Genetic Analyses of Growth, Real-Time Ultrasound, Carcass, and Pork Quality Traits in Duroc and Landrace Pigs: II. Heritabilities and Correlations

L. L. Lo, D. G. McLaren², F. K. McKeith, R. L. Fernando, and J. Novakofski

Department of Animal Sciences, University of Illinois, Urbana 61801

ABSTRACT: Knowledge of the genetic control of pork quality traits and relationships among pork quality, growth, and carcass characteristics is required for American swine populations. Data from a 2 x 2 diallel mating system involving Landrace and Duroc pigs were used to estimate heritabilities and genetic correlations among growth (ADG), real-time ultrasonic (US) measures of backfat thickness (BF) and longissimus muscle area (LMA), carcass characteristics, and various pork quality traits. Data were collected from 5,649 pigs, 960 carcasses, and 792 loin chops representing 65, 49, and 49 sires, respectively. Genetic parameters were estimated by REML assuming animal models. Heritability estimates were moderate to high for ADG, USBF, USLMA, carcass BF, and LMA, percentage of LM lipid (IMF), pork tenderness, and overall acceptability. Estimates were low to moderate for percentage of cooking loss, pH, shear force, percentage of LM water, water-holding capacity (WHC), pork flavor, and juiciness. Genetic correlations between US and carcass measures of BF and LMA indicate that selection based on US data will result in effective improvement in carcass characteristics. Selection for increased LMA and(or) decreased BF using US is, however, expected to result in decreased IMF and WHC, increased percentage of LM water and shear value, and in decreased juiciness, tenderness, and pork flavor. Average daily gain was favorably correlated with IMF and unfavorably correlated with shear force. Selection for increased ADG is expected to improve WHC but to decrease the percentage of LM water, with an associated decrease in juiciness. The results of this study suggest the feasibility of including meat quality in selection objectives to improve product quality. Favorable genetic correlations between IMF and eating quality traits suggest the possible merit of including IMF in the selection objective to improve, or restrict change in, pork eating quality.

Key Words: Pigs, Heritability, Genetic Correlation, Variance Components, Carcass Composition, Meat Quality

Introduction

Meat quality is likely to become increasingly important to meat processors and consumers as ready-made meat products and microwave food consumption and the incidence of eating outside the home increase (Sloan et al., 1984). Estimates of heritabilities for eating quality characteristics and of genetic correlations between these and other traits of economic importance are, however, extremely limited. Additionally, real-time ultrasonic measurements of backfat thickness and longissimus muscle depth or area are being used increasingly in swine selection programs. Genetic parameter estimates for these traits have not, to our knowledge, been published before.

In light of such industry changes, knowledge of the genetic control of pork quality traits and relationships among pork quality, growth, and carcass characteristics is required for American swine populations to implement selection pro-
grams that emphasize product quality. The objectives of this study were 1) to estimate heritabilities for growth, real-time ultrasonic measures of backfat thickness and longissimus muscle area, carcass characteristics, and various pork quality traits and 2) to estimate phenotypic and genetic correlations between these traits.

**Experimental Procedure**

*Animals.* Duroc and Landrace pigs were maintained at the University of Illinois Moorman swine research farm from 1987 to 1990. A 2 x 2 diallel mating system involving these two breeds began at the farm in February 1987. The objective was to farrow six litters of each of the four genotypes (purebred Duroc, purebred Landrace, and each reciprocal cross) each month sired by six Duroc and six Landrace boars, each boar producing one purebred and one crossbred litter. Purebred lines each of 60 sows and 6 boars were maintained at the farm with annual replacement rates of 40% on sows and 60% on boars. Gilt replacements were randomly selected on a within-litter basis. Duroc and Landrace boars were purchased from different sources to broaden the genetic base of the lines. Semen from five Duroc and three Landrace boars was also purchased and used. Of a total of 65 boars used in the study, 39 (60%) were purchased and 26 (40%) were farm-raised. Average inbreeding coefficients for pigs produced in this experiment were < 1% for both Landrace and Duroc. A total of 5,649 purebred and crossbred pigs were produced by 424 sows and 65 boars and growth rate data and backfat thickness and longissimus muscle area (obtained with real-time ultrasound) measurements were collected. In addition, carcass composition data on 960 barrows and pork quality measurements on 792 carcasses from 310 sows and 49 boars were analyzed in this study. Further details of the origins, management, and numbers of animals are described by Lo et al. (1992).

**Traits.** The traits investigated were off-test age, ADG from 39.5 to 103.6 kg BW, real-time ultrasonic backfat thickness and longissimus muscle area at the last rib at 103.6 kg BW, hot carcass weight, carcass length, backfat thickness at the first rib, 10th rib, last rib, and last lumbar vertebra, longissimus muscle area at the 10th rib, longissimus muscle color, firmness, and marbling scores, ham muscling score, longissimus muscle ultimate pH value, percentage of cooking loss, shear-force value, water content, intramuscular fat content, water-holding capacity (measured as percentage of free water), and eating quality traits (juiciness, tenderness, pork flavor, off-flavor, and overall acceptability). A complete description of data collection and traits measured is given by Lo et al. (1992).

**Statistical Analysis.** All traits were initially analyzed using the GLM procedure of SAS (1985) assuming fixed models with all possible first-order interactions. Models for final analyses were obtained after eliminating interactions that were not statistically important (P > .20). Final models assumed for ADG [11], off-test age, scanned backfat thickness, and longissimus muscle area [2], carcass traits [3], and pork quality traits [4] were as follows:

\[
Y_{ijklmn} = F_1 + P_j + G_k + B_l + S_m + (FP)_{ij} + (FG)_{lk} + (PG)_{jk} + (GB)_{kl} + (BS)_{lm} + \beta_1 X_{ijklmn} + \beta_2 W_{ijklmn} + \beta_3 W_{ijklmn} + a_{ijklmn} + e_{ijklmn} \]  

[1]

\[
Y_{ijklmn} = F_1 + P_j + G_k + B_l + S_m + (FP)_{ij} + (FG)_{lk} + (PG)_{jk} + (GB)_{kl} + (BS)_{lm} + \beta_1 X_{ijklmn} + \beta_3 W_{ijklmn} + a_{ijklmn} + e_{ijklmn} \]  

[2]

\[
Y_{ijklmn} = F_1 + P_j + G_k + B_l + (FP)_{ij} + (FG)_{lk} + (GB)_{kl} + \beta_4 W_{ijklmn} + a_{ijklmn} + e_{ijklmn} \]  

[3]

\[
Y_{ijklmn} = F_1 + P_j + G_k + B_l + D_m + (FP)_{ij} + (FG)_{lk} + (PG)_{jk} + (GB)_{kl} + \beta_4 W_{ijklmn} + a_{ijklmn} + e_{ijklmn} \]  

[4]

where

\[
Y_{ijklmn} = \text{an observation;}
\]

\[
(F_{ijkl}) = \text{fixed effect of the } i^{th} \text{ farrowing season (} i = 1, \ldots, 10); \]

\[
P_j = \text{fixed effect of the } j^{th} \text{ parity of the dam (} j = 1, \ldots, 4), \text{ where } j = 4 \text{ represented parities } \geq 4; \]

\[
G_k = \text{fixed effect of } k^{th} \text{ breed group (} k = 1, \ldots, 4); \]

\[
B_l = \text{fixed effect of } l^{th} \text{ finishing barn (} l = 1, \ldots, 6); \]

\[
S_m = \text{fixed effect of } m^{th} \text{ sex (barrow, gilt);} \]

\[
D_m = \text{fixed effect of } m^{th} \text{ date of slaughter (} m = 1, \ldots, 50); \]

\[
(FP)_{ij} = \text{fixed farrowing season } \times \text{ parity of the dam interaction effect;} \]

\[
(FG)_{lk} = \text{fixed farrowing season } \times \text{ parity of the dam interaction effect;} \]

\[
(GB)_{kl} = \text{fixed breed group } \times \text{ barn of rearing interaction effect;} \]

\[
(BS)_{lm} = \text{fixed barn of rearing } \times \text{ sex interaction effect;} \]

\[
(PB)_{jl} = \text{fixed parity of the dam } \times \text{ barn of rearing interaction effect;} \]
PARAMETERS FOR CARCASS AND QUALITY TRAITS

\( \text{(PG)jk} = \text{fixed parity of the dam x breed group interaction effect}; \)

\( \beta_1 = \text{partial linear regression of the dependent variable on birth litter size,} \ X_{ijklmn}; \)

\( \beta_2 = \text{partial linear regression coefficient of the dependent variable on on-test weight,} \ W_{ijklmn}; \)

\( \beta_3 = \text{partial linear regression coefficient of the dependent variable on off-test weight,} \ W_{ijklmn}; \)

\( \beta_4 = \text{partial linear regression coefficient of the dependent variable on off-farm weight,} \ W_{ijklmn}; \)

\( a_{ijklmn} = \text{additive genetic effect of the oth (nth) animal,} \ a_{ijklmn} \sim N(0, \mathbf{A}_a^2), \) where \( \mathbf{A} = \text{Wright's numerator relationship matrix, and uncorrelated with random litter effects; and} \)

\( e_{ijklmn} = \text{random residual effect,} \ e_{ijklmn} \sim iid \text{N}(0, \sigma_e^2) \) and uncorrelated with random additive and litter effects.

Farrowing groups were defined as 3-mo periods (June to August, September to November, etc.) within each year except for the last group (September to December, 1989). Farrowings occurred every month for 31 mo, but in some months no carcass data were obtained. Smaller groupings of farrowing dates would have resulted in cells with missing carcass data.

The two extremes of low pork quality, PSE and DFD meat, are related to animal stress associated with environmental factors such as preslaughter handling and slaughter methods (Eikelenboom, 1988). Slaughter date was, therefore, included as a fixed effect in the analysis of pork quality traits. Haley (1989) pointed out that negative maternal effects may be exerted on growth traits in pigs via litter size (i.e., fraternity size may affect subsequent postweaning growth performance). The model, therefore, included the size of the litter the pig was born in as a covariable to adjust for such effects. On-test weight was included as a covariable in the model for ADG because the objective was to compare growth rate for a fixed-weight interval (i.e., between 40 and 104 kg). All pigs did not go on-test at the same weight or come off-test at the same weight; hence, both on- and off-test weight were included as covariables in [1].

Variance components were estimated by the REML method (Patterson and Thompson, 1971) using downhill simplex for maximization (Nelder and Mead, 1965). Initial values of the variance components used to start the iterative process for univariate models were from Lo (1990). The criterion for convergence was that successive estimates were the same up to a minimum of eight decimal places. Convergence occurred after 14 to 105 iterations. In addition, because < 1% of coefficients in the coefficient matrices for animal models (including relationships) were different from zero, sparse matrix techniques were applied to reduce the computational resources required (Misztal, 1990).

Phenotypic and genotypic correlations were estimated using bivariate animal models in the REML analysis. Fixed effects were the same as in the univariate analyses. The starting values for residual and additive genetic variances for pairs of traits were chosen from the estimates under univariate analyses. Starting values for residual and additive genetic covariances for pairs of traits were obtained by varying the phenotypic and genetic correlations from -1.0 to 1.0 in increments of .1 and choosing the set of values that maximized the likelihood function. Convergence occurred after approximately 200 to 700 iterations. The criterion of convergence was a minimum of eight decimal places.

Heritabilities were estimated as follows:

\[ h^2 = \frac{\sigma^2_a}{\sigma^2_a + \sigma^2_e} \]  

[5]

Standard errors of heritability estimates were calculated using the approximate method of Swiger et al. (1964) for unbalanced data based on the following expression:

\[ \text{SE}(h^2) = 4 \sqrt{\frac{2(N-k)S^2 \sigma_e^2 + (k-1)t^2}{k^2(N-S)(S-1)}} \]  

[6]

where \( N = \text{the total number of observations,} \ S = \text{the number of sires,} \ k = (\frac{1}{S-1}) \times \left[ N - \left( \frac{\Sigma n_i^2}{N} \right) \right], \) \( n_i = \text{the number of observations of the ith sire and} \) \( t = \text{the intraclass correlation, .25} h^2. \) The approximation of the variance of \( t \) from which \( \text{SE}(h^2) \) is taken is based on results of analysis of variance with sire models. In the present study, REML was used for estimation using animal models, contributing to the approximate nature of the method used to estimate standard errors of heritability estimates.

Correlations coefficients were computed from additive and residual variances and covariances estimated using REML assuming bivariate animal models. Genetic correlations \( \hat{r}_A \) between traits were computed as follows:

\[ \hat{r}_A = \frac{\text{COV}_{A_{x,y}}}{\sqrt{\text{var}_{A_x} \text{var}_{A_y}}} \]  

[7]
where $\text{cov}_{AX}(x,y)$ is the additive genetic covariance between traits $x$ and $y$. $\text{Var}_{AX}$, $\text{Var}_{AY}$ are the additive genetic variances for traits $x$ and $y$, respectively. Phenotypic correlations $\hat{r}_p$ between traits were computed as follows:

$$\hat{r}_p = \frac{\text{COV}_{P(x,y)}}{\sqrt{\text{Var}_{Px} \times \text{Var}_{Py}}}$$

where $\text{COV}_{P(x,y)}$ is the phenotypic covariance between traits $x$ and $y$, the sum of the genetic and residual covariance (i.e., $\text{COV}_P = \text{COV}_A + \text{COV}_E$; $\text{Var}_{PX}, \text{Var}_{PY}$ are the phenotypic variances for traits $x$ and $y$, respectively).

Standard errors of genetic correlations ($\delta\hat{r}_A$) were estimated using the approximate formula given by Falconer (1989):

$$\delta\hat{r}_A = \frac{1}{\sqrt{2}} \sqrt{\frac{\sigma^{2}_{h_x^2} + \sigma^{2}_{h_y^2}}{h_x^2 \times h_y^2}}$$

where $h_x^2$, $h_y^2$ are the heritabilities of traits $x$ and $y$, respectively, and $\sigma^{2}_{h_x^2}$, $\sigma^{2}_{h_y^2}$ are the standard errors of heritability estimates of traits $x$ and $y$, respectively. The (covariance component estimates used to calculate genetic and phenotypic correlations were calculated using only records that had measurements on both the traits to be correlated.

**Results and Discussion**

**Genetic Parameters Estimation.** Genetic parameters were estimated based on individual records using additive genetic models for direct effects and assuming common genetic variances across breed groups (purebred Duroc, purebred Landrace, and each reciprocal cross). However, non-additive genetic effects within and between breeds and crosses may be important for some traits, as evidenced by heterosis for growth rate (Lo et al., 1992). The additive relationship matrix (A) accounts for the correlated structure among animals and has widespread acceptance in animal breeding applications of mixed model methodology. The A matrix is, however, a true relationship matrix among individuals only when all the animals come from the same breed population (Van Vleck et al., 1987). Smith and Maki-Tanila (1990) presented a recursive method for evaluating the genotypic covariances between relatives for models allowing dominance and inbreeding within populations and suggested that dominance should be considered as an essential feature of genetic models for loci affecting quantitative traits. Methodology for multibreed analysis of additive and non-additive effects is yet to be developed. Although breed group differences existed for some traits in this population (Lo et al., 1992), it is assumed that means and variances are unrelated. Sellier (1988) suggested that there were few differences between breeds in heritabilities for meat quality traits.

The quality of pig meat depends greatly on the incidence of halothane sensitivity in the population involved, which may vary from 5 to 50% for Landrace breeds. The quality of meat in a Landrace population composed of 5 to 10% halothane reactor is close to that of the Duroc (Sellier, 1988). Lo et al. (1992) classified 7.2% of carcasses in the present study as having pale and soft longissimus muscles based on color and firmness scores of one. Incidence of poor meat quality was 2.4% in the Duroc and 9.6% in the Landrace. In the absence of halothane test results, Lo et al. (1992) concluded that the stress gene was likely present in both the populations and suggested that dominance should be considered as an essential feature of genetic models for loci affecting quantitative traits. Methodology for multibreed analysis of additive and non-additive effects is yet to be developed. Although breed group differences existed for some traits in this population (Lo et al., 1992), it is assumed that means and variances are unrelated. Sellier (1988) suggested that there were few differences between breeds in heritabilities for meat quality traits.

**Table 1. Heritability estimates ± approximate standard errors for growth and ultrasound traits**

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of sires</th>
<th>No. of dams</th>
<th>No. of pigs</th>
<th>$\hat{h}^2 \pm SE$</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGE</td>
<td>65</td>
<td>424</td>
<td>5,849</td>
<td>.43 ± .06</td>
</tr>
<tr>
<td>ADG</td>
<td>65</td>
<td>424</td>
<td>5,849</td>
<td>.36 ± .07</td>
</tr>
<tr>
<td>USBF</td>
<td>65</td>
<td>409</td>
<td>4,647</td>
<td>.54 ± .09</td>
</tr>
<tr>
<td>USLMA</td>
<td>65</td>
<td>409</td>
<td>4,647</td>
<td>.48 ± .08</td>
</tr>
</tbody>
</table>

*AGE = days to 103.6 kg BW; ADG = average daily gain from 50.5 to 103.6 kg BW, grams; USBF = real-time ultrasonic backfat thickness at the last rib at 103.6 kg BW, millimeters; and USLMA = real-time ultrasonic longissimus area at the last rib at 103.6 kg BW, square centimeters.*

A-mode scanners, however, have been in use since the late 1950s to measure backfat thickness in pigs and genetic parameters for ultrasonically probed backfat thickness are based on data from such instruments. The heritability estimate for real-time scanned backfat thickness (.54, Table 1), although larger than many estimates for A-mode scanners,
The heritability estimate obtained for muscle pH 24 h postmortem is similar to weighted average heritability estimates given by Sellier (1988) and Lo (1990). Cameron (1990b) reported a heritability of 20 for muscle pH at 24 h postmortem. Shear force values are a quantitative measure of tenderness and correlate fairly well with taste panel scores for tenderness (see below). Heritability estimates for shear value (.17), longissimus muscle firmness score (.29), and loin chop tenderness score (.45) were somewhat variable, but with standard errors > .10 they were not significantly different (Tables 2 and 3).

Because weight loss during storage, freezing, thawing, and cooking of meat is related to the binding of water within muscle, water-holding capacity (measured as percentage of free water content) of meat is of considerable economic interest (Hamm, 1986). Percentage free of water was estimated to be moderately heritable (.25, Table 3) in this study, similar to the weighted average of previous estimates (.31) reported by Lo (1990). Cooking loss is also used as a measure of the water-holding capacity of meat (Hamm, 1986). The heritability estimate for percentage of cooking loss (.06) was lower than that for water-holding capacity. Schepers (1979) also found differences in cooking loss and water-holding capacity heritability estimates (.10 vs .43). Malmfors and Nilsson (1979) did not detect any additive genetic variation in frying, drip, and cooking loss for Landrace pigs. As Hamm (1986) pointed out, water-holding capac-

Table 2. Heritability estimates ± approximate standard errors for carcass characteristics

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of sires</th>
<th>No. of dams</th>
<th>No. of carcasses</th>
<th>$h^2$ ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>LENG</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.62 ± .14</td>
</tr>
<tr>
<td>BFTR</td>
<td>49</td>
<td>310</td>
<td>950</td>
<td>.56 ± .13</td>
</tr>
<tr>
<td>AVBF</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.61 ± .14</td>
</tr>
<tr>
<td>LMA</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.60 ± .18</td>
</tr>
<tr>
<td>COLOR</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.11 ± .08</td>
</tr>
<tr>
<td>FIRM</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.29 ± .09</td>
</tr>
<tr>
<td>MARB</td>
<td>49</td>
<td>310</td>
<td>980</td>
<td>.18 ± .07</td>
</tr>
<tr>
<td>MS</td>
<td>49</td>
<td>310</td>
<td>890</td>
<td>.17 ± .07</td>
</tr>
</tbody>
</table>

$LENG =$ carcass length, centimeters; $BFTR =$ backfat at the 10th rib, millimeters; $AVBF =$ average of first rib, last rib, and last lumbar vertebra backfat measurements, millimeters; $LMA =$ longissimus muscle area at the 10th rib, square centimeters; $COLOR$, $FIRM$, and $MARBLing$ scores on a 1 to 3 integer scale with $1$ representing pale/soft/no marbling and 3 representing dark/very firm/excess marbling. $MS =$ ham muscling score on a 1 to 3 integer scale with 1 representing light, 2 average, and 3 very heavy muscling.

is within the range of previous estimates (Arganosa et al., 1969; Lundström, 1975; Kennedy et al., 1985; Bereskin, 1987; Merks, 1987; Van Diepen and Kennedy, 1989; Kaplon et al., 1991). In a literature review conducted by Hutchens and Hintz (1981), heritability for probed backfat averaged .38. The National Swine Improvement Federation (NSIF) assumed heritabilities of .40 for average backfat thickness and .50 for longissimus muscle area in constructing selection indexes (NSIF, 1987).

The heritability estimate for carcass length of .62 (Table 2) is consistent with estimates of .54, .49, and .60 reported by Johansson et al. (1987) for Landrace, Yorkshire, and Hampshire pigs, respectively. Heritability estimates as high as .96 and .71 have, however, been reported by Arganosa et al. (1989) and Bereskin and Steele (1988), respectively. Warwick and Legates (1979) gave heritability for carcass length in pigs as between .40 and .60. Heritability estimates for different measures of carcass backfat thickness and of carcass longissimus muscle area (Table 2) tend to the high side of estimates reported in the literature.

Longissimus muscle color, firmness, and marbling scores and ham muscling score were estimated to be low to moderately heritable (Table 2). Meat color, one of the most frequently measured meat quality traits, is a function of both the density and structural condition of muscle fibers (Briskey and Kauffman, 1978) and can be evaluated by subjective and objective methods. In a review, Sellier (1988) reported a .27 weighted average heritability for muscle reflectance using the EEL (Evans Electroselenium Limited) reflectometer, in contrast to the low heritability estimate for subjective muscle color score in the present study (.11).

The heritability estimate obtained for muscle pH 24 h postmortem is similar to weighted average heritability estimates given by Sellier (1988) and Lo (1990). Cameron (1990b) reported a heritability of 20 for muscle pH at 24 h postmortem. Shear force values are a quantitative measure of tenderness and correlate fairly well with taste panel scores for tenderness (see below). Heritability estimates for shear value (.17), longissimus muscle firmness score (.29), and loin chop tenderness score (.45) were somewhat variable, but with standard errors > .10 they were not significantly different (Tables 2 and 3).

Because weight loss during storage, freezing, thawing, and cooking of meat is related to the binding of water within muscle, water-holding capacity (measured as percentage of free water content) of meat is of considerable economic interest (Hamm, 1986). Percentage free of water was estimated to be moderately heritable (.25, Table 3) in this study, similar to the weighted average of previous estimates (.31) reported by Lo (1990). Cooking loss is also used as a measure of the water-holding capacity of meat (Hamm, 1986). The heritability estimate for percentage of cooking loss (.06) was lower than that for water-holding capacity. Schepers (1979) also found differences in cooking loss and water-holding capacity heritability estimates (.10 vs .43). Malmfors and Nilsson (1979) did not detect any additive genetic variation in frying, drip, and cooking loss for Landrace pigs. As Hamm (1986) pointed out, water-holding capac-

Table 3. Heritability estimates ± approximate standard errors for pork quality measurements

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of sires</th>
<th>No. of dams</th>
<th>No. of carcasses</th>
<th>$h^2$ ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.14 ± .08</td>
</tr>
<tr>
<td>PCL</td>
<td>49</td>
<td>270</td>
<td>791</td>
<td>.06 ± .06</td>
</tr>
<tr>
<td>SH</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.17 ± .08</td>
</tr>
<tr>
<td>PWAT</td>
<td>49</td>
<td>270</td>
<td>791</td>
<td>.14 ± .06</td>
</tr>
<tr>
<td>IMF</td>
<td>49</td>
<td>270</td>
<td>791</td>
<td>.52 ± .13</td>
</tr>
<tr>
<td>FWAT</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.25 ± .09</td>
</tr>
<tr>
<td>JC</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.12 ± .07</td>
</tr>
<tr>
<td>TEN</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.45 ± .12</td>
</tr>
<tr>
<td>PFI</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.13 ± .07</td>
</tr>
<tr>
<td>OFI</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.03 ± .06</td>
</tr>
<tr>
<td>OA</td>
<td>49</td>
<td>270</td>
<td>792</td>
<td>.34 ± .11</td>
</tr>
</tbody>
</table>

$pH =$ longissimus muscle pH value at 24 h postmortem; $PCL =$ percentage of cooking loss; $SH =$ shear force, kilograms; $PWAT =$ percentage H_{2}O in ground and mixed samples of longissimus muscle; $IMF =$ intramuscular fat, percentage of extractable lipid from the longissimus muscle; and $FWAT =$ percentage of free water content of the muscle. High values indicate poor water-holding capacity. The following five variables are scores assigned by a sensory panel using a continuous 15-cm scale, 0 representing least desirable and 15 most desirable: $JC =$ juiciness; $TEN =$ tenderness; $PFI =$ pork flavor intensity; $OFI =$ off-flavor intensity; $OA =$ overall acceptability.
from 39.5 to 103.6 kg BW, grams; USBF reported for Landrace pigs in Denmark and in backfat thickness at the last rib at 103.5 kg BW, millimeters; reported a .35 heritability estimate for German ity measurements with raw, unground muscle do not necessarily reflect water retention during cooking or other types of meat processing.

Intramuscular fat content of the longissimus muscle was estimated to be determined in large part by additive genetic effects (h² = .52, Table 3). Malmfors and Nilsson (1979) obtained heritability estimates of .58 and .68 for Swedish Landrace and Large White pigs, respectively. Scheper (1979) reported a .35 heritability estimate for German Landrace pigs, and heritabilities of .55 were reported for Landrace pigs in Denmark and in Switzerland (Just et al., 1986; Schwörer et al., 1987, respectively). The average heritability weighted by number of sires for intramuscular fat content from previous reports is .53 (Sellier, 1988), similar to the estimate obtained in the present study. Percentage of water in the longissimus muscle was estimated to be lowly heritable (.14, Table 3).

Cameron (1990b) reported heritability estimates for tenderness, pork flavor, and overall acceptability of .23, .14, and .16, respectively, from data on 40 full-sib litter groups of Duroc and halothane-negative British Landrace pigs, in contrast to estimates of .45, .13, and .34 for these traits in the present study (Table 3). Malmfors and Nilsson (1979) estimated that heritabilities for sensory panel evaluation of pork taste and juiciness did not differ from zero. Juiciness was estimated to have a heritability of .12 in the present study, but that did not differ significantly from zero. Based on results of a small number of studies, eating quality traits in general seemed to be lowly to moderately heritable, of the order of .10 to .20 (Lo, 1990). Estimates were, however, quite variable, as would be expected given the relatively small sample sizes involved in their estimation. Overall, results indicate that meat quality is determined to some extent by additive genetic effects and as such might be improved by selection.

Correlations. Growth rate was estimated to have a low to moderate unfavorable genetic correlation with scanned backfat thickness (Table 4) and a moderate unfavorable genetic correlation with carcass backfat thickness (Table 5). Several studies (McPhee et al., 1979; Cleveland et al., 1982; Bereskin and Steele, 1988) have demonstrated an undesirable genetic relationship between growth rate and backfat thickness. The high genetic correlations between real-time ultrasonic measures of backfat and longissimus muscle area at the last rib and carcass measurement made at the 10th rib (Table 5), plus the moderate to high

### Table 4. Genetic (above diagonal) and phenotypic (below diagonal) correlations among growth and ultrasound traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>ADG</th>
<th>AGE</th>
<th>USBF</th>
<th>USLMA</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG</td>
<td>-83 ± 0.8</td>
<td>.28 ± 0.18</td>
<td>.28 ± 0.53</td>
<td></td>
</tr>
<tr>
<td>AGE</td>
<td>-70</td>
<td>-13 ± 0.12</td>
<td>.35 ± 0.18</td>
<td></td>
</tr>
<tr>
<td>USBF</td>
<td>.21</td>
<td>-.10</td>
<td>-.56 ± 0.09</td>
<td></td>
</tr>
<tr>
<td>USLMA</td>
<td>.13</td>
<td>.24</td>
<td>-.45</td>
<td></td>
</tr>
</tbody>
</table>

aAGE = days to 103.6 kg BW; ADG = average daily gain from 39.6 to 103.6 kg BW, grams; USBF = real-time ultrasonic backfat thickness at the last rib at 103.6 kg BW, millimeters; USLMA = real-time ultrasonic longissimus area at the last rib at 103.6 kg BW, square centimeters.

### Table 5. Genetic and phenotypic correlations between growth and ultrasound and carcass and pork quality traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>ADGa</th>
<th>AGEa</th>
<th>USBFa</th>
<th>USLMAa</th>
</tr>
</thead>
<tbody>
<tr>
<td>LMA</td>
<td>-19 ± 0.9</td>
<td>.06</td>
<td>.14 ± 0.11</td>
<td>-.01</td>
</tr>
<tr>
<td>BFTR</td>
<td>.43 ± .13</td>
<td>.03</td>
<td>-.35 ± .07</td>
<td>-.11</td>
</tr>
<tr>
<td>IMF</td>
<td>.27 ± .32</td>
<td>.06</td>
<td>-.33 ± .14</td>
<td>-.23</td>
</tr>
<tr>
<td>FWAT</td>
<td>-.28 ± .17</td>
<td>-.43</td>
<td>.37 ± .16</td>
<td>-.28</td>
</tr>
<tr>
<td>FWAT</td>
<td>-.55 ± .14</td>
<td>-.15</td>
<td>.53 ± .00</td>
<td>.30</td>
</tr>
<tr>
<td>SH</td>
<td>-.27 ± .10</td>
<td>-.19</td>
<td>.49 ± .18</td>
<td>.06</td>
</tr>
<tr>
<td>JC</td>
<td>.30 ± .08</td>
<td>-.17</td>
<td>.16 ± .25</td>
<td>.01</td>
</tr>
<tr>
<td>TEN</td>
<td>.00 ± .14</td>
<td>.00</td>
<td>-.46 ± .11</td>
<td>-.14</td>
</tr>
<tr>
<td>PFI</td>
<td>.88 ± .87</td>
<td>-.03</td>
<td>-.19 ± .16</td>
<td>-.05</td>
</tr>
<tr>
<td>OA</td>
<td>-.17 ± .15</td>
<td>-.33</td>
<td>.08 ± .19</td>
<td>.04</td>
</tr>
</tbody>
</table>

aAGE = days to 103.6 kg BW; ADG = average daily gain from 39.6 to 103.6 kg BW, grams; USBF = real-time ultrasonic backfat thickness at the last rib at 103.6 kg BW, millimeters; USLMA = real-time ultrasonic longissimus area at the last rib at 103.6 kg BW, square centimeters; LMA = longissimus muscle area at the 10th rib, square centimeters; BFTR = backfat at the 10th rib, millimeters; IMF = intramuscular fat, percentage of extractable lipid from the longissimus muscle; FWAT = percentage of H2O in ground and mixed samples of longissimus muscle; PFI = pork flavor intensity; OA = overall acceptability.
heritability estimates for scanned backfat and longissimus muscle area (Table 1), indicate that selection based on real-time ultrasonic data is expected to result in effective improvement in carcass characteristics.

Genetic correlation estimates between growth rate and scanned or carcass longissimus muscle area, although not detected as differing from zero, tended to be unfavorable (Tables 4 and 5). Schwörer et al. (1980) reported an unfavorable genetic relationship of -0.35 between ADG and percentage of premium cuts in Swiss Large White and Swiss Landrace pigs. Cameron (1990a) reported a genetic correlation of -0.47 between ADG and lean weight for Duroc and British Landrace pigs. Bereskin and Steele (1988) estimated a genetic correlation of -0.22 for ADG and longissimus muscle area based on American pig populations.

Moderate genetic correlation estimates between growth rate and pork quality traits (Table 5) indicate that selection for increased ADG or decreased off-test age would result in increased intramuscular fat content and decreased shear value. That genetically faster-growing pigs might be expected to yield more tender pork is indicated by the genetic correlation with age (-0.46), but no genetic relationship was detected between ADG and tenderness (Table 5). Schwörer et al. (1990) summarized genetic correlation estimates between intramuscular fat content and ADG in European studies and reported correlation coefficients ranging from 0.23 to 0.44. Selection for increased growth rate is expected to improve water-holding capacity but to decrease muscle water content, with an associated decrease in juiciness (Table 5).

Scanned backfat thickness was positively correlated with pork juiciness, tenderness, and flavor, whereas scanned longissimus muscle area was negatively correlated with these quality traits (Table 5). Selection to increase longissimus area and(or) decrease backfat thickness based on real-time ultrasound data is expected to result in pork that is less juicy and less tender with less flavor, associated with a decreased intramuscular fat content and water-holding capacity. Overall pork acceptability was not correlated with scanned backfat thickness but was negatively correlated with scanned longissimus muscle area. Correlations between real-time ultrasonic data and pork quality traits and between carcass measures of backfat and longissimus muscle area and pork quality traits were, in general, similar (Tables 5 and 6).

Jensen et al. (1967) estimated relationships between carcass backfat and meat quality and suggested that selection for decreased backfat thickness and increased percentage of lean cuts would also decrease water-holding capacity, lower intramuscular fat content, increase shear value, and decrease scores for juiciness and flavor. Several studies (Rhodes, 1970; Wood et al., 1981; Cameron, 1990b), however, found that there were no differences in eating quality due to carcass fatness. This can be explained, at least in part, by mean levels of fat and the amount of variation in the populations studied. A smaller effect is observed for pigs having low variability and average to high levels of fat compared with pigs having highly variable fat content (Wood, 1991). The mean 10th rib backfat thickness in the present study was 29 mm, ranging from 8 to 51 mm, with an average of 3.75% intramuscular fat, ranging from 0.52 to 13.72% (Lo et al., 1992). Fat content was lower than

### Table 6. Genetic and phenotypic correlations between carcass and pork quality traits

<table>
<thead>
<tr>
<th>Trait*</th>
<th>AVBF*</th>
<th>BFTR*</th>
<th>LMA*</th>
</tr>
</thead>
<tbody>
<tr>
<td>IMF</td>
<td>0.32</td>
<td>0.41</td>
<td>-0.40</td>
</tr>
<tr>
<td>PWAT</td>
<td>-0.31</td>
<td>-0.81</td>
<td>0.74</td>
</tr>
<tr>
<td>FWAT</td>
<td>-0.34</td>
<td>-0.15</td>
<td>0.46</td>
</tr>
<tr>
<td>SH</td>
<td>-0.45</td>
<td>-0.20</td>
<td>0.46</td>
</tr>
<tr>
<td>JC</td>
<td>0.31</td>
<td>0.37</td>
<td>-0.37</td>
</tr>
<tr>
<td>TEN</td>
<td>0.19</td>
<td>0.30</td>
<td>-0.24</td>
</tr>
<tr>
<td>PFI</td>
<td>0.19</td>
<td>0.37</td>
<td>-0.24</td>
</tr>
<tr>
<td>OA</td>
<td>0.76</td>
<td>0.45</td>
<td>-0.41</td>
</tr>
</tbody>
</table>

*AVBF = average of first rib, last rib, and last lumbar vertebra backfat measurements, millimeters; BFTR = backfat at the 10th rib, millimeters; LMA = longissimus muscle area at the 10th rib, square centimeters; IMF = intramuscular fat, percentage of extractable lipid from the longissimus muscle; PWAT = percentage of H2O in ground and mixed samples of longissimus muscle; FWAT = percentage of free water content of the muscle (high values indicate poor water-holding capacity); and SH = shear force, kilograms. The following five variables are scores assigned by a sensory panel using a continuous 15-cm scale, 0 representing least desirable and 15 most desirable: JC = juiciness; TEn = tenderness; PFI = pork flavor intensity; OA = overall acceptability.
phenotypic correlations between intramuscular fat and subcutaneous fat thickness and intramuscular fat content, which was greater than the typical for pigs used in other (European) studies. Several authors have reported low genetic and phenotypic correlations between intramuscular fat content and backfat thickness and suggested that eating quality is associated with intramuscular fat content and not with backfat thickness (Malmfors and Nilsson, 1979; Schwörer et al., 1980). At low levels of intramuscular fat content (< 1.0%), Wood et al. (1986) reported a phenotypic correlation of .56 between subcutaneous fat thickness and intramuscular fat content, which was greater than the estimates of the above studies (.10 and .06, respectively). Skelley et al. (1973) and Cameron (1990b) found phenotypic correlations of .26 and .22 between these two traits, close to the values of .20 to .25 estimated in this study (Table 6).

The finding that selection for increased longissimus muscle area would be expected to reduce intramuscular fat content and water-holding capacity, increase water content and shear force values, and reduce pork juiciness, tenderness, and overall acceptability agrees with results reported by Jensen et al. (1967) and Cameron (1990b). Malmfors and Nilsson (1979) also found that increased water content and frying loss and decreased intramuscular fat content were associated with increased longissimus muscle area. Juiciness, tenderness, and flavor, however, showed no relationships with longissimus muscle area in their studies.

Genetic correlations between water content of the longissimus muscle and tenderness, pork flavor, and overall acceptability were all negative, whereas water-holding capacity was positively correlated with these traits (Table 7). The reverse was true for juiciness, however. Intramuscular fat content was positively correlated with all eating quality traits, indicating that fat plays a role in these properties. The relationship between eating quality and intramuscular fat content is dependent on the amount of intramuscular fat, however. Bejerholm and Barton-Gade (1986) considered a level of 2.5 to 3.0% intramuscular fat to be optimum for eating quality. DeVol et al. (1988) suggested a threshold value of 2.5 to 3.0% fat to explain low correlations between intramuscular fat content and juiciness, tenderness, and flavor. There seems to be little effect on pork juiciness, tenderness, and flavor when intramuscular fat content on loin chops is above this threshold. DeVol et al. (1988) reported correlation coefficients of .21, .32, and .23 for intramuscular fat content with juiciness, tenderness, and flavor, respectively. Intramuscular fat in the present study averaged 3.75%. Based on these same data, Lo et al. (1992) detected a breed difference for intramuscular fat content (5.0% for Duroc vs 2.8% for Landrace) but no breed effects were found for the eating quality traits studied. Eating quality traits decreased with increased shear force (Table 7).

Practically, muscle pH1 and pH2 are used, respectively, to identify PSE and DFD meat (Greaser, 1986). Water-holding capacity is of direct economic importance to the meat industry and its genetic improvement should also have desirable effects on cooking loss and pork eating quality traits (Hamm, 1986). However, Lundström (1975) and Malmfors et al. (1980), in simulation studies in which meat color was included in selection indices, did not include muscle pH or water-holding capacity in the selection criteria for genetic improvement of meat quantity and quality.

Cameron (1990b) examined the correlated selection differentials to selection in various meat quality and carcass traits and reported that when P2 backfat depth, muscle pH, and light reflectance were included in the selection index, the correlation between the index and breeding objective was .44, similar to that (.43) when only P2 and muscle pH were included. He concluded that the measurement of muscle reflectance for selection purpose would be of little value. Another potential trait to include in an index designed to improve meat quality is intramuscular fat content. Barton-Gade

<table>
<thead>
<tr>
<th>Trait</th>
<th>SHa</th>
<th>IMFa</th>
<th>PWAt</th>
<th>FWAt</th>
</tr>
</thead>
<tbody>
<tr>
<td>JC</td>
<td>-.88 ± .19  -.17</td>
<td>.24 ± .27  .16</td>
<td>.57 ± .13  .11</td>
<td>.14 ± .24  -.04</td>
</tr>
<tr>
<td>TEN</td>
<td>-.70 ± .05  -.73</td>
<td>.53 ± .13  .23</td>
<td>-.15 ± .19  -.08</td>
<td>-.41 ± .14  -.11</td>
</tr>
<tr>
<td>PFI</td>
<td>-.44 ± .27  -.06</td>
<td>.03 ± .08  .17</td>
<td>-.32 ± .00  .08</td>
<td>-.35 ± .24  -.00</td>
</tr>
<tr>
<td>OA</td>
<td>-.52 ± .08  -.57</td>
<td>.08 ± .11  .22</td>
<td>-.23 ± .32  .08</td>
<td>-.48 ± .15  -.11</td>
</tr>
</tbody>
</table>

*SH = shear force, kilograms; IMF = intramuscular fat, percentage of extractable lipid from the longissimus muscle; PWAT = percentage of H2O in ground and mixed samples of longissimus muscle; and FWAT = percentage of free water content of the muscle (high values indicate poor water-holding capacity). The following five variables are scores assigned by a sensory panel using a continuous 15-cm scale, 0 representing least desirable and 15 most desirable: JC = juiciness; TEN = tenderness; PFI = pork flavor intensity; OA = overall acceptability.
(1990) described phenotypic changes in meat quality in breeds used in Denmark between 1983 and 1988 and commented that it may be necessary to include intramuscular fat content in breeding goals in the future. Favorable genetic correlations between intramuscular fat content and eating quality traits suggest the possible merit of including this trait in the selection objective to improve or restrict change in pork eating quality.

Conclusions. Heritability estimates obtained in this study indicate that there is sufficient genetic variation to allow improvement in meat quality by selection. Although eating quality characteristics could not, practically, be measured as part of swine improvement (testing and selection) programs, muscle color, and/or other technological traits could be measured on carcasses of relatives and included in selection indices designed to hold constant or to improve eating quality at the same time as genetically improving lean tissue growth rate and feed conversion efficiency, as has been practiced for some time in Europe (Lindhé et al., 1980). Meat color, for example, is included in the aggregate genotype in several European countries (Austria, Finland, France, Germany, the Netherlands, Norway, Sweden, and Switzerland; Lundström, 1990). Switzerland has included intramuscular fat content in the selection index, and breeders in Norway have included intramuscular fat content as an additional selection criteria in their breeding programs (Lundström, 1990). Based on the genetic correlation estimates obtained, selection for increased longissimus muscle area and/or decreased backfat thickness using real-time ultrasonography would be expected to result in decreased intramuscular fat content and water-holding capacity and in increased water content and shear value. Such selection is also expected to result in pork that is less juicy and less tender with less flavor. Water seemed to have a positive influence on pork juiciness: increased water content and free water in the longissimus muscle resulted in juicier pork. Average daily gain was found to be positively correlated with intramuscular fat content and negatively correlated with shear force. Selection for increased growth rate is expected to improve water-holding capacity but to decrease muscle water content, with an associated decrease in juiciness. The results of this study suggest the feasibility of including meat quality in selection objectives to improve product quality.

Implications

High genetic correlations between real-time ultrasonic and carcass measures of backfat and longissimus muscle area, plus moderate to high heritability estimates for the ultrasound traits, indicate that selection based on real-time ultrasonic data will result in effective improvement in carcass characteristics. However, genetic correlations between growth, real-time scan, carcass, and pork quality traits indicate the potential for a decrease in pork eating quality with selection for improved lean growth characteristics. Favorable genetic correlations between intramuscular fat content and eating quality traits suggest the possible merit of including this trait in the selection objective to improve or restrict change in pork eating quality.

Literature Cited


