Genetic parameters for measures of residual feed intake and growth traits in seven generations of Duroc pigs

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Abstract
Residual feed intake (RFI) represents the deviation of the actual feed consumption of an animal from that predicted from combination of growth traits. Data on 1642 Duroc (380 boars, 868 gilts, and 394 barrows) pigs in seven generations were used to estimate genetic parameters for measures of RFI, daily feed intake (FI), average daily gain (ADG), backfat (BF), and loin eye area (LEA). Four measures of RFI were estimated from models that included initial test age and weight, and ADG (RFI1); initial test age and weight, ADG, and BF (RFI2); initial test age and weight, ADG and LEA (RFI3); and initial test age and weight, ADG, BF, and LEA (RFI4). Genetic parameters were estimated using an animal model by the REML method. Heritability estimates for measures of RFI were moderate (ranged from 0.22 to 0.38). The corresponding estimates for FI, ADG, and LEA were also moderate (ranging from 0.45 to 0.49), while the estimate for BF was high (0.72). Genetic correlations of FI with ADG (0.84) and BF (0.67) were high. LEA negatively correlated with FI (−0.42), ADG (−0.11) and BF (−0.44). Genetic correlations of BF with measures of RFI were higher when BF was not included in the estimation of RFI (0.77 with RFI1 and 0.76 with RFI3 vs. 0.11 with RFI2 and 0.07 with RFI4). Genetic correlations of LEA with measures of RFI were all negative (ranged from −0.30 to −0.60). Selection for ADG, LEA, BF, and intramuscular fat has resulted in small but favourable genetic changes in measures of RFI. Phenotypic correlations between measures of RFI were zero, and genetic correlations between them were low (0.17 to 0.23). FI was strongly correlated with all the measures of RFI, both genetically (ranged from 0.56 to 0.77) and phenotypically (ranged from 0.56 to 0.66). The results suggested that selection against RFI may cause a reduction in FI. BF should also decrease, and LEA should increase. The amount of change in BF or LEA would vary depending on whether RFI was adjusted for BF.

Keywords:
Residual feed intake
Growth traits
Genetic parameters
Breeding value

1. Introduction
The cost of feeding animals is a major determinant of profitability in almost any animal production system and thus any effort at improving the efficiency of feed use will help to reduce feed cost. This has long been recognized by the swine industries, where feed cost accounts for about two third of total production expenses. Selection programmes that emphasize efficiency rather than growth rate on ad libitum feeding have led to a reduction of daily feed intake, which may be detrimental in the long term (Web, 1989; Smith et al., 1991). Selection against that portion of feed intake not required for growth rate, i.e. residual feed intake (RFI), may provide an alternative measure (Hoque et al., 2006).

Feed efficiency is difficult to measure for individual pigs and results in high labor and equipment costs. Direct selection for improving feed efficiency has not always been effective because...
efficiency of feed use is not a directly measurable trait. It is usually computed as the ratio of feed intake to product, and direct selection on feed efficiency ratio may not be the best way to improve this component trait because of complex additive and multiplicative relations (Luiting, 1990). It may even result in undesired correlated selection responses because of the ratio aspect (i.e., feed over gain). Therefore, feed efficiency in swine may be improved indirectly by selection for growth rate and against backfat (Cleveland et al., 1983). RFI is estimated by the difference between actual and predicted feed intake for an animal. The predicted feed intake is the amount of feed the animal is expected to consume on the basis of its maintenance and production. Variation in RFI may reflect differences in the efficiency with which animals digest and utilize energy for maintenance and production. Therefore, selection against RFI might improve efficiency of energy utilization without reducing appetite required for production of product (Mrode and Kennedy, 1993). Inclusion of this trait in a breeding programme depends on its heritability and its relationships with other traits of interest. The objective of this study was to estimate genetic parameters for and genetic relationships between measures of RFI and growth traits, and to examine the genetic trends of these traits in Duroc pigs over seven generations of selection based on average daily gain (ADG), loin eye area (LEA), backfat thickness (BF), and intramuscular fat (IMF).

2. Materials and methods

2.1. Animals at performance test

Duroc pigs used in this study were of a line that had been selected for ADG, LEA, BF, and IMF through seven generations at the Miyagi Prefecture Animal Industry Experiment Station, Japan during 1995–2001. A total of 1642 (380 boars, 868 gilts, and 394 barrows) pigs were tested, which were the progeny produced from 125 sires and 356 dams. For estimating the variance components, a pedigree file was constructed and the total number of animals, including testing animals, was 1780 pigs in the pedigree. Gilts farrowed only once, and boars were retained for use during one 4 to 6-week breeding period. Thereby, a new generation was obtained each year. Thereby, a new generation was obtained each year. Pigs were weaned at 4 weeks. At 8 weeks of age, 1 barrow and 1 gilt were retained for use during one 4 to 6-week breeding period. Thereby, a new generation was obtained each year. Pigs were weaned at 4 weeks. At 8 weeks of age, 1 boar and 1 gilt were retained for use during one 4 to 6-week breeding period. Thereby, a new generation was obtained each year. Gilts and barrows were reared in growing pens, with group feeding in a concrete-floored building with eight pigs per pen, which allowed 1.2 m² of floor area per pig.

2.2. Selection method

The detailed procedure for selection has been described by Suzuki et al. (2005). Because of limited facility space, selection was conducted without a control line. The first and second generations of selection were performed using an index selection method based on relative desired gains (Yamada et al., 1975). Traits used as selection criteria were ADG, LEA, BF, and IMF. Genetic and phenotypic parameters used to derive the selection criteria were obtained from performance test data of the first and second generations. Relative desired gains were estimated as 1.35 kg, 3.9 cm², −0.54 cm and 0.7%, respectively, for ADG, LEA, BF, and IMF. Consequently, the selection index equation was $I = 0.018 \times ADG + 1.38 \times LEA - 15.10 \times BF - 12.63 \times IMF - 56.68$. Breeding values of ADG, LEA, BF, and IMF were estimated using multiple-trait, animal-model BLUP from the third generation onward. The breeding values were calculated using the Prediction and Estimation (PEST) programme after estimating genetic parameters using the Variance Component Estimation (VCE) programme (ver. 4.2.5) (Neumaier and Groeneveld, 1998), with the generation and sex as fixed effects and random effects of individual additive genetic effect and error. Relative economic weights of selection traits were calculated from the relative desired gains of ADG, LEA, BF, and IMF, which were established from performance test data of the first generation, as described above. The aggregate breeding values were calculated by multiplying the relative economic weights to the EBV of each trait; then selection was executed. To avoid rapid disappearance of the base generation lines from the population, selection was made among sires for boars, and within litters for gilts at the first generation. Approximately 15 boars and 50 gilts were selected at each generation. For each generation, inbreeding coefficients for individual pigs were computed. Based on inbreeding information, all matings were planned to minimize the rate of increase in inbreeding.

2.3. Traits in study

The studied traits were ADG, LEA, BF, daily feed intake (FI), and residual feed intake (RFI). The weekly body weight of each individual pig during the test period was recorded, and ADG (kg/day) for each animal was calculated. Using an ultrasound (B-mode) color scanning technology (SR-100, Kajio Corp., Tokyo, Japan), LEA and BF were measured on all live animals at 105 kg on the left side at the location of half body length. FI was measured in kg per day for individual boars by the difference between supplied and leftover feed. Then, a set of initial test age and weight, ADG, BF and LEA. Model 1 included initial test age and weight as covariates. Model 2 included initial test age and weight, ADG, and BF. Model 3 included initial test age and weight, ADG, and LEA. Model 4 included initial test age and weight, and RFI. The studied traits were ADG, LEA, BF, daily feed intake (FI), and residual feed intake (RFI). The weekly body weight of each individual pig during the test period was recorded, and ADG (kg/day) for each animal was calculated. Using an ultrasound (B-mode) color scanning technology (SR-100, Kajio Corp., Tokyo, Japan), LEA and BF were measured on all live animals at 105 kg on the left side at the location of half body length. FI was measured in kg per day for individual boars by the difference between supplied and leftover feed. Then, a set of initial test age and weight, ADG, BF and LEA. Model 1 included initial test age and weight as covariates. Model 2 included initial test age and weight, ADG, and BF. Model 3 included initial test age and weight, ADG, and BF. Model 4 included initial test age and weight, ADG, and LEA. Model 4 included initial test age and weight,

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### Table 1

Mean values and heritabilities for and genetic (above the diagonal) and phenotypic (below the diagonal) correlations among feed intake and growth traits

<table>
<thead>
<tr>
<th>Traits</th>
<th>Mean ± s.d.</th>
<th>h² ± s.e.</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG (kg/d)</td>
<td>0.87±0.11 (1642)</td>
<td>0.48±0.03 –</td>
<td>0.11 ± 0.36 ± 0.84 ± 0.02</td>
</tr>
<tr>
<td>LEA (cm²)</td>
<td>36.99±4.05 (1642)</td>
<td>0.45±0.05 –</td>
<td>–0.20 –0.44 –0.42 ± 0.05</td>
</tr>
<tr>
<td>BF (cm)</td>
<td>2.37±0.43 (1642)</td>
<td>0.72±0.04 0.09 –0.28 –0.67 ± 0.04</td>
<td></td>
</tr>
<tr>
<td>FI (kg/d)</td>
<td>2.62±0.23 (360)</td>
<td>0.49±0.06 0.73 –0.11 0.49 –</td>
<td></td>
</tr>
</tbody>
</table>

Figures in the parentheses indicate the number of observations.

a ADG, average daily gain; LEA, loin eye area; BF, backfat thickness; FI, daily feed intake.

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### Table 2

Estimates of partial regressions of daily feed intake on starting weight and growth traits

<table>
<thead>
<tr>
<th>Model</th>
<th>Starting age (kg)</th>
<th>Starting weight (kg)</th>
<th>ADG</th>
<th>BF</th>
<th>LEA</th>
<th>R²-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st</td>
<td>–0.0059</td>
<td>0.0148</td>
<td>1.9927</td>
<td>–</td>
<td>–</td>
<td>0.59</td>
</tr>
<tr>
<td>2nd</td>
<td>–0.0061</td>
<td>0.0120</td>
<td>1.7706</td>
<td>0.2214</td>
<td>–</td>
<td>0.68</td>
</tr>
<tr>
<td>3rd</td>
<td>–0.0066</td>
<td>0.0159</td>
<td>1.9775</td>
<td>–</td>
<td>–0.0070</td>
<td>0.61</td>
</tr>
<tr>
<td>4th</td>
<td>–0.0064</td>
<td>0.0128</td>
<td>1.7684</td>
<td>0.2152</td>
<td>–0.0039</td>
<td>0.69</td>
</tr>
</tbody>
</table>

a Included initial test age and weight, and average daily gain (ADG).

b Included initial test age and weight, ADG and backfat (BF).

c Included initial test age and weight, ADG and loin eye area (LEA).

d Included initial test age and weight, ADG, BF and LEA.
ADG, BF, and LEA. Regression coefficients for these covariates from models 1, 2, 3, and 4 were used to estimate RFI1, RFI2, RFI3, and RFI4, respectively.

2.4. Statistical analysis

The covariance components for all traits were estimated by the REML method with the VCE programme (Neumaier and Groeneveld, 1998). The optimization in VCE was done with a quasi-Newton procedure and includes setting up the mixed model equation, numerical factorization, solving the triangular system, computing the sparse inverse, and assembling the gradients. The convergence criterion (i.e., variance of the simplex values) for all runs was 10−2. The following multi-trait animal model was used to estimate genetic parameters:

\[ Y_{Ijklm} = \mu_i + G_k + S_{l} + c_{l} + a_{lm} + e_{ijklm} \]

where \( Y_{Ijklm} \) = observation of trait \( i \); \( \mu_i \) = common constant for trait \( i \); and \( G_k \) = fixed effect of selection generation \( j \) for trait \( i \). The selection generation included the genetic effect of selection and the environmental effect at each generation; \( S_{l} \) = fixed effect of sex \( k \) for trait \( i \); \( c_{l} \) = random effect of common environment \( l \) of litters for trait \( i \); and \( a_{lm} \) = random additive genetic effect of animal \( m \) for trait \( i \), and \( e_{ijklm} \) = random residual effect for trait \( i \).

The (co)variance components for FI, ADG, LEA, and BF were estimated using a four-trait animal model. The corresponding components for growth and feed efficiency traits were estimated in series of five-trait animal model (FI, ADG, BF, and LEA were common with one feed efficiency trait). The breeding values for all the studied traits were estimated with the VCE programme using the same model.

### 3. Results

Mean values, heritabilities, and genetic and phenotypic correlations among FI and growth traits are summarized in Table 1. The mean values for these traits are consistent with other reports (Mrode and Kennedy, 1993; Suzuki et al., 2005) in the same breed. For growth traits, heritability estimates for ADG and LEA were moderate, whereas the corresponding estimate for BF was high (0.72). Appetite, as measured by FI, was moderately heritable (0.49). Common environmental effects on these traits were close to zero (not shown in table). Unfavourable genetic correlations were found between ADG and BF (0.36). Genetic correlations of FI with ADG (0.84) and BF (0.67) were positive and high, which indicated that fast-growing pigs had greater daily feed requirements as did fatter pigs. However, the genetic correlation between FI and LEA (−0.42) was negative and moderate.

Estimates of partial regressions of FI on starting age, starting weight, and growth traits in different combinations are shown in Table 2. These correlation coefficients, obtained from different models, were used to estimate measures of RFI (RFI1 to RFI4). It can be found from Table 2 that delayed starting ages reduced FI, and heavier starting weights resulted in higher FI. Partial regression coefficients of FI on ADG were 1.8–2.0.

Mean values, variance components, and heritabilities for measures of RFI are summarized in Table 3. The mean values for all measures of RFI were zero as expected by definition. The standard errors of these traits ranged from 0.13 to 0.15. All four measures of RFI were moderately heritable (\( h^2 = 0.38, 0.22, 0.33, \) and 0.20 for RFI1, RFI2, RFI3, and RFI4, respectively), indicating that variation in RFI of Duroc pigs contains genetic components, which should respond to selection. However, relatively high common environmental effects were found on these traits (ranged from 0.16 to 0.23).

Genetic and phenotypic correlations of measures RFI with FI and growth traits (ADG, BF, and LEA) are presented in Table 4. Genetic correlations between ADG and measures of RFI were low and positive (ranging from 0.16 to 0.23), which indicated that genetically fast growing pigs had appetite requirements greater than needs for growth. BF was genetically strongly correlated with RFI, when RFI was not adjusted for BF (i.e., \( r_g \) with RFI1 and RFI3 were 0.77 and 0.76, respectively). All the measures of RFI favourably correlated with FI (ranging from 0.56 to 0.78) and LEA (ranging from −0.30 to −0.60). As expected, phenotypic correlations between ADG and measures of RFI were close to zero, because residuals from the population regression are uncorrelated with all variables in the regression. Likewise, RFI would be uncorrelated with BF, when it is in the model, and present results confirmed this, i.e., phenotypic correlations of BF with RFI2 and RFI4 were close to zero. However, BF was phenotypically correlated with RFI1 (0.46) and RFI3 (0.42).

Estimated average breeding values by selection generations in different traits are presented in Table 5. Genetic changes in measures of RFI were small but favourable over seven generations of the existing selection programme. Selection

### Table 3

Means, variance components, and heritability estimates for measures of residual feed intake

<table>
<thead>
<tr>
<th>Estimates</th>
<th>Measures of residual feed intake</th>
<th>(kg/day)</th>
<th>(kg/day)</th>
<th>(kg/day)</th>
<th>(kg/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RFI1</td>
<td>0.00±0.15</td>
<td>0.00±0.13</td>
<td>−0.01±0.15</td>
<td>−0.01±0.13</td>
</tr>
<tr>
<td></td>
<td>RFI2</td>
<td>0.00±0.09</td>
<td>0.00±0.04</td>
<td>0.00±0.08</td>
<td>0.00±0.03</td>
</tr>
<tr>
<td></td>
<td>RFI3</td>
<td>0.00±0.04</td>
<td>0.00±0.04</td>
<td>0.00±0.04</td>
<td>0.00±0.04</td>
</tr>
<tr>
<td></td>
<td>RFI4</td>
<td>0.01±0.01</td>
<td>0.00±0.01</td>
<td>0.01±0.01</td>
<td>0.01±0.01</td>
</tr>
<tr>
<td></td>
<td>RFI2 ±s.e.</td>
<td>0.16±0.03</td>
<td>0.23±0.02</td>
<td>0.18±0.04</td>
<td>0.23±0.03</td>
</tr>
<tr>
<td></td>
<td>RFI3 ±s.e.</td>
<td>0.38±0.05</td>
<td>0.22±0.07</td>
<td>0.33±0.04</td>
<td>0.20±0.07</td>
</tr>
</tbody>
</table>

Figures in the parentheses indicate the number of observations.

a ADG, average daily gain; BF, backfat thickness; LEA, loin eye area; FI, daily feed intake; RFI1, RFI2, RFI3, and RFI4: residual feed intakes estimated from models 1, 2, 3, and 4, respectively.

b Measures of residual feed intake.

### Table 4

Estimates of genetic \( (r_g) \) and phenotypic \( (r_p) \) correlations between measures of residual feed intake and growth traits

<table>
<thead>
<tr>
<th>Traits</th>
<th>ADG</th>
<th>BF</th>
<th>LEA</th>
<th>FI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( r_g )</td>
<td>( r_p )</td>
<td>( r_g )</td>
<td>( r_p )</td>
</tr>
<tr>
<td></td>
<td>0.22±0.05</td>
<td>0.01</td>
<td>0.77±0.04</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>0.16±0.06</td>
<td>0.01</td>
<td>0.11±0.07</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>0.23±0.05</td>
<td>0.01</td>
<td>0.76±0.05</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>0.17±0.07</td>
<td>0.01</td>
<td>0.07±0.06</td>
<td>0.00</td>
</tr>
</tbody>
</table>

a ADG, average daily gain; BF, backfat thickness; LEA, loin eye area; FI, daily feed intake; RFI1, RFI2, RFI3, and RFI4: residual feed intakes estimated from models 1, 2, 3, and 4, respectively.
responses in FI were increased as selection progressed. However, selection responses in LEA were favourable, and in BF were unfavourable.

4. Discussion

Estimated heritabilities for ADG in the present study were close to the estimate (0.43) reported by Mrode and Kennedy (1993) in Duroc, Yorkshire and Landrace breeds, and to the literature average (0.45) reported by Hutchens and Hintz (1981). However, Bereskin (1986) reported a considerably lower heritability (0.10) for ADG of group fed Duroc and Yorkshire gilts. The reasons for differences in estimates of heritability might be due to feeding method (Jungst et al., 1981). Higher values of heritability for ADG can be expected when pigs are individually fed (Robison and Berruecos, 1973). Estimated heritability for BF was slightly higher than the estimate reported by Li and Kennedy (1994). They measured BF ultrasonically at the midback and loin on both sides 5 cm from the midline. In their study, average BF was adjusted to 100 kg, and average heritability for four breeds was 0.52. Mrode and Kennedy (1993) estimated heritability for BF to be 0.59, which was slightly higher than the present estimate. However, Bryner et al. (1992), using Yorkshire records from U.S. central test stations, reported heritability estimates for ADG of 0.24, and for BF of 0.56. Ferraz and Johnson (1993), using four animal models for breeds of Landrace and Large White pigs, estimated heritability for direct animal effects of 0.23 to 0.34 for ADG, and of 0.39 to 0.50 for BF. Appetite, as measured by FI, appeared moderately heritable and was comparable to the estimate of 0.45 by Mrode and Kennedy (1993), but slightly higher than the estimate of 0.34 for boars given feed ad libitum reported by Cameron et al. (1990).

Unfavourable genetic correlations between ADG and BF were found, implying that as ADG increases so does BF. These results are supported by Johnson et al. (1999) and Mrode and Kennedy (1993). Johnson et al. (1999) estimated genetic and phenotypic correlations between ADG and BF to be 0.37 and 0.46, respectively in Large White swine. Mrode and Kennedy (1993) reported the corresponding correlations between ADG and BF to be 0.32 and 0.28, respectively in Duroc, Yorkshire, and Landrace pigs. However, Lo et al. (1992), using Duroc and Landrace pigs, reported genetic and phenotypic correlations between ADG and BF to be 0.28 and 0.21, respectively. The genetic and phenotypic correlations between ADG and FI in the present study are in agreement with the findings of Mrode and Kennedy (1993) and Johnson et al. (1999). Mrode and Kennedy (1993) estimated genetic and phenotypic correlations between ADG and FI to be 0.80 and 0.74, respectively. Corresponding correlations estimated by Johnson et al. (1999) for Large White swine were 0.82 and 0.72, respectively. The large estimated genetic and phenotypic correlations between ADG and FI indicate that faster-growing pigs had greater daily feed consumption.

Litter effects were a significant source of variation for all measures of RFI examined, and the litter variation as proportion to phenotypic variation ($c^2$) accounted for a range of 0.16 to 0.23. Johnson et al. (1999) used a similar procedure to estimate measures of RFI in Large White swine, and found the common environmental litter effects to be 0.10 to 0.17 for four different measures of RFI. Foster et al. (1983) reported corresponding estimates of 0.10 to 0.27 for RFI in Landrace, Large White, and Welsh pigs. Estimates of heritability of direct genetic effect with litter effect in the model were approximately 10% less than those obtained with only random animal effects in the model (Johnson et al., 1998).

There are few estimates of heritability of RFI for comparison, but the estimates obtained here, 0.20 to 0.38, are consistent with the previous studies. Foster et al. (1983) had a pooled estimate, across breeds, of 0.30 for RFI adjusted for ADG and BF. Haer (1992) reported a heritability of 0.45 for RFI adjusted for ADG and lean growth rate. The current estimates also fall within the 0.13–0.47 range of the literature results reported in pigs (reviewed by Nguyen et al., 2004; Mrode and Kennedy, 1993). Measures of RFI that included BF had lower estimates of heritability than those without BF included (RFI2 and RFI4 vs. RFI1 and RFI3). Variation in RFI has many causes such as variation in feed digestibility, variation in energetic efficiencies for maintenance and for protein and fat accretions, and variation in other maintenance requirements such as physical activity, body temperature regulation, maintenance of body tissues and basal metabolic rate (Haer, 1992). Wastage of feed at the trough can also contribute to variation in RFI as can errors in measurement and in prediction equations used in its estimation. Despite the numerous causes contributing to variability in RFI, the estimates of heritability suggest that selection of this aggregate measure may have the potential for genetic improvement of feed efficiency.

BF was genetically strongly correlated with RFI, when RFI was not adjusted for BF, which indicated that selection for decreased RFI would result in decreased BF. Mrode and Kennedy (1993) found higher genetic correlations for BF with measures of RFI not adjusted for BF (0.34 and 0.61 for RFI adjusted for ADG and lean growth rate, respectively). Johnson et al. (1999) also estimated strong genetic correlations for BF

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**Table 5**

Average breeding values per generation of selection in different traits

<table>
<thead>
<tr>
<th>Generations</th>
<th>Traits</th>
<th>ADG</th>
<th>FI</th>
<th>LEA</th>
<th>BF</th>
<th>RFI1</th>
<th>RFI2</th>
<th>RFI3</th>
<th>RFI4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>0.04</td>
<td>0.20</td>
<td>-0.285</td>
<td>0.033</td>
<td>0.012</td>
<td>0.005</td>
<td>0.009</td>
<td>0.004</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>0.017</td>
<td>0.046</td>
<td>-0.069</td>
<td>0.012</td>
<td>0.012</td>
<td>0.013</td>
<td>0.012</td>
<td>0.013</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>0.021</td>
<td>0.017</td>
<td>0.851</td>
<td>0.054</td>
<td>-0.026</td>
<td>0.004</td>
<td>-0.020</td>
<td>0.007</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>0.039</td>
<td>0.032</td>
<td>1.454</td>
<td>0.057</td>
<td>-0.024</td>
<td>-0.011</td>
<td>-0.025</td>
<td>-0.003</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>0.070</td>
<td>0.112</td>
<td>1.296</td>
<td>0.120</td>
<td>-0.027</td>
<td>-0.003</td>
<td>-0.018</td>
<td>0.002</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>0.092</td>
<td>0.160</td>
<td>1.695</td>
<td>0.085</td>
<td>-0.023</td>
<td>-0.006</td>
<td>-0.012</td>
<td>-0.002</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>0.108</td>
<td>0.201</td>
<td>1.648</td>
<td>0.123</td>
<td>-0.045</td>
<td>-0.011</td>
<td>-0.022</td>
<td>-0.006</td>
</tr>
</tbody>
</table>

*ADG, average daily gain; FI, daily feed intake; LEA, loin eye area; BF, backfat thickness; RFI1, RFI2, RFI3, and RFI4: residual feed intakes estimated from models 1, 2, 3, and 4, respectively.*
with measures of RFI not adjusted for BF (0.67 for RFI1 and RFI2). Similar results were reported by Nguyen et al. (2005), who noted that selection for low RFI would improve carcass leanness in Large White pigs. Negative genetic correlations were found between LEA and all measures of RFI, which are in agreement with the estimates reported by Johnson et al. (1999), who also found negative genetic correlations between LEA and four measures of RFI (ranged from −0.31 to −0.51). These results indicate that measures of RFI without BF adjustment had higher heritabilities and they were favourably strongly correlated with BF and FI than those with BF adjustment, which suggested that RFI without BF adjustment might be better to include in selection programme for improving efficiency of feed and reducing amount of backfat.

Selection responses in measures of RFI were small, but in the expected direction over seven generations of selection based on ADG, LEA, BF, and IMF. The responses in LEA were also small, probably because of small selection differentials (Suzuki et al., 2005). The relative desired gain for BF was not achieved at the seventh generation, since the relative desired gain for BF was established at −0.54 cm in the third generation. Consequently, the failure of BF improvement resulted in a decrease in meat quality over seven generations of selection. The effect of selection for improved growth rate on appetite is not clear. Some studies have shown a correlated reduction in appetite (Sather and Fredeen, 1978), and others have shown small increases in FI (Ollivier, 1986; Mrode and Kennedy, 1993). Theoretical arguments have been made that selection for ADG under ad libitum feeding would have a neutral effect on FI, at least initially, but that increases in intake might follow in later generations (Fowler et al., 1976). The genetic correlation estimates from this study suggest that selection for ADG would increase FI.

5. Conclusion

Results of this study indicate that residual feed intake was moderately heritable, and should respond to selection. Genetic correlations indicate that it should be possible to select for reduced residual feed intake without adversely affecting average daily gain. Daily feed intake and backfat would also decrease, and eye muscle area would increase. The amount of change in backfat or eye muscle area would depend on which measure of residual feed intake one uses.

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