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ANALYSIS OF A DUROC x PIETRAIN F_2 PIG RESOURCE POPULATION FOR QUANTITATIVE TRAIT LOCI AFFECTING GROWTH, BODY COMPOSITION, AND MEAT QUALITY TRAITS

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By

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ABSTRACT

ANALYSIS OF A DUROC x PIETRAIN F_2 PIG RESOURCE POPULATION FOR QUANTITATIVE TRAIT LOCI AFFECTING GROWTH, BODY COMPOSITION, AND MEAT QUALITY TRAITS

By

David Bowen Edwards

A Duroc x Pietrain F_2 pig resource population was created to discover quantitative trait loci (QTL) affecting growth, body composition, and meat quality traits. These pigs (1259 born) were finished in either a Modified Open Front (MOF) or a Test Station (TS) building. Body weight and ultrasound estimates of tenth rib backfat, last rib backfat, and *longissimus* muscle area were serially measured throughout development. Random regression analyses were performed to evaluate body weight gain and its components over time. Carcass and meat quality data collection included primal cut weights, backfat thickness, muscle pH, objective and subjective color information, marbling and firmness scores, and drip loss of boneless *longissimus* muscle chops. Additionally, chops were analyzed for moisture, protein, and fat composition as well as cook yield and shear force measurements. Palatability of chops was determined by a trained sensory taste panel.

Models that included genetic, permanent environment, and residual error variance components were used to evaluate the influence of finisher facilities on these traits. Pigs finished in the MOF were heavier at harvest and had more backfat at 22 wk of age and at harvest at the tenth and last rib than pigs raised in the TS. Body weight random regression analysis revealed that pigs reared in the TS grew more slowly at first, but then grew more quickly later in the finisher phase for the same overall weight gain from 10 to 22 wk of age as pigs in the MOF. Pigs raised in the MOF had a greater backfat accretion

rate from 10 to 22 wk of age than pigs raised in the TS. Additionally, pigs raised in the MOF had greater decline in pH from 45 min to 24 h postmortem and had lower Warner-Bratzler shear force measurements than pigs raised in the TS. Thus, animals of similar genetic merit can show differences in phenotypes as influenced by finisher facilities.

A total of 510 F_2 animals were genotyped for 124 microsatellite markers evenly spaced across the entire genome. Data were analyzed with line cross least squares regression interval mapping methods using sex and litter as fixed effects with covariates of carcass weight or harvest age for specific carcass and meat quality traits. Significance thresholds of the F-statistic for additive, dominance, and imprinted QTL were determined on chromosome- and genome-wise levels by permutation tests.

A total of 54 QTL for 22 of the 29 measured growth traits, 33 QTL for 15 of the 16 animal random regression terms, and 94 QTL for 35 of the 38 carcass merit and meat quality traits were found to be significant at the 5% chromosome-wise level. Growth and body composition putative QTL were discovered for tenth and last rib backfat on SSC 6, body composition traits on SSC 9, backfat and lipid composition traits on SSC 11, tenth rib backfat and total body fat tissue on SSC 12, and linear regressions of body weight, *longissimus* muscle area, and tenth rib backfat on SSC 18. Carcass merit and meat quality putative QTL were discovered for 45 min pH and pH decline on SSC 3, marbling score and carcass backfat on SSC 6, carcass length and number of ribs on SSC 7, marbling score on SSC 12, and color measurements and tenderness score on SSC 15. These results will facilitate fine mapping efforts to identify genes controlling growth and body composition of pigs that can be incorporated into marker-assisted selection programs to accelerate genetic improvement in pig populations.

This dissertation is dedicated to my family, who have fostered my learning and stimulated my thinking from day one, and to Christy, who has made my life whole.

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LIST OF ABBREVIATIONS

ADG = average daily gain

BF10 = tenth rib backfat

BW = body weight

DNA = deoxyribonucleic acid

EBLIPID = empty body lipid

EBPRO = empty body protein

FFTOLN = fat-free total lean

LMA = *longissimus* muscle area

LRF = last rib backfat

MOF = Modified Open Front building

QTL = quantitative trait loci

RYR-1 = ryanodine receptor gene

SSC = *Sus scrofa* chromosome

TOFAT = total body fat tissue

TS = Test Station building

WBS = Warner-Bratzler shear force

INTRODUCTION

Genetic progress in livestock has been based upon direct selection for phenotype or on predicted breeding values based upon phenotype. These breeding values are predicated on accurate measurements of the traits and proper accounting for environmental influences. Knowledge gained on the effects of certain genes can augment selection programs and increase the rate of genetic progress. Molecular genetics enables the identification of regions of the genome known as quantitative trait loci (QTL) that can affect many economically important traits. These QTL can be incorporated into selection programs and used to enhance genetic progress by allowing selection for traits in both sexes, on all animals, earlier in life, and with less phenotypic data collection. Dekkers (2003) identified four key steps of development for the eventual application of these molecular genetics techniques in livestock breeding programs. The first area is the development of molecular markers and genetic maps. Creation of resource populations and analysis for QTL is the second major step. Thirdly, once these QTL are identified, these genes or markers linked to the genes can be used in genetic evaluation, and, finally, these data can be utilized in selection.

In order to attain these goals, researchers have developed anonymous markers that are located across the entire genome in many species of interest. Dinucleotide microsatellite markers have been developed for use in swine maps and QTL identification. Combining these markers with phenotypic information from well characterized swine populations has allowed the detection of QTL for various classes of traits including growth, composition, meat quality, and reproduction. A valuable source of phenotypic data is a resource population since the known pedigrees allow tracking of

alleles through the generations; these populations also can be used to study management and other environmental effects on these phenotypes. Many previously reported swine resource populations have used rustic breeds crossed with commercial breeds to study QTL segregating between diverse populations (e.g. Andersson et al., 1994; Rohrer and Keele, 1998a). While analysis of these populations was able to reveal QTL for important phenotypes, a resource population generated from breeds already utilized in commercial populations would allow more rapid introduction of beneficial QTL into the breeding program.

Enhancement of production efficiency and improvement of product quality are major concerns for producers of food animals. Unfortunately, selection for rapid lean growth rate in swine frequently results in production of animals that yield inferior quality meat. Locating and utilizing specific favorable genes for lean growth and meat quality will help overcome this natural antagonistic relationship and allow improvement to be realized for both efficient production and product quality. A major step towards this goal can be achieved through the development and analysis of a genetic resource population that exhibits variation for lean growth and meat quality traits. Duroc and Pietrain breeds, used in many modern commercial populations and divergent for many growth, composition, and meat quality traits (Kanis et al., 1990; Affentranger et al., 1996; Ellis et al., 1996; Garcia-Macias et al., 1996; Edwards et al., 2003; Edwards et al., 2006), were selected as the basis for the resource population developed at Michigan State University.

Discovery of previously unreported QTL can lead to further understanding of the influence of growth QTL on meat quality. Furthermore, traits such as meat quality are difficult and expensive to measure and require slaughter of the animal. Discovering QTL

for meat quality traits and then implementing these QTL into breeding systems will allow the pork industry to more rapidly improve production efficiency and profitability and at the same time provide consumers a better quality product. Implementing marker-assisted selection using information gained from QTL discovery can augment traditional selection strategies.

A Duroc x Pietrain F_2 pig resource population was developed at Michigan State University. Analysis of the phenotypic and genotypic data from this population for the discovery of QTL was the main emphasis of this dissertation. Additionally, an analysis of the data to determine influence of management practices on phenotypes was undertaken. Three objectives were evaluated in this research program:

1. To determine the influence of finisher facilities on pig growth, composition, and meat quality traits.
2. To discover positions and effects of QTL affecting pig growth and body composition traits.
3. To discover positions and effects of QTL affecting pig carcass merit and meat quality traits.

CHAPTER I

LITERATURE REVIEW

Growth and Composition Prediction

Breeds and lines used in commercial pork production each have their unique patterns of growth. "Growth may be considered from at least two different aspects: 1) an increase in body mass with time and 2) changes in form or composition resulting from different growth rates of component parts," (Robison, 1976). Robison (1976) further stated that efforts in the past to change the growth curve have been directed at simply changing rate of body mass growth.

Change in body mass can be partitioned into its component parts. This partitioning provides more information concerning biological differences between different animals within populations as well as further description of different populations. In order to study these compositional changes, animals have been dissected or chemically analyzed at different slaughter weights (Siemens et al., 1989; Schinckel and de Lange, 1996; Wagner et al., 1999). The high cost of these procedures makes them prohibitive to be routinely conducted on a large number of pigs (Schinckel and de Lange, 1996). In addition, animals slaughtered would not be available for breeding purposes, which allows only information on relatives to be used for predicting genetic merit.

Methods to predict these components of growth on live animals are desirable and have been developed. One method is ultrasound technology. Terry et al. (1989) used ultrasound estimates of backfat and loin muscle area to attempt to predict the four lean cuts as a percent of side weight. Targeting protein accretion specifically with attention paid to an adequate amount of fat within pork is a production goal that can be achieved.

Several studies have reported non-invasive measures to predict body protein and fat composition at various stages of the growth phase (McLaren et al., 1989; Siemens et al., 1989; Houghton and Turlington, 1992; Schinckel and de Lange, 1996; NPPC, 2000). The ability to estimate composition on breeding animals allows optimization of breeding schemes and production practices for desired end products.

A review by Houghton and Turlington (1992) showed that ultrasound could accurately assess body measurements of swine. Overall accuracy of composition measurements (e.g., backfat at first rib, tenth rib, last rib, and last lumbar and loin muscle depth, width, and area), as assessed by correlation coefficients, was approximately 0.9. These high correlations to carcass measures allow for non-invasive measures of an animal's phenotype.

Ultrasound technology has been used to characterize growth and composition throughout the life of the pig. Serial real-time ultrasound measures have been taken on pigs at regular intervals to predict body composition measures at market weight and to model growth. McLaren et al. (1989) took ultrasound measures starting at 42 d of age and every 2 wk thereafter until slaughter (mean of 98.5 kg, 170 d). Both measures of backfat and loin muscle area were obtained and used to predict lean gain per day. They reported that serial measures appeared promising, and cost-effective, as a technique for monitoring composition of growth in the pig. Johnson et al. (2004) compared several methods to estimate fat-free lean in swine including carcass measurements, ultrasound measurements, and automated collection systems of composition estimates utilized in packing plants. In order to compare these systems, physical and chemical dissection of the carcass was undertaken. To calculate fat-free lean an adjustment has to be made for

the weight of dissected lean tissue to a fat-free basis by using the ratio of percentage of lipid in lean tissue to percentage of lipid in fat tissue. An assumption held is that the lipid percentages in dissected fat tissue and in the fat depots remaining within dissected lean tissue are equal (Johnson et al., 2004). Another procedure to estimate lipid-free lean from weight of dissected lean and the percentage of lipid in the tissue involves calculation of the percentage of lipid-free lean from the weight of dissected lean and the percentage of lipid in the tissue (Johnson et al., 2004). These two procedures produce different estimates because, besides lipid, fat contains cytoplasmic fluids, protein, and ash and the percentages of lipid in the dissected fat tissue and different fat depots within the carcass vary (Higbie et al., 2002). Although these two measures can be substantially different (Schinckel et al., 2001), the correlation between them is high (Schinckel et al., 2003). This high correlation results in only minor differences in ranking of animals between the two procedures (Schinckel et al., 2003) allowing either to be used in selection with no detriment to rate or direction of improvement.

Growth Modeling

Successful simulation of growth performance of an individual pig depends not only on the correct parameterization of its genotypic parameters but also on a detailed description of its environment (Knap, 2000). Growth curves are an effective way to summarize measurement information into only a few parameters (Mignon-Grasteau et al., 1999). Many different approaches have been used to summarize growth parameters in different species. These include changes in body mass as well as changes in composition of body mass. Change in body mass has been an important growth characterization in meat animal species. Whittemore et al. (2003) used Landrace, Pietrain, and Meishan

crossbred pigs to estimate growth phenotypes between pigs with genetic predisposition to different body types. Serial slaughter and dissection was carried out to estimate carcass composition and describe these changes using regression over time. Estimation of growth curves in chickens (Mignon-Grasteau et al., 1999) has shown that parameters of the growth curve are heritable. Four lines of chickens were selected for change of body weight at 8 or 36 weeks of age. One line was selected for high body weight at both ages. Another was selected for low body weight at both ages. A third was selected for high body weight at 8 weeks and low body weight at 36 weeks. The fourth was selected for low body weight at 8 weeks and high body weight at 36 weeks. Offspring from these selected animals were measured for body weight growth and had growth patterns similar to their parents. Thus, patterns of growth as described by parameters of the functions, not just overall growth, are heritable (Mignon-Grasteau et al., 1999).

A further refinement of growth is to measure the change in mass of its components. In meat animals the relationship of lean growth (protein) to fat is especially important. Knap (2000) fitted body protein and lipid mass growth functions and assumed that the rate parameter would be the same for both components. Knap concluded that selection between 'meat-type' pig populations has greatly reduced mature body lipid mass while leaving mature body protein mass practically unchanged. Also, the growth rate of both body fractions had substantially increased and the peak of the protein accretion curve had shifted towards more mature stages of development.

Random Regression

Random regression analysis is a method to fit longitudinal data, such as body weight, where the trait of interest is changing, gradually but continually, over time.

Random regression allows regression of a trait on age to model growth and allows separation of between and within animal variation. Henderson Jr. (1982) first considered random regression coefficients in a linear mixed model context. Recent applications include evaluation of dairy cattle using test day records (Jamrozik and Schaeffer, 1997; Jamrozik et al., 1997), and description of growth curves in beef cattle (Varona et al., 1997; Meyer, 2004), lambs (Fischer et al., 2004), and pigs (Andersen and Pedersen, 1996; Huisman et al., 2002, Edwards et al., 2006).

Random regression, as opposed to multiple trait analysis, can be used as an effective tool to reduce the number of traits to analyze, such as body weight or body component weights, for those traits measured over time. Traits can be described by parameters of a function, instead of by many measures taken over a time period. The fixed regression parameter of the function can model population trajectory, while the random regression coefficients represent individuals' deviation from this curve (Meyer, 1998). Random coefficients allow a (co)variance structure to be specified for related factors (Fischer et al., 2004). Additionally, Fischer et al. (2004) also fit a heterogeneous residual error variance over age, which is common amongst growth data. Inclusion of random genetic components of regressions in animal models may be applicable to any situation in which repeated time-dependent observations are taken on a given animal, and when the time-dependent response function exhibits genetic variation (Schaeffer and Dekkers, 1994).

Andersen and Pedersen (1996) applied random regression methodology to growth rate and daily food intake in pigs. Gilts and barrows were on test from 30 to 115 kg live weight. They postulated that the growth curve of each individual followed a fourth

degree polynomial. The (co)variance parameters were estimated using REML, and then fixed effects were estimated and random effects were predicted assuming the estimated (co)variance parameters as the true parameters. The difficulty in introducing random effects or variance components in non-linear functions was the reason that linear polynomial models were chosen. When animals are not taken to mature weights, such as growth evaluation to standard or contemporary market weights, it is not necessary to consider curves which approach asymptotic values (Andersen and Pedersen, 1996). This is an advantage of the random regression approach over non-linear models, in which an asymptotic value is estimated by extrapolating from collected data. Huisman et al. (2002) also utilized random regression to model body weight in pigs. They used a sire model and accounted for repeated measures on each animal, but did not allow the random residual variance to vary over time. This restriction may have led to incorrect estimation of some of their parameters. Overall, Huisman et al. (2002) concluded that random regression models had better log likelihood values than spline or multivariate models and were valuable to model body weight growth data. Fischer et al. (2004) did fit a heterogeneous measurement error variance structure to growth data in lambs and investigated the opportunity to select on a phenotype derived from random regression analyses. They also mentioned the flexibility inherent to random regression to account for differences in measurement dates across experiments or management structures. Meyer (2004) applied random regression to beef cattle and reported that accuracy of genetic evaluation for growth can be improved by 5% by replacing a multi-trait model with a random regression model. Most of this improvement came from more appropriate modeling of variances and genetic parameters and relied on the assumption that the

random regression model correctly described the covariance structure in the data (Meyer, 2004). Random regression allows the advantage of individually modeled random terms that more accurately account for environmental variation and compute estimates of genetic merit for selection and evaluation of breeding animals.

Meat Quality

While growth and composition are major concerns in the swine industry, meat quality of pork products is also affected by genetic influences. Selection for pigs that have a higher proportion of muscle and reduced amounts of fat may negatively affect meat quality characteristics. Wood (1985) reported that work with leaner pigs (below 10 mm P2 fat thickness) suggested increased occurrence of slightly less juicy pork products. Genetic correlations of carcass leanness to ultimate pH (-0.13), reflectance (0.16), and drip loss (0.05) (Sellier, 1998) suggest decreased meat quality with leaner pigs. Brewer et al. (2002) characterized quality attributes of pork derived from pigs of divergent genetic background in closed terminal sire lines. These lines were Duroc, Pietrain (Hal-1843 normal), Pietrain (Hal-1843 positive), Berkshire, Hampshire (rn^+), Hampshire (RN^-), and a synthetic line. They reported differences in meat quality color characteristics, cooking loss, and shear force between these breeds, but did not find differences in pH or flavor characteristics. Breeds or lines introduced into commercial application should improve these meat quality characteristics or at least not detract from current levels of meat quality.

Heavier slaughter-weight pigs can also be a concern for meat quality. Slaughter weights for swine in the United States have been increasing steadily over recent years from a mean of 108 kg in 1977 to 121 kg in 2004 (USDA, 1998; USDA, 2005a).

Cisneros et al. (1996) reported significant linear regression coefficients on slaughter weight (in kg) for lighter color (-0.006), less firmness (-0.009), a lower 24-h pH (-0.002), higher drip loss (0.029), and decreased tenderness (-0.015) in heavier pigs. All these measures led to a decrease in overall pork quality as market weight increased. In the same study, non-significant effects of slaughter weight on growth rate and feed efficiency were reported. As breeding scheme choices are made for growth and composition goals, meat quality must also be considered.

Impact of Management on Growth and Carcass Quality

Growth performance can be dependent on environmental and housing differences with animals of similar genetic merit showing differing patterns of growth performance due to differences in management (Hamilton et al., 2003). Gentry et al. (2002) reported few differences in growth and meat quality traits between pigs reared in a deep bedded semi-open building and those reared on a slatted floor in a conventional building. Although only 46 and 56 pig carcasses from deep bedded versus slatted floored pens, respectively, were tested for differences in carcass characteristics, some measures were significantly different. Pigs from deep bedded environments had a heavier cold carcass weight, more backfat at the first rib, last rib, and last lumbar positions, shorter carcasses, and higher firmness scores on *longissimus* muscle chops. No differences were reported for 24 h pH, *longissimus* muscle area, color score, marbling score, or objective color scores of L*, a*, or b*. Edwards (2003) stated that energy requirements of outdoor pigs in Northern Europe were generally higher because of increased climatic energy demand, while protein requirements were relatively unaffected. These climatic factors would be similar for pigs raised in the upper Midwest of the United States. Additionally, Edwards

(2005b) reviewed studies measuring meat quality attributes in indoor versus outdoor systems and concluded that no difference in many meat quality attributes were discovered, including measures of juiciness, tenderness, or meat flavor, but pigs reared in outdoor systems had a reduced muscle pH at harvest. While these diverse environmental conditions changed phenotypes of genetically similar pigs, research remains to be done to determine if phenotype differences will occur between different types of indoor finisher facilities. Knowledge of how these different systems affect phenotypes can affect management and marketing practices and decisions for pork producers.

Duroc and Pietrain Breeds

Throughout the years, the Duroc breed has served as a terminal sire population and as a reference sire breed in many research evaluations. Duroc animals and their progeny have been compared in nation-wide breed comparisons in different countries (Kennedy et al., 1996; Moeller et al., 1998), as reference sires to newly imported breeds (Young, 1992a,b), and in studies of heterosis and mating schemes (McLaren et al., 1987a,b; Langlois and Minvielle, 1989a,b; Kuhlers et al., 1994; Blanchard et al., 1999). In general, Duroc pigs and their offspring have been found to grow faster, but also have more backfat than other breeds (Blasco et al., 1994; Kennedy et al., 1996; Moeller et al., 1998; Blanchard et al., 1999). At the same time, Duroc animals tend to have greater rates of lean gain because of their faster overall rate of gain. Durocs tended to have heavier ham and shoulder weight, but similar loin weight compared to other domestic breeds of Hampshire, Landrace, and Yorkshire (Langlois and Minvielle, 1989b). One study has reported that Duroc pigs were more efficient converters of feed to gain (McLaren et al., 1987a), while another study reported Durocs to be less efficient (Mrode and Kennedy,

1993). One area in which Duroc pigs excel is meat quality. Pork from Duroc and Duroc sired pigs tends to have lower shear force and cooking loss, better color and marbling scores, and higher pH than other breeds (Langlois and Minvielle, 1989b; Oliver et al., 1994; Blanchard et al., 1999; Jeremiah et al., 1999). Duroc pigs have been characterized as fast growing, slightly less lean, but favorable for meat quality.

The Pietrain breed has been used in European production systems, but little comparative data have been reported regarding their merit in U.S. production systems. Lean et al. (1972) conducted an early study of purebred Pietrain pigs in Europe and found they were lower in fat content, similar in feed efficiency, but had more meat quality defects than Landrace pigs. McKay et al. (1985) reported Pietrains grew slower, but had larger hams than Yorkshire or Minnesota No.1 pigs. McKay also reported that slower body weight growth combined with less backfat allowed Pietrains to have similar lean tissue growth rates to Yorkshire pigs. Fortin et al. (1987) noted that Pietrains demonstrated early maturing characteristics with leaner carcasses compared with Large Whites. Quiniou and Noblet (1995) used Pietrain boars in their study of equations to predict composition because of their propensity towards leanness, and found them to be leaner than either Large White or Meishan pigs ($P < 0.05$), but similar in leanness to a synthetic line used in the study. Whittemore et al. (2003) conducted a serial slaughter experiment using crossbred pigs that were sired by Landrace, Pietrain, or 50% Meishan/25% Large White/25% Landrace boars. These sires were mated to JSR Genepacker 90 primiparous females to generate types with tendencies to be 'lean', 'blocky', or 'fatty' (Whittemore et al., 2003). The Pietrain crossbred pigs were the leanest and had a slower rate of fatty tissue deposition while also having the largest

longissimus muscle area. Estimates of whole body protein and lipid content as a function of pig live weight also indicated that the Pietrain pigs were the leanest of the three groups. Purebred Pietrain and Pietrain crosses are generally leaner animals with a higher proportion of muscle in valuable wholesale cuts than other breeds.

Duroc vs. Pietrain Studies

Few studies have been undertaken to compare Duroc and Pietrain animals for growth, composition, and meat quality. Those that have been reported have conflicting results for the traits studied, but varying ending weights across the studies may have contributed to these observed differences. Kanis et al. (1990) used Duroc and Pietrain animals to study the effects of recombinant porcine somatotropin (rpST). Among control animals (those not receiving rpST), Pietrain animals had better feed efficiency and lean growth rate in early growth and were leaner at all weights, but had similar feed efficiency and lean growth rate over the entire growth period to Durocs. Affentranger et al. (1996) reported faster growth rate with more backfat, but worse feed efficiency for Duroc animals as compared to Pietrains. Meat quality measures of pH and water holding capacity were better for Duroc pigs in this study. Average daily gain was similar for Duroc and Pietrain influenced animals in a study by Ellis et al. (1996) with Pietrain influenced pigs having less backfat and a larger loin muscle area. Meat quality measures again favored Duroc animals for marbling and Warner-Bratzler shear force. No differences were reported for color score or cooking loss. Garcia-Macias et al. (1996) also reported less backfat and larger loin muscle area for Pietrain animals as compared to Durocs. Similar weight of ham, loin, and shoulder primal cuts were reported for both Duroc and Pietrain progeny with larger belly cuts in Pietrain progeny in this study.

Again, Duroc progeny had better 24-h pH, but no difference was discovered for subjective or objective color scores.

Discrepancies reported in these studies may be due to different end weights used. Many studies found Pietrain-sired pigs to have favorable characteristics at lighter slaughter weights, but these differences may not be as apparent at heavier weights typically seen in U.S. production systems. These studies also used Pietrain animals that carried the malignant hyperthermia mutation in the RYR-1 gene. Pietrain animals that do not carry this allele are now available for use in the U.S. pork industry. Edwards et al. (2006) compared growth traits between pigs that did not carry the mutation in the RYR-1 gene sired by Duroc or Pietrain boars and grown to a common age. Duroc-sired pigs grew faster, but had more backfat than Pietrain-sired pigs. The combination of these differences led to similar rates of fat-free lean accretion from 10 to 26 wk of age. Using the same experimental animal group, Edwards et al. (2003) also reported on carcass composition and meat quality differences. Pietrain-sired pigs were leaner and had larger *longissimus* muscle area than Duroc-sired animals, but Duroc-sired animals excelled in meat quality measures of color, marbling, firmness, pH 24 h postmortem, and drip loss percentage. Similar results were also reported by Cassady et al. (2002) in a study of heterosis and recombination effects on pig growth and carcass traits. Purebred Duroc pigs had faster ADG from 10 to 26 wk of age and more backfat than Pietrain pigs, but Duroc pigs also had smaller loin muscle area than purebred Pietrain pigs. Rauw et al. (2003) compared pigs sired by Duroc or Large White/Pietrain boars and reported no difference in growth for progeny, but did report that Duroc-sired pigs were mostly fatter and had more marbling. Duroc- versus Pietrain-sired crossbred pigs from F_1 German

Landrace by Large White and Leicoma by (German Landrace by Large White) females were compared for carcass composition and meat quality traits (Kuhn et al., 2005). Again, Duroc-sired animals had lower lean percentage, but better meat quality measurements of color, drip loss, and intramuscular fat. Thus, Duroc and Pietrain animals can both be used in selection programs to obtain phenotypes that match commercial production objectives.

Swine Resource Populations

While individual breeds can be studied for improvement of traits, the creation of resource populations allows researchers to discover the underlying alleles that influence these traits. Development of backcross or F_2 resource populations for the discovery of QTL has occurred at several research institutions worldwide. These populations have involved many rustic or indigenous breeds as well as commercial populations, and a summary of the worldwide reported populations is presented in Table I.1. The publications listed in Table I.1 represent the initial genome scan publication for each resource population. Additional phenotypic data and marker genotypes have been collected for many of these populations and reported in subsequent publications which are not listed in Table I.1. Publications that divided phenotypes into multiple publications but that were published simultaneously are listed together.

Table I.1. Summary of F_2 resource populations including original QTL manuscript for each population, founder breeds, number of offspring, number of markers used, and types of phenotypic data analyzed for QTL analysis.

Original QTL manuscript and year	F_0 sire breed[a]	F_0 dam breed[a]	F_1 M[b]	F_1 F[b]	P[c]	G[d]	Trait classes[e]
Andersson et al., 1994	EWB, 2	LW, 8	4	22	193	117	G, C
Rathje et al., 1997[f]	I,5; C,4	C,14; I,12	10	50	114	55	R
Rohrer and Keele, 1998a,b	M,5; WC,5	WC,5; M,5	BC[g]	41	540	156	C
Walling et al., 1998	LW,2; M,2	M,2; LW,2	7	25	390	9	G
Wang et al., 1998[h]	Meishan, 2	Duroc, 2	2	7	99	15	G, C, MQ
(330 F_2 analyzed jointly)	Meishan, 2	Hampshire, 2	3	5	111		
	Meishan, 2	Landrace, 2	2	4	46		
	Minzhu, 2	Hampshire, 2	2	4	69		
	Minzhu, 2	Landrace, 2	2	4	5		
de Koning et al., 1999	Meishan, 19	LW&DL, 126	19	131	619	127	G, R
Paszek et al., 1999	Meishan, 3	Yorkshire, 7	(18 total)		298	119	G
Pérez-Enciso et al., 2000	Iberian, 3	Landrace, 31	6	73	250	7	C
Wada et al., 2000	Göttingen, 1	Meishan, 2	2	19	265	318	G, C
Bidanel et al., 2001	LW, 6	Meishan, 6	6	23	1090	137	G
Grindflek et al., 2001	Duroc, 5	Landrace, 5	5	8[i]	305	29	C, MQ
Malek et al., 2001a,b	Berkshire, 2	Yorkshire, 9	8	26	512	125	G, C, MQ
Nezer et al., 2002	Pietrain, 27	LW, 20	31	82	528	137	G, C
Su et al., 2002	LW, 3	Meishan, 7	5	23	66	48	G
Geldermann et al., 2003	Meishan, 1	Pietrain, 8	3	19	316	185	G, C, MQ
	EWB, 1	Pietrain, 9	2	26	315		
	EWB, 1	Meishan, 4	2	21	335		
Lee et al., 2003	KN, 5	Landrace, 9	11	36	240	24	G
Sato et al., 2003	Duroc, 1	Meishan, 1	4	24	864	180	G, C, MQ
Zuo et al., 2003	LW, 3	Meishan, 7	5	23	140	24	MQ
Stearns et al., 2005	Berkshire, 3	Duroc, 18	6	56	806	30	G, C

[a] Breed abbreviations: DL = Dutch Landrace, EWB = European wild boar, KN = Korean native, LW = Large White, M =Meishan, WC = White Composite

[b] M = Males, F = Females

[c] Largest number of animals for any one trait in each manuscript

[d] Number of genetic markers used in genotyping in each manuscript

[e] Traits analyzed in the manuscript
G = Growth, C = Carcass characteristics, MQ = Meat quality, R = Reproduction

[f] I = Increased ovulation rate and embryonal survival line, C = Random selection control line (Neal et al., 1989)

[g] BC = Backcross design

[h] Family structures from Yu et al. (1995)

[i] Norwegian Slaughter Pig cross sows (50% Norwegian Landrace-50% Yorkshire)

The seminal F_2 resource population was created by Andersson et al. (1994) and involved breeding two European wild boars with eight Large White sows. This cross of an undomesticated breed with a commercially used breed resulted in 200 F_2 animals which exhibited variation in traits of growth and backfat thickness. Although the small number of F_2 animals prohibited finding QTL with smaller effects, QTL affecting 7.5 to 18.7 % of F_2 variance were discovered. This population spawned other efforts to create resource populations from several other breeds.

A breed utilized in many resource populations is the Meishan breed from China, which excels for reproductive traits (Rohrer and Keele, 1998a,b). These animals were often crossed with commercially used breeds, and traits of growth, composition, meat quality, and reproduction were studied. Of the 25 populations in Table I.1, 14 included Meishan germplasm. Recently, resource populations have been created from breeds utilized in commercial production (Grindflek et al., 2001; Malek et al., 2001a,b; Nezer et al., 2002; Stearns et al., 2005). The advantage of these populations is the ability to quickly incorporate QTL results into breeding schemes that are already in use in commercial production.

The number of F_2 animals generated in the populations listed in Table I.1 varied from 5 to 1090 animals with many of the populations containing 200 to 350 animals and three of the populations having more than 800 animals included in the initial publications. As more animals are included in the analyses, QTL that control a smaller percentage of phenotypic variation can be discovered. A sample size of 1050 animals is required to find a QTL that controls 1% of phenotypic variation at an error rate of 0.05 with 90% power (Weller, 2001). Although the populations with 100 to 200 animals have identified

putative QTL (e.g. Andersson et al., 1994), more F_2 animals allows more recombination events to take place, so more QTL can also be found in larger populations.

These populations also differed greatly in the number of genetic markers analyzed. The studies that genotyped more than 115 markers were able to obtain a full scan of the genome, while those studies that genotyped fewer than this number of markers chose to target specific chromosomes with their genotyping efforts. As more markers are genotyped on each animal, the distance between markers decreases and the confidence interval for the estimated position of putative QTL is reduced. The ultimate goal of a resource population is to identify a chromosomal region containing a gene that controls a significant portion of the variation for a trait of interest. Further saturation of potential positions of QTL on chromosomes with additional linked markers allows a more accurate description of the QTL position (e.g. Rattink et al., 2000; Thompsen et al., 2004) and facilitates fine mapping to possibly identify the causative gene at the QTL.

An ideal resource population would be derived from breeds that are phenotypically distinct, but with alleles in both breeds that are segregating and could be identified in commercial breeds used in pork production. If these breeds are used in current breeding schemes, it is a straightforward task to incorporate selection for beneficial QTL into breeding objectives and ultimately influence commercial production. Ideally, resource populations would be fixed for alternative alleles at each marker, which would allow more power of test at each marker position (Weller, 2001). The creation of a population should involve the generation of enough F_2 animals and possibly subsequent later generations to discover QTL that affect a smaller percentage of phenotypic variation, and the measurement of phenotypes should be numerous enough to allow

discovery of QTL that affect traits important to pork production. Finally, the markers used should cover the entire genome, as traits of interest have been found on every autosome and the X chromosome (Hu et al., 2005). Proper design and creation of a resource population will lead to discovery of important QTL and will allow for their implementation into breeding programs.

Growth QTL

Many recent studies have undertaken the task of determining QTL for various growth phenotypic traits. Description of growth can involve weights at different ages, gain in weight between ages, and weight gain partitioned into protein and fat components. Difficulties in comparison of traits from one population to another arise as phenotypes are defined in many different ways across populations. Table I.2 represents QTL for birth weight and ADG during the finishing phase although ADG is reported in many different formats in different studies. A summary of QTL studies published through mid-2004 (Hu et al., 2005) attempted to combine some, but not all, similar phenotypes. Comparison of off-test or harvest weight QTL across studies is difficult due to the many different protocols for growth evaluation and marketing pigs for harvest. These QTL for growth have been discovered on most of the autosomes except 5, 11, 15, 16, 17, and 18.

Table I.2. Summary of reported QTL chromosomal locations for growth traits.

Trait[a]	Manuscript	Chromosome
Birth weight	Knott et al., 1998	1, 12, 13
	Paszek et al., 1999	4
	Wada et al., 2000	1
	Bidanel et al., 2001	4, 7
	Malek et al., 2001a	3
	Knott et al., 2002	4
	Quintanilla et al., 2002	3
	Sato et al., 2003	7
ADG on test	Knott et al., 1998	2, 4, 10
	Malek et al., 2001a	2, 4, 8, 9
ADG, 10 to 22 wk of age	Bidanel et al., 2001	3, 4, 6, 7
	Knott et al., 2002	4
	Quintanilla et al., 2002	8, 9
Growth rate, 25-90 kg	de Koning et al., 2001	1, 2, 4, 6, 7, 8, 12, 13, 14
	Sato et al., 2003	6

[a] Hu et al. (2005) summary is the basis for trait names

Carcass Merit QTL

Backfat thickness (in varying locations) is the most commonly reported class of QTL for carcass traits. One reason that so many backfat QTL have been reported is the possible pleiotropic effects of these QTL that affect fat deposition at many body locations. Regions that have been reported to contain QTL in several studies include SSC 1, 4, 6, and 7 (Table I.3). Not all studies have conducted entire genome scans when searching for QTL. Several studies have targeted these previously mentioned chromosomes, which may have disproportionately increased the number of reported QTL on them.

Average backfat has been measured in several studies because of its significant QTL reported in Andersson et al. (1994). However, the location of measurement and the number of measurements combined to calculate average backfat has not been consistent across studies, so the trait is not summarized here. Instead, locations of QTL for individual points of measurement for backfat traits have been reported in Table I.3. While some QTL for the backfat thickness at the first rib, tenth rib, last rib, and last lumbar vertebra share the same location, individual studies have reported unique QTL for each trait. Another aspect of carcass composition is the size of the *longissimus* muscle area. This important muscling measure has QTL that have been identified in several studies, but generally with only one QTL location in each study. Nevertheless, QTL for *longissimus* muscle area have been reported on SSC 2, 4, and 6, and these locations were identified in eight of the ten publications in Table I.3.

Table I.3. Summary of reported QTL chromosomal locations for carcass traits.

Trait	Manuscript	Chromosome
First rib backfat	Rohrer and Keele, 1998a	7, 10, X
	Wang et al., 1998	7
	Varona et al., 2002	4, 6
	Stearns et al., 2005	6
Tenth rib backfat	Rohrer and Keele, 1998a	1, 7, 13, X
	Malek et al., 2001a	1, 6, 7, 13
	Stearns et al., 2005	2, 18
Last rib backfat	Rohrer and Keele, 1998a	1, 7, X
	Wang et al., 1998	7
	Malek et al., 2001a	1, 4, 5, 7, 12, 13, 14
	Milan et al., 2002	2, 7, X
	Varona et al., 2002	4, 6
	Stearns et al., 2005	6, 18
Last lumbar vertebra backfat	Rohrer and Keele, 1998a	1, 5, 7, 14, X
	Wang et al., 1998	7
	Malek et al., 2001a	1, 4, 5, 7
	Stearns et al., 2005	2
Longissimus muscle area	Andersson-Eklund et al., 1998	3
	Rohrer and Keele, 1998b	1, 8, 11, 14, X
	Jeon et al., 1999	2
	Pérez-Enciso et al., 2000	4
	Malek et al., 2001a	1, 4
	Ovilo et al., 2002b	6
	Varona et al., 2002	2, 4, 6
	Wimmers et al., 2002	4
	Sato et al., 2003	6
	Stearns et al., 2005	2, 6

Meat Quality QTL

While growth and body composition measurements can be obtained on live animals, other traits can only be measured after harvest. The inability to collect meat quality phenotypes on the live animal increases the importance of discovering meat quality QTL for use in selection of prospective parents of the next generation. Table I.4 lists reported locations of QTL for meat quality traits grouped by similar trait classification. The trait of 24 h pH is an important indication of meat quality in the carcass and QTL for this trait have been reported on 13 different chromosomes. Only SSC 6, 14, and 15 contain QTL that have been reported in multiple studies. Subjective color, marbling, and firmness scores are fresh meat quality attributes that have QTL that have been reported in two studies (Malek et al., 2001b; Stearns et al., 2005). A QTL has been reported on SSC 2 in both studies for color. In addition, Stearns et al. (2005) reported a QTL on SSC 2 for marbling. Objective color scores measure reflectance (L*), redness, (a*), and yellowness (b*) and have been measured across several resource populations. While all autosomes except 9, 10, 11, and 12 have QTL reported for objective color scores, regions on SSC 4, 7, and 14 have been reported in multiple studies to affect these traits.

Specific QTL have been identified for water retention parameters, shear force measurements, and sensory taste panel attributes. The analysis of water retention measurements (drip loss, cook loss, and water holding capacity) is important to processors of pork products and can determine how well these products will perform in further value-added processing. Five studies have reported putative QTL for these water retention traits. Shear force has been measured with differing procedures (e.g. Warner-

Bratzler or Instron), but they attempt to quantify a similar attribute of cooked products. Although significant QTL for shear force have been reported in three studies, none of the QTL positions have been replicated across the studies. An additional tool to measure cooked product palatability is the trained sensory panel. While individual sensory panels evaluate meat products with different organoleptic descriptions on differing scales, QTL for the traits of juiciness, tenderness, and off-flavor were discovered in Malek et al. (2001b) and Stearns et al. (2005). Similar to subjective fresh meat scores, QTL were found on SSC 2 for two of these three traits in both studies. Only Stearns et al. (2005) reported a QTL on SSC 2 for juiciness. Intramuscular fat percentage can be directly determined through chemical extraction (AOAC, 2000) and has been reported in several studies (Table I.4). Most studies have reported just one QTL for intramuscular fat in their results, and multiple studies have reported the location of this putative intramuscular fat QTL on either SSC 4 or SSC 6 (Table I.4).

Table I.4. Summary of reported QTL chromosomal locations for meat quality traits.

Trait	Manuscript	Chromosome
24 h pH	Bertram et al., 2000	15
	de Koning et al., 2001	4, 9, 11, 14, 18, X
	Malek et al., 2001b	5, 6, 14, 15
	Ovilo et al., 2002a	3
	Geldermann et al., 2003	6, X
	Su et al., 2004	2, 6, 7
Color	Malek et al., 2001b	2, 12, 17
	Stearns et al., 2005	2
Marbling	Malek et al., 2001b	1, 8, 10
	Stearns et al., 2005	2
Firmness	Malek et al., 2001b	2
	Stearns et al., 2005	2
L*	de Koning et al., 2001	1, 3, 4, 14
	Malek et al., 2001b	2, 4, 5, 7, 14, 15, 17, 18
	Ovilo et al., 2002a	4, 7
	Sato et al., 2003	3
a*	Bertram et al., 2000	15
	de Koning et al., 2001	13, 14, 15
	Ovilo et al., 2002a	4, 7, 8
	Geldermann et al., 2003	6
	Stearns et al., 2005	2, 13
b*	de Koning et al., 2001	13, 14
	Stearns et al., 2005	2
Drip loss	Bertram et al., 2000	15
	de Koning et al., 2001	4, 6, 14, 18
	Malek et al., 2001b	1, 2, 11
	Stearns et al., 2005	2
Water holding capacity	Malek et al., 2001b	2, 13
	Su et al., 2004	1, 4, 6
Cook loss	de Koning et al., 2001	7, 18
	Malek et al., 2001b	14
	Stearns et al., 2005	13

Table I.4 (cont'd).

Shear force	de Koning et al., 2001	9, 13
	Malek et al., 2001b	10, 15
	Stearns et al., 2005	2
Juiciness	Malek et al., 2001b	17
	Stearns et al., 2005	2
Tenderness	Malek et al., 2001b	2, 14, 15
	Stearns et al., 2005	2
Off-flavor	Malek et al., 2001b	2, X
Intramuscular fat	de Koning et al., 1999	6
	Harlizius et al., 2000	X
	Rattink et al., 2000	4
	de Koning et al., 2001	4
	Grindflek et al., 2001	6
	Ovilo et al., 2002b	6
	Szyda et al., 2002	6
	Zuo et al., 2003	4
	Su et al., 2004	4
	Stearns et al., 2005	2, 6, 13, 18

F_2 Population QTL Analysis Procedures

Methodology to analyze F_2 or backcross populations for putative QTL has evolved as more emphasis on error structures and accounting for environmental variance components have become increasingly more complex. Initially, line cross analyses focused on associating single markers with phenotypes, but were soon replaced by methods to estimate likelihood of any region of the genome controlling part of the variance of the trait. This method is called interval mapping and involves calculating the probability of recombination between markers and the QTL position and how this QTL relates to the phenotype of interest (Lander and Botstein, 1989). Further simplification of this methodology used least squares regression to regress the phenotypes against the probabilities that an individual has a certain genotype at each position in the genome (Haley and Knott, 1992; Haley et al., 1994). This analysis includes probabilities for an F_2 individual to inherit a particular allele from which parent at points throughout the genome. In most analyses this evaluation is performed at continuous 1 cM intervals across the entire region with segregating markers in the population. The full model that includes the QTL effects is tested against the reduced model without the effects to obtain an F-test and that is compared to significance threshold levels. The development of an extension of this regression analysis to account for QTL that segregate in both breeds at similar frequency was reported in Knott et al. (1996). This extension involves the analysis of groups of progeny from one sire or dam and is referred to as the half-sib analysis. This half-sib analysis can detect QTL that are missed in the line cross analysis, and can be utilized in populations with outbred founders that have the same alleles present in both founder breeds. Dekkers et al. (2003) proposed combined regression

interval mapping, in which line cross and half-sib analyses are performed jointly. The QTL discovered in the Dekkers et al. (2003) joint analyses were classified as significant for line cross only, significant for half-sib only, or significant for the combined analysis, but not significant for either type of analysis individually. Since significance of a QTL cannot be obtained from the standard F-tables because of the large number of correlated tests conducted from the same marker data, permutation tests are typically used to derive proper significance thresholds (Churchill and Doerge, 1994). Additionally, the accuracy of the position of QTL can be described through the use of confidence intervals. Bootstrap methods have been developed to estimate these intervals (Visscher et al., 1996). The separate line cross and half-sib analyses have been combined with permutation tests for significance thresholds and bootstrap methods for confidence intervals into a web interface to create the QTL Express software (Seaton et al., 2002).

Although the regression interval mapping procedures have been used in many analyses and are a good beginning step to find QTL that have been subsequently reconfirmed in other experiments (e.g. Walling et al., 1998), it does inherently contain only fixed effects and can be improved upon for analysis of populations derived from outbred populations. To improve the estimation of QTL effects, Fernando and Grossman (1989) proposed modeling the QTL effect as a normally distributed random variable with mean zero and variance to be estimated. This variance is estimated by assessing the degree of phenotypic similarity between relatives according to the probability of sharing identical by descent alleles at specified positions. An alternative analysis scheme has been proposed by Pérez-Enciso and Varona (2000) in which a mixed-model approach allows for QTL segregation within lines as well as for differences in mean QTL effects

between lines. This method allows the estimation of differences in additive variances between the parental lines. Pérez-Enciso and Varona (2000) simulated data to exhibit its implementation; however, no studies have been reported that have used this method of analysis. QxPak, a software package that has recently been released, incorporates these methods into QTL estimation (Pérez-Enciso and Misztal, 2004). Most reported F_2 animal studies have implemented line cross least squares regression analysis for QTL discovery.

CHAPTER II

INFLUENCE OF FINISHER FACILITIES ON PIG GROWTH PERFORMANCE[1]

Abstract

Pigs from the F_2 generation of a Duroc by Pietrain resource population were finished in either a Modified Open Front or a Test Station building with bedded, solid floors to evaluate finisher influence on growth, composition, and meat quality traits. Serial data of body weight, tenth rib backfat, *longissimus* muscle area, and last rib fat were obtained at three week intervals from 10 to 22 wk of age. From these measurements, estimates of fat-free total lean, total body fat, empty body protein, and empty body lipid were calculated. At harvest, carcass composition traits, carcass temperature, and *longissimus* muscle pH were obtained. Primal cut weights, meat quality evaluation traits, proximate analysis measurements, and sensory taste panel phenotypes were also recorded. Models that included genetic, permanent environment, and residual error variance components were used to evaluate these traits. Many of the traits did not differ significantly between pigs raised in the two building types. Pigs finished in the Modified Open Front building were heavier at harvest, had more backfat at 22 wk of age at the tenth rib and last rib, and had more backfat at harvest at the tenth rib, last rib, and last lumbar vertebra. Serial data analyses revealed differences in patterns of weight, leanness, and fatness accretion not apparent in single time point measurements. Although body weight did not differ at 10 or 22 wk of age, the pigs reared in the Test Station building grew more slowly at first, but then grew more quickly later in the finisher phase

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to achieve the same overall weight gain from 10 to 22 wk of age. Pigs raised in the Modified Open Front building had a greater backfat accretion rate from 10 to 22 wk of age than pigs raised in the Test Station building. Additionally, these pigs had a greater decline in pH from 45 min to 24 h after harvest and were more tender based on Warner-Bratzler shear force measurements. Heritability of the serial traits generally increased for all traits from 10 to 22 wk of age. Body weight and *longissimus* muscle area had similar increasing heritability patterns, whereas tenth rib backfat and last rib backfat had similar heritability patterns, increasing from 10 to 16 wk of age and remaining constant thereafter. Thus, animals of similar genetic merit can show differences in growth patterns as influenced by differing finisher facilities.

Introduction

Growth performance can be dependent on environmental and housing differences with animals of similar genetic merit showing differing patterns of growth performance due to differences in management (Hamilton et al., 2003). Gentry et al. (2002) reported differences in growth and meat quality traits between pigs reared indoors or outdoors. While these diverse environmental conditions changed phenotypes of genetically similar pigs, further research is needed to determine if differences in growth will occur when pigs are housed in different types of enclosed facilities. Knowledge of how these different systems affect phenotypes can affect management and marketing practices and decisions for pork producers. To determine the influence that differing facility types may have on pig growth, a genetic resource population with known pedigrees can be an ideal study group. With known pedigrees and similar genetic merit amongst animals in a

resource population, those genetic factors can be accounted for and actual differences in management practices can be tested.

Traits that are measured once in the lifetime of an animal do not represent how the phenotype of that animal may change as the animal matures. Phenotypes such as body weight and composition traits can be measured serially over time and modeled through the use of random regression (Meyer, 2004). These procedures allow (co)variance matrices to be estimated that model the relationship of the trait at different points throughout the measurement period. Previous reports have demonstrated the usefulness of random regression modeling of weight data in pigs (Huisman et al., 2002; Edwards et al., 2006). Evaluation of serially measured traits allows more in depth characterization of phenotypic differences. The objective of this study was to compare growth, composition, and meat quality traits for pigs of similar genetic merit finished in two different types of finishing buildings.

Materials and Methods

Population Development

A three-generation resource population was developed at Michigan State University and used to study traits of growth, body composition, and meat quality. Semen from four F_0 Duroc sires from a closed unselected control population (Kuhlers et al., 2003) and sixteen F_0 Pietrain dams from a closed herd propagated the F_1 generation. All F_0 animals were determined homozygous normal for the RYR-1 gene by a DNA test (Fujii et al., 1991). All animals were produced through artificial insemination at the Michigan State University Swine Teaching and Research Farm. From F_1 progeny, 51 females and six males (sons of three F_0 sires) were retained to produce 1259 F_2 pigs born

in 142 litters across 11 farrowing groups. Females were retained across multiple parities to produce F_2 progeny.

Animal Management

Sows were placed into farrowing crates one week prior to farrowing. Baby pigs were processed (individually identified by ear tag, given 0.5 ml penicillin and 1 ml iron dextran subcutaneously, and tails clipped) at approximately 1 d of age. Pigs were weaned at 16-25 (mean of 19.8) d of age and were sorted into nursery pens by sex and weight. All pigs were managed similarly in farrowing and nursery stages. At 10 wk of age, F_2 pigs were placed into one of two finishing facilities at the Michigan State University Swine Teaching and Research Farm. Farrowing groups 1, 3, 5, 7, 9, and 11 (n = 521 pigs) were placed into a Modified Open Front (MOF) building with eight pens, in which four pens differed in size from the other four. Four larger pens (2.03 m by 6.91 m) with two-space feeders were targeted to contain 16 pigs. Four smaller pens (1.42 m by 6.91 m) with one-space feeders were targeted to contain 12 pigs. Each pen had two-thirds solid, one-third slatted floors and wet-dry feeders. Farrowing groups 2, 4, 6, 8, and 10 (n = 465 pigs) were placed into a test station (TS) facility in which pens had solid floors and were bedded with straw or wood shavings and had single-space dry feeders and cup drinkers. All 25 pens utilized (1.42 m by 4.93 m) were targeted to contain four pigs. All diets fed were Michigan State University standard swine farm diets that met or exceeded NRC (1998) requirements for all nutrients at each production stage. Pigs in both facilities had ad libitum access to feed and water.

Trait Collection

Live animal traits collected on F_2 animals included BW at birth, weaning, 6, 10, 13, 16, 19, and 22 wk of age. An ADG from 10 to 22 wk of age was calculated. Additionally, B-mode ultrasound (Pie Medical 200SLC, Classic Medical Supply, Inc., Tequesta, FL) estimates of tenth rib backfat (BF10), last rib backfat (LRF), and *longissimus* muscle area (LMA) were recorded at 10, 13, 16, 19, and 22 wk of age. At each of these time points, estimates of fat-free total lean (FFTOLN), total body fat tissue (TOFAT), empty body protein (EBPRO), and empty body lipid (EBLIPID) were calculated using equations similar to those used by Wagner et al. (1999). Animals were also weighed prior to leaving the farm for harvest.

At harvest, pigs were transported to one of two abattoirs. A total of 176 pigs were harvested at the Michigan State University Meats Laboratory (East Lansing, MI), and the remainder of the pigs were transported to a small federally inspected plant in western Michigan (DeVries Meats, Coopersville, MI). Both groups were fasted and allowed to rest overnight with access to water. Ear tag and tattoo numbers were collected at slaughter to maintain identity of each carcass. Carcass traits that were collected included hot carcass weight and pH and temperature in *longissimus dorsi* at 45 min and 24 h postmortem. After overnight chilling, measurements taken according to National Pork Producers Council guidelines (NPPC, 2000) included midline first rib backfat, last rib backfat, last lumbar backfat, and carcass length. Weights of primal cuts of ham, closely trimmed loin, picnic shoulder, Boston shoulder, belly, and spareribs were recorded. During carcass fabrication, measurements of tenth rib backfat and *longissimus* muscle area were also recorded. A section of loin from the tenth rib to the last rib was returned

to Michigan State University for further meat quality analysis. All measurements were taken from the left side of each carcass.

Boneless *longissimus dorsi* were removed from loin sections and external fat removed. A small portion of *longissimus dorsi* was diced and frozen for proximate analysis. Two 2.54 cm thick chops were cut from the anterior end for fresh meat quality analysis. The two chops were allowed to bloom for a minimum of 10 minutes and evaluated for subjective scores of color and marbling (NPPC, 2000) and firmness (NPPC, 1991). The color score scale ranged from 1 (pale pinkish gray) to 6 (dark purplish red). The marbling score scale was 1 to 10 (closely approximating fat percentage). The firmness score scale was 1 (very soft and watery) to 5 (very firm and dry). Additionally, objective color scores of CIE L* (lightness), a* (redness), and b* (yellowness) were obtained using a Minolta CR-310 colorimeter (Ramsey, NJ) with a D_{65} illuminant and a two-degree standard observer. Chops were weighed, hung in sealed plastic bags for 24 h at 4°C, and then weighed again for drip loss measurement. The remaining section of the *longissimus dorsi* was vacuum packaged, aged 7 d at 4°C, and frozen for further meat quality tests of cook yield, shear force, and sensory taste panel analysis.

From frozen loin sections, two 2.54 cm thick chops were cut for cook yield and Warner-Bratzler shear force (WBS) analysis. For cook yield measurements, each chop was thawed, weighed, cooked to 71°C internal temperature on a Taylor clamshell grill (Model QS24, Taylor Co., Rockton, IL), cooled to room temperature, and weighed again. From these chops six cores (three cores from each chop) were taken parallel to the muscle fiber direction using a drill press-mounted corer. Cores were sheared perpendicular to muscle fibers using a Warner-Bratzler head on a TA-HDi texture

analyzer (Texture Technologies Corp., Scarsdale, NY). The cross-head speed was 3.30 mm/s. Samples for proximate analysis were ground using dry ice and measured for moisture (oven drying), fat (soxhlet ether extraction), and protein (nitrogen combustion, Model FP-2000, Leco Inc., St. Joseph, MI) following AOAC procedures (2000).

A trained panel of seven healthy adults (ages 20-65) was utilized to determine specific sensory attributes of each *longissimus* chop. The sensory panel was trained according to Meilgaard et al. (1991) and AMSA (1995). All panelists had experience in sensory evaluation and were previously trained to evaluate various meat products. Each sample was evaluated for juiciness, muscle fiber and overall tenderness, connective tissue, and off-flavor using an 8 point hedonic scale. Higher scores were more favorable in each of the first four categories and indicated extremely juicy, extremely tender, or no connective tissue for each of these attributes, respectively, while lower scores for off-flavor were indicative of less off-flavor.

Frozen chops were thawed for 24 h at 2.6°C and then cooked on a Taylor clamshell grill (Model QS24, Taylor Co., Rockton, IL). The upper plate was set to 104.4°C and the bottom plate was set to 102.8°C with a 2.16 cm gap between plates. Temperature was monitored by inserting a copper constantan thermocouple (0.051 cm diameter, 15.2 cm length, Omega Engineering Inc., Stamford, CT) into the geometric center of the pork chop. Chops were cooked to a final internal temperature of 71°C. Sample preparation included cutting 1.27 cm cubes from the center portion of each chop, and two cubes were placed in 2 oz. soufflé cups and covered with a lid. Soufflé cups were placed in a Pyrex two quart bowl with a lid, and the bowl was covered with warm

towels to keep the samples warm. The insulated bowl was placed in an insulated container and transferred to the sensory evaluation room.

Testing took place in climate controlled, partitioned booths with cool incandescent light. The order of sample preparation was randomized within each session to minimize positional bias and a 3 digit random code was used to label the samples. The samples were picked up with a toothpick, chewed with the molars, and evaluated. Expectorant cups were provided to prevent taste fatigue and distilled, deionized water was used to clean the palate between samples. The panelists were standardized each day by evaluating a warm-up sample and discussing the results. A total of 18-24 samples were evaluated on each day, and the day was divided into three sessions with a 15 min break between each session. A total of 958 animals had carcass and meat quality traits measured.

Trait Analysis

The 22 wk of age off-test traits, carcass phenotypes, and meat quality traits were analyzed with a mixed model that included the fixed effects of sex and finisher and the random effect of farrowing group for off-test traits or harvest group for carcass and meat quality traits. An animal random effect augmented with a (co)variance matrix that accounted for genetic relationships among animals was also included in all models. For off-test traits, age at measurement was included as a covariate in the analysis. Table II.1 lists whether carcass weight, harvest age, or neither covariate was used for carcass and meat quality trait models. All covariates included in each model were those that were found to be important to the model ($P < 0.20$) when each trait was analyzed by ordinary

least squares analysis of variance without random effects included. The following model was used for analysis:

$Y_{ijklm} = \mu + sex_i + fin_j + grp(fin)_{jk} + pen(grp)_{kl} + g_m + \beta x_{ijklm} + e_{ijklm}$
where

Y_{ijklm} = record on the m^{th} pig within i^{th} sex, j^{th} finisher, k^{th} group, and l^{th} pen,
μ = overall mean of trait,
sex_i = fixed effect of sex of animal i (Barrow or Gilt),
fin_j = fixed effect of finisher j (MOF or TS),
$grp(fin)_{jk}$ = random effect of farrowing group (1-11) or harvest date (1-33) nested within finisher where grp ~$N(\mathbf{0}, \mathbf{I}\sigma_{grp}^2)$,
$pen(grp)_{kl}$ = random effect of pen (1-25) nested within farrowing group where pen ~$N(\mathbf{0}, \mathbf{I}\sigma_{pen}^2)$,
g_m = random effect for animal m,
x_{ijklm}= covariate appropriate to each trait such that β is the partial regression coefficient on x_{ijklm}, and
e_{ijklm} = random error ~$N(\mathbf{0}, \mathbf{I}\sigma_e^2)$.

Here, $\mathbf{g} = \{g_m\} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ where **A** is the numerator relationship matrix among animals and σ_a^2 is the additive genetic variance. The relationship matrix accounted for relationships among progeny plus the three generations of sire and dam ancestors.

Serial Data Analysis

Serial BW and ultrasound estimates from 10 to 22 wk of age were used to generate random regression equations to model pig BW, BF10, LMA, LRF, FFTOLN, TOFAT, EBPRO, and EBLIPID on age at measurement. Age at measurement was modeled as week on-test, calculated as age in weeks minus nine (i.e. 1, 4, 7, 10, and 13 as distinct covariate values used in the analysis). A random intercept for each animal and a linear regression on age for each animal was included in each model. Table II.2 lists the polynomial order of week of age and interactions used in models for these eight traits as determined by log likelihood tests of significance. During preliminary analysis of these traits a trend for increasing residual variance as age increased was noted. To account for

heterogenous residual variances across serial measurement and the relationship between time points, the $\mathbf{e} = \{e_{ijklm}\}$ was specified as normally distributed with a general (co)variance structure calculated from the data and specified within and across weeks with five variance and 10 covariance terms. The (co)variances of the random animal intercept as well as the animal linear by week term were also modeled. The following model was used:

$Y_{ijklmn} = \mu + \Sigma week_i^{\phi} + sex_j + \Sigma(sex*week^{\phi})_j + fin_k + \Sigma(fin*week^{\phi})_k + grp(fin)_{kl} + pen(grp)_{lm} + g_n + \alpha_n*Zi + e_{ijklmn}$

where

Y_{ijklmn} = record on the n^{th} pig within j^{th} sex, k^{th} finisher, l^{th} group, and m^{th} pen regressed on ϕ^{th} polynomial week i,
μ = overall mean of trait,
$week_i^{\phi}$ = fixed regression coefficients for polynomial terms ϕ (1-4) of week i,
sex_j = fixed effect of sex of animal j (Barrow or Gilt),
fin_k = fixed effect of finisher k (MOF or TS),
$grp(fin)_{kl}$ = random effect of farrowing group l (1-11) nested within finisher where grp ~$N(\mathbf{0}, \mathbf{I}\sigma_{grp}^2)$,
$pen(grp)_{lm}$ = random effect of pen m (1-25) nested within farrowing group where pen ~$N(\mathbf{0}, \mathbf{I}\sigma_{pen}^2)$,
g_n = random intercept for animal n,
α_n = random linear regression coefficient on age for animal n,
Z_i = week on test as a covariate, and
e_{ijklmn} = random error.

The distributional assumptions on $\mathbf{g} = \{g_n\}$ and $\boldsymbol{\alpha} = \{g_n\}$ were such that:

$$\begin{bmatrix}\mathbf{g}\\ \boldsymbol{\alpha}\end{bmatrix} \sim N\left(\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\end{bmatrix}, \begin{bmatrix}\mathbf{A}\sigma_g^2 & \mathbf{A}\sigma_{g\alpha}\\ \mathbf{A}\sigma_{g\alpha} & \mathbf{A}\sigma_{\alpha}^2\end{bmatrix}\right),$$ where σ_g^2 is the intercept genetic variance for the individuals, σ_{α}^2 is the linear age by animal genetic variance, and $\sigma_{g\alpha}$ is the genetic covariance between the intercept and linear term for each animal.

Results and Discussion

Off-Test, Carcass Composition, and Meat Quality

Many of the off-test, carcass composition, and meat quality traits did not differ significantly between pigs raised in the MOF building and those raised in the TS building (Tables II.3 and II.4). These findings are consistent with Gentry et al. (2002), who reported no differences for carcass measurements, 24 h pH, drip loss, sensory panel, and shear force values for pigs raised in deep bedding versus those raised on slatted floors. At 22 wk of age, BW was not significantly different between the two finishers, but once pigs reached harvest age, BW was significantly higher in animals from the MOF than the TS finisher (113.4 vs. 110.7 kg, respectively). This difference led to a trend for hot carcass weight to be heavier in pigs from the MOF finisher compared to the TS finisher, contrary to Gentry et al. (2002) who reported heavier cold carcass weights in pigs from bedded facilities versus those on slatted floors. Since BW and hot carcass weight both varied in the same proportion in this study, dressing percentages for pigs raised in these two finishers was not different. While neither carcass temperature nor pH were different between carcasses from pigs in these two finishers, the decline in pH from 45 min to 24 h after harvest was greater among carcasses from pigs raised in the MOF versus the TS finisher (0.89 vs. 0.83, respectively).

Off-test BF10 and LRF were significantly greater in pigs from the MOF building than the TS building (Table II.3). These differences were also discovered at slaughter with carcass tenth rib backfat and last rib backfat greater in carcasses from pigs reared in the MOF versus those reared in the TS building. Additionally, backfat at the last lumbar vertebra was greater among carcasses from MOF reared pigs than those reared in the TS

building (Table II.4). Gentry et al. (2002) reported similar results of more backfat on pigs raised in deep bedded pens versus those raised on slatted floors.

All primal cut weights, meat quality evaluation traits, proximate analysis traits, and sensory taste panel measurements were not significantly different between carcasses from pigs raised in the MOF compared to those from the TS building (Table II.4). Additionally, drip loss and cook yield percentages were not significantly different. Warner-Bratzler shear force values of *longissimus* chops from pigs raised in the MOF were lower than values for chops from pigs raised in the TS building (3.14 vs. 3.36 kg, respectively).

The observed differences in fat measurements may be a result of either differing feeder types in the two buildings or changes in maintenance energy requirements. Wet-dry feeders have been reported to cause pigs to have more subcutaneous fat than pigs fed on dry feeders (Barnes et al., 1999). Since the MOF was equipped with wet-dry feeders, this could explain part of the differences discovered in our study. An environmental difference between the MOF and TS finishers was the amount of climate control inherent to each building. The MOF building was naturally ventilated and had supplemental heat in the winter. While the TS building had a curtain, wind blocks, and hovers in winter, it did not have supplemental heat, and pigs were more exposed to the ambient temperature. Considering these environmental differences, pigs in the TS may have had less fat because they may have had an increased maintenance energy requirement in the TS environment versus those raised in the MOF building. Since the energy requirement of the pigs raised in the MOF may have been less, the excess energy may have been stored as fat. These differences in subcutaneous fat may be partially responsible for the trend

($P = 0.116$) of 24 h carcass temperature to be higher for pigs raised in the MOF versus the TS building. Since higher carcass temperatures can allow faster pH declines, the carcass temperature difference may have led to the greater pH decline from 45 min to 24 h after harvest for pigs finished in the MOF building than for those finished in the TS building.

Serial Data Results

Although differences between finishers may not have been significant for some of the off-test data, further evaluation of the serial data revealed some differences in growth patterns between the MOF raised pigs and the TS raised pigs. The eight serial traits analyzed were BW, BF10, LMA, LRF, FFTOLN, TOFAT, EBPRO, and EBLIPID. These traits were plotted against week of age with standard error bars included in Figures II.1-8. Figure II.1 shows how BW changes differed between MOF and TS raised pigs. While 10 wk and 22 wk BW did not differ, the shape of the BW curves differed slightly with the pigs in the MOF building being heavier through the three midpoints of the finisher phase. Pigs in the TS building grew faster in the latter stages of the 10 to 22 wk of age period and BW was not different at 22 wk of age.

Figure II.2 depicts the trend for increasing differences in BF10 as pigs became older. Pigs reared in the MOF building had more BF10 than those reared in the TS and continued this trend through harvest as indicated by the differences reported in the carcass data. In Figure II.3, LMA took a similar pattern to that reported for BW in this study with no differences at 10 wk or 22 wk of age. Again, small differences occurred in the shape of the LMA growth curve between pigs raised in the MOF compared to those raised in the TS building; however, none were significant. Figure II.4 for LRF indicated

a similar pattern to BF10 over time with pigs from the MOF building having an increasing trend for more backfat than those from the TS building. These differences in backfat were significant at 22 wk of age, and the harvest data suggested that the differences between pigs raised in the MOF building versus the TS building continued to increase through harvest.

These noted differences in backfat measurements combined with BW and LMA measurements led to no differences between MOF and TS raised pigs for FFTOLN (Figure II.5). Conversely, differences in TOFAT continued to increase as the finishing period from 10 to 22 wk of age progressed (Figure II.6). The differences noted for BF10 and LRF contributed to the differences in TOFAT where the MOF reared pigs had increasingly more TOFAT than the TS reared pigs. Regressions of EBPRO followed a similar pattern to LMA with no differences between pigs raised in the two buildings (Figure II.7). Measures of EBLIPID followed BF10, LRF, and TOFAT trends for pigs raised in the MOF versus those raised in the TS building, but were not statistically different between pigs raised in the two buildings (Figure II.8).

Serial Heritability Results

Estimates of heritability over time were calculated for all eight serial traits. The heritability plotted over the time period in the finisher facilities from 10 to 22 wk of age for the 4 measured traits of BW, BF10, LMA, and LRF increased over time (Figure II.9). Heritability for BW and LMA increased gradually throughout the period, and heritability for BW reached 0.11 at 22 wk of age while heritability for LMA reached 0.25 at 22 wk of age. Kuhlers et al. (2003) reported a similar heritability of 0.13 for body weight of Duroc pigs at 168 d. Heritability for loin eye area, adjusted to 113.5 kg BW, of 0.32 was

reported by Chen et al. (2002). Estimates for BF10 and LRF heritability followed similar trends to one another with a rapid increase from 10 to 16 wk of age and then a plateau for the rest of the finishing period to 22 wk of age. Chen et al. (2002) and Kuhlers et al. (2003) both reported higher tenth rib backfat heritability estimates for Duroc pigs when adjusted to either 113.5 kg (0.48) or adjusted to 168 d (0.58), respectively.

Heritability estimates for the composition traits of FFTOLN, TOFAT, EBPRO, and EBLIPID were also calculated from 10 to 22 wk of age (Figure II.10). Estimates of heritability of the two leanness traits of FFTOLN and EBPRO were generally low, but did increase from 10 to 22 wk of age. Heritability for TOFAT increased from 10 to 16 wk of age, but then declined to a similar level as that observed at 10 wk of age. The EBLIPID heritability generally increased from 10 to 22 wk of age, and was 0.23 at 22 wk of age. Huisman et al. (2002) also fit random regression models to serial data of BW in pigs. Although residual error was kept constant throughout their study, heritability for the models fluctuated around 0.17. Further research may be necessary on models that account for genetic variance, permanent environment variance, and residual error variance changes across time as they may have lower heritability estimates than some other studies since more of the sums of squares are accounted for in variances other than the genetic variance.

Implications

Analysis of data from the Michigan State University Duroc by Pietrain F_2 resource population revealed some insight into the influence of finisher facilities on growth, carcass merit, and meat quality. While many traits, including 22 wk body weight, composition traits, and most meat quality traits, did not significantly differ

between finisher types in animals of similar genetic merit, some traits, including backfat measurements, were influenced by finisher type. Collection of serial data allowed for further characterization of animal growth data and allowed for estimation of serial heritability from 10 to 22 wk of age. Animals of similar genetic merit can show differences in growth patterns as influenced by differing finisher facilities. These differences can lead to changes in feeding and management decisions, including diet choices and marketing possibilities, based upon finisher facilities utilized.

Table II.1. Covariates for carcass and meat quality trait analyses.

Trait	Covariates[a]	
	Carcass Weight	Harvest Age
Carcass measures		
Off-farm BW, kg	-	X
Hot carcass weight, kg	-	X
Dressing percentage, %	-	-
45 min carcass temperature, °C	X	-
24 h carcass temperature, °C	X	-
45 min pH	X	-
24 h pH	X	-
45 min-24 h pH decline	X	-
Carcass length, cm	X	-
Number of ribs	-	-
First rib backfat, mm	X	-
Last rib backfat, mm	X	-
Last lumbar vertebra backfat, mm	X	-
Tenth rib backfat, mm	X	-
Longissimus muscle area, cm^2	X	-
Primal cut weights		
Ham weight, kg	X	-
Loin weight, kg	X	-
Boston shoulder weight, kg	X	-
Picnic shoulder weight, kg	X	-
Belly weight, kg	X	-
Spareribs weight, kg	X	-
Meat quality evaluation		
Color, 1-6	-	-
Marbling, 1-10	-	X
Firmness, 1-5	-	X
L*	-	-
a*	-	-
b*	-	-
Proximate analysis		
Moisture,%	X	-
Fat, %	X	-
Protein, %	X	-
Laboratory analyses		
Drip loss,%	-	X
Cook yield, %	-	-
Warner-Bratzler shear force, kg	-	-
Sensory taste panel		
Juiciness, 1-8	-	-
Tenderness, 1-8	-	-
Overall tenderness, 1-8	-	-
Connective tissue, 1-8	-	-
Off-flavor, 1-8	-	-

[a]X indicates used in model, - indicates not used in model

Table II.2. Order of polynomial on week of age terms and other significant terms for random regression analyses of serial growth data.

Trait	Week of age	Significant term[a]	
		Sex* week^2	Finisher* week^2
Body weight, kg	4	-	X
Tenth rib backfat, mm	2	X	-
Longissimus muscle area, cm^2	3	-	-
Last rib backfat, mm	4	X	-
Fat-free total lean, kg	4	-	X
Total body fat tissue, kg	4	X	-
Empty body protein, kg	2	-	X
Empty body lipid, kg	4	-	-

[a]X indicates used in model, - indicates not used in model

Table II.3. Number of observations, least squares means, standard error of the mean, and *P*-value of the difference between finisher means for 22 wk of age off-test traits.

	MOF[a]		TS[a]			
Trait	n	Mean	n	Mean	SEM	*P*-value
Body weight, kg	513	99.6	460	100.4	3.23	0.687
Tenth rib backfat, mm	513	21.6	460	18.9	1.25	0.050
Longissimus muscle area, cm^2	513	37.5	460	36.6	1.36	0.444
Last rib backfat, mm	513	15.1	460	13.6	0.87	0.050
Fat-free total lean, kg	513	38.1	460	38.6	1.22	0.571
Total body fat tissue, kg	513	25.5	460	24.7	1.92	0.519
Empty body protein, kg	513	14.9	460	15.1	0.48	0.414
Empty body lipid, kg	513	22.5	460	21.6	1.00	0.244
ADG (10-22 wk), g/d	513	874.5	460	876.0	31.1	0.961

[a]MOF = Modified Open Front finisher, TS = Test Station finisher

Table II.4. Number of observations, least squares means, standard error of the mean, and *P*-value of the difference between finisher means for carcass and meat quality traits.

	MOF[a]		TS[a]			
Trait	n	Mean	n	Mean	SEM	*P*-value
Carcass measures						
Off-farm BW, kg	50	113.4	45	110.7	1.77	0.015
Hot carcass weight, kg	50	82.5	45	80.7	1.31	0.074
Dressing percentage, %	50	72.8	45	72.9	0.46	0.883
45 min carcass temperature, °C	50	39.2	45	39.3	0.50	0.892
24 h carcass temperature, °C	50	3.02	45	2.46	0.26	0.116
45 min pH	49	6.41	45	6.36	0.03	0.125
24 h pH	48	5.52	45	5.55	0.02	0.358
45 min-24 h pH decline	47	0.89	45	0.83	0.01	0.019
Carcass length, cm	50	78.8	45	78.7	0.49	0.880
Number of ribs	29	15.1	33	14.9	0.17	0.416
First rib backfat, mm	44	41.6	42	40.5	1.13	0.385
Last rib backfat, mm	50	29.8	45	27.3	1.00	0.006
Last lumbar vertebra backfat, mm	50	23.0	45	21.3	1.08	0.021
Tenth rib backfat, mm	50	25.6	44	23.1	0.99	0.001
Longissimus muscle area, cm^2	50	40.4	44	41.0	0.95	0.273
Primal cut weights						
Ham weight, kg	50	9.48	45	9.60	0.10	0.087
Loin weight, kg	50	8.17	45	8.33	0.11	0.218
Boston shoulder weight, kg	50	3.78	45	3.81	0.14	0.857
Picnic shoulder weight, kg	50	3.92	45	3.84	0.14	0.679
Belly weight, kg	50	4.96	45	5.07	0.08	0.215
Spareribs weight, kg	50	1.47	44	1.48	0.04	0.717
Meat quality evaluation						
Color, 1-6	50	3.06	45	3.14	0.17	0.392
Marbling, 1-10	50	2.84	43	2.96	0.12	0.193
Firmness, 1-5	50	2.76	45	2.88	0.14	0.178
L*	45	54.02	45	53.77	0.53	0.290
a*	45	17.09	45	17.11	0.52	0.967
b*	45	9.22	45	9.10	0.36	0.781
Proximate analysis						
Moisture,%	49	73.92	44	73.73	0.33	0.453
Fat, %	49	3.24	44	3.20	0.32	0.837
Protein, %	49	23.57	44	23.60	0.21	0.832
Laboratory analyses						
Drip loss,%	50	1.62	45	1.73	0.25	0.444
Cook yield, %	49	77.65	44	77.72	0.63	0.840
Warner-Bratzler shear force, kg	49	3.14	44	3.36	0.13	0.044
Sensory taste panel						
Juiciness, 1-8	50	5.18	44	5.34	0.23	0.074
Tenderness, 1-8	50	5.48	44	5.55	0.22	0.441
Overall tenderness, 1-8	50	5.56	44	5.63	0.20	0.362
Connective tissue, 1-8	50	6.36	44	6.38	0.16	0.783
Off-flavor, 1-8	50	1.14	44	1.12	0.04	0.255

[a]MOF = Modified Open Front finisher, TS = Test Station finisher

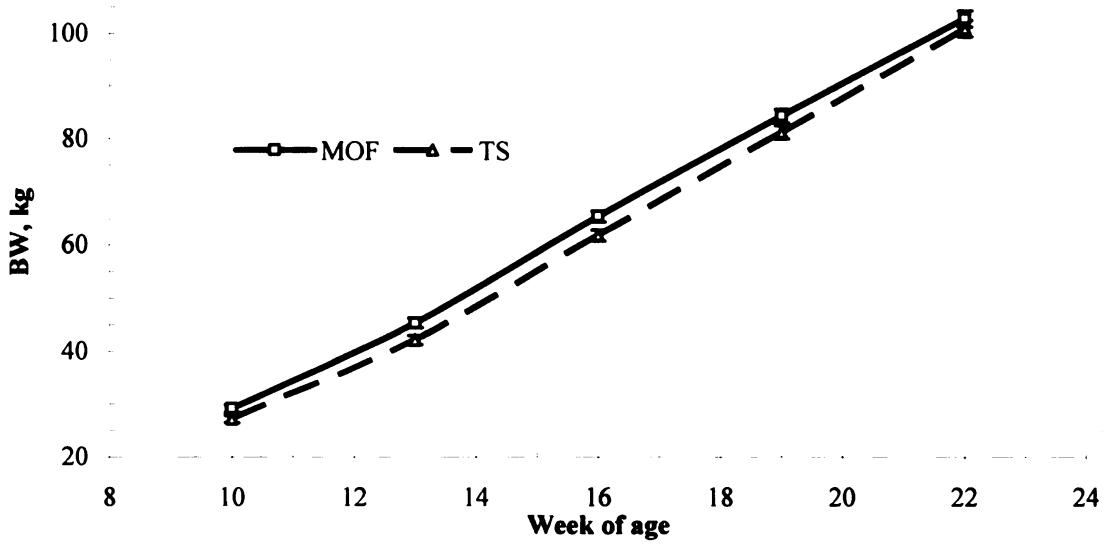

Figure II.1. Body weight means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

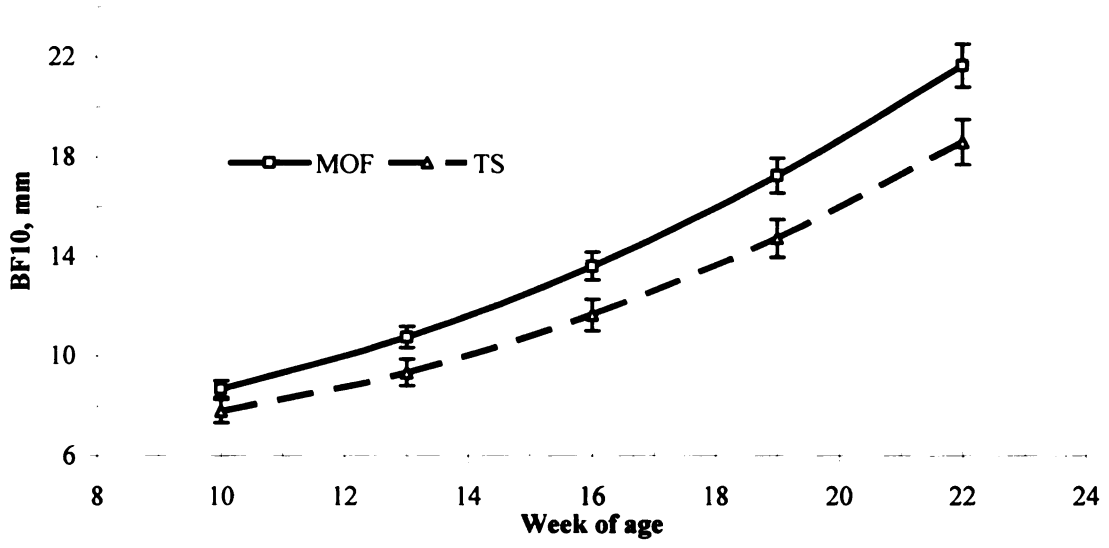

Figure II.2. Tenth rib backfat means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

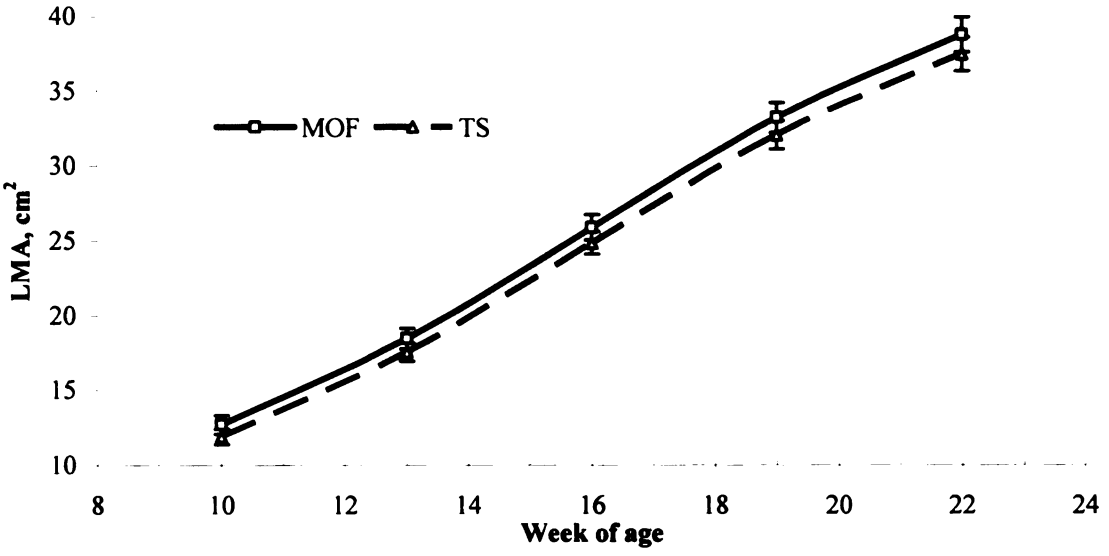

Figure II.3. *Longissimus* muscle area means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

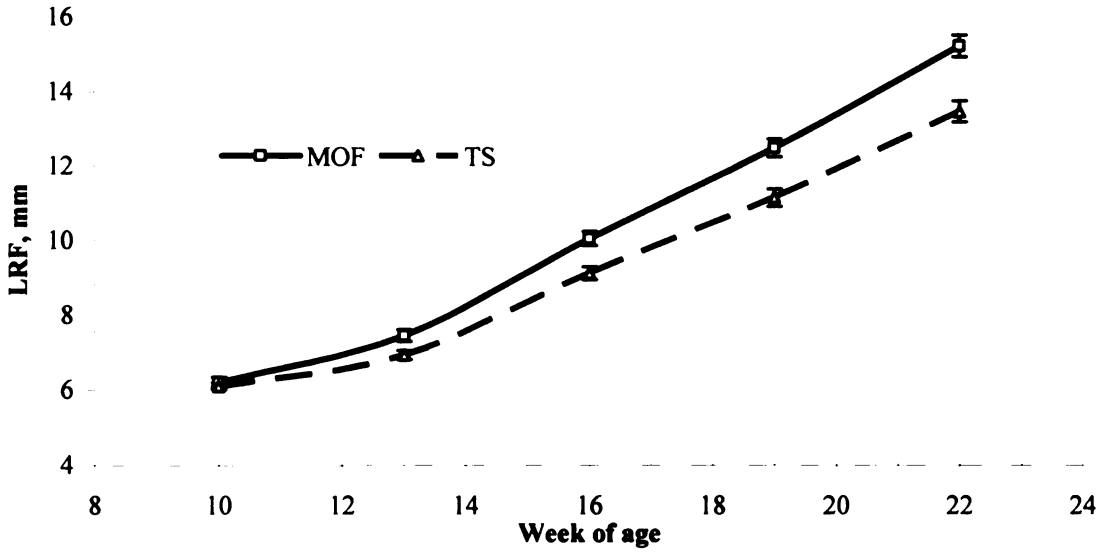

Figure II.4. Last rib backfat means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

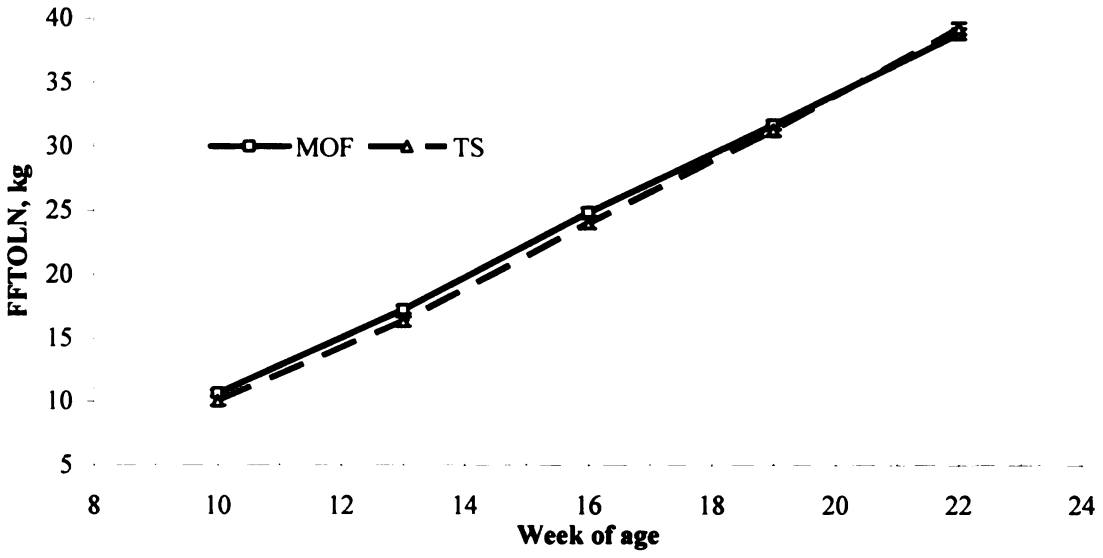

Figure II.5. Fat-free total lean means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

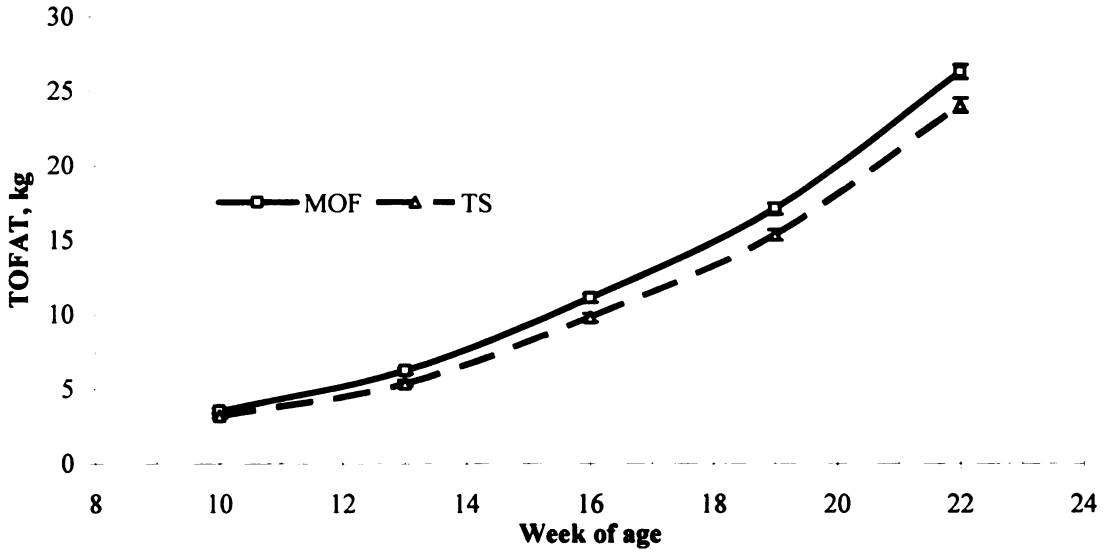

Figure II.6. Total body fat tissue means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

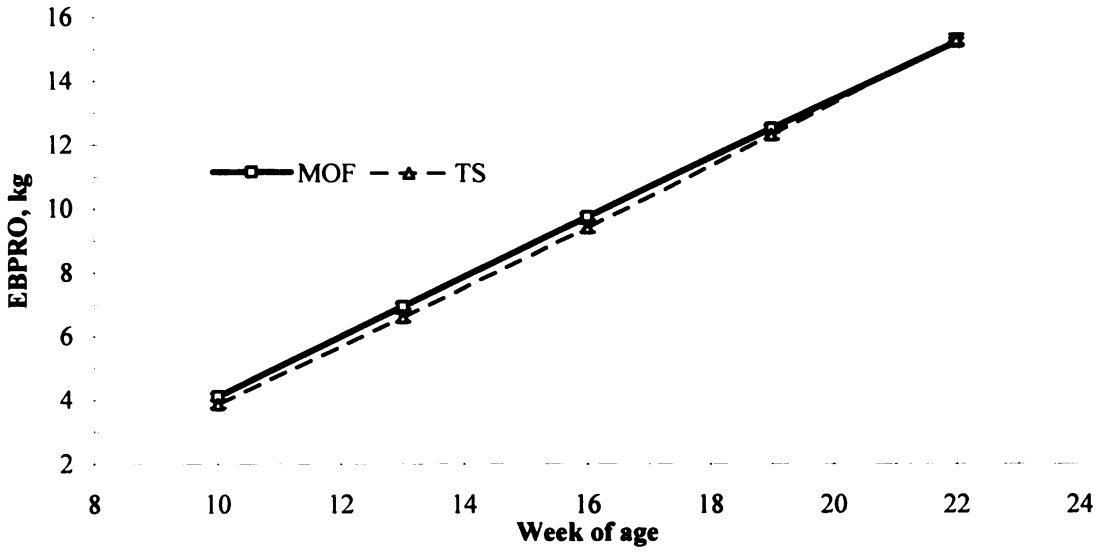

Figure II.7. Empty body protein means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

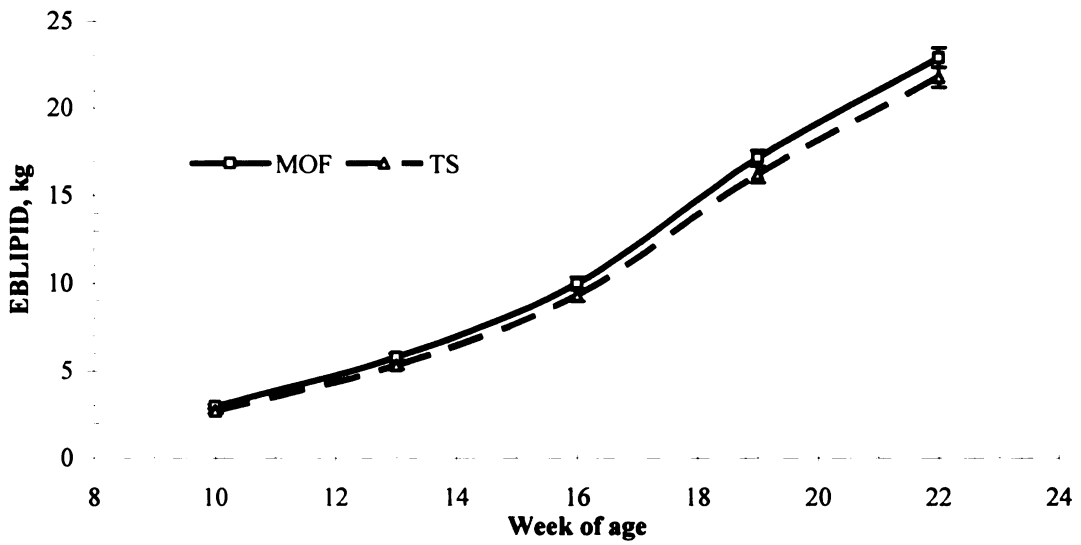

Figure II.8. Empty body lipid means with standard errors from 10 to 22 wk of age for Modified Open Front building (MOF) vs. Test Station building (TS) raised pigs.

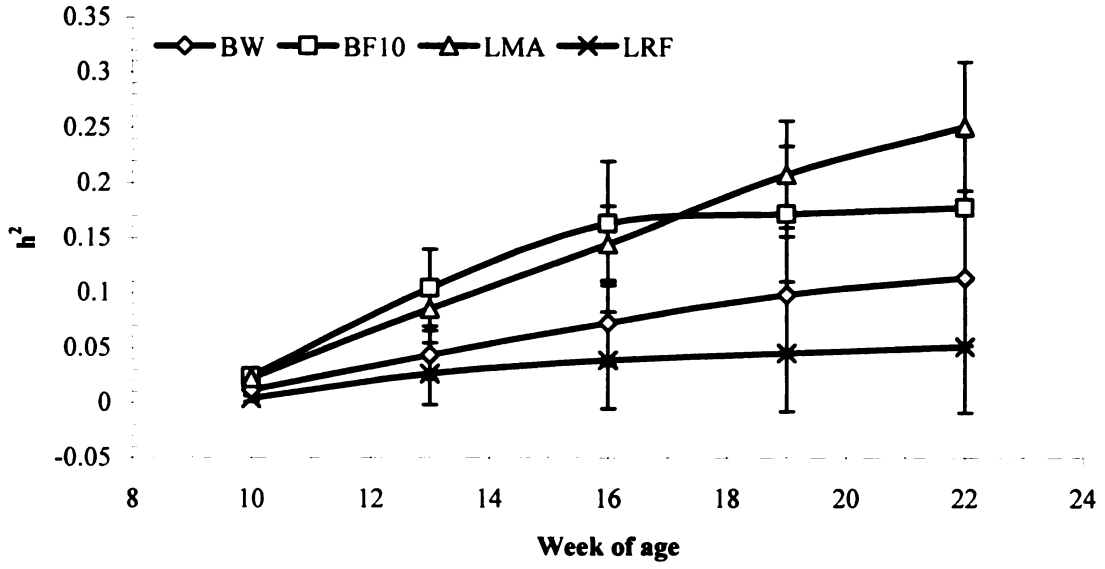

Figure II.9. Heritability for measured traits from 10 to 22 wk of age. BW = body weight, BF10 = tenth rib backfat, LMA = *longissimus* muscle area, LRF = last rib backfat

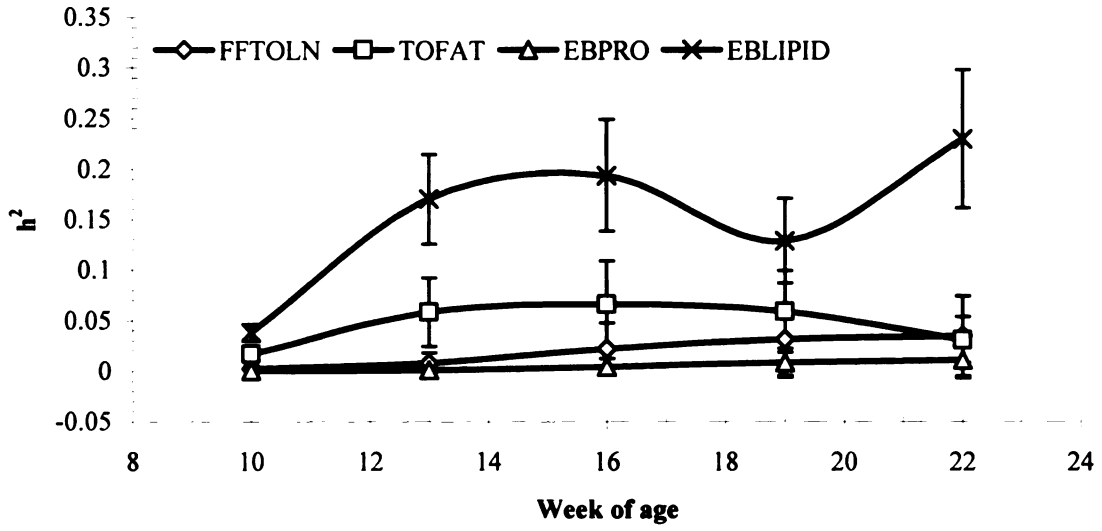

Figure II.10. Heritability for calculated traits from 10 to 22 wk of age. FFTOLN = fat-free total lean, TOFAT = total fat tissue, EBPRO = empty body protein, EBLIPID = empty body lipid

CHAPTER III

QTL MAPPING IN AN F_2 DUROC x PIETRAIN RESOURCE POPULATION: I. GROWTH TRAITS[2]

Abstract

Pigs from the F_2 generation of a Duroc x Pietrain resource population were evaluated to discover quantitative trait loci (QTL) affecting growth and composition traits. Body weight and ultrasound estimates of tenth rib backfat, last rib backfat, and *longissimus* muscle area were serially measured throughout development. Estimates of fat-free total lean, total body fat, empty body protein, empty body lipid, and average daily gain from 10 to 22 wk of age were calculated, and random regression analyses were performed to evaluate phenotypes representing intercept and linear rates of increase in these eight serial traits. A total of 510 F_2 animals were genotyped for 124 microsatellite markers evenly spaced across the entire genome. Data were analyzed with line cross least squares regression interval mapping methods using sex and litter as fixed effects. Significance thresholds of the F-statistic for additive, dominance, and imprinted QTL were determined at chromosome- and genome-wise levels by permutation tests. A total of 55 QTL for 22 of the 29 measured traits were found to be significant at the 5% chromosome-wise level. Of these 55 QTL, 16 were significant at the 1% chromosome-wise, 11 at the 5% genome-wise, and 10 at the 1% genome-wise significance thresholds. A total of 33 QTL for 15 of the 16 animal random regression terms were found to be significant at the 5% chromosome-wise level. Of these 33 QTL, 11 were significant at the 1% chromosome-wise, 2 at the 5% genome-wise, and 2 at the 1% genome-wise

[2] This research was financially supported by the Michigan State University Department of Animal Science, the Michigan Agricultural Experiment Station, a Michigan Animal Initiative Coalition Grant, and USDA-CSREES NRI Award 2004-35604-14580.

significance thresholds. Putative QTL were discovered for tenth rib and last rib backfat on SSC 6, body composition traits on SSC 9, backfat and lipid composition traits on SSC 11, tenth rib backfat and total body fat tissue on SSC 12, and linear regression of body weight, *longissimus* muscle area, and tenth rib backfat on SSC 18. These results will facilitate fine mapping efforts to identify genes controlling growth and body composition of pigs that can be incorporated into marker-assisted selection programs to accelerate genetic improvement in pig populations.

Introduction

Enhancement of production efficiency and improvement of product quality are major concerns for producers of food animals. Selection of improved breeding animals is essential for achieving this goal, and more information on prospective parents leads to better selection decisions. Advances in genetic technologies have allowed for more information to be collected on prospective parents which has included identification of quantitative trait loci (QTL). The search for regions of the genome that control these traits has led to the creation of resource populations and the discovery of putative QTL.

The Duroc and Pietrain breeds are utilized worldwide as sire breeds, and these breeds differ in growth phenotypes. In general, Duroc pigs and their offspring have been found to grow faster, but also have more backfat than other breeds (Kennedy et al., 1996; Blanchard et al., 1999; Edwards et al., 2006). Quiniou and Noblet (1995) used Pietrain boars in their study of equations to predict composition because of their propensity towards leanness, and Edwards et al. (2006) reported slower, but leaner, growth in Pietrain-sired pigs versus Duroc-sired pigs. While each of these breeds has been utilized individually in resource populations with some rustic and some commercial breeds

(Duroc: Grindflek et al., 2001; Sato et al., 2003; Stearns et al., 2005) (Pietrain: Nezer et al., 2002), no study has reported a resource population utilizing both Duroc and Pietrain breeds. The objective of this study was to conduct a full genome scan using microsatellite markers to search for QTL affecting growth traits in an F_2 Duroc x Pietrain resource population.

Materials and Methods

Population Development

A three-generation resource population was developed at Michigan State University to study traits of growth, body composition, and meat quality. Semen from four F_0 Duroc sires from a closed unselected control population (Kuhlers et al., 2003) and sixteen F_0 Pietrain dams from a closed herd propagated the F_1 generation. All grandparents were determined homozygous normal for the RYR-1 gene by a DNA test (Fujii et al., 1991). All animals were produced through artificial insemination at the Michigan State University Swine Teaching and Research Farm. From F_1 progeny, 51 females and six males (sons of three F_0 sires) were retained to produce the 1259 F_2 pigs born alive in 142 litters across 11 farrowing groups. Females were retained across multiple parities to produce F_2 progeny.

Animal Management

All pigs were managed similarly in farrowing and nursery stages with dams placed into farrowing crates one week prior to farrowing. Baby pigs were processed (individually identified by ear tag, given 0.5 ml penicillin and 1 ml iron dextran subcutaneously, and tails clipped) at approximately one d of age. At seven d of age, males not kept for breeding purposes were castrated. Pigs were weaned at 16-25 (mean

of 19.8) d of age and sorted into nursery pens by sex and weight. All diets fed were Michigan State University standard swine farm diets that met or exceeded NRC (1998) requirements for all nutrients at each production stage. At 10 wk of age, F_2 pigs were placed into one of two finishing facilities at the Michigan State University Swine Teaching and Research Farm. Farrowing groups 1, 3, 5, 7, 9, and 11 (n = 521 pigs) were placed into a Modified Open Front (MOF) building with two-thirds solid, one-third slatted floors and wet-dry feeders. Four larger pens (2.03 m by 6.91 m) with two-space feeders were targeted to contain 16 pigs per group. Four smaller pens (1.42 m by 6.91 m) with one-space feeders were targeted to contain 12 pigs per group. Farrowing groups 2, 4, 6, 8, and 10 (n = 465 pigs) were placed into a test station (TS) facility with solid floors bedded with straw or wood shavings with one-space dry feeders and cup drinkers. All 25 pens utilized (1.42 m by 4.93 m) were targeted to contain four pigs per group. Pigs in either facility had ad libitum access to feed and water.

Phenotype and Genotype Collection

Live animal traits collected on F_2 animals included BW at birth, weaning, 6, 10, 13, 16, 19, and 22 wk of age. Additionally, B-mode ultrasound (Pie Medical 200SLC, Classic Medical Supply, Inc., Tequesta, FL) estimates of tenth rib backfat (BF10), last rib backfat (LRF), and *longissimus* muscle area (LMA) were recorded at 10, 13, 16, 19, and 22 wk of age. The ADG from 10 to 22 wk of age and the number of days to reach 105 kg were calculated from these BW measures. At each of these time points measures of fat-free total lean (FFTOLN), total body fat tissue (TOFAT), empty body protein (EBPRO), and empty body lipid (EBLIPID) were calculated using equations similar to those used by Wagner et al. (1999).

Whole blood was collected from all F_0, F_1, and F_2 animals for DNA isolation. White blood cells were separated and frozen for subsequent DNA extraction. A total of 206 dinucleotide microsatellite genetic markers were considered for genotyping, and 128 informative markers that would amplify were chosen. Markers were selected from the published pig genome linkage map (http://www.marc.usda.gov/genome/swine/swine.html, USDA, 2005b), and the initial set of markers was tested for informativeness (markers segregating between F_0 breeds and estimated to have three or more alleles) using fluorescent primers distributed by the US Pig Genome Coordinator (supported by the USDA-CREES through the National Research Support Project 8). These 128 markers were genotyped for 510 F_2 animals, their parents, and grandparents at a commercial laboratory (GeneSeek Inc., Lincoln, NE). These 510 animals were sampled across all farrowing groups from 61 entire litters. Pigs represented all F_1 sires with at least 100 grand progeny from each F_0 sire. Fifteen of the 16 F_0 dams had a son or daughter as a parent that produced multiple litters of the selected F_2 pigs with the remaining F_0 dam represented by a single F_1 daughter with one litter in this group. Mendelian inheritance of alleles could not be verified within F_2 animals for SW1349 on SSC 9, SW2067 on SSC 10, SW1632 on SSC 11, and S0229 on SSC 12, and these markers were removed from the data set. The remaining 124 markers were utilized for a whole genome scan of approximately 20 cM spacing across the 18 autosomes and X chromosome. Among these 124 markers several individual animal genotypes could not be verified as they did not match expected Mendelian inheritance patterns from pedigree analysis and were removed. Markers used in this genome scan are listed in Table III.1 along with the number of alleles segregating for each marker, the relative positions of

each marker, and number of unverified genotypes for each marker. Genetic linkage maps were constructed for each of the 18 autosomes and the X chromosome using Crimap version 2.4 software (Green et al., 1990).

Random Regression

Serial BW and ultrasound estimates from 10 to 22 wk of age were used to generate random regression equations to model pig BW, BF10, LMA, LRF, FFTOLN, TOFAT, EBPRO, and EBLIPID on age at measurement for individual animals. Age at measurement was modeled as week on-test, calculated as age in weeks minus nine, (i.e. 1, 4, 7, 10, and 13 as distinct covariate values used in the analysis). A random intercept for each animal and a linear regression on age for each animal were included in each model. Main effects and interactions that contributed significantly to the increase of the log likelihood were kept in the model. Table III.2 lists the polynomial order of week of age and interactions used in models for these eight traits as determined by log likelihood tests of significance. The following model was used:

$$Y_{ijklmn} = \mu + \Sigma week_i^{\phi} + sex_j + \Sigma(sex*week^{\phi})_j + fin_k + \Sigma(fin*week^{\phi})_k + grp(fin)_{kl} + pen(grp)_{lm} + g_n + \alpha_n*Zi + e_{ijklmn}$$

where

Y_{ijklmn} = record on the n^{th} pig within j^{th} sex, k^{th} finisher, l^{th} group, and m^{th} pen regressed on ϕ^{th} polynomial week i,
μ = overall mean of trait,
$week_i^{\phi}$ = fixed regression coefficient for polynomial terms ϕ (1-4) of week i,
sex_j = fixed effect of sex of animal j (Barrow or Gilt),
fin_k = fixed effect of finisher k (MOF or TS),
$grp(fin)_{kl}$ = random effect of farrowing group l (1-11) nested within finisher where grp ~$N(\mathbf{0}, \mathbf{I}\sigma_{grp}^2)$,
$pen(grp)_{lm}$ = random effect of pen m (1-25) nested within farrowing group where pen ~$N(\mathbf{0}, \mathbf{I}\sigma_{pen}^2)$,
g_n = random intercept for animal n,
α_n = random linear regression coefficient on age for animal n,
Z_i = week on test as a covariate, and
e_{ijklmn} = random error.

The distributional assumptions on $\mathbf{g} = \{g_n\}$ and $\boldsymbol{\alpha} = \{g_n\}$ were such that:

$\begin{bmatrix} \mathbf{g} \\ \boldsymbol{\alpha} \end{bmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{A}\sigma_g^2 & \mathbf{A}\sigma_{g\alpha} \\ \mathbf{A}\sigma_{g\alpha} & \mathbf{A}\sigma_\alpha^2 \end{bmatrix}\right)$, where σ_g^2 is the intercept genetic variance for the individuals, σ_α^2 is the linear age by animal genetic variance, and $\sigma_{g\alpha}$ is the genetic covariance between the intercept and linear term for each animal. To account for residual variances across serial measurement and the relationship between time points, the $\mathbf{e} = \{e_{ijklmn}\}$ was specified as normally distributed with a general (co)variance structure calculated from the data and specified within and across weeks with five variance and 10 covariance terms.

QTL Analysis

The genetic linkage maps constructed for each chromosome were used in an F_2 least squares interval mapping framework for QTL analysis (Haley et al., 1994). Briefly, this method proceeded in two steps. In the first step, marker positions and genotypes were used to calculate the probability an individual inherited 0, 1, or 2 alleles from each of the two founder lines. Secondly, phenotypic data were regressed on coefficients derived from these probabilities. The F_2 analysis option of the QTL Express software (Seaton et al., 2002) was used to search for single QTL with additive, dominance, or imprinting effects on the 18 autosomes and additive effects on the X chromosome. For traits listed in Table III.3 the model used included the fixed effects of sex of animal and litter. For birth and 3 wk BW the model also included parity of the female as a fixed effect and number born alive as a covariate. The model for 10 to 22 wk ADG also

included a covariate of 10 wk BW to account for differences in BW when pigs were placed into the finishers.

Tests of the full model including additive, dominance, and imprinting effects versus the reduced model without these effects were carried out to determine F-ratios at intervals of 1 cM across the entire genome for the traits listed in Table III.3. Analyses of the animal random regression terms were also carried out with QTL Express, but only for additive effects. During the course of estimation of the animal intercept and linear terms, dominance effects were confounded with common environment (as stated in Hill, 1999). Since these traits have already been adjusted for fixed and random effects in random regression models, no further effects were included in their QTL analyses.

Additive effects were defined as half the difference between Pietrain and Duroc genotypes at the QTL. Dominance effects were defined as the difference between the heterozygote genotype and the average of the homozygote genotypes. Imprinting effects were defined as the difference between the heterozygous genotypes when the Duroc allele was inherited from parents of opposite sex. Haley et al. (1994) and Knott et al. (1998) describe further details on the parameterization of these effects. Significance thresholds of 5% and 1% at the chromosome-wise and 5% and 1% at the genome-wise levels were determined through the use of permutation tests (Churchill and Doerge, 1994) in QTL Express. These thresholds were determined for genome-wise levels and for each chromosome based upon appropriate models for each chromosome and 30,000 permutations. For each QTL determined to be significant at the 5% genome-wise level, confidence intervals of the QTL position were determined using a bootstrap method with 5,000 permutations in QTL Express (Visscher et al., 1996).

Results and Discussion

QTL Analysis

Trait means and standard deviations are listed in Table III.3, and are similar to those measured in other resource populations for similar traits (e.g. Malek et al., 2001b; Stearns et al., 2005). Table III.1 contains the list of the 124 markers used in this analysis along with their linkage map positions on each chromosome, the number of alleles segregating in this population, and the number of missing genotypes for F_2 animals. The average distance between markers was 24 cM, although the distance between some markers was larger due to the difficulty in identifying informative markers in those regions. Overall, our map generally agreed with or was slightly longer than the USDA map (Rohrer et al., 1996; http://www.marc.usda.gov/genome/swine/swine.html, USDA, 2005b) except for two marker pairs that switched order in our analysis. On SSC 9, SW21 and SW983 inverted order and were 13.2 cM apart on our map, whereas they were 11.2 cM apart on the USDA map. On SSC X, SW1608 and SW2059 inverted order and were 23.0 cM apart on our map and 17.4 cM apart on the USDA map. The longer length of our map as compared to the USDA map was not unexpected since the marker density of our map was much lower.

The permutation test results to determine significance thresholds for the F statistics for models testing additive, dominance, and imprinting effects ranged from 3.44 to 4.35 across chromosomes for the 5% chromosome-wise thresholds and from 4.71 to 5.64 for the 1% chromosome-wise thresholds. Genome-wise threshold levels were 6.34 and 7.63 for 5% and 1% thresholds, respectively. Significance threshold levels for the additive effect only models ranged from 5.39 to 7.64 and 8.68 to 10.99 for 5% and 1%

chromosome-wise levels, respectively, and they were 12.86 and 16.05 for 5% and 1% genome-wise levels, respectively.

Estimates of positions and F-ratios of QTL significant at the 5% chromosome-wise level for traits listed in Table III.3 are listed in Table III.4. These results were derived from single QTL on each chromosome models. Information in the table is sorted by chromosome and position within each chromosome. Additionally, the additive, dominance, and imprinting effect at each QTL along with their standard errors are listed in Table III.4. A total of 55 QTL for traits in Table III.3 were found to be significant at 5% chromosome-wise levels. Of these 55 QTL, 16 were significant at the 1% chromosome-wise, 11 at the 5% genome-wise, and 10 at the 1% genome-wise significance thresholds. No significant QTL were detected in this population for 3, 6, 10, 13, or 16 wk BW, 13 wk LMA, or 22 wk FFTOLN.

For each of the random regression analyses conducted, the animal-specific intercept and linear random regression terms were tested for QTL. Estimates of QTL positions and F-ratios for animal random regression terms significant at the 5% chromosome-wise level are listed in Table III.5. These results are for the most significant position for each QTL as only single QTL on each chromosome models were analyzed. Additionally, the additive effect at each QTL along with the standard error is listed in Table III.5. A total of 33 QTL for 15 of the 16 animal random regression terms were found to be significant at 5% chromosome-wise levels. Of these 33 QTL, 11 were significant at the 1% chromosome-wise, 2 at the 5% genome-wise, and 2 at the 1% genome-wise significance thresholds. Only linear regression on FFTOLN did not have a significant QTL that was detected in this population.

All chromosomes, except 2, 4, 12, 15, and 17, contained at least one QTL for these traits related to growth and body composition. Although these two breeds have both been selected for terminal sire breeding programs for several years, many important QTL causing phenotypic differences between the breeds still exist and are possible candidates to explore more thoroughly. Some QTL had breed effects in the same direction as for traits in Duroc- and Pietrain-sired animals reported in Edwards et al. (2006), but a few cryptic alleles exist that act in an opposite direction to the general trend for the overall breed effects.

Body Weight

Four QTL influenced BW growth at different ages at the 5% chromosome-wise level (Table III.4). A QTL for birth weight occurred on SSC 5 with an imprinting effect that indicated paternal expression. This QTL has not been reported before in other pig resource populations (Hu et al., 2005). No QTL for growth between 3 and 16 wk of age were detected in this analysis. However, a QTL on SSC 16 for BW was significant for growth at 19 and 22 wk of age and influenced 10 to 22 wk ADG. This was a cryptic allele, as the Duroc alleles caused lower BW and 10 to 22 wk ADG, which contrasted with results from Edwards et al. (2006), who reported faster growth from Duroc-sired versus Pietrain-sired progeny. The 1 cM F-ratio tests for these QTL are illustrated for SSC 16 in Figure III.1 with the F-ratio plotted versus relative marker position. Another QTL affected BW growth on SSC 7 and showed an imprinting inheritance pattern. Other studies have reported a QTL for average daily gain on SSC 7, but for differing time periods of development than in this study (Knott et al., 1998; Nezer et al., 2002) or in different positions on the chromosome (Bidanel et al., 2001). Two QTL were found that

influenced the animal random regression intercept of BW (Table III.5). One QTL was on SSC 5 with the Pietrain allele increasing the intercept and another QTL was on SSC 8 with the Duroc allele increasing the intercept. Two additional QTL influencing the linear rate of BW gain from 10 to 22 wk of age were found. One QTL on SSC 16 had an additive effect with Pietrain alleles that increased the rate of BW gain. The other, on SSC 18, suggested that Duroc alleles increased the rate of BW gain. Neither of these linear rate QTL, or traits with similar definitions, was reported in a summary of other pig QTL studies (Hu et al., 2005). In addition, a QTL for days to 105 kg was discovered on SSC 9. Although ADG from 10 to 22 wk of age and days to 105 kg are similar traits, differences in growth from birth to 10 wk of age that are included in the days to 105 kg calculation may have caused QTL for these traits to be located on different chromosomes.

Backfat

Several regions of the genome contributed to fat tissue phenotypes at many ages of development. When considering the associated traits of BF10 and LRF, a region on SSC 6 influenced both of these traits at all measured time points of 10, 13, 16, 19, and 22 wk of age with all of them significant at the 1% genome-wise level (Table III.4). The estimate of the peak position of this QTL ranged from 134 to 143 cM from the most proximal marker (S0099), so this may be the same pleiotropic QTL for all of these related traits. Figure III.2 demonstrates the F-ratio curves plotted versus relative marker positions on SSC 6 and illustrates the similar shapes of F-ratios for 22 wk BF10 and 22 wk LRF. The estimate of this QTL in this analysis indicated that Duroc alleles contributed to larger measures of BF10 and LRF. A QTL in the same region affected the animal linear random regression terms of BF10 and LRF (Table III.5). Again, Duroc

alleles contributed to a faster rate of backfat deposition at BF10 and LRF. While most backfat QTL on SSC 6 found in other populations occur more proximal than what was reported here, Malek et al. (2001a) and Ovilo et al. (2002b) also reported putative QTL for backfat in the same region as those reported in this study. Two other regions were significant for multiple backfat phenotypes. One of these was on SSC 11, which influenced BF10 at 19 and 22 wk of age and LRF at 19 wk of age (Figure III.3). The only other study which reported a backfat QTL on SSC 11 was Milan et al. (2002), but their QTL was more proximal to the one reported here. Another region, on SSC 16, that influenced BF10 at 19 wk of age and LRF at 22 wk of age is at 64 cM with an additive effect characterized by Duroc alleles that caused less BF10 and LRF (Figure III.1). Only one QTL, for small intestine length (Hu et al., 2005), has been identified on SSC 16, but several of the traits in this study were influenced by QTL on SSC 16. A QTL on SSC 18 at 54 cM was significantly related to BF10 at 10 wk of age and LRF at 16 wk of age. Additional locations of QTL affecting BF10 and LRF at different time points from 10 to 22 wk of age occur on SSC 3, 8, and 9 (Table III.4). The random regression linear animal terms for BF10 and LRF were also affected by a QTL on SSC 16. These effects on SSC 16 were estimated to increase backfat when Pietrain alleles were present, which would be considered a cryptic allele in comparison to results of Edwards et al. (2006). Other QTL affecting random regression animal intercept and linear terms were found on SSC 10, 11, 18, and X.

Longissimus Muscle Area

Numerous QTL controlling LMA in this population were detected with most of them significant only at the 5% chromosome-wise level. One chromosome with three

regions significant for LMA QTL was SSC 6 (Tables III.4 and III.5). One region that was significant for 10 and 19 wk of age LMA had a dominance effect where Duroc alleles contributed to a larger LMA. Another region was significant for 16 wk of age LMA with a dominance effect where Pietrain alleles contributed to a larger LMA. Lastly, a third region was significant for LMA random regression animal intercept where Duroc alleles contributed to a larger LMA. A QTL influencing lean percentage was reported in the same region in two other populations containing Duroc animals (Grindflek et al., 2001; Szyda et al., 2003; Stearns et al., 2005). Additionally, SSC 1 had a QTL region that affected 13 wk of age LMA where Pietrain alleles had additive effects that contributed to larger LMA. The SSC 4 had a QTL region that affected 22 wk of age LMA additively where Pietrain alleles contributed to a larger LMA. A few populations have identified a region that influences LMA just distal to the findings reported here (Pérez-Enciso et al., 2000; Malek et al., 2001a; Varona et al., 2002), while one used AFLP markers and identified a QTL in the same region as reported here for LMA (Wimmers et al., 2002). A region at the proximal end of SSC 18 affected the linear random regression of LMA and was significant at the 1% genome-wise level (Figure III.4). For this QTL, Duroc alleles caused a faster rate of increase in LMA.

Composition Traits

Estimates of body composition (FFTOLN, TOFAT, EBPRO, and EBLIPID) at 22 wk of age as well as random regression analyses from serial data of 10 to 22 wk of age were tested for QTL. The use of random regression terms as traits for QTL analysis has not been previously reported in other swine resource populations. Two QTL with dominance effects for FFTOLN at 22 wk of age were discovered, with one on SSC 6 and

another on SSC 9 (Table III.4). The Duroc alleles increased the amount of FFTOLN at 22 wk of age. Two QTL also affected the random regression intercept of FFTOLN with one QTL on SSC 5 and another on SSC X (Table III.5). In this case the Pietrain alleles increased the FFTOLN intercept. Results for QTL for TOFAT indicated three QTL with one each on SSC 6, 9, and 16 affecting TOFAT at 22 wk of age (Table III.4). The random regression animal intercept for TOFAT was influenced by QTL on SSC 5, 8, 14, and 18 while random regression animal linear TOFAT was influenced by QTL on SSC 8 and 16 (Table III.5). These QTL for TOFAT were all significant at the 5% chromosome-wise level. Putative QTL with dominance effects were found on SSC 6 and 9 where Duroc alleles contributed to an increase in EBPRO. Both of the protein composition traits of FFTOLN and EBPRO had similar patterns for F-ratio curves on SSC 6 as indicated in Figure III.2. Random regression animal intercept for EBPRO was influenced by QTL on SSC 5 and X with a decrease in EBPRO intercept by Duroc alleles. For random regression linear EBPRO, QTL occurred on SSC 9 where Duroc alleles increased the rate of EBPRO deposition. Another QTL was discovered on SSC X where Pietrain alleles increased the rate of EBPRO deposition. This QTL also affected FFTOLN intercept in the same region (Figure III.5). Effects of QTL on SSC 6 and 11 were evident for EBLIPID at 22 wk of age, as well as in the same region of SSC 9 that contributed to differences in EBPRO (Table III.4). A similar region on SSC X to the one that influenced random regression EBPRO intercept also contributed to differences in random regression EBLIPID intercept (Table III.5). Additionally a region on SSC 6 also contributed to an increase in random regression EBLIPID intercept when Duroc alleles were present. The F-ratios for TOFAT and EBLIPID on SSC 6 were generally

concurrent (Figure III.2), which indicated that the same chromosomal regions influenced both traits. The random regression animal linear EBLIPID term associated with QTL regions on SSC 18 and X was significant at the 5% chromosome-wise level for QTL. Traits related to body composition of FFTOLN, TOFAT, EBPRO, and EBLIPID were influenced by a QTL in between the two most proximal markers on SSC 9 (SW21 and SW983) used in this study (Figure III.6). These traits are highly related, and appeared to be influenced by similar regions of the genome. No other studies have reported QTL for these or similar traits on SSC 9 (Hu et al., 2005).

Confidence Intervals

For QTL that were significant at the 5% genome-wise level, 95% confidence intervals were estimated using bootstrapping with resampling in QTL Express (Seaton et al., 2002). These confidence intervals are listed in Table III.6. Confidence intervals were not calculated for QTL significant at the 5 or 1% chromosome-wise level since preliminary analyses indicated that many of these intervals tended to encompass the entire chromosome on which they reside.

Implications

Discovery of QTL in an F_2 Duroc-Pietrain resource population revealed many regions of the genome that potentially influence a portion of the phenotypic differences in growth and composition traits. Not only were QTL found for measured traits, but also for the animal terms from random regression analysis. Employing both measured and composite traits allowed unique characterization of growth and composition phenotypes from this population. The utilization of the Duroc and Pietrain breeds in this population will allow for identified QTL to be incorporated quickly into breeding schemes as these

two populations are already a major part of commercial pig production. While further analyses and refining of QTL positions are in progress, results of this study are useful in discovering potential QTL regions and leading to further understanding the role certain regions of the genome have in determining phenotype differences among potential parents for selection of breeding animals.

Table III.1. Markers used in the QTL analysis, map positions determined for the F_2 Duroc x Pietrain resource population, number of alleles segregating for each marker, and number of missing genotypes for each marker. Distances (in Kosambi cM) are relative to position of first marker on each chromosome in this population.

Marker	Chr	Position	Alleles	DG[a]	Marker	Chr	Position	Alleles	DG[a]
SW1514	1	0	5	10	S0099	6	0	5	42
SW1515	1	21.1	5	13	SW2406	6	22.4	5	6
S0008	1	49.7	5	20	SW2525	6	50.7	4	10
S0331	1	77.5	9	7	S0087	6	81.4	4	10
SW974	1	108.9	8	15	S0220	6	98.2	2	13
S0056	1	179.7	5	15	SW122	6	103.9	5	9
SW1301	1	235.1	5	8	SW1881	6	135.8	4	26
SWR2516	2	0	3	4	SW322	6	164.8	7	3
SW240	2	41.0	4	13	SW2419	6	181.1	7	12
S0170	2	53.7	2	5	S0025	7	0	5	6
SW1026	2	64.8	8	10	S0064	7	28.1	7	17
S0370	2	93.4	6	13	SW1369	7	48.0	7	14
SW1844	2	103.2	5	1	SW859	7	92.5	4	41
S0378	2	110.1	4	9	S0115	7	135.8	7	7
S0036	2	142.0	6	7	SWR773	7	151.6	3	10
SW274	3	0	6	1	S0101	7	164.0	4	9
SW2021	3	22.7	11	8	SW764	7	186.7	3	5
S0206	3	68.7	4	3	SW2410	8	0	4	0
ACTG2	3	86.4	7	9	SW905	8	22.9	3	3
SW2047	3	101.3	5	17	SWR1101	8	55.0	7	44
SW2408	3	124.3	4	2	S0017	8	95.1	5	10
S0002	3	132.4	5	5	SW2160	8	110.7	3	9
SW1327	3	141.2	9	5	SW1085	8	124.4	3	3
SW2532	3	159.6	6	8	S0178	8	165.5	4	21
SW2404	4	0	7	8	SW21	9	0	4	9
S0301	4	29.2	5	26	SW983	9	13.2	5	8
SW871	4	54.1	6	25	SW911	9	43.1	6	8
SW2454	4	61.8	4	6	SW2401	9	63.7	3	4
S0107	4	73.8	6	5	SW539	9	72.4	2	7
S0214	4	88.0	5	10	SW989	9	97.0	6	9
S0097	4	131.3	3	11	SW2116	9	127.4	4	14
SW413	5	0	3	36	SWR136	10	0	7	26
ACR	5	11.5	5	2	SW249	10	20.2	4	9
SWR453	5	53.4	3	7	SWC19	10	44.3	5	17
SW2	5	81.5	6	9	SW1041	10	56.8	2	10
S0005	5	108.9	10	12	SW920	10	79.4	2	0
S0018	5	127.4	6	9	S0391	11	0	4	9
SW995	5	147.6	5	5	S0071	11	53.0	4	6
SW378	5	159.7	3	3	S0230	11	65.2	5	11
					SW66	11	119.0	7	20

[a]DG = number of unverified genotypes deleted for each marker (out of 510 F_2 pigs)

Table III.1 (cont'd).

Marker	Chr	Position	Alleles	DG[a]	Marker	Chr	Position	Alleles	DG[a]
SW2490	12	0	6	10	S0111	16	0	7	27
SW957	12	31.2	6	12	SW419	16	30.9	5	13
SW874	12	47.2	4	17	SW2517	16	64.8	3	14
S0090	12	61.0	5	11	S0061	16	99.5	4	18
SW2180	12	94.1	6	17	SWR1004	17	0	5	25
S0219	13	0	3	8	SW2441	17	22.7	7	8
SWR1941	13	13.7	7	12	SW1031	17	42.9	2	7
SW344	13	40.9	7	7	SW2427	17	94.9	6	17
SWR1008	13	54.2	7	28	SW1023	18	0	4	3
S0068	13	65.1	5	13	SW1984	18	43.1	3	0
SW398	13	85.8	5	12	S0062	18	54.9	4	7
SW2440	13	103.2	5	5	SW949	X	0	6	13
S0215	13	122.6	3	3	SW980	X	14.8	5	9
SW857	14	0	5	6	SW2534	X	37.3	4	10
SW510	14	26.6	3	6	SW2126	X	47.7	5	4
SW210	14	45.9	3	6	SW2470	X	56.1	4	9
SW886	14	64.7	7	13	SW1426	X	89.2	3	3
SW55	14	85.2	4	10	SW2059	X	146.6	5	18
SW1557	14	95.6	3	25	SW1608	X	169.6	4	11
SWC27	14	117.6	3	2					
SW1204	15	0	3	45					
S0148	15	24.7	5	11					
S0088	15	54.8	2	9					
SW1683	15	64.5	4	1					
SW1983	15	82.2	6	11					
SW1119	15	96.0	5	9					

[a]DG = number of unverified genotypes deleted for each marker (out of 510 F_2 pigs)

Table III.2. Order of polynomial on week of age terms and other significant terms for random regression analyses of serial growth data.

Trait	Week of age	Significant term[a]	
		Sex* week^2	Finisher* week^2
Body weight, kg	4	-	X
Tenth rib backfat, mm	2	X	-
Longissimus muscle area, cm^2	3	-	-
Last rib backfat, mm	4	X	-
Fat-free total lean, kg	4	-	X
Total body fat tissue, kg	4	X	-
Empty body protein, kg	2	-	X
Empty body lipid, kg	4	-	-

[a]X indicates used in model, - indicates not used in model

Table III.3. Number of records, means, and standard deviations for growth traits measured.

Trait	N	Mean	SD
Birth weight, kg	510	1.50	0.32
3 wk weight, kg	510	5.61	1.46
6 wk weight, kg	510	11.94	2.78
10 wk weight, kg	510	26.38	4.91
10 wk tenth rib backfat, mm	510	7.94	1.80
10 wk *longissimus* muscle area, cm^2	510	11.63	2.60
10 wk last rib backfat, mm	510	6.09	1.09
13 wk weight, kg	510	41.56	6.55
13 wk tenth rib backfat, mm	510	9.71	2.66
13 wk *longissimus* muscle area, cm^2	510	17.03	3.33
13 wk last rib backfat, mm	510	7.13	1.35
16 wk weight, kg	510	62.01	8.21
16 wk tenth rib backfat, mm	510	12.34	3.44
16 wk *longissimus* muscle area, cm^2	510	25.03	3.92
16 wk last rib backfat, mm	510	9.53	2.29
19 wk weight, kg	510	80.85	10.15
19 wk tenth rib backfat, mm	510	16.03	5.12
19 wk *longissimus* muscle area, cm^2	510	31.72	4.51
19 wk last rib backfat, mm	510	11.89	3.38
22 wk weight, kg	510	100.00	10.93
22 wk tenth rib backfat, mm	510	19.97	6.30
22 wk *longissimus* muscle area, cm^2	510	37.47	5.04
22 wk last rib backfat, mm	510	14.43	4.13
10-22 wk ADG, g/d	510	880.21	107.99
Days to 105 kg	510	157.37	14.54
22 wk total body fat tissue, kg	510	25.01	7.00
22 wk fat-free total lean tissue, kg	510	38.45	4.41
22 wk empty body protein, kg	510	15.01	1.67
22 wk empty body lipid, kg	510	21.97	4.27

Table III.4. Position and significance levels of single point QTL significant at 5% chromosome-wise level with additive, dominance, and imprinting effects and standard errors of the QTL.

		Pos.	Additive		Dominance		Imprinting		
Chr	Trait	(cM)	Effect	SE	Effect	SE	Effect	SE	F-ratio[a]
1	13 wk *longissimus* muscle area, cm^2	87	-0.66	0.22	0.56	0.36	0.33	0.23	4.55
3	10 wk tenth rib backfat, mm	45	-0.03	0.15	-0.06	0.32	0.58	0.15	5.34
4	22 wk *longissimus* muscle area, cm^2	45	-1.30	0.36	-1.02	0.59	-0.26	0.34	5.20
5	Birth weight, kg	58	-0.05	0.02	-0.04	0.04	0.07	0.03	4.44
6	10 wk *longissimus* muscle area, cm^2	104	0.11	0.15	0.75	0.21	-0.06	0.14	4.48
6	19 wk *longissimus* muscle area, cm^2	104	-0.05	0.29	1.56	0.42	-0.41	0.29	4.98
6	22 wk fat-free total lean, kg	104	-0.74	0.29	1.23	0.42	-0.54	0.29	5.97*
6	22 wk empty body protein, kg	104	-0.31	0.11	0.35	0.16	-0.18	0.11	5.11
6	10 wk last rib backfat, mm	134	0.40	0.06	-0.37	0.10	-0.07	0.07	17.59***
6	10 wk tenth rib backfat, mm	137	0.67	0.10	-0.76	0.14	-0.04	0.11	25.77***
6	19 wk tenth rib backfat, mm	138	1.81	0.25	-1.80	0.38	-0.25	0.28	24.97***
6	19 wk last rib backfat, mm	138	1.36	0.18	-1.21	0.27	-0.25	0.20	26.15***
6	13 wk last rib backfat, mm	139	0.55	0.08	-0.50	0.13	-0.04	0.09	20.07***
6	22 wk last rib backfat, mm	139	1.44	0.23	-1.11	0.36	-0.10	0.25	16.45***
6	22 wk total body fat tissue, kg	139	1.32	0.42	-0.87	0.66	-1.06	0.47	5.48
6	13 wk tenth rib backfat, mm	140	0.97	0.15	-0.93	0.23	-0.18	0.16	20.36***
6	16 wk last rib backfat, mm	140	0.85	0.14	-0.92	0.22	-0.16	0.15	19.31***
6	16 wk tenth rib backfat, mm	141	1.37	0.19	-1.09	0.30	0.09	0.21	22.09***
6	22 wk tenth rib backfat, mm	142	2.09	0.35	-1.98	0.58	-0.03	0.39	15.17***
6	22 wk empty body lipid, kg	142	0.91	0.26	-1.04	0.43	-0.43	0.29	6.48**
6	16 wk *longissimus* muscle area, cm^2	150	0.30	0.27	-1.45	0.48	-0.57	0.29	4.87
7	10-22 wk ADG, g/d	148	15.76	6.53	-3.07	11.3	20.08	6.73	4.75
8	13 wk tenth rib backfat, mm	115	0.51	0.15	-0.10	0.25	-0.33	0.16	5.20
9	22 wk fat-free total lean, kg	4	-0.16	0.30	1.43	0.46	0.63	0.33	4.26
9	Days to 105 kg	5	0.42	0.96	-5.02	1.47	-2.22	1.06	5.08
9	22 wk empty body lipid, kg	6	0.05	0.26	1.56	0.40	0.80	0.29	7.21**
9	22 wk empty body protein, kg	6	-0.10	0.11	0.58	0.17	0.16	0.13	4.30
9	22 wk total body fat tissue, kg	8	-0.20	0.44	2.40	0.66	0.84	0.48	5.26
9	22 wk tenth rib backfat, mm	86	-1.02	0.43	-2.46	0.82	0.44	0.44	4.67
11	10 wk last rib backfat, mm	0	0.04	0.10	0.51	0.22	-0.24	0.10	3.97
11	19 wk weight, kg	65	-1.27	0.62	-2.08	0.87	1.06	0.63	4.36
11	19 wk last rib backfat, mm	65	-0.21	0.19	-1.10	0.27	0.16	0.20	6.34*
11	19 wk tenth rib backfat, mm	68	-0.64	0.28	-1.30	0.42	-0.01	0.29	5.25*
11	22 wk tenth rib backfat, mm	75	-0.34	0.42	-2.33	0.73	0.29	0.43	3.80
11	22 wk empty body lipid, kg	75	-0.46	0.30	-1.87	0.52	0.21	0.31	5.30*
16	22 wk last rib backfat, mm	64	-1.10	0.30	-0.17	0.50	0.47	0.30	5.35*
16	19 wk tenth rib backfat, mm	65	-1.42	0.33	-0.26	0.55	0.04	0.34	6.40**
16	22 wk total body fat tissue, kg	65	-2.06	0.52	-1.24	0.86	0.89	0.53	7.08**
16	22 wk weight, kg	67	-2.71	0.88	-1.59	1.51	0.98	0.91	4.02
16	19 wk weight, kg	69	-2.96	0.80	-0.18	1.42	1.17	0.83	4.97
16	10-22 wk ADG, g/d	97	-14.67	5.98	-15.61	8.83	16.50	6.04	5.45*
18	10 wk tenth rib backfat, mm	54	0.30	0.11	0.30	0.16	0.18	0.12	4.14
18	16 wk last rib backfat, mm	54	0.40	0.14	0.42	0.21	0.06	0.16	3.75

[a] Significant at * = 1% chromosome-wise, ** = 5% genome-wise, *** = 1% genome-wise levels

Table III.5. Position and significance levels of random regression QTL significant at 5% chromosome-wise level with additive effects and standard errors of QTL at those positions.

Chr	Trait	Location (cM)	Additive Effect	Additive SE	F-ratio[a]
5	Total fat tissue intercept, kg	57	-0.0078	0.0027	8.48
5	Body weight intercept, kg	120	-0.0217	0.0070	9.52
5	Fat-free total lean tissue intercept, kg	123	-0.0075	0.0022	11.56*
5	Empty body protein intercept, kg	126	-0.0024	0.0008	8.12
6	Last rib backfat intercept, mm	36	0.0059	0.0017	12.27*
6	Empty body lipid intercept, kg	104	0.0114	0.0036	9.91
6	Last rib backfat linear, mm/wk	140	0.0052	0.0018	8.07
6	Tenth rib backfat linear, mm/wk	145	0.0211	0.0061	12.08*
6	*Longissimus* muscle area intercept, cm^2	181	0.0138	0.0048	8.35
8	Total fat tissue linear, kg/wk	55	0.0093	0.0033	8.11
8	Body weight intercept, kg	114	0.0278	0.0067	17.10***
8	Total fat tissue intercept, kg	116	0.0068	0.0024	7.95
8	Last rib backfat intercept, mm	117	0.0044	0.0015	8.41
9	Empty body protein linear, kg/wk	63	0.0036	0.0012	9.53
10	Tenth rib backfat intercept, mm	26	0.0125	0.0042	8.75
11	Last rib backfat linear, mm/wk	119	0.0077	0.0024	10.14*
14	Last rib backfat intercept, mm	109	-0.0053	0.0018	8.99
14	Total fat tissue intercept, kg	117	-0.0078	0.0028	7.94
16	Tenth rib backfat linear, mm/wk	0	-0.0171	0.0057	9.14
16	Total fat tissue linear, kg/wk	0	-0.0090	0.0032	8.12
16	Body weight linear, kg	0	-0.0298	0.0094	10.03*
16	Last rib backfat linear, mm/wk	3	-0.0055	0.0019	8.04
18	*Longissimus* muscle area linear, cm^2/wk	0	0.0517	0.0128	16.30***
18	Empty body lipid linear, kg/wk	0	0.0166	0.0069	5.87
18	Body weight linear, kg	0	0.0455	0.0138	10.80*
18	Tenth rib backfat linear, mm/wk	7	0.0295	0.0087	11.45*
18	Total fat tissue intercept, kg	49	0.0064	0.0024	7.17
X	Fat-free total lean tissue intercept, kg	35	-0.0069	0.0021	10.71*
X	Empty body protein linear, kg/wk	37	-0.0034	0.0010	10.86*
X	Empty body protein intercept, kg	160	-0.0026	0.0009	7.39
X	Last rib backfat linear, mm/wk	169	-0.0061	0.0019	9.81
X	Empty body lipid intercept, kg	169	-0.0108	0.0040	7.48
X	Empty body lipid linear, kg/wk	169	-0.0130	0.0050	6.84

[a] Significant at * = 1% chromosome-wise, ** = 5% genome-wise, *** = 1% genome-wise levels

Table III.6. Position and 95% confidence interval lower and upper limits of growth QTL significant at the 5% genome-wise level.

Chr	Trait	Position (cM)	Lower limit (cM)	Upper limit (cM)
6	10 wk last rib backfat, mm	134	122	144
6	10 wk tenth rib backfat, mm	137	129	143
6	19 wk tenth rib backfat, mm	138	127	144
6	19 wk last rib backfat, mm	138	127	144
6	13 wk last rib backfat, mm	139	125	145
6	22 wk last rib backfat, mm	139	124	146
6	13 wk tenth rib backfat, mm	140	127	146
6	16 wk last rib backfat, mm	140	126	147
6	16 wk tenth rib backfat, mm	141	128	147
6	22 wk tenth rib backfat, mm	142	124	149
6	22 wk empty body lipid, kg	142	23	181
8	Body weight intercept, kg	114	2	139
9	22 wk empty body lipid, kg	6	0	104
16	19 wk tenth rib backfat, mm	65	0	79.5
16	22 wk total fat tissue, kg	65	0	80
18	*Longissimus* muscle area linear, cm^2/wk	0	0	10

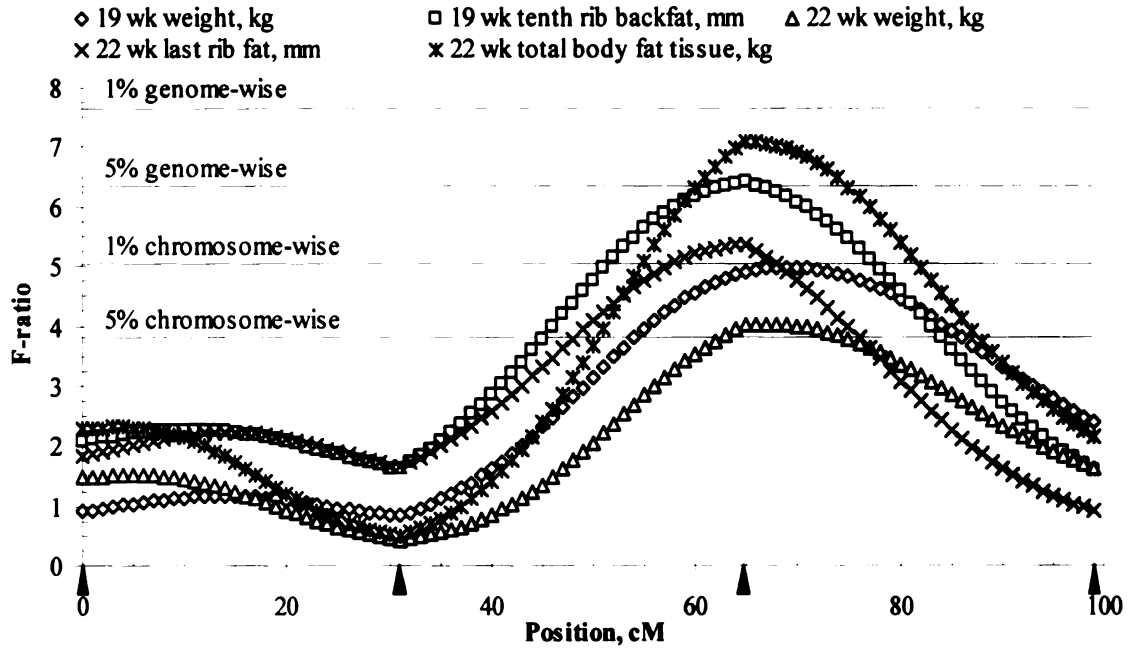

Figure III.1. F-ratio plots versus relative positions on SSC 16. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

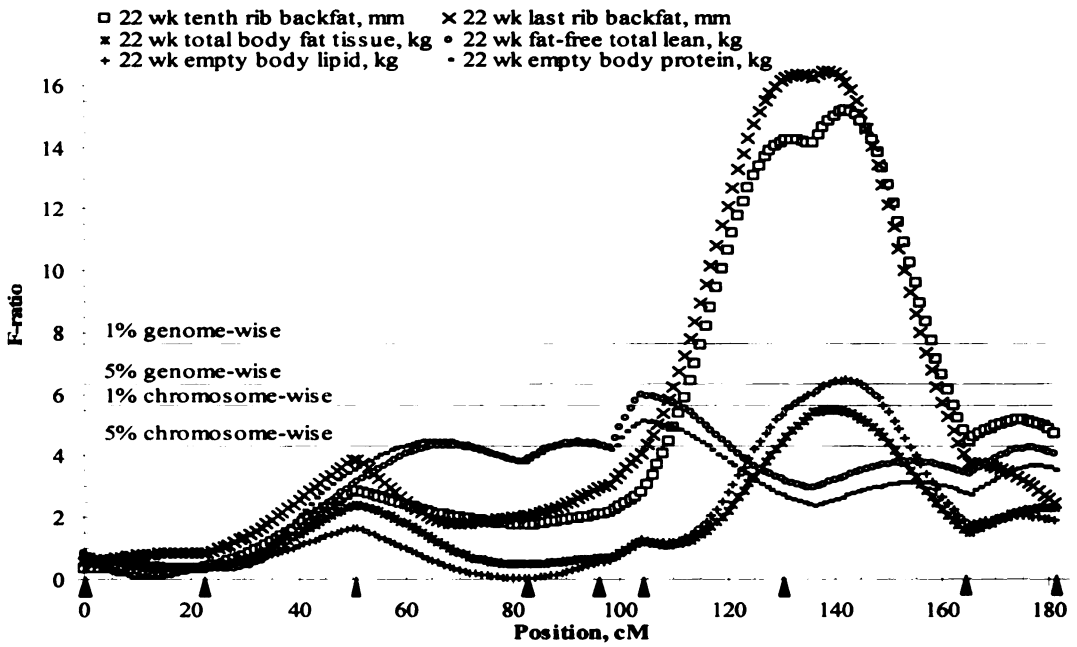

Figure III.2. F-ratio plots versus relative positions on SSC 6. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

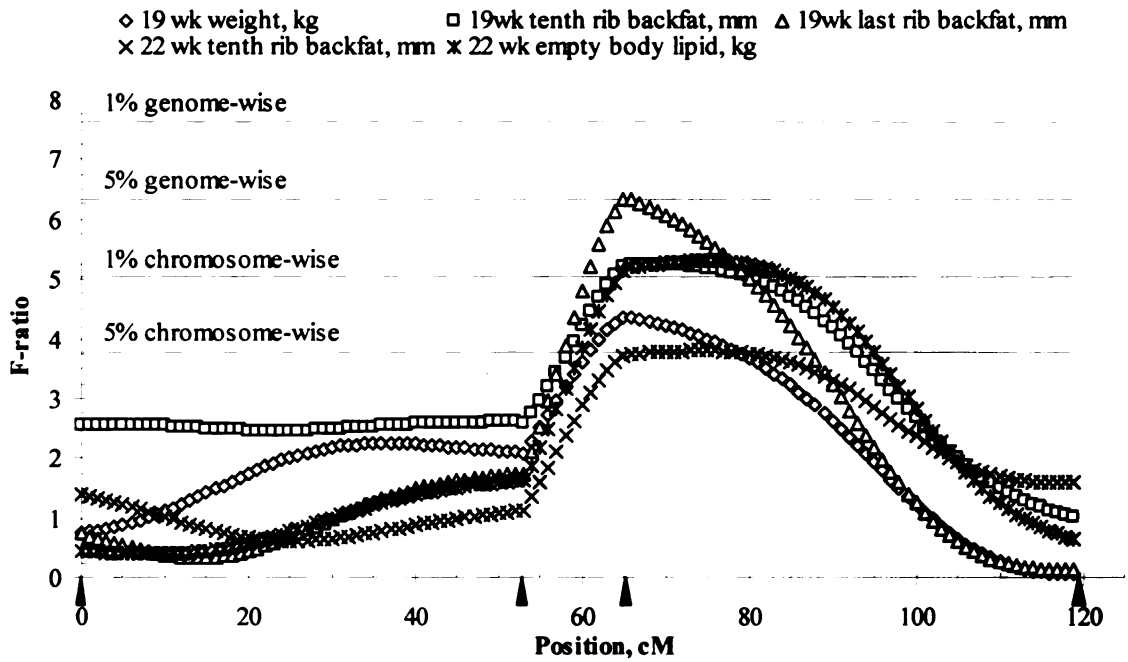

Figure III.3. F-ratio plots versus relative positions on SSC 11. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

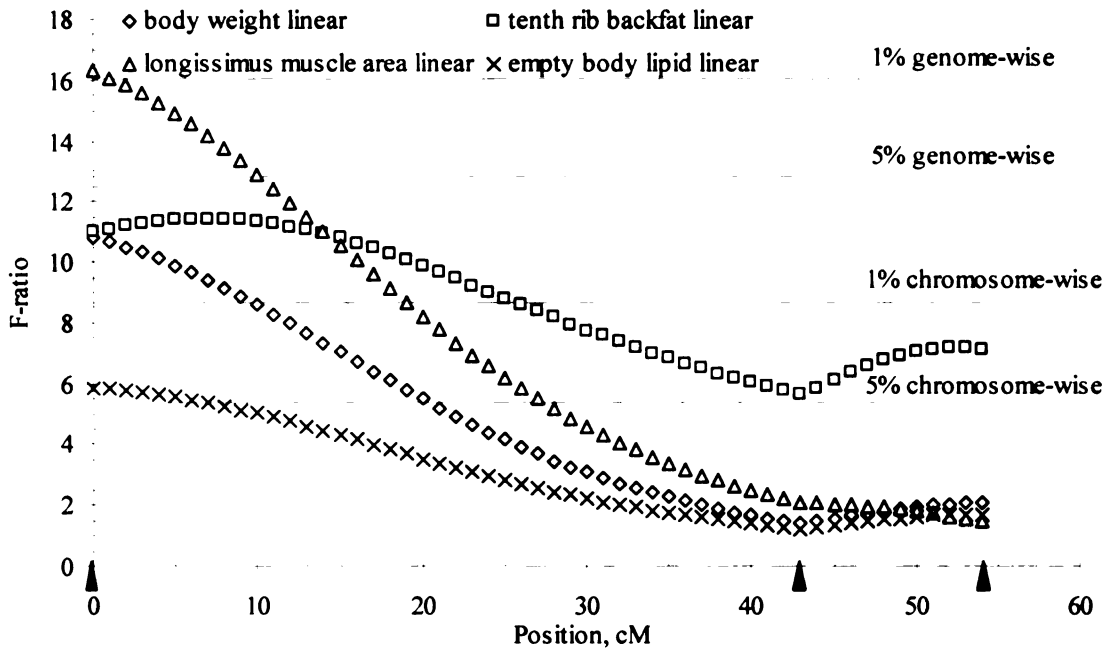

Figure III.4. F-ratio plots versus relative positions on SSC 18. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

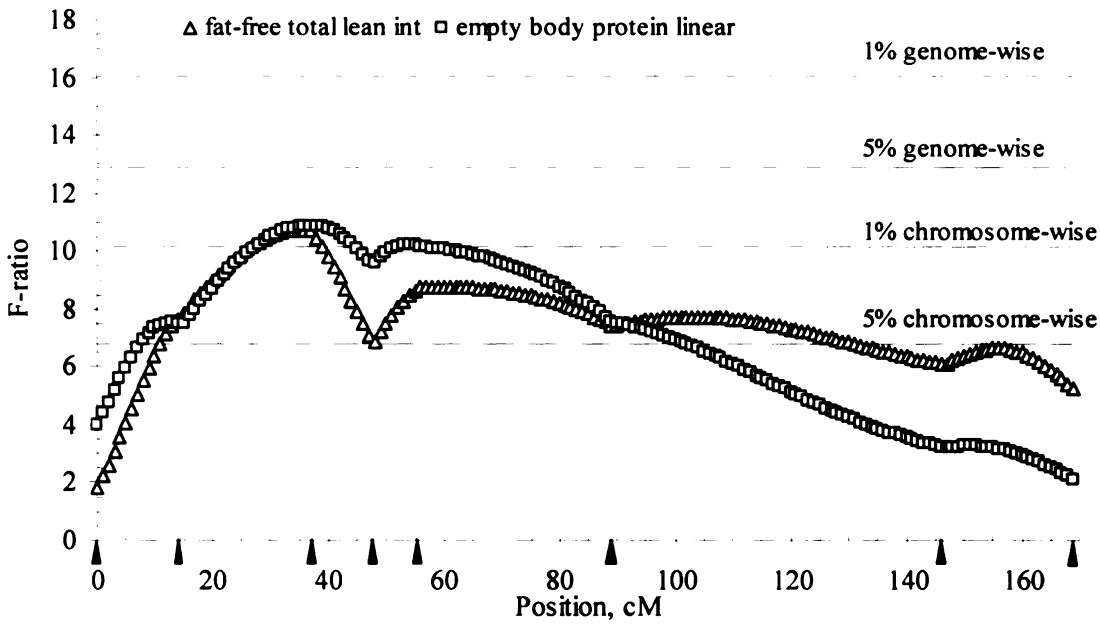

Figure III.5. F-ratio plots versus relative positions on SSC X. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

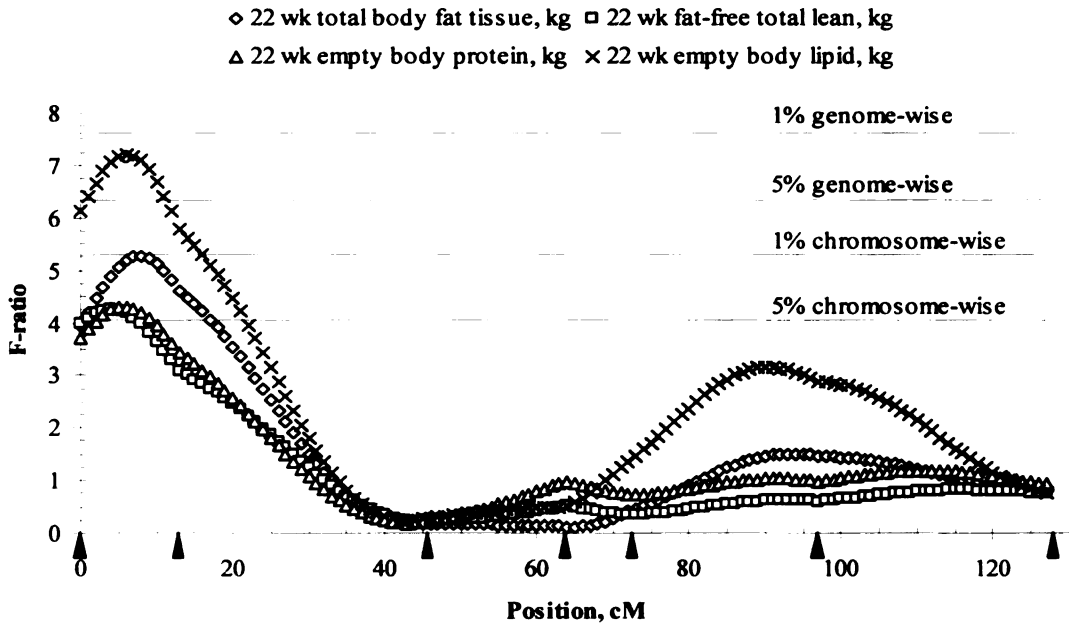

Figure III.6. F-ratio plots versus relative positions on SSC 9. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

CHAPTER IV

QTL MAPPING IN AN F_2 DUROC x PIETRAIN RESOURCE POPULATION: II. CARCASS AND MEAT QUALITY TRAITS[3]

Abstract

Pigs from the F_2 generation of a Duroc x Pietrain resource population were evaluated to discover quantitative trait loci (QTL) affecting carcass composition and meat quality traits. Carcass composition phenotypes included primal cut weights, skeletal characteristics, backfat thickness, muscle pH, and temperature. Meat quality data collected on boneless *longissimus* muscle chops included objective and subjective color information, marbling and firmness scores, and drip loss. Additionally, chops were analyzed for moisture, protein, and fat composition as well as cook yield and Warner-Bratzler shear force measurements. Palatability of chops was determined by a trained sensory taste panel. A total of 510 F_2 animals were genotyped for 124 microsatellite markers evenly spaced across the entire genome. Data were analyzed with line cross least squares regression interval mapping methods using sex and litter as fixed effects and carcass weight or harvest age as covariates. Significance thresholds of the F-statistic for additive, dominance, and imprinted QTL were determined on chromosome- and genome-wise levels by permutation tests. A total of 94 QTL for 35 of the 38 traits analyzed were found to be significant at the 5% chromosome-wise level. Of these 94 QTL, 43 were significant at the 1% chromosome-wise, 27 at the 5% genome-wise, and 14 at the 1% genome-wise significance thresholds. Putative QTL were discovered for 45 min pH and pH decline on SSC 3, marbling score and carcass backfat on SSC 6, carcass length and

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number of ribs on SSC 7, marbling score on SSC 12, and color measurements and tenderness score on SSC 15. These results will facilitate fine mapping efforts to identify genes controlling carcass composition and meat quality traits that can be incorporated into marker-assisted selection programs to accelerate genetic improvement in pig populations.

Introduction

Enhancement of production efficiency and improvement of product quality are major concerns for producers of food animals. Swine have been selected for increased lean growth, but the antagonistic relationship with meat quality, shown by significant genetic correlations of carcass leanness to ultimate pH (-0.13), reflectance (0.16), and drip loss (0.05) (Sellier, 1998), has caused a decrease in meat quality. Additionally, Wood (1985) reported increased occurrence of less juicy pork products with leaner pigs. Locating specific favorable quantitative trait loci (QTL) for meat quality and using this information in genetic improvement programs will help overcome this natural relationship and allow improvement in both efficient production and product quality.

The Duroc and Pietrain breeds are utilized worldwide as sire breeds, and these breeds differ in carcass and meat quality phenotypes. Quiniou and Noblet (1995) used Pietrain boars in their study because of the breed's propensity towards leanness. Affentranger et al. (1996) compared Duroc and Pietrain pigs and reported more backfat for Duroc animals as compared to Pietrain animals. In Edwards et al. (2003), Duroc-sired pigs had longer carcass lengths than Pietrain-sired pigs, while Pietrain-sired pigs had less backfat at the tenth rib and larger *longissimus* muscle area at harvest than Duroc-sired pigs. Meat quality was more favorable for Duroc- versus Pietrain-sired pigs in

Affentranger et al. (1996) and Edwards et al. (2003). In general, Duroc and Duroc-sired pigs have favorable meat quality (Langlois and Minvielle, 1989b; Jeremiah et al., 1999), whereas Pietrain and Pietrain-sired animals are leaner with average meat quality (Edwards at al., 2003). The objective of this study was to conduct a full genome scan using microsatellite markers to search for QTL affecting carcass and meat quality traits in an F_2 Duroc x Pietrain resource population.

Materials and Methods

Population Development

A three-generation resource population was developed from four F_0 Duroc sires and sixteen F_0 Pietrain dams at Michigan State University to study traits of growth, body composition, and meat quality. All grandparents were determined homozygous normal for the RYR-1 gene by a DNA test (Fujii et al., 1991). Further details of population development and animal management are found in Edwards (2005a).

Phenotype Collection

At harvest, pigs were transported to one of two abattoirs. A total of 176 pigs were harvested at the Michigan State University Meats Laboratory (East Lansing, MI), and the remaining pigs were transported to a small federally inspected plant in western Michigan (DeVries Meats, Coopersville, MI). Both groups were fasted and allowed to rest overnight with access to water. Ear tag and tattoo numbers were collected at harvest to maintain identity of each carcass. Carcass traits collected included hot carcass weight and *longissimus dorsi* pH and temperature at 45 min and 24 h postmortem. Dressing percentage was calculated by dividing hot carcass weight by harvest live weight. After overnight chilling, measurements were taken according to National Pork Producers

Council guidelines (NPPC, 2000) and included midline first rib backfat, last rib backfat, last lumbar backfat, number of ribs, and carcass length. Weights of primal cuts of ham, closely trimmed loin, picnic shoulder, Boston shoulder, belly, and spareribs were recorded. During carcass fabrication, measurements of tenth rib backfat and *longissimus* muscle area were also recorded. A section of loin from the tenth rib to the last rib was further evaluated for meat quality traits at Michigan State University. All measurements were taken from the left side of each carcass.

Boneless *longissimus dorsi* were removed from loin sections and external fat removed. A small portion of *longissimus dorsi* was diced and frozen for proximate analysis. Two 2.54 cm thick chops were cut from the anterior end of the *longissimus dorsi* for fresh meat quality analysis. The two chops were allowed to bloom for a minimum of 10 minutes and evaluated for subjective scores of color and marbling (NPPC, 2000) and firmness (NPPC, 1991). The color score scale ranged from 1 (pale pinkish gray) to 6 (dark purplish red). The marbling score scale was 1 to 10 (closely approximating fat percentage). The firmness score scale was 1 (very soft and watery) to 5 (very firm and dry). Additionally, objective color scores of CIE L* (lightness), a* (redness), and b* (yellowness) were obtained using a Minolta CR-310 colorimeter (Ramsey, NJ) with a D_{65} illuminant and a two-degree standard observer. Chops were weighed, hung in sealed plastic bags for 24 h at 4°C, and then weighed again for drip loss measurement. The remaining section of the *longissimus dorsi* was vacuum packaged, aged at 4°C until 7 d postmortem, and frozen for further meat quality tests of cook yield, shear force, and sensory taste panel analysis.

From frozen loin sections, two chops were cut for cook yield and Warner-Bratzler shear force (WBS) analysis. For cook yield measurements, each chop was thawed, weighed, cooked to 71°C internal temperature on a Taylor clamshell grill (Model QS24, Taylor Co., Rockton, IL), cooled to room temperature, and weighed again. From these chops, six cores (three cores from each chop) were taken parallel to the muscle fiber direction using a drill press-mounted corer. Cores were sheared perpendicular to muscle fibers using a Warner-Bratzler head on a TA-HDi texture analyzer (Texture Technologies Corp., Scarsdale, NY). The cross-head speed was 3.30 mm/s. Samples for proximate analysis were ground using dry ice and measured for moisture (oven drying), fat (soxhlet ether extraction), and protein (nitrogen combustion, Model FP-2000, Leco Inc., St. Joseph, MI) following AOAC procedures (2000). A total of 958 animals had carcass and meat quality traits measured.

Trained Sensory Panel Evaluation

A trained panel of seven healthy adults (ages 20-65) was utilized to determine specific sensory attributes of each *longissimus* chop. The sensory panel was trained according to Meilgaard et al. (1991) and AMSA (1995). All panelists had experience in sensory evaluation and were previously trained to evaluate various meat products. Each sample was evaluated for juiciness, muscle fiber and overall tenderness, connective tissue, and off-flavor using an 8 point hedonic scale. Higher scores in each of the first four categories were more favorable and indicated extremely juicy, extremely tender, or no connective tissue for each of these attributes, respectively, while lower scores for off-flavor were indicative of less off-flavor.

Frozen chops were thawed for 24 h at 2.6°C and then cooked on a Taylor clamshell grill (Model QS24, Taylor Co., Rockton, IL). The upper plate was set to 104.4°C and the bottom plate was set to 102.8°C with a 2.16 cm gap between plates. Temperature was monitored by inserting a copper constantan thermocouple (0.051 cm diameter, 15.2 cm length, Omega Engineering Inc., Stamford, CT) into the geometric center of the pork chop. Chops were cooked to a final internal temperature of 71°C. Sample preparation included cutting 1.27 cm cubes from the center portion of each chop, and two cubes were placed in 2 oz. soufflé cups and covered with a lid. Soufflé cups were placed in a Pyrex two quart bowl with a lid and the bowl was covered with warm towels to keep the samples warm. The insulated bowl was placed in an insulated container and transferred to the sensory evaluation room.

Testing took place in climate controlled, partitioned booths with cool incandescent light. The order of sample preparation was randomized within each session to minimize positional bias and a 3 digit random code was used to label the samples. The samples were picked up with a toothpick, chewed with the molars, and evaluated. Expectorant cups were provided to prevent taste fatigue and distilled, deionized water was used to clean the palate between samples. The panelists were standardized each day by evaluating a warm-up sample and discussing the results. A total of 18-24 samples were evaluated on each day, and the day was divided into three sessions with a 15 min break between each session.

Genotype Collection

Whole blood was collected from all F_0, F_1, and F_2 animals for DNA isolation. White blood cells were separated and frozen for subsequent DNA extraction.

Dinucleotide microsatellite genetic markers were utilized in this study to obtain genotypes for a whole genome scan of approximately 20 cM spacing across the 18 autosomes and X chromosome. Markers were selected from the published pig genome linkage map (http://www.marc.usda.gov/genome/swine/swine.html, USDA, 2005b), and the initial set of markers were tested for informativeness (markers segregating between F_0 breeds and estimated to have three or more alleles) using fluorescent primers distributed by the US Pig Genome Coordinator (supported by the USDA-CREES through the National Research Support Project 8). The resulting 124 markers were genotyped for 510 F_2 animals, their parents, and grandparents at a commercial laboratory (GeneSeek Inc., Lincoln, NE). These 510 animals were sampled across all farrowing groups from 61 entire litters. Pigs represented all F_1 sires with at least 100 grand progeny from each F_0 sire. Fifteen of the 16 F_0 dams had a son or daughter as a parent that produced multiple litters of the selected F_2 pigs with the remaining F_0 dam represented by a single F_1 daughter with one litter in this group. Markers used in this genome scan were those reported in Edwards (2005a).

QTL Analysis

Genetic linkage maps were constructed for all 18 autosomes and the X chromosome using Crimap version 2.4 software (Green et al., 1990) and are reported in Edwards (2005a). These maps were used in an F_2 least squares interval mapping framework for QTL analysis (Haley et al., 1994) similar to that in Edwards (2005a). The F_2 analysis option of the QTL Express software (Seaton et al., 2002) was used to search for single QTL with additive, dominance, or imprinting effects on the 18 autosomes and additive effects on the X chromosome for the carcass and meat quality traits with the

fixed effects and covariates as listed in Table IV.1. The terms that were included in each model were those that were found to be important to the model ($P < 0.20$) when each trait was analyzed by ordinary least squares analysis of variance without QTL effects. Fixed effects of sex of the animal and harvest date were included in every model. Some models contained the covariates of carcass weight or harvest age, while others had neither covariate (Table IV.1).

Tests of the full model including additive, dominance, and imprinting effects versus the reduced model without these effects were carried out to determine F-ratios at 1 cM intervals across the entire genome. Significance thresholds of 5% and 1% at the chromosome-wise and 5% and 1% at the genome-wise levels were determined through the use of permutation tests (Churchill and Doerge, 1994) in QTL Express using 30,000 permutations. For each QTL determined to be significant at the 5% genome-wise level, confidence intervals of the QTL position were determined using a bootstrap method with 5,000 permutations in QTL Express (Visscher et al., 1996).

Results and Discussion

QTL Analysis

Trait means and standard deviations for genotyped animals with measured phenotypes are reported in Table IV.2. These means and standard deviations are similar to those measured in other resource populations reporting similar traits (e.g. Malek et al., 2001b; Stearns et al., 2005). The permutation test results of F-ratio calculations to determine significance thresholds for the model testing additive, dominance, and imprinting effects ranged from 3.44 to 4.35 across different chromosomes for the 5% chromosome-wise levels and from 4.71 to 5.64 for the 1% chromosome-wise levels.

Genome-wise F-ratio threshold levels were 6.34 and 7.63 for 5% and 1% levels, respectively. Significance levels of the F-statistic for the additive effect only model for SSC X were 6.68 and 9.93 for 5% and 1% chromosome-wise levels, respectively, whereas the significant F-ratios were 12.86 and 16.05 for 5% and 1% genome-wise levels, respectively.

Estimates of position and F-ratio for carcass and meat quality QTL significant at the 5% chromosome-wise level are listed in Table IV.3. The table is sorted by chromosome and position within each chromosome. Additionally, the additive, dominance, and imprinting effect of each QTL along with the standard errors are listed in Table IV.3. A total of 94 QTL for 35 of the 38 traits were found to be significant at 5% chromosome-wise levels. Of these 94 QTL, 43 were significant at the 1% chromosome-wise, 27 at the 5% genome-wise, and 14 at the 1% genome-wise significance thresholds. No significant QTL were detected in this population for subjective firmness, Boston shoulder weight, or picnic shoulder weight.

All chromosomes, except 13, contained at least one QTL for these 38 traits. Although these two breeds are used in similar capacities in many pork production chains, many important QTL that impact phenotypic differences between the two breeds still exist and are possible candidates to explore more thoroughly. Differences in carcass and meat quality traits between animals sired by Duroc or Pietrain boars in a crossbred progeny study (Edwards et al., 2003) have been previously reported. Some of the breed allelic QTL effects in the current study had effects in the same direction as breed effects reported in Edwards et al. (2003), but a few cryptic alleles were detected that acted in an opposite direction to the general trend for the overall breed effects.

Carcass Measurements

The carcass measurement traits included many of the classically measured carcass traits that impact prices paid for market pigs. Measures of off-farm BW and hot carcass weight are related and QTL for these two traits appeared in similar positions. Two significant QTL were identified, one on SSC 4, expressing an additive effect where Pietrain alleles increased these weights, and one on SSC 10, which indicated an imprinting effect where alleles from Pietrain dams increased these weights. These QTL were significant at the 5% genome-wise and 1% chromosome-wise levels, respectively. While other studies have reported QTL for live weight at harvest on SSC 4 (Cepica et al., 2003; Marklund et al., 1998), the position of these QTL were more distal than the 12 cM distance from the first marker observed in this study. By utilizing the population of Cepica et al. (2003), another analysis by Dragos-Wendrich et al. (2003) found a QTL for live weight at harvest on SSC 10, but, again, not in the same position as reported here. Several studies have reported QTL for carcass weight on SSC 4, but all of these studies reported positions more distal (85 to 121 cM from SW2404) than was discovered in this population (Pérez-Enciso et al., 2000; Malek et al., 2001a; Cepica et al., 2003).

Carcass temperature and pH at 45 min and 24 h postmortem are important early indicators of meat quality. The decline between these two points is a rarely studied trait, but is indicative of changes in meat properties that affect further quality parameters. Figure IV.1 demonstrates the F-ratio curves plotted versus relative marker positions on SSC 3 and illustrates the similar shapes of F-ratios for 45 min pH and pH decline from 45 min to 24 h postmortem. On SSC 3, a QTL that was significant at the 1% chromosome-wise level was discovered in this population which was additive and increased 45 min pH

when Pietrain alleles were present. In addition this QTL also caused a smaller decrease in pH from 45 min to 24 h with Pietrain alleles. The Pietrain alleles caused favorable change for these two traits which should improve meat quality. These can be considered cryptic alleles since previous studies reported lower pH values for Pietrain or Pietrain-cross pigs compared to animals from other breeds (Affentranger et al., 1996; Garcia-Macias et al., 1996; Edwards et al., 2003). This QTL affecting pH on SSC 3 was in a similar location to a pH QTL reported by Beeckmann et al. (2003) in a population that contained Pietrain germplasm. Additional QTL significant at the 5% genome-wise level were found for 24 h carcass temperature on SSC 5, which was estimated to have a positive dominance effect and another on SSC 6, which was additive in its effect and indicated animals with Duroc alleles increased 24 h carcass temperature. On SSC 9, QTL for 45 min temperature and 24 h temperature were found, but in separate regions of the chromosome. No other QTL studies have reported taking carcass temperature measurements, but our work indicated that significant QTL did control carcass temperature at 45 min and 24 h after harvest.

Measurements of skeletal characteristics of a carcass are important in determining size and ability to grow to heavier weights while maintaining leanness. Carcass length QTL were present on SSC 6 and 7 with both significant at the 1% genome-wise level. The QTL on SSC 6 showed a positive dominance effect while the one on SSC 7 affected both carcass length and dressing percentage in an additive manner (Figure IV.2). Duroc alleles caused a lengthening of the carcass and decreased dressing percentage. A similar dominance effect QTL was reported on SSC 6 by Malek et al. (2001a), while the QTL on SSC 7 was in a similar position to one reported by Rohrer and Keele (1998b). Two

putative QTL were detected for the number of ribs counted in each carcass with one on SSC 7 and one on SSC 18. The QTL for number of ribs on SSC 7 was found in the same location as one detected in several populations by Mikawa et al. (2005). Of nine families reported in their study, the one that contained Duroc germplasm had the highest F-ratio corresponding to a significant QTL on SSC 7. Their study reported an additive effect for this QTL, but they did not test imprinting effects. Our QTL was estimated to have an imprinting effect with animals that received a Duroc allele from the sire having an increase of 0.34 ribs.

Carcass backfat thickness and *longissimus* muscle area are predictive of body composition, and have been used to determine pricing structure at packing plants. Traditionally, carcass measurements of backfat have been taken along the midline at the first rib, last rib, and last lumbar vertebra in pigs, while measurements of backfat and *longissimus* muscle area at the tenth rib have been taken on a ribbed carcass. All of these measures can be used to determine body composition estimates. A region of SSC 6 (Figure IV.3) contained a significant QTL that affected many of these related backfat traits as well as carcass *longissimus* muscle area. This was an additive QTL in which Duroc alleles increased backfat and reduced *longissimus* muscle area. These results were consistent with overall breed results reported in Edwards et al. (2003) where Duroc germplasm contributed to an increase in backfat compared to Pietrain-sired pigs. The region of SSC 6 that affected tenth rib backfat was also found significant by Malek et al. (2001a). Ovilo et al. (2002b) also reported that the same region of SSC 6 affected *longissimus* muscle area as reported here. An additional QTL on SSC 18 that was dominant and increased last rib and tenth rib backfat when Duroc alleles were present

was discovered in this analysis. Finally, a QTL significant at the 1% chromosome-wise level was found for first rib backfat on SSC 5, and no previous pig QTL studies have identified a first rib backfat QTL in this region (Hu et al., 2005). Su et al. (2004) reported a QTL for carcass *longissimus* muscle area on SSC 7 in a similar region to the QTL significant at the 1% chromosome-wise level discovered in this study. Sato et al. (2003) also discovered a QTL for *longissimus* muscle area on SSC 7 in a population with a Duroc founder boar, but their QTL was located in a more proximal position than the QTL reported here.

Primal Cut Weights

Since primal cut weights were adjusted for carcass weight in the model to determine significance of QTL, these adjusted primal weights have a similar interpretation to primal cut weights as a percentage of carcass weight. Although QTL were not found in this study for Boston shoulder and picnic shoulder weights, these primal cut weights were highly dependent on where they were separated from one another and had higher standard deviations than other primal cuts compared to their mean weights (Table IV.2), so larger environmental variation may have prevented discovery of significant QTL. Other primal cuts had several putative QTL in this study. Again, SSC 6 contained a QTL that indicated more muscling in the ham and loin for animals with Pietrain alleles, which paralleled results of Edwards et al. (2003) that reported Pietrain-sired pigs had larger ham and loin primal weights than Duroc-sired pigs. Other pig QTL studies that reported loin weight, summarized by Hu et al. (2005), had not found QTL on SSC 6. Geldermann et al. (2003) reported a QTL for ham weight on SSC 6, but it was slightly more proximal to S0099, our first marker, than the QTL reported here. An

additional loin weight QTL, significant at the 5% genome-wise level, was found on SSC 3 and was estimated to have a negative dominance effect. Two QTL for belly weight were found, one on SSC 12 and one on SSC 14, at the 1% chromosome-wise and 5% genome-wise levels, respectively. The QTL on SSC 12 indicated that Duroc alleles additively increased belly weight whereas the QTL on SSC 14 was dominant and negative in its effect. These two QTL have not been previously reported (Hu et al., 2005). The analysis for sparerib weight indicated QTL located on SSC 1, 4, 6, 7, 8, and 18, although only the QTL on SSC 1 exceeded the 5% chromosome-wise significance threshold.

Meat Quality

Consumer perception of fresh meat products is affected at least in part by color, marbling, and firmness. Evaluation of these parameters on chops cut from *longissimus dorsi* in this study revealed QTL affecting traits of color and marbling, but not firmness. Putative QTL for subjective color were located on SSC 4, 6, 7, and 15. The QTL on SSC 15 was significant at the 1% chromosome-wise level for subjective color as well as for a* and at the 1% genome-wise level for L* (Figure IV.4). The additive effects indicate that Duroc alleles lowered the color score and raised the L* value while they lowered the a* value. The population studied by Malek et al. (2001b) also contained a QTL for L* on SSC 15, but it was slightly more distal than the position reported here. A QTL in a similar position to the one reported here for a* was also reported by de Koning et al. (2001). A QTL for L* was also discovered in this study at the same position on SSC 7 as the QTL reported for subjective color score. While not in the same position on SSC 7 as the QTL reported here, Ovilo et al. (2002a) also reported a QTL for L* on SSC 7. A

QTL at the 5% genome-wise level for a* was located on SSC 6 and was additive in its effect where Duroc alleles increased the a* value. The only QTL for b* found in this study was on SSC 9 and was significant only at the 5% chromosome-wise level.

Another factor that impacts a consumer's choice of meat and subsequent eating experience is marbling. The subjective marbling score analysis revealed three significant QTL on SSC 6, 10, and 12. The QTL on SSC 6 was additive and indicated that Duroc alleles increased marbling and was significant at the 1% genome-wise level while the one on SSC 12 was significant at the 5% genome-wise level. Marbling score and intramuscular fat percentage showed similar F-ratio curves when plotted versus relative marker position on SSC 6 (Figure IV.3), which indicated QTL within this region are controlling these traits.

The three traits of percentage moisture, fat, and protein from proximate analysis of *longissimus dorsi* are highly related as they are derived from percentages of the same whole. As subjective marbling score approximates fat percentage in each chop, two significant QTL for fat percentage were found at the same locations as the QTL for marbling score on SSC 6 and 12, again significant at the 1% and 5% genome-wise levels, respectively. Nearly the same position on SSC 6 for a QTL affecting intramuscular fat was reported by Ovilo et al. (2002b). The QTL on SSC 6 also affected moisture percentage, and was previously reported by Su et al. (2004). This chromosomal region also affected protein percentage, while the QTL on SSC 12 affected moisture percentage. An additional QTL, significant at the 1% genome-wise level, for protein percentage was located on SSC 15. Selection for any of these QTL will directly impact the other two

traits since these three traits are not strictly independent, as evidenced by similar F-ratio curves for fat and moisture percentages on SSC 12 (Figure IV.5).

Several traits measured are directly related to storage, preparation, and eating quality of chops. One was drip loss, and a QTL was found on SSC 9 with an estimated dominance effect that indicated that Duroc alleles caused a higher percentage of drip loss. Cook yield, which measured moisture loss during cooking, had two QTL, with one on SSC 5 significant at the 1% chromosome-wise level and an additional one on SSC 15. None of the drip loss or cook yield QTL discovered in this study, including related traits, were previously reported in a summary of pig QTL studies (Hu et al., 2005). Our analyses indicated significant QTL for WBS on SSC 7 and 15, with both significant at the 1% chromosome-wise level. A similar trait, Instron (star probe) force, was reported to have a QTL on SSC 15 (Malek et al., 2001b) in a similar position to the WBS QTL in our study, but the QTL on SSC 7 had not been reported previously (Hu et al., 2005). These same two QTL regions on SSC 7 and 15 reported here for WBS also affected tenderness and overall tenderness as determined by the trained sensory taste panel and were significant at the 5% genome-wise level for these two important eating quality traits. The QTL on SSC 7 acted in an additive mode of inheritance where Pietrain alleles led to lower, and less favorable, tenderness scores. On SSC 15, the mode of inheritance followed an imprinting pattern where Pietrain alleles from the sire again led to lower tenderness scores. Furthermore, tenderness, overall tenderness, and WBS were controlled by the same chromosomal region on SSC 15 (Figure IV.6). Malek et al. (2001b) also reported a similar position for a tenderness QTL on SSC 15. Additional QTL for both tenderness and overall tenderness were located on SSC 9 and 10. There

was only one QTL for sensory taste panel juiciness, on SSC 2, possibly due to its high propensity to be affected by meat preparation conditions. A QTL on SSC 2 for juiciness was also reported by Stearns et al. (2005), but it was located more proximal than the QTL discovered here. Additionally, a QTL for off-flavor was located on SSC 2, a chromosome in which Malek et al. (2001b) reported two QTL for off-flavor. A QTL significant at the 1% chromosome-wise level which impacted connective tissue scores was discovered on SSC 10. This QTL had a dominance mode of inheritance. Refining the location for these QTL for sensory taste panel attributes will provide potentially important information for selection of prospective parents in swine populations since these attributes ultimately impact a consumer's dining experience.

Confidence Intervals

For QTL that were significant at the 5%genome-wise level, 95% confidence intervals were estimated using bootstrapping with resampling in QTL Express (Seaton et al., 2002). These confidence intervals are listed in Table IV.4. Confidence intervals were not calculated for QTL significant at the 5 or 1% chromosome-wise level since preliminary analyses indicated that many of these intervals tended to encompass the entire chromosome on which they reside.

Implications

Numerous QTL that control economically important traits of carcass composition and meat quality were revealed in this F_2 Duroc-Pietrain resource population. These QTL are extremely important as they give us insight into traits that are not easily measured in breeding animals but add value to end products. These QTL will become even more important as the traits they influence achieve greater economic value. Many

QTL for meat quality, with both desirable and undesirable alleles, existed in the Duroc and Pietrain breeds utilized in this study, and desirable QTL could be incorporated systematically into breeding schemes as these two populations are already a major part of commercial pig production. Chromosomal regions of interest discovered in these populations are being subjected to further analyses and refinement of QTL positions may lead to their incorporation into selection programs for prospective parents and subsequently increase value in these pork products.

Table IV.1. Fixed effects and covariates for carcass and meat quality trait QTL analyses.

	Fixed Effects[a]		Covariates[a]	
Trait	Sex	Harvest Date	Carcass Weight	Harvest Age
Carcass measures				
Off-farm BW, kg	X	X	-	X
Hot carcass weight, kg	X	X	-	X
Dressing percentage, %	X	X	-	-
45 min carcass temperature, °C	X	X	X	-
24 h carcass temperature, °C	X	X	X	-
45 min pH	X	X	X	-
24 h pH	X	X	X	-
45 min-24 h pH decline	X	X	X	-
Carcass length, cm	X	X	X	-
Number of ribs	X	X	-	-
First rib backfat, mm	X	X	X	-
Last rib backfat, mm	X	X	X	-
Last lumbar vertebra backfat, mm	X	X	X	-
Tenth rib backfat, mm	X	X	X	-
Longissimus muscle area, cm^2	X	X	X	-
Primal cut weights				
Ham weight, kg	X	X	X	-
Loin weight, kg	X	X	X	-
Boston shoulder weight, kg	X	X	X	-
Picnic shoulder weight, kg	X	X	X	-
Belly weight, kg	X	X	X	-
Spareribs weight, kg	X	X	X	-
Meat quality evaluation				
Color, 1-6	X	X	-	-
Marbling, 1-10	X	X	-	X
Firmness, 1-5	X	X	-	X
L*	X	X	-	-
a*	X	X	-	-
b*	X	X	-	-
Proximate analysis				
Moisture,%	X	X	X	-
Fat, %	X	X	X	-
Protein, %	X	X	X	-
Laboratory analyses				
Drip loss,%	X	X	-	X
Cook yield, %	X	X	-	-
Warner-Bratzler shear force, kg	X	X	-	-
Sensory taste panel analyses				
Juiciness, 1-8	X	X	-	-
Tenderness, 1-8	X	X	-	-
Overall tenderness, 1-8	X	X	-	-
Connective tissue, 1-8	X	X	-	-
Off-flavor, 1-8	X	X	-	-

[a] X indicates used in model, - indicates not used in model

Table IV.2. Number of records, means, and standard deviations for carcass and meat quality traits measured.

Trait	N	Mean	SD
Carcass measures			
Off-farm BW, kg	504	111.89	9.12
Hot carcass weight, kg	504	81.35	7.19
Dressing percentage, %	504	72.69	2.12
45 min carcass temperature, °C	503	39.20	2.26
24 h carcass temperature, °C	502	2.74	1.19
45 min pH	497	6.38	0.23
24 h pH	484	5.53	0.15
45 min-24 h pH decline	478	0.84	0.23
Carcass length, cm	503	78.92	2.59
Number of ribs	357	14.84	0.86
First rib backfat, mm	417	40.67	7.19
Last rib backfat, mm	503	28.65	6.29
Last lumbar vertebra backfat, mm	502	22.29	6.59
Tenth rib backfat, mm	499	24.15	7.25
Longissimus muscle area, cm^2	500	40.94	4.60
Primal cut weights			
Ham weight, kg	503	9.56	0.81
Loin weight, kg	503	8.17	0.86
Boston shoulder weight, kg	503	3.72	0.63
Picnic shoulder weight, kg	503	3.89	0.65
Belly weight, kg	503	4.94	0.69
Spareribs weight, kg	502	1.48	0.20
Meat quality evaluation			
Color, 1-6	502	3.21	0.82
Marbling, 1-10	503	2.88	0.80
Firmness, 1-5	489	2.86	0.81
L*	487	53.63	2.21
a*	487	17.26	1.91
b*	487	9.10	1.61
Proximate analysis			
Moisture,%	494	73.88	1.50
Fat, %	494	3.27	1.33
Protein, %	493	23.39	1.09
Laboratory analyses			
Drip loss,%	503	1.71	1.18
Cook yield, %	498	77.46	2.94
Warner-Bratzler shear force, kg	497	3.19	0.69
Sensory taste panel analyses			
Juiciness, 1-8	501	5.28	0.58
Tenderness, 1-8	501	5.59	0.61
Overall tenderness, 1-8	501	5.65	0.55
Connective tissue, 1-8	501	6.39	0.38
Off-flavor, 1-8	501	1.14	0.21

Table IV.3. Position and significance level of carcass and meat quality QTL significant at the 5% chromosome-wise level with additive, dominance, and imprinting effects and standard errors.

Chr	Trait	Pos. (cM)	Additive Effect	Additive SE	Dominance Effect	Dominance SE	Imprinting Effect	Imprinting SE	F-ratio[a]
1	*Longissimus* muscle area, cm^2	10	-1.23	0.31	0.44	0.56	0.13	0.30	5.47
1	Dressing percentage, %	71	-0.42	0.12	0.05	0.20	-0.38	0.13	6.03*
1	Spareribs wt, kg	172	0.02	0.01	-0.11	0.02	-0.04	0.01	11.24***
2	Juiciness, 1-8	54	-0.10	0.04	-0.16	0.07	-0.08	0.04	4.64
2	Off-flavor, 1-8	70	-0.05	0.01	0.01	0.02	-0.02	0.02	4.70
3	45 min-24 h pH decline	86	-0.05	0.02	-0.03	0.02	0.04	0.02	5.70*
3	45 min pH	91	-0.06	0.02	-0.02	0.02	0.03	0.02	6.49**
3	Loin wt, kg	114	0.06	0.04	-0.21	0.06	-0.08	0.04	6.60**
3	*Longissimus* muscle area, cm^2	155	0.16	0.27	-1.37	0.41	-0.27	0.27	4.29
4	*Longissimus* muscle area, cm^2	0	-0.33	0.26	-1.09	0.35	0.35	0.24	4.71
4	Hot carcass weight, kg	12	-2.18	0.50	0.94	0.83	-0.47	0.47	7.14**
4	Off-farm BW, kg	13	-2.70	0.65	0.76	1.08	-0.71	0.61	6.56**
4	Color, 1-6	45	0.02	0.06	0.35	0.10	0.04	0.06	4.21
4	Spareribs wt, kg	53	0.02	0.01	-0.03	0.01	0.00	0.01	4.31
5	First rib backfat, mm	86	0.64	0.47	1.16	0.74	1.79	0.47	6.28*
5	24 h carcass temperature, °C	117	0.02	0.03	0.20	0.05	0.09	0.03	7.13**
5	Cook yield, %	159	-0.28	0.20	0.37	0.32	0.82	0.22	5.52*
6	a*	24	0.24	0.07	0.15	0.11	-0.14	0.08	6.49**
6	Color, 1-6	92	0.17	0.06	0.04	0.10	-0.15	0.06	4.77
6	Warner-Bratzler shear force, kg	101	-0.14	0.05	-0.14	0.07	0.05	0.05	4.64
6	Marbling, 1-10	116	0.43	0.06	-0.15	0.11	0.04	0.06	18.41***
6	Fat, %	117	0.71	0.10	-0.37	0.17	0.14	0.10	20.01***
6	Ham wt, kg	121	-0.17	0.03	0.18	0.06	-0.04	0.03	11.79***
6	Tenth rib backfat, mm	125	3.66	0.39	-2.09	0.70	0.42	0.42	32.18***
6	Last lumbar backfat, mm	129	2.11	0.42	-2.31	0.70	0.03	0.46	11.87***
6	Carcass length, cm	139	-0.57	0.13	1.02	0.20	0.16	0.14	14.57***
6	Loin wt, kg	141	-0.18	0.03	0.17	0.06	0.04	0.04	12.25***
6	Last rib backfat, mm	144	1.04	0.38	-2.19	0.65	-0.17	0.41	6.10*
6	Protein, %	150	-0.39	0.08	0.24	0.14	-0.17	0.09	10.06***
6	Spareribs wt, kg	154	-0.03	0.01	0.04	0.02	-0.01	0.01	4.84
6	*Longissimus* muscle area, cm^2	156	-1.27	0.28	-0.69	0.48	0.06	0.30	7.40**
6	24 h carcass temperature, °C	176	0.14	0.03	-0.04	0.05	0.01	0.04	6.70**
6	Moisture,%	181	-0.19	0.09	-0.34	0.17	-0.34	0.10	6.21*

[a] Significant at * = 1% chromosome-wise, ** = 5% genome-wise, *** = 1% genome-wise levels

Table IV.3 (cont'd).

Chr	Trait	Pos. (cM)	Additive Effect	Additive SE	Dominance Effect	Dominance SE	Imprinting Effect	Imprinting SE	F-ratio[a]
7	L*	1	0.23	0.14	0.24	0.21	-0.50	0.16	4.32
7	Color, 1-6	2	-0.05	0.05	-0.07	0.08	0.21	0.06	4.52
7	Protein, %	6	-0.24	0.07	-0.21	0.13	0.02	0.08	4.48
7	Carcass length, cm	67	0.81	0.17	0.40	0.34	0.19	0.18	9.01***
7	Dressing percentage, %	70	-0.73	0.15	-0.65	0.31	-0.05	0.16	10.13***
7	*Longissimus* muscle area, cm^2	108	-1.28	0.36	-1.61	0.72	0.17	0.37	6.28*
7	Number of ribs	124	0.19	0.06	0.10	0.11	0.34	0.06	15.13***
7	Spareribs wt, kg	135	0.01	0.01	-0.01	0.01	0.03	0.01	4.93
7	Warner-Bratzler shear force, kg	158	0.19	0.05	0.05	0.08	0.07	0.05	5.74*
7	Overall tenderness, 1-8	159	-0.15	0.04	0.00	0.06	-0.01	0.04	4.72
7	Tenderness, 1-8	160	-0.16	0.04	-0.01	0.07	-0.01	0.04	4.75
7	45 min-24 h pH decline	164	0.04	0.02	0.01	0.02	0.04	0.02	4.35
8	Spareribs wt, kg	62	0.03	0.01	0.02	0.02	-0.01	0.01	4.41
8	*Longissimus* muscle area, cm^2	96	-0.82	0.24	-0.38	0.36	-0.15	0.26	4.68
8	Moisture,%	152	-0.35	0.12	0.45	0.21	-0.03	0.12	4.19
9	Drip loss,%	1	-0.04	0.07	0.36	0.10	-0.05	0.07	4.75
9	Off-farm BW, kg	3	-0.37	0.56	2.89	0.83	0.77	0.59	4.39
9	Hot carcass weight, kg	3	-0.40	0.44	2.38	0.65	0.76	0.46	5.25
9	Overall tenderness, 1-8	5	0.00	0.04	0.04	0.06	0.14	0.04	4.42
9	Ham wt, kg	8	-0.11	0.03	0.01	0.05	-0.04	0.03	5.09
9	24 h carcass temperature, °C	13	0.09	0.03	-0.02	0.04	-0.06	0.03	4.08
9	Warner-Bratzler shear force, kg	17	-0.01	0.04	-0.09	0.07	-0.18	0.05	4.77
9	Tenderness, 1-8	28	-0.02	0.05	0.07	0.09	0.19	0.05	4.85
9	Fat, %	62	-0.14	0.10	-0.11	0.16	0.35	0.10	4.66
9	Moisture,%	64	0.21	0.10	-0.01	0.17	-0.34	0.11	4.14
9	45 min carcass temperature, °C	108	0.06	0.10	0.67	0.19	0.03	0.11	4.27
9	b*	127	-0.13	0.05	0.14	0.07	0.01	0.07	4.25
10	Tenderness, 1-8	0	0.06	0.04	0.19	0.06	0.01	0.04	4.08
10	Overall tenderness, 1-8	0	0.05	0.04	0.19	0.05	-0.02	0.04	4.65
10	Connective tissue, 1-8	61	0.08	0.04	0.15	0.07	-0.05	0.03	5.36*
10	Off-farm BW, kg	74	-0.59	0.82	2.22	1.35	-2.72	0.77	5.62*
10	Hot carcass weight, kg	75	-0.37	0.63	0.93	1.03	-2.38	0.60	5.93*
10	Marbling, 1-10	79	-0.12	0.08	0.30	0.11	-0.14	0.07	4.22
11	45 min-24 h pH decline	107	0.07	0.02	-0.08	0.06	0.03	0.03	3.80
11	Fat, %	119	0.28	0.12	-0.43	0.25	0.36	0.13	4.78
11	Moisture,%	119	-0.40	0.13	0.30	0.27	-0.28	0.14	4.69
12	Belly wt, kg	53	0.11	0.03	0.01	0.04	0.01	0.03	6.04*
12	Moisture,%	54	-0.37	0.10	0.31	0.16	-0.11	0.10	7.26**
12	Fat, %	57	0.30	0.09	-0.32	0.15	0.11	0.09	6.99**
12	24 h pH	61	-0.02	0.01	-0.04	0.01	0.01	0.01	4.23
12	Marbling, 1-10	67	0.21	0.06	-0.24	0.10	0.02	0.06	7.04**

[a] Significant at * = 1% chromosome-wise, ** = 5% genome-wise, *** = 1% genome-wise levels

Table IV.3 (cont'd).

Chr	Trait	Pos. (cM)	Additive Effect	Additive SE	Dominance Effect	Dominance SE	Imprinting Effect	Imprinting SE	F-ratio[a]
14	a*	51	-0.28	0.07	0.05	0.12	0.01	0.07	5.05
14	Belly wt, kg	114	0.06	0.03	-0.24	0.06	-0.05	0.03	7.53**
15	Protein, %	57	0.38	0.08	-0.01	0.14	0.41	0.08	14.89***
15	L*	60	0.70	0.17	-0.70	0.29	0.18	0.17	8.03***
15	a*	64	-0.25	0.07	0.15	0.11	-0.13	0.07	5.60*
15	Color, 1-6	64	-0.16	0.06	0.16	0.09	-0.13	0.06	5.03*
15	Tenderness, 1-8	65	-0.12	0.04	0.00	0.07	-0.17	0.04	7.57**
15	Overall tenderness, 1-8	65	-0.10	0.04	0.00	0.06	-0.15	0.04	7.25**
15	Warner-Bratzler shear force, kg	70	0.08	0.05	0.04	0.08	0.18	0.05	5.02*
15	Cook yield, %	75	0.55	0.21	-0.15	0.34	0.42	0.21	3.86
16	24 h pH	81	0.02	0.01	-0.04	0.02	0.03	0.01	4.90
17	Protein, %	23	-0.03	0.07	0.38	0.11	0.04	0.07	3.98
17	45 min-24 h pH decline	51	-0.06	0.02	-0.14	0.06	-0.01	0.03	3.94
18	Last rib backfat, mm	0	1.33	0.54	1.45	0.78	1.36	0.56	4.10
18	24 h pH	0	-0.01	0.01	0.07	0.02	-0.01	0.01	4.60
18	Tenth rib backfat, mm	5	0.21	0.59	3.46	0.97	1.06	0.63	4.77*
18	Spareribs wt, kg	19	-0.02	0.01	0.01	0.03	-0.05	0.01	3.83
18	Number of ribs	48	-0.11	0.05	0.15	0.08	0.06	0.06	3.45
X	Moisture,%	14	-0.36	0.13	NA		NA		8.02
X	Fat, %	169	0.31	0.11	NA		NA		7.68

[a] Significant at * = 1% chromosome-wise, ** = 5% genome-wise, *** = 1% genome-wise levels

Table IV.4. Position and 95% confidence interval lower and upper limits of carcass merit QTL significant at 5% genome-wise level.

Chr	Trait	Position (cM)	Lower limit (cM)	Upper limit (cM)
1	Spareribs wt, kg	172	146	184
3	45 min pH	91	43	149.5
3	Loin wt, kg	114	88	156
4	Hot carcass weight, kg	12	0	61
4	Off-farm BW, kg	13	0	61
5	24 h carcass temperature, °C	117	12	123
6	a*	24	4	117
6	Marbling, 1-10	116	94	144
6	Fat, %	117	96	144
6	Ham wt, kg	121	113	175
6	Tenth rib backfat, mm	125	118	148
6	Last lumbar vertebra backfat, mm	129	99	146
6	Carcass length, cm	139	99	144
6	Loin wt, kg	141	122	149
6	Last rib backfat, mm	144	0	173.5
6	Protein, %	150	30	164
6	*Longissimus* muscle area, cm^2	156	80.5	166
6	24 h carcass temperature, °C	176	81	181
7	Carcass length, cm	67	41	152
7	Dressing percentage, %	70	56	80
7	Number of ribs	124	106	144
12	Fat, %	57	12	75
12	Marbling, 1-10	67	17	79
14	Belly wt, kg	114	36	117
15	Protein, %	57	46	71
15	L*	60	41	67
15	Overall tenderness, 1-8	65	34	93
15	Tenderness, 1-8	65	33	86.5

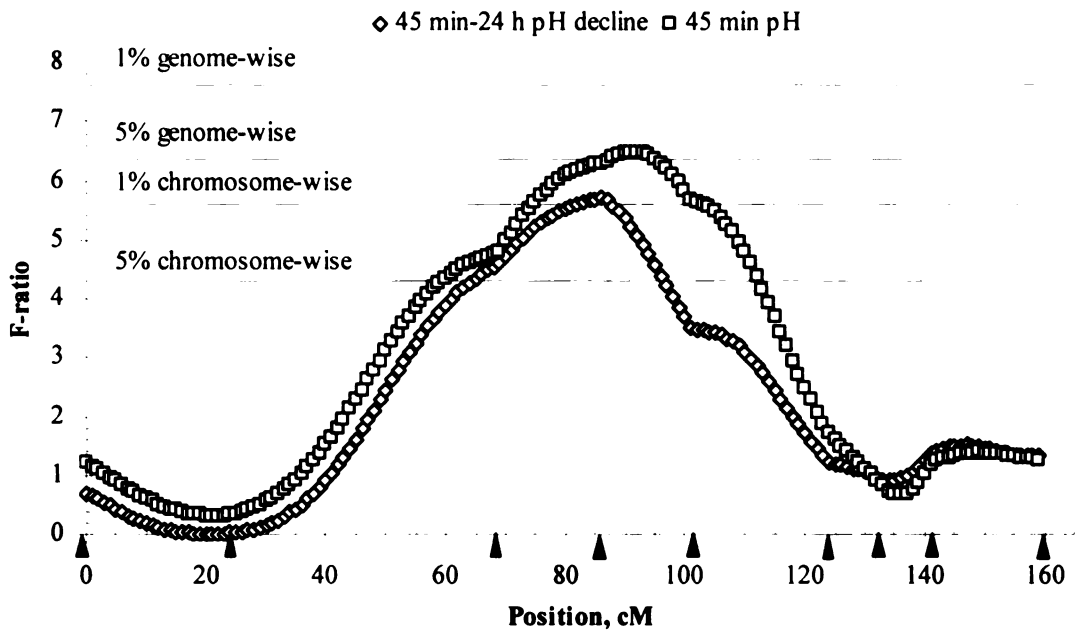

Figure IV.1. F-ratio plots versus relative positions on SSC 3. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

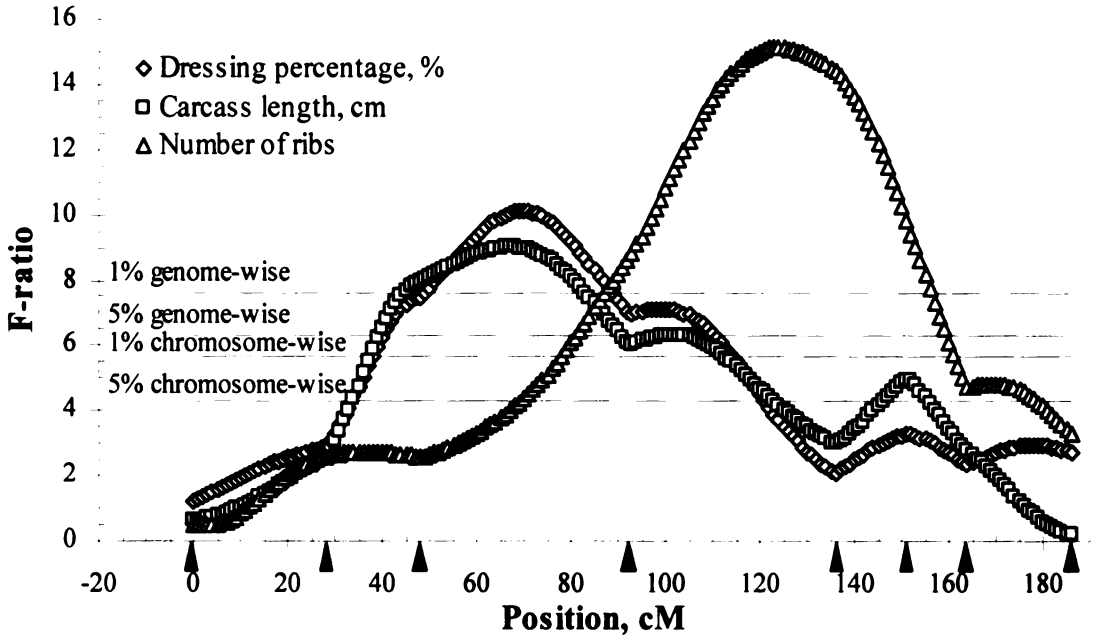

Figure IV.2. F-ratio plots versus relative positions on SSC 7. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

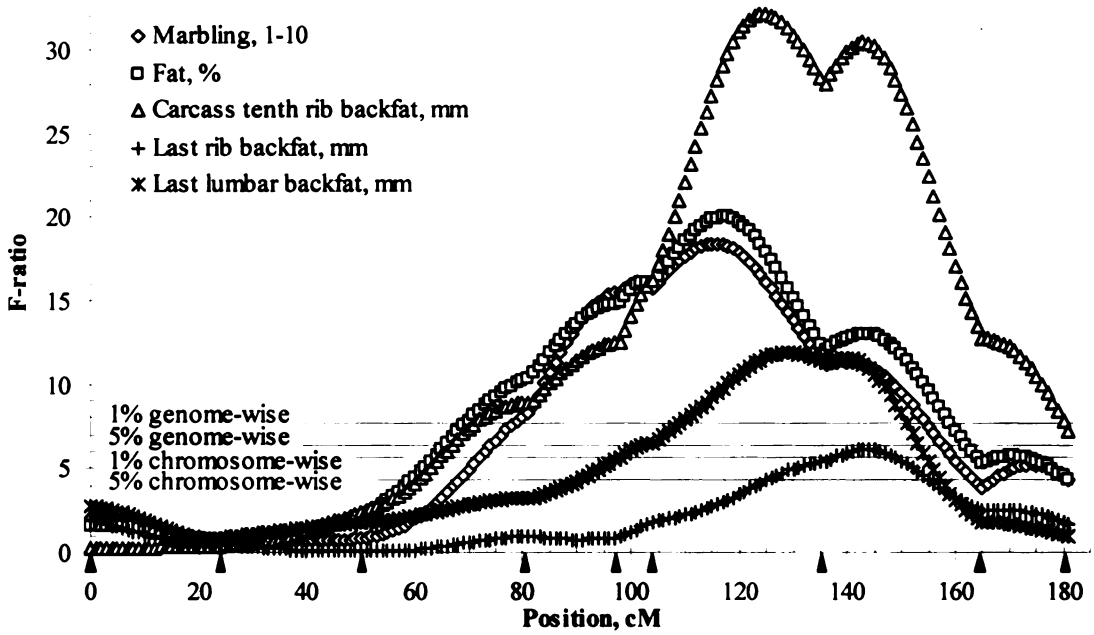

Figure IV.3. F-ratio plots versus relative positions on SSC 6. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

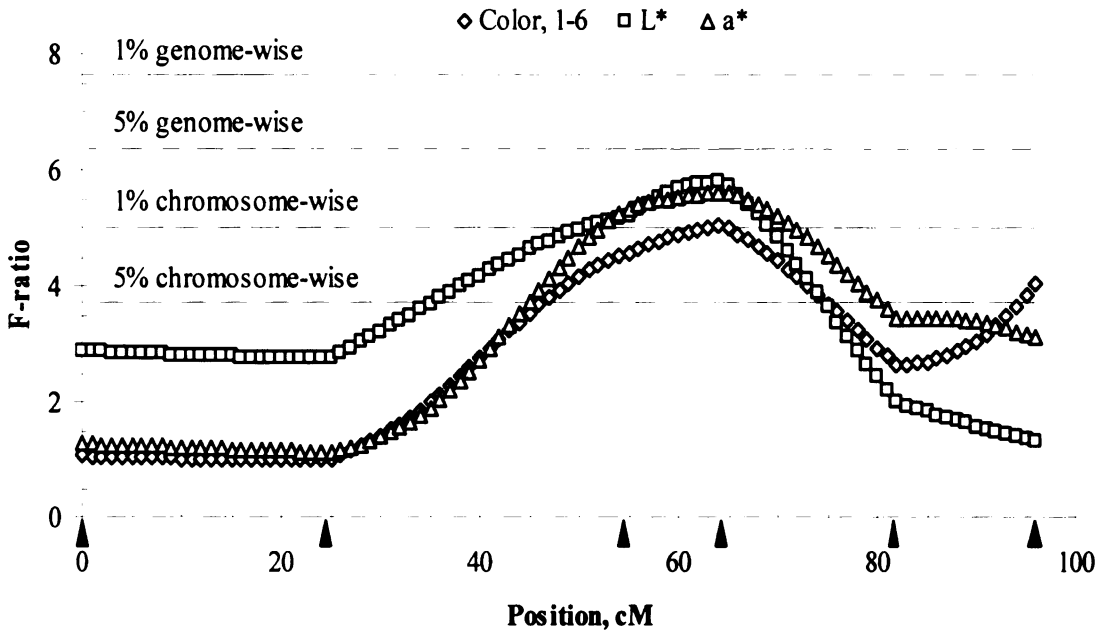

Figure IV.4. F-ratio plots versus relative positions on SSC 15. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

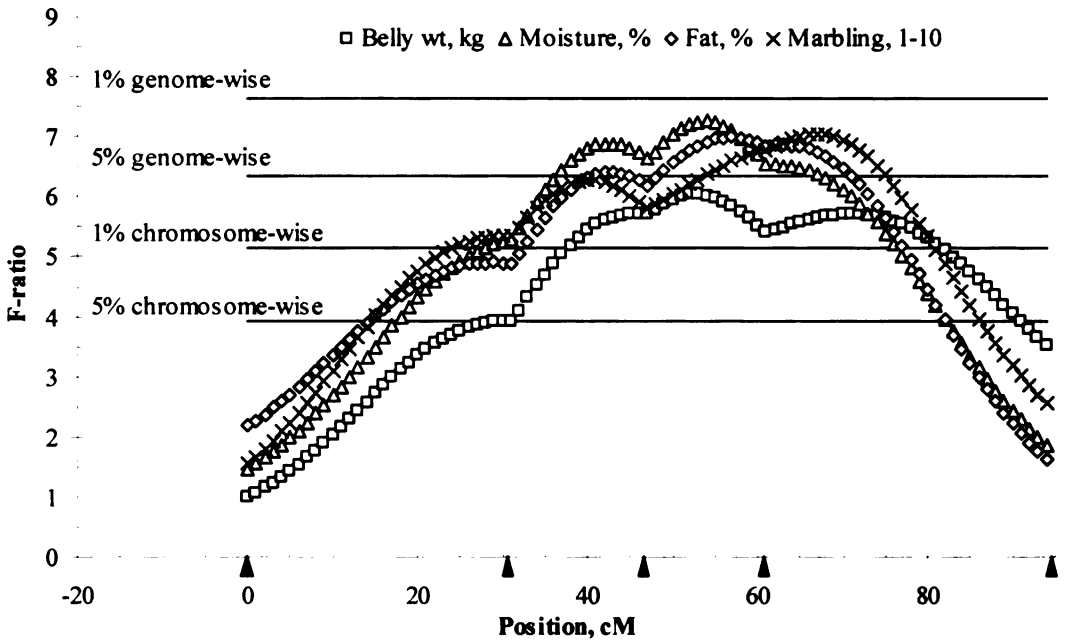

Figure IV.5. F-ratio plots versus relative positions on SSC 12. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

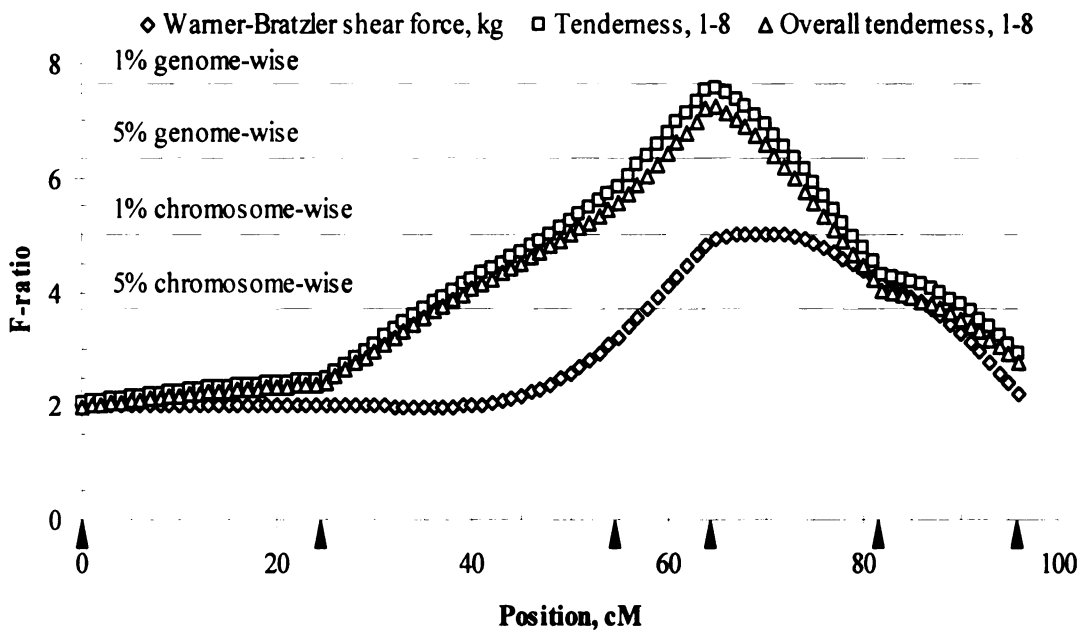

Figure IV.6. F-ratio plots versus relative positions on SSC 15. Arrows on x-axis indicate relative positions of markers on the linkage map. Significance thresholds are indicated by horizontal lines for 5 and 1% genome- and chromosome-wise significance levels.

SUMMARY AND CONCLUSIONS

Creation and analysis of the Michigan State University Duroc x Pietrain F_2 pig resource population allowed for the discovery of quantitative trait loci (QTL) affecting growth, body composition, and meat quality. In order to supplement these objectives, an analysis regarding the influence of two different finishing facility types used to rear pigs within the population was undertaken. These analyses were designed to determine what phenotypes, if any, may have been influenced by the type of finisher pigs were housed in during their growth phase. A total of 1259 F_2 pigs were born in 11 farrowing groups with 958 pigs completing all growth and meat quality trait collection. These pigs were managed similarly during farrowing through nursery stages and placed into one of two different finishers at 10 wk of age. The Modified Open Front building (MOF) had eight pens, in which four pens differed in size from the other four. Four larger pens (2.03 m by 6.91 m) with two-space feeders were targeted to contain 16 pigs. Four smaller pens (1.42 m by 6.91 m) with one-space feeders were targeted to contain 12 pigs. Each pen had two-thirds solid, one-third slatted floors and wet-dry feeders. The Test Station building (TS) had pens with solid floors that were bedded with straw or wood shavings and had single-space dry feeders and cup drinkers. All 25 pens utilized in the TS (1.42 m by 4.93 m) were targeted to contain four pigs.

Although 10 to 22 wk ADG of pigs was not different between the two finisher types, shapes of the growth curve derived from random regression analyses revealed some differences. Pigs finished in the MOF were heavier at harvest and had more backfat at 22 wk of age and at harvest at the tenth and last rib than pigs raised in the TS. Backfat differences as determined through random regression analyses were significantly

different between pigs raised in the two buildings during the test period and continued to increase through harvest. This increased backfat thickness may have been more insulating during carcass chilling and led to a trend for higher 24 h carcass temperatures in the pigs raised in the MOF versus those raised in the TS (3.02 vs. 2.46 °C, $P = 0.116$). These higher temperatures may have led to a greater decline in pH from 45 min to 24 h postmortem for those pigs raised in the MOF than those raised in the TS (0.89 vs. 0.83, $P = 0.019$). Most measures of carcass composition and meat quality did not differ between pigs raised in the two finishing facilities. Ham primal cut weight indicated a trend for heavier hams in pigs raised in the TS versus the MOF (9.60 vs. 9.48 kg, $P = 0.077$), while sensory panel juiciness also indicated a trend for a higher score (more favorable) in TS raised pigs versus MOF raised pigs (5.34 vs. 5.18, $P = 0.064$). Warner-Bratzler shear force was significantly higher in TS raised pigs versus MOF raised pigs (3.36 vs. 3.14 kg, $P = 0.036$). The knowledge that finisher facilities influenced some traits was incorporated into QTL analyses to account for these finisher differences.

The remaining two objectives related to the the detection of QTL. The first objective was to discover QTL affecting traits that described growth and body composition, and the second estimated QTL effects for carcass merit and meat quality traits. Whole blood was collected from all animals for DNA isolation. White blood cells were separated and frozen for subsequent DNA extraction. A total of 206 dinucleotide microsatellite markers were considered for genotyping, and 128 informative markers were selected. Inheritance patterns of four marker genotypes could not be resolved and were not included in the analysis, therefore 124 markers were utilized encompassing the entire genome with an average spacing of 24 cM between the markers. A total of 510 F_2

pigs, their parents, and grandparents were genotyped, and these 510 F_2 pigs were sampled across all farrowing groups from 61 entire litters. Pigs represented all F_1 sires with at least 100 grand progeny from each F_0 sire. Fifteen of the 16 F_0 dams had a son or daughter as a parent that produced multiple litters of the selected F_2 pigs with the remaining F_0 dam represented by a single F_1 daughter with one litter in this group. Genetic linkage maps were constructed for each of the 18 autosomes and the X chromosome, and least squares interval mapping was used for QTL detection. Additive, dominance, and imprinting effects were tested with significance thresholds determined by permutation tests.

Several measures of growth and body composition were obtained and tested for significance of QTL associated with the traits measured in the population. Weight at birth, weaning, and six wk of age was recorded. Additionally, weight and ultrasound estimates of tenth rib backfat, *longissimus* muscle area, and last rib backfat were obtained at three week intervals from 10 to 22 wk of age. From these estimates, body composition estimates were calculated at each of the three week intervals from 10 to 22 wk of age. Random regression analyses were performed on these growth data to calculate random regression terms for each animal. The BLUP animal intercept and animal linear regression coefficients were predicted and included as traits for QTL discovery. The QTL analyses for these growth traits revealed 55 QTL for 22 of the 29 measured traits that were significant at the 5% chromosome-wise significance threshold, and 33 QTL for 15 of the 16 random regression BLUP animal terms that were significant at the 5% chromosome-wise significance threshold. Highly significant regions with putative QTL were discovered for tenth rib and last rib backfat on SSC 6, body composition traits on

SSC 9, backfat and lipid composition traits on SSC 11, tenth rib backfat and total body fat tissue on SSC 12, and linear regression of body weight, *longissimus* muscle area, and tenth rib backfat on SSC 18.

Carcass composition phenotypes included primal cut weights, skeletal characteristics, backfat thickness, muscle pH, and carcass temperature. Meat quality data collected on boneless *longissimus* muscle chops included objective and subjective color information, marbling and firmness scores, and drip loss. Additionally, chops were analyzed for moisture, protein, and fat composition as well as cook yield and Warner-Bratzler shear force measurements. Palatability of chops was determined by a trained sensory taste panel. A total of 94 QTL for 35 of the 38 carcass composition and meat quality traits were found to be significant at the 5% chromosome-wise significance threshold. Highly significant regions with putative QTL were discovered for 45 min pH and pH decline on SSC 3, marbling score and carcass backfat on SSC 6, carcass length and number of ribs on SSC 7, marbling score on SSC 12, and color measurements and tenderness score on SSC 15.

While important QTL were uncovered for both growth and carcass merit traits, the antagonistic relationship of these traits makes discovery of regions that control both sets of traits valuable. An example of this relationship was illustrated by QTL affecting differing fat depots of backfat and intramuscular fat. Many putative QTL in this study affected measures of backfat. One region on the genome that affected backfat measurements on the live animal and carcass backfat measurements was located on SSC 6. While these QTL for measures of subcutaneous fat were located in similar positions with QTL for marbling on this chromosome, marbling also had a significant QTL on SSC

12. Discovering QTL in different regions of the genome for distinct fat depots may improve the ability to specifically select for amounts of fat in these separate regions. This selection scheme would allow concurrent genetic improvement in both backfat and intramuscular fat traits. In general, growth and meat quality QTL were not located in similar regions of the genome. This presents the opportunity to select for certain advantageous alleles for one class of traits in one region while selecting for advantageous alleles for the other class of traits in another region, which would allow improvement to be made in both types of traits at the same time. These QTL discovery results will facilitate fine mapping efforts to identify genes controlling growth, body composition, and meat quality traits that can be incorporated into marker-assisted selection programs to accelerate genetic improvement in pig populations.

LITERATURE CITED

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