ABSTRACT: Residual feed intake (RFI), defined as the difference in the observed and expected feed intake while accounting for growth and backfat, has gained much attention, but little is known about why pigs selected for reduced RFI are more efficient. To this end, a line of Yorkshire pigs selected for reduced RFI was developed. The objective of this study was to evaluate the 5th generation of this select line against a randomly selected control line for performance, carcass and chemical carcass composition, and overall efficiency toward the later part of the growth phase. Eighty barrows, 40 from each line, were paired by age (~132 d, \( P < 0.60 \)) and BW (74.8 ± 9.9 kg, \( P < 0.49 \)) and randomly assigned to 1 of 4 feeding treatments in 10 replicates: 1) ad libitum, 2) 75% of ad libitum, 55% of ad libitum, and BW stasis, with weekly adjustments in intake to keep BW constant for each pig. Pigs were individually penned (group housing was used for selection) and on treatment for 6 wk. Initial BW did not differ between the lines (\( P < 0.49 \)). The ad libitum select pigs consumed 10% less feed (\( P < 0.09 \)) than the ad libitum control with no significant difference in BW (\( P < 0.80 \)) and slight differences in carcass fat composition (\( P < 0.20 \)) and backfat (\( P < 0.11 \)), which resulted in significantly less carcass energy (\( P < 0.03 \)). Under restricted feeding, the select line had an increase in BW (\( P = 0.10 \)) while consuming the same ration of feed as the control line with no significant difference in chemical carcass composition and lighter visceral weights, which was significant for the 75% of ad libitum treatment (\( P < 0.01 \)). Under BW stasis feeding the select line consumed 7.6% less feed overall (\( P = 0.21 \)) and 18% less feed at the end of the 6 wk (\( P < 0.08 \)), to maintain static BW with no significant difference in chemical carcass composition compared with the control line. Overall, the select line had lighter visceral weight (\( P < 0.02 \)) and a greater dressing percentage (\( P < 0.03 \)) compared with the control line. Using regression, the select line had reduced energy retention (\( P < 0.04 \)) and feed energy utilization (\( P < 0.34 \)); however, the select line appeared to have reduced maintenance requirements (\( P < 0.13 \)). In conclusion, selection for reduced RFI decreases feed intake with no significant difference (\( P > 0.05 \)) in growth performance, reduced backfat, increased dressing percentage, and reduced maintenance requirements. All of these traits are appealing to the producer and result in increased profits in the production setting.

Key words: feed efficiency, pig, residual feed intake, selection

©2011 American Society of Animal Science. All rights reserved.

INTRODUCTION

Profitability of pork production heavily depends upon the cost of feed and the efficiency with which pigs utilize feed energy for maintenance and growth. Residual feed intake (RFI) is a unique measure of feed efficiency (FE), which accounts for growth and backfat and is calculated as observed minus expected feed intake (Koch et al., 1963; Luiting, 1990). In swine, RFI has been shown to be moderately heritable, with estimates ranging from 0.15 to 0.38 (Nguyen et al., 2005; Gilbert et al., 2007; Cai et al., 2008; Hoque et al., 2009). To investigate the genetic and biological basis of RFI, a selection experiment for reduced RFI (i.e., im-
Proved FE) in purebred Yorkshire pigs was undertaken at Iowa State University. After 4 generations, selection responses were evaluated by Cai et al. (2008) under group pen and ad libitum feeding conditions; gilt from the low RFI line consumed substantially less feed (165 g/d) but also had a slightly slower growth rate (33 g/d) and backfat (1.99 mm) relative to gilts from the randomly selected control. The difference in RFI was 96 g/d. The main biological factors that contribute to RFI have been partially quantified in mice (McDonald et al., 2009), poultry (Luiting, 1990), pigs (Barea et al., 2010; Boddicker et al., 2010), and beef cattle (Richardson and Herd, 2004) and more recently reviewed by Herd and Arthur (2009). In beef cattle, approximately 73% of the variation in RFI is accounted for by factors that may include activity, feed intake patterns, behavior, stress, digestibility, protein turnover, and tissue metabolism (Herd and Arthur, 2008). In pigs, the difference in feed intake between reduced RFI and control pigs at a young age can be partially attributed to carcass composition. Aside from these findings from Barea et al. (2010) and Boddicker et al. (2010), the importance of these processes for RFI in pigs is relatively unknown. Furthermore, Cai et al. (2010) reported divergence in feed intake and BW at 110 d and 70 kg, respectively, between a reduced RFI line and randomly selected control line. Therefore, the objective of this study was to evaluate the 5th generation of the Iowa State University reduced RFI and control lines for feed intake, growth performance, body composition, and chemical carcass composition under ad libitum and restricted feed intake toward the end of the growth curve. The latter included feeding an amount required to maintain a constant BW. We hypothesized that, compared with the control line, pigs from the reduced RFI line would have 1) decreased feed intake under ad libitum feeding but a similar rate of BW gain and carcass composition, 2) a greater rate of BW gain under restricted feeding, with similar carcass composition, and 3) require less feed to maintain constant BW.

MATERIALS AND METHODS

All animal procedures were approved by the Animal Care and Use Committee of Iowa State University.

Study Design

Using a randomized complete block design, 80 Yorkshire barrows (74.8 ± 9.9 kg) from the 5th generation of the Iowa State University RFI lines, 40 from the reduced RFI line (select line) and 40 from the randomly selected control line (control line), were paired based on age and BW, and each pair was randomly assigned to neighboring individual pens. Pigs were allowed to acclimate for 3 d on ad libitum feeding and had free access to water at all times. After the acclimation period, all pigs were offered feed ad libitum for 7 d and ad libitum feed intake was established (wk −1). Pairs were then randomly allocated to 1 of 4 feed intake treatments: 1) ad libitum (Ad), 2) 75% of feed intake of the Ad control pigs (Ad75), 3) 55% of feed intake of the Ad control pigs (Ad55), and 4) a BW stasis (WS) treatment. In the WS treatment, feed intake was individually adjusted to maintain initial BW. The experiment was conducted in 10 replicates of 8 pigs (1 pig per line × treatment combination), and the duration of the test period was 6 wk. All pigs received the same diet, which was formulated to meet or exceed nutrient requirements for this size pig (NRC, 1998) over the 6-wk test period (Table 1). Pigs on restricted feed intake treatments were provided 2 equal-portioned meals at 0700 and 1700 h each day. Feed allotments for the Ad75 and Ad55 treatments were based upon the ADFI of the control line Ad-fed pigs in the previous week within the replicate of each pig. The initial feeding amount used for the WS treatment was based on estimated energy requirements for maintenance based on 106·BW0.75, where BW was the BW of the pig on d −1 before treatment. The energy required per day to support maintenance energy requirements of each pig was then calculated according to NRC (1998) guidelines for swine. Pigs on the WS treatment were weighed twice per week, and their feed intake was adjusted based on BW gain or loss relative to their starting BW. All pigs were genotyped for the melanocortin-4 receptor gene following Kim et al. (2000) because it is associated with growth, feed intake, and backfat (BF).

Performance Traits

All pigs were weighed at the beginning and end of the pretreatment week (d −7 and −1, of wk −1). Week −1 ADFI was based on feed offered minus feed refused for each pig during wk −1 and used to determine d-0 feed allotted for the pigs on the Ad75 and Ad55 treatments. Pretreatment ADG was based on BW at d −7 and −1. On d −1, pigs were fasted overnight, representing the beginning of the 6-wk test period.

All pigs were weighed individually at the start of the treatment period (d 0), and pigs on the Ad, Ad75, and Ad55 treatments were weighed weekly thereafter until the conclusion of the treatment period (d 42). Pigs on the WS treatment were weighed on d 3 and 7 of each week to adjust feed intake to maintain static BW. Average daily feed intake for the Ad pigs was calculated as feed offered minus feed refused every 7 d. Average daily gain was calculated for each week of the treatment period. Feed efficiency was calculated as kilograms of BW gain divided by kilograms of feed consumed and multiplied by 100. Ultrasonic measurements of 10th-rib BF and loin eye area (LEA) were collected on d 0, 14, 28, and 42 of the test period. Two 10th rib images were collected by a National Swine Improvement Federation certified technician using an Aloka 500V SSD ultrasound machine fitted with a 3.5 MHz, 12.5 cm, linear-
array transducer (Corometrics Medical Systems Inc., Wallingford, CT).

Upon completion of the performance study, pigs from 8 replicates were fasted overnight, weighed, anesthetized via an intravenous injection (0.04 mL/kg of BW) of a 1:1:1 mixture of Telazol-HCl (Fort Dodge Animal Health, Fort Dodge, IA), Xylazine-HCl (Lloyd Laboratories, Shenandoah, IA), and ketamine-HCl (Fort Dodge Animal Health). After a surgical plane of anesthesia was reached, pigs were killed by exsanguination. Immediately thereafter, visceral weights, including stomach and intestinal tract (both with digesta), kidneys, lungs, and heart were obtained, and empty BW recorded. The head was removed, and the carcass weight was recorded. The carcass was then split medially, and the right half was frozen at −20°C for later chemical analyses. Dressing percentage was calculated as the empty BW, including the head, divided by BW at slaughter.

**Carcass Composition**

For chemical analysis, each frozen one-half carcass was sectioned and was twice passed through a mechanical grinder (Buffalo No. 66BX Enterprise, St. Louis, MO) and twice through a Hobart 52 grinder with a 5-mm die. The ground carcass was thoroughly mixed and a homogenized sample was collected and stored at −20°C for laboratory analysis. For analyses, samples were thawed and aliquots were freeze-dried and re-ground for determination of moisture, protein, lipid, and ash. Briefly, water content was determined in triplicate by drying 7.5-g subsamples to a constant weight in a Fisher Scientific Isotemp oven (Pittsburgh, PA). Moisture-free subsamples were placed in a muffle furnace for determination of ash. Nitrogen was determined in quadruplicate using the Kjeldahl method in a Fisher Scientific digestion and distillation system. Crude protein was calculated by multiplying the N content by 6.25. Lipid content was determined in duplicate samples of approximately 3.5 g by ether extract using a Goldfisch fat extraction system (AOAC, 1980).

**Carcass Energy and Consumed Energy**

The GE content of the diet and carcasses was determined in triplicate by adiabatic bomb calorimetry and also calculated based on proximate analysis values for protein and lipid using 5.6 and 9.4 kcal per gram, respectively (Ewan, 2001). To calculate carcass energy using the bomb calorimetry values, carcass DM was calculated in kilograms and multiplied by the energy content per kilogram of carcass. To acquire carcass energy based on protein and lipid (Ewan, 2001), kilogram of protein and fat were calculated from the carcass composition data and multiplied by their respective energy values.

**Statistical Analysis**

All data were analyzed using the MIXED procedure (SAS Inst. Inc., Cary, NC). All models included replicate, line, and melanocortin-4 receptor genotype as fixed factors. Random effects were included for litters and replicate × treatment interaction terms. The litter random effects were included to account for covariances among litter mates, whereas the interaction random effects account for pairing of control and select animals because there was 1 control-select pair for each combination of replicate and treatment. However, when traits were analyzed within each treatment, the litter and interaction random effects were removed because there were no litter mates within a treatment and the replicate effects alone already account for control-select pairs when only a single treatment is considered.

Pretreatment traits of BW at d −7 and −1, ADFI for wk −1, and BF and LEA on d 0 were analyzed as discussed previously; however, the replicate × treatment interaction terms were not included as random effects because of the absence of treatment in the pretreatment trait model. Starting BW on d −7 was included as an additional covariate for d −1 BW and ADFI for wk −1. Day 0 BW was included as an additional covariate for d 0 BF and LEA.

Because of the treatment design, the performance traits of BW, ADFI, BF, and LEA while pigs were on treatment were analyzed as repeated measures separately for each treatment, with d-0 BW as a covariate and additional fixed factors of week and the interaction of line and week. For BF and LEA, in addition to d-0
BW, d-0 BF and d-0 LEA, respectively, were used as covariates. A first-order autoregressive, AR(1), covariance structure was used to model correlations among pig-specific residuals across time. Overall ADG and FE were analyzed with d-0 BW as a covariate and additional fixed factors of treatment and the interaction of line and treatment. However, because the WS treatment was designed to maintain static BW of the pigs, the WS treatment was not included in the analysis of ADG and FE.

The carcass traits of carcass weight, viscera weight, dressing percentage, and chemical carcass composition were analyzed with additional fixed effects of treatment and the interaction of line and treatment. However, because the WS treatment was designed to maintain static BW of the pigs, the WS treatment was not included in the analysis of ADG and FE.

The carcass traits of carcass weight, viscera weight, dressing percentage, and chemical carcass composition were analyzed with additional fixed effects of treatment and the interaction of line and treatment, d-0 BW as a covariate, and random effects as previously stated. Litter was removed as a random factor for dressing percentage and protein percentage because its variance component estimate was not positive for those variables. Slaughter BW (results not shown) was included as an additional covariate for carcass and viscera weight. Because of the large differences in slaughter BW between treatments, this covariate was fitted as the BW minus the average slaughter BW of each pig for that treatment, such that least squares means were computed for the average BW for each treatment.

For carcass energy, d-0 BW, d-0 BF, and d-0 LEA were included as additional covariates to adjust for differences in carcass energy at the start of the test, such that differences estimated are estimates of differences in retained energy. This analysis assumes that BW, BF, and LEA are adequate estimates of carcass energy. This assumption was validated by analyzing carcass energy by the same model but with BW, ultrasound BF, and LEA at slaughter (d 42) as covariates. This model had an R² value of 0.92. Gross energy consumed over the 6-wk test period was analyzed separately for each treatment with d-0 BW as a covariate.

Maintenance requirements and efficiency of energy retention were estimated by regressing carcass energy on gross energy consumed, following the procedures outlined in Ewan (2001). The carcass energy used in this analysis was adjusted for carcass energy at the start of treatment by adjusting for the effects of d 0 BW, BF, and LEA using regression coefficients obtained from the analysis of carcass energy described previously. Adjusted carcass energy was used as a response variable in a general linear model with fixed effects of line, treatment group, and the interactions of line and treatment group, and covariates of feed energy consumed and its interactions with line and treatment group. Because the linear relationship between energy retained and energy consumed is expected to be consistent for all treatments except for the WS, the Ad, Ad75, and Ad55 treatments were combined into treatment group 1 for this analysis, and the WS treatment made up treatment group 2. The interaction of line and treatment group allows separate estimates of maintenance requirements and efficiency for the 2 treatment groups. To estimate line specific maintenance requirements and efficiency, the interaction of feed energy consumed with line was included in the model. Finally, to test for separate slopes between the 2 treatment groups, the interaction of feed energy consumed and treatment group was included in the model. The 3-way interaction of feed energy consumed with line and treatment group was included in initial analyses but removed because it was not significant (P > 0.05).

### RESULTS

#### Performance and Ultrasound

Results for BW and feed intake data for wk −1, along with d 0 BF and LEA, are presented in Table 2. Select line pigs consumed 6.7% less feed (P < 0.06), with no significant difference (P > 0.05) in start or end BW or ADG compared with the control line. At d 0, select line pigs had significantly less BF (P < 0.02) but similar (P < 0.41) LEA. Although d 0 BW did not differ between lines (P = 0.26), subsequent results were adjusted by including d 0 BW as a covariate in the models. At d 0, there were no significant differences (P < 0.75) in BW, BF, or LEA between the groups of pigs that were randomly assigned to each treatment (results not shown).

Table 2. Effects of selection for residual feed intake on BW and feed intake of pigs from the select or control line

<table>
<thead>
<tr>
<th>Item</th>
<th>Select line</th>
<th>Control line</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>d -7 to -1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Start BW, kg</td>
<td>68.4 ± 1.5</td>
<td>68.9 ± 1.6</td>
<td>0.81</td>
</tr>
<tr>
<td>End BW,1 kg</td>
<td>76.2 ± 0.28</td>
<td>75.9 ± 0.29</td>
<td>0.53</td>
</tr>
<tr>
<td>Feed intake, kg/d</td>
<td>2.36 ± 0.06</td>
<td>2.53 ± 0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>Daily BW gain, g/d</td>
<td>890.2 ± 38.3</td>
<td>863.3 ± 38.9</td>
<td>0.60</td>
</tr>
<tr>
<td>BW,2 kg</td>
<td>73.7 ± 1.6</td>
<td>75.4 ± 1.7</td>
<td>0.26</td>
</tr>
<tr>
<td>Backfat, mm</td>
<td>15.6 ± 0.50</td>
<td>17.4 ± 0.54</td>
<td>0.02</td>
</tr>
<tr>
<td>Loin eye area, cm²</td>
<td>32.4 ± 0.65</td>
<td>31.8 ± 0.69</td>
<td>0.41</td>
</tr>
</tbody>
</table>

1Start and end of the week before dietary treatment, along with ultrasonic backfat and loin eye area at the start of treatment. Data represent least squares means ± SEM, n = 40 pigs per line.

2Body weights differ due to an overnight fast from d −1 to 0.

43
Least squares means for the repeated measures analysis of BW and ADFI over the 6-wk test period are in Figure 1. These data were analyzed separately for each treatment and adjusted for d-0 BW within treatment. As expected, BW increased incrementally as feed intake increased from treatment WS to Ad. The Ad select pigs consumed less feed than the Ad control (AdC) pigs (P < 0.09, Table 3) over the entire 6-wk period. There was no significant difference (P > 0.05) in BW between the Ad select (AdS) and AdC for any 1 wk. Control Ad75 (C75) and select Ad75 (S75), and control Ad55 (C55) and select Ad55 (S55) pigs consumed the same amount of feed by study design. For Ad75 the 2 lines had very similar BW throughout the treatment period. For the Ad55 treatment, however, the select line tended to have greater BW than the control line, and this difference increased as the study progressed. At the end of treatment, the S55 pigs weighed 2.5% more than the C55 pigs (P = 0.10).

Despite attempts to keep the WS pigs at a constant BW for 6 wk, the main effect of week was highly significant (P < 0.01), indicating a change in BW from wk 0 to 6. The select WS (SWS) pigs weighed 3.5% more (P = 0.08) at the end of treatment than the control WS (CWS) pigs (Figure 1), although their feed intake across the 6 wk tended to be less (7.6%, P = 0.21, Table 3). The difference in feed intake between the 2 lines was significant in wk 5 (14%, P < 0.04) and 6 (18%, P < 0.02; Figure 1B). The amount of feed required to maintain BW for the CWS pigs at wk 6 did not differ from the requirement calculated at wk 1 based on NRC requirements (P = 0.82); however, for the SWS pigs, there was a significant decrease in feed intake from wk 1 to 6 (0.82 vs. 0.67 kg, respectively, P < 0.01).

The development of BF and LEA, as measured by ultrasound, over the 6-wk period is shown in Figure 2. These repeated measures were analyzed separately for each treatment and adjusted for d-0 BW, along with d-0 BF and d-0 LEA for BF and LEA, respectively. On average, BF increased with the amount of feed provided by treatment (Figure 2A), although differences were not always clearly apparent because C75 pigs had similar BF as the Ad pigs and the S75 pigs had similar BF as the Ad55 pigs. For the Ad treatment, the AdS pigs had less BF than the AdC pigs across the treatment period, although this was nonsignificant (P = 0.21) within any 1 wk. There was no significant difference in LEA development between the AdS and AdC, except that on d 28 AdS tended (P < 0.08) to have a smaller LEA than the AdC.

Within the Ad75 treatment, the S75 pigs had less BF at d 14, 28, and 42 (P < 0.01) and no significant difference in LEA overall (P = 0.47), nor any significant differences in LEA within any particular week (Figure 2). For the Ad55 treatment, the main effect of week was not significant (P = 0.30) for BF but was significant (P < 0.01) for LEA. For the first 28 d of treatment, the 2 lines had very similar BF, but at d 42 the S55 had 4% more BF than the C55. Although BF did not drastically change, there was a steady divergence in LEA between the 2 lines under the Ad55 treatment, with the S55 pigs having 3.5% larger LEA at d 42 (P = 0.23).

For the WS treatment, the main effect of week was not significant for BF (P = 0.14) or LEA (P = 0.65; Figure 2). The main effect of line was also not significant for either trait (P = 0.64 and P = 0.33, respectively), although the SWS had an overall 4% larger

---

**Figure 1.** Effects of feed restriction on BW (A) and ADFI (B) of control and reduced residual feed intake finisher barrows. Panel A represents BW every 7 d (least squares means ± SEM); n = 10 barrows per line per treatment. Panel B represents weekly ADFI (least squares means ± SEM); n = 10 barrows per line per treatment. *P < 0.10, **P < 0.05. Ad = ad libitum; Ad75 = 75% of feed intake of the Ad control pigs; Ad55 = 55% of feed intake of the Ad control pigs; and WS = BW stasis treatment.
The SWS pigs had a steady loss of BF during treatment, whereas the CWS pigs initially had a sharp decrease in BF and then a slight increase in BF from wk 4 to 6 (Figure 2A). Although both lines under the WS treatment had a loss in BF, there was no change in LEA over the test period in the CWS or SWS pigs \((P > 0.05)\).

Average daily gain was not different \((P > 0.05)\) between lines within each treatment (Table 3). As expected, the main effect of treatment was significant \((P < 0.01)\), where the Ad pigs had the greatest ADG and the AdS5 pigs had the least. Furthermore, there was no difference \((P > 0.05)\) for the main effect of line or the interaction of line and treatment. For FE, the main effect of line and the interaction of line and treatment were not different \((P > 0.05)\), whereas the main effect of treatment was different \((P < 0.05)\). Overall, the majority of the line \(\times\) treatment interactions were not different. However, the C55 pigs had reduced \((P < 0.03)\) FE compared with the C75, S75, and AdS pigs. As previously stated, the WS treatment was excluded from the analysis of ADG and FE due to treatment design.

The main effects of line and treatment were significant \((P < 0.01)\) for d-42 BF, when analyzed simultaneously across treatments, with the select line having less BF than the control line (Table 3). For LEA, the main effect of treatment was significant \((P < 0.01)\), whereas the main effect of line and the interaction of line and treatment were not different \((P > 0.05)\) in the CWS and SWS pigs. Average daily gain was not different \((P > 0.05)\) between lines within each treatment (Table 3). As expected, the main effect of treatment was significant \((P < 0.01)\), where the Ad pigs had the greatest ADG and the AdS5 pigs had the least. Furthermore, there was no difference \((P > 0.05)\) for the main effect of line or the interaction of line and treatment. For FE, the main effect of line and the interaction of line and treatment were not different \((P > 0.05)\), whereas the main effect of treatment was different \((P < 0.05)\). Overall, the majority of the line \(\times\) treatment interactions were not different. However, the C55 pigs had reduced \((P < 0.03)\) FE compared with the C75, S75, and AdS pigs. As previously stated, the WS treatment was excluded from the analysis of ADG and FE due to treatment design.

The main effects of line and treatment were significant \((P < 0.01)\) for d-42 BF, when analyzed simultaneously across treatments, with the select line having less BF than the control line (Table 3). For LEA, the main effect of treatment was significant \((P < 0.01)\), whereas the main effect of line and the interaction of line and treatment were not \((P > 0.12\) and 0.84, respectively).

Melanocortin-4 receptor was not different in the majority of the analyses but tended to be different for d \(-7 (P = 0.06)\) and d \(-1 (P = 0.08),\) and was different \((P = 0.04)\) for wk \(-1 (P = 0.04)\) ADFI. For d \(-7\) and \(-1 (P = 0.08),\) animals homozygous for the 1 allele had the lightest BW and the heterozygous animals had the heaviest BW. For wk \(-1 (P = 0.04)\) ADFI, heterozygotes consumed the most feed and pigs homozygous at the 2 allele consumed the least.

### Body and Carcass Composition

The main effect of treatment was significant \((P < 0.01)\) for all carcass traits, with the exception of dressing percentage \((P < 0.011; Table 4).\) Carcass weight within any given treatment, adjusted for d 0 BW and slaughter weight, was not different \((P = 0.26)\) between lines. However, when averaged over all treatments, there was a difference of 0.57 kg of carcass weight in favor of the select line compared with the control line \((P < 0.05).\) The select line also had a 0.62\% greater dressing percentage than the control \((P < 0.03),\) but there was no significant difference in carcass weight within treatments. For each treatment, the select line had the lightest visceral mass, although this was only significant \((P < 0.02)\) for Ad75. Averaged over treatments, the select line had 0.36 kg less visceral mass \((P < 0.05).\) The effects of treatment and line on chemical carcass composition are also shown in Table 4. Percentages

### Table 3. Least squares means of line and treatment on performance of pigs selected for decreased residual feed intake and a randomly selected control line

<table>
<thead>
<tr>
<th>Item</th>
<th>Select</th>
<th>Control</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADFI, kg/d</td>
<td>2.2 ± 0.03</td>
<td>2.2 ± 0.04</td>
<td>0.77 ± 0.04</td>
</tr>
<tr>
<td>ADG, g/d</td>
<td>703 ± 31b</td>
<td>704 ± 31b</td>
<td>455 ± 42b</td>
</tr>
<tr>
<td>Feed efficiency, %</td>
<td>28.2 ± 1</td>
<td>28.0 ± 1b</td>
<td>26.5 ± 1ab</td>
</tr>
<tr>
<td>d 42 BF, mm</td>
<td>22.6 ± 0.61</td>
<td>21.9 ± 0.61</td>
<td>31.3 ± 0.61</td>
</tr>
<tr>
<td>d 42 LEA, cm2</td>
<td>14.7 ± 0.81</td>
<td>14.7 ± 0.81</td>
<td>37.6 ± 0.81</td>
</tr>
</tbody>
</table>

Values are least squares means based on 10 pigs per line per treatment.

* Different letters within a row represent significant differences at \(P < 0.05.\)
* Analysis included d-0 BW.
* Analysis included d-0 ultrasonic backfat (BF).
* Analysis included d-0 ultrasonic loin eye area (LEA).
* Differences between control minus select.

*Main effect of line.
*Main effect of treatment.
*Analysis included d-0 BW.
of the main chemical components of carcass protein, lipid, ash, and water added up to 100.1 ± 0.15% of the subsample weight, which confirms the accuracy of the procedures used. The main effect of treatment was significant for water percentage \( (P < 0.01) \), protein percentage \( (P < 0.03) \), and fat percentage \( (P < 0.01) \), with no significant difference between treatments for ash percentage \( (P < 0.13) \). In general, as feed restriction increased, the water and protein percentage increased, and the fat percentage decreased. Averaged over treatments, there was no difference \( (P = 0.18) \) between the lines for any of the chemical carcass composition traits. However, there was a trend for the select line to have more water, slightly more protein, and less fat than the control line. For water, fat, and ash percentages, there were no significant differences between any of the line \( \times \) treatment combinations. However, when litter was removed from the model with fat percentage as the response variable, there was a significant \( (P < 0.01) \) difference between the AdS and AdC pigs, which is consistent with the reduced BF found in the select line. Protein percentage in the carcass did not differ between the 2 lines within a given feeding treatment; however, CWS and SWS had significantly more protein percentage than the AdC.

**Carcass Energy**

The effects of treatment and line on carcass energy when using the values from bomb calorimetry (BCE) are shown in Table 4. The main effect of treatment was significant \( (P < 0.01) \), and as expected, greater feed restriction resulted in less carcass energy. The main effect of line was also significant for BCE \( (P < 0.04) \), indicating that the select line had less carcass energy relative to the control; averaged over the treatments, the select line had 4% less carcass energy. For the analysis of BCE, there was a significant effect of line on carcass energy for the Ad \( (P < 0.03) \) and 75Ad \( (P < 0.02) \) treatments, with the select line having less carcass energy.

Gross energy consumed was analyzed separately for each treatment; therefore, the main effects of treatment and the interaction of line and treatment were not estimated. No differences \( (P > 0.05) \) were found between the select and control lines for the Ad and WS treatments. By study design, the Ad75 and Ad55 treatments were to consume the same amount of energy. However, one C75 pig had a reduction in feed intake due to health reasons, causing the control line to consume slightly less feed. No reductions in growth or other performance measurements were observed on that pig; therefore, the pig was not removed from the analysis.

A scatter plot of adjusted carcass energy vs. energy consumed, including separate regression lines for each line and group, is shown in Figure 3. As expected, carcass energy increased with increased energy intake \( (R^2 = 0.94) \). The difference in the intercepts between the select and control lines is an estimate of the difference in maintenance requirements between the 2 lines. Although the difference \( (16.5 ± 10.8 \text{ Mcal}) \) between the intercepts for the select and control lines was not significant \( (P < 0.13) \), the intercept of the select line was larger than that of the control. This suggests that the select line had a reduced maintenance requirement.

![Figure 2](image-url)

Figure 2. Effects of feed restriction on backfat (A) and loin eye area (B) of control and decreased residual feed intake finisher barrows. Panel A represents backfat every 2 wk (least squares means ± SEM); \( n = 10 \) barrows per line per treatment. Panel B represents loin eye area every 2 wk (least squares means ± SEM); \( n = 10 \) barrows per line per treatment. \( *P < 0.10, ***P < 0.001 \). Ad = ad libitum; Ad75 = 75% of feed intake of the Ad control pigs; Ad55 = 55% of feed intake of the Ad control pigs; and WS = BW stasis treatment.
<table>
<thead>
<tr>
<th>Item</th>
<th>Ad libitum</th>
<th>75% of ad libitum</th>
<th>55% of ad libitum</th>
<th>BW stasis</th>
<th>Line × Trt&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Line&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Trt&lt;sup&gt;4&lt;/sup&gt;</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcass weight&lt;sup&gt;6,7&lt;/sup&gt; kg</td>
<td>98.0 ± 0.41&lt;sup&gt;d&lt;/sup&gt;</td>
<td>90.3 ± 0.41&lt;sup&gt;c&lt;/sup&gt;</td>
<td>82.7 ± 0.43&lt;sup&gt;b&lt;/sup&gt;</td>
<td>66.3 ± 0.41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>−0.57 ± 0.29</td>
<td>0.07</td>
<td>0.01</td>
<td>0.99</td>
</tr>
<tr>
<td>Dressing %&lt;sup&gt;5,3&lt;/sup&gt;</td>
<td>85.3 ± 0.39&lt;sup&gt;b&lt;/sup&gt;</td>
<td>84.4 ± 0.39&lt;sup&gt;b&lt;/sup&gt;</td>
<td>84.8 ± 0.42&lt;sup&gt;b&lt;/sup&gt;</td>
<td>85.1 ± 0.41&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.62 ± 0.62</td>
<td>0.03</td>
<td>0.11</td>
<td>0.99</td>
</tr>
<tr>
<td>Viscera, kg&lt;sup&gt;7,10&lt;/sup&gt;</td>
<td>13.8 ± 0.32</td>
<td>13.8 ± 0.32</td>
<td>12.4 ± 0.31&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.9 ± 0.30&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.36 ± 0.17</td>
<td>0.05</td>
<td>0.01</td>
<td>0.46</td>
</tr>
<tr>
<td>Chemical composition, % of carcass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water&lt;sup&gt;9&lt;/sup&gt;</td>
<td>55.3 ± 1.1</td>
<td>54.6 ± 0.98</td>
<td>57.4 ± 1.1</td>
<td>60.7 ± 1.0</td>
<td>−2.18 ± 0.64</td>
<td>0.18</td>
<td>0.01</td>
<td>0.56</td>
</tr>
<tr>
<td>Protein&lt;sup&gt;9&lt;/sup&gt;</td>
<td>17.6 ± 0.57&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17.5 ± 0.52&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18.7 ± 0.58&lt;sup&gt;b&lt;/sup&gt;</td>
<td>18.8 ± 0.54&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.20 ± 0.38</td>
<td>0.60</td>
<td>0.03</td>
<td>0.40</td>
</tr>
<tr>
<td>Fat&lt;sup&gt;9&lt;/sup&gt;</td>
<td>24.1 ± 1.4</td>
<td>25.6 ± 1.3</td>
<td>21.6 ± 1.5</td>
<td>16.8 ± 1.4</td>
<td>2.72 ± 0.95</td>
<td>0.21</td>
<td>0.01</td>
<td>0.53</td>
</tr>
<tr>
<td>Ash&lt;sup&gt;9&lt;/sup&gt;</td>
<td>2.9 ± 0.13</td>
<td>2.9 ± 0.12</td>
<td>2.9 ± 0.13</td>
<td>3.1 ± 0.13</td>
<td>−0.15 ± 0.10</td>
<td>0.37</td>
<td>0.13</td>
<td>0.95</td>
</tr>
<tr>
<td>Carcass energy, Mcal/pig</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE&lt;sup&gt;11&lt;/sup&gt;</td>
<td>302.8 ± 7.0&lt;sup&gt;f&lt;/sup&gt;</td>
<td>263.0 ± 6.7&lt;sup&gt;c&lt;/sup&gt;</td>
<td>232.6 ± 6.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>163.3 ± 6.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.50 ± 4.2</td>
<td>0.04</td>
<td>0.01</td>
<td>0.13</td>
</tr>
<tr>
<td>GEC&lt;sup&gt;12&lt;/sup&gt;</td>
<td>464.3 ± 18.4</td>
<td>360.3 ± 3.3</td>
<td>264.4 ± 0.0</td>
<td>141.1 ± 1.9</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

<sup>a</sup>Different letters within a row represent significant differences at P < 0.05.
<sup>1</sup>Values are least squares means based on 8 pigs per line per treatment.
<sup>2</sup>Difference of control minus select.
<sup>3</sup>Main effect of line.
<sup>4</sup>Main effect of treatment.
<sup>5</sup>Interaction of line by treatment.
<sup>6</sup>Carcass equals empty BW, including head and hair.
<sup>7</sup>Analysis included d-0 BW and adjusted slaughter weight (average BW at slaughter within each treatment minus the BW at slaughter of the individual pig) as covariates.
<sup>8</sup>Dressing percentage is carcass weight as a percentage of slaughter weight.
<sup>9</sup>Analysis included d-0 BW as a covariate.
<sup>10</sup>Viscera includes entire intestinal tract with contents, kidney, heart, and lungs.
<sup>11</sup>CE = carcass energy determined from adiabatic bomb calorimetry.
<sup>12</sup>GEC = GE consumed over the 6-wk test period (analyzed per treatment).
Additionally, the difference in the slopes between the select and control lines is an estimate of the efficiency with which feed energy consumed above maintenance is retained (i.e., a steeper slope corresponds to greater energy retention). The 3-way interaction between feed energy consumed, line, and treatment group was not significant \((P > 0.88)\) and was removed from the model; therefore, the difference of 0.047 in the slope between the 2 lines is the same across the 2 treatment groups. Although not significant \((P < 0.34)\), the control line had a steeper slope. Within a line, there was a significant difference \((P < 0.05)\) in the slopes between the 2 treatment groups \((0.426)\), with the WS group having a steeper slope.

**DISCUSSION**

Consistent with results published previously (Cai et al., 2008; Boddicker et al., 2010), the AdS pigs consumed less feed for a similar rate of BW gain compared with the AdC pigs, which resulted in a slight increase in FE, although not significant. Collectively, these findings confirm our hypothesis that, under ad libitum feeding, pigs selected for reduced RFI consume less feed for a given rate of BW gain. Additionally, the fact that the S55 pigs had a slightly greater BW gain on the same amount of feed is consistent with our hypothesis that under identically restricted feeding, pigs selected for reduced RFI have a greater rate of BW gain compared with the control pigs. However, the fact that the S75 pigs did not have greater BW gain did not support this hypothesis and could be the result of sample size and individual housing rather than group housing. Similar results were found in a study that had identical treatments and pigs of a younger age and BW (Boddicker et al., 2010). Furthermore, for the WS treatment, the NRC-based calculation used to determine the initial maintenance energy need was a reasonably accurate estimation for the control line because there was essentially no need to change the feed intake from d 0 to 42. However, the initial NRC requirements appeared to be overestimated for select line because feed intake had to be reduced by nearly 20% from d 0 to 42. Interestingly, despite the decrease in feed provided, the select pigs on the WS treatment continued to increase in BW. This may indicate that the select line has less maintenance requirements than the control line, which will be discussed later.

Genetic correlations between RFI and BF are generally found to be positive in pigs, ranging from 0.07 to 0.77 (Johnson et al., 1999; Gilbert et al., 2007; Hoque et al., 2009). Although Cai et al. (2008) found a slightly negative genetic correlation between RFI and BF \((-0.14)\) in the lines used in this study, they did find that the select line had less BF than the control line, which would be consistent with a positive genetic cor-

![Figure 3. Carcass energy, adjusted for initial carcass energy, against total feed energy consumed over the 6-wk test period. Ad = ad libitum; Ad75 = 75% of feed intake of the Ad control pigs; Ad55 = 55% of feed intake of the Ad control pigs; and WS = BW stasis treatment.](image-url)
relation. Genetic correlations between RFI and LEA in pigs have generally been found to be negative, ranging from −0.18 to −0.60 (Johnson et al., 1999; Cai et al., 2008; Hoque et al., 2009), and Cai et al. (2008) also reported that the select line had greater LEA than the control. In this study, the select line had less BF and more LEA in almost all treatments, although not always significant. This is consistent with the line differences observed by Cai et al. (2008) under ad libitum feeding and group housing. These results indicate that the select line may have a greater lean deposition rate. Boddicker et al. (2010) found that young pigs under WS feeding had more BF and increased LEA. For the WS treatment in the current study, the select pigs had a similar amount of BF, an increased LEA, and decreased feed consumption compared with the control pigs, which is consistent to previously reported results, with the exception of feed intake where there was no significant difference (Boddicker et al., 2010). This indicates that the select line is partitioning less of the consumed energy for maintenance requirements than the control line. These results, however, disagree with the findings from Cleveland et al. (1983). These authors reported that leaner pigs partition more of their ME for maintenance relative to fat pigs. In the current study, the select line was leaner than the control, yet required less energy to maintain static BW. The results indicate that the select line and selection for reduced RFI per se may alter the relationship between lean and maintenance generally reported for animals selected for increased lean, FE, or both.

Carcass weight tended to be heavier for the select line, which corresponds to a difference in dressing percentage, with the select line having a 0.62% greater dressing percentage. Part of the explanation of the increase in dressing percentage is that the select line had an average of 0.36 kg less visceral mass. This decreased visceral mass may also be part of the reason for the increased efficiency of the select line because visceral organs have increased maintenance requirements. There was a treatment effect on visceral mass, which was expected based on the differences between the treatments in the amount of feed provided. However, there was no difference in visceral mass between the Ad75 and Ad treatments. Furthermore, the C75 pigs had the largest visceral mass overall. Although not significant, the select line had lighter visceral weights than the control within each treatment. Similar results were found by Wiseman et al. (2007) who found that pigs offered feed ad libitum had greater feed intake and larger intestinal tracts and liver weights. Although we did not separate the intestinal tract from the rest of the viscera, our findings suggest that pigs that consume more feed tend to have larger visceral mass. Our data also suggest that pigs selected for decreased RFI have smaller visceral mass, which was validated by including ADFI as an additional covariate. The select line still had lighter visceral mass compared with the control.

As the extent of feed restriction increased, water content and protein content of the carcass increased and fat content decreased, indicating an increase in leanness. These same trends were also seen within all treatments between the 2 lines; overall, there was a trend for the select line to have less carcass fat content, which is consistent with decreased BF in the select line, and slightly increased carcass protein content and increased carcass water content, which is consistent with the findings from Boddicker et al. (2010), where pigs were at the beginning of their growth phase, rather than the end. This implies that selecting for decreased RFI increases carcass leaness.

In beef cattle, steer progeny of parents with decreased or greater RFI exhibited similar differences in carcass characteristics as in the present study. Progeny from parents with reduced RFI had less BF and more protein than progeny from parents with greater RFI (Richardson et al., 2001). These differences in steer progeny chemical carcass composition, however, accounted for only 5% of the difference in RFI (Richardson et al., 2001). In young pigs, Boddicker et al. (2010) estimated that, under ad libitum feeding, the difference in carcass composition between a decreased RFI and control line may explain 87% of the difference in feed intake. To evaluate the extent to which differences in feed intake could be explained by differences in carcass composition in our study, NE consumed was estimated to be 56% of GE consumed (Oresanya et al., 2008), using the least squares means of Table 3. Then, line differences in net energy consumed were compared with estimated line differences in carcass energy retained, using LSM of Table 3. For the Ad treatment, the line difference in net energy consumed was (487.1 − 464.3) × 0.56 = 12.8 Mcal, whereas the line difference in retained energy was 322.0 − 302.8 = 19.2. Similar results (i.e., that the difference in retained carcass energy was greater than the estimated differences in net energy consumed) were observed for the other 3 treatments. Assuming that the assumptions that underlie these calculations are correct, this suggests that the difference in feed intake between the 2 lines may be partially explained by the differences in carcass composition. The difference in carcass composition was primarily caused by differences in fat content between the 2 lines. The AdC pigs consumed more energy and had greater carcass fat. The C75 pigs appear to be more efficient at retaining the energy consumed by storing it as fat. The S55 pigs had slightly greater carcass energy, but again, this may be due to the greater increase in BW, and as seen from chemical carcass composition, the C55 pigs had greater chemical carcass fat. If there was no significant difference in final BW, the control line may have had greater carcass energy.

Maintenance energy requirements are believed to be associated with RFI (Barea et al., 2010). Selection for decreased RFI resulted in reduced maintenance requirements in beef cattle (Herd and Bishop, 2000). Based on
the regression analysis, the select line appears to have less maintenance requirements than the control line. The select line had a greater intercept. Decreased maintenance requirements of the select line are also indicated by the select line requiring substantially less feed to maintain constant BW under the WS treatment and by the select line having smaller viscera mass. However, as previously discussed, most, if not all, of the differences in feed intake between the 2 lines were accounted for by the difference in carcass energy between the select and control lines. In addition, the slopes of the regression lines, which are estimates of the efficiency of retaining the energy consumed, suggest that the control line, by having a steeper slope, may in fact be more efficient in converting feed energy above maintenance into retained energy. However, it appears that the control line is retaining the extra energy consumed as fat rather than lean, which is not necessarily desirable from a production standpoint. This is further supported by findings from Boddicker et al. (2010) who found no significant differences in the slopes between reduced RFI and control pigs at a young age. This supports the current findings because the variation in BF increases with an increase in BW, explaining the steeper slope of the control line because they have more BF than the select. Further work is needed to investigate the somewhat contradictory results that were obtained in this study on the importance of maintenance requirements, carcass composition, and energy retention for the difference between the select and control lines. The results obtained herein must be viewed with caution because the sample size was small. Nevertheless, the results do show that selection for decreased RFI in Yorkshire pigs reduced feed intake by approximately 9% when feed was offered ad libitum at no expense to carcass yield or growth rates and a greater lean percentage, which increases profitability to the producer. Under restricted feeding, the select line had slightly heavier carcass weights than the control line, indicating that the reduced RFI line is more efficient in partitioning, not retaining, the energy consumed. Furthermore, carcass composition and maintenance energy requirements are the main biological factors that are affected by selection for RFI in pigs. Together, these data are supported by the findings of Barea et al. (2010) in swine selected based on RFI and Eggert and Nielsen (2006) in rodents selected on heat production. Both these studies found that animals with greater heat production had greater physical activity and basal metabolic rates. This difference in heat production and basal metabolic rates may explain why animals have different maintenance costs and FE.

**Implications**

The results of this study show that selection for decreased RFI does indeed improve FE, with few differences in growth. In addition, this study indicates that selection also changes carcass composition, yet the overall carcass composition may explain most, if not all, of the difference in feed intake. This project paves the way for future work, which is examining tissue accretion rates, protein turnover, ion pump activity, and mitochondrial biogenesis differences between our control and decreased RFI lines. Residual feed intake may be another important measure of FE to use as the basis for genetic selection to improve FE.

**LITERATURE CITED**


