigree-matrix-based and the hybrid-matrix-based methods are valuable for understanding the impact genomics has on the selection process. However, with 39 traits of interest, it becomes imperative to explore other possibilities for enabling efficient selection. By performing a PCA on the additive genetic (co)variance matrix ($\mathbf{A^T}$) the traits will be able to be compared based on common biotypes while maintaining variance, potentially reducing the number of phenotypes and records needed to perform genomic selection in this population in the future. Furthermore, utilizing a GWAS with the results of the PCA has the potential to identify candidate genes and QTLs related to the biotypes, thereby adding to the biological understanding of the many traits included in the following studies.

The main hypothesis of this thesis was that there is genetic variability for traits related to growth, carcass, and meat quality in pigs, and through the use of genetic parameters, principal components, and genome-wide association studies, we can more accurately select for pork quality and carcass traits simultaneously with conventional pork production traits Duroc pigs.

1.5 References

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CHAPTER 2. ESTIMATION OF GENETIC PARAMETERS FOR PORK QUALITY, NOVEL CARCASS, PRIMAL-CUT AND GROWTH TRAITS IN DUROC PIGS

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2.1 Abstract

More recently, swine breeding programs have aimed to include pork quality and novel carcass (e.g., specific primal cuts such as the Boston butt or belly that are not commonly used in selection indexes) and belly traits together with growth, feed efficiency, and carcass leanness in the selection indexes of terminal-sire lines, in order to efficiently produce pork with improved quality at a low cost to consumers. In this context, the success of genetic selection for such traits relies on accurate estimates of heritabilities and genetic correlations between traits. The objective of this study was to estimate genetic parameters for 39 traits in Duroc pigs (three growth, eight conventional carcass (commonly measured production traits; e.g., backfat depth), 10 pork quality, and 18 novel carcass traits). Phenotypic measurements were collected on 2,583 purebred Duroc gilts, and the variance components were estimated using both univariate and bivariate models and REML procedures. Moderate to high heritability estimates were found for most traits, while genetic correlations tended to be low to moderate overall. Moderate to high genetic correlations were found between growth, primal-cuts, and novel carcass traits, while low to moderate correlations were found between pork quality and growth and carcass traits. Some genetic antagonisms were observed, but they are of low to moderate magnitude. This indicates that genetic progress can be achieved for all traits when using an adequate selection index.

2.2 Introduction

The North American swine industry produces over 146 million pigs per year, which accounts for over 15 million tons of pork products [1]. Pork production in the United States generated over 21 billion dollars in gross income from meat sales in 2018 [2], which is expected to increase due

to a greater demand for pork [3,4]. In order to meet this growing demand, worldwide swine breeding programs have focused upon increasing the lean growth rate and feed efficiency of pigs by selecting for rapid growth and reduced backfat depth [5–7].

Currently, consumers desire high-quality meat products, which are perceived as more tender, juicier, and possessing of desirable flavor [8,9]. Pork quality in this context can be defined as consumers' sensory acceptance of pork products, which have a stable pH, pinkish-red color, and moderate marbling (i.e., intra-muscular fat) content [8,10,11]. Therefore, it is becoming important to include pork quality with growth and carcass leanness traits in the selection objectives in order to attend to consumers' growing demands for higher quality pork [8,12,13]. Additionally, as the value of primal cuts (e.g., picnic shoulder, Boston butt, loin, ham, and belly) increases, producers need to consider additional carcass traits when making selection decisions to increase carcass cut-out value.

Pork quality traits have been previously estimated to have low to moderate heritabilities, while carcass traits have moderate to high heritabilities [13–16]. However, there are few [13,14,16] to no previously estimated genetic parameters for primal and subprimal carcass cuts with pork quality and growth traits measured in the same population. For instance, traits such as the belly flop test, belly width, and belly length have not been previously genetically evaluated, and the difference between trimmed and untrimmed primal cuts has only been evaluated in a crossbred population [13]. As crossbred animals are used primarily for meat products, it is important to understand the genetics of their pork quality. However, it is also valuable to estimate meat quality and carcass traits in the terminal sire line as, within swine breeding, the sire line's most valuable contribution is their meat quality and carcass attributes. Duroc is the most common terminal sire line in North America, likely due to their high pork quality (darker meat with more marbling) and fast rate of growth [17–19]. Favorable genetic correlations between these traits may exist and could enable simultaneous selection for improved pork quality and primal-cut yield. However, there could also be unfavorable correlations, and in order to prevent potential negative effects to pork quality, carcass characteristics or growth the relationships between these traits must be quantified and considered in selective breeding schemes.

The main objective of this study was to estimate heritability and genetic correlations for various novel pork quality, carcass cut weight, belly, carcass leanness, and growth traits in a population of purebred, terminal-line Duroc gilts.

2.3 Materials and Methods

2.3.1 Ethics Statement

The animals included in this study were managed in accordance with the "Code of practice for the care and handling of pigs" (National Farm Animal Care Council, 2014). All the samples for genotyping were collected in a nucleus breeding farm and the animal owners agreed to be involved in the project. The slaughters, data collection and trait measurements were done by well-trained staff following industry best practices.

2.3.2 Datasets

Phenotypic records for 39 growth, carcass, pork quality, and conventional carcass traits were available for 2,583 pigs (all female) born between 2010 and 2018. All animals were born and raised on the same nucleus farm and slaughter information was collected at the same slaughter plant on pigs from 159 to 219 days of age. Only female records were collected as the males were used for genetic dissemination from the nucleus farm. The initial pedigree file contained 193,764 animals, in which 3,796 were sires and 19,802 were dams. The pedigree was trimmed to 10 generations back from the phenotyped animals. The number of animals in the pedigree file ranged from 2,544 to 4,917 for the different traits (average ± SD: 4,579 ± 689).

2.3.3 Trait Description

A total of 39 growth, conventional, carcass, and pork quality traits were included in this study. The descriptive statistics are shown in Tables 2.1 and 2.2. Traits were grouped into four categories: growth, pork quality, and conventional and novel carcass traits.

Table 2.1. Complete descriptive statistics for growth, pork quality, and conventionally measured carcass traits.

Trait	Abbreviation	*n*	Mean	SD	Min.	Max.
Growth traits						
Average Daily Gain (g/day)	ADG	2,226	670.07	49.14	518.00	813.00
Hot Carcass Weight (kg)	HCW	2,237	100.61	5.92	83.60	118.00
Live Weight (kg)	LW	2,210	121.17	7.18	100.00	143.00
Pork quality traits						
25 cm Chop Initial Weight (g)[1]	DL1	2,152	188.68	26.45	120.70	269.00
25 cm Chop Post Weight (g)[1]	DL2	2,150	186.25	26.19	114.40	261.80
Drip Loss Percentage (%)	DLP	1,114	1.15	0.53	0.06	3.14
Japanese Loin Color Scale	LJPC	2,203	3.54	0.38	2.50	4.50
Minolta L*	L*	2,089	49.22	2.30	41.80	57.40
Minolta a*	a*	2,092	4.17	1.64	0.25	17.85
Minolta b*	b*	2,082	9.12	1.07	5.70	12.50
NPPC Loin Color Scale	LNC	2,202	3.60	0.50	2.50	5.00
NPPC Loin Marbling Scale	LNM	2,209	2.11	0.67	1.00	4.00
Loin pH	LPHA	2,155	5.72	0.15	5.25	6.18
Conventionally measured carcass traits						
Dressing Percentage (%)	DP	2,159	83.13	2.77	74.73	91.90
Grading Back Fat (cm)	GBF	2,218	14.16	3.13	7.10	24.10
Grade Index[2]	GI	2,216	113.07	4.18	70.00	115.00
Grading Loin Depth (cm)	GLD	2,224	66.62	5.41	51.00	82.40
Loin Area (cm2)	LA	1,921	56.90	7.04	31.94	80.41
Loin Circumference (cm)	LC	777	29.78	2.51	21.22	53.55
Loin Length (cm)	LL	2,209	67.46	2.52	60.00	75.00
Ruler Muscle Depth (cm)	RMD	2,215	70.87	5.12	55.00	85.00

[1]Initial chop weight was the weight of the 25 cm loin sample taken prior to packaging, while post chop weight was the weight of the 25 cm loin sample taken after the loin was packaged for 48 hours. [2]Grade index is a measure of the economic value of each carcass based upon lean content and fat content.

Table 2.2. Complete descriptive statistics for novel carcass traits.

Trait	Abbreviation	*n*	Mean	SD	Min.	Max.
Belly Flop Test (cm)	BLFT	570	15.21	4.50	3.00	29.50
Belly Length (cm)	BL	1,036	62.93	2.92	54.00	72.00
Boneless Loin Weight (kg)	BLW	2,221	4.83	0.45	3.52	6.18
Back Ribs Weight (kg)	BRW	2,211	0.90	0.13	0.50	1.28
Belly Width (cm)	BW	1,824	26.67	1.84	13.00	34.00
Belly Width Rear (cm)	BWR	572	19.05	2.36	11.00	26.00
Side Ribs Weight (kg)	SRW	2,190	1.75	0.23	1.09	2.42
Sirloin Weight (kg)	SW	2,206	1.12	0.19	0.58	1.73
Tenderloin Weight (kg)	TW	2,212	0.49	0.08	0.28	0.74
Trimmed Belly Weight (kg)	TBLW	2,181	5.87	0.63	3.96	7.80
Trimmed Boston Butt Weight (kg)	TBW	2,222	4.69	0.59	3.04	6.34
Trimmed Ham Weight (kg)	THW	2,204	9.42	0.71	7.33	11.60
Trimmed Picnic Shoulder Weight (kg)	TPW	2,219	4.18	0.48	2.74	5.54
Untrimmed Belly Weight (kg)	UBLW	2,211	7.63	0.75	5.50	9.84
Untrimmed Boston Butt Weight (kg)	UBW	2,224	5.65	0.62	4.00	7.34
Untrimmed Ham Weight (kg)	UHW	2,219	11.42	0.78	9.12	13.80
Untrimmed Shoulder Weight (kg)	USW	2,216	11.71	0.89	9.04	14.38
Untrimmed Loin Weight (kg)	ULW	2,223	11.18	0.83	8.69	13.72

Growth traits. Average daily gain (ADG; g/day) was defined as total body weight gain divided by days-on-test. Pre-slaughter live weight (LW; kg) was measured five days before slaughter. Hot carcass weight (HCW; kg) was defined as the whole carcass weight taken after exsanguination and evisceration, including the head, leaf lard, kidneys, and trotters [20].

Pork quality traits. Drip loss (DL) measurements were obtained following a retail method by cutting a 2.5 cm thick chop from the center of the loin and weighing it to obtain the preliminary value (DL1). Subsequently, the loin was packaged in a retail tray with a moisture pad for 48 hours and weighed a second time to obtain the difference in moisture weight (DL2). Percent drip loss was calculated as the difference between DL2 and DL1 divided by DL1 [20]. Both the Japanese color scale (LJPC) [21] and NPPC color scale (LNC) [22] were used to classify the loin cuts by color. As outlined by Fortier et al. [20], the LJPC scale ranges from 0.5 to 6.0 while the LNC scale ranges from 1.0 to 6.0. Loins were also assigned a marbling score according to the NPPC marbling scale (LNM) [22] on a scale from 1 to 10, which corresponds to the indirect percentage of intramuscular lipid content. Each loin was scored a single time by technicians at the time of processing. In addition, Minolta color measurements were taken using the Minolta Colorimeter (Minolta Camera Co., LTD, Osaka, Japan), in which L* (lightness), a* (redness), and b* (yellowness) values were determined as averages of two measurements. At 24 h after slaughter, loins were measured twice with a pH meter [20] to obtain the loin ultimate pH average (LPHA).

Conventional carcass traits. Conventional carcass traits were defined as traits that are commonly measured by processors or producers. Dressing percentage (DP; %) was calculated by dividing HCW by LW and was recorded as a percentage. Both backfat (GBF) and loin (GLD) depth measurements were obtained using a Destron optical probe (Destron-Fearing, Saint Paul, MN) at the third to fourth from the last rib. A grade index (GI) was measured on each carcass in order to assess economic quality of the carcass on a percentage-based scale. The GI is a grid created by packers to reward the most desirable carcasses, whether by size or lean yield. Technicians were responsible for measuring loin length (LL; cm), measured from midway between 2^{nd} and 3^{rd} ribs to the posterior end of the loin cut, 2.5 centimeters in front of the pelvis and ruler muscle depth (RMD; cm)—a hand measure of the diameter of the loin-eye between 3^{rd} and 4^{th} last ribs taken seven centimeters from the midline and perpendicular to the skin surface [20]. Loin area (LA; cm^2) and loin circumference (LC; cm) were measured using the ImageJ software [23]. Loin images were

processed using the ImageJ software [23] and used to validate the RMD measurement. All loin measurements were taken from the cross section of the 3rd and 4th last ribs [20].

Novel carcass traits. In this context, novel carcass traits were defined as traits that are not commonly used for genetic parameter estimation or included in selection indexes. Carcasses were separated into primal cuts to attain both untrimmed and trimmed weights. Untrimmed belly weight (UBLW; kg), untrimmed Boston butt weight (UBW; kg), untrimmed ham weight (UHW; kg), untrimmed loin weight (ULW; kg), and untrimmed shoulder weight (USW; kg) were weighed with skin, fat, and bones remaining. Then, trimmed belly weight (TBLW; kg), trimmed Boston butt weight (TBW; kg), trimmed picnic shoulder weight (TSW; kg), and trimmed ham weight (THW; kg) were taken post removal skin with fat trimmed to commercial levels. A boneless loin weight (BLW; kg) was measured with skin, bone, tenderloin, and sirloin removed with fat trimmed to 6.35 millimeters. Sirloin weight (SW; kg) and tenderloin weight (TW; kg) were taken after removal from the primal loin. Two sub-primal rib cuts were measured as back ribs weight (BRW; kg) and side ribs weight (SRW; kg) after extraction from the primal loin and the primal belly, respectively. In order to quantify the belly fat quality, the belly flop test (BLFT; cm) was performed by hanging the belly, skin down over a metal pipe. After two minutes, the distance between the sides of the belly was measured [20] in centimeters. In addition, belly length (BL; cm) was measured as the length of the whole belly; belly width (BLW; cm) was measured at the center of the cut; and width of the rear (BWR; cm) was measured at the end of the cut. All individual carcass measurements were taken during slaughter by a single well-trained technician per day of slaughter.

2.3.4 Definition of Statistical Models

Evaluation of fixed and random effects included in the statistical model was performed in the R software [24] using the lm (linear model) and AIC (Akaike information criterion) functions. The fixed effects tested were: slaughter technician (SLT; i.e., the technician who took the carcass measurements), slaughter date (SLD; date of animal slaughter), season-year (SY; season (1: November–January; 2: February–April; 3: May–July; 4: August–October) and year at time of birth), parity of the dam (P1vP2up; parity one dams versus parity two and greater dams, and P1vP2vP3up; parity one dams versus parity two dams versus parity three and greater dams), age (AGE; age of the animal at the time of slaughter), hot carcass weight (HCW) and dam-litter (DL;

dam and birth litter information). First degree interactions were also tested, but only SLD by SLT was found to be significant (p-value < 0.05).

The process of backwards selection was used to remove non-significant effects one at a time per trait until each remaining effect or interaction effect was significant at an α of 0.05 and produced the lowest residual error. Additionally, the Tukey test was performed for traits significant for the parity effects to determine which parity grouping should be used. The results indicated that P1vP2up should be used as the parity effect. AIC values were used to compare models containing random effects. Those models with the lowest AIC values were chosen for further analysis. The random effects tested were DL as a common environmental (common litter) effect and animal additive genetic effects. The final models for each trait can be found in Table 2.3.

2.3.5 Estimation of Variance Components

Variance components were estimated using the pedigree-based relationship matrix and the restricted maximum likelihood (REML) procedure with the average-information algorithm implemented in the AIREMLF90 package [25]. Genetic correlations and their corresponding standard errors were obtained from the bivariate analysis of traits, while phenotypic correlations were obtained by adjusting the phenotypes by their fixed effects and using the Pearson correlation in the R software [24]. Heritabilities were estimated on a single-trait basis.

The animal model used when one random effect was present is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

with

$$\begin{pmatrix} u \\ e \end{pmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & 0 \\ 0 & \sigma_e^2 \end{pmatrix}\right]$$

where **y** is the vector of phenotypic observation, **b** is the vector of fixed effects (found to be significant for each trait), **u** is the vector of additive genetic effects, and **e** is a vector of random error. The **X** and **Z** are the incidence matrices associating **b** and **u** to the observations, respectively. The σ_a^2 and σ_e^2 are the additive and residual error variances, respectively.

The animal model used when both DL and animal additive genetic random effects were present is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wd} + \mathbf{e}$$

with

$$\begin{pmatrix} u \\ d \\ e \end{pmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & 0 & 0 \\ 0 & \sigma_d^2 & 0 \\ 0 & 0 & \sigma_e^2 \end{pmatrix}\right]$$

where **y** is the vector of phenotypic observation, **b** is the vector of fixed effects (found to be significant for each trait), **u** is the vector of additive genetic effects, **d** is the vector of common environment (dam-litter) effect, and **e** is a vector of random error. The **X**, **Z,** and **W** are the incidence matrices associating **b**, **u,** and **d** to the observations, respectively. σ_a^2 , σ_d^2, and σ_e^2 are the additive genetic, common environmental (dam-litter), and residual error variances, respectively.

2.4 Results

2.4.1 Descriptive Statistics

The descriptive statistics of the phenotypic records are shown in Tables 2.1 and 2.2. There are a total of 18 carcass traits including primal and subprimal cuts, 10 pork quality traits, three growth traits, and eight conventionally measured traits. The average number of observations among growth traits was 2224 (±14), while for pork quality, conventional and novel carcass trait averages were 2045 (±331), 1992 (±502), and 1942 (±575), respectively. The variation in the number of observations is due to the data trimming process. The BLFT, BWR, and LC had less observations (570, 572, and 777, respectively) as they were added later in the data collection process.

On average, trimmed primal cut weights were 24.79 ± 7.01 percent less than the untrimmed cuts.

2.4.2 Statistical Models

The final models for each trait are shown in Table 2.3 (categorical fixed effects, covariates, and random effects), Table 2.4, and Table 2.5 (significance levels and AIC values, respectively). Fixed effects such as SLDxST and SY were used to account for variation in the slaughter process and the season and year when the animal was born, respectively. Similarly, the parity effect was used to account for the differences in performance among pigs born from gilts, as it has been shown that pigs born from earlier parity dams have lower performances [26–28].

Table 2.3. Fixed and random effects included in the statistical models used for the single and two-trait analysis.

Traits[1]	Fixed Effect(s)[2]	Covariate(s)[3]	Random Effect(s)[4]
DP	SLDxST	Age	Animal
DLP, b*, LPHA	SLDxST	Age	Animal, DL
GI	SLDxST	HCW	Animal
BRW, BW, GLD, RMD, BLFT	SLDxST	HCW	Animal, DL
LNC	SLDxST, P1vP2up		Animal, DL
a*, L*, LNM	SLDxST, P1vP2up	Age	Animal, DL
LJPC	SLDxST, P1vP2up	HCW	Animal
DL1, DL2, GBF	SLDxST, P1vP2up	HCW	Animal, DL
HCW, LW	SLDxST, SY	Age	Animal, DL
BWR	SLDxST, SY	HCW	Animal
BL, LL, SRW, TBLW, TPW, TW, UBLW, UBW, ULW, USW	SLDxST, SY	HCW	Animal, DL
BLW, LA, LC, SW, TBW, THW, UHW	SLDxST, SY, P1vP2up	HCW	Animal, DL
ADG	SLDxST, SY		Animal, DL

[1]DP: dressing percentage; DLP: drip loss percentage; b*: loin Minolta b* score; LPHA: loin pH average; GI: grade index; BRW: back ribs weight; BW: belly width; GLD: grading loin depth; RMD: ruler muscle depth; BLFT: belly flop test; LNC: loin NPPC color score; a*: loin Minolta a* score; L*: loin Minolta L* score; LNM: loin NPPC marbling score; LJPC: loin Japanese color score; DL1: drip loss measurement 1; DL2: drip loss measurement 2; GBF: grading back fat; HCW: hot carcass weight; LW: live weight; BWR: belly width at the rear; BL: belly length; LL: loin length; SRW: side ribs weight; TBLW: trimmed belly weight; TPW: trimmed picnic shoulder weight; TW: tenderloin weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; ULW: untrimmed loin weight; USW: untrimmed picnic shoulder weight; BLW: boneless loin weight; LA: loin-eye area; LC: loin-eye circumference; SW: sirloin weight; TBW: trimmed Boston butt weigh; THW: trimmed ham weight; UHW: untrimmed ham weight; ADG: average daily gain. [2]SLDxST: date of animal slaughter by the slaughter technician; P1vP2up: grouping of parity one dams versus parity two and greater dams; SY: season and year of animal birth. [3]Age: age of animal at time of slaughter; HCW: hot carcass weight of animal at time of slaughter. [4]DL: effect of dam and birth litter; common environmental factor.

Table 2.4. Significance of covariate and categorical fixed effects tested for growth, pork quality, and conventionally measured carcass traits; and the different AIC values obtained among the models with and without the random effect of dam-litter (DL).

	Fixed effects[1]					Random effects[2]	
Trait[3]	**SLDxST**	**P1vP2up**	**SY**	**Age**	**HCW**	**DL**	**Animal + DL**
Growth traits							
ADG	****		****			21,550.43	−135,190.70
HCW	****		****			13,603.34	−149,532.60
LW	****		****	**		14,047.96	−141,882.40
Pork quality traits							
DL1	****	**			****	18,696.57	−127,322.10
DL2	****	**			****	18,612.74	−128,274.10
DLP	****			***		1,059.23	-Inf
LJPC	****	***				-	−160,829.40
L*	****	**		*		8,359.99	−160,829.40
a*	****	**		***		6,159.43	−142,888.80
b*	****			***		5,031.52	−144,782.00
LNC	****	*				1,321.70	−156,996.80
LNM	****	**		*		2,795.43	−145,330.40
LPHA	****			**		−4,144.23	−155,993.50
Conventionally measured carcass traits							
DP	****			**		-	−163,952.10
GBF	****	**	*		****	9,988.46	−147,518.00
GI	****				****	-	−159,068.30
GLD	****				****	12,787.05	−138,065.40
LA	****	**	*		****	11,061.23	−122,852.30
LC	****	**	**		****	2,630.98	−42,713.54
LL	****		**		****	8,653.23	−138,682.60
RMD	****				****	12,476.45	−139,640.40

**** < 0.0001, *** < 0.001, ** < 0.01, * < 0.05. [1]SLDxST: date of animal slaughter by the slaughter technician; P1vP2up: grouping of parity one dams versus parity two and greater dams; SY: season and year of animal birth; Age: age of animal at time of slaughter; HCW: hot carcass weight of animal at time of slaughter. [2]DL: effect of dam and birth litter; common environmental factor. [3]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 2.5. Significance of covariate and categorical fixed effects tested for novel carcass traits; and the different AIC values obtained among the models with and without the random effect of dam-litter (DL).

	Fixed effects[1]					Random effects[2]	
Trait	**SLDxST**	**Parity**	**SY**	**Age**	**HCW**	**DL**	**Animal + DL**
BLFT	****				**	2,440.94	−35,504.03
BL	****		*		****	4,036.71	−55,987.57
BLW	****	***	****		****	802.40	−153,389.30
BRW	****				****	−4,818.93	−159,264.60
BW	****				****	-	−129,307.10
BWR	****		**		****	-	−37,851.27
SRW	****		***		****	−2,727.63	−152,472.80
SW	****	*	*		****	−2,189.68	−146,506.50
TW	****		*		****	−7,239.72	−156,483.90
TBLW	****		****		****	1,720.85	−150,733.80
TBW	****	*	****		****	845.88	−145,625.50
THW	****	**	****		****	2,967.29	−143,913.60
TPW	****		*		****	563.55	−146,284.40
UBLW	****		***		****	2,090.03	−150,757.10
UBW	****		**		****	1,056.23	−146,604.20
UHW	****	**	****		****	845.88	−141,628.50
USW	****		****		****	2,167.23	−143,398.00
ULW	****		****		****	3,070.93	−146,928.40

**** < 0.0001, *** < 0.001, ** < 0.01, * < 0.05. [1]SLDxST: date of animal slaughter by the slaughter technician; P1vP2up: grouping of parity one dams versus parity two and greater dams; SY: season and year of animal birth; Age: age of animal at time of slaughter; HCW: hot carcass weight of animal at time of slaughter. [2]DL: effect of dam and birth litter; common environmental factor. [3]BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

2.4.3 Heritabilities

The heritability estimates are shown in Tables 2.6 and 2.7. Results were categorized using the following heritability scale: low: from 0.01 to 0.14; moderate: from 0.15 to 0.39; and high: greater than or equal to 0.40.

Table 2.6. Estimates of heritability (h^2), additive genetic variance (σ^2_a) and variance for the permanent environmental effect of dam-litter (σ^2_d) for growth, pork quality, and conventionally measured carcass traits.

Trait[1]	h^2	σ^2_a	σ^2_d	c^2
Growth traits				
ADG	0.28 ± 0.07	522.490	416.2300	0.223
HCW	0.30 ± 0.06	8.442	0.1030	0.004
LW	0.26 ± 0.06	10.337	1.1060	0.028
Pork quality traits				
DL1	0.24 ± 0.06	124.740	63.6810	0.123
DL2	0.23 ± 0.06	115.630	60.3760	0.120
DLP	0.28 ± 0.09	0.052	0.0054	0.000
LJPC	0.22 ± 0.05	0.023		
L*	0.36 ± 0.07	1.310	0.0324	0.009
a*	0.30 ± 0.06	0.392	0.1320	0.101
b*	0.32 ± 0.06	0.224	0.0005	0.001
LNC	0.14 ± 0.05	0.015	0.0029	0.026
LNM	0.42 ± 0.06	0.097	0.0000	0.000
LPHA	0.39 ± 0.07	0.004	0.0007	0.069
Conventionally measured carcass traits				
DP	0.14 ± 0.05	0.627	-	-
GBF	0.38 ± 0.07	2.852	0.4542	0.061
GI	0.00 ± 0.00	0.000	-	-
GLD	0.27 ± 0.06	6.308	0.3462	0.015
LA	0.47 ± 0.08	14.042	0.4351	0.015
LC	0.23 ± 0.09	0.616	0.0000	0.000
LL	0.32 ± 0.06	1.220	0.2395	0.063
RMD	0.39 ± 0.07	8.245	0.3323	0.016

[1]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 2.7. Estimates of heritability (h^2), additive genetic variance (σ^2_a), and variance for the permanent environmental effect of dam-litter (σ^2_d) for novel carcass traits.

Trait[1]	h^2	σ^2_a	σ^2_d	c^2
BLFT	0.31 ± 0.11	2.950	0.0000	0.000
BL	0.19 ± 0.08	0.889	0.7091	0.152
BLW	0.40 ± 0.06	0.039	0.0000	0.000
BRW	0.19 ± 0.05	0.001	0.0003	0.034
BW	0.10 ± 0.04	0.197	-	-
BWR	0.17 ± 0.12	0.722	0.1186	0.028
SRW	0.28 ± 0.06	0.006	0.0005	0.022
SW	0.12 ± 0.05	0.003	0.0012	0.053
TW	0.30 ± 0.06	0.001	0.0001	0.047
TBLW	0.18 ± 0.06	0.031	0.0177	0.104
TBW	0.26 ± 0.05	0.025	0.0000	0.000
THW	0.40 ± 0.07	0.111	0.0067	0.024
TPW	0.14 ± 0.05	0.013	0.0038	0.042
UBLW	0.16 ± 0.05	0.033	0.0184	0.090
UBW	0.15 ± 0.05	0.016	0.0014	0.013
UHW	0.23 ± 0.06	0.058	0.0092	0.036
USW	0.22 ± 0.06	0.048	0.0209	0.028
ULW	0.25 ± 0.06	0.072	0.0081	0.095

[1]BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

In general, growth and weight traits had moderate heritabilities, with values of 0.28 ± 0.07, 0.30 ± 0.06, and 0.26 ± 0.06 estimated for ADG, HCW, and LW, respectively. Pork quality traits were lowly to highly heritable, ranging from 0.14 ± 0.05 (LNC) to 0.42 ± 0.06 (LNM). The Minolta color scores were moderate in magnitude with an average of 0.33. The LNC and LJPC had lower heritabilities of 0.14 ± 0.05 and 0.22 ± 0.05, respectively, and DLP (h2 = 0.28 ± 0.09) and LPHA (h2 = 0.39 ± 0.07) were moderately heritable. Conventionally-measured carcass traits were lowly to highly heritable with a range of 0.14 ± 0.05 (DP) to 0.47 ± 0.08 (LA) with the exception of GI (its heritability was estimated as 0.00 ± 0.00). This range in heritabilities was expected, as these traits have been used in swine selection for years due to their moderate to high heritabilities. Measurements taken on the loin ranged from 0.23 ± 0.09 (LC) to 0.47 ± 0.08 (LA) with an average heritability of 0.34 ± 0.10. GBF had a heritability of 0.38 ± 0.07.

The heritability estimates for novel carcass traits ranged from 0.10 ± 0.04 (BW) to 0.40 ± 0.06 (BLW) and 0.40 ± 0.07 (THW). The novel belly traits had low to moderate heritabilities with an average of 0.19 ± 0.08, while subprimal cuts ranged from low to highly heritable with an

average of 0.25 ± 0.10. The heritability estimated for BLFT of 0.31 ± 0.11 was the highest among the belly traits. Trimmed and untrimmed primal cuts ranged from lowly to highly heritable. Trimmed cuts tended to have a higher heritability (average of 0.25 ± 0.11) compared to untrimmed cuts (average of 0.20 ± 0.04), which could be due to trimmed cuts having skin and some excess fat tissue removed.

2.4.4 Genetic Correlations

The genetic correlations are shown in Tables 2.8–2.13. In general, genetic correlations between conventionally-measured carcass traits and pork quality traits were moderate in magnitude with the exception of a few highly correlated traits. The genetic correlations estimated between pork quality and novel carcass traits, and between conventional and novel carcass traits, were moderate.

Among the growth and conventional carcass traits, high to moderate genetic correlations were observed, with high and favorable correlations being prominent among growth traits specifically. Similarly, genetic correlations among pork quality traits were moderate to high. Novel carcass traits tended toward a moderate degree of association with fewer trait pairs having high correlations.

Phenotypic correlations are not discussed in the paper, but for completeness they are presented as Supplementary Material (available online at http://www.mdpi.com/2076-2615/10/5/779/s1).

Table 2.8. Genetic correlations between conventionally measured carcass traits and pork quality traits.

Trait[1]	DL1	DL2	DLP	LJPC	L*	a*	b*	LNC	LNM	LPHA
ADG	0.18 ± 0.18	−0.14 ± 0.19	−0.12 ± 0.30	−0.18 ± 0.18	−0.05 ± 0.17	−0.02 ± 0.17	0.01 ± 0.16	−0.10 ± 0.23	0.04 ± 0.14	0.11 ± 0.16
HCW	−0.48 ± 0.13	−0.46 ± 0.14	−0.01 ± 0.26	−0.36 ± 0.04	−0.06 ± 0.15	−0.13 ± 0.16	−0.04 ± 0.14	−0.14 ± 0.41	0.07 ± 0.13	0.05 ± 0.05
LW	−0.12 ± 0.19	−0.11 ± 0.19	−0.02 ± 0.25	−0.28 ± 0.04	−0.08 ± 0.17	−0.18 ± 0.17	−0.11 ± 0.14	−0.08 ± 0.23	0.13 ± 0.14	0.18 ± 0.16
DP	−0.12 ± 0.22	−0.10 ± 0.23	0.26 ± 0.34	−0.50 ± 0.30	0.18 ± 0.21	−0.06 ± 0.20	0.10 ± 0.05	−0.47 ± 0.30	−0.09 ± 0.05	N/A
GBF	−0.63 ± 0.12	−0.65 ± 0.13	0.14 ± 0.25	−0.12 ± 0.04	0.26 ± 0.15	0.38 ± 0.14	0.37 ± 0.15	−0.37 ± 0.21	0.30 ± 0.11	−0.14 ± 0.13
GI	0.14 ± 0.09	0.13 ± 0.10	0.42 ± 0.06	−0.05 ± 0.48	0.17 ± 0.13	0.12 ± 0.04	0.12 ± 0.60	−0.05 ± 0.09	0.10 ± 0.42	−0.15 ± 0.05
GLD	0.91 ± 0.09	0.92 ± 0.09	0.06 ± 0.26	−0.11 ± 0.04	0.08 ± 0.16	−0.04 ± 0.16	0.06 ± 0.15	−0.07 ± 0.22	−0.37 ± 0.13	−0.23 ± 0.15
LA	0.95 ± 0.05	0.96 ± 0.05	−0.07 ± 0.15	−0.09 ± 0.04	0.13 ± 0.13	0.08 ± 0.15	0.12 ± 0.14	0.03 ± 0.20	−0.15 ± 0.12	−0.17 ± 0.12
LC	0.82 ± 0.14	0.74 ± 0.01	−0.98 ± 0.08	0.14 ± 0.07	−0.10 ± 0.27	0.04 ± 0.27	−0.05 ± 0.26	0.09 ± 0.49	−0.26 ± 0.23	0.13 ± 0.18
LL	0.24 ± 0.17	0.21 ± 0.18	0.13 ± 0.22	0.18 ± 0.04	−0.09 ± 0.15	−0.04 ± 0.16	−0.12 ± 0.15	0.41 ± 0.23	−0.06 ± 0.13	0.15 ± 0.15
RMD	0.80 ± 0.10	0.82 ± 0.10	0.06 ± 0.24	−0.11 ± 0.15	0.16 ± 0.14	−0.05 ± 0.15	0.13 ± 0.14	−0.19 ± 0.20	−0.12 ± 0.12	−0.14 ± 0.14

N/A represents when convergence was unable to be achieved. [1]DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 2.9. Genetic correlations between pork quality and novel carcass traits.

Trait[1]	DL1	DL2	DLP	LJPC	L*	a*	b*	LNC	LNM	LPHA
BLFT	−0.50 ± 0.39	−0.48 ± 0.31	0.12 ± 0.07	−0.42 ± 0.03	0.15 ± 0.28	−0.14 ± 0.24	0.02 ± 0.26	−0.47 ± 0.51	0.32 ± 0.25	0.02 ± 0.31
BL	0.48 ± 0.52	0.51 ± 0.55	−0.14 ± 0.19	0.28 ± 0.40	−0.06 ± 0.32	0.23 ± 0.41	0.10 ± 0.30	0.17 ± 0.48	0.14 ± 0.25	0.23 ± 0.30
BLW	0.99 ± 0.00	0.99 ± 0.00	0.01 ± 0.35	−0.07 ± 0.14	0.12 ± 0.13	−0.02 ± 0.14	0.08 ± 0.13	0.15 ± 0.22	−0.21 ± 0.12	−0.17 ± 0.05
BRW	0.25 ± 0.21	0.26 ± 0.22	−0.56 ± 0.32	0.07 ± 0.20	−0.01 ± 0.16	−0.10 ± 0.19	−0.19 ± 0.15	−0.09 ± 0.27	0.09 ± 0.08	0.36 ± 0.18
BW	0.37 ± 0.36	0.34 ± 0.43	0.61 ± 0.96	−0.24 ± 0.06	−0.23 ± 0.28	−0.15 ± 0.28	−0.19 ± 0.32	−0.19 ± 0.34	−0.52 ± 0.37	−0.39 ± 0.16
BWR	−0.32 ± 0.06	−0.36 ± 0.06	0.44 ± 0.06	0.01 ± 0.46	−0.38 ± 0.15	0.03 ± 0.03	−0.22 ± 0.38	0.01 ± 0.09	−0.39 ± 0.33	0.03 ± 0.05
SRW	0.36 ± 0.17	0.34 ± 0.17	0.26 ± 0.27	−0.30 ± 0.16	0.07 ± 0.15	−0.21 ± 0.16	−0.14 ± 0.13	−0.22 ± 0.25	−0.09 ± 0.09	0.12 ± 0.15
SW	0.59 ± 0.27	0.62 ± 0.27	−0.26 ± 0.38	−0.14 ± 0.00	−0.04 ± 0.17	−0.37 ± 0.36	−0.19 ± 0.17	−0.05 ± 0.17	−0.16 ± 0.09	0.07 ± 0.23
TBLW	−0.17 ± 0.22	−0.17 ± 0.22	0.10 ± 0.34	0.20 ± 0.04	−0.07 ± 0.19	0.34 ± 0.20	0.16 ± 0.16	0.08 ± 0.28	0.18 ± 0.16	−0.17 ± 0.19
TBW	0.08 ± 0.17	0.06 ± 0.18	−0.48 ± 0.27	0.24 ± 0.16	−0.09 ± 0.15	−0.26 ± 0.16	−0.34 ± 0.15	0.12 ± 0.21	−0.18 ± 0.14	0.29 ± 0.07
THW	0.72 ± 0.10	0.74 ± 0.10	0.02 ± 0.24	−0.11 ± 0.05	−0.03 ± 0.14	−0.33 ± 0.14	−0.22 ± 0.13	0.07 ± 0.21	−0.29 ± 0.11	−0.14 ± 0.13
TPW	0.21 ± 0.23	0.22 ± 0.23	0.12 ± 0.33	−0.21 ± 0.23	−0.09 ± 0.18	−0.26 ± 0.26	−0.13 ± 0.11	−0.10 ± 0.30	−0.32 ± 0.15	0.28 ± 0.23
TW	0.39 ± 0.16	0.39 ± 0.16	0.24 ± 0.29	0.03 ± 0.16	−0.11 ± 0.14	−0.27 ± 0.16	−0.24 ± 0.13	−0.09 ± 0.22	−0.26 ± 0.09	0.05 ± 0.15
UBLW	0.00 ± 0.24	0.00 ± 0.24	0.28 ± 0.33	0.01 ± 0.04	0.08 ± 0.20	0.25 ± 0.20	0.17 ± 0.17	−0.07 ± 0.30	0.15 ± 0.16	−0.08 ± 0.19
UBW	−0.33 ± 0.22	−0.34 ± 0.23	−0.40 ± 0.17	0.21 ± 0.08	−0.17 ± 0.15	−0.38 ± 0.24	−0.41 ± 0.20	−0.08 ± 0.22	0.03 ± 0.15	0.41 ± 0.19
UHW	0.52 ± 0.15	0.55 ± 0.15	0.02 ± 0.27	−0.15 ± 0.04	0.12 ± 0.15	−0.19 ± 0.16	−0.08 ± 0.12	−0.12 ± 0.23	−0.10 ± 0.13	−0.19 ± 0.15
ULW	0.64 ± 0.14	0.65 ± 0.14	0.21 ± 0.22	−0.22 ± 0.06	0.25 ± 0.15	0.06 ± 0.16	0.17 ± 0.15	−0.39 ± 0.17	−0.09 ± 0.14	−0.25 ± 0.14
USW	0.02 ± 0.20	0.01 ± 0.20	−0.22 ± 0.28	−0.06 ± 0.04	−0.14 ± 0.17	−0.52 ± 0.19	−0.44 ± 0.11	−0.24 ± 0.24	−0.29 ± 0.14	0.44 ± 0.16

[1]DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

Table 2.10. Genetic correlations between conventionally measured carcass traits and novel carcass traits.

Trait[1]	ADG	HCW	LW	DP	GBF	GI	GLD	LA	LC	LL	RMD
BLFT	−0.00 ± 0.29	0.31 ± 0.25	0.09 ± 0.28	−0.29 ± 0.05	0.99 ± 0.07	−0.14 ± 0.70	−0.38 ± 0.28	−0.49 ± 0.25	−0.68 ± 0.62	−0.02 ± 0.26	−0.15 ± 0.26
BL	0.02 ± 0.38	0.71 ± 0.01	0.23 ± 0.34	−0.20 ± 0.57	−0.74 ± 0.33	0.52 ± 0.06	−0.26 ± 0.35	0.03 ± 0.30	−0.07 ± 0.61	0.97 ± 0.59	−0.08 ± 0.27
BLW	−0.22 ± 0.14	0.47 ± 0.11 **	0.11 ± 0.14	0.01 ± 0.05	−0.45 ± 0.11	0.12 ± 0.56	0.77 ± 0.08	0.79 ± 0.06	0.88 ± 0.18	0.21 ± 0.13	0.72 ± 0.07
BRW	−0.02 ± 0.20	0.33 ± 0.03 **	0.07 ± 0.20	N/A	−0.75 ± 0.13	0.22 ± 0.07	0.06 ± 0.19	0.19 ± 0.17	0.10 ± 0.09	0.54 ± 0.17	0.11 ± 0.17
BW	0.26 ± 0.22	0.13 ± 0.30	0.56 ± 0.30	−0.25 ± 0.05	0.01 ± 0.39	0.05 ± 0.83	−0.02 ± 0.29	0.08 ± 0.26	0.00 ± 0.45	−0.28 ± 0.31	0.13 ± 0.27
BWR	0.24 ± 0.06	−0.84 ± 0.02	0.46 ± 0.06	−0.38 ± 0.59	0.12 ± 0.06	N/A	−0.39 ± 0.07	−0.56 ± 0.06	−0.47 ± 0.62	0.11 ± 0.05	−0.41 ± 0.57
SRW	0.14 ± 0.17	0.88 ± 0.00	0.45 ± 0.14	−0.33 ± 0.19	−0.67 ± 0.11	0.79 ± 0.18	−0.17 ± 0.16	−0.10 ± 0.14	−0.16 ± 0.20	0.70 ± 0.13	−0.15 ± 0.15
SW	0.23 ± 0.40	0.53 ± 0.22 **	0.32 ± 0.25	N/A	−0.28 ± 0.23	0.22 ± 0.19	0.59 ± 0.27	0.62 ± 0.22	0.71 ± 0.04	−0.44 ± 0.30	0.76 ± 0.36
TBLW	0.46 ± 0.18	0.74 ± 0.06	0.52 ± 0.15	0.14 ± 0.25	0.51 ± 0.16	0.03 ± 0.04	−0.37 ± 0.17	−0.17 ± 0.18	−0.32 ± 0.10	−0.15 ± 0.20	−0.17 ± 0.17
TBW	−0.02 ± 0.17	0.37 ± 0.05	0.08 ± 0.17	−0.22 ± 0.05	−0.43 ± 0.13	0.15 ± 0.50	0.03 ± 0.16	0.06 ± 0.14	−0.04 ± 0.28	0.06 ± 0.16	−0.01 ± 0.15
THW	−0.12 ± 0.15	−0.38 ± 0.05	−0.01 ± 0.16	0.05 ± 0.19	−0.73 ± 0.08	0.29 ± 0.08	0.45 ± 0.13	0.54 ± 0.10	0.56 ± 0.26	0.16 ± 0.13	0.47 ± 0.11
TPW	0.18 ± 0.26	−0.11 ± 0.15	0.20 ± 0.22	0.12 ± 0.30	−0.39 ± 0.21	0.11 ± 0.07	0.25 ± 0.22	0.37 ± 0.19	0.64 ± 0.28	0.07 ± 0.22	0.26 ± 0.18
TW	−0.26 ± 0.17	0.15 ± 0.16 **	0.08 ± 0.17	N/A	−0.45 ± 0.13	0.14 ± 0.07	0.46 ± 0.14	0.43 ± 0.10	0.44 ± 0.15	0.02 ± 0.16	0.43 ± 0.13
UBLW	0.50 ± 0.19	0.73 ± 0.07	0.63 ± 0.14	−0.03 ± 0.26	0.18 ± 0.19	0.38 ± 0.04	−0.36 ± 0.18	−0.19 ± 0.11	−0.27 ± 0.13	0.14 ± 0.20	−0.22 ± 0.17
UBW	0.12 ± 0.23	0.92 ± 0.03	0.37 ± 0.19	−0.19 ± 0.26	0.13 ± 0.19	0.22 ± 0.12	−0.30 ± 0.21	−0.21 ± 0.19	−0.12 ± 0.24	−0.29 ± 0.20	−0.20 ± 0.19
UHW	−0.10 ± 0.18	−0.44 ± 0.13	0.15 ± 0.18	0.21 ± 0.21	−0.44 ± 0.14	0.46 ± 0.05	0.38 ± 0.16	0.55 ± 0.13	0.59 ± 0.28	−0.12 ± 0.16	0.49 ± 0.13
ULW	−0.02 ± 0.17	0.71 ± 0.08	0.42 ± 0.14	0.27 ± 0.22	0.06 ± 0.14	0.41 ± 0.10	0.36 ± 0.15	0.62 ± 0.10	0.65 ± 0.15	−0.03 ± 0.15	0.53 ± 0.12
USW	0.19 ± 0.20	0.77 ± 0.08 **	0.31 ± 0.17	−0.05 ± 0.22	−0.27 ± 0.16	0.42 ± 0.04	−0.06 ± 0.18	0.11 ± 0.16	0.28 ± 0.20	−0.02 ± 0.17	−0.04 ± 0.16

Results marked with ** had HCW removed from the model in order to achieve convergence. N/A represents when convergence was unable to be achieved.
[1]BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight; ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 2.11. Genetic correlations among growth and conventionally measured carcass traits.

Trait[1]	HCW	LW	DP	GBF	GI	GLD	LA	LC	LL	RMD
ADG	0.93 ± 0.04	0.97 ± 0.04	0.44 ± 0.19	−0.14 ± 0.16	0.74 ± 0.78	−0.24 ± 0.16	−0.08 ± 0.15	0.42 ± 0.28	−0.12 ± 0.17	−0.09 ± 0.15
HCW		0.90 ± 0.04	0.51 ± 0.17	0.12 ± 0.14	0.79 ± 0.61	−0.36 ± 0.14	−0.66 ± 0.08	−0.63 ± 0.08 **	−0.23 ± 0.14	−0.16 ± 0.14
LW			0.17 ± 0.22	−0.02 ± 0.16	0.36 ± 0.67 *	−0.40 ± 0.16	0.00 ± 0.16	0.48 ± 0.33	0.24 ± 0.16	0.00 ± 0.16
DP				0.17 ± 0.22	−0.20 ± 0.59	−0.20 ± 0.59	−0.03 ± 0.19	0.03 ± 0.05	−0.30 ± 0.20	0.28 ± 0.25
GBF					0.04 ± 0.19	−0.32 ± 0.13	−0.49 ± 0.11	−0.60 ± 0.24	−0.61 ± 0.12	−0.23 ± 0.13
GI						−0.23 ± 0.09	0.14 ± 0.10	0.62 ± 0.01	0.10 ± 0.05	−0.04 ± 0.11
GLD							0.90 ± 0.06	0.83 ± 0.27	−0.20 ± 0.16	0.91 ± 0.06
LA								0.99 ± 0.01	−0.03 ± 0.13	0.86 ± 0.06
LC									−0.20 ± 0.28	0.95 ± 0.31
LL										−0.23 ± 0.14

Results marked with a ** had HCW removed from the model in order to achieve convergence. [1]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 2.12. Genetic correlations among pork quality traits.

Trait[1]	DL2	DLP	LJPC	L*	a*	b*	LNC	LNM	LPHA
DL1	N/A	0.21 ± 0.36	−0.03 ± 0.18	0.03 ± 0.17	−0.13 ± 0.18	−0.09 ± 0.16	0.13 ± 0.24	−0.35 ± 0.13	−0.13 ± 0.16
DL2		0.18 ± 0.29	−0.01 ± 0.19	0.02 ± 0.18	−0.14 ± 0.18	−0.10 ± 0.17	0.15 ± 0.24	−0.34 ± 0.18	−0.12 ± 0.17
DLP			−0.74 ± 0.24	0.70 ± 0.21	0.24 ± 0.24	0.61 ± 0.21	−0.70 ± 0.13	−0.30 ± 0.19	−0.76 ± 0.25
LJPC				−0.79 ± 0.02	0.19 ± 0.04	−0.34 ± 0.11	0.96 ± 0.00	0.07 ± 0.13	0.67 ± 0.08
L*					0.47 ± 0.13	0.82 ± 0.06	−0.84 ± 0.13	0.34 ± 0.13	−0.48 ± 0.11
a*						0.86 ± 0.05	0.20 ± 0.24	0.54 ± 0.12	−0.38 ± 0.13
b*							−0.45 ± 0.18	0.45 ± 0.12	−0.59 ± 0.10
LNC								−0.07 ± 0.16	0.56 ± 0.08
LNM									0.17 ± 0.05

N/A represents when convergence was unable to be achieved. [1]DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH.

Table 2.13. Genetic correlations among novel traits.

Trait[1]	BL	BLW	BRW	BW	BWR	SRW	SW	TBLW
BLFT	−0.66 ± 0.64	−0.21 ± 0.01	−0.36 ± 0.07	−0.53 ± 0.66	0.21 ± 0.64	−0.58 ± 0.15	0.04 ± 0.46	0.37 ± 0.30
BL		0.36 ± 0.31	0.33 ± 0.41	−0.12 ± 0.52	0.08 ± 0.06	0.81 ± 0.53	−0.66 ± 0.51	−0.40 ± 0.40
BLW			0.20 ± 0.07	0.14 ± 0.54	−0.48 ± 0.33	0.21 ± 0.11	0.52 ± 0.07	−0.01 ± 0.17
BRW				−0.37 ± 0.06	0.31 ± 0.06	0.71 ± 0.14	−0.30 ± 0.33	−0.31 ± 0.24
BW					0.87 ± 0.83	0.25 ± 0.14	−0.12 ± 0.15	0.19 ± 0.37
BWR						0.41 ± 0.09	−0.45 ± 0.05	0.48 ± 0.04
SRW							−0.27 ± 0.09	−0.06 ± 0.21
SW								−0.19 ± 0.31

	TBW	THW	TPW	TW	UBLW	UBW	UHW	ULW	USW
BLFT	−0.47 ± 0.01	−0.87 ± 0.06	−0.58 ± 0.31	−0.25 ± 0.06	0.09 ± 0.38	−0.16 ± 0.37	−0.49 ± 0.14	0.29 ± 0.23	−0.45 ± 0.31
BL	−0.23 ± 0.35	0.28 ± 0.33	−0.52 ± 0.71	−0.00 ± 0.49	0.02 ± 0.39	−0.78 ± 0.66	−0.03 ± 0.33	0.05 ± 0.33	−0.65 ± 0.67
BLW	−0.08 ± 0.14	0.46 ± 0.10	0.09 ± 0.17	0.30 ± 0.05	0.09 ± 0.17	−0.47 ± 0.17	0.29 ± 0.13	0.72 ± 0.08	−0.21 ± 0.15
BRW	0.25 ± 0.07	0.44 ± 0.16	0.32 ± 0.25	0.40 ± 0.17	0.06 ± 0.24	0.04 ± 0.28	0.13 ± 0.20	0.02 ± 0.20	0.31 ± 0.21
BW	0.00 ± 0.01	0.30 ± 0.45	0.22 ± 0.08	0.13 ± 0.21	0.30 ± 0.40	−0.24 ± 0.36	0.37 ± 0.18	0.08 ± 0.26	0.01 ± 0.14
BWR	0.34 ± 0.45	−0.20 ± 0.39	0.33 ± 0.06	−0.42 ± 0.05	0.70 ± 0.03	0.43 ± 0.09	−0.06 ± 0.06	−0.24 ± 0.10	0.67 ± 0.03
SRW	0.24 ± 0.11	0.21 ± 0.14	−0.03 ± 0.23	0.03 ± 0.06	0.41 ± 0.18	−0.11 ± 0.13	−0.06 ± 0.17	0.03 ± 0.16	0.13 ± 0.17
SW	0.26 ± 0.19	0.47 ± 0.26	0.02 ± 0.37	0.62 ± 0.04	−0.28 ± 0.31	0.10 ± 0.19	0.42 ± 0.30	0.29 ± 0.20	0.06 ± 0.27
TBLW	−0.60 ± 0.16	−0.33 ± 0.17	−0.77 ± 0.30	−0.42 ± 0.17	0.87 ± 0.04	−0.55 ± 0.25	−0.15 ± 0.21	0.30 ± 0.19	−0.72 ± 0.18
TBW		0.18 ± 0.14	0.40 ± 0.22	0.23 ± 0.07	−0.43 ± 0.18	0.80 ± 0.05	−0.19 ± 0.16	−0.38 ± 0.16	0.75 ± 0.10
THW			0.37 ± 0.16	0.57 ± 0.11	−0.24 ± 0.15	−0.16 ± 0.17	0.88 ± 0.03	0.19 ± 0.14	0.16 ± 0.16
TPW				0.21 ± 0.21	−0.71 ± 0.37	0.23 ± 0.23	0.38 ± 0.24	−0.10 ± 0.23	0.77 ± 0.08
TW					−0.41 ± 0.18	0.01 ± 0.21	0.34 ± 0.16	0.31 ± 0.07	0.20 ± 0.17
UBLW						−0.51 ± 0.26	−0.17 ± 0.21	0.24 ± 0.19	−0.61 ± 0.20
UBW							−0.28 ± 0.18	−0.36 ± 0.23	0.82 ± 0.07
UHW								0.20 ± 0.16	−0.03 ± 0.19
ULW									−0.27 ± 0.18

[1]BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

2.5 Discussion

2.5.1 Statistical Models

For some groups of traits (i.e., growth and carcass traits), multiple covariates were found to be significant during the model development process. The final covariates fitted in the models (Tables 2.3–2.5) were chosen based on biological and industry considerations, and precedents established in the literature. For example, HCW and LW included age as a covariate, as they are measures of body weight and carcass growth. Another example was adjusting carcass traits for HCW to have the estimates be analyzed by content of lean muscle and fat instead of weight by accounting for lighter or heavier carcasses. For other traits, such as ADG, no covariate was added to the model due to potential confounding factors, as ADG was calculated directly from the age and weight of the animal.

Other studies have used age and cold carcass weight (CCW) as covariates to estimate genetic parameters. Miar et al. [29] used age and CCW as covariates, while van Wijk et al. [16] also used CCW. Age is a common fixed effect due to older animals growing larger and naturally having greater body mass and measurement than a younger animal. CCW has been used in other studies to adjust for the size of the carcass, similar to the use of HCW in this study.

Color traits were significantly affected by both AGE and HCW in some instances. In one study [30], the effect of age on meat color was studied using the Minolta scale. Age was observed to have a significant effect on L* and b*, and on the ratio between a* and b*, whereas a* was not significant. Other studies have reported that meat becomes redder with age due to the concentration of myoglobin [31]. Pork color has also been related to the type of muscle fiber present, as lighter meat will often have more Type IIB fibers [32]. For these reasons, both were considered valid covariates for the statistical models used in this study.

The models in this study do not include some of the typical fixed effects, as seen for estimates of genetic parameters, due to the nature of the datasets. Studies available in the literature commonly use farm, sex, herd-year-season or slaughter plant (in the case of carcass traits) to define their contemporary groups [13,15,33,34]. However, this study dealt with only female pigs that were raised on the same farms from birth to slaughter and were also slaughtered at the same slaughter plant. Therefore, our models did not consider these factors due to the lack of variability. Past literature has shown that there is a significant difference in results between the sexes in pigs

[35–37], and as such, further study in this area should be conducted with information from boars and barrows. However, the impact in the genetic parameter estimates is expected to be minimal, as sex is usually accounted for in statistical genetic models.

2.5.2 Heritabilities

Growth, pork quality, and conventional carcass trait heritabilities and variance components are presented in Table 2.6. Growth and weight traits had moderate heritabilities with estimates of 0.28 ± 0.07, 0.30 ± 0.06, and 0.26 ± 0.06 for ADG, HCW, and LW, respectively. The heritability estimated for ADG in this study is lower than estimates reported in other studies for the same trait (e.g., 0.36 ± 0.07 and 0.47 ± 0.02) in the Duroc breed [14,38]. However, it is similar to estimates found for other breeds: 0.24 (no SE presented) in Large White [39] and 0.27 ± 0.03 in Landrace [40] pigs. The estimate of 0.30 ± 0.06 for HCW falls within the range seen in the literature (0.24 – 0.36) [41–43]. The heritability estimate for LW is in agreement with the body weight by age heritability curve presented by Edwards et al. [44]. The heritability and additive genetic variance estimates indicate that growth traits are under moderate genetic control and can be improved through direct genetic selection. For instance, high genetic progress for growth traits has been reported in various pig populations [45–47].

Pork quality traits had moderate heritabilities with the only low heritability estimated for LNC (0.14 ± 0.05). To the best of our knowledge, a heritability for color score based on the NPPC scale has not been previously reported. There is more information available in the literature for the Japanese color scale, possibly due to the popularity of this color scale. Suzuki et al. [14] estimated a heritability of 0.18 ± 0.02 for LJPC, while this study found a slightly higher heritability of 0.22 ± 0.05. Meanwhile, another study found a heritability of 0.83 ± 0.12 [48], which is above the common range observed for meat quality traits in livestock species.

The Minolta color scale (L*, a*, and b*) is used to quantify the color of pork based upon lightness, redness, and yellowness values given by a machine. The heritability estimate for L* (0.36 ± 0.07) is within the range of 0.15−0.57 [5, p 358] reported in literature, though it is greater than the value of 0.16 ± 0.02 estimated in another Duroc population [14]. The heritability estimated for a* (0.30 ± 0.06) is similar to that estimated in a crossbred commercial population (0.36 ± 0.06) [13], but is different from another estimate of 0.52 ± 0.10 [40]. Our estimate of b* (0.32 ± 0.06) is different from those found in literature, as it is higher than 0.20 ± 0.06 found by Miar et al. [13]

and less than the 0.94 ± 0.11 found by Newcom et al. [48]. However, Newcom et al. [48] stated that the high heritability estimates in their study could have been due to the study design and limited environmental variation.

Pork color scales generally had lower heritability (average of 0.18) compared to the Minolta color measurements (average of 0.33). This difference could be due to human error, as color scores were given by a technician while Minolta L*, a*, and b* were measurements taken using a machine. Thus, these measurements would be expected to have less error.

The DLP heritability found here (0.28 ± 0.09) is within the range of what was found in literature [49], though it is higher than the heritability of 0.14 ± 0.01 estimated by Suzuki et al. [14] with a Japanese population of Duroc pigs. The main factors that influence DLP are the rate of pH decline postmortem and the ultimate pH of the meat. Additionally, sarcomere length and other environmental factors may also influence the amount of drip loss from a pork product [50].

Previous heritability estimates for LNM range from 0.16 ± 0.07 to 0.23 ± 0.05 to 0.31 ± 0.12 [13,16,38], which are lower than the estimated 0.42 ± 0.06 found in this study. Heritability for LPHA has a range from 0.07 to 0.39 ([9] p. 358); the estimate in this study (0.39 ± 0.07) is among the higher estimates. The higher heritabilities found for these traits could be due to the amount of variation in this population of Duroc pigs, as it is comprised of a combination of purebred animals from Europe, Canada, and the United States. In addition, there are other factors that influence the heritability estimates, including the statistical method used, variables included in the models, sample size, and trait recording.

Conventional carcass traits were generally moderately to highly heritable, with the exception of GI, which had an estimated heritability of 0.00 ± 0.00. This indicates that GI is not under genetic control, as grades are determined by individual packing plants and fluctuate based on plant and time of the year, making genetic prediction difficult. Therefore, GI (as currently measured) is not a trait that should be included in a genetic or genomic evaluation scheme.

A heritability of 0.14 ± 0.05 was found for DP in this study as compared to estimates of 0.32 ± 0.04, 0.40 ± 0.03, and 0.31 ± 0.06 for maternal breeds (Landrace, Large White Sire, and Large White Dam, respectively) [51]. In another study on the Duroc breed, a heritability of 0.22 (no SE presented) was found [52], which is similar to our estimate, indicating that heritability for dressing percentage in terminal lines is lower than in maternal lines. Additionally, the lower

heritability observed in this study could be due to the delay in collecting live weight to carcass weight data, as live weight was measured three days prior to slaughter.

A heritability of 0.38 ± 0.07 was estimated for GBF, which is below the average of the range shown in Clutter [53]: 0.12 – 0.74. In another population of Duroc pigs, the heritability for backfat was 0.65 ± 0.06 [54], while in a population of Berkshire pigs it was 0.57 ± 0.06 [49]. On the other hand, Miar et al. [13] found a heritability of 0.31 ± 0.06 in a population of crossbred pigs. GLD had a heritability of 0.27 ± 0.06, which falls within the range (0.13 ± 0.06 to 0.41 ± 0.06) estimated by Van Wijk et al. [16] and Miar et al. [13]. Similarly, our estimate for LA (0.47 ± 0.08) is average compared to estimates (0.22 to 0.80) found by Miar et al. [13] and Lo et al. [38], respectively, and is similar to another estimate in a population of Duroc pigs of 0.45 ± 0.02 [14]. The heritability for LL was estimated to be 0.32 ± 0.06, which is slightly lower than another estimate of 0.46 ± 0.09 [55] reported in Large White pigs, but is close to an estimate of 0.39 (no SE presented) in Landrace pigs [56]. Specific heritability estimates for LC (0.23 ± 0.09) and RMD (0.39 ± 0.07) are scarce, though they can be related to other measurements of the loin, such as LA, which indicate the size of the loin muscle.

The moderate to high heritabilities estimated for traits such as GBF, LA, and RMD indicate that substantial progress can be made by selecting for these traits. Due to their higher heritabilities, genetic progress will be faster while also providing more accurate estimated breeding values.

Novel carcass traits had low to high heritabilities (Table 2.7). To our knowledge, there have been few estimates of these heritabilities in the literature, especially concerning a purebred terminal line of Duroc pigs. Miar et al. [13] estimated genetic parameters for similar traits in a crossbred population (Duroc x (Landrace x Large White)) and found estimates of 0.32 ± 0.06, 0.53 ± 0.06, 0.29 ± 0.05, 0.63 ± 0.04, 0.44 ± 0.06, 0.49 ± 0.06, 0.46 ± 0.06, 0.63 ± 0.06, and 0.55 ± 0.06 for SRW, TBLW, TBW, THW, TPW, UBLW, UHW, ULW, and USW, respectively, as compared to the estimates received in this study of 0.28 ± 0.06, 0.18 ± 0.06, 0.26 ± 0.05, 0.40 ± 0.07, 0.14 ± 0.05, 0.16 ± 0.05, 0.23 ± 0.06, 0.25 ± 0.06, and 0.22 ± 0.06 for the same traits. The SRW and TBW have similar estimates between the studies, while the remaining traits (TBLW, THW, TPW, UBLW, UHW, ULW, and USW) had lower estimates in this study. TW was estimated to have a heritability of 0.30 ± 0.06, which is similar to the estimate of 0.29 ± 0.11 found by Van Wijk et al. [16]. Neither BL (0.19 ± 0.08) nor BW (0.10 ± 0.04) heritability estimates are similar to those

found (0.28 ± 0.08 and 0.49 ± 0.08, respectively) by Kang et al. [57] in a population of Yorkshire pigs, which could be due to the populational (breed) difference.

To our best knowledge, the current study is the first report of heritability estimates for BLFT, BRW, BLW, BWR, SW, and UBW. Thus, the heritability estimates in this study were 0.31 ± 0.11, 0.19 ± 0.05, 0.40 ± 0.06, 0.17 ± 0.12, 0.12 ± 0.05, and 0.15 ± 0.05 for these traits, respectively.

Carcass traits had low to high heritability, with the novel and less studied traits tending towards a low to moderate heritability. These results show that these traits are under some degree of genetic control and can be used for the purpose of selecting for specific gains on the primal and subprimal cuts of the carcass. Additionally, the moderate estimate for BLFT indicates that it may be a candidate for consideration to account for belly quality in a selection index.

2.5.3 Genetic Correlations between Growth and Conventional Carcass and Pork Quality Traits

Genetic correlations between conventional carcass traits and pork quality traits can be found in Table 2.8. In general, genetic correlations of interest had moderate relationships with the exception of the strong and favorable relationships between DL1 and DL2 with GLD (0.91 ± 0.09 and 0.92 ± 0.09, respectively), LA (0.95 ± 0.05 and 0.96 ± 0.05, respectively), LC (0.82 ± 0.14 and 0.74 ± 0.01, respectively) and RMD (0.80 ± 0.10 and 0.82 ± 0.10, respectively). As DL1 and DL2 are weights of 2.4 cm thick cuts of the loin, these favorable correlations were expected; this group of traits is all related to loin size. Similarly, DL1 and DL2 have moderately unfavorable correlations with GBF (−0.63 ± 0.12 and −0.65 ± 0.13, respectively). As lean loin and backfat depth are known to be inversely correlated [5,58], this was an expected finding within this population. However, this relationship is favorable and has been used for decades within the swine industry to decrease backfat depth and increase leanness in swine carcasses.

Both color score measurements (LJPC and LNC) had a moderately unfavorable correlation with DP, (−0.50 ± 0.30 and −0.47 ± 0.30, respectively) which indicates that selection for an increased ratio of internal body contents to lean muscle tissue could lead to paler pork color. A similar correlation was found between LJPC and HCW (−0.36 ± 0.04). However, Miar et al. [13] found that the Japanese color Animals 2020, 10, 779 18 of 25 scale was lowly genetically correlated with HCW. Meanwhile, another study reported that body weight did not have an impact

on the loin color [59]. This indicates that there may be a genetic relationship between these traits, but phenotypically the effect may not be observed. Overall, more studies in independent populations are needed to better understand the genetic correlation between pork color and carcass weight traits.

Backfat depth had moderate correlations of 0.26 ± 0.15, 0.38 ± 0.14, and 0.37 ± 0.15 with L*, a*, and b*, respectively. This indicates that selection for backfat is likely to moderately increase the Minolta color score. Inversely, GBF and LNC have a moderate and negative correlation of −0.37 ± 0.21, which indicates that selection for backfat has an inverse relationship with the NPPC color score. The NPPC color scale is based on Minolta L* values, and as NPPC score decreases, the L* value increases. As such, these correlations align

The moderate and favorable correlation between GBF and LNM of 0.30 ± 0.11, was expected, as these traits have been reported to be positively correlated previously [9,60]. Additionally, Suzuki et al. [14] found a correlation of 0.28 ± 0.03 in another population of Duroc pigs. Similarly, LNM had a moderate and unfavorable correlation with GLD of −0.37 ± 0.13. It is commonly known that increased back fat depth will also increase the amount of marbling in a carcass [60].

2.5.4 Genetic Correlations between Pork Quality and Novel Carcass Traits

Genetic correlations between pork quality and novel carcass traits are shown in Table 2.9. A moderate and inverse correlation was found between BLFT and LJPC (−0.42 ± 0.03), which may indicate an effect of fat texture on the color score given to a pork loin. If the LJPC were selected to increase, we would expect to see the distance between the ends of the BLFT decrease, indicating a softer textured fat. Another correlation of interest is between BLFT and LNM, for which a positive and moderate value of 0.32 ± 0.25 was found, which indicates that selection for greater marbling will increase the distance between ends of the belly in the belly flop test. However, this estimate had a high standard error.

Marbling score also had a moderate inverse correlation with TPW (−0.32 ± 0.15). This indicates that if intra-muscular fat is selected for, there may be higher total fat on the carcass, which will lower the lean yield elsewhere, such as on the picnic shoulder. The moderate correlations between LNM and THW and TW (−0.29 ± 0.11 and −0.26 ± 0.09, respectively) confirm this observation. In addition, several studies confirm this genetic correlation between

leanness and fat, and summaries of correlations can be found in reviews by Ciobanu et al. [9] and Stewart and Schinckel [60].

The moderate and inverse correlations between DLP and BRW, TBW, and UBW (−0.56 ± 0.32, −0.48 ± 0.27, and −0.40 ± 0.17) indicate an unfavorable relationship between carcass leanness and drip loss when compared with estimates found in other studies. Suzuki et al. [14] reported a genetic correlation between drip loss and loin area of 0.64 ± 0.05, and an estimate of −0.25 ± 0.06 between drip loss and backfat depth. If BRW, TBW, and UBW are considered to have more fat, then drip loss could potentially be decreased by selecting for these carcass traits.

2.5.5 Genetic Correlations between Growth and Conventionally-Measured and Novel Carcass Traits

Table 2.10 displays the genetic correlations between conventional carcass and novel carcass traits. Moderate to high correlations were found for HCW and LW and the trimmed and untrimmed primal cuts, and subprimal cut weight. Those that were high, positive, and favorable (HCW by SRW (0.88 ± 0.00), TBLW (0.74 ± 0.06), UBLW (0.73 ± 0.07), UBW (0.92 ± 0.03), and ULW (0.71 ± 0.08)]) and moderate, positive, and favorable (HCW by TBW (0.37 ± 0.05) and LW by SRW (0.45 ± 0.14), SW (0.32 ± 0.25), TBLW (0.52 ± 0.15), UBLW (0.63 ± 0.14), UBW (0.37 ± 0.19), ULW (0.42 ± 0.14), and USW (0.31 ± 0.17)) indicate a strong genetic correlation between HCW and LW and the growth and lean deposition process of this population. Additionally, the moderate and inverse correlation between HCW and THW (−0.38 ± 0.05) and UHW (−0.44 ± 0.13), and the moderate and positive correlation with ADG and TBLW (0.46 ± 0.18) and UBLW (0.50 ± 0.19), indicate that the belly contains more fat than the ham.

For those traits that had HCW removed as a covariate from the analysis in order to meet convergence criteria, there were both high and moderately positive correlations with HCW (HCW by BLW (0.47 ± 0.11), BRW (0.33 ± 0.03), SW (0.53 ± 0.22), and USW (0.77 ± 0.08)). It is explainable that both primal and subprimal cuts would increase in weight if selection for increased HCW was implemented. In the study performed by Miar et al. [13], high correlations were also found between HCW and primal and subprimal cuts of the carcass, but our findings contrast concerning the ham's correlations. However, this could be due to the difference in the statistical models used for the analysis. Miar et al. [13] used age as a covariate, where this study used HCW (unless it was removed due to non-convergence), which makes the interpretation of the results

different. As Miar et al. [13] mentioned previously, more studies should be done on these traits in independent populations for further validation.

A highly favorable correlation was found between GBF and BLFT (0.99 ± 0.07), indicating a high degree of genetic similarity between these two traits. Additionally, a moderately favorable genetic correlation was found between GBF and TBLW (0.51 ± 0.16), a strong and negative correlation was estimated between GBF and THW (−0.73 ± 0.08), and a moderate and negative correlation was observed between BLFT and loin size traits GLD (−0.38 ± 0.28), LA (−0.49 ± 0.25) and LC (−0.68 ± 0.62). GBF also had moderately unfavorable correlations (average of −0.49) with most primal and subprimal cuts except TBLW, as shown above. This correlation is unfavorable because if GBF is included in a selection index, producers do not want to decrease the amount of lean product produced in the rest of the carcass. In this context, these correlations can be explained by considering the fat and lean contents the traits possess, as the literature indicates that fat content and lean content will have an inverse genetic correlation [53,60].

2.5.6 Genetic Correlations among Growth and Conventionally-Measured Carcass Traits

Genetic correlations among growth and conventional carcass traits can be found in Table 2.11. Among growth traits specifically, there are high and favorable correlations (ADG with HCW (0.93 ± 0.04) and LW (0.97 ± 0.04) and HCW by LW (0.90 ± 0.04)), indicating each of these traits could be used as a predictor for the others. In this study, ADG was calculated directly from the weight of the animal, which explains this high degree of genetic correlation. Past research found similar correlation between ADG and HCW [29,58]. Similarly, correlations measured on the loin (GLD and LA (0.90 ± 0.06), LC (0.83 ± 0.27), and RMD (0.91 ± 0.06); LA and LC (0.99 ± 0.01) and RMD (0.86 ± 0.06); RMD and LC (0.95 ± 0.31)) have high and favorable correlations. Because of this high degree of genetic correlation, it can be concluded that a similar set of genes influences this group of traits and suggests one trait could be used as a predictor for all the traits.

A moderate, but favorable correlation of 0.44 ± 0.19 was found between DP and ADG, and HCW by GI had a highly favorable correlation of 0.79 ± 0.61, indicating first that selection for increased feed gain will increase the ratio in a carcass of lean and fat to body contents, and, second, that selection for a higher carcass weight will likely create a higher value product on a scale like the grade index used in this study.

2.5.7 Genetic Correlations among Pork Quality Traits

Genetic correlations amongst the pork quality traits can be found in Table 2.12. Drip loss, ultimate pH (pH at 24 h post mortem) and pork color have strong correlations [61,62], as when pH drops too low, pork that is pale in color, soft and squishy in texture and highly exudative (PSE) can occur. Inversely, if ultimate pH is too high, pork that is dark in color, firm in texture, and dry in appearance (DFD) can occur [63]. Both are detrimental characteristics for pork quality and should be avoided. Within this population, several correlations can further define this relationship genetically. Several correlations indicate that if LPHA (−0.76 ± 0.25), LJPC (−0.74 ± 0.24) or LNC (−0.70 ± 0.13) are selected for, DLP will change in an inverse direction. For example, if the breeding goal was to increase the color score, DLP would be expected to decrease. Similarly, if selecting for an increase in L*, DLP will increase due to the high and favorable genetic correlation (0.70 ± 0.21). LPHA had comparable, albeit more moderate, correlations with L* (−0.48 ± 0.11), LJPC (0.67 ± 0.08), and LNC (0.56 ± 0.08), indicating selection for color should generally have a favorable impact upon ultimate pH. Miar et al. [13] found similar correlations between L* and DL (0.55 ± 0.24), LPHA and DL (−0.99 ± 0.49), and LPHA and L* (−0.65 ± 0.21).

The favorable correlation between LNC and LJPC of 0.96 ± 0.00 suggests that these traits are nearly genetically identical. L* also shows a high degree of correlation with both LNC (−0.84 ± 0.13) and LJPC (−0.79 ± 0.02). Suzuki et al. [14] also found a correlation of −0.80 (no SE presented) between LJPC and L*. As the NPPC color score is based on Minolta L* values, this inverse correlation is explainable because the NPPC score decreases as L* increases, and if LNC and LJPC are genetically the same trait, then the Japanese color score should also decrease.

Among the Minolta values, moderate to high correlations were observed. Correlations between L* and a* (0.47 ± 0.13), L* and b* (0.82 ± 0.06) and a* and b* (0.86 ± 0.05) are all positively related. Lee et al. [49] found a similar estimate for L* and b* of 0.75 (no SE presented) and a* and b* of 0.41 (no SE presented), but a lower correlation between L* and a* of 0.03 (no SE presented). Miar et al. [13] reported moderate to high correlations among the Minolta color scale (L* and a* were −0.40 ± 0.15, L* and b* were 0.51 ± 0.12, and a* and b* were 0.46 ± 0.13), but estimated an inverse correlation between L* and a*, contrary to this study. However, in general the Minolta color scale has a positive and moderate to high correlation.

Moderate correlations were found between LNM and DLP (−0.30 ± 0.19), L* (0.34 ± 0.13), a* (0.54 ± 0.12) and b* (0.45 ± 0.12). Marbling and drip loss had a low and negative correlation

of −0.06 ± 0.19 as estimated previously by Miar et al. [13]; however, this estimate had high standard error. Miar et al. [13] and Khanal et al. [15] also estimated correlations between LNM and the Minolta scale (L* of −0.12 ± 0.16; a* of −0.03 ± 0.15; b* of −0.13 ± 0.17 and L* of 0.11 ± 0.30; a* of 0.02 ± 0.34; b* of 0.17 ± 0.44, respectively), but none of these estimates are similar. The differences among these estimates could be due to the different breeds of animals used in each study. Where this study worked with terminal Durocs, Miar et al. [13] worked with commercial crossbreds and Khanal et al. [15] worked with maternal lines. Additionally, fat does not carry any myoglobin, the primary molecule that provides pigment in meat products, so it would stand to reason that the presence of more marbling may reflect more light, giving a higher L* value [64]. However, more studies should be done to better understand the genetic correlations between marbling and the Minolta scale within the Duroc breed.

2.5.8 Genetic Correlations among Novel Carcass Traits

Genetic correlations for novel carcass traits can be found in Table 2.13. As would be expected due to their part-whole correlation, the trimmed and untrimmed primal cuts are highly correlated. TBLW and UBLW had a correlation of 0.87 ± 0.04; TBW and UBW had a correlation of 0.80 ± 0.05; UHW and THW had a correlation of 0.88 ± 0.03; USW and TBW had a correlation of 0.75 ± 0.10 and USW by TPW had a correlation of 0.77 ± 0.08. Another study also found positive estimates between these cuts. UHW and THW had a correlation of 0.70 ± 0.01, TBLW and UBLW had a correlation of 0.21 ± 0.03, while TBW and TPW were correlated with USW with values of 0.42 ± 0.03 and 0.47 ± 0.02 [13]. These correlations are similar in direction, though not in magnitude, and indicate that this study confirms what has been previously observed in the literature. Similarly, UBW and USW had a high and positive correlation of 0.82 ± 0.07, which was not studied by Miar et al. [13] and may be the first estimate presented between these two subprimal cuts.

The genetic correlation between trimmed and untrimmed primal cuts and subprimal cuts are most commonly moderate but have a few high correlations as well. SRW and BRW had a highly favorable correlation of 0.71 ± 0.14, indicating these two cuts can be selected together in a positive direction. To contrast, TBLW and UBLW tend to be strongly and inversely correlated with TPW (−0.77 ± 0.30 and −0.71 ± 0.37, respectively) and USW (−0.72 ± 0.18 and −0.61 ± 0.20, respectively). TBLW also shares moderately inverse correlations with TBW (−0.60 ± 0.16), THW

(−0.33 ± 0.17), TW (−0.42 ± 0.17), BRW (−0.31 ± 0.24), and UBW (−0.55 ± 0.25). UBLW has similar correlations with UBW (−0.51 ± 0.26), TBW (−0.43 ± 0.18), and TW (−0.41 ± 0.18). As the belly would be expected to have more fat than lean mass, these inverse correlations are explainable.

These estimates do not agree with what was found by Miar et al. [13] where correlations between trimmed and untrimmed primal cuts tend to be either strong or moderate and positive. This may be due to difference in breed composition or the use of different covariates in the statistical analysis. Where this study adjusted all carcass traits with HCW, Miar et al. [13] adjusted their traits by AGE instead. Therefore, the results may be interpreted slightly differently

Meanwhile, cuts that contain more lean mass tend to have a moderate and positive relationship amongst each other. THW had positive correlations with TPW (0.37 ± 0.16), BRW (0.44 ± 0.16), and SW (0.47 ± 0.26). UHW has similar correlations with these traits as well. Among the loin traits (ULW, TW, and SW) the average correlation was 0.47. TPW and TBW had a correlation of 0.40. These correlations indicate that the genetic relationship between leanness traits will be positive and favorable. Generally, these estimates are in agreement with previous estimates between leaner carcass traits [13].

The belly flop test was developed to determine the degree of firmness of the fat as a measurement of overall belly quality and is phenotypically related to fatty acid profile [65]. The distance measured between the ends of the belly are indicative of firmer (wider) or softer (closer) fat. Previous literature has explored the genetic correlation between the belly and fat traits, such as fat percentage in the belly, backfat depth, subcutaneous fat area and inter- and intra-muscular fat content [66]. Recently, pork processors have begun using the belly flop test to test bacon fat quality in packing plants, where firmer fat is preferred for the later stages of processing of bacon. With this knowledge, the genetic definition of this trait could be a valuable asset for swine breeders as well. To our knowledge, this is the first paper reporting the genetic correlations between the belly flop test (and other belly traits) and carcass traits.

Only THW was highly correlated with BLFT (−0.87 ± 0.06), though it is a strong and negative correlation. This indicates that selection for increased lean in the ham may decrease the distance measured between the ends of the bacon in the belly flop test, which is ultimately an undesirable impact upon the belly. Likewise, BLFT is moderately and inversely correlated with BRW (−0.36 ± 0.07), SRW (−0.58 ± 0.15), TBW (−0.47 ± 0.01), TPW (−0.58 ± 0.31), UHW

(−0.49 ± 0.14), and UPW (−0.45 ± 0.31). With this unfavorable relationship, if producers consider including BLFT as a trait in a selection index, it may be important to include it alongside other carcass traits such as trimmed or untrimmed primal cuts to prevent any negative impacts upon bacon quality.

One expected correlation found was between BL and BLFT with a correlation of −0.66 ± 0.64, meaning that a longer belly may produce a smaller distance between the ends of the belly during the belly flop test will be closer together. BW and BWR are also closely related (0.87 ± 0.83), indicating they are similar traits and may not need to be measured separately. Using the BLFT to determine quality and BW to determine the preferable width of the belly could be beneficial to selection programs that wish to meet a packer's preferences, and these results show promise in regard to the degree of genetic correlation between belly traits while also providing a measure of caution when selecting for primal or sub-primal cuts.

2.6 Conclusions

Pork quality, conventionally-measured and novel carcass, and growth traits in purebred Duroc pigs are heritable and can be improved through genetic selection. Genetic correlations between growth and conventional carcass traits and pork quality traits were predominantly low to moderate and unfavorable, while growth and conventional and novel carcass traits were mostly moderate and favorable in relation, with few high correlations. Meanwhile, among growth and conventional carcass traits, pork quality traits and novel carcass traits, there were higher and moderate correlations which tended to be favorable. An important finding in this study was that some trait measurements may be redundant due to their high and positive correlations, such as the correlations estimated between HCW, LW, and ADG; between L*, LNC, and LJPC; and between trimmed and untrimmed cuts. It may not be necessary to measure all of these traits or to include every color score in a selection index for example. Carcass and pork quality traits are not good predictors for one another due to their moderate correlation. Similarly, growth and conventional carcass traits may not have a large impact on pork quality traits, as many correlations were low (but also had large standard errors). However, growth and conventional and novel carcass traits had many favorable correlations and show potential for use within a selection index. The estimation of genetic parameters for belly traits is a valuable contribution of this paper as it fills a gap in knowledge and provides insight into using a measurement such as the belly flop test as a

predictor for belly quality. These estimated parameters show potential for developing a selection index combining growth, pork quality, and carcass traits.

2.7 References

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CHAPTER 3. GENOMIC BACKGROUND OF VARIOUS GROWTH, CARCASS AND MEAT QUALITY TRAITS IN DUROC PIGS VIA PRINCIPAL COMPONENT ANALYSIS

3.1 Abstract

As the swine industry continues to explore the inclusion of pork quality traits alongside growth, feed efficiency, and carcass leanness traits, it becomes imperative to understand their underlying genetic relationships. Due to this increase in the number of desirable traits, animal breeders must also consider methods to efficiently select for them all while only utilizing a few within selection indexes. Principal component analysis (PCA) and genome-wide association studies (GWAS) can be combined in order to understand the genetic architecture and biological mechanisms by defining biological types (biotypes) that relate these valuable traits. Therefore, the main objectives of this study were to: 1) estimate genome-based genetic parameters; 2) define animal biotypes utilizing PCA; and 3) utilize GWAS to link the biotypes to candidate genes and quantitative trail loci (QTLs). The phenotypic data set included 2,583 phenotypic records from female Duroc pigs from a terminal sire line. The pedigree file contained 193,764 ancestors and the genotype file included 21,309 animals with 35,651 single nucleotide polymorphisms (SNPs). Eight principal components (PCs), accounting for 99.7 percent of the population variation, were defined for three growth, eight conventional carcass, 10 pork quality, and 18 novel carcass traits. The eight biotypes defined from the PCs were found to be related to growth rate, maturity, meat quality and body structure, which were then related to candidate genes. Of the 175 candidate genes found, six genes [*LDHA* (SSC1), *PIK3C3* (SSC6), *PRKAG3* (SSC15), *VRTN* (SSC7), *DLST* (SSC7), and *PAPPA* (SSC1)] related to four PCs were found to be associated with previously defined QTLs, linking the biotypes with biological processes involved with muscle growth, fat deposition, glycogen levels, and skeletal development. Further functional analysis helped to make connections between biotypes, relating them through common KEGG pathways and gene ontology (GO) terms. These findings indicate a rich genetic relationship between growth, carcass, and meat quality traits, enabling breeders to better understand the biological mechanisms behind these traits in order to improve the genetic selection process.

3.2 Introduction

Meat quality and carcass traits have become more prevalent in the swine industry's breeding programs as consumers continue to demand high quality products at a low cost from animals raised under exemplary welfare conditions [1]. In this context, it becomes important to consider how both meat quality and carcass traits can be included in a breeding program to increase meat quality while maintaining a lower overall cost of production and caring for animal welfare. In order to simultaneously select for these traits, it becomes important to explore the biological and genetic components underlying meat quality, carcass, and growth traits [2,3]. By integrating this knowledge, swine breeding programs can identify alternative ways to include fewer variables in selection indexes while also influencing many traits simultaneously.

The first step to gathering this knowledge is through the estimation of genetic parameters for the traits of interest. The predominant methods of estimating variance components (VCs) are restricted maximum likelihood (REML) and average information REML (AIREML), which can utilize either the pedigree-based relationship matrix (**A**) or the hybrid relationship matrix (**H**) [4–7], which is a combination of the genomic (**G**) and the pedigree-based (**A**) matrices. In a previous study, VCs were estimated for 39 growth, carcass, primal cuts, and meat quality traits in a Duroc population using the **A** matrix [8]. However, including genomic information in the estimation process can change the genetic parameter estimates. For instance, Forni et al. [9] showed that heritability estimates and their standard errors tend to decrease when genomic information is used. These findings are related to the fact that genomics can yield more accurate estimates due to the better estimation of the relationships between animals and tracing of more distant relationships not captured through the pedigree. Studies done in cattle have found similar results, where pedigree-based estimates tend to have higher standard errors and higher heritabilities than the single-step genomic approach [10,11]. Utilizing the **A** or **H** matrix in the estimation procedures may produce different estimates for the traits included in this study and may impact the inclusion of new traits in a selection index.

The next step to consider is the number of traits desired and how feasible it is for pig breeders to include them all in their breeding goals. While developing a selection index is one option, deriving economic values for several traits would be difficult and complex, especially for genetic companies that export to multiple countries. A simpler method to decrease the number of variables and break groups of traits down to an understandable, biological level is through principal

component analysis (PCA). PCA derives principal components (PCs) from matrices that have been constructed using the (co)variance matrix of the estimated breeding values (EBVs) [12–15], the correlation-coefficient matrix of related phenotypes [16], or the (co)variance matrix of the additive genetic effects of the traits being analyzed [12,17]. Lee et al. [16] used PCA analysis previously to study pork quality traits. The authors used PCA to develop integrated phenotypes and genome-wide association analysis (GWAS) in order to facilitate the discovery of candidate genes that would aide in the selection process for improved meat quality characteristics.

Similarly, Vargas et al. [17] used a combined PCA and GWAS methodology to identify candidate genes for growth and reproduction traits using "pseudo-phenotypes" created from the EBVs of the animals. They also introduced the application of the eigen-decomposition of the $\mathbf{A}_T$ matrix (a variance-covariance matrix constructed from the additive genetic variance) to animal breeding and proposed that this method better accounts for the genetic relationship between traits because of its direct correspondence to the additive genetic relationships. By utilizing these pseudo-phenotypes (or new genetic traits), Vargas et al. [17] were able to identify several promising candidate genes and quantitative trait loci (QTLs) through single-step GWAS (ssGWAS) analysis. Prior to their work, Zhang et al. [18] discovered the value in combining PCA and GWAS as multiple-trait GWAS studies had more power in detecting QTLs and in exploring pleiotropy than single-trait GWAS.

This method has not, to the best of our knowledge, been applied to a large number of growth, carcass, and meat quality traits in pigs. Applying PCA to a plethora of traits of importance to terminal sire lines will vastly aid in the selection of biologically relevant variables that can ensure gain across multiple traits [19]. Therefore, the objectives of this study were to: 1) estimate genome-based variance components for 39 growth, carcass, and meat quality traits in Duroc pigs; 2) apply PCA to derive novel biotypes related to terminal sire performance; and 3) to uncover candidate genes related to those phenotypes through GWAS in order to facilitate more accurate selection of multiple traits simultaneously.

3.3 Materials and Methods

3.3.1 Ethics Statement

The animals included in this study were managed in accordance with the "Code of practice for the care and handling of pigs" (National Farm Animal Care Council, 2014). All samples used for genotyping were collected in a nucleus breeding farm and the animal owners agreed to be involved in the project. The slaughters, data collection, and trait measurements were done by well-trained staff following industry best practices.

3.3.2 Datasets

Phenotypic data and traits were previously described in detail in Willson et al. [8]. A brief description of the 39 traits included in this study and their abbreviations can be found in Table 3.1. In total, 21,309 genotypes were available for this study. The genotypes were collected from four different panels [4,742 genotyped with GGP Porcine HD v1, 856 genotyped with ILMN PorcineSNP60, 10,444 with GGP Porcine HD v1, and 5,267 with a custom panel] and accurately imputed [20] to the GGP Porcine v2 panel. These panels were developed based on the 10.2 *Sus scrofa* reference genome. Before quality control, genotypes were available for 2,183 animals with phenotypic records and 21,294 animals in the pedigree.

3.3.3 Data Editing and Quality Control

Quality control on the genotypes was performed using the PREGSF90 program from the BLUPf90 family [21]. SNPs with call rates lower than 90% and minor allele frequency (MAF) lower than 0.05 were removed. A threshold p-value lower than 0.00001 was set for a chi-squared test for extreme deviation from the Hardy-Weinberg equilibrium (HWE). Animals with call rate lower than 90% were removed. Additionally, genotyped animals without parents or grandparents in the pedigree file were removed. After performing these quality control requirements, 35,651 SNPs and 21,219 genotyped animals remained in the analysis with 193,764 animals in the pedigree.

Table 3.1. All traits abbreviations and descriptions.

Abbreviation	Description
ADG	Average Daily Gain (g/day)
HCW	Hot Carcass Weight (kg)
LW	Live Weight (kg)
DL1	25 cm Chop Initial Weight (g)
DL2	25 cm Chop Post Weight (g)
DLP	Drip Loss Percentage (%)
LJPC	Japanese Loin Color Scale
L*	Minolta L*
a*	Minolta a*
b*	Minolta b*
LNC	NPPC Loin Color Scale
LNM	NPPC Loin Marbling Scale
LPHA	Loin pH
DP	Dressing Percentage (%)
GBF	Grading Back Fat (cm)
GI	Grade Index
GLD	Grading Loin Depth (cm)
LA	Loin Area (cm2)
LC	Loin Circumference (cm)
LL	Loin Length (cm)
RMD	Ruler Muscle Depth (cm)
BLFT	Belly Flop Test (cm)
BL	Belly Length (cm)
BLW	Boneless Loin Weight (kg)
BRW	Back Ribs Weight (kg)
BW	Belly Width (cm)
BWR	Belly Width Rear (cm)
SRW	Side Ribs Weight (kg)
SW	Sirloin Weight (kg)
TW	Tenderloin Weight (kg)
TBLW	Trimmed Belly Weight (kg)
TBW	Trimmed Boston Butt Weight (kg)
THW	Trimmed Ham Weight (kg)
TPW	Trimmed Picnic Shoulder Weight (kg)
UBLW	Untrimmed Belly Weight (kg)
UBW	Untrimmed Boston Butt Weight (kg)
UHW	Untrimmed Ham Weight (kg)
USW	Untrimmed Shoulder Weight (kg)
ULW	Untrimmed Loin Weight (kg)

3.3.4 Variance Component Estimation

Statistical model development were previously described in detail in Willson et al. [8]. The models included the fixed effects of slaughter date by slaughter technician, season-year (a definition of contemporary group) and parity of the dam at birth; covariates included age of the animal at slaughter or hot carcass weight; and the random effects of animal and dam-litter (DL; common environment effect) were included in the models where significant for each trait.

The animal model used when one random effect was present was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

with

$$\begin{pmatrix} u \\ e \end{pmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & 0 \\ 0 & \sigma_e^2 \end{pmatrix}\right]$$

where **y** is the vector of phenotypic observation, **b** is the vector of fixed effects (found to be significant for each trait), **u** is the vector of additive genetic effects, and **e** is a vector of random residuals. The **X** and **Z** are the incidence matrices associating **b** and **u** to the observations, respectively. The σ_a^2 and σ_e^2 are the additive and residual error variances, respectively.

The animal model used when both DL and animal additive genetic random effects were present was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wd} + \mathbf{e}$$

with

$$\begin{pmatrix} u \\ d \\ e \end{pmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_a^2 & 0 & 0 \\ 0 & \sigma_d^2 & 0 \\ 0 & 0 & \sigma_e^2 \end{pmatrix}\right]$$

where **y** is the vector of phenotypic observation, **b** is the vector of fixed effects (found to be significant for each trait), **u** is the vector of additive genetic effects, **d** is the vector of common environment (dam-litter) effect, and **e** is a vector of random error. The **X**, **Z,** and **W** are the incidence matrices associating **b**, **u,** and **d** to the observations, respectively. σ_a^2 , σ_d^2, and σ_e^2 are the additive genetic, common environmental (dam-litter) and residual error variances, respectively.

The univariate and PCA pseudo-phenotypes variance components were estimated including genomic and pedigree relationship information following the single-step approach using the hybrid (**H**) matrix [4,7] with the average-information algorithm present in the AIREMLF90

program [21]. All default settings were used for the construction of the inverse of the **H** matrix, where $\tau = 1$ and $\omega = 1$, $\alpha = 0.95$ and $\beta = 0.05$, and $\gamma = 0$ and $\delta = 0$.

The inverse of the **H** matrix was defined as [7]:

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \tau(\alpha\mathbf{G} + \beta\mathbf{A}_{22})^{-1} - \omega\mathbf{A}_{22}^{-1} \end{bmatrix},$$

where **A** is the pedigree relationship matrix, $\mathbf{A_{22}}$ is a subset of the pedigree relationship matrix for only the genotyped animals, and **G** is the genomic relationship matrix for all genotyped animals.

The **G** matrix used was defined as [22]:

$$\boldsymbol{G} = \frac{\boldsymbol{ZZ'}}{2\sum p_i(1 - p_i)}$$

where $\mathbf{Z} = \mathbf{M} - \mathbf{P}$, in which **M** contains the centered genotypes (i.e., -1, 0, and 1 to represent AA, Aa and aa, respectively), **P** contains the allele frequency for SNP_i (p_i) in its k^{th} column, expressed as $2(p_i - 0.5)$; $2\sum p_i(1 - p_i)$ is a scaling parameter; and **A** is the traditional (pedigree-based) additive relationship matrix.

3.3.5 Principal Component Analysis

Principal components (PCs) were estimated following the approach outlined by Vargas et al. [12] and Vargas et al. [17]. Bivariately estimated genetic parameters from a previous study [8] were used to construct the $\mathbf{A_T}$ matrix as follows:

$$\boldsymbol{A_T} = (G_a)$$

where, $\mathbf{G_a}$ is a variance-covariance matrix with the additive genetic variance (σ_a^2) on the diagonal and additive genetic covariances between traits in the off-diagonals. The final matrix dimension was 39 x 39.

Principal components were calculated from the eigen-decomposition of the $\mathbf{A_T}$ matrix using the *eigen* function available in the R software [23]. This function calculates both eigenvalues and eigenvectors, which explain the magnitude and direction of the variance of the interactions between all traits included in the principal component analysis [12]. Together, these values can be used to define biological groups for traits of importance.

In order to determine which of these PCs explained the largest proportion of genetic variance, the Kaiser criterion [24] was used. Thus, only PCs with eigenvalues above 1.0 were considered as significant for further analysis.

Psuedo-phenotypes were calculated for use in the GWAS analysis. For the purpose of this study, the pseudo-phenotypes were obtained based on animal GEBV and eigenvectors. The EBVs associated with each significant PC (EBV_{PC_i} – pseudo-phenotype) were calculated as [17]:

$$EBV_{PC_{ij}} = \sum_{k}^{j} e_{ik} EBV_{jk}$$

where $EBV_{PC_{ij}}$ is the estimated breeding value for the ith PC pseudo-phenotype of the jth animal, $e_{ik}$is the coefficient of the eigenvector of the ith PC for the kth trait (e.g. ADG), and EBV_{jk} is the EBV for the jth animal for the kth trait. The coefficients *i*, *j*, and *k* represent PC (equivalent number to the Kaiser Criterion cutoff), animal, and traits (39 original traits), respectively.

Two separate PCAs were performed for this study. The first included all traits as previously described in Table 3.1, while the second analysis was performed on a smaller set of traits excluding some potentially redundant traits (DL1, DL2, LJPC, LNC. RMD, UBLW, UBW, UHW, ULW, and USW) to see if a difference existed in the biological types represented by the different PCs and to hopefully place more emphasis on carcass and meat quality traits. The GWAS was carried out using the results of the first PCA.

3.3.6 Genome-wide Association Analysis

Following the use of AIREMLF90 to estimate variance components for the pseudo-phenotypes, BLUPF90 and POSTGSF90 [21] were used to estimate breeding values and SNP effects, respectively, in order to perform the GWAS analysis following the single-step GWAS (ssGWAS) method [25]. The model used was:

$$\boldsymbol{y}^{*} = \mu + \boldsymbol{Z}_{a}\boldsymbol{a} + \boldsymbol{e}$$

where $\mathbf{y}^{*}$ is a vector of the pseudo-phenotypes ($EBV_{PC_{ij}}$), $\boldsymbol{\mu}$ is a vector of the overall mean, $\boldsymbol{Z}_{a}$ is an incidence matrix that relates animals to the vector of pseudo-phenotypes, $\boldsymbol{a}$ is the vector of direct additive genetic effects, and $\boldsymbol{e}$ is the vector of random residuals. It was assumed that $\boldsymbol{a} \sim N(0, \boldsymbol{H}\sigma_a^2)$ where $\mathbf{H}$ represents the hybrid relationship matrix of pedigree and genomic information and σ_a^2 is the additive genetic variance.

As the pseudo-phenotypes had different reliabilities, a weight was applied during variance component and SNP effect estimation in order to compensate for this difference. The weight was calculated as:

$$w = 1 - \left(\frac{SEP^2}{\sigma_a^2}\right)$$

where SEP is the standard error of prediction for the GEBVs of HCW, which had records present for all animals in the analysis and σ_a^2 is the additive genetic variance.

Genome-wide association plots were created using the default script provided within the BLUPF90 family programs [21] and inputting them into R [23]. The significance of the SNPs was determined after adjusting for multiple testing through Bonferroni. The Bonferroni correction was performed on an individual chromosome basis (chromosome-wise correction) considering an alpha level of 0.05.

3.3.7 Functional Analysis

A window of 50kb was used on either side of the significant SNPs identified in the GWAS analysis to detect candidate genes and QTLs associated with each significant PC. Gene detection was performed using the biomaRt package **[26,27]** in R. Subsequently, the results from biomaRt were used to search for previously reported associations between our candidate genes and QTLs in the AnimalQTLdb (https://www.animalgenome.org/cgi-bin/QTLdb/index). Gene Ontology (GO) terms and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways were detected for all candidate genes using DAVID (https://david.ncifcrf.gov/home.jsp). All default options were used for this analysis, but the main areas of interest to this study were the biological pathways (GOTERM_BP_DIRECT) under Gene Ontology and KEGG_PATHWAY under Pathways in DAVID's annotation summary tool. Bonferroni correction ($p < 0.05$) was used to detect significant pathways and GO terms.

3.4 Results

3.4.1 Heritabilities

The genomic-based heritability estimates are shown in Tables 3.2 and 3.3. Results were categorized using the following heritability scale: low (from 0.01 to 0.14), moderate (from 0.15 to 0.39), and high (greater than or equal to 0.40).

In general, growth traits had moderate heritabilities with values of 0.23 ± 0.03, 0.25 ±0.04 and 0.20 ±0.03 for ADG, HCW, and LW, respectively. Pork quality traits were moderately heritable, ranging from 0.17 ± 0.03 (LNC) to 0.34 ± 0.04 (DL1 and DL2) and 0.34 ±0.03 (LNM). The color scales tended to have lower heritabilities (0.17 ± 0.03 for LNC and 0.20 ±0.03 for LJPC), as compared to the Minolta color scores (0.32 ± 0.04 for L*, 0.29 ± 0.04 for a*, and 0.30 ± 0.04 for b*).

Conventionally-measured carcass traits were lowly to highly heritable, displaying the largest range of all groups of traits. GI had the lowest heritability of 0.01 ± 0.02, while LA had the highest heritability of 0.45 ± 0.04. Other loin traits had moderate heritabilities of 0.28 ± 0.03, 0.28 ± 0.03, 0.19 ± 0.06, 0.32 ± 0.04, and 0.35 ± 0.04 for GLD, LC, LL, and RMD, respectively. GBF had a moderate heritability of 0.33 ± 0.04.

Novel carcass traits ranged from lowly (0.09 ± 0.03 for BW) to highly heritable (0.42 ± 0.03 for BLW). Novel belly traits ranged from lowly to moderately heritable, with BW having the lowest heritability of 0.09 ± 0.03 and BWR having the highest heritability of 0.24 ± 0.08. When comparing trimmed and untrimmed cuts, TBLW (0.28 ± 0.04) had a lower heritability than the untrimmed counterpart (0.29 ± 0.04). Otherwise, trimmed cuts (0.15 ± 0.03 and 0.40 ± 0.04 for TBW and THW, respectively) tended to have higher heritabilities than untrimmed cuts (0.11 ±0.03 and ± 0.26 ± 0.04 for UBW and UHW, respectively). Subprimal cuts had low to high heritability estimates, ranging from 0.14 ± 0.03 (SW) to 0.42 ± 0.03 (BLW). Subprimal rib cuts had moderate heritabilities of 0.20 ± 0.03 and 0.21 ± 0.03 for BRW and SRW, respectively.

Table 3.2. Heritabilities, standard errors, additive genetic variance (σ^2_A), common environment (dam-litter) variance (σ^2_{DL}), and common-litter ratio effect (c^2) for growth, pork quality, and conventional carcass traits.

Trait[1]	h^2	SE	σ^2_A	σ^2_{DL}	c^2
		Growth traits			
ADG	0.23	0.03	437.390	433.8400	0.2281
HCW	0.25	0.04	7.086	1.2109	0.0427
LW	0.20	0.03	8.161	2.7061	0.0663
		Pork quality traits			
DL1	0.34	0.04	180.390	53.5360	0.1009
DL2	0.34	0.04	175.990	49.2160	0.0951
DLP	0.18	0.05	0.034	0.0124	0.0651
LJPC	0.20	0.03	0.021		
L*	0.32	0.04	1.160	0.1667	0.0460
a*	0.29	0.04	0.389	0.1235	0.0921
b*	0.30	0.04	0.215	0.0153	0.0214
LNC	0.17	0.03	0.019	0.0021	0.0186
LNM	0.34	0.03	0.079	0.0000	0.0001
LPHA	0.30	0.04	0.003	0.0010	0.1044
		Conventionally measured carcass traits			
DP	0.08	0.03	0.000	-	-
GBF	0.33	0.04	2.542	0.7642	0.0992
GI	0.01	0.02	0.13794	-	-
GLD	0.28	0.03	6.497	0.6167	0.0266
LA	0.45	0.04	13.868	0.8485	0.0275
LC	0.19	0.06	0.503	0.0000	0.0000
LL	0.32	0.04	1.226	0.2267	0.0592
RMD	0.35	0.04	7.651	0.5228	0.0239

[1]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth.

Table 3.3. Heritabilities, standard errors, additive genetic variance (σ^2_A), common environment (dam-litter) variance (σ^2_{DL}), and common-litter ratio effect (c^2) for novel carcass traits.

Trait[1]	h^2	SE	σ^2_A	σ^2_{DL}	c^2
BLFT	0.25	0.09	2.381	0.0177	0.0019
BL	0.22	0.06	1.041	0.6286	0.1328
BLW	0.42	0.03	0.042	0.0001	0.0006
BRW	0.20	0.03	0.002	0.0003	0.0390
BW	0.09	0.03	0.186	0.0000	0.0000
BWR	0.24	0.08	1.042	-	-
SRW	0.21	0.03	0.005	0.0011	0.0486
SW	0.14	0.03	0.003	0.0010	0.0397
TW	0.34	0.04	0.001	0.0001	0.0281
TBLW	0.28	0.04	0.049	0.0123	0.0711
TBW	0.15	0.03	0.015	0.0000	0.0001
THW	0.40	0.04	0.117	0.0129	0.0441
TPW	0.15	0.03	0.014	0.0039	0.0428
UBLW	0.29	0.04	0.062	0.0107	0.0496
UBW	0.11	0.03	0.011	0.0029	0.0283
UHW	0.26	0.04	0.066	0.0085	0.0334
USW	0.16	0.03	0.035	0.0259	0.1185
ULW	0.21	0.03	0.061	0.0133	0.0456
USW	0.16	0.03	0.035	0.0259	0.1185

[1]BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

3.4.3 Principal component analysis

By the definition of the Kaiser criterion [24], only the PCs with eigenvalues above 1.0 were considered as significant. Therefore, for the first PCA scenario (all 39 traits), eight PCs were significant, while in the second PCA scenario (29 traits) had six significant PCs.

For the first PCA, the first three PCs accounted for 97.17 percent of the total variation. The remaining five PCs accounted for 2.43 percent of the variation. For the second PCA, the first three PCs accounted for 98.02 percent of the variation, while the remaining three accounted for 1.53 percent of the variation. Collectively across both PCAs, the significant PCs accounted for nearly 100 percent of the variation in both analyses.

Results are shown in Tables 3.4 and 3.5. The heat map applied denotes the signal and magnitude of each trait's relationship with each PC. Red denotes positive values where blue denotes negative values. Traits that share signals respond in the same direction, while the number value reflects the amount of variation explained by that trait for each PC.

Principal Component Analysis – First Scenario

The first principal component (PC1) is most notably related to ADG (0.9582), HCW (0.1577), and LW (0.172), suggesting that this biotype is likely related to the growth rate and slaughter weight of the animal. The second principal component (PC2) had moderate and negative coefficients for DL1 (-0.6420), DL2 (-0.5344), and LA (-0.3495), low and negative coefficients for ADG (-0.1588), GLD (-0.2118), LC (-0.1665), and RMD (-0.2239) and a low, positive relationship with GBF (0.1073), suggesting that this PC's biotype is related to an earlier maturing animal that has begun depositing more fat on the carcass. The third principal component (PC3) had only notable coefficients with DL1 (-0.6603) and DL2 (0.7492), and considering the similarity of these traits, the biotype is difficult to distinguish at this time.

As the variation explained decreases, it becomes harder to definitively define the smaller biotypes. However, the traits still displayed some strong relationships with the remaining PCs. The fourth principal component (PC4) had low to moderate, positive coefficients with BWR (0.4016), LA (0.2493), LC (0.1890), and LW (0.2586), and low to moderate negative coefficients with BL (-0.2953), GLD (-0.3000), HCW (-0.5821), and RMD (-0.3536), suggesting a biotype that is shorter bodied with wider bellies and less lean musculature. The fifth principal component (PC5)

had moderate negative coefficients with BLFT (-0.4586), GBF (-0.5403), and RMD (-0.3648) and moderate but positive coefficients with BL (0.4165) and LL (0.2904), suggesting a longer bodied biotype with a slower growth rate and less muscle and fat deposition. Inversely, the sixth principal component (PC6) had moderate and negative coefficients with BLFT (-0.5559), BL (-0.3637), and LL (-0.5751) and one moderately positive coefficient with GLD (0.2632), indicating the sixth biotype is related to shorter bodied animals with more lean deposits and softer belly fat. The seventh principal component (PC7) had low to moderate and positive coefficients with the Minolta color scale [L* (0.6632), a* (0.3149), b* (0.2860)], LA (0.3168), and LNM (0.1308) while also possessing moderate negative coefficients with BWR (-0.2971) and GLD (-0.2616), indicating this biotype is primarily related to the color of the loin. The eighth principal component (PC8) was primarily related to LC (0.7184) with low and positive coefficients with GBF (0.1923) and GI (0.2412) and low to moderately negative coefficients with BWR (-0.2049), LA (-0.2126), LL (-0.2329), and RMD (-0.3927), indicating that this biotype may be related to an increase in fat deposition and a decrease in lean accretion.

Table 3.4. Table of eigenvalues (λ), eigenvectors and proportion (prop) of variance explained for the first eight principal components (PC1 to PC8) of the first principal component analysis.

Trait[1]	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
ADG	0.9582	-0.1588	-0.004	0.0304	-0.0144	0.0358	-0.0016	0.0131
HCW	0.1577	0.0761	-0.0122	-0.5821	0.0978	-0.0071	-0.0108	0.0311
LW	0.172	-0.0614	-0.0066	0.2586	-0.0765	-0.1876	0.0023	-0.1606
DL1	-0.121	-0.642	-0.6603	-0.0242	0.0368	-0.037	-0.0161	0.0465
DL2	-0.0942	-0.5344	0.7492	-0.0156	0.0426	-0.044	-0.0179	0.0611
DLP	-0.0012	-0.0026	-0.0002	-0.0092	-0.0066	-0.0279	0.0391	-0.0605
LJPC	-0.0011	0.001	0.0002	0.0083	0.022	0.0142	-0.0421	0.0091
L*	-0.0026	-0.003	-0.0005	-0.0515	-0.1307	-0.0267	0.6632	0.0366
a*	-0.0003	0.0073	-0.0006	0.0172	-0.0332	0.0668	0.3149	0.0526
b*	0.0003	0.0029	-0.0004	-0.0142	-0.057	0.0327	0.286	-0.0182
LNC	-0.0006	-0.0012	0.0003	0.0067	0.0257	0.0054	-0.034	0.0033
LNM	0.0011	0.0096	-0.0007	0.0045	-0.0257	-0.0319	0.1308	-0.0221
LPHA	0.0003	0.0006	0	0.0028	0.0045	-0.0054	-0.0155	-0.0001
DP	0.0002	0	0	-0.0009	-0.0007	0.0038	0.0001	-0.0025
GBF	-0.0046	0.1073	-0.0104	-0.0087	-0.5403	-0.0999	0.0818	0.1923
GI	0.0264	-0.0246	-0.0007	-0.0678	0.0934	-0.0025	0.1298	0.2412
GLD	-0.0378	-0.2118	0.0229	-0.3	-0.1597	0.2632	-0.2616	0.082
LA	-0.0318	-0.3495	0.034	0.2493	-0.1332	0.0863	0.3168	-0.2126
LC	0.0058	-0.1665	0.0004	0.189	0.0635	-0.1812	-0.1173	0.7184
LL	-0.0062	-0.0168	-0.0005	0.0749	0.2904	-0.5751	0.0584	-0.2329
RMD	-0.0219	-0.2239	0.0227	-0.3536	-0.3648	-0.1529	-0.1271	-0.3927
BLFT	0.0041	0.0787	-0.0037	-0.0655	-0.4586	-0.5559	-0.1084	0.1442
BL	0.0005	-0.0368	0.0046	-0.2953	0.4165	-0.3637	0.1085	-0.0049
BLW	-0.0025	-0.0173	0.0014	-0.0513	0.0126	-0.0606	0	0.0258
BRW	-0.0001	-0.0009	0.0001	-0.0024	0.0079	-0.0036	-0.0011	-0.0125
BW	0.0043	-0.0168	-0.0001	0.0354	0.0182	0.0276	-0.1188	-0.1029
BWR	0.0097	0.0258	-0.0051	0.4016	-0.0295	-0.0921	-0.2971	-0.2049
SRW	0.0005	-0.0024	0	-0.0267	0.0321	-0.0187	-0.0016	0.0028
SW	0.0004	-0.0036	0.0004	-0.0089	-0.007	0.0029	-0.009	0.0011
TW	-0.0003	-0.0009	0.0001	-0.0034	0.0013	-0.001	-0.0028	-0.0063
TBLW	0.004	0.0014	-0.0004	-0.0088	-0.0204	-0.0174	0.0008	0.0054
TBW	-0.0001	-0.0009	-0.0001	-0.0131	0.0217	0.0286	-0.0194	-0.038
THW	-0.0031	-0.0245	0.0026	0.0049	0.0642	0.022	-0.0159	-0.0458
TPW	0.0007	-0.0032	0.0002	0.0101	0.0033	0.0289	-0.0106	-0.0352
UBLW	0.0046	-0.0015	-0.0003	-0.0057	0.0054	-0.0375	0.0054	0.0053
UBW	0.0011	0.0039	-0.0006	-0.0427	0.0059	0.0261	-0.0209	-0.0065
UHW	-0.0019	-0.0143	0.0018	0.0163	0.0087	0.0078	0.0136	-0.0513
USW	0.002	-0.0012	-0.0002	-0.0266	0.023	0.0482	-0.0401	-0.0277
ULW	-0.0008	-0.0183	0.0014	-0.0735	-0.0226	-0.1294	0.0458	0.0653
λ	565.48	163.94	119.82	8.44	6.89	2.6	2.05	1.22
Prop (%)	64.7	18.76	13.71	0.97	0.79	0.3	0.23	0.14

[1]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DL1: 25 cm chop initial weight; DL2: 25 cm chop post weight; DLP: drip loss percentage; LJPC: Japanese loin color scale; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNC: NPPC loin color scale; LNM: NPPC loin marbling scale; LPHA: loin pH; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; RMD: ruler muscle depth; BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight; UBLW: untrimmed belly weight; UBW: untrimmed Boston butt weight; UHW: untrimmed ham weight; USW: untrimmed shoulder weight; ULW: untrimmed loin weight.

Principal Component Analysis – Second Scenario

Similar to the results of the first PCA, PC1 had a high relationship with ADG (0.9709) and a lower relationship with HCW (0.1554) and LW (0.1758), indicating a similar biotype to the first analysis. PC1 is most likely related to animals with higher growth rate and increased live and carcass weight at the time of slaughter. PC2 had a high, positive coefficient with LA (0.7736) and a positive and moderate coefficient with GLD (0.3903) and LC (0.2192), while it also had moderate and negative coefficients with HCW (-0.3296), GBF (-0.1904), and BLFT (-0.1982), indicating this biotype is related to leaner animals with less fat on the carcass. The third PC had moderate coefficients overall, but had a positive relationship with HCW(0.4726), GLD (0.3440), and BL (0.4099) and a negative relationship with LC (-0.1720), GBF (-0.3180), BLFT (-0.2838), and BWR (-0.4254). PC3 likely explains a biotype related to animals with longer bodies, producing a longer, but narrower belly. Overall, these animals are likely to be leaner and have less fat.

The fourth PC was found to have moderate, but positive coefficients with GBF (0.5047), GLD (0.4492), and BLFT (0.4278) and moderate, negative coefficients with LL (-0.3556), BL (-0.2406), and BWR (-0.2676), indicating that this PC is representative of a biotype that is shorter bodied and likely to mature sooner, thus depositing more fat on the carcass. PC5 had a moderate and positive coefficient with GLD (0.2723) but primarily had negative coefficients with L* (-0.4736), LA (-0.2629), LL (-0.4939), BLFT (-0.3285), and BL (-0.3302). The fifth PC is most likely related to a biotype with darker meat color and shorter bodied animals. The final PC had moderate and positive coefficients with the Minolta L* (0.4848), a* (0.3226), and b* (0.2457), while it also had negative coefficients with GLD (-0.3010), LL (-0.4443), and BLFT (-0.4833). PC6 is likely representative of a biotype with paler meat color and shorter body length.

Table 3.5. Table of eigenvalues (λ), eigenvectors and proportion (prop) of variance explained for the first six principal components (PC1 to PC6) of the second principal component analysis.

Trait[1]	PC1	PC2	PC3	PC4	PC5	PC6
ADG	0.9709	0.0552	-0.0166	0.0146	0.0230	0.0099
HCW	0.1553	-0.3296	0.4726	0.1719	-0.0095	-0.0369
LW	0.1758	0.0904	-0.2761	-0.1084	-0.1269	-0.0987
DLP	-0.0010	-0.0046	-0.0021	0.0113	-0.0412	0.0282
L*	-0.0025	0.0143	0.0076	0.1823	-0.4736	0.4848
a*	-0.0007	0.0045	-0.0120	0.0370	-0.1563	0.3226
b*	0.0001	0.0065	0.0025	0.0705	-0.1722	0.2457
LNM	0.0006	-0.0130	-0.0175	0.0156	-0.1163	0.0726
LPHA	0.0003	-0.0013	-0.0018	-0.0078	0.0061	-0.0156
DP	0.0002	0.0001	0.0009	0.0012	0.0028	0.0029
GBF	-0.0097	-0.1904	-0.3180	0.5047	-0.0990	0.0665
GI	0.0277	0.0154	0.1098	-0.0148	-0.0758	0.1403
GLD	-0.0281	0.3903	0.3440	0.4492	0.2723	-0.3010
LA	-0.0158	0.7736	-0.0284	0.0938	-0.2629	-0.0115
LC	0.0141	0.2192	-0.1720	-0.0702	0.0574	0.0997
LL	-0.0053	-0.0005	0.0209	-0.3556	-0.4939	-0.4443
BLFT	0.0005	-0.1982	-0.2838	0.4278	-0.3285	-0.4833
BL	0.0025	-0.0459	0.4099	-0.2406	-0.3302	-0.0962
BLW	-0.0017	0.0216	0.0555	0.0267	-0.0549	-0.0710
BRW	0.0000	0.0010	0.0060	-0.0075	-0.0029	-0.0054
BW	0.0051	0.0140	-0.0392	-0.0508	0.1428	0.0705
BWR	0.0085	-0.0117	-0.4254	-0.2676	0.2001	-0.0812
SRW	0.0007	-0.0052	0.0349	-0.0152	-0.0107	-0.0053
SW	0.0006	0.0055	0.0066	0.0134	0.0058	-0.0122
TW	-0.0003	0.0018	0.0044	0.0003	-0.0001	-0.0064
TBLW	0.0040	-0.0104	-0.0088	0.0270	-0.0082	-0.0043
TBW	0.0000	-0.0005	0.0236	-0.0153	0.0328	0.0064
THW	-0.0020	0.0424	0.0356	-0.0650	0.0340	0.0334
TPW	0.0008	0.0103	-0.0022	-0.0107	0.0272	0.0107
λ	555.01	25.09	7.03	5.34	2.18	1.66
Prop (%)	92.66%	4.19%	1.17%	0.89%	0.36%	0.28%

[1]ADG: average daily gain; HCW: hot carcass weight; LW: live weight; DLP: drip loss percentage; L*: Minolta L*; a*: Minolta a*; b*: Minolta b*; LNM: NPPC loin marbling scale; LPHA: loin pH; DP: dressing percentage; GBF: backfat depth; LA: loin area; LC: loin circumference; LL: loin length; BLFT: belly flop test; BL: belly length; BLW: boneless loin weight; BRW: back ribs weight; BW: belly width; BWR: belly width rear; SRW: side ribs weight; SW: sirloin weight; TW: tenderloin weight; TBLW: trimmed belly weight; TBW: trimmed Boston butt weight; THW: trimmed ham weight; TPW: trimmed picnic shoulder weight.

3.4.4 Genome-wide association analysis

All PCs from the first PCA, except PC7, had significant SNPs according to the results of the GWAS using p-values after performing the Bonferroni correction. Two sets of Manhattan plots were generated from these results. These plots are primarily used to help researchers visualize peaks (areas of interest) across the genome. The first set of plots were created based on the log transformation of each SNP's p-value, which can be found in Figures 3.1 through 3.8. The second set of plots were created based on SNP effects and are presented as Supplementary Material in Appendix A as Figures A.1 to A.8. All significant SNPs, their base pair position, chromosome number, and related genes can be found in Tables 3.6 to 3.12.

PC1 had two significant SNPs as well as two related genes across on SSC1. PC2 had 179 significant SNPs and 59 related genes across eight chromosomes (SSC1, SSC2, SSC5, SSC6, SSC7, SSC8, SSC10, SSC16, and SSC17). PC3 had 165 significant SNPs and 50 related genes across eight chromosomes (SSC 3, SSC4, SSC5, SSC6, SSC12, SSC13, SSC15, and SSC18). PC4 had 11 significant SNPs and four related genes across two chromosomes (SSC6, SSC14). PC5 had 164 significant SNPs and 39 related genes across six chromosomes (SSC1, SSC4, SSC7, SSC9, SSC12, and SSC13). PC6 had four significant SNPs, but no related genes were found. PC8 had 90 significant SNPs with 21 related genes across five chromosomes (SSC1, SSC4, SSC12, SSC14, and SSC18). In total, there were 615 significant SNPs found with 175 candidate genes related to seven principal components.

Of the 175 candidate genes found, only six (*LDHA*, *PIK3C3*, *PRKAG3*, *VRTN*, *DLST*, and *PAPPA*) were related to previously documented QTLs, and only one of the six (i.e., *DLST*) overlapped with a significant SNP position. The summary of related QTLs can be found in Tables 3.13 to 3.16.

A functional analysis was then performed for each PC's group of candidate genes individually to investigate potential relationship with known biological pathways. Though there were many gene ontology (GO) terms associated with the genes included in the functional analysis, only the significant biological processes will be discussed as it would go beyond the scope of this paper to include all of them. Two GO terms were found to be significant, GO:0009952 and GO:0048704, which were both associated with PC3. Next, all candidate genes across PCs were analyzed simultaneously to investigate overall pathways that may be linked across multiple principal components. In addition to the two GO terms found previously, two KEGG pathways

were also significant. The first pathway, “oxytocin signaling pathway,” was associated with seven candidate genes, while the second pathway, “MAPK signaling pathway,” was associated with five candidate genes.

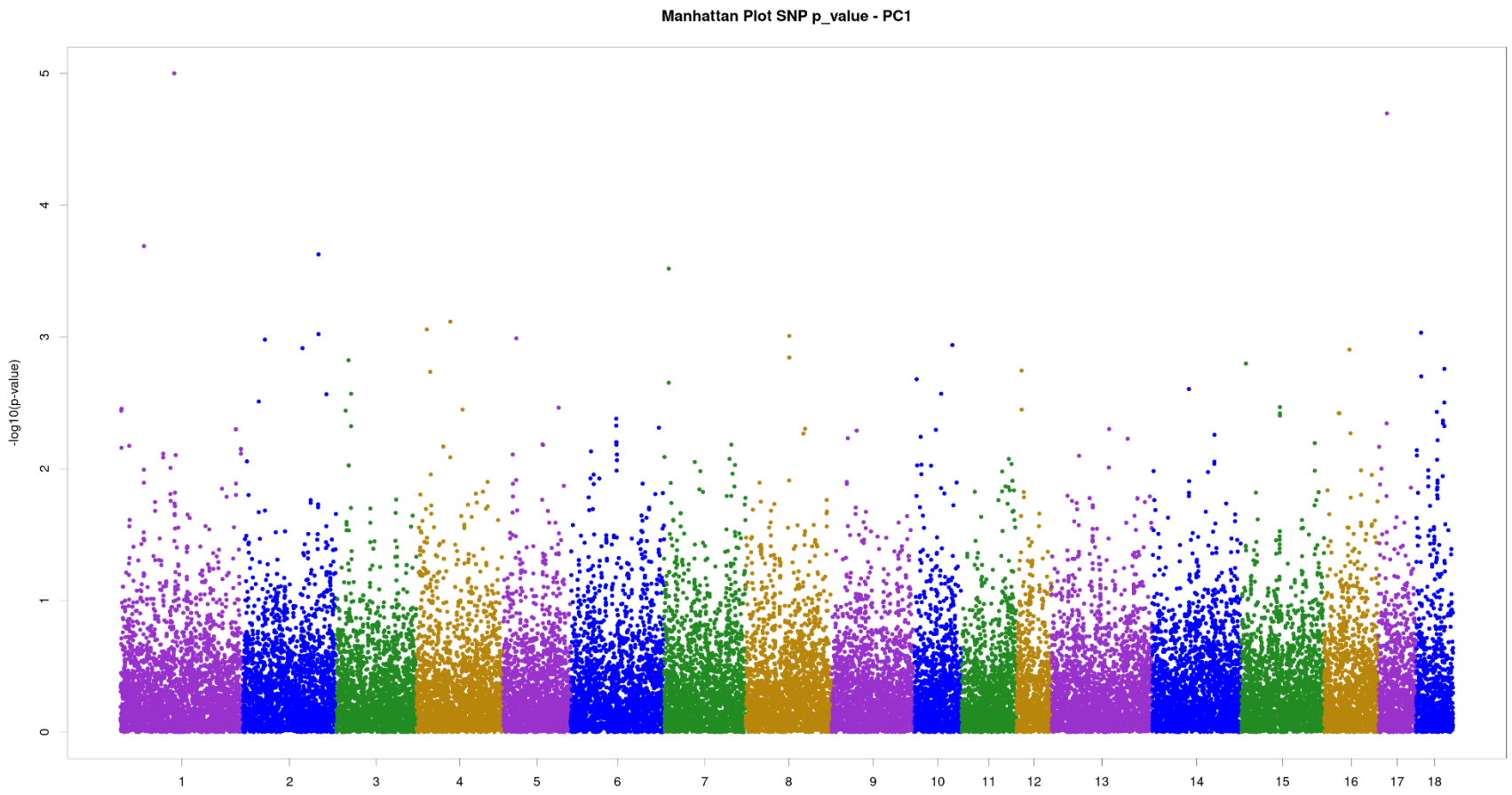

Figure 3.1. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 1 (PC1).

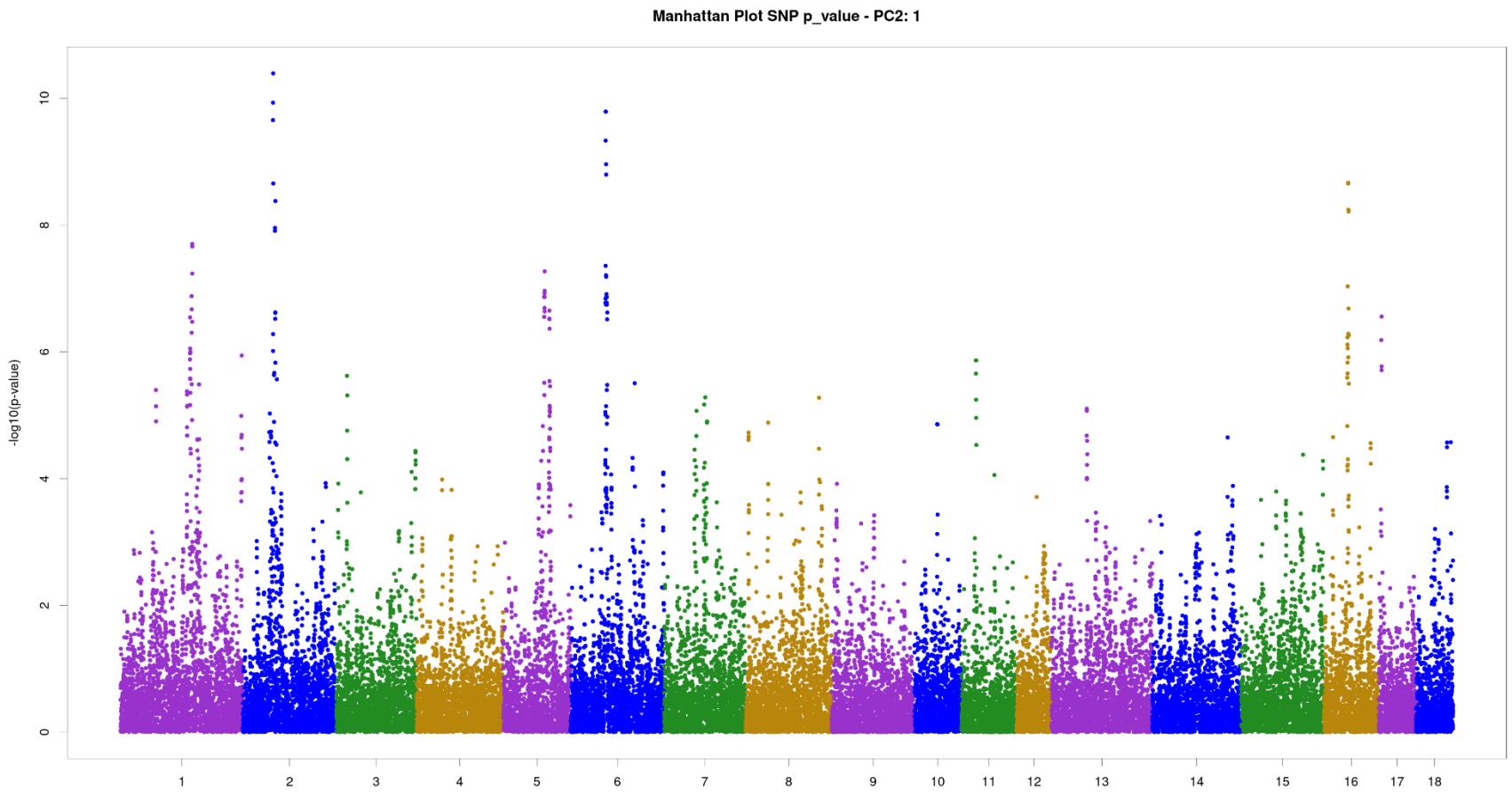

Figure 3.2. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 2 (PC2).

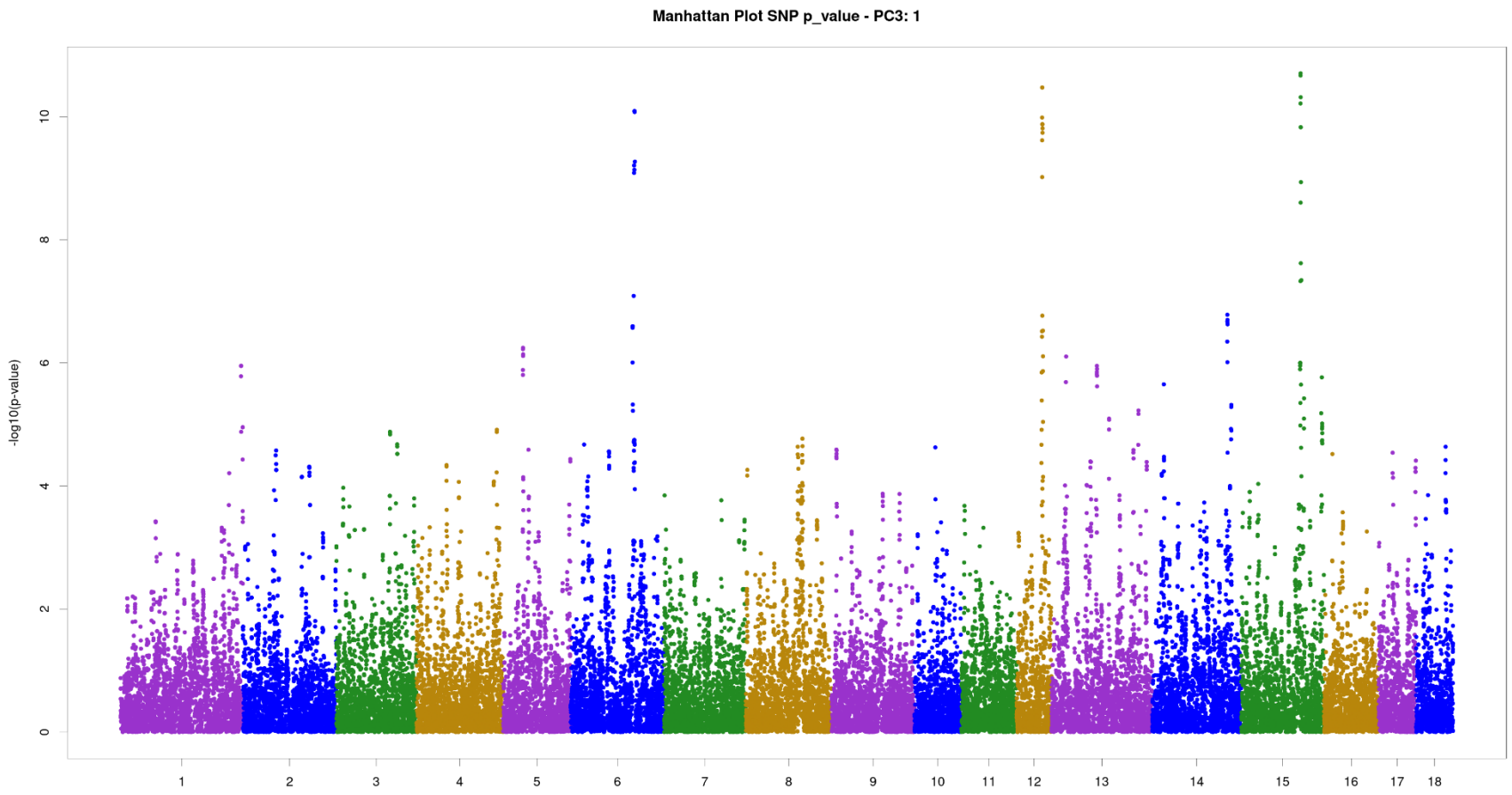

Figure 3.3. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 3 (PC3).

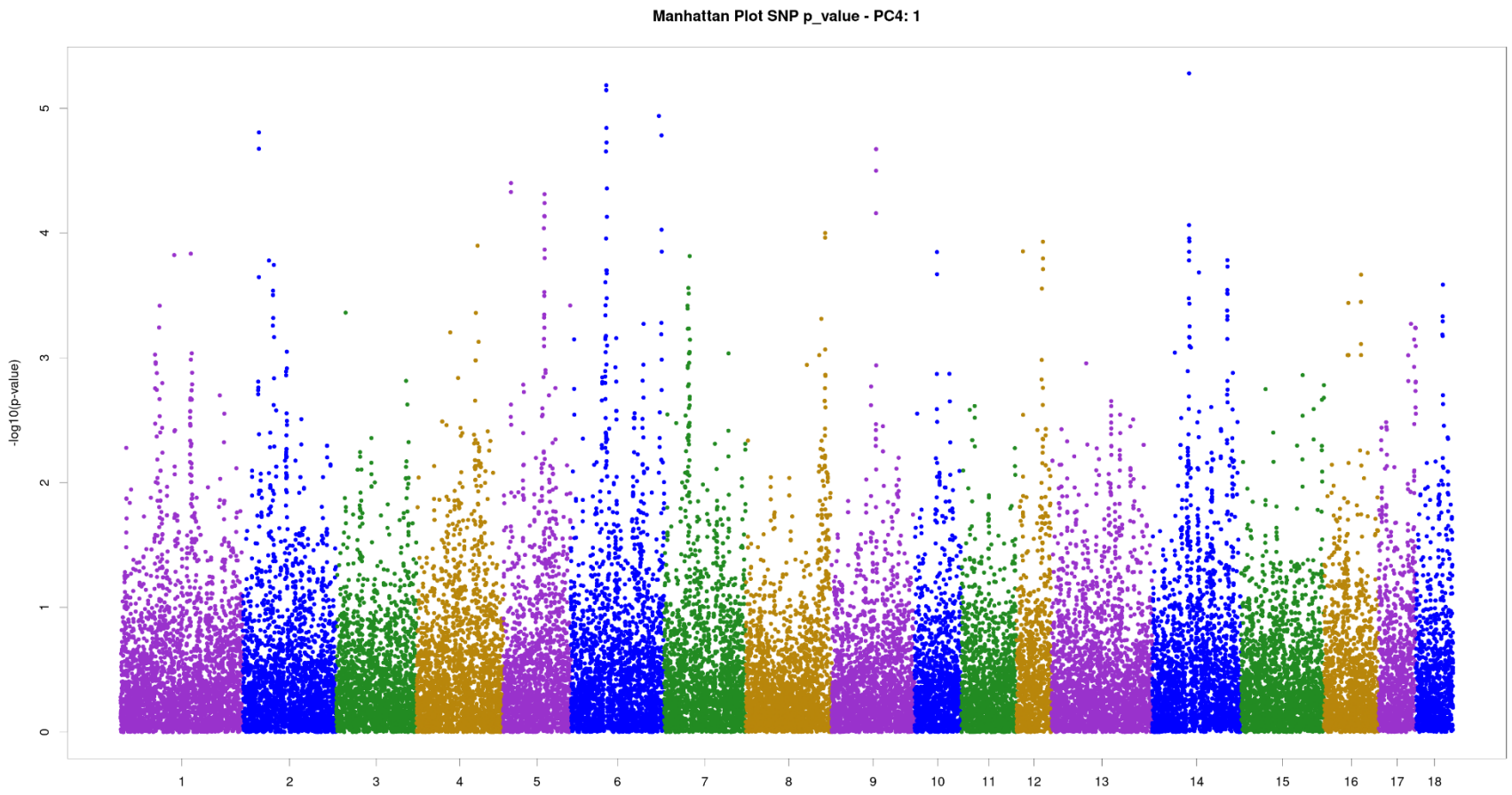

Figure 3.4. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 4 (PC4).

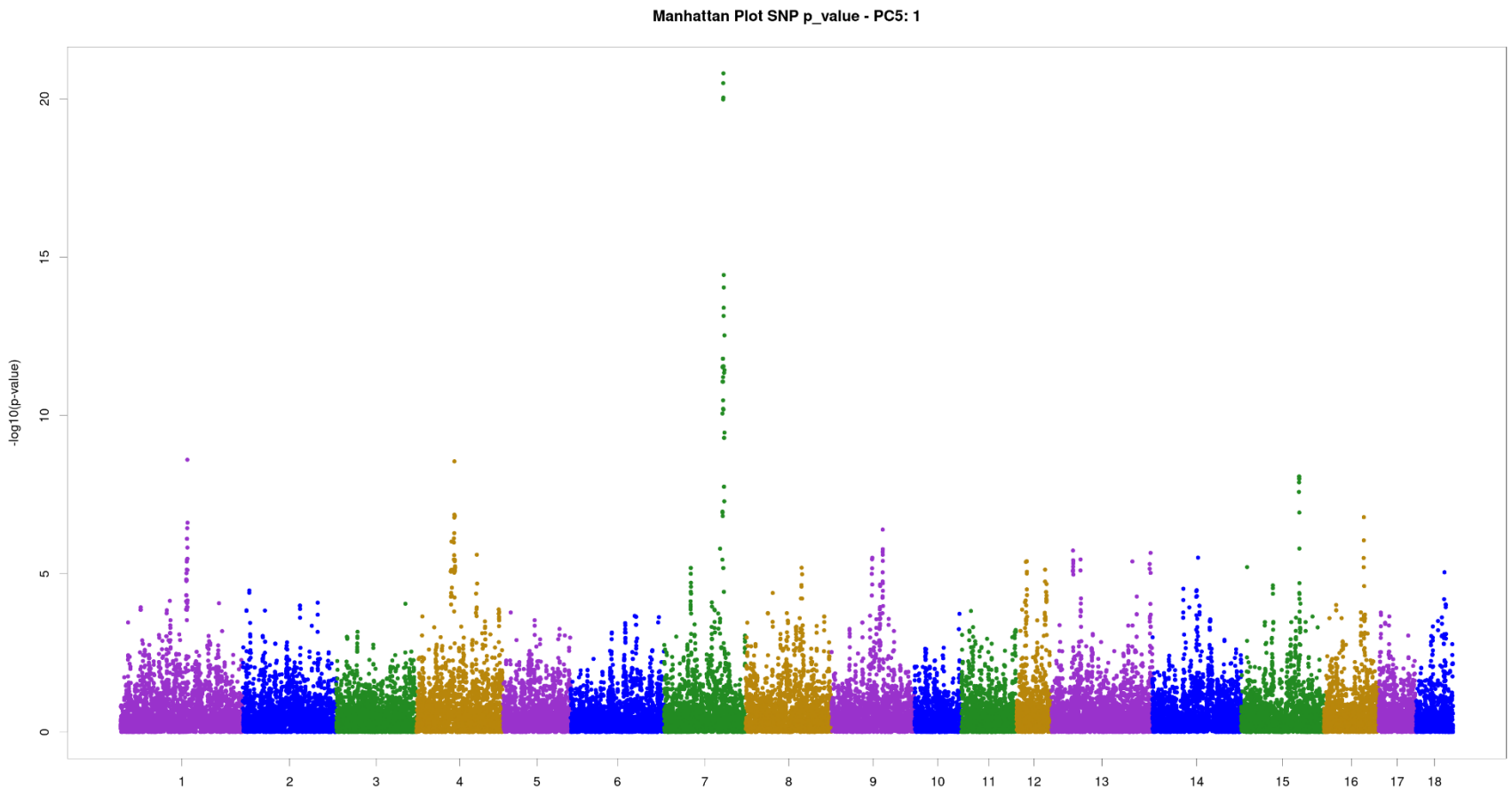

Figure 3.5. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 5 (PC5).

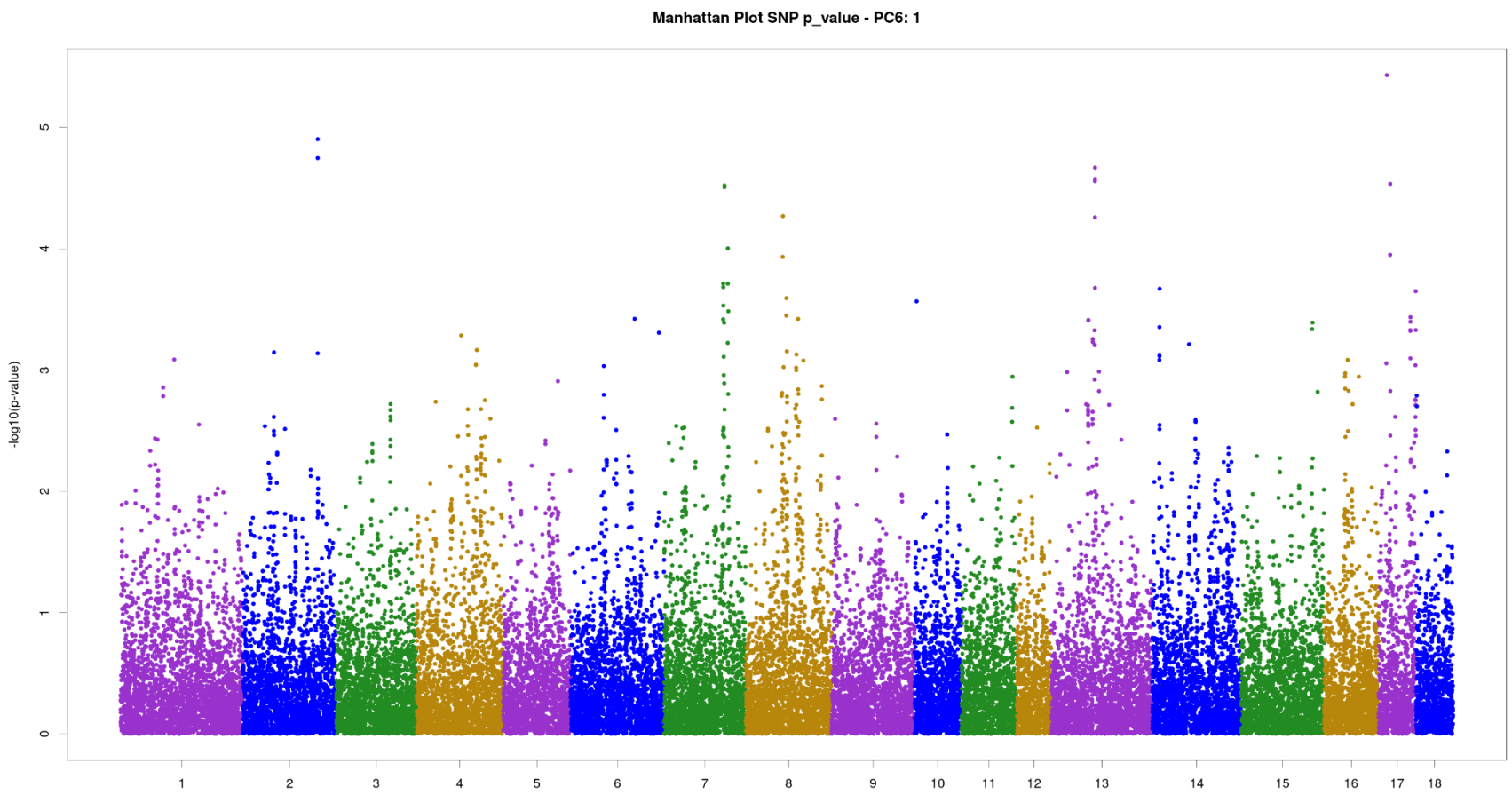

Figure 3.6. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 6 (PC6).

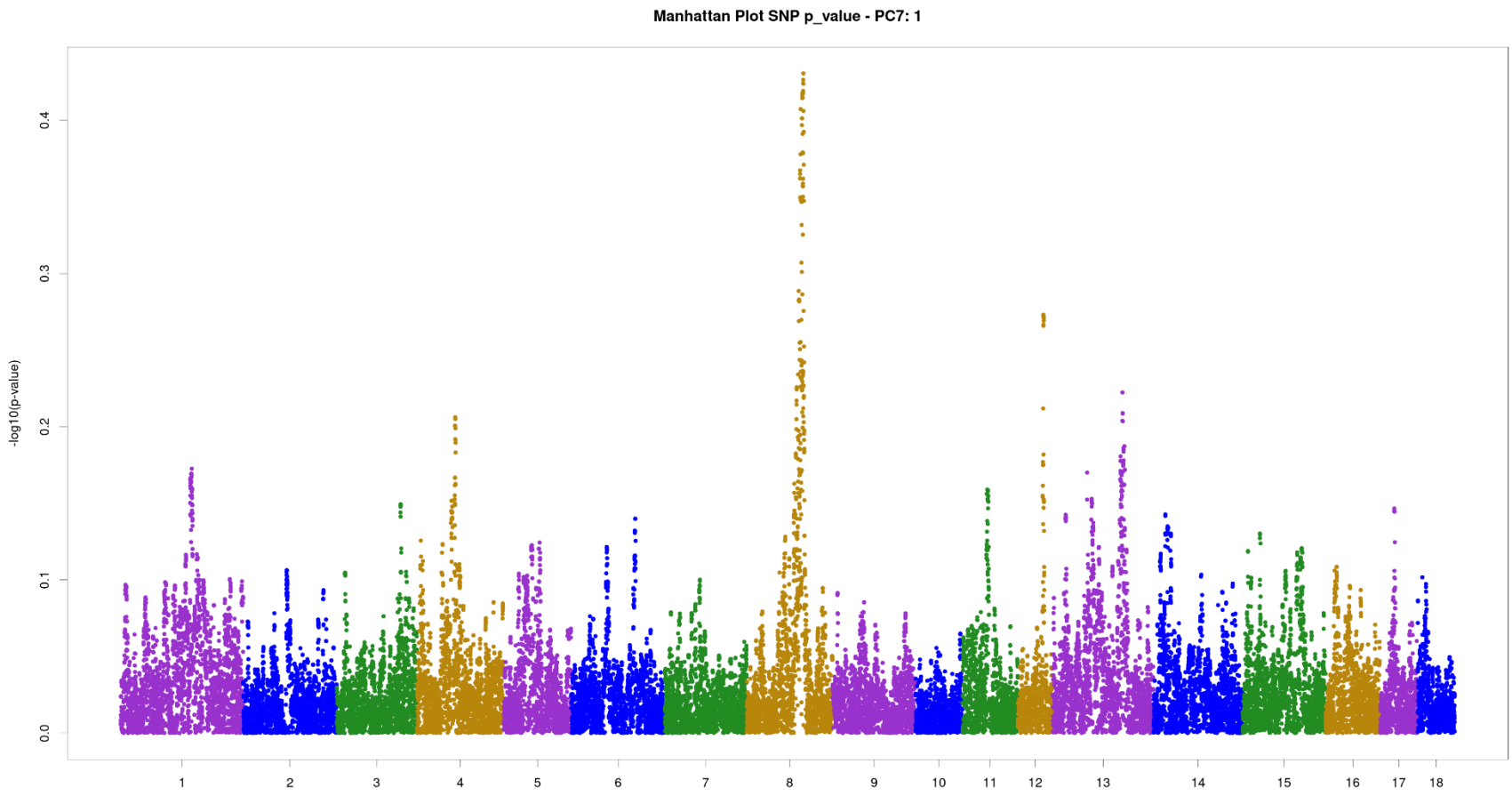

Figure 3.7. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 7 (PC7).

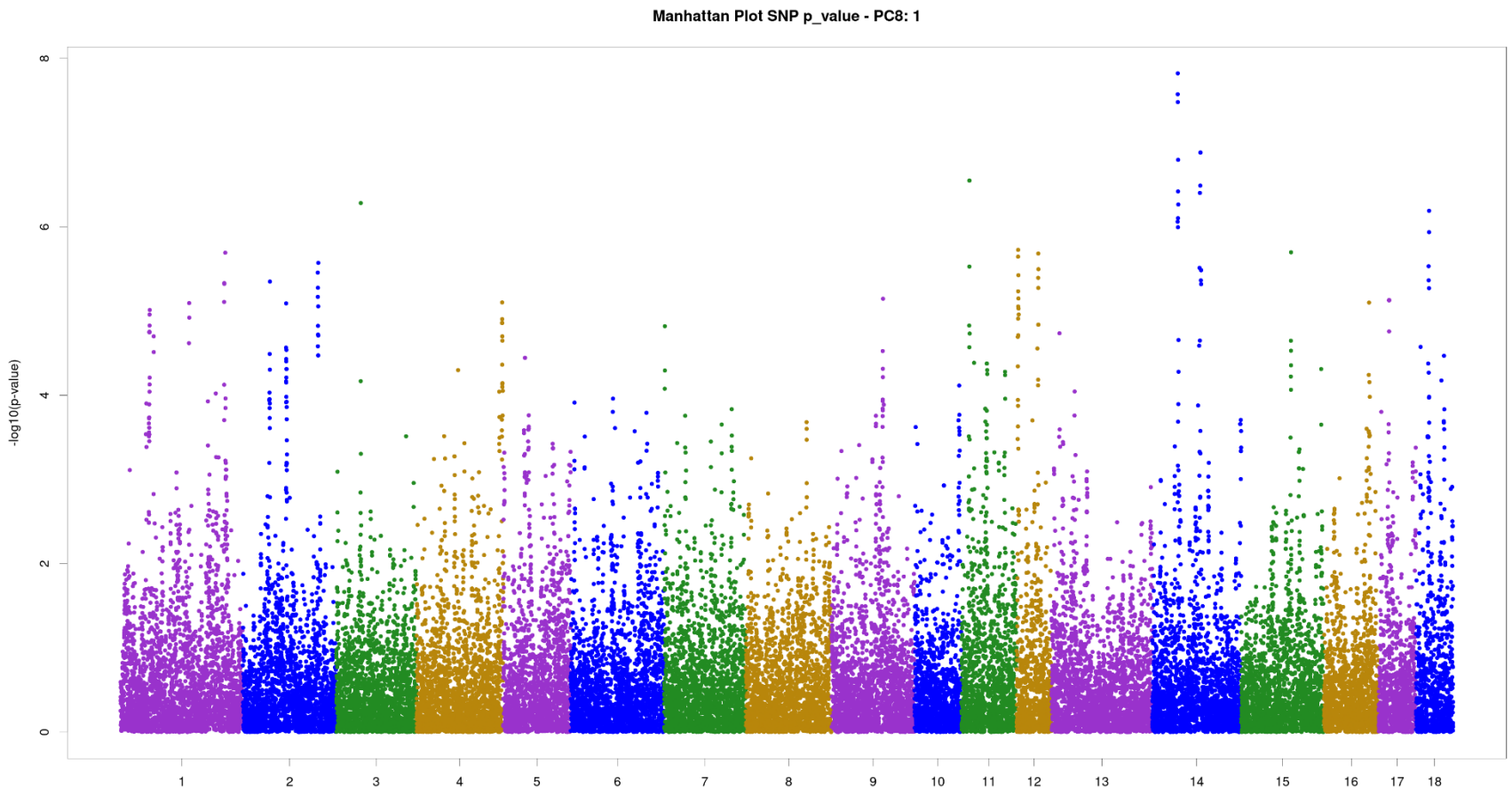

Figure 3.8. Manhattan plot of p-values for each single nucleotide polymorphisms (SNPs) for principal component 8 (PC8).

Table 3.6. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 1 (PC1) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
1	127,724,193	1.00E-05	*ZNF280D, LOC100621861*
17	13,254,721	2.02E-05	

Table 3.7. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 2 (PC2) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
1	53,023,914	4.01E-06	
1	53,359,712	7.23E-06	
1	53,385,720	7.23E-06	
1	53,420,432	1.25E-05	
1	177,006,345	4.19E-06	
1	177,201,808	4.72E-06	
1	177,412,813	7.31E-06	
1	177,662,261	7.09E-06	*7SK*
1	189,388,692	1.31E-06	
1	189,552,361	1.06E-06	
1	189,558,732	2.86E-07	
1	189,595,354	6.90E-06	
1	189,896,026	2.63E-06	
1	190,244,449	8.87E-07	
1	190,278,915	1.86E-06	
1	190,422,856	2.69E-06	
1	190,469,312	4.42E-06	
1	190,614,150	1.01E-06	*U6*
1	190,897,093	1.01E-06	
1	194,987,488	1.32E-07	*snoU13, FAM179B*
1	195,015,099	1.32E-07	
1	195,182,279	5.00E-07	*PRPF39, SNORD127*
1	195,434,873	2.14E-07	
1	195,518,093	3.24E-06	
1	196,589,225	1.19E-05	
1	196,630,945	3.36E-07	
1	196,657,090	1.98E-08	
1	196,704,846	2.17E-08	
1	196,836,959	5.84E-08	
1	220,102,612	3.26E-06	
1	220,139,546	3.26E-06	

Table 3.7 continued

Chromosome	Position (bp)	p-value	Positional genes
1	311,027,658	1.03E-05	*TARSL2*
1	311,418,877	1.14E-06	
2	37,665,702	1.85E-05	
2	39,135,539	9.39E-06	
2	41,455,130	1.81E-05	
2	43,939,277	2.21E-10	*LDHA, HPS5*
2	43,971,719	2.21E-10	*HPS5*
2	44,080,004	1.17E-10	*SAAL1*
2	44,112,723	9.69E-07	*TPH1*
2	44,381,318	5.26E-07	*SERGEF*
2	44,483,806	4.03E-11	
2	44,625,308	2.20E-09	*USH1C*
2	45,737,986	2.33E-06	
2	45,910,764	1.27E-05	
2	46,154,413	2.14E-06	
2	47,473,825	1.23E-08	*U6*
2	47,485,301	1.11E-08	*U6*
2	48,125,078	3.01E-07	
2	48,203,263	2.43E-07	
2	48,332,744	2.39E-07	
2	48,461,410	1.49E-06	
2	48,612,084	4.17E-09	
2	51,244,889	2.71E-06	
3	11,948,584	2.39E-06	
3	12,041,491	1.75E-05	
3	12,121,767	4.87E-06	
5	68,910,635	1.49E-05	
5	71,774,499	2.80E-07	
5	71,796,853	1.34E-07	
5	71,889,421	3.08E-06	
5	72,044,251	4.82E-06	*CECR2, BCL2L13*
5	72,230,141	1.37E-07	
5	72,245,513	1.37E-07	
5	72,352,991	2.03E-07	
5	72,400,948	1.19E-07	
5	72,424,166	1.09E-07	
5	72,474,945	2.31E-07	
5	72,500,090	5.37E-08	*USP18*
5	79,322,855	2.25E-05	
5	79,353,130	2.40E-05	
5	79,469,764	3.01E-07	
5	79,493,111	3.01E-07	
5	79,574,309	2.24E-07	*ARID2*

Table 3.7 continued

Chromosome	Position (bp)	p-value	Positional genes
5	79,634,609	1.03E-05	
5	79,682,793	3.04E-07	
5	79,714,980	3.04E-07	
5	79,848,149	2.89E-06	
5	79,893,040	4.32E-07	
5	79,977,136	7.11E-06	
5	80,036,469	8.35E-06	
5	80,247,257	7.53E-06	
5	80,284,434	8.97E-06	
5	80,318,867	3.49E-06	
5	80,358,518	1.63E-05	
6	53,001,243	8.92E-06	*PRKCG, CACNG7, CACNG8*
6	53,668,870	1.68E-07	*NCR1*
6	53,802,649	1.45E-07	*PigE-173F2.4*
6	53,966,129	9.88E-06	*PigE-108A11.5, PigE-108A11.3, KIR2DL1, FCAR*
6	54,194,696	4.39E-08	
6	54,277,959	4.64E-10	*PTPRH, SYT5, TNNI3, TNNT1, PPP1R12C*
6	54,529,501	1.62E-10	*ISOC2*
6	54,630,380	1.62E-10	
6	55,261,304	1.79E-07	
6	55,576,768	6.19E-08	*NLRP5*
6	55,727,201	1.10E-09	
6	55,867,767	7.21E-06	*ZNF667*
6	55,956,683	1.60E-09	*ZNF582*
6	56,131,941	6.54E-08	
6	56,719,535	1.37E-07	*ZNF134*
6	56,879,701	1.23E-07	*ZSCAN4*
6	57,167,528	1.37E-07	
6	57,292,829	1.37E-07	
6	57,423,143	1.37E-07	*SNORA19*
6	57,496,711	1.67E-07	
6	57,741,392	1.81E-07	*RPS5, ZNF584*
6	57,809,637	4.00E-06	
6	57,849,875	1.36E-05	
6	58,206,514	3.07E-07	*7SK*
6	58,241,766	3.32E-06	*TMEM88B*
6	58,424,941	1.06E-05	
6	58,514,948	2.40E-07	*TMEM52*
6	118,286,246	3.13E-06	
7	46,369,439	2.13E-05	*RUNX2*
7	46,550,649	8.53E-06	
7	56,866,248	6.80E-06	

Table 3.7 continued

Chromosome	Position (bp)	p-value	Positional genes
7	60,615,114	5.22E-06	*GDPGP1, SEC23A*
7	65,683,817	1.31E-05	*GDPGP1, SEC23A*
7	65,712,373	1.26E-05	*SEC23A*
8	3,028,065	1.88E-05	
8	21,987,255	1.31E-05	
8	136,942,252	5.32E-06	
10	36,609,671	1.38E-05	*C9orf24, KIF24*
10	37,326,100	1.40E-05	*NOL6, AQP3*
11	20,434,828	2.20E-06	
11	20,455,635	1.36E-06	
11	20,476,314	1.36E-06	
11	20,567,616	5.69E-06	
11	20,589,875	1.10E-05	
11	20,717,628	2.95E-05	
13	45,672,671	7.88E-06	
13	45,682,967	8.55E-06	
16	14,090,875	2.22E-05	
16	35,378,050	2.56E-06	
16	35,473,650	1.48E-05	
16	35,521,313	7.67E-07	
16	35,539,595	5.91E-07	
16	35,614,082	2.19E-06	
16	35,661,077	1.48E-06	
16	35,775,083	9.26E-08	*HSPB3*
16	35,829,257	8.80E-07	
16	36,455,971	2.15E-09	
16	36,472,679	2.20E-09	*CCNO*
16	36,506,690	1.22E-06	*GPX8*
16	36,540,209	5.18E-07	*SKIV2L2*
16	36,653,844	5.71E-09	*SKIV2L2*
16	36,835,185	2.07E-07	
16	36,933,143	6.11E-09	
16	37,584,102	5.40E-07	
16	37,608,638	3.18E-06	
16	77,593,861	2.76E-05	
16	77,611,594	3.33E-05	
17	3,989,769	6.53E-07	*SNORA40*
17	4,396,914	2.77E-07	
17	4,468,083	1.95E-06	
17	4,491,131	1.70E-06	
18	52,153,781	3.20E-05	
18	52,154,666	2.70E-05	
18	58,317,336	2.67E-05	

Table 3.8. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 3 (PC3) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
1	310,650,145	1.65E-06	
1	310,695,569	1.12E-06	
1	310,738,813	1.12E-06	
1	310,757,789	1.12E-06	
1	310,816,401	1.32E-05	
1	314,983,259	1.11E-05	
1	315,159,384	1.11E-05	
3	110,714,214	1.32E-05	
3	110,748,277	1.35E-05	
3	110,785,943	1.46E-05	
3	119,766,912	2.11E-05	*HADHA*
3	119,779,851	2.29E-05	*HADHA*
4	134,053,124	1.33E-05	*ALG14*
4	134,108,119	1.22E-05	*ALG14*
5	18,937,830	1.30E-06	*PFDN5, C12orf10, SPRYD3*
5	18,962,460	1.57E-06	*PFDN5, C12orf10*
5	18,992,892	5.97E-07	*PFDN5, C12orf10, ESPL1*
5	19,053,403	5.70E-07	*SP1, AMHR2, PRR13*
5	19,089,049	5.70E-07	*SP1, AMHR2, PRR13*
5	19,089,049	5.70E-07	*U6*
5	19,151,113	7.71E-07	*PRR13, PCBP2, U6*
5	19,207,741	7.26E-07	*TARBP2*
5	34,176,673	2.58E-05	
6	113,231,677	9.86E-07	*FHOD3*
6	113,353,240	2.69E-07	
6	113,414,724	2.54E-07	
6	113,488,317	2.54E-07	
6	113,590,864	2.54E-07	*KIAA1328*
6	113,680,401	4.76E-06	*KIAA1328*
6	113,818,056	6.01E-06	
6	116,602,688	8.15E-08	
6	116,675,908	1.93E-05	
6	116,724,062	1.93E-05	
6	116,768,032	1.93E-05	
6	116,830,227	1.93E-05	
6	116,861,357	1.93E-05	
6	116,969,069	1.93E-05	
6	117,268,481	1.84E-05	
6	117,341,966	8.17E-10	
6	117,461,675	6.18E-10	
6	117,546,718	1.93E-05	

Table 3.8 continued

Chromosome	Position (bp)	p-value	Positional genes
6	117,673,658	1.98E-05	
6	117,787,421	1.79E-05	
6	117,800,422	1.79E-05	
6	117,892,357	7.28E-10	
6	118,009,798	8.09E-11	*PIK3C3*
6	118,036,589	8.09E-11	*PIK3C3*
6	118,181,406	8.37E-11	
6	118,862,387	5.37E-10	
8	106,615,641	1.70E-05	
8	106,661,347	1.70E-05	
10	32,138,866	2.36E-05	
12	46,804,217	4.23E-05	
12	46,855,900	2.14E-05	
12	47,211,746	1.22E-05	*FLOT2, ssc-mir-451, U6, TIAF1*
12	47,262,207	1.43E-06	*TIAF1*
12	47,352,945	4.08E-06	
12	47,709,979	3.76E-07	*TAOK1, TP53I13*
12	47,799,622	3.06E-07	*SSH2*
12	47,809,068	3.06E-07	*SSH2*
12	47,862,623	1.03E-10	
12	47,873,596	2.42E-10	
12	47,931,054	9.57E-10	
12	48,040,569	3.35E-11	
12	48,060,726	3.35E-11	
12	48,107,944	1.33E-10	
12	48,121,999	1.71E-07	
12	48,272,702	1.33E-10	
12	48,297,863	1.33E-10	
12	48,416,845	1.82E-10	
12	48,475,167	1.55E-10	
12	48,968,569	1.36E-06	
12	49,048,547	2.99E-07	
12	49,202,373	7.81E-07	*NXN, GLOD4*
12	49,247,551	9.09E-06	*NXN, GLOD4*
13	13,063,614	2.05E-06	
13	13,172,438	7.87E-07	
13	72,895,609	1.52E-06	*SETD5, LHFPL4*
13	73,023,057	1.41E-06	*LHFPL4, MTMR14, TADA3*
13	73,058,596	1.12E-06	*CAMK1*
13	73,107,395	1.61E-06	
13	73,121,216	1.61E-06	*ARPC4*
13	73,139,546	1.26E-06	*ARPC4*
13	73,179,575	2.41E-06	*ARPC4*

Table 3.8 continued

Chromosome	Position (bp)	p-value	Positional genes
13	118,575,955	1.21E-05	
13	118,601,930	8.07E-06	*U6*
13	118,712,827	8.39E-06	
13	205,099,656	6.75E-06	
13	205,111,625	5.93E-06	
14	13,189,517	2.23E-06	
14	140,112,366	4.51E-07	
14	140,146,239	2.11E-07	
14	140,163,299	1.65E-07	
14	140,217,030	9.75E-07	
14	140,228,777	2.26E-07	
14	140,245,302	2.00E-07	
14	140,351,512	2.36E-07	
14	142,638,165	1.18E-05	
14	142,686,795	1.75E-05	
14	142,779,125	5.20E-06	
14	142,815,394	4.82E-06	
14	142,848,082	4.96E-06	
14	142,874,271	1.25E-05	
15	133,232,635	1.27E-06	*RUFY4*
15	133,251,066	1.11E-06	*RUFY4*
15	133,269,167	1.00E-06	*RUFY4*
15	133,287,223	1.00E-06	*RUFY4*
15	133,321,393	1.00E-06	*SNORA42*
15	133,342,361	1.00E-06	*SNORA42*
15	133,369,010	1.04E-05	*SNORA42*
15	133,427,999	1.01E-06	*SNORA42*
15	133,441,683	4.47E-06	*SNORA42*
15	133,465,593	4.69E-08	*VIL1*
15	133,730,356	6.08E-11	
15	133,738,342	2.14E-11	
15	133,810,036	1.97E-11	*PRKAG3*
15	133,929,898	2.49E-09	
15	133,988,527	4.82E-11	
15	134,006,803	1.48E-10	
15	134,006,845	1.48E-10	
15	134,033,273	2.40E-08	
15	134,172,205	1.15E-09	
15	134,216,979	2.26E-06	*FAM134A*
15	134,661,069	4.53E-08	
15	136,569,986	1.16E-05	
15	136,590,429	8.06E-06	
15	136,652,953	3.77E-06	

Table 3.8 continued

Chromosome	Position (bp)	p-value	Positional genes
15	153,573,791	6.58E-06	
15	154,470,711	1.72E-06	*ANKMY1*
15	154,557,138	1.87E-05	*ANKMY1*
15	154,768,168	1.17E-05	*44076*
15	154,922,054	9.66E-06	
15	154,940,255	1.08E-05	*SNED1*
15	155,061,138	1.81E-05	*PPP1R7*
15	155,104,199	1.39E-05	
15	155,121,123	2.04E-05	
16	12,569,621	3.03E-05	
17	25,366,971	2.89E-05	
17	68,820,284	3.87E-05	
18	50,072,344	3.79E-05	*HOXA11, ssc-mir-196b-1, HOXA7, HOXA6, HOXA5*
18	50,123,715	2.30E-05	*HOXA4, HOXA3, HOXA2, HOXA1*

Table 3.9. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 4 (PC4) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
2	18,722,196	1.56E-05	
6	56,570,180	7.17E-06	
6	56,600,329	6.56E-06	
6	56,654,232	7.17E-06	
6	56,833,928	1.44E-05	
6	57,001,823	1.88E-05	*SNORA70*
6	150,117,288	1.15E-05	
6	152,731,890	1.65E-05	*POMGMT1*
9	68,691,015	2.13E-05	
9	68,778,125	2.13E-05	
14	51,732,537	5.25E-06	*DEPDC5, U6*

Table 3.10. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 5 (PC5) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
1	173,741,598	1.51E-05	
1	174,298,531	9.60E-06	
1	176,159,526	7.37E-06	
1	176,231,881	4.11E-06	
1	176,700,629	3.59E-06	
1	177,046,933	7.84E-07	
1	177,123,870	7.84E-07	
1	177,534,097	3.62E-07	
1	178,024,855	2.50E-09	
1	178,188,861	1.49E-06	
1	179,002,367	3.36E-06	*CCBE1*
1	179,053,686	7.60E-06	*CCBE1*
1	179,327,620	2.44E-07	
4	49,752,068	8.42E-06	
4	49,917,991	8.42E-06	
4	50,507,516	8.42E-06	
4	50,530,735	8.42E-06	
4	50,611,693	8.42E-06	
4	51,225,096	7.53E-06	*CALB1*
4	51,237,941	7.53E-06	*CALB1*
4	51,268,855	7.53E-06	
4	51,298,876	9.56E-07	
4	51,556,918	7.53E-06	
4	51,815,961	7.53E-06	*5S_rRNA*
4	61,282,546	3.55E-06	*ZBTB10*
4	61,401,615	1.03E-06	
4	61,457,845	7.61E-07	
4	62,044,724	2.59E-06	
4	62,079,318	9.20E-06	*HEY1*
4	62,131,797	5.20E-07	*HEY1, U6*
4	62,177,861	1.67E-07	
4	62,303,926	1.36E-07	
4	62,391,576	2.82E-09	
4	62,557,898	6.99E-06	
4	62,599,388	6.99E-06	
4	62,835,433	3.60E-06	
4	62,885,525	3.99E-06	*IL7*
4	62,925,054	1.50E-07	*IL7*
4	62,943,196	1.50E-07	*IL7*
4	63,054,580	3.67E-06	
4	63,221,227	8.32E-06	
4	63,290,072	7.76E-06	*U6*

Table 3.10 continued

Chromosome	Position (bp)	p-value	Positional genes
4	63,316,010	6.42E-06	*U6*
4	63,328,211	6.42E-06	*U6*
4	63,362,857	5.79E-06	
4	63,491,767	6.40E-06	
4	110,606,323	2.50E-06	
4	111,494,301	2.04E-05	*ZNF697*
7	35,880,196	6.52E-06	
7	35,935,629	9.97E-06	
7	36,004,578	6.52E-06	
7	36,202,231	1.92E-05	
7	99,021,825	1.61E-06	
7	101,863,838	3.58E-06	
7	101,915,921	8.67E-11	
7	101,941,152	1.09E-07	
7	102,013,846	1.16E-07	
7	102,041,850	8.55E-12	
7	102,065,903	1.14E-07	
7	102,121,878	2.99E-12	
7	102,142,510	2.99E-12	
7	102,344,072	2.86E-12	*PSEN1*
7	102,377,016	1.50E-07	*PSEN1*
7	102,538,447	1.61E-12	
7	102,588,283	1.61E-12	
7	102,593,598	1.61E-12	
7	102,864,333	8.57E-12	
7	102,881,143	6.15E-12	
7	103,148,794	3.32E-11	*BBOF1*
7	103,182,352	6.13E-11	*LIN52*
7	103,232,787	1.05E-20	*LIN52*
7	103,241,824	3.20E-21	*LIN52*
7	103,288,546	6.57E-06	
7	103,328,224	6.57E-06	
7	103,411,844	9.16E-21	*VSX2, VRTN*
7	103,460,706	1.56E-21	*VRTN*
7	103,495,170	6.51E-11	*VRTN*
7	103,574,383	2.79E-12	*ISCA2*
7	103,594,753	2.79E-12	*ISCA2*
7	103,715,448	7.16E-14	
7	103,866,076	3.96E-14	
7	103,910,821	3.65E-15	*DLST*
7	103,933,199	9.05E-15	*DLST*
7	104,313,655	1.79E-08	*FOS*
7	104,327,946	1.76E-08	*FOS*

Table 3.10 continued

Chromosome	Position (bp)	p-value	Positional genes
7	104,416,561	5.09E-10	*FLVCR2*
7	104,420,693	5.09E-10	*FLVCR2*
7	104,470,681	4.47E-12	*FLVCR2*
7	104,576,288	5.14E-08	
7	104,807,152	2.95E-13	*7SK*
7	105,130,451	3.69E-12	*TTLL5*
7	105,182,819	3.47E-10	*TTLL5*
8	104,388,741	6.43E-06	
8	105,991,646	1.03E-05	
9	56,060,274	1.01E-05	*TMEM225, U3, OR4D5*
9	57,173,925	3.47E-06	
9	57,362,823	6.72E-06	
9	57,579,479	2.18E-05	*ROBO3*
9	57,814,665	3.12E-06	*SLC37A2*
9	96,414,274	2.19E-05	
9	96,447,542	2.19E-05	
9	111,186,377	2.03E-06	
9	111,235,830	9.00E-06	
9	111,310,406	1.74E-05	
9	111,322,763	4.03E-07	
9	111,345,607	2.50E-06	
9	111,398,156	1.68E-06	
9	111,425,368	1.68E-06	
9	111,488,497	3.92E-06	
9	111,563,850	1.98E-05	
12	15,320,259	4.21E-06	
12	18,228,133	4.07E-06	*PLEKHM1, ARHGAP27*
12	18,305,409	4.00E-06	*ARHGAP27*
12	18,398,838	9.82E-06	*MAP3K14, SPATA32*
12	18,451,814	3.11E-05	*SPATA32*
12	18,499,751	8.63E-06	*PLCD3*
12	18,667,503	4.70E-05	*C1QL1, KIF18B, GFAP*
12	53,288,290	1.75E-05	
12	53,322,741	7.38E-06	
12	55,135,676	3.76E-05	
12	55,166,260	3.76E-05	
12	55,575,876	2.10E-05	
12	55,602,201	4.86E-05	
13	20,788,585	8.26E-06	*UBP1*
13	20,852,831	8.26E-06	*UBP1*
13	20,956,491	1.84E-06	
13	21,030,064	7.63E-06	
13	21,100,364	5.95E-06	

Table 3.10 continued

Chromosome	Position (bp)	p-value	Positional genes
13	21,140,885	3.74E-06	
13	21,287,606	4.70E-06	*PDCD6IP*
13	21,397,590	3.94E-06	
13	21,493,849	1.06E-05	
13	29,349,306	7.84E-06	*SNRK*
13	29,385,584	3.52E-06	*SNRK*
13	198,960,675	4.07E-06	
13	216,267,790	6.93E-06	
13	216,277,671	4.89E-06	
13	216,986,355	2.18E-06	*AIRE*
13	216,993,686	9.38E-06	*AIRE*
14	69,813,273	3.09E-06	
15	5,856,540	6.14E-06	
15	132,271,433	2.60E-08	
15	132,382,690	1.30E-08	
15	132,411,519	8.48E-09	
15	132,418,651	8.48E-09	
15	132,520,074	9.99E-09	
15	132,542,374	9.99E-09	
15	132,590,789	1.16E-07	
15	132,641,501	1.60E-06	
15	132,703,653	1.97E-05	
16	70,175,862	3.17E-06	
16	70,212,915	6.19E-06	
16	70,319,503	8.79E-07	
16	70,369,347	1.63E-07	
16	70,578,692	2.44E-05	
18	47,853,852	8.96E-06	

Table 3.11. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 6 (PC6) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
2	141,366,250	1.79E-05	
2	141,401,458	1.25E-05	
17	13,254,721	3.71E-06	
17	19,978,814	2.93E-05	

Table 3.12. Significant single nucleotide polymorphisms (SNPs) and related genes for principal component 8 (PC8) in Duroc pigs.

Chromosome	Position (bp)	p-value	Positional genes
1	32,130,380	1.10E-05	*AHI1*
1	32,166,894	1.49E-05	*AHI1*
1	32,337,588	9.74E-06	
1	184,917,301	8.07E-06	*GLCE*
1	185,093,424	1.20E-05	
1	287,718,489	7.81E-06	
1	287,858,838	4.67E-06	*PAPPA*
1	287,886,926	4.77E-06	*PAPPA*
1	288,840,564	2.04E-06	
2	39,465,141	4.48E-06	
2	92,524,243	8.13E-06	
2	141,417,043	3.50E-06	
2	141,434,133	6.80E-06	
2	141,554,977	5.30E-06	
2	141,569,133	1.50E-05	
2	141,584,719	1.91E-05	
2	141,675,357	8.82E-06	
2	141,680,215	1.96E-05	
2	141,696,144	2.68E-06	
3	30,187,510	5.23E-07	
4	141,823,043	1.39E-05	
4	142,201,639	7.92E-06	
4	142,242,525	1.25E-05	*ODF2L*
4	142,317,862	1.39E-05	*ODF2L*
4	142,384,587	2.00E-05	
7	1,336,203	1.52E-05	
9	111,817,735	7.16E-06	
11	10,974,888	1.49E-05	
11	11,084,336	2.70E-05	
11	11,119,332	2.97E-06	
11	11,150,563	2.83E-07	
11	11,175,837	2.83E-07	
11	11,542,003	1.85E-05	
12	1,673,966	2.03E-05	
12	1,699,203	4.55E-05	
12	1,998,701	2.27E-06	
12	2,081,249	1.23E-05	
12	2,097,504	1.88E-06	
12	2,149,118	5.84E-06	
12	2,202,804	8.85E-06	
12	2,240,535	1.94E-05	*EIF4A3*
12	2,553,605	3.76E-06	*TBC1D16*

Table 3.12 continued

Chromosome	Position (bp)	p-value	Positional genes
12	2,601,965	7.10E-06	*CBX4, CBX8*
12	2,707,026	9.35E-06	
12	2,922,849	1.10E-05	
12	40,271,308	2.79E-05	*U6*
12	41,251,526	4.04E-06	*CCL5, HEATR9*
12	41,344,517	2.08E-06	
12	41,369,481	5.33E-06	
12	41,406,009	1.46E-05	*PEX12*
12	41,445,302	1.45E-05	*PEX12*
12	41,521,930	3.19E-06	*NLE1, RAD51D*
13	9,181,945	1.84E-05	
14	33,278,520	8.72E-07	*CAMKK2*
14	33,341,083	2.67E-08	
14	33,452,528	1.51E-08	
14	33,673,401	3.31E-08	*ARPC3*
14	33,833,169	1.01E-06	*ARPC3, RAD9B*
14	33,939,592	7.91E-07	*TCTN1*
14	34,028,866	3.81E-07	
14	34,058,099	1.61E-07	*CCDC63*
14	34,321,513	5.45E-07	
14	73,042,114	3.08E-06	
14	73,695,090	3.97E-07	
14	74,648,813	3.25E-07	
14	74,953,294	1.32E-07	
14	74,990,114	1.32E-07	
14	75,479,251	4.33E-06	
14	75,632,971	3.28E-06	
14	75,856,377	4.80E-06	
14	75,927,172	3.28E-06	
15	108,978,696	2.26E-05	
15	109,450,090	2.01E-06	
16	76,174,540	7.95E-06	
17	17,981,232	7.48E-06	
17	18,040,810	1.75E-05	
17	18,057,468	7.48E-06	
17	18,106,530	7.41E-06	
18	5,991,322	2.67E-05	
18	17,576,116	4.21E-05	
18	18,396,728	2.94E-06	
18	18,464,906	4.33E-06	
18	18,843,195	5.36E-06	
18	18,867,886	1.16E-06	
18	18,911,413	6.47E-07	
18	47,383,209	3.40E-05	*SCRN1*

Table 3.13. Quantitative trait loci (QTL) linked to significant single nucleotide polymorphisms (SNPs) for principal component 2 (PC2).

QTL Trait Description	Chromosome	Region (Mbp)	Gene
Average backfat thickness	2	23.0-27.7 40.8-40.8	*LDHA*
Average daily gain	2	40.8-40.8 23.0-27.7	*LDHA*
Backfat at last lumbar	2	23.0-27.7	*LDHA*
Backfat at rump	2	12.2-12.4	*LDHA*
Backfat at tenth rib	2	23.0-27.7	*LDHA*
Drip loss	2	23.0-27.7	*LDHA*
Feed conversion ratio	2	40.8-40.8	*LDHA*
Fiber type II myosin isoform ratio	2	23.0-27.7	*LDHA*
Ham weight	2	40.8-40.8	*LDHA*
Lean cuts weight	2	40.8-40.8	*LDHA*
Loin muscle area	2	23.7-27.7	*LDHA*
Marbling	2	23.0-27.7	*LDHA*

Table 3.14. Quantitative trait loci (QTL) linked to significant single nucleotide polymorphisms (SNPs) for principal component 3 (PC3).

QTL Trait Description	Chromosome	Region (Mbp)	Gene
Average backfat thickness	6	76.6-77.5	*PIK3C3*
Average daily gain	6	76.6-77.5	*PIK3C3*
Intramuscular fat content	6	76.6-77.5	*PIK3C3*
Loin muscle area	6	76.6-77.5	*PIK3C3*
Average glycogen	15	145.2-145.3	*PRKAG3*
Average glycolytic potential	15	120.9-120.9	*PRKAG3*
		120.9-120.9	
Average lactate	15	120.9-120.9	*PRKAG3*
		120.9-120.9	
Conductivity 24 hours postmortem (ham)	15	138.6-138.9	*PRKAG3*
Conductivity 24 hours postmortem (loin)	15	145.2-145.3	*PRKAG3*
Drip loss	15	145.2-145.3	*PRKAG3*
		145.2-145.3	
		145.2-145.3	
		145.2-145.3	
		134.4-134.4	
		145.2-145.3	
		120.9-120.9	
		145.2-145.3	
		145.2-145.3	
		120.9-120.9	
		120.9-120.9	
		145.2-145.3	
		145.2-145.3	
Intramuscular fat content	15	145.2-145.3	*PRKAG3*
		145.2-145.3	
		145.2-145.3	
Meat color L*	15	127.4-127.4	*PRKAG3*
		120.9-120.9	
		145.2-145.3	
		134.4-134.4	
Meat color a*	15	120.9-120.9	*PRKAG3*
		120.9-120.9	
		120.9-120.9	
		120.9-120.9	

Table 3.14 continued

QTL Trait Description	Chromosome	Region (Mbp)	Gene
Meat color b*	15	120.9-120.9 120.9-120.9 145.2-145.3 145.2-145.3 134.4-134.4	*PRKAG3*
Meat color score	15	120.9-120.9 127.4-127.4 120.9-120.9	*PRKAG3*
Muscle cathepsin B activity	15	133.8-133.8	*PRKAG3*
pH for *longissimus dorci*	15	120.9-120.9 120.9-120.9 126.8-126.8	*PRKAG3*
Residual glycogen	15	129.8-129.8 120.9-120.9 120.9-120.9	*PRKAG3*
pH 24 hr postmortem (ham)	15	145.2-145.3 145.2-145.3 120.9-120.9	*PRKAG3*
pH 24 hr postmortem (loin)	15	145.2-145.3 145.2-145.3 145.2-145.3 145.2-145.3 157.3-157.3	*PRKAG3*
pH 45 minutes postmortem	15	145.2-145.3 145.2-145.3 145.2-145.3 145.2-145.3 145.2-145.3	*PRKAG3*

Table 3.15. Quantitative trait loci (QTL) linked to significant single nucleotide polymorphisms (SNPs) for principal component 5 (PC5).

QTL Trait Description	Chromosome	Region (Mbp)	Gene
Carcass length	7	97.6-97.6	*VRTN*
		97.6-97.6	
		97.6-97.6	
Intramuscular fat content	7	97.6-97.6	
		122.5-122.6	*VRTN*
		122.5-122.6	*VRTN*
Loin muscle area	7	103.5-103.5	*VRTN*
Loin muscle depth	7	103.5-103.5	*VRTN*
Number of ribs	7	103.5-103.5	*VRTN*
Teat number	7	95.9-97.8	
		99.1-105.4	*VRTN*
		100.1-105.2	
Thoracic vertebra number	7	97.6-97.6	*VRTN*
Teat number	7	98.1-98.1	*DLST*

Table 3.16. Quantitative trait loci (QTL) linked to significant single nucleotide polymorphisms (SNPs) for principal component 8 (PC8).

QTL Trait Description	Chromosome	Region (Mbp)	Gene
Body depth	1	256.6-256.6	*PAPPA*
Fat androsterone level	1	191.9-193.7	*PAPPA*
Front feet conformation	1	256.6-256.6	*PAPPA*
Hind feet conformation	1	256.6-256.6	*PAPPA*
Rib shape	1	256.6-256.6	*PAPPA*
Body length	1	256.6-256.6	*PAPPA*

3.5 Discussion

3.5.1 Heritabilities

Several differences where observed when comparing the heritabilities estimated in the present study (shown in Tables 3.2 and 3.3) with the estimates presented in a previous study using only pedigree information [8] (Chapter 2). Growth traits (ADG, HCW, and LW) tended to have lower heritabilities and lower standard errors in this study when compared to the previous estimates. The additive genetic variance was lower in these traits, while both the common environmental variance and the environmental variance were higher, indicating that some genetic variance was lost.

Meat quality and conventional carcass traits followed a similar trend. Meat quality traits had seven heritability estimates that were lower (DLP, LJPC, L*, a*, b*, LNM, and LPHA) and three estimates that were higher (DL1, DL2, and LNC) than pedigree-based estimates, while conventional carcass traits had five lower estimates (DP, GBF, LA, LC, and RMD), two higher estimates (GI and GLD) and one unchanged estimate (LL). Additionally, all standard errors were lower for meat quality and conventional carcass traits (with the exception of GI, which had a higher SE), indicating more accurate heritability estimates overall. However, when comparing the variance components, meat quality traits tended to have a higher variance across the board, where conventional carcass traits tended to have lower additive genetic variance with higher common environment (DL) variance and environmental variance.

Novel carcass traits displayed the opposite trend, tending to have more traits with higher heritability estimates as compared to pedigree-based estimates. Overall, there were 11 traits with higher heritability estimates (BL, BLW, BRW, BWR, SW, TBLW, TPW, TW, UBLW, UHW, and ULW), six traits with lower estimates (BLFT, BW, SRW, TBW, UBW, and USW) and one estimate that was the same (THW). All standard errors for novel carcass traits were also lower than previous estimated. When comparing variance components, however, there are several differences. For the belly traits, additive genetic variance tended to be higher, while DL variance decreased, and environmental variance remained unchanged. For trimmed and untrimmed cuts, the environmental variance did not change much, but trimmed cuts tended to have lower additive genetic variance while untrimmed cuts had higher additive genetic variance and higher DL variance. The subprimal cuts had similar variance components estimated in both studies.

Heritabilities and variance components estimated with genomic information have been shown to yield lower standard errors and lower heritabilities [9], due to the ability to better estimate the genomic effect on each trait. Lower standard errors are indicative of higher accuracy, which also makes genomic estimated variance components and heritabilities valuable when compared with only pedigree-based estimates.

All trait groups fell within reasonable range of the heritabilities reviewed in the previous study and previous findings in literature are described in further detail in Willson et al. [8].

3.5.2 Principal component analysis

PCA Scenarios One and Two Biotypes – Biological Background

Across the eight proposed biotypes for the first PCA and the six biotypes for the second PCA, there are several common themes. Firstly, the biotype of PC1 for both PCAs was primarily related to ADG, HCW, and LW. A biological and genetic connection has well been established between these traits in literature [28–30]. ADG has a direct relationship with the weight of the animal, as it is calculated based on the amount of weight gain an individual has experienced through the growing phase. Often, an animal with a higher ADG will also have a heavier body weight [28].

When comparing PC4 and PC6 from PCA1 with PC4 from PCA2, similar biotypes exist where animals are likely to be shorter bodied with more or less lean or fat. Similarly, PC5 and PC8 from PCA1 and PC2 and PC3 from PCA2 were related to longer bodied animals that tended to be leaner and have less fat. While this study did not include body conformation traits, the length of the belly and loin can be used to approximate the length of the body. A shorter belly and loin might indicate a shorter bodied animal, and vice versa for longer bodied animals. Otherwise, the relationship between fat and lean has been well documented previously in literature. Genetically, it has been shown that GBF and GLD have an inverse relationship [8,31,32], which is commonly used in swine breeding programs to influence the ratio of lean and fat on a pig carcass [2].

The third common biotype between the two PCA were related to PC7 from PCA1 and PCs 5 and 6 from PCA2. PC7 and PC5 from PCA1 and PCA2, respectively, shared the same biotype of darker lean color, while PC6 from PCA2 seemed to be related to lighter meat color. In the case of all of these traits, a moderate relationship with the Minolta color scales (L*, a*, and b*) was

found. These three color scores are commonly used in meat science to describe the color of pork, which is essential now that consumers are becoming more concerned with the color of their pork products. In a previous study with the same population of animals [8], L* was found to have a high and favorable genetic correlation with LNC, which gives strong predicting power for NPPC color from the L* value. Meat color was also favorably associated with LPHA and DLP, other meat quality traits of high interest, in the same study [8]. Ultimate pH is one of the primary drivers behind pork color, and it has been related to rate of protein denaturation and rate of water release, which result in differences in pork color [33]. When pH drops too low, protein denaturation increases, which releases more water from lean protein, creating a more reflective surface with a lighter color. Inversely, when pH is too high, the cut will release less water, thus absorbing more light and appearing darker in color [33,34]. The three commonly used acronyms for pork color are PSE (pale, soft, and exudative), DFD (dark, firm, and dry), and RFN (reddish-pink, firm, and non-exudative), each corresponding to more acidic, less acidic, and good acidity, respectively [35,34]. With three biotypes across two PCAs within this population related to the color of the loin, these biotypes could be used to increase not only color, but pH and DLP as well.

Across all of these results, the biotypes found by both PCA1 and PCA2 are generally favorable for exploration of these traits. Several biotypes affirmed the presence of well documented biological interactions between traits present in this population, which can be invaluable relationships when performing genetic selection.

3.5.3 Genome-wide association analysis

For the four PCs with candidate genes associated with QTLs, the results displayed in Tables 3.13 to 3.16 can be summarized into four categories: genes associated to muscle mass, growth, fat deposition, and meat quality. PCs 2, 5, and 8 have stronger associations to growth, muscle, backfat, and marbling, whereas PC3 was representative of all categories but has stronger ties to meat quality.

The QTLs detected by PC2 were previously associated with average backfat thickness and average daily gain [36,37], backfat at last lumbar, backfat at tenth rib, drip loss, fiber type II myosin isoform ratio, loin muscle area, marbling [36], backfat at rump [38], feed conversion ratio, ham weight, and lean cuts weight [37]. For PC3, the QTLs detected were previously associated with average backfat thickness, average daily gain, intramuscular fat content, and loin muscle area [39]

as well as meat quality traits like drip loss [40,41], meat color [40–42], pH [40,42–44], and glycolysis [41,44]. For PC5, the QTLs detected were previously associated with carcass and body length [45,46], teat number [47,48], marbling [49], and loin-eye area and depth [50]. For PC8, the QTLs detected were previously associated with conformation traits, such as body length, body depth, and front and hind feet conformation [51].

Candidate genes for PC2

The primary candidate gene related to QTLs for PC2 was lactate dehydrogenase A (*LDHA*). *LDHA*'s primary function is to catalyze the conversion of pyruvate into lactate during glycolysis when the body is subjected to periods of low oxygen, thus releasing energy. *LDHA* is also responsible for ensuring the balanced regulation of lactate in muscle cells [36]. Qui et al. [36] associated *LDHA* with GBF, ADG, DLP, LA, and LNM. Their results indicate the *LDHA* is highly expressed in the skeletal muscle, suggesting that it plays a crucial role in muscle development in a population of Berkshire x Yorkshire crossbreds. Fontanesi et al. [37] related *LDHA* to GBF, ADG, feed conversion ratio, ham weight, and lean cuts weight in a population of Italian Large White pigs, however the strongest association was made with ADG of all the traits studied. Similarly, Cepica et al. [38] associated this gene with backfat thickness at the rump. When comparing these findings with the results in the present study, the second PC's biotype supports this conclusion. PC2 had a biotype related to muscle and fat content, which corresponds to *LDHA's* biological effect upon muscle development. Overall, this indicates a population likely to have contrast between muscle and fat deposition. To the best of our knowledge, a Duroc population has yet to be linked to the *LDHA* gene, and additional candidate traits that may be linked are GLD, LC, and RMD.

Candidate genes for PC3

The third PC had two candidate genes reported to be related to QTLs. The first candidate gene was *PIK3C3* (phosphatidylinositol 3-kinase catalytic subunit type 3), a gene that is involved in receptor-mediated signal transduction and intracellular trafficking [39,52,53]. PI3-kinases (phosphatidylinositol 3-kinase) are known for their regulatory properties which are responsible for signals that control the growth of cells [54,55], but are also known to participate in glycogen

synthesis and transport as well as antilipolysis among other roles [53,56]. *PIK3C3* has been previously linked to ADG, LA, GBF, and intramuscular fat (IMF) content in a Duroc population [39,57], and Hirose et al. [39] found that the C/C genotype had higher ADG, GBF, and IMF but less LA.

The second candidate gene was *PRKAG3* (protein kinase, AMP-activated, gamma 3 non-catalytic subunit) which is primarily involved with glycogen levels in muscles and meat quality traits [58]. Previous studies have linked this gene with four missense mutations (one being the AMPK$\gamma 3^{R200Q}$ or RN^- mutation) that have resulted in excessive levels of glycogen in muscle tissue and low ultimate pH after slaughter [59], leading to low water holding capacity [58,60–62] which is dangerously close in nature to the Halothane (H+) mutation [63] that causes pale, soft, and exudative pork products. *PRKAG3* has been studied in Duroc [42,44], Erhualian [44], Large White [43], commercial crossbred [41] and Pietran [40] populations, and has been related to many meat quality traits in all of them. Ryan et al. [40] related *PRKAG3* to DLP, IMF, L*, b*, LPHA, and pH at 45 minutes postmortem in Pietrans, while Liu et al. [41] related this gene to glycolytic potential, lactate levels in the loin, DLP, L*, a*, b*, LJPC, LPHA, and residual glycogen. Additionally, Choi et al. [42] found a* and LPHA to be related as well. Two additional studies confirmed the relationship between *PRKAG3* and LPHA [43,44].

When comparing these two genes to the results of the PCA, there are only two coefficients that could be used for comparison: DL1 and DL2, and they are not easy to interpret. These traits are measurements of weight on the loin to obtain the drip loss, and in this context, association with the *PIK3C3* gene could be explained by the genetic relationship between growth rate (ADG) and loin traits. A previous correlation was estimated between ADG and LC to be 0.42 ± 0.28 [8]. However, the relationship between PC3, *PRKAG3*, and meat quality traits is unclear in this population, as the magnitude of all meat quality traits were small with differing signals. Further study should be performed on this population to determine a stronger relationship with *PRKAG3*.

Candidate genes for PC5

The fifth PC had two candidate genes reported to be related to QTLs. The first candidate gene was *VRTN* (vertebrae development associated) and has been associated to the development of the thoracic vertebrae and is likely essential during the development of the embryo [64]. One study has shown that *VRTN* is critical to the vertebrae development in mammals, as mice embryos

that were *VRTN*-null displayed developmental issues such as abnormal spinal development and tended to have fewer ribs (12 pairs instead of 13) and did not survive or fully develop while embryos that were heterozygous for the *VRTN* gene also displayed some abnormal development, though they did survive and were reported to be of good health [65]. Thus far in swine, this gene has been linked to carcass length and thoracic vertebra number [66], teat number [48], IMF [49], LA, and GLD [50] in Duroc populations and number of ribs in a crossbred population [46].

The second candidate gene was *DLST* (dihydrolipoamide S-succinyltransferase). This gene has been less documented in swine, thus it is difficult to relate its expression to this population, but has been linked to a family of complexes [67]. One study related the presence of the *DLST* gene to the number of teats in a population of Large White pigs [47], however there is not yet a clear explanation for this relationship.

As PC5 presented a biotype related to longer bodied animals with less lean and fat mass, these genes present a supporting explanation. As swine breeders have continued to select for larger, longer bodied animals, selection for the *VRTN* gene has happened simultaneously. During domestication, humans bred wild boar with 19 thoracic vertebrae into the domestic meat animal with an average of 21-23 vertebrae, effectively creating a larger, longer animal [64,68] that would ultimately yield more pork product.

Candidate genes for PC8

The eighth PC had one candidate gene reported to be related to QTLs: *PAPPA* (pappalysin 1). In humans, the *PAPPA* gene encodes a metalloproteinase which cleaves insulin-like growth factor binding proteins, which ultimately results in the activation of the IGF pathway. This protein was found to effect bone formation, healing, and fertility, and, when overexpressed, can effect cancer formation [69]. Previous research done in swine has related this gene to a number of conformation and body shape and size traits [51,70]. However, the study at hand has no confirmation traits, but traits such as BL and LL can be used to approximate longer bodied animals. In addition to being longer bodied, the biotype from PC8 suggests that the *PAPPA* gene may also be related to backfat depth, loin area, live weight, loin muscle depth, and the width of the belly cut. To the best of our knowledge, this is the first study to make a link between conventional carcass traits like GBF and RMD and the *PAPPA* gene. As such, more study should be performed to validate these findings.

3.5.4 Functional analysis

The only PC to display significant clustering of GO terms was PC3, which was enriched with pathways related to the regional growth and development of the animal. For example, the GO term "anterior/posterior pattern specification" (GO:0009952) is the regionalized process of cell differentiation that is determined along the anterior-posterior axis of the animal - a line that runs from the head to the tail end of the animal's body. This term is related to the homeobox genes *HOXA11*, *HOXA2*, *HOXA3*, *HOXA5*, *HOXA6,* and *HOXA7*, which are an integral part of embryonic development through gene expression regulation and cell differentiation. The other notable biological process was the GO term "embryonic skeletal system morphogenesis" (GO:0048704) which is the process of the generation of the anatomical structures of the skeleton during embryonic development. The homeobox genes HOXA3, HOXA5, HOXA6, and HOXA7 were also related to this GO term. The finding of these terms and genes suggests that PC3's biotype may be more complex than initially seen, as it seems to play a critical role in the development of the animal from the time of conception.

When all PCs were included in the functional analysis, the only significant GO terms related to biological processes were GO:0009952 and GO:0048704 again, which can be explained by their prominent presence in the analysis of PC3 as none of the other PCs had a homeobox gene included in their list of candidate genes.

Two KEGG pathways were also found to be significant and involved many candidate genes across PCs. The first pathway is the "oxytocin signaling pathway," which involves the FOS (fos proto-oncogene, *AP-1* transcription factor subunit), *CACNG7* (calcium voltage-gated channel auxiliary subunit gamma 7), *CAMK1* (calcium/calmodulin dependent protein kinase I), *CAMKK2* (calcium/calmodulin dependent protein kinase kinase 2), *PRKCG* (protein kinase C gamma), *PRKAG3* (protein kinase, AMP-activated gamma 3 non-catalytic subunit), and *PPP1R12C* (protein phosphatase 1 regulatory subunit 12C) genes. These genes are involved in the pathway in many varied ways, such as the signaling of protein synthesis, glucose uptake in skeletal muscle cells, migration of endothelial cells, cell proliferation and differentiation, and vasodilation in the cardiovascular system.

The second pathway is the "MAPK signaling pathway," which involves the *FOS* (fos proto-oncogene, *AP-1* transcription factor subunit), *TAOK2* (TAO kinase 1), *CACNG7* (calcium voltage-gated channel auxiliary subunit gamma 7), *MAP3K14* (mitogen-activated protein kinase kinase

kinase 14), and *PRKCG* (protein kinase C gamma) genes. These genes are notably involved in the pathway as influencers in the process of cell proliferation, inflammation, and differentiation.

Both the GO terms and the KEGG pathways are intertwined with biological processes that influence the growth and development of the animal, specifically pertaining to the skeletal system and skeletal muscling. Though not all PCs could be analyzed deeper, the indicators found here for PC3 and the pathways for all PCs are in line with the previously defined biotypes and indicate that these genes could be used as indicators for the purpose of genomic selection.

3.6 Conclusions

The results from the genomic estimation of variance components showed that when including genomic information, the resulting heritability is more precise, though it is likely to be lower in most cases. Regardless, all growth, meat quality, conventional, and novel carcass traits were shown to have moderate to high heritabilities, indicating they are valid candidates for inclusion in breeding programs. Additionally, the use of principal components and the development of pseudo-phenotypes has proved to be successful in simultaneously associating many candidate genes with valuable traits such as growth rate, lean and fat content, and pH and meat color. These associations will enable breeders to select for a pool of genes that lay within valuable quantitative trait loci on the genome, which will facilitate rapid genetic progress in those traits of interest. The candidate genes' involvement in the biological development of the Duroc breed was evidenced by the functional analysis results, where QTLs, GO terms, and KEGG pathways related the pseudo-phenotypes to biological processes involving common production traits, pork quality, growth, and development of skeletal structures, synthesis of proteins and cell proliferation. The candidate genes, biological processes and pathways identified in this study provide valuable insight into the biological interpretation of the biotypes defined by the principal components. Together, this information shows potential for the genetic selection based on these biotypes, rather than individual traits alone.

3.7 References

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CHAPTER 4. GENERAL CONCLUSIONS

The results of Chapter 2 provided valuable missing insight into the genetic parameters of the 39 growth, primal and sub-primal carcass, and pork quality traits included in this thesis. As was described, there has been little quantification of these traits in literature, especially concerning primal and sub-primal carcass traits and belly traits. With this contribution, more researchers can choose to verify the results seen here so that more information will be distributed to breeding companies and packers.

The results of Chapter 3 fill a similar void in the literature by applying the combined PCA and ssGWAS approach to use pseudo-phenotypes in order to define groups of biotypes that can then be used to identify candidate genes, related QTLs and biological mechanisms. Both of these studies have shown promise for the use of novel traits and novel methodologies in the development of selection indexes. Growth, carcass, and meat quality traits have been shown to have intertwined genetic relationships through PCA and this information should be utilized to supplement their simultaneous selection in terminal sire lines.

When the results of these two chapters are brought together, there are several trends that should be noted. Firstly, the second chapter identified four groups of traits that were likely to be strongly genetically related based on their high (above 0.80) and positive genetic correlations. The first (ADG, LW, and HCW) and second (GLD, LA, LC, and RMD) groups of traits tended to respond in the same direction with a similar magnitude across the first three principal components. Most notable was the positive relationship between ADG, LW, and HCW which lead to the definition of the biotype of PC1 as being related to growth and carcass weight. As was discussed in the discussion of Chapter 4, these traits have long been known to be biologically linked, as ADG is directly related to the weight of the animal as it continues to grow. The similar magnitude and signal of these groups of traits in the PCA, in addition to their genetic correlations, further indicate that they are biologically related traits.

Additionally, a third grouping of traits (LJPC, L*, a*, b*, and LNC) was found to respond similarly across the first three PCs. While only LNC and L* were found to have a highly positive genetic correlation, the other color traits had moderate to high correlations as well. While these traits shared a similar response across PCs, none of them were of great magnitude, and unfortunately a biotype specifically for meat color could not be well defined. However, the genes

identified for PC3 (*PIK3C3* and *PRKAG3*) have been previously linked to meat quality traits, specifically those that were closely related in Chapter 3. All of the color scores are closely related to one another genetically and also have strong correlations with LPHA and DLP. Pork color, drip loss, and ultimate pH are commonly linked traits within meat science and have been well documented to be biologically related. The discovery of these genes and their relationship with meat quality provide a direct connection for animal breeders to use in genomic selection schemes.

The final traits that were found to respond similarly across all PCs were BLFT, BW, and BWR. BW and BWR were considered to be similar traits in the results of Chapter 2, though BLFT was found to have more minimal genetic correlations with them. PC4 in particular suggested that a biotype related to the width of the belly exists. However, little study has been performed on these traits in current literature, and if more study could be done, perhaps another, stronger biotype, or similar genetic parameters, for belly traits could be defined. The supplementation of these findings in literature would aid in verifying the results of the two studies described in this thesis.

Considering the limitations of these studies, research should not end with the conclusion of this thesis. While one of the advantages of this research was the use of complete and well-documented datasets in a terminal Duroc population, it also consisted of records taken only on female animals. It is difficult for breeders to sacrifice male animals when they are invaluable to a selection program, but perhaps with the implementation of genomic selection, the data of males could also be added to the population. However, it is also important to consider how preselection will affect the results coming from a study that only included a subset of the male population.

Additionally, as these studies were performed only on purebred animals, it is imperative that more research and investigation be done in a crossbred population, as those animals are the primary source of pork products in North America. While it is valuable to understand the terminal sire line for the purposes of sire selection and proliferation of meat quality traits, half of the genetics expressed by commercial crossbreds come from their mothers, which are mostly commonly crosses between Large White and Landrace. With the introduction of different genetic material comes the possibility to detect other candidate genes, biological types, and QTLs.

As the study presented in Chapter 3 was, to the best of our knowledge, the first PCA analysis of this type and magnitude to be performed on a swine dataset, it should be replicated in other swine populations to validate this methodology use in pigs. Previously, this method has been

applied to cattle populations successfully, but it would be of use to the swine industry to further explore PCA's applications with its important traits.

When considering what more could be done with this data set, there are several other analyses that would add to the information we have received so far. The next step that is imperative to complete is the estimation of all genetic parameters for all 39 traits utilizing the **H** matrix. Chapter 3 presented the difference between heritabilities estimated with the **A** matrix and the **H** matrix, but it is critical to do an additional comparison between genetic correlations, as previous literature has shown that differences are likely to exist between the estimates received from the two different matrices.

Additionally, the results of Chapter 3 only presented GWAS plots and significant SNPs received from the use of the PCA. Individual GWAS studies should be performed for all 39 traits in addition to the PCA GWAS, and the results should be compared to see if similar, or new, candidate genes, SNPs, or QTLs are detected. The PCA should also be repeated on smaller subsets of traits (growth, conventional carcass, novel carcass, and meat quality) and used as pseudo-phenotypes for more GWAS analysis for similar reasons. It would also be of interest to explore the different biotypes defined by the individual groupings of traits, and to see if more genes related to those biotypes could be found, or, if existing or new QTLs could also be associated with the traits.

By performing the additional analysis described here, we could gain a deeper understanding of these traits, which are invaluable to the pork production system. Additional studies performed by other researches will increase the knowledge available to producers, validate the methodology used in this thesis, and provide more scientific insight into the genetic architecture and background of carcass, growth, meat quality, and more traits.

APPENDIX A. SUPPLEMENTARY MANHATTAN PLOTS

This is the appendix for Chapter 3, containing additional Manhattan plots relevant to the results presented therein.

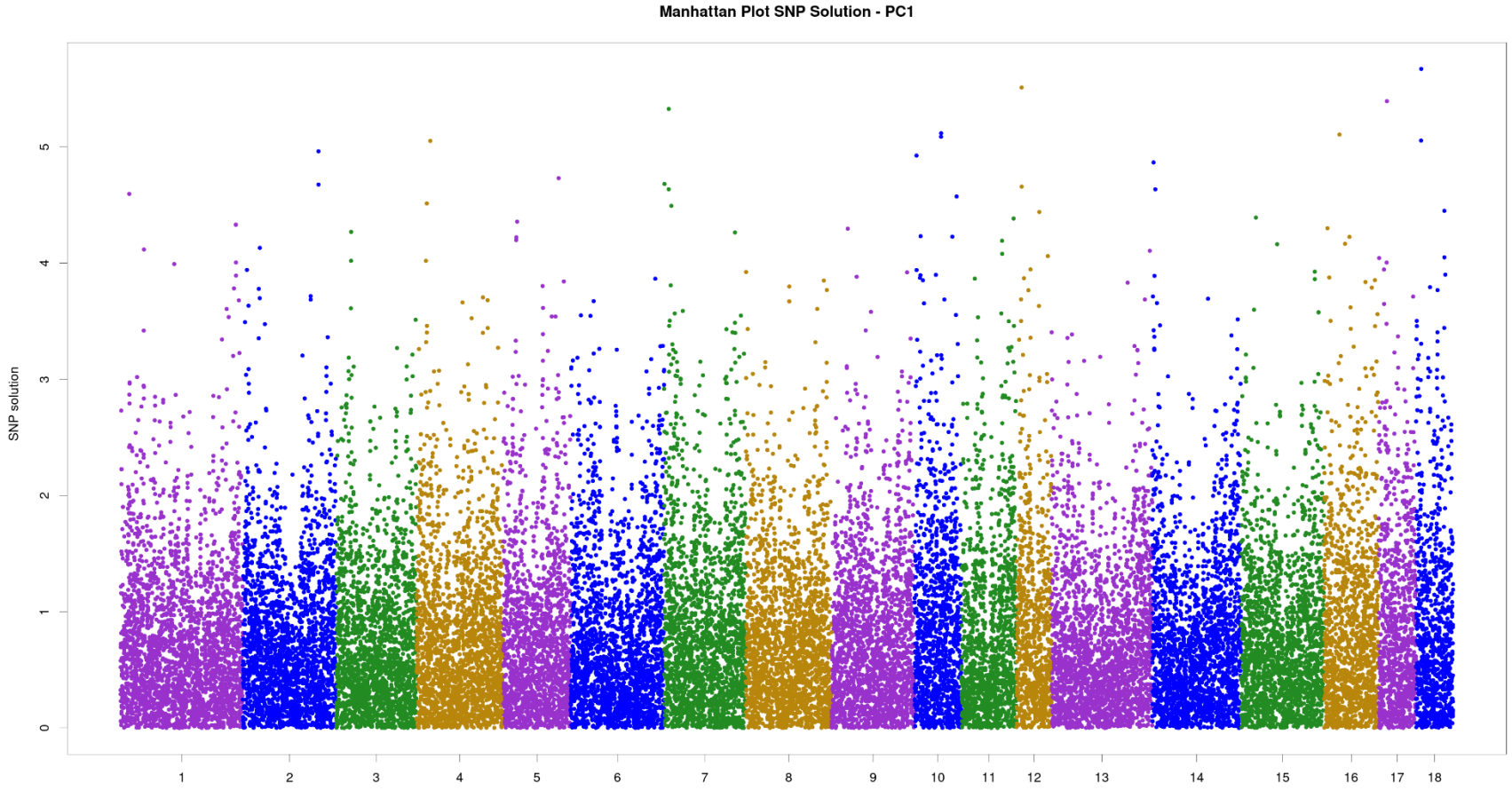

Figure A.1. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 1 (PC1).

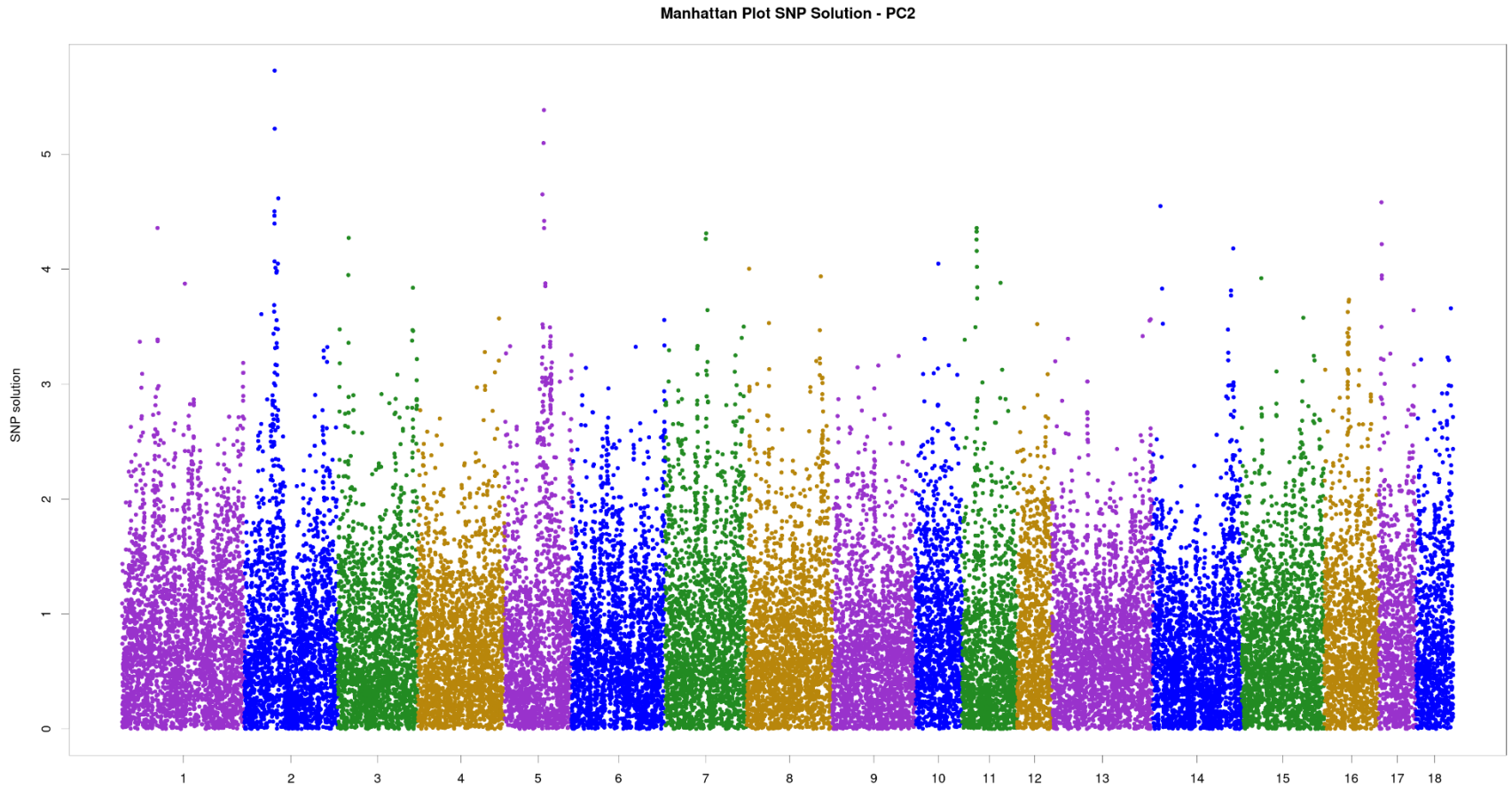

Figure A.2. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 2 (PC2).

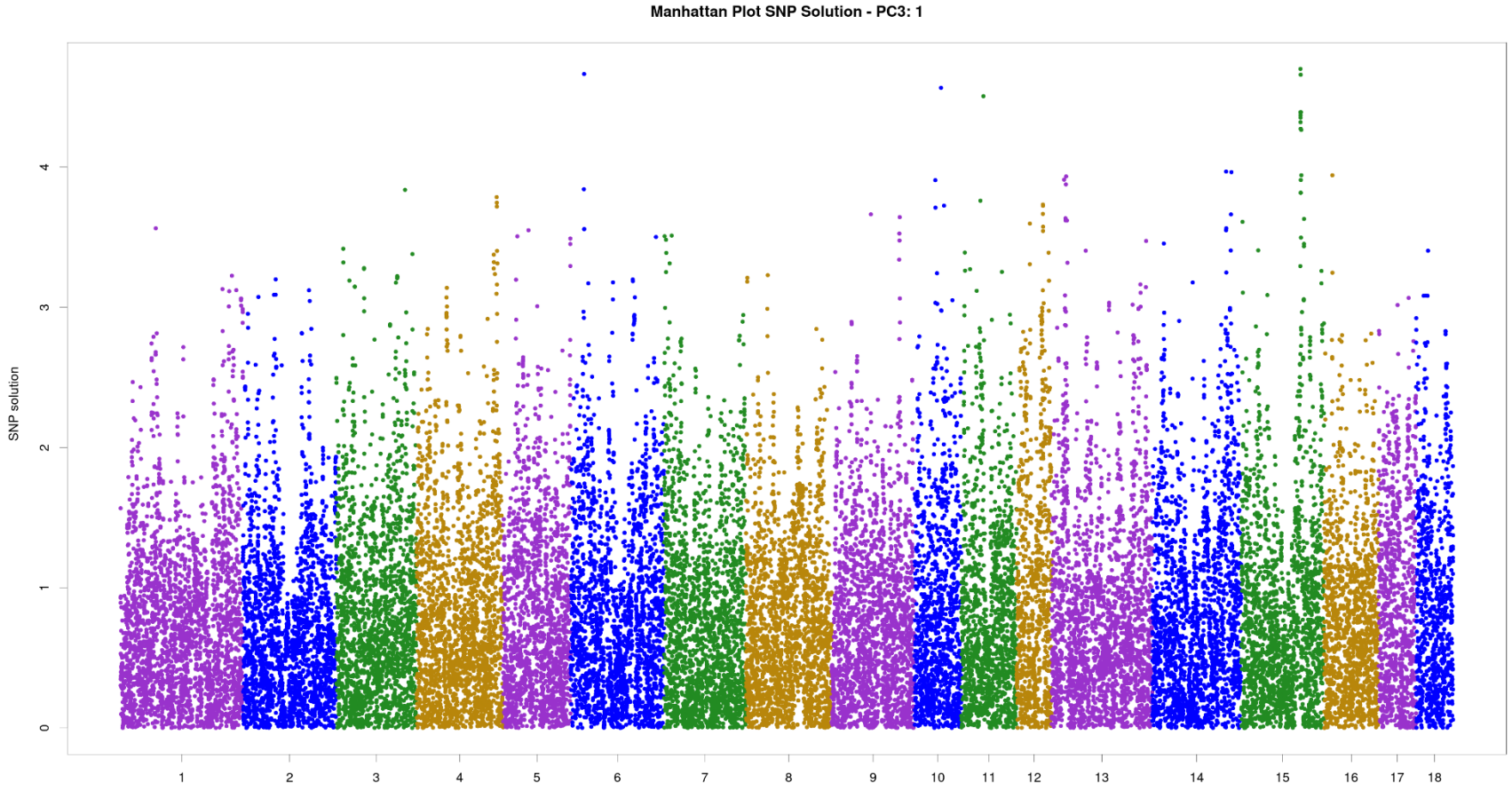

Figure A.3. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 3 (PC3).

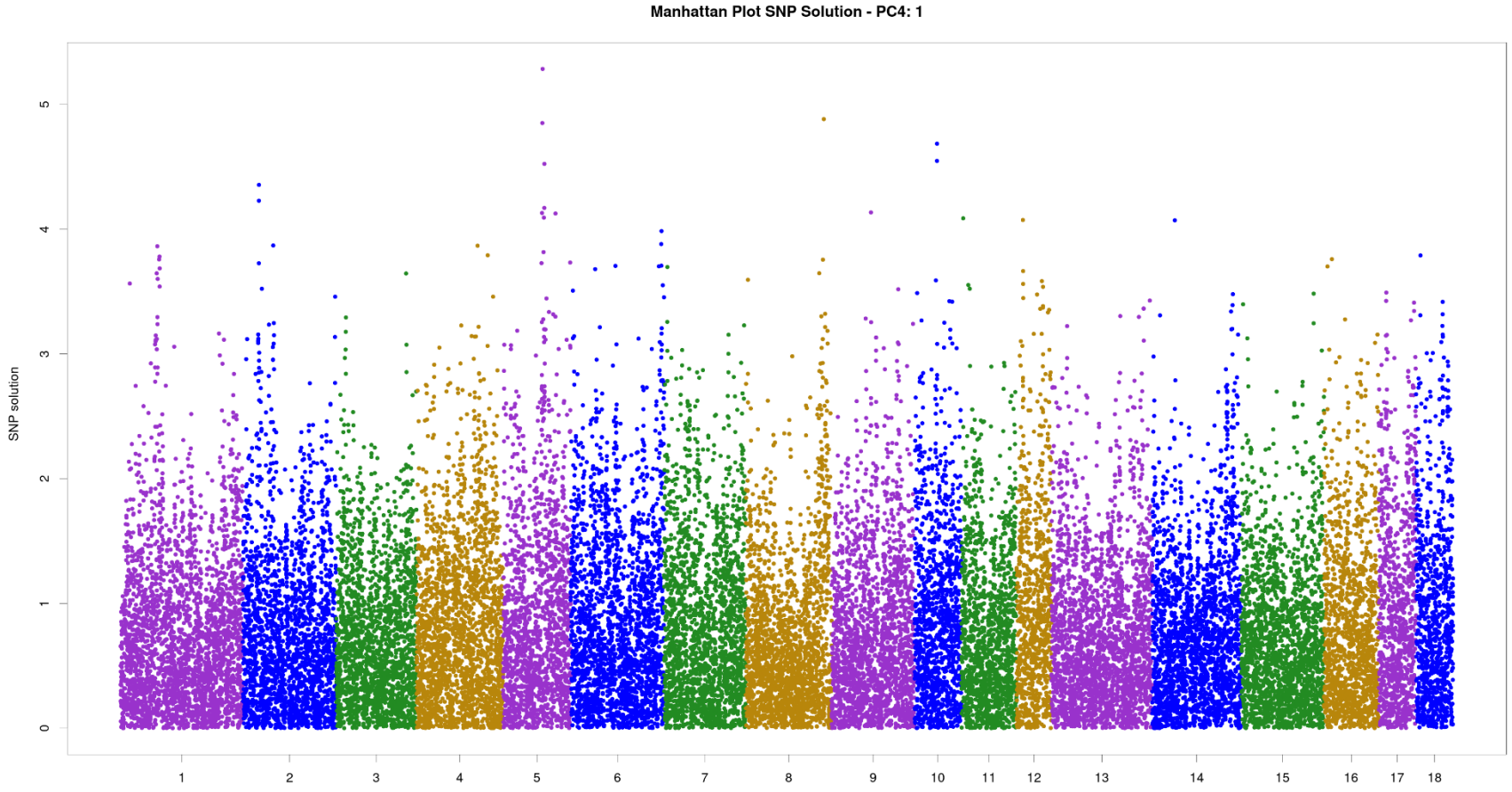

Figure A.4. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 4 (PC4).

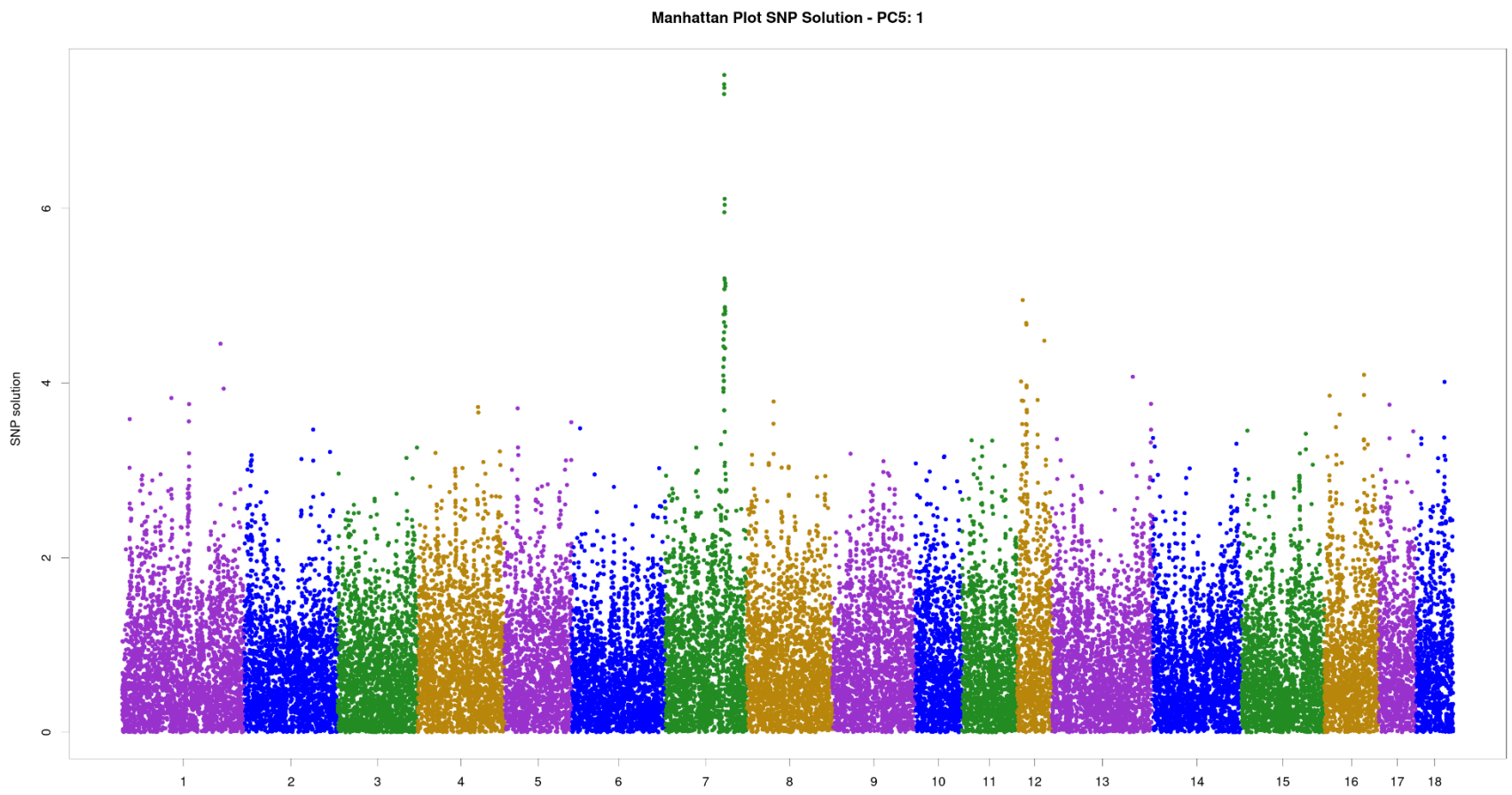

Figure A.5. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 5 (PC5).

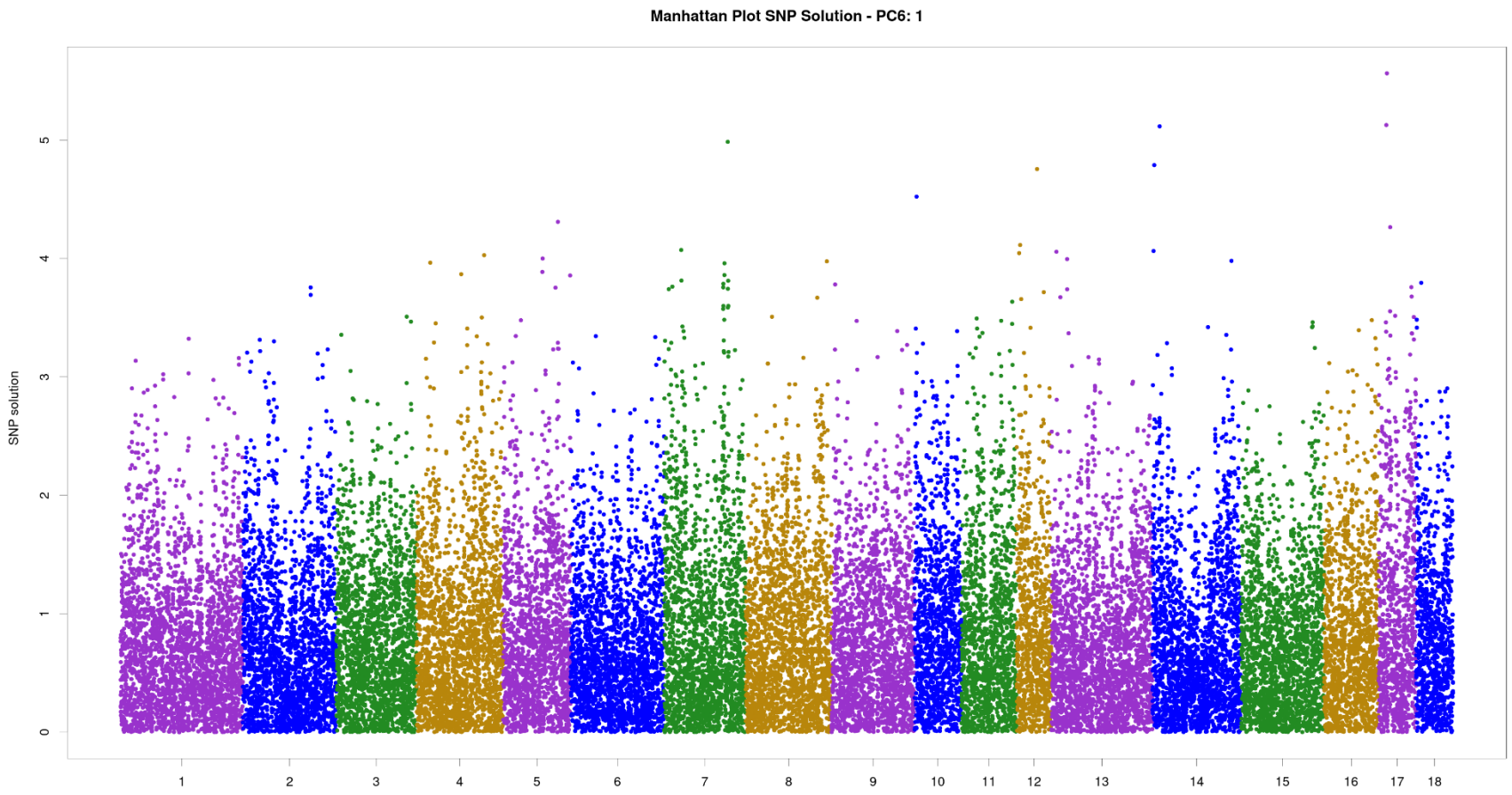

Figure A.6. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 6 (PC6).

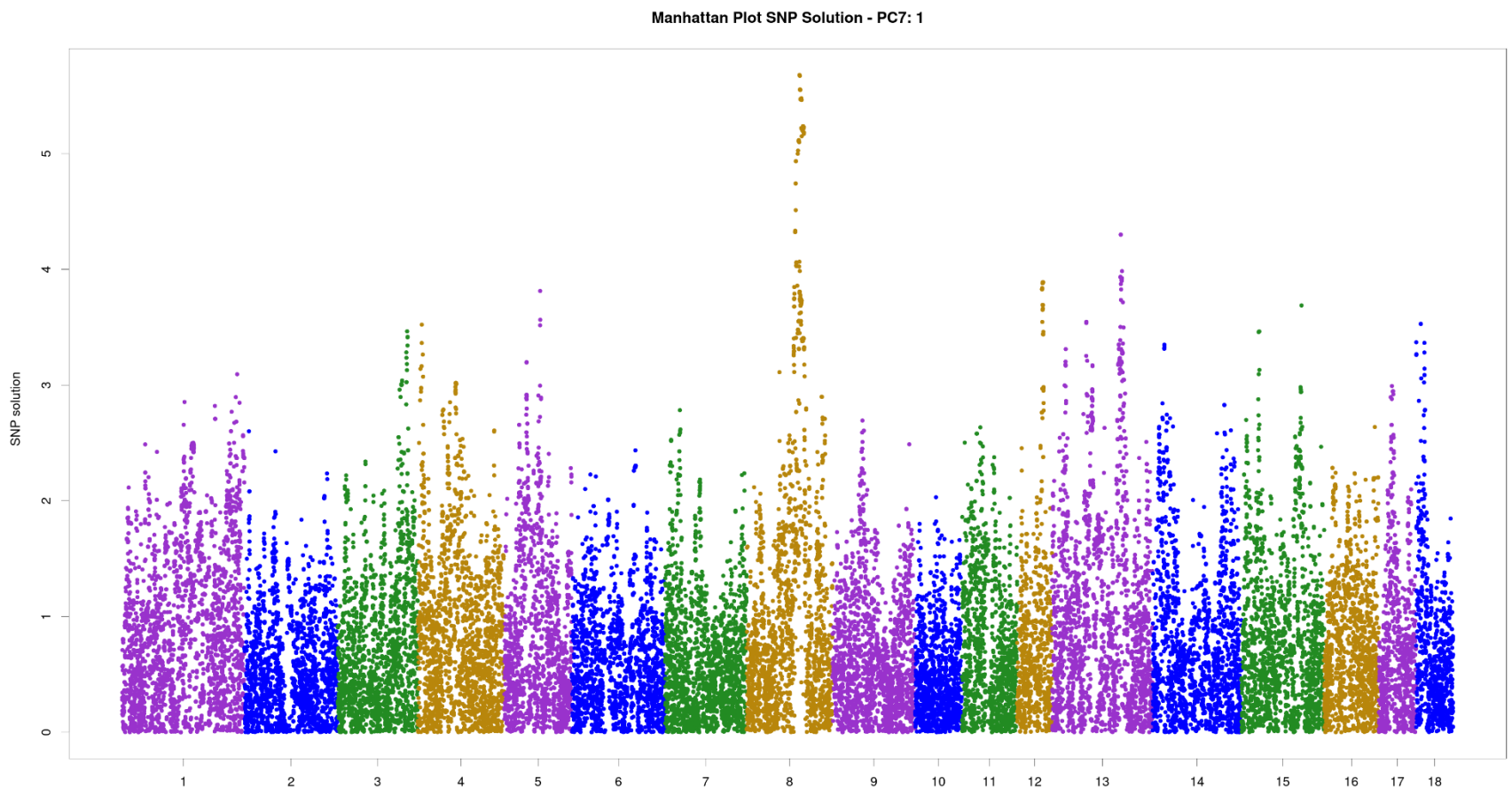

Figure A.7. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 7 (PC7).

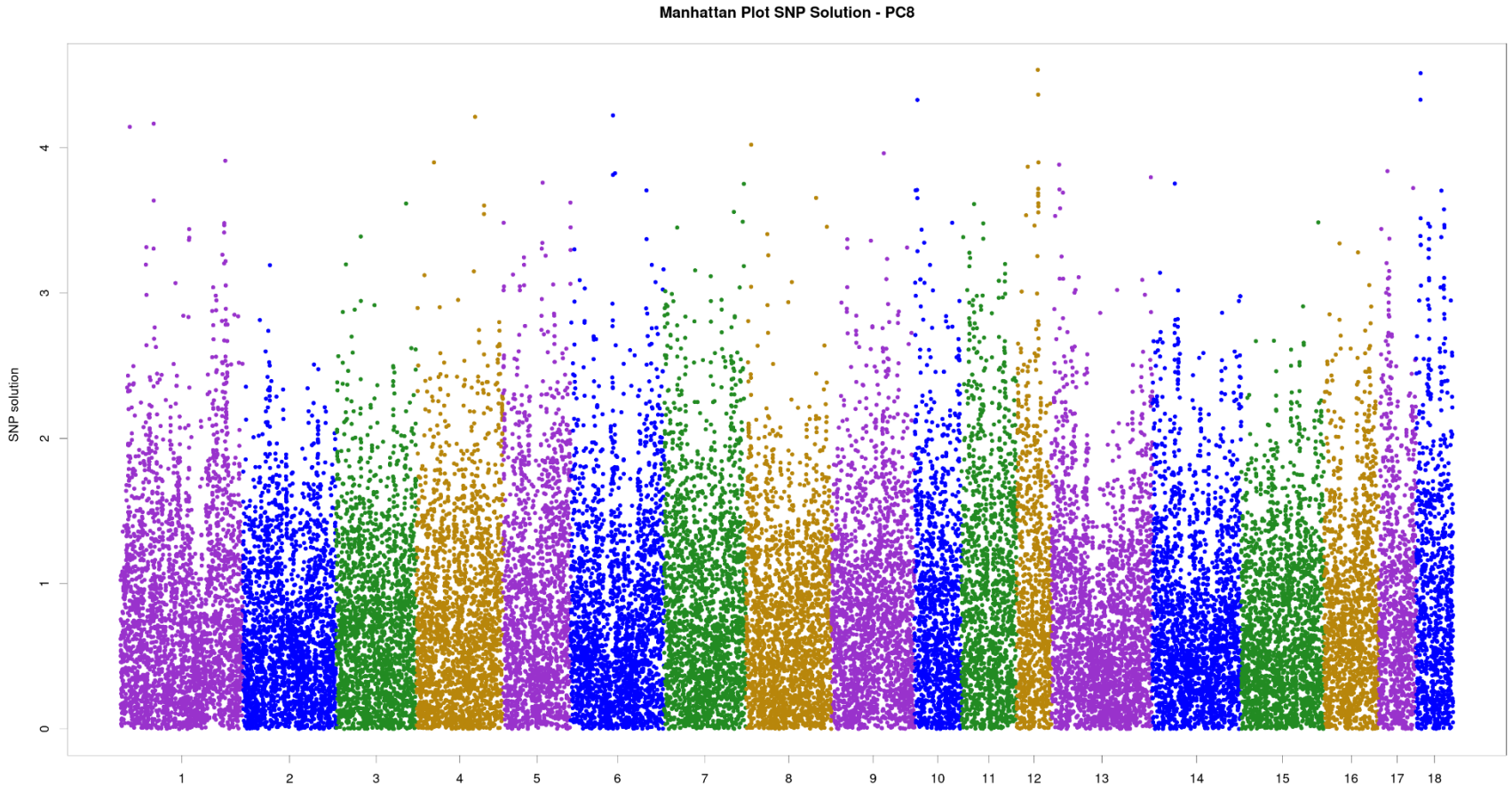

Figure A.8. Manhattan plot of single nucleotide polymorphisms (SNPs) solutions for principal component 8 (PC8).

PUBLICATIONS

Willson, H.E.; de Oliveira, H.R.; Schinckel, A.P.; Grossi, D.; Brito, L.F. Estimation of genetic parameters for pork quality, novel carcass, primal-cut and growth traits in Duroc pigs. *Animals* **2020**, doi:10.3390/ani10050779.

Willson, H.E.; de Oliveira, H.R.; Schinckel, A.P.; Grossi, D. Estimation of genetic parameters for novel meat quality and carcass traits in Duroc pigs. *Journal of Animal Science* **2019**.