A molecular genome scan analysis to identify chromosomal regions influencing economic traits in the pig. I. Growth and body composition.

Massoud Malek[1], Jack C.M. Dekkers[1], Hakkyo K. Lee[2], Thomas J. Baas[1], Max F. Rothschild[1]

[1] Department of Animal Science, Iowa State University, Ames, Iowa, 50011, USA.
[2] Present address: National Livestock Research Institute, Korea

Abstract

Genome scans can be employed to identify chromosomal regions and eventually genes (quantitative trait loci or QTL) that control quantitative traits of economic importance. A three-generation resource family was developed using two Berkshire grand sires and nine Yorkshire grand dams to detect QTL for growth and body composition traits in pigs. A total of 525 F2 progeny were produced from 65 matings. All F2 animals were phenotyped for birth weight, 16 day weight, growth rate, carcass weight, carcass length, back fat thickness, and loin eye area. Animals were genotyped for 125 microsatellite markers covering the genome. Least squares regression interval mapping was used for QTL detection. All carcass traits were adjusted for live weight at slaughter. A total of 16 significant QTL, as determined by permutation test, were detected at the 5% chromosome-wise level for growth traits on chromosomes 1, 2, 3, 4, 6, 7, 8, 9, 11, 13, 14, and X, of which 2 were significant at the 5% genome-wise level and 2 at the 1% genome-wise level (on chromosomes 1, 2 and 4). For composition traits, 20 QTL were significant at the 5% chromosome-wise level (on chromosomes 1, 4, 5, 6, 7, 12, 13, 14, 18), of which 1 was significant at the 5% genome-wise level and 3 were significant at the 1% genome-wise level (on chromosomes 1, 5 and 7). For several QTL the favorable allele originated from the breed with the lower trait mean.

Introduction

The development of molecular biology techniques and the application of these techniques to farm animals have progressed rapidly and have opened new vistas for investigators wishing to identify genes that control quantitative traits (quantitative trait loci or QTL). Comprehensive genetic linkage maps for the pig have been developed over the past few years with an international mapping effort (Archibald et al. 1994, Archibald, personal communication), and a USDA/ARS effort (Rohrer et al. 1996). At present, approximately 2,000 genes and markers have been mapped in the pig, with a majority of these being anonymous molecular markers (http://www.ri.bbsrc.ac.uk/pigmap/).

Based on these linkage maps and data from F2 breed cross resource populations, several recent studies have reported the discovery of a number of QTL affecting growth and body composition traits in the pig on a variety of chromosomes (Andersson et al. 1994; Wang et al. 1998; Rohrer and Keele, 1998a, b; Marklund et al. 1999; Paszek et al. 1999; De Koning et al. 1999; Perez-Enciso et al. 2000). Walling et al. (2000) conducted the first joint QTL analysis for growth and back fat on SSC 4 based on a large data set from several F2 crosses and detected several QTL. Recently, QTL analyses have expanded from the search for Mendelian QTL to QTL with non-Mendelian inheritance. This has resulted in the identification of several QTL with imprinted effects for body composition traits. (Knott et al. 1998; Jeon et al. 1999; Nezer et al. 1999; De Koning et al. 2000b).

Most QTL studies in pigs to date have involved exotic crosses with breeds of commercial interest crossed either to Chinese breeds (e.g. Meishan), or the Wild Boar. The QTL detected in such crosses are not of immediate practical interest because of the poor performance of the exotic breeds for several traits of importance to modern swine breeding. Resource families using commercial breeds or lines did not exist at the initiation of this project. Therefore, the objectives of this study were to develop a three generation resource family using the Berkshire and Yorkshire breeds and to identify chromosomal regions responsible for breed differences for a comprehensive set of growth, body composition, muscle and meat quality and sensory traits. Choice of these two commercial breeds was based on results from the National Pork Producers Council Genetic Evaluation Program (Goodwin and Burroughs, 1995), which revealed that considerable differences in meat quality exist between commercial breeds and that the Berkshire breed, in particular, has very positive meat quality characteristics. In this paper we present results of the QTL analyses for growth and body composition traits. Results for meat quality traits are presented in a companion paper (Malek et al. 2001). Only single QTL models with Mendelian inheritance were investigated here. Additional statistical analysis to consider multiple QTL, within breed QTL effects and gametic imprinting are in progress.

Material and Methods

Family structure. A three-generation resource family was created using two purebred Berkshire grand sires and nine Yorkshire grand dams. The two boars used were from the Casino and Count sire families that are well known within the breed. Sows were mated by artificial insemination at the Iowa State University Swine Breeding Farm, using semen from two boar studs, to produced nine litters of F1 individuals. From the 9 F1 litters, 8 boars and 26 females were chosen to produce the 525 F2 animals that were used in this study. A total of 65 matings were made to produce four sets of F2 offspring.

Management. The F1 animals that were kept for breeding were put in outside lots with shelter. The F1 gilts were bred at eight to nine months of age and sows were bred after weaning their respective litters during the course of the experiment. The females farrowed in rooms that contained 12 farrowing crates and were fed a 15% protein lactation diet *ad libitum*. The F2 pigs were weaned at 16 to 21 days of age. Feed was made available at 10 to 14 days of age. Litters were kept together during the growing and finishing phases. At weaning, males were castrated and the pigs were moved to a nursery, where they received a 21% protein complete feed for 5 to 7 days and then a 20% protein complete feed for three weeks. This was changed to an 18% protein ration for another 2 to 3 weeks. When the pigs left the nursery they were placed in pens that allowed for an average of eight sq. ft. per pig. The diet was changed to an 18.8% protein diet until the pig's weight reached 34 kg on a pen average. At that time, the diet was changed to a 17.5% protein diet until pigs reached 72 kg and then to a 16 % protein diet until the pigs went to market. All diets were fortified with vitamins and minerals for the age of the pig. Water was provided *ad libitum*. Pigs were sent to slaughter at a target weight of 115 kg. The slaughter point was determined by weighing pigs at weekly intervals when they approached 115 kg.

Traits measured. The traits measured on the live animal included birth weight, 16 day weight, average daily gain from birth to weaning, and average daily gain on test from weaning to slaughter. After slaughter and chilling, carcass traits were evaluated at the plant by trained personnel according to National Pork Producers Council guidelines (NPPC, 1991). Traits recorded for the purpose of the present paper were live weight at slaughter, carcass weight, carcass length, tenth rib back fat, lumbar back fat, last rib back fat, average back fat and loin eye area. See Table 1 for a description of the traits.

DNA isolation, marker selection and genotyping. Blood samples were collected from all F2 animals and their parents (F1) and grandparents (F0), and DNA was isolated. Likely parentage (or collection) problems existed for 13 F2 animals and these were removed, leaving 512 animals for QTL analysis. Genotyping was sub-contracted to a commercial laboratory (GeneSeek Inc, Lincoln NE). In total 180 markers were tested on the F0 and F1 animals to determine the final 125 informative markers used for genotyping the F2 animals (see Table 2).

Marker alleles were amplified by PCR and scored following electrophoresis using infrared fluorescent technology. Markers were amplified using either end-labeled forward primers, or M13-tailed forward primers. Labeled forward primers were synthesized by LI-COR (Lincoln, Nebraska, USA), while M13-tailed forward primers and all reverse primers were synthesized by Research Genetics (Huntsville, Alabama, USA). End-labeled reactions used 25 ng genomic DNA, 200μM of each dNTP, 0.15 picomol of labeled forward primer (either IR700 or IR800; LI-COR, Lincoln, NE), 1 picomol of unlabeled reverse primer, 0.5 U Taq-Gold polymerase with supplied $MgCl_2$-free buffer (Perkin-Elmer, Foster City, California, USA), and 2.5 mM $MgCl_2$. M13-tailed reactions were the same, except that 0.3 picomol of each primer was used. Each forward primer had a 19-bp 5' tail consisting of M13 sequence, and each PCR included 0.3 picomol of a fluorescently labeled 19-bp M13 primer (either IR700 or IR800). The PCR began with a 95 °C incubation temperature for 5 min, followed by "touchdown" PCR with annealing temperatures beginning at 68 °C and decreasing by 2 °C per cycle to 54 °C. A total of 33 cycles were performed at a 54 °C annealing temperature. PCR ended with a 7 min extension at 72 °C. PCR products were denatured at 95 °C prior to electrophoresis (1500 V, 50mA, 50W, 45 °C) in 7.0% denaturing polyacrylamide gels in LI-COR (Model 4200 IR^2) sequencers. Alleles were scored based on size relative to known DNA size standards.

Statistical analysis. Marker linkage maps were computed using Crimap version 2.4 software (Green et al. 1990), using the flips and all options to get the best order of the markers and the fixed option to obtain the map distances. The maps were then used for QTL analysis of the 18 autosomes and the X chromosome using the line cross least squares regression interval mapping program developed by Haley et al. (1994). Marker information was used to calculate the probabilities that an F2 offspring inherited none, one, or two alleles from each breed for a putative QTL at each 1 cM position in the genome. Based on these probabilities, additive and dominance coefficients were derived for the putative QTL, contrasting average QTL alleles from the two breed origins, as represented by the F0 grandparents. Information content of each marker was calculated on an individual marker basis and on a linked marker basis. Designating P_{BB} and P_{YY} as the average probability of a given F2 progeny to have received both marker alleles from the Berkshire and Yorkshire breeds, respectively, polymorphism information content for a given marker was computed as $(P_{BB} - P_{YY})$. Information content on a linked marker basis includes information from flanking markers, in addition to information from the marker itself, for determining the breed origin of marker alleles in F2 progeny, following Haley et al. (1994).

The least squares regression model used for QTL analysis included the fixed effects of sex and year-season for all traits, along with additive and dominance coefficients for the putative QTL. Litter size was added as a covariable for birth weight, 16 day weight and for average daily gain from birth to weaning, and live weight was added as a covariable for carcass traits. Note that adjusting carcass weight for live weight corresponds to analysis of carcass yield.

Detection of QTL was based on an F statistic that was computed from sums of squares explained by the additive and dominance coefficients for the QTL. Significance thresholds of the F statistic were derived at the chromosome and genome-wise levels on a single trait basis by the

permutation test of Churchill and Doerge (1994). A total of 10,000 random permutations of the data were used. Because computational requirements prevented permutation tests to be conducted for all traits, significance thresholds were derived based on five representative traits: carcass weight, last rib back fat, loin eye area, cholesterol content and marbling. See Malek et al. (2001) for a description of the latter two traits. Average thresholds across these five traits were used for significance testing for all traits. See Lee et al. (2001) for more details on the permutation tests conducted for this project.

Results and Discussion

Arithmetic means and standard deviations of traits measured on the F2 animals are listed in Table 1. Trait measurements were within the usual range of scores. Relationships between traits are discussed in Huff-Lonergan et al. (2001).

Chromosome linkage map results. Marker mapping results are presented by chromosome in Table 2. The 125 markers genotyped in this study represent reasonable genome coverage. The total map length was 20.8 Morgans, which compares well to previous swine linkage maps. In all cases but one, map order of the markers was the same as in the USDA map (Rohrer et al. 1996). The exception was a switch in order for SSC 2 between SW2157 and SW1408. In our map these markers are 4 cM apart while the order is reversed in the USDA map and they are 2 cM apart. Our results and those of Rohrer et al. (1996) however differed from those of Paszek et al. (1999) for chromosomes 1, 4, 8 and 10. Map lengths for these chromosomes were considerably longer in the study of Paszek et al. (1999). This may have been caused by genotyping errors, which are known to increase map lengths. The average distance in our study between adjacent markers was 17 cM but 8 gaps existed of greater than 30 cM. Finding markers for these gaps was limited by the need to use markers that were easy to use and informative. Average information content was 0.76 and 0.82 on the individual and linked marker basis (Table 2). For some markers, however, information content on an individual basis was less than 0.5. The lowest information content on a linked marker basis, however, was 0.64.

Significance thresholds. Individual chromosome significance levels at the 5% level, as determined by the permutation test, differed slightly by trait (Lee et al. 2001) but more substantially by chromosome. For significance testing, average thresholds across the five evaluated traits were used. See the footnote on Table 3 for a list of average thresholds by chromosome. Average 5% chromosome-wise thresholds ranged from 4.34 to 5.32. Thresholds for chromosome-wise significance at the 5% level correspond approximately to suggestive significance at the genome-wise level (De Koning et al. 1999, Lander and Kruglyak, 1995).

Genome-wise significance thresholds also differed slightly by trait (Lee et al. 2001). Average genome-wise thresholds across traits were 8.22, and 9.96 for the 5%, and 1% levels. Genome-wise threshold values were similar to those obtained by De Koning et al. (1999), who analyzed data with a similar marker density and family structure.

General QTL mapping results. Estimates for QTL significant at the 5% chromosome-wise level are presented in Tables 3 and 4. The QTL graphs, representing plots of the F statistic across chromosomes, are shown in Figure 1 for chromosomes with QTL significant at the 5% genome-wise level. Although some graphs suggest evidence for multiple QTL in adjacent intervals for the same trait (Fig. 1E), only results for the most significant position were included in Tables 3 and 4 because only single QTL models were tested.

A total of 36 QTL were detected at the 5% chromosome level for the 11 traits evaluated in this study, not counting potential multiple QTL in adjacent intervals. Over the 11 traits examined

we would expect 11 QTL to be significant at the 5% chromosome-wise level by chance alone. Thus, over three times as many QTL were detected at this level than expected by chance.

Of the 36 suggestive QTL, 3 and 5 QTL were significant at the 5% and 1% genome-wise levels (Table 4). Over the 11 traits examined we would expect 0.5 and 0.1 QTL to be significant at these levels by chance alone. Thus, clearly, more QTL were identified at these levels than expected. In addition, several of the QTL found here have been identified in previous studies based on exotic crosses, as will be discussed in the following on a trait by trait basis. Other QTL found in this study have not been identified previously and vice versa. Differences between this and previous studies may be the result of false negatives and false positives in this or literature studies, or be due to differences in QTL that segregate between the different breeds used.

There were QTL identified at the 5% chromosome level for nearly all traits and on all chromosomes except 10, 12, 15, 16, and 17 (Tables 3 and 4). Most QTL accounted for 3 to 5% of the F2 variance but some reached 7% (Table 3). Note that these variance estimates may be biased upward because they are based on only significant results. Total trait variances explained by QTL reported in Table 4 may, however, be biased downward because potential multiple QTL in adjacent regions were ignored.

A priori we might expect to find fewer QTL in this cross of commercial breeds compared to the divergent crosses reported on in previous studies, which involved an exotic breed (Wild Boar or Chinese breeds). Expected differences between the Berkshire and Yorkshire breeds for the traits evaluated here are given in Table 1, based on crossbred results from the National Pork Producers Council genetic evaluation program (Goodwin and Burroughs 1995). It is recognized, though, that the grandparents used in our cross represent only a small sample of their respective breeds.

Birth weight. Only one suggestive QTL at the genome-wise level, which is equivalent to significance at the 5% chromosome-wise level, was detected for birth weight. This QTL was on SSC 3 (Tables 3 and 4). The additive effect suggested that Berkshire alleles tended to be associated with lower birth weight in comparison with Yorkshires but heterozygotes had the lowest birth weight (Table 3). The variance accounted for by this QTL was 2.9%. There are no previous reports of QTL affecting birth weight on SSC 3. However, Paszek et al. (1999) found suggestive QTL for birth weight on SSC 4, 5, 6, 9 and 16. Also, Rothschild et al. (1995) found an association of the TNFalpha gene with birth weight. This gene lies within the swine major histocompatibility complex on SSC 7.

Average daily gain. A total of five QTL were detected for average daily gain to weaning and average daily gain on test, of which two were significant at the 5% genome-wise level (Table 4, Fig. 1B, 1C). Berkshire alleles were superior to Yorkshire alleles for three of five QTL (Table 3). Heterozygotes had greatest growth for two out of five QTL. One QTL was for average daily gain to weaning, on SSC 9. The other four QTL were for average daily gain from weaning to slaughter, on SSC 2, SSC 4, SSC 8 and SSC 9.

The QTL on SSC 4 confirms results of several other studies that found a QTL for late growth in a similar region of SSC 4 (Andersson et al. 1994; Knott et al. 1998; Milan et al. 1998; Wang et al. 1998; Marklund et al. 1999; Paszek et al. 1999; Walling et al. 2000). Rohrer (2000) did not find evidence of a QTL for growth on SSC 4. Paszek et al. (1999) reported thirty QTL for various early and late growth traits on SSC 1, 5, 6, 7, 10, 11, 12, 13 and 16. None of these were confirmed in this study. Their QTL on SSC 13 was also found by Andersson et al. (1994), Knott et al. (1998) and Yu et al. (1999). Paszek et al. (1999) also found eleven QTL for late growth, on SSC 2, 4 and 8. We were able to confirm some of these, with QTL detected in similar regions on SSC 2, 4, and 8. Rohrer (2000) reported a QTL on SSC 1 (at 128 to134 cM) that significantly

affected early growth, which confirmed the result of Pazek et al. (2000). Milan et al. (1998), Wang et al. (1998) and Rohrer (2000) also reported a QTL for late growth on SSC 7 that was not confirmed in our study. Cassas-Carrillo et al. (1997) reported the detection of QTL affecting late growth on SSC 3. We did not find the same result but their QTL for growth and the QTL for birth weight from our study (Table 3) were mapped to the same region. We also detected two suggestive QTL for early and late gain on SSC 9 but these QTL were not confirmed by other studies.

Back fat thickness. We found 20 significant QTL at the 5% chromosome-wise level for the different traits associated with back fat thickness (Table 3). It should be noted, however, that these traits tend to be highly correlated (Huff-Lonergan et al. 2001). Thus, several of these QTL may have pleiotropic effects. On the other hand, several QTL regions could represent more than one QTL. Multi-trait and multi-QTL analyses will be needed to separate these QTL and their effects. The detected QTL for back fat traits jointly explained from 14 to 24% of the phenotypic variance in the F2 population (Table 4). Our results indicated that Berkshire alleles tended to be associated with less fat for QTL on SSC 1, 4, 6, 12, 14, and 18 but were fatter for QTL on SSC 5, 7, and 13 (Table 3). Heterozygotes were leanest for QTL on SSC 1 and 13 and fattest for QTL on SSC 4, 6, 12, and 14.

We found QTL on SSC 1 for tenth rib, last rib, lumbar, and average back fat, but in different regions of the chromosome than the QTL detected by Rohrer and Keele (1998). We did not detect QTL for backfat on SSC2, for which Nezer et al. (1999) and Jeon et al. (1999) found strong evidence for a paternally expressed QTL for fatness in the region of the IGF2 locus. The IGF2 locus is approximately 5-10 cM distal to our first marker on SSC2. De Koning et al. (2000b) also found a paternally expressed QTL for back fat thickness near our second marker for SSC2 We did not detect QTL in this region but only considered Mendelian inheritance. Our results confirmed the existence of QTL for back fat on SSC 4, as reported by Andersson et al. (1994), Marklund et al. (1999), Knott et al. 1998 and Perez-Enciso et al. (2000), but not in the same region of the chromosome.

De Koning et al. (2000b) found two QTL affecting intramuscular back fat with maternal and paternal imprinting in the short and long arm of SSC 6, respectively. We also found a QTL for back fat on SSC 6, although our QTL was more to the distal end of the chromosome. Rohrer and Keele (1998) and Rohrer (2000) also identified QTL and suggestive QTL for back fat measures on chromosomes 5, 8, 9,10, 13, 14 and X. We found QTL in the same regions on SSC 5 for lumbar back fat, and average back fat, and on SSC 13 for tenth rib back fat.

By far the greatest evidence for QTL for back fat in our population was on chromosome 7. The F statistic showed convincing evidence of QTL for all back fat traits over a 80 cM range around the center of SSC 7 (from 40 to 120 cM) (Fig. 1E). These results confirm QTL that have been detected in several studies (Marklund et al. 1999; Moser et al. 1998; Rohrer and Keele, 1998a; Walling et al. 1998; Wang et al. 1998; De Koning et al. 1999; Rohrer, 2000). While the fatter Meishan breed in these studies had a cryptic allele for leanness on SSC 7, Berkshire alleles were associated with considerably greater fatness in our study (Table 3), as expected based on breed differences (Table 1). Recently Harlizius et al. (2000) reported a QTL for fatness on the X chromosome using a Meishan cross. This QTL was not confirmed in our study.

Loin eye area. We detected two QTL for loin eye area, on SSC 1 and 4, of which one was significant at the 5% genome-wise significance level (Tables 3 and 4). The QTL on SSC 1 confirms results of Rohrer and Keele (1998b), who found a QTL for loin depth on SSC 1 in the same region. Our QTL on SSC 4 was not confirmed by previous studies. Previous studies also reported evidence for QTL for loin depth in exotic crosses on chromosomes 2 (Nezer et al. 1999; Jeon et al. 1999), 3 (Andersson-Eklund et al. 1998), 6 (Moser et al.1998), 7 (Rothschild et al.

1995; De Koning et al. 2000a, b), 8 (Andersson-Eklund et al. 1998; Rohrer and Keele, 1998b), 9 (De Koning et al. 2000a), 11, 14 (Rohrer and Keele, 1998b), 16 (De Koning et al. 2000a), and on the X chromosome (Rohrer and Keele, 1998). We were not able to confirm any of these findings.

Carcass Length. Our results revealed suggestive QTL on SSC 6, 11 and X, with the Berkshire alleles resulting in greater length for two out of three QTL (Table 3). These effects accounted for nearly 10.6% of the variation (Table 4). The QTL on the X chromosome was in the same region as a QTL found by Rohrer and Keele (1998b). Other QTL have been reported for carcass length on SSC 1 (Rohrer and Keele, 1998b), SSC 4 (Andersson-Eklund et al. 1998, Rohrer and Keele, 1998b), SSC 7 (Rohrer and Keele, 1998b), and SSC 8 (Andersson-Eklund et al. 1998, Rohrer and Keele, 1998b).

Carcass weight. The statistical model included a covariable for slaughter weight. Therefore, results for carcass weight reported here reflect an indirect measure of yield or dressing percentage. When interpreting the QTL effect, a difference of 0.5 kg in carcass weight translates into an effect of 0.4% for dressing percent for a pig of average live weight of 118kg.

Five QTL were identified for carcass weight (Table 4), on SSC 4, 7, 8, 13, and 14 (Table 3), of which one (on SSC 4) was significant at the 1% genome-wise level. The QTL on SSC 4 was in the same region as the QTL found for last rib back fat (Table 3). Individuals that were homozygous for Berkshire alleles had higher yield or carcass weight than those with Yorkshires alleles for all QTL, except for the QTL on SSC 8 and 13. Four of the five QTL showed high degrees of overdominance. For these QTL, heterozygotes with regard to breed origin had lower yield than either of the homozygotes.

Andersson-Eklund et al. (1998) also reported QTL for carcass weight on SSC 4, 7 and 8, in agreement with this study. Rohrer and Keele (1998) reported carcass weight QTL on SSC 3 and 7. We also found a QTL for carcass weight on SSC 7 in the same region. Other studies (Moser et al. 1998) have reported effects on SSC 6 when certain alleles of the RYR1 gene were involved but this was not the case in our families.

Conclusions

Despite limited breed differences, a total of 36 QTL were found to segregate between the Berkshire and Yorkshire breeds for a total of 11 growth and body composition traits, of which 3 and 5 QTL were significant at the 5 and 1% genome-wise levels. These QTL explained from 2.9 to 24.1 % of the phenotypic variance for the individual traits in the F2.

Both breeds had favorable QTL on separate chromosomes for many of the growth and composition traits studied here. There was some evidence on several chromosomes that cryptic alleles existed which favored the breed least expected to have them. Use of these QTL in marker assisted selection could result in substantial improvements.

In this study, we reported QTL significant at the 5 and 1% genome-wise level, as well as those significant at the 5% chromosome-wise level. Although several of these QTL may be false positives, the reporting of QTL at this level of significance is justified by the need to provide other researchers a complete picture of QTL segregating in our family, which will allow them to confirm our results or attempt to identify the individual genes responsible for the traits.

In this study we only considered single QTL models with Mendelian inheritance, with the aim to detect QTL that segregate between the two breeds. Additional statistical analyses to consider multiple QTL, gametic imprinting, and within breed QTL effects is in progress.

Table 1. Means and standard deviations for traits of interest measured on 525 F2 animals and expected differences between breed means (Berkshire minus Yorkshire)[a].

Traits Analyzed for QTL Mapping	**Mean**	*Std Dev*	Berk –York[a]
Birth Weight (kg)	1.55	0.325	NA[b]
16 Day Weight (kg)	4.95	1.311	NA
Average Daily Gain to Weaning (kg/day)	0.24	0.074	0.005
Average Daily Gain on Test (kg/day)	0.69	0.065	0.009
Carcass Weight (kg)	87.08	5.733	NA
Carcass Length (cm)	84.16	2.454	-1.524
Tenth Rib Back Fat (cm)	3.19	0.779	1.016
Lumbar Back Fat (cm)	3.58	0.757	1.016
Last Rib Back Fat (cm)	3.16	0.609	0.664
Average Back Fat (cm)	3.31	0.641	NA
Loin Eye Area (cm^2)	35.59	5.684	-5.548
Additional Traits			
Live Weight at Slaughter (kg)	118.11	6.964	NA
Dressing Percent (%)	73.72	1.95	0.0

[a]Expected difference between breed means based on twice the difference observed in crossbreds in the NPPC genetic evaluation program (Goodwin and Burroughs 1995).
[b]NA: Not available

Table 2. Markers used in the QTL mapping project, their map position based on the F2 data and information content. Distances are in cM relative to position of the first marker on each chromosome. For comparison see USDA Map (Rohrer et al. 1996).

Marker	SSC	Position	Number of alleles	IIC**	EIC*
SW1515	1	0	7	0.97	0.97
SWR2300	1	18.1	3	0.25	0.75
S0008	1	27.4	3	0.90	0.90
S0312	1	42.9	5	0.94	0.94
S0331	1	56.5	5	0.96	0.96
SW974	1	75.5	11	0.92	0.94
SW1301	1	117.6	5	0.80	0.80
SW2623	2	0	5	0.90	0.93
SW2445	2	27.9	4	0.89	0.91
SW766	2	71.3	3	0.73	0.84
SW2157	2	86.3	6	0.89	0.92
SW1408	2	90.1	6	0.44	0.88
SW1844	2	111.6	3	0.72	0.84
SWR308	2	136.9	5	0.86	0.92
S0036	2	143.3	6	0.97	0.97
SW274	3	0	4	0.66	0.77
SW2021	3	19.7	7	0.78	0.83
SW2429	3	31.5	3	0.32	0.71
SW1443	3	58	3	0.33	0.87
S0206	3	60.9	5	0.85	0.89
ACTG2	3	77.6	4	0.78	0.88

SW2408	3	111.9	5	0.95	0.95
SW349	3	128.1	7	0.84	0.92
SW2404	4	0	6	0.89	0.94
SW2509	4	13.7	4	0.55	0.81
S0301	4	33.4	5	0.58	0.75
SW45	4	65.6	4	0.52	0.73
SW512	4	86.4	3	0.62	0.83
SW2435	4	101.9	3	0.60	0.83
SW58	4	110.2	6	0.75	0.89
SW1461	4	130.6	7	0.96	0.96
ACR	5	0	4	0.48	0.88
SW413	5	2.2	5	0.80	0.90
SW1482	5	29.6	8	0.84	0.88
SW2	5	61.8	5	0.44	0.68
SW904	5	86.1	5	0.93	0.95
SW995	5	102.1	5	0.73	0.88
SW378	5	113.9	3	0.62	0.81
SW2535	6	0	3	0.59	0.82
SW2406	6	12.1	5	0.92	0.95
SW1038	6	40.2	3	0.58	0.81
SWR1130	6	53.6	7	0.84	0.91
SW122	6	66.2	6	0.95	0.97
SW1059	6	78.3	8	0.88	0.93
DG93	6	96.5	6	0.74	0.84
SW322	6	119.8	5	0.90	0.92
SW2052	6	142.9	6	0.97	0.97
S0025	7	0	4	0.87	0.91
S0064	7	28.9	5	0.61	0.79
TNFB	7	48.3	8	0.83	0.91
SWR1928	7	64.2	4	0.76	0.88
SW252	7	83	4	0.90	0.93
SW1083	7	95.6	2	0.30	0.76
S0101	7	116.9	4	0.87	0.91
SW764	7	139.1	4	0.93	0.95
S0098	8	0	4	0.55	0.71
SWR1101	8	25.4	7	0.81	0.88
S0086	8	48.2	4	0.77	0.90
SW2160	8	59.9	5	0.97	0.97
SW1551	8	75.7	3	0.46	0.77
SPP1	8	99.8	7	0.84	0.91
S0178	8	115.9	4	0.97	0.97
SWR68	9	0	2	0.05	0.51
SW21	9	14.1	4	0.58	0.71
SW911	9	37	3	0.66	0.78
SW827	9	50.8	3	0.57	0.74
SW1491	9	76.5	3	0.49	0.75
SW2093	9	94.5	5	0.80	0.82
SW2116	9	116.4	3	0.67	0.77
SW1349	9	143.3	4	0.52	0.64
SWR136	10	0	5	0.57	0.70
SW443	10	18.2	5	0.50	0.74
SW2491	10	38.8	4	0.83	0.89
SWR198	10	56.1	5	0.97	0.97
SWR493	10	79.2	3	0.54	0.77

SW1626	10	102.8	6	0.92	0.92
SW2067	10	120.4	6	0.88	0.92
S0385	11	0	5	0.74	0.81
SW1632	11	18	4	0.40	0.69
S0071	11	45.1	5	0.92	0.93
SW13	11	85.8	5	0.83	0.83
S0229	12	0	6	0.96	0.97
SW874	12	34.1	7	0.97	0.97
S0090	12	46.9	5	0.69	0.84
S0147	12	61.9	4	0.79	0.88
SW2180	12	90.4	4	0.69	0.77
SWR1941	13	0	5	0.70	0.84
SW1407	13	20.8	6	0.97	0.97
SW344	13	32.3	5	0.97	0.97
S0068	13	45.9	5	0.95	0.96
SW398	13	58	5	0.97	0.98
SW1056	13	73.7	4	0.41	0.73
SW2097	13	98.8	3	0.81	0.83
SW857	14	0	5	0.62	0.82
SW1027	14	16.4	7	0.92	0.94
SWR84	14	38.2	4	0.97	0.97
S0007	14	46.2	8	0.95	0.96
SW77	14	57	5	0.97	0.97
SW1557	14	70.4	5	0.85	0.92
SWC27	14	110.3	5	0.58	0.64
SW1416	15	0	5	0.97	0.98
S0148	15	21.5	5	0.89	0.93
SW964	15	38.2	5	0.86	0.92
SW1683	15	59.3	4	0.70	0.88
SW936	15	69.1	4	0.76	0.91
SW1983	15	80.5	7	0.90	0.94
SW1119	15	96	5	0.61	0.83
SW2411	16	0	5	0.76	0.82
SW2517	16	31.8	4	0.95	0.95
S0105	16	58.4	5	0.96	0.96
SW335	17	0	5	0.96	0.97
SWR1004	17	7	5	0.94	0.97
S0292	17	48.5	5	0.80	0.89
S0359	17	59	4	0.76	0.90
S0332	17	82.1	4	0.92	0.95
SW2427	17	94.4	7	0.44	0.80
SW1023	18	0	5	0.86	0.92
SW1984	18	21.1	5	0.91	0.94
S0062	18	32.1	4	0.56	0.83
S0177	18	59.4	6	0.96	0.96
SW949	X	0	6	0.84	0.84
SW1903	X	54.9	4	0.68	0.93
SW2126	X	55.1	4	0.83	0.96
SW1943	X	74.9	4	0.96	0.96
SW2588	X	96.8	3	0.96	0.96

**IIC: Information content based on data for this marker only.
*EIC: Effective information content including information on linked markers.

Table 3. Evidence for QTL significant at the 5% chromosome-wise level for various growth and composition traits by chromosome. Estimated significance levels (F value), location, gene effects and % of F2 variance explained by each QTL.

SSC	Trait	F-value[a]	Location (cM)	**Additive**		Dominance		%
				Effect[b]	S.E.	effect	S.E.	variance[c]
1	Average Back Fat (cm)	6.79	29	-0.09	0.03	-0.12	0.05	2.83
1	Tenth Rib Back Fat (cm)	11.32**	29	-0.11	0.04	-0.23	0.06	4.78
1	Last Rib Back Fat (cm)	6.61	66	-0.13	0.04	-0.01	0.06	3.03
1	Lumbar Back Fat(cm)	6.96	64	-0.15	0.44	-0.08	0.07	3.12
1	Loin Eye Area (cm2)	10.34**	29	1.11	0.31	1.33	0.47	4.21
2	Average Daily Gain on Test (kg/day)	8.31*	87	0.015	0.00	0.010	0.006	3.65
3	Birth Weight (kg)	5.20	19	-0.02	0.020	-0.09	0.03	2.88
4	Average Daily Gain on Test (kg/day)	8.87*	97	-0.006	0.004	0.03	0.007	5.71
4	Carcass Weight (kg)	11.76**	123	0.71	0.16	0.41	0.25	5.97
4	Loin Eye Area (cm2)	7.87	92	1.38	0.36	-0.64	0.59	4.20
4	Last Rib Back Fat (cm)	5.86	101	-0.03	0.04	0.19	0.07	3.18
4	Lumbar Back Fat(cm)	5.29	107	-0.03	0.04	0.27	0.07	2.92
5	Average Back Fat (cm)	7.35	113	0.15	0.04	-0.002	0.06	3.75
5	Last Rib Back Fat (cm)	9.51*	113	0.17	0.04	0.04	0.06	4.83
5	Lumbar Back Fat(cm)	7.25	107	0.17	0.05	0.11	0.07	3.79
6	Tenth Rib Back Fat (cm)	6.14	128	-0.14	0.05	0.15	0.08	3.63
6	Carcass Length (cm)	5.44	141	0.46	0.14	0.05	0.19	2.59
7	Average Back Fat (cm)	11.10**	58	0.17	0.04	0.05	0.06	5.34
7	Lumbar Back Fat (cm)	13.81**	72	0.24	0.05	-0.07	0.08	6.88
7	Tenth Rib Back Fat (cm)	5.60	58	0.14	0.05	0.09	0.07	2.83
7	Last Rib Back Fat (cm)	7.27	74	0.14	0.04	-0.04	0.06	3.69
7	Carcass Weight (kg)	7.69	95	0.41	0.16	-0.77	0.26	4.68
8	Average Daily Gain on Test (kg/day)	6.28	48	-0.014	0.004	0.005	0.006	2.76
8	Carcass Weight (kg)	7.33	48	-0.34	0.15	0.67	0.21	3.36
9	Average Daily Gain to Weaning (kg/day)	6.38	37	0.008	0.005	0.023	0.007	3.66
9	Average Daily Gain on Test (kg/day)	5.32	116	0.014	0.004	-0.002	0.007	2.86
11	Carcass Length (cm)	5.72	13	-0.36	0.15	0.60	0.27	4.06
12	Last Rib Back Fat (cm)	4.78	81	-0.14	0.05	-0.12	0.08	4.52
13	Average Back Fat (cm)	5.84	27	0.09	0.04	-0.13	0.05	2.81

13	Tenth Rib Back Fat (cm)	7.08	23	0.12	0.04	-0.14	0.06	3.05
13	Last Rib Back Fat (cm)	5.35	36	0.07	0.04	-0.15	0.05	2.69
13	Carcass Weight (kg)	5.52	54	-0.19	0.15	-0.67	0.22	2.61
14	Last Rib Back Fat (cm)	5.29	57	-0.04	0.03	0.14	0.05	2.09
14	Carcass Weight (kg)	5.51	58	0.19	0.14	0.62	0.20	2.30
18	Average Back Fat (cm)	4.46	5	-0.12	0.04	0.02	0.06	2.33
X	Carcass Length (cm)	5.17	75	0.55	0.17	-0.02	0.18	3.95

[a]Chromosome-wise F-statistic thresholds at the 5% level, as determined by permutation test were as follows: (1) 5.08, (2) 5.12, (3) 5.14, (4) 5.14, (5) 4.99, (6) 5.32, (7) 5.25, (8) 5.03, (9) 5.09, (10) 5.11, (11) 4.59, (12) 4.78, (13) 5.03, (14) 5.02, (15) 5.02, (16) 4.34, (17) 4.86, (18) 4.45, (X) 4.80.
[b]Additive (a) and dominance (d) QTL effects correspond to genotype values of +a, d, and –a for, respectively, individuals having inherited two Berkshire alleles, heterozygotes, and individuals with two Yorkshire alleles. Positive additive effects indicate that Berkshire alleles increased the trait, negative that the Berkshire alleles decreased it. Dominance effects are relative to the mean of the two homozygotes.
[c] % variance = genetic variance at the QTL based on estimated additive and dominance effects and allele frequencies of ½, as a percent of the residual variance in the F2.
* Significant at the 5% genome-wise level (F>8.22)
** Significant at the 1% genome-wise level (F> 9.96)

Table 4. Summary of QTL significant at the 5% chromosome-wise level (%5 chr), the 5% genome-wise level (%5 gen) (F>8.22) and the 1% genome-wise level (%1 gen) (F>9.96) by trait.

Trait	# of significant QTL			% of F2 variance explained
	%5 chr	%5 gen	%1 gen	
Birth Weight	1			2.9
Average Daily Gain to Weaning	1			3.7
Average Daily Gain on Test	2	2		15.0
Tenth Rib Back Fat	3		1	14.3
Lumbar Back Fat	3		1	16.7
Last Rib Back Fat	6	1		24.1
Average Back Fat	4		1	17.0
Loin Eye Area	1		1	8.4
Carcass Length	3			10.6
Carcass weight	4		1	19.0

[a]The real variance could be higher, because we did not account for multiple QTL in adjacent intervals.

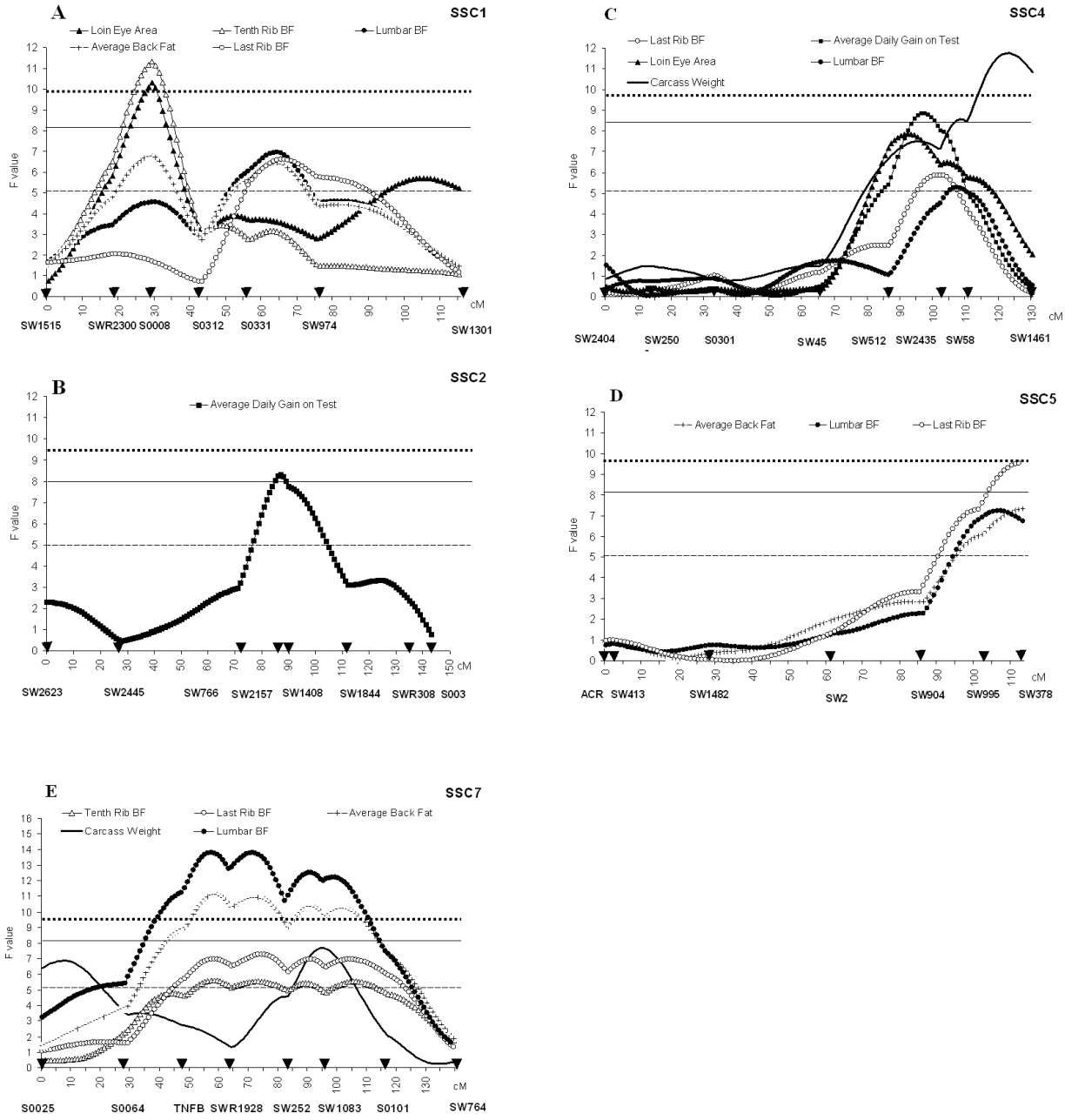

Figure 1. F-ratio curves for evidence of QTL. The x-axis indicates the relative position on the linkage map. The y-axis represents the F-ratio. Arrows on the x-axis indicate the position where a marker was present. Three lines are provided for 5% chromosome-wise (------), 5% genome-wise (_____) and the 1% genome-wise (.....) significance.

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