

JOURNAL OF ANIMAL SCIENCE

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J Anim Sci 2008.86:287-298.

doi: 10.2527/jas.2007-0396 originally published online Nov 12, 2007;

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<http://jas.fass.org/cgi/content/full/86/2/287>



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Selection response and genetic parameters for residual feed intake in Yorkshire swine¹

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ABSTRACT: Residual feed intake (RFI) is a measure of feed efficiency defined as the difference between the observed feed intake and that predicted from the average requirements for growth and maintenance. The objective of this study was to evaluate the response in a selection experiment consisting of a line selected for low RFI and a random control line and to estimate the genetic parameters for RFI and related production and carcass traits. Beginning with random allocation of purebred Yorkshire littermates, in each generation, electronically measured ADFI, ADG, and ultrasound backfat (BF) were evaluated during a ~40- to ~115-kg of BW test period on ~90 boars from first parity and ~90 gilts from second parity sows of the low RFI line. After evaluation of first parity boars, ~12 boars and ~70 gilts from the low RFI line were selected to produce ~50 litters for the next generation. Approximately 30 control line litters were produced by random selection and mating. Selection was on EBV for RFI from an animal model analysis of ADFI, with on-test group and sex (fixed), pen within group and litter (random), and covariates for interactions of on- and off-test BW, on-test age, ADG, and BF with generations. The RFI explained 34% of phenotypic variation in ADFI. After 4 generations of selection, estimates of heritability

for RFI, ADFI, ADG, feed efficiency (FE, which is the reciprocal of the feed conversion ratio and equals ADG/ADFI), and ultrasound-predicted BF, LM area (LMA), and intramuscular fat (IMF) were 0.29, 0.51, 0.42, 0.17, 0.68, 0.57, and 0.28, respectively; predicted responses based on average EBV in the low RFI line were -114, -202, and -39 g/d for RFI (= 0.9 phenotypic SD), ADFI (0.9 SD), and ADG (0.4 SD), respectively, and 1.56% for FE (0.5 SD), -0.37 mm for BF (0.1 SD), 0.35 cm² for LMA (0.1 SD), and -0.10% for IMF (0.3 SD). Direct phenotypic comparison of the low RFI and control lines based on 92 low RFI and 76 control gilts from the second parity of generation 4 showed that selection had significantly decreased RFI by 96 g/d ($P = 0.002$) and ADFI by 165 g/d ($P < 0.0001$). The low RFI line also had 33 g/d lower ADG ($P = 0.022$), 1.36% greater FE ($P = 0.09$), and 1.99 mm less BF ($P = 0.013$). There was not a significant difference in LMA and other carcass traits, including subjective marbling score, despite a large observed difference in ultrasound-predicted IMF (-1.05% with $P < 0.0001$). In conclusion, RFI is a heritable trait, and selection for low RFI has significantly decreased the feed required for a given rate of growth and backfat.

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

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J. Anim. Sci. 2008. 86:287–298
doi:10.2527/jas.2007-0396

INTRODUCTION

Feed for the growing phase is the largest variable cost in swine production. Therefore, feed intake (**FI**), as a vital component of feed efficiency (**FE**: kg of product/kg of feed), remains one of the most important considerations in pig breeding programs. Feed intake is genetically related to the economically important traits of growth and backfat (**BF**), but these relationships are not perfect; estimates of genetic correlations average

¹FIRE feeders used in this experiment were donated by Pig Improvement Company. Funds for development and maintenance of the selection lines were from the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, U.S.A. (Project No. 3600) and supported by Hatch Act and State of Iowa Funds and from the ISU Center for Integrated Animal Genomics. Monsanto Co. is acknowledged for providing partial support for Weiguo Cai. Benny Mote, Doug Newcom, Jay Lampe, and Jeremy Burkett are acknowledged for help with ultrasound evaluation, John Newton and his crew at the Lauren Christian Swine Research Center and Bilsland Memorial Farm for their tremendous assistance on this project, Chad Stahl and Lindsey Alexander for DNA genotyping, and Kim Bunter for input on this manuscript. The authors also thank both anonymous reviewers and the section editor for their useful comments.

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Received July 3, 2007.
Accepted October 31, 2007.

0.65 (0.32 to 0.89) with growth rate and 0.37 (0.08 to 0.59) with backfat thickness (Clutter and Brascamp, 1998). Thus, although a large proportion (36 to 64%; Luiting, 1998) of variation in FI is related to production traits, there is considerable variation that is independent of growth and composition. This is referred to as residual FI [**RFI**: i.e., feed consumed over and above expected requirements for production and maintenance (Luiting, 1990)]. Variation in RFI is not utilized in genetic selection for growth and composition, but is heritable; estimates in the pig range from 0.15 to 0.40 (Foster et al., 1983; Mrode and Kennedy, 1993; Von Felde et al., 1996; Johnson et al., 1999). Factors that contribute to genetic variation in RFI include feeding behavior, nutrient digestion, maintenance requirements, and energy homeostasis and partitioning (Luiting, 1998). Genetic differences in the ability to digest nutrients are small, but differences in maintenance requirements play a major role (Luiting, 1998). Although reduced maintenance requirements are desirable for improved FE, this may result in reduced fitness and increased susceptibility to stressors and diseases (Rauw et al., 1998). To enable the study of the genetic and physiological basis of FE, we initiated a selection experiment for RFI in Yorkshire pigs, with the goal of creating lines that differ in RFI. The objective of this study was to evaluate direct and correlated responses to selection and to estimate genetic parameters based on the first 4 generations.

MATERIALS AND METHODS

Experimental protocols for this study were approved by the Iowa State University Institutional Animal Care and Use Committee.

Selection Experiment

Experimental Design and Data Collection. Using purebred Yorkshire pigs, a selection line for reduced RFI (low RFI line) was begun in 2001, along with a randomly selected control. An outline of the selection line protocol is presented in Figure 1. Beginning with random allocation of littermates from generation 0 (the base population) to the low RFI and control lines, in each generation the following traits were evaluated on ~90 boars from first parity and ~90 gilts from second parity sows of the low RFI line: electronically measured FI, weekly BW, and 10th-rib BF, LM area (**LMA**), and intramuscular fat (**IMF**, in generations 0 through 4 only) by ultrasound 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). After evaluation of first parity boars based on EBV for RFI (see below), ~12 select line boars and 70 gilts were selected to produce ~50 litters for the next generation. After selection, full- or half-sisters of the selected boars, produced in the second parity of their dams, were evaluated for RFI to provide additional data

for the next generation (Figure 1). Each generation approximately 30 control line litters from approximately 10 boars and 40 gilts were produced by random selection and mating.

For feed intake recording, pigs were put in pens of 15 to 16 pigs, each of which had an electronic 1-space feeder (FIRE, Osborne Industries Inc., Osborne, KS), at ~90 d of age and ~40 kg of BW. Pigs were allowed to acclimate to the FIRE feeders for approximately 1 wk before they were put on test in groups by on-test date (typically in 2 or 3 age groups per generation) based on age and BW. In general, pigs were taken off test on an individual basis when they reached 115 kg of BW, but were removed at a lighter BW if only 3 pigs were left in a pen, in which case they were all taken off test. All pigs with off-test BW greater than 102 kg were used for analysis. Because of limited capacity to measure FI, in general, only low-RFI line pigs were evaluated for FI.

Database and edit systems developed by Casey (2003) and Casey et al. (2005) to handle the large amount of FI data from the FIRE feeders were used. The main steps in the edit procedures were to

- (i) identify errors in each visit (a feeding event from a pig's entrance into the feeder to its exit) by 16 criteria (Casey et al., 2005) and count the number of errors of each type for each day (about 5% of the visits contained at least 1 error);
- (ii) compute error-free FI for each pig and day by summing feed consumed in visits without identified errors;
- (iii) estimate the effect of error counts on error-free daily FI by fitting a linear mixed model to error-free daily FI observations with sex, generation by parity, and on-test weeks within generation by parity as fixed effects, variables created from the 16 error counts, BW on that day, and ADG as covariates, and pig as a random effect (Casey, 2003);
- (iv) adjust error-free daily FI for each pig and day for feed consumed in error visits by adding estimates of covariates from step iii);
- (v) estimate daily FI for each pig for days with missing FI data (no records or too many error visits) by fitting a quadratic regression of daily FI against on-test day for each pig; and
- (vi) compute ADFI for each pig by averaging daily FI during the test period.

For each pig, ADG was estimated as the slope from simple linear regression of weekly BW on number of days on test. The IMF content was predicted based on a longitudinal ultrasound scan when the pigs were taken off test using the model developed by Schwab and Baas (2006) on purebred Duroc barrows and gilts from the IMF selection project at Iowa State University. The R^2 and root mean square error for this prediction model were 0.36 and 1.31% (Schwab and Baas, 2006).

Genetic Evaluation. Each generation, selection of boars and gilts used to produce the next generation of

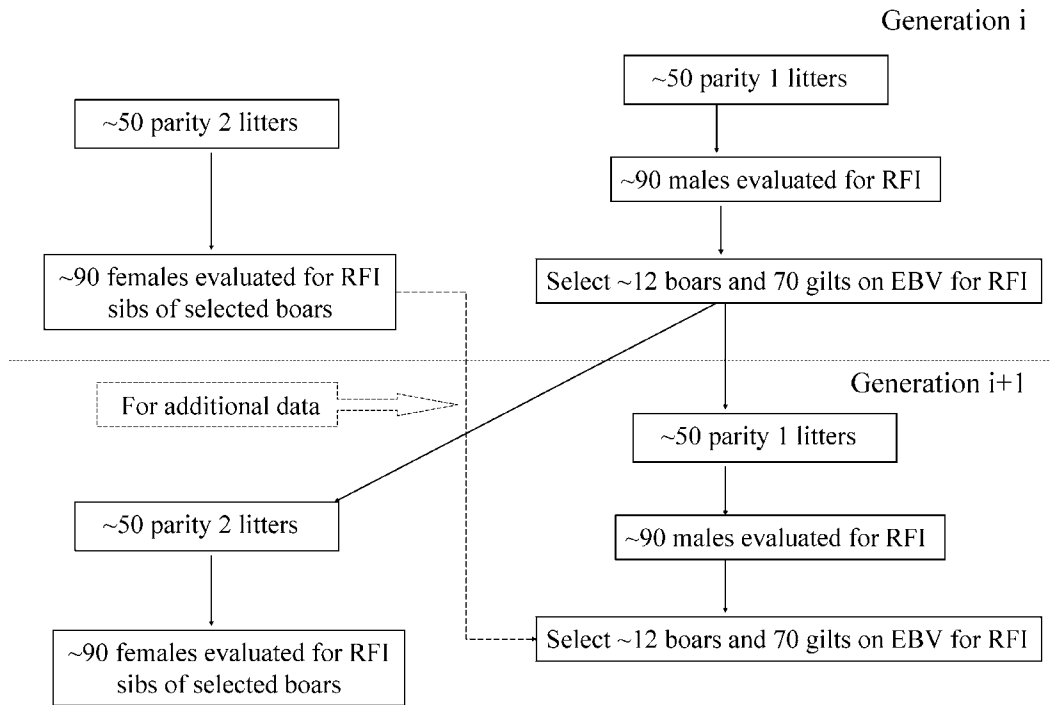


Figure 1. Design of the selection line for reduced residual feed intake (RFI).

the low RFI line was based on EBV for RFI, with some consideration of avoiding selection of full-sib brothers. Using data from all generations up to that point, including data from the base population (generation 0) and the generation that created the base population (generation -1), EBV for RFI were obtained from a single-trait animal model analysis of ADFI, with fixed effects of on-test group and sex, random effects of litter and pen within on-test group, and linear covariates for interactions of on- and off-test BW, on-test age, ADG adjusted to an on-test age of 90 d (= ADGA), and BF adjusted to an off-test BW of 115 kg (= BFA) with generation. Adjusted values for ADG (**ADGA**) and BF (**BFA**) were used as covariates rather than unadjusted ADG and BF because ADGA and BFA are expected to better reflect the impact of growth and BF on ADFI in a model that includes these same adjustments (i.e., for on-test age and off-test BW) for ADFI. Regression coefficients used for adjustment of ADG and BF to derive ADGA and BFA were obtained from models described later. Inclusion of interactions of covariates with generation was based on significance ($P < 0.05$) using backward elimination. Inclusion of metabolic midBW as a covariate to account for average maintenance requirements, as suggested by Nguyen et al. (2005), was considered. However, the correlation between EBV of RFI with and without metabolic midBW was 0.98 in our data, indicating that maintenance requirements are accounted for by ADG and on- and off-test BW. The heritability used for genetic evaluation of RFI was reestimated each generation using all available data and ranged from 0.27 to 0.36 for generations 0 to 4.

Estimation of Response to Selection and Genetic Parameters. After 4 generations of selection, genetic parameters and responses to selection for RFI, ADFI, ADG, FE (which is the reciprocal of the feed conversion ratio and equals $ADG/ADFI$), BF, LMA, and IMF were estimated by 2-trait animal model analyses using AS-Reml (Gilmour et al., 2002), using data from pigs evaluated for FI from generations -1 to 0 (the base population) and in the low RFI line from generation 1 up to and including generation 4 parity 1. The 2-trait animal models for all traits were the same as the single-trait genetic evaluation model for RFI, except covariates for the interaction of on-test age with generation were added for ADFI, ADG, and FE, and covariates for the interaction of off-test BW with generation were added for BF, LMA, and IMF. On- and off-test BW were not included as covariates for analysis of ADFI and ADG because they included some biological variation related to FI and growth in view of the fact that high-growing pigs tend to have higher on- and off-test BW. A summary of covariates included for each trait is in Table 1. Estimates of heritability, variance components, and selection response for all traits are reported from 2-trait animal models that always included RFI as one of the traits to account for the effect of selection on RFI.

Two-trait models, such as those that include ADFI to estimate RFI as one trait and ADG as the other trait result in a recursive system of equations with simultaneous feedback because ADG is used as a trait and also as a covariate in the model that analyzes ADFI to obtain genetic parameters for RFI. As outlined by Gianola and Sorensen (2004), this results in biased and

Table 1. Covariates included in the model for traits in the selection experiment and the direct line comparison experiment

Experiment and trait ¹	Covariate by gen ²				
	On-age	On-weight	Off-weight	ADG	BF
Selection line					
RFI	✓	✓	✓	✓	✓
ADFI, ADG, FE	✓				
BF, LMA, IMF			✓		
Direct line comparison					
RFI	✓	✓	✓	✓	✓
ADFI, ADG, FE	✓				
BF, LMA, IMF			✓		
Carcass traits	Live BW before slaughter				

¹RFI = residual feed intake, ADFI = average daily feed intake, FE = ADG/ADFI, BF = backfat, LMA = loin muscle area, and IMF = intramuscular fat.

²By gen = interaction with generation; this interaction was not included for the direct line comparison because it involved only 1 generation.

inconsistent estimates of genetic parameters when solved by maximum likelihood. To avoid this, RFI was preadjusted for on- and off-test BW, and for ADGA and BFA before it was fitted in the 2-trait animal model analyses. Regression coefficients used for preadjustment were obtained from the single-trait RFI model.

Direct Line Comparison Experiment

Experimental Design and Data Collection. Because FI was not routinely recorded in the control line, a phenotypic comparison experiment was conducted to allow direct comparison of line differences for RFI, ADFI, ADG, FE, BF, LMA, IMF, and several carcass traits using gilts from the second parity of generation 4. The same boars and sows that produced parity 1 of generation 4 were used to produce these gilts. This experiment was also used to evaluate the effects of a polymorphism in the calcitron receptor gene (*calcr*), as a candidate gene for bone strength (Hittmeier, 2005), on performance and bone strength. Because the *calcr* genotype had limited effects on the traits considered here, results for bone strength will be reported elsewhere. As illustrated in Figure 2, the experiment was designed as a split-plot with 2 factors: line (low RFI vs. control) and *calcr* genotype (11, 12, and 22), with litter as the main experimental unit to test for line differences, and pig as the split-plot experimental unit to test for genotype differences. To increase power to detect genotype differences, pigs included in the comparison were selected to obtain adequate numbers within each genotype by line class. A total of 92 low RFI gilts from 27 litters and 76 control gilts from 17 litters were evaluated. They were grouped in 12 pens by BW and age, balancing to the extent possible across line and genotype. Because only 6 pens were available for FI recording, pens were switched every 2 wk. Alternate pens were in the same room and had feeding equipment equivalent to the FIRE feeders, so as not to induce an acclimation period. The FI data from the day of switching were not used.

Pigs were taken off test in 3 groups (different off-test dates) and sent for slaughter at a commercial abattoir (Hormel Foods, Austin, MN) at a minimum BW of 102 kg. In contrast to standard procedures in the selection experiment, where pigs were taken off test individually at a target BW of 115 kg, taking pigs off test in just 3 groups to allow for sufficient numbers per slaughter day resulted in substantial variation in off-test BW. Carcass measurements were obtained 24 h postmortem using standard carcass collection procedures, as outlined in the Pork Composition and Quality Assessment Procedures (NPPC, 2000) for carcass length, carcass weight, 10th-rib BF, last-rib BF, last lumbar BF, and 10th-rib LMA. Ultimate pH was measured on the 10th-rib face of the loin using a pH star probe (SFK Ltd., Hvidovre, Denmark). Hunter L score and Minolta Y reflectance (a measure of light reflectance, where lower values indicate a darker and more desirable color) were measured on the 10th-rib face of the loin using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm diam. aperture, D65 illuminant, and calibrated to the white calibration plate. Subjective scores for color (National Pork Board standards 6-point scale, 1 = pale pinkish gray to white; 6 = dark purplish red), firmness (National Pork Board standards 3-point scale, 1 = soft; 3 = very firm), and marbling (National Pork Board standards 10-point scale, 1 = 1.0% IMF; 10 = 10.0% IMF) were also recorded.

Statistical Analysis. Data from the production traits RFI, ADFI, ADG, FE, BF, LMA, and IMF were analyzed by a linear mixed model with on-test group ($n = 2$), off-test group ($n = 3$), line, *calcr*, and the interaction of line with *calcr* as fixed effects, litter and pen within on-test group as random effects, and covariates, as specified in Table 1. Carcass traits were analyzed with a linear mixed model or a generalized linear mixed model (using a multinomial response distribution and cumulative logit link function for color, firmness, and marbling score), with live BW before slaughter as the covariate, and the same fixed and random effects as for

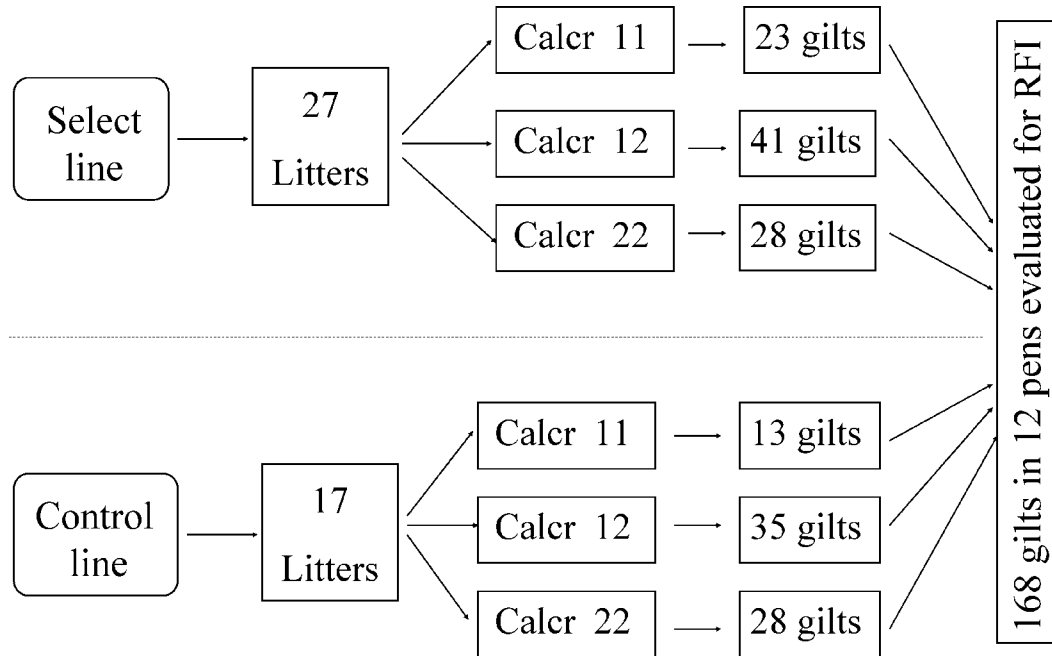


Figure 2. Design of the direct phenotypic line comparison experiment.

the production traits analysis, except that on-test group and pen within on-test group were not included in the models. To enable the GLIMMIX procedure (SAS Inst. Inc., Cary, NC) to converge, class 5 of the color score, which had only 2 observations, was merged into class 4, and for marbling score class 4 (2 observations) and class 3 (3 observations) were merged into class 2. The interaction of line with *calcr* was dropped after it was found to be nonsignificant ($P > 0.20$), other than for ADG and ADFI. Also, interactions of all covariates with line were not significant ($P > 0.05$) for all traits and were dropped from the models.

RESULTS

Estimates of Genetic Parameters

Table 2 shows estimates of heritability and variance due to environmental components from the 2-trait animal model analyses. Estimates of genetic parameters and responses to selection for RFI were similar among 2-trait models of RFI with all other traits and are reported from the 2-trait animal model of RFI with ADFI. The RFI had a substantial heritability (0.29), which is within the upper range of estimates (0.15 to 0.40) for RFI in pigs observed in the literature (Foster et al., 1983; Mrode and Kennedy, 1993; Von Felde et al., 1996; Johnson et al., 1999). About 34% of phenotypic variation in ADFI was contributed by RFI (= phenotypic variance ratio of RFI to ADFI), the rest being explained by variation in growth rate and backfat. The estimated heritability for ADFI (0.51) was in the upper range of literature estimates, with estimates averaging 0.29 and ranging from 0.13 to 0.62 (Clutter and Brascamp, 1998).

Estimates of heritability for ADG and BF were 0.42 and 0.68, respectively, also in the upper range of literature estimates for ADG (0.03 to 0.49) and BF (0.12 to 0.74), as specified by Clutter and Brascamp (1998). The estimated heritability for FE was 0.17, similar to the 0.16 heritability of feed conversion ratio (i.e., ADFI/ADG) from Large White boars estimated by Johnson et al. (1999). Table 2 also shows that the estimated common environmental effect of litter was close to zero for RFI, ADFI, ADG, and FE, but was not negligible for BF, LMA, and IMF. Pen accounted for 30, 13, and 16% of the phenotypic variation in RFI, ADFI, and FE, respectively, which is likely due to the operation and measurement errors associated with the FIRE feeder located in each pen. Although the pen variance ratio was much greater for RFI (30%) than for ADFI (13%), the absolute value of the pen variance component was not much different between RFI and ADFI. Estimated pen within group common environmental effects were close to zero for ADG, BF, LMA, and IMF.

Estimates of phenotypic and genetic correlations are in Table 3. Genetic correlations of ADFI with ADG and BF were estimated at 0.88 and 0.57, in the upper range of literature estimates of ADFI with ADG (0.32 to 0.89) and of ADFI with BF (0.08 to 0.59; Clutter and Brascamp, 1998). Estimated phenotypic correlations of RFI with ADG and BF were close to zero, as expected from adjusting for ADG and BF in the model for RFI. However, because adjustment for ADG and BF was at the phenotypic level, genetic correlations of RFI with ADG (0.17) and with BF (−0.14) were nonzero, although these estimates had large standard errors and were not significantly different from zero. Johnson et al. (1999) obtained similar estimates of genetic correlations of RFI

Table 2. Estimates (\pm SE) of heritability and of variance due to litter, pen (group), and residual, based on data from the low RFI line, expressed as a percentage of phenotypic variance¹

Trait ²	n	Mean	SD ¹	Heritability	Litter ³	Pen(group) ³	Residual
RFI, g/d	756	0	126	0.29 \pm 0.07	0.01 \pm 0.00	0.30 \pm 0.06	0.40 \pm 0.07
ADFI, g/d	756	1,989	216	0.51 \pm 0.08	0.00 \pm 0.00	0.13 \pm 0.04	0.36 \pm 0.08
ADG, g/d	756	768	91	0.42 \pm 0.08	0.00 \pm 0.00	0.02 \pm 0.02	0.56 \pm 0.08
FE, %	756	38.76	3.30	0.17 \pm 0.07	0.05 \pm 0.00	0.16 \pm 0.04	0.62 \pm 0.07
BF, mm	756	15.88	3.48	0.68 \pm 0.09	0.08 \pm 0.01	0.00 \pm 0.00	0.24 \pm 0.09
LMA, cm ²	756	42.67	4.67	0.57 \pm 0.10	0.11 \pm 0.01	0.02 \pm 0.02	0.30 \pm 0.09
IMF, %	492	1.75	0.40	0.28 \pm 0.11	0.27 \pm 0.02	0.01 \pm 0.02	0.44 \pm 0.10

¹Phenotypic variance and SD after adjustment for fixed effects and covariates.

²RFI = residual feed intake, ADFI = average daily feed intake, FE = ADG/ADFI, BF = backfat, LMA = loin muscle area, and IMF = intramuscular fat.

³An SE or estimate of 0.00 denotes that the number was smaller than 0.005.

with ADG (0.17), but a slightly positive genetic correlation of RFI with BF (0.22) from Large White boars on individual pen testing, when RFI was adjusted for initial test age and BW, test ADG, and BF. However, Nguyen et al. (2005) reported a slightly negative genetic correlation of RFI (adjusted for test ADG and BF) with BF (−0.20) from Large White boars and gilts on individual pen feeding, similar to our result. Apart from sampling errors, differences in these estimates can result from population differences in phenotypic and genetic correlations among traits; the genetic correlation of RFI with ADG and BF is a direct result of the phenotypic and genetic parameters of FI, ADG, and BF in the population (Kennedy et al., 1993). Genetic correlations of RFI with FE, LMA, and IMF were estimated as −0.74, −0.18, and 0.40, respectively. The estimated negative genetic correlation (−0.13) between BF and IMF is opposite to literature estimates (Lo et al., 1992; Suzuki et al., 2005), but the large standard error (0.26) of this estimate could explain this discrepancy.

Direct and Correlated Responses to Selection

Predicted from Average EBV in the Low RFI Line.

Predicted selection responses for RFI and production traits are shown in Figure 3, in which the average EBV of boars with data in the low RFI line for each generation was plotted on a genetic SD scale and deviated

from the average EBV of boars with data in the base population (generation 0). Single-trait selection for decreasing RFI resulted in the expected selection response (close to 2 genetic SD in generation 4). As expected, selection on RFI also led to a substantial reduction in ADFI. Selection on RFI also resulted in small negative correlated responses in ADG, BF, and IMF, and a slight increase in LMA, consistent with the estimated genetic correlations of RFI with ADFI, ADG, IMF, and LMA of 0.52, 0.17, 0.40, and −0.18, respectively (Table 3). Selection on RFI also slightly reduced BF, which was opposite to the estimated genetic correlation of −0.14 between RFI and BF (Table 3), but which had a large standard error that could explain this discrepancy. Although there was a small reduction in ADG, selection for decreasing RFI, as expected, resulted in substantial improvements in FE (about 1.2 genetic SD in generation 4) because of a substantial reduction in ADFI.

Estimates from Direct Line Comparison. The 27 selection litters (92 gilts) and the 17 control litters (76 gilts) finished test with average on- and off-test BW (\pm SD) of approximately 60 (\pm 8) kg and 110 (\pm 6) kg and these were used to estimate line differences in performance. Results are shown in Table 4 and also in Figure 3. The low RFI line gilts had significantly lower RFI (96 g/d, $P = 0.002$), lower ADFI (165 g/d, $P < 0.0001$), and greater FE (1.36%, $P = 0.09$) than the control line gilts, although the select line gilts also had significantly

Table 3. Estimates of phenotypic (above diagonal) and genetic (below diagonal) correlations based on bivariate analyses of the low RFI line data

Trait ¹	RFI \pm SE	ADFI \pm SE	ADG \pm SE	FE \pm SE	BF \pm SE	LMA \pm SE	IMF \pm SE
RFI	—	0.61 \pm 0.03	0.06 \pm 0.05	−0.69 \pm 0.03	−0.01 \pm 0.04	−0.06 \pm 0.05	0.03 \pm 0.06
ADFI	0.52 \pm 0.12	—	0.73 \pm 0.02	−0.26 \pm 0.05	0.49 \pm 0.04	−0.01 \pm 0.05	0.08 \pm 0.06
ADG	0.17 \pm 0.18	0.88 \pm 0.05	—	0.46 \pm 0.04	0.36 \pm 0.04	0.11 \pm 0.05	0.16 \pm 0.05
FE	−0.74 \pm 0.13	−0.26 \pm 0.21	0.30 \pm 0.21	—	−0.09 \pm 0.04	0.14 \pm 0.05	0.11 \pm 0.05
BF	−0.14 \pm 0.16	0.57 \pm 0.10	0.45 \pm 0.13	−0.24 \pm 0.22	—	−0.10 \pm 0.05	−0.01 \pm 0.06
LMA	−0.18 \pm 0.18	−0.09 \pm 0.16	0.16 \pm 0.17	0.27 \pm 0.27	−0.10 \pm 0.17	—	0.03 \pm 0.06
IMF	0.40 \pm 0.28	0.37 \pm 0.24	0.38 \pm 0.23	−0.23 \pm 0.47	−0.13 \pm 0.26	0.22 \pm 0.28	—

¹RFI = residual feed intake, ADFI = average daily feed intake, FE = ADG/ADFI, BF = backfat, LMA = loin muscle area, and IMF = intramuscular fat.

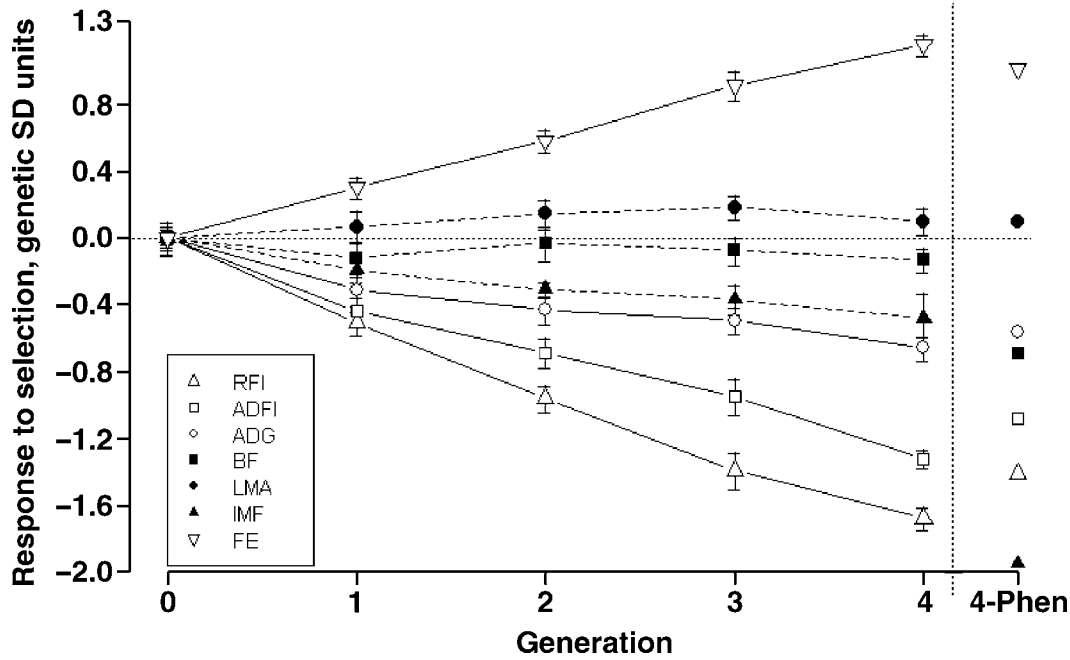


Figure 3. Direct and correlated responses to selection on residual feed intake (RFI) based on average EBV (connected symbols) and direct phenotypic line comparison in generation 4 (4-Phen). Average EBV and SE bars are based on only boars with data in the low RFI line. 4-Phen: Phenotypic line differences (low RFI-control) based on the direct line comparison in generation 4; ADFI = average daily feed intake; FE (feed efficiency) = ADG/ADFI; BF = backfat; LMA = loin muscle area; IMF = intramuscular fat. *The direct phenotypic line comparison for IMF in generation 4 was -5 genetic SD.

lower growth (33 g/d, $P = 0.022$), less BF (1.99 mm, $P = 0.013$), less IMF (1.05%, $P < 0.0001$), and tended to have greater LMA (0.35 cm², $P = 0.7$). The estimated line difference for IMF was 5 genetic SD, which may be due to the poor quality of the IMF prediction (see Discussion section).

Because the phenotypic comparison experiment had substantial on- and off-test BW variation, in contrast to standard procedures in the selection experiment, the

impact of including these BW as covariates in the models for analysis of RFI, ADG, and ADFI was evaluated. Results in Table 4 show limited impact of including these covariates on estimates of line differences, except when both on- and off-test BW were included, in which case estimates of line differences were reduced for ADFI and in particular for ADG (-4 vs. -33 g/d). The on- and off-testing procedures caused variation in on- and off-test BW to be correlated with true biological variation

Table 4. Estimates of line differences (low RFI – control) in generation 4 based on average EBV from analysis of the low RFI line and based on direct line comparison of the low RFI and control lines, depending on the inclusion of additional covariates in the model

Trait ¹	Covariates included in model	Difference based on EBV ± SEM ²	Difference based on direct line comparison ± SED with inclusion of covariates in addition to on-age			
			None	On-weight	Off-weight	On-weight off-weight
RFI, g/d	On-age, ADG, BF	-114 ± 5	-89** ± 30	-100** ± 30	-97** ± 28	-96 ³ ** ± 28
ADFI, g/d	On-age	-202 ± 8	-165 ³ *** ± 35	-171*** ± 35	-164*** ± 34	-139*** ± 34
ADG, g/d	On-age	-39 ± 4	-33 ³ * ± 14	-26* ± 13	-30* ± 12	-4 ^{NS} ± 5
FE, %	On-age	1.56 ± 0.08	1.36 ³ † ± 0.78	1.73* ± 0.73	1.39† ± 0.78	2.31** ± 0.69
BF, mm	Off-weight	-0.37 ± 0.20	-1.99 ³ * ± 0.76	—	—	—
LMA, cm ²	Off-weight	0.35 ± 0.28	0.35 ³ NS ± 0.93	—	—	—
IMF, %	Off-weight	-0.10 ± 0.03	-1.05 ³ *** ± 0.23	—	—	—

¹RFI = residual feed intake, ADFI = average daily feed intake, FE = ADG/ADFI, BF = backfat, LMA = loin muscle area, and IMF = intramuscular fat.

²Average EBV and SEM are based on only boars with data in the low RFI line.

³Indicates results for the preferred model.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$, and ^{NS} $P > 0.10$.

Table 5. Estimates of line differences for production and carcass traits based on the direct line comparison (n = 168)

Trait ¹	Mean	SD ²	Line difference (select-control) ± SED
Production trait			
RFI, g/d	0	165	-96** ± 28
ADFI, g/d	1,990	193	-165*** ± 35
ADG, g/d	702	72	-33* ± 14
FE, %	38.76	3.30	1.36† ± 0.78
BF, mm	15.88	3.02	-1.99* ± 0.76
LMA, cm ²	45.02	4.08	0.35 ^{NS} ± 0.93
IMF, %	3.60	0.95	-1.05*** ± 0.23
Carcass trait			
Carcass length, cm	83.32	1.78	-0.35 ^{NS} ± 0.39
Carcass weight, ³ kg	83.94	1.53	-0.03 ^{NS} ± 0.31
10th-rib BF, mm	16.68	4.08	-2.62* ± 1.01
Last-rib BF, mm	22.41	4.55	-1.28 ^{NS} ± 0.88
Last-lumbar BF, mm	27.12	4.65	-1.11 ^{NS} ± 0.89
LMA, cm ²	46.73	6.18	0.73 ^{NS} ± 1.48
Color ⁴	3.35	0.65	0.09 ^{NS} ± 0.37
Firmness ⁴	2.30	0.61	-0.35 ^{NS} ± 0.31
Marbling ⁴	1.38	0.59	-0.52 ^{NS} ± 0.39
pH	5.62	0.11	-0.02 ^{NS} ± 0.02
Minolta Y	23.14	2.55	-0.26 ^{NS} ± 0.48
Hunter L	48.02	2.65	-0.25 ^{NS} ± 0.49

¹RFI = residual feed intake, ADFI = average daily feed intake, FE = ADG/ADFI, BF = backfat, LMA = loin muscle area, and IMF = intramuscular fat.

²SD = phenotypic SD after adjustment for fixed effects and covariates.

³Live BW was included as covariate such that the results apply to dressing percent.

⁴Subjective score: SD without adjustment; line difference in logarithm odds ratio scale.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.10$, and ^{NS} $P > 0.10$.

in ADG. Thus, including on- and off-test BW as covariates in the models for ADG and ADFI not only removes noise, but also removes some biological variation in ADG and ADFI, which is undesirable. Thus, for these traits, the model that included neither of these covariates was deemed the preferred model. Although the impact of including one or both of these covariates in the model for RFI was limited, for this trait all variation associated with ADG must be removed, such that the model that includes all covariates is the preferred model. This model resulted in an estimated line difference of -96 g/d in RFI (Table 4).

Phenotypic Comparison for Carcass Traits

Estimates of line differences for carcass traits are presented in Table 5, which also includes estimates for production traits for completeness. Line differences for the subjective scores of color, firmness, and marbling are expressed as logarithm odds ratios. A ratio close to zero means no difference between the lines and a positive ratio means a higher score for the low RFI line. Except for 10th-rib BF, none of the carcass traits had a significant ($P > 0.10$) difference between the low RFI and control lines. The estimated line differences for 10th-rib BF and LMA measured on the carcass were

-2.62 mm and 0.73 cm², respectively, which are in the same direction and order of magnitude as the line difference of -1.99 mm ($P < 0.05$) for BF and 0.35 cm² ($P > 0.10$) for LMA measured in live pigs by real-time ultrasound on the farm. The line difference for marbling score was -0.52 on the logarithm odds ratio scale, which is in the same direction as the line difference of IMF predicted by longitudinal ultrasound scan, but was not significant ($P > 0.10$), in contrast to the high level of significance for IMF estimated by ultrasound. This result is probably because IMF data were of poor quality, which may have resulted in an overestimate of the line difference. The line difference for color by subjective scores was positive, though not significant ($P > 0.10$). Nevertheless, this estimate was in the same direction as estimates for objective reflectance measures by Minolta Y and Hunter L, in that the low RFI line tended to have greater color and less reflectance.

Regression Coefficients for ADG and BF

Estimates of regression coefficients on ADGA and BFA when analyzing ADFI to obtain RFI represent the average increase in FI per unit of change in ADG or BF and are shown in Table 6 for the different analyses. The mixed model used for analysis of the low-RFI line data across generations included interactions of generation with ADGA and BFA to allow for different regression coefficients as a result of selection or year effects. Both interactions were significant ($P < 0.05$).

The regression coefficient for ADGA was fairly stable up to generation 4, at which point it dropped dramatically (Table 6). A possible reason for this result was that the growth test in generation 4 was during a long hot period. The regression coefficient for BFA was fairly stable, except for generation 3, but this coefficient had a large standard error because only 51 pigs from parity 1 in that generation had data. Estimates of the regression coefficients for ADGA and BFA from the direct phenotypic comparison were similar to those obtained from the genetic analysis (Table 6).

Estimates of regression coefficients on ADGA were affected by the inclusion of other covariates in the model (Table 6). When on-test or off-test BW were included as additional covariates, compared with only including on-test age, the regression coefficient on ADGA decreased, especially when on- or off-test BW had large variation (e.g., at generation 3 of the genetic analysis and in the direct phenotypic comparison), indicating that on- and off-test BW capture some biological variation in ADGA. The regression coefficients for BFA did not change much across generations. To obtain partial regression coefficients for ADGA and BFA when analyzing RFI, the model that includes on-test age is preferred because it does not remove biological variation in ADGA.

Regression coefficients for ADGA ranged from 1.37 to 1.99 kg·d⁻¹·kg⁻¹·d, which was similar to the 1.29 kg·d⁻¹·kg⁻¹·d reported by Nguyen et al. (2005), but the

Table 6. Estimates of partial regression coefficients of average daily feed intake (ADFI, kg/d) on ADG (kg/d) and backfat (BF, mm), when analyzing ADFI to calculate residual feed intake, based on data from the low RFI line by generation and the direct line comparison

Experiment and trait	Gen ¹	Estimate of regression coefficient ± SE with inclusion of covariates in addition to on-age		
		None	On-weight	On-weight off-weight
Selection²				
ADG	-1	1.61 ± 0.10	1.23 ± 0.10	1.14 ± 0.10
	0	1.46 ± 0.12	1.33 ± 0.11	1.24 ± 0.11
	1	1.44 ± 0.13	1.27 ± 0.13	1.20 ± 0.13
	2	1.37 ± 0.12	1.33 ± 0.11	1.18 ± 0.12
	3	1.99 ± 0.22	1.52 ± 0.23	0.88 ± 0.27
	4	0.80 ± 0.17	0.76 ± 0.16	0.58 ± 0.16
BF	-1	0.014 ± 0.003	0.018 ± 0.003	0.020 ± 0.003
	0	0.016 ± 0.003	0.015 ± 0.003	0.015 ± 0.003
	1	0.011 ± 0.003	0.012 ± 0.003	0.013 ± 0.003
	2	0.019 ± 0.003	0.019 ± 0.003	0.019 ± 0.003
	3	-0.007 ± 0.007	-0.003 ± 0.007	0.001 ± 0.006
	4	0.018 ± 0.006	0.019 ± 0.006	0.019 ± 0.006
Direct line comparison³				
ADG	4	1.51 ± 0.17	1.69 ± 0.17	0.78 ± 0.40
BF	4	0.023 ± 0.004	0.023 ± 0.004	0.023 ± 0.004

¹Gen = generation.

²Data were on gilts and boars from the low RFI line.

³Data were on gilts from the low RFI and control lines.

coefficients for BFA, which ranged from 0.011 to 0.023 kg·d⁻¹·mm⁻¹, were about 10 times larger than the 0.00185 kg·d⁻¹·mm⁻¹ reported by Nguyen et al. (2005). A possible reason for the latter difference is that in Nguyen et al. (2005) RFI was evaluated on Large White pigs selected for BW gain on restricted feeding when they were housed individually and fed ad libitum vs. our group-housed Yorkshire pigs selected for reduced RFI on ad libitum feeding.

DISCUSSION

Comparison of Responses Based on Genetic Evaluation and Direct Line Comparison

The limited capacity to measure FI did not allow systematic measurement of RFI in the control line, which reduces the accuracy of the estimation of response to selection. This was addressed by evaluating RFI on both lines in the direct line comparison in the final generation. Estimated responses of RFI and ADFI in the fourth generation based on direct comparison of lines were -96 and -165 g/d and were slightly smaller than the predicted response of -114 and -202 g/d based on average line EBV of boars from analysis of data observed in the low RFI line. In addition to sampling errors (SE of line differences from direct comparison were 28 and 35 g/d), this slightly lower response in the direct comparison may be because it was evaluated on gilts, whereas most selection was on RFI observed on boars. Some differences also existed in on- and off-test

BW; pigs were evaluated from ~60 kg to ~110 kg in the direct comparison and from ~40 kg to 115 kg in the selection line.

Selection slightly reduced ADG and BF in the low RFI line, probably because of nonzero genetic correlations of RFI with ADG and BF when using these traits to adjust ADFI to obtain RFI on a phenotypic level (Kennedy et al., 1993). Because of a large reduction in ADFI relative to the reduction in ADG, selection on RFI increased feed efficiency by 1.56% kg of growth per kg of feed (Table 4) from generation 0 (base population) to generation 4 based on average EBV of boars with data in the low RFI line, which is close to the difference in feed efficiency (1.36% kg of growth per kg of feed) based on direct comparison of the 2 lines in generation 4.

Genetic analysis of the low RFI line resulted in a small line difference for ultrasound IMF (-0.10%), but the direct phenotypic line comparison resulted in a large difference in ultrasound IMF (-1.05%), although the difference in subjective marbling scores was not significant (Table 5). One explanation for the large difference in ultrasound IMF in the phenotypic comparison is that the variance for IMF was much higher in the phenotypic line comparison (based on gilts) than in the data used for the genetic evaluation, which was primarily on boars; the mean and phenotypic SD of IMF (after adjustment for fixed effects and covariates) were 3.60 and 0.95%, respectively, in the phenotypic line comparison vs. 1.75 and 0.40%, respectively, based on the genetic evaluation data. Another explanation is that these differences may be because the IMF ultrasound

Table 7. Frequencies of the *calcr* genotype for the low residual feed intake and control line in generation 4 parity 2

Line	Calcr genotype	Frequency in all pigs genotyped	Frequency in pigs evaluated
Select	11	0.21	0.25
	12	0.58	0.45
	22	0.21	0.30
Control	11	0.15	0.17
	12	0.45	0.46
	22	0.40	0.37

predictions had limited accuracy and may be biased in view of the fact that the prediction model was developed based on a Duroc population and had low R^2 and high root mean square error even for that population (Schwab and Baas, 2006).

Differences in body composition (fat to lean) can cause differences in RFI because depositing fat requires more energy per gram than depositing lean. The model used for evaluating RFI corrects for differences in body composition to the extent they are related to ultrasound backfat. Thus, to evaluate differences in IMF as a potential contributor to observed line differences in RFI in the phenotypic comparison experiment, the impact of including IMF (preadjusted for off-test BW) as an additional covariate in the model for RFI was evaluated. Results showed that this only slightly decreased the estimated line difference in RFI, from -96 to -87 g/d. Thus, IMF was not a large factor associated with differences in RFI. This does not, however, preclude differences in other fat depots to contribute to the observed line differences in RFI. Also, LMA was not included in the model adjustment for RFI because, as Johnson et al. (1999) indicated, LMA was not a large factor beyond ADG and BF associated with RFI. Johnson et al. (1999) compared RFI adjusted for ADG and BF with RFI adjusted for ADG, BF, and LMA, and the results showed RFI heritability (0.11 vs. 0.10, respectively), litter variance, and error variance components were little affected by inclusion of LMA.

There are a number of aspects of the design and analysis of the direct line comparison that could have affected results from this comparison, although none are expected to have a major effect that changes conclusions from this comparison, as explained in the following. The gilts that were evaluated in the direct line comparison were not a random sample of gilts produced in the second parity of the fourth generation, but were partially chosen based on their genotype for *calcr* to obtain sufficient numbers per genotype. However, as shown in Table 7, genotype frequencies for the *calcr* gene polymorphism among pigs that were included in the comparison for the low RFI and control lines (92 and 76 gilts) were very similar to the frequencies observed among all pigs that were genotyped (175 gilts in the low RFI line and 91 gilts in the control line). Therefore,

including *calcr* genotypes in the experiment and evaluating a sample of pigs that was not completely random is expected to have very limited impact on observed line differences. Also, in the direct line comparison, pigs from the 2 lines were mixed, which may result in some bias by behavioral interactions between lines because selection for low RFI may lead to changes in behavior. However, this bias is not expected to be large. Moreover, the alternative design of separating pigs by pen would have substantially reduced the power to detect differences. Thirdly, the standard errors of differences estimated in the direct line comparison accounted for drift variance only partially by including litter as a random effect, which accounts for relationships due to sire and dam, and by using litter as the experimental unit to test for line differences. Including all of the drift variance will increase standard errors of differences to some degree, and, correspondingly, will increase P -values to some degree. These changes will not, however, alter our conclusions because the line differences for RFI and ADFI were highly significant ($P = 0.002$ and $P < 0.0001$, respectively) and a larger SE would make differences in the other traits even less significant.

In this experiment, selection was on RFI, derived using phenotypic regression of FI on ADG and BF. There are other ways of selection to improve feed efficiency, as Kennedy et al. (1993) suggested. One option is to use genetic, rather than phenotypic, regressions to adjust FI for ADG and BF. An equivalent strategy is to select on a restricted selection index (i.e., an index of ADFI, ADG, and BF, restricted to hold ADG and BF constant). These 2 selection strategies may have reduced correlated responses in ADG and BF, but require accurate estimates of genetic correlations among ADG, BF, and ADFI, which were not available at the start of the selection experiment.

Comparison with Other Selection Experiments

Results of a similar selection experiment on RFI that is ongoing in France have been reported by Gilbert et al. (2006). In that study, divergent selection for RFI is practiced in a Large White population, with RFI measured on group-housed males between 35 and 95 kg of BW, selection of males based on their phenotype for RFI predicted from a selection index of ADFI, ADG, and BF that was derived from prior studies in the same population, and random selection of females. To evaluate response to selection, castrated males and females from second parity litters were slaughtered at an average BW of 107 kg and measured for carcass traits (Gilbert et al., 2006). Using data from the first 3 generations, Gilbert et al. (2006) estimated heritabilities for RFI, ADFI, ADG, and BF at 0.15, 0.17, 0.25, and 0.62, respectively. The estimated difference between the high and low RFI lines after 3 generations was about 0.3 phenotypic SD for RFI and about 0.2 SD for ADFI. These responses are substantially lower than those we observed between the low RFI and control lines after

4 generations (about 0.9 phenotypic SD for RFI and 0.9 SD for ADFI), especially considering the uni- vs. bidirectional design of our experiment.

To gain some understanding of potential causes for the differences in responses in RFI between the 2 studies [the study of Gilbert et al. (2006) and the current study], predicted asymptotic (based on the Bulmer effect) responses in RFI for these 2 studies given their respective estimated genetic parameters were calculated using the SelAction program (Rutten and Bijma, 2001). For the Gilbert et al. (2006) study, using a realized selection intensity of 1.6 (selected proportion of 6.7%) for males and 0 for females, and selection on own phenotype for a trait with a heritability of 0.15, predicted divergent response in RFI over 3 generations was $0.114\sigma_p \times 2 \times 3 \approx 0.7\sigma_p$, which is relatively higher than the observed response of 0.3 SD. In our study, response to selection on BLUP EBV was approximated by a pseudo BLUP index of own phenotype and phenotype on 1 full-brother for males and phenotype on 2 full-brothers for females, in addition to information from sire and dam BLUP EBV for both males and females. Using a heritability of 0.29, resulting asymptotic accuracies of selection were 0.54 for males and 0.31 for females, which using selection intensities of 1.63 for males (13% selected) and 1.06 for females (35% selected), resulted in a predicted response of $0.3\sigma_p \times 4 = 1.2\sigma_p$ after 4 generations, which is close to the 0.9 SD of response we observed based on EBV. These calculations show that there may be other potential reasons for the large difference in response for RFI between our study and that of Gilbert et al. (2006) besides use of different electronic feeders (ACEMO vs. FIRE), selection in a different breed population (Large White vs. Yorkshire), use of a different test period (35 to 95 kg vs. 40 to 115 kg of BW), and their selection only on the male side and based on own phenotype for RFI rather than EBV.

Gilbert et al. (2006) reported that the low RFI line tended to have less BF, similar to our result. In contrast to our results, Gilbert et al. (2006) reported significant correlated responses in several carcass traits; the low RFI line had significantly lower pH, lighter meat color, heavier carcass weight (increased dressing percent) and lean cuts (weight of loin). In comparison, our data showed no significant differences ($P > 0.10$) between the lines for pH, meat color, carcass weight, or LMA, although the low RFI line tended to have slightly lower pH, darker meat color, lighter carcass weights, and larger LMA. These differences in correlated responses between the 2 studies may be because of population and other differences; our study only evaluated gilts for carcass traits vs. castrated males and gilts in the Gilbert et al. (2006) study.

Gilbert et al. (2006) reported estimates of genetic correlations of RFI with ADFI, ADG, and BF of 0.38, -0.16, and -0.15, respectively, which are similar to the estimates of genetic correlations of RFI with ADFI (0.52) and BF (-0.14) in our results, but the estimate of the genetic correlation between RFI and ADG was

of opposite sign than our estimate (0.17). Kennedy et al. (1993) showed that, although RFI is phenotypically independent of the component traits, it is not genetically independent, and the sign and magnitude of the genetic correlations are influenced by the genetic and environmental correlations with FI.

Out of interest, we also predicted correlated responses to selection on RFI in our study, using the estimated genetic correlations and the program SelAction. Correlated responses for ADFI and ADG from selection on RFI were predicted at -178 and -22 g/d, respectively, in the fourth generation, similar to the observed values of -202 and -39 g/d. The predicted correlated response for BF was 0.9 mm, which is of opposite sign from the observed -0.37 mm. The reason is that the estimated genetic correlation of -0.14 between RFI and BF with a large standard error is in opposite direction to the observed selection response.

Regression Coefficients for ADG and BF

The partial regression coefficients of ADFI on ADG and BF, when analyzing ADFI to calculate RFI, approximately can be interpreted as the average daily feed (kg) required for lean meat growth (kg) and for deposition of an additional 1 mm of BF, respectively. These coefficients can be compared with expected energy requirements for lean meat growth and for BF deposition. The NRC (1998) showed that estimates for the energy costs of protein retention range from 6.8 to 14.0 Mcal of ME/kg, with a mean of 10.6 Mcal of ME/kg. Estimates for the energy costs of fat deposition range from 9.5 to 16.3 Mcal of ME/kg with a mean of 12.5 Mcal of ME/kg. Based on these estimates, the average energy required for 1 kg of carcass fat-free lean tissue growth can be calculated as $10.6/(2.55 \times 3.44) = 1.21$ kg of feed per kilogram of growth (range from 0.78 to 1.60), where 2.55 represents the kilograms of carcass fat-free lean tissue per kilogram of whole-body protein (NRC, 1998) and 3.44 is the energy density of feed used in the RFI selection project in megacalories per kilogram. This result is very close to the partial regression coefficients for ADG, while holding on-test age and BF constant, found in our analyses, which ranged from 1.37 to 1.99, excluding the apparent outlier result from parity 1 of generation 4 (Table 6). Feed required for a 1-mm increase in 10th-rib BF was calculated as follows: a 1-mm increase in last-rib BF was estimated to correspond to 1.12×0.78 kg of whole body lipid retention by Whittemore et al. (2001); the estimated regression coefficient of last rib BF on 10th-rib BF from our carcass data was 0.57; the test length was 105 d on average in our Yorkshire population; so, after ignoring on-test BF, which was small, this results in $0.57 \times 1.12 \times 0.78 \times 12.5/(3.44 \times 105) = 0.017$ (range from 0.013 to 0.023) kg of extra feed required per day on average for a 1-mm increase in off-test 10th-rib BF. This number is close to the partial regression coefficients for BF obtained while holding on-test age and ADG constant, which ranged from 0.011

to 0.023, excluding the apparent outlier result from parity 1 of generation 3 (Table 6).

Summary and Implications

The results of this study show that a substantial proportion of variation in feed consumption in growing pigs is unrelated to growth and backfat. The RFI is a heritable trait and selection for RFI can significantly decrease the feed required for a given rate of growth and backfat. These results are important for developing strategies to select for feed efficiency in pigs. Feed efficiency has increased in importance in recent years and is expected to remain important because of the increasing demand on feed crops and on land for biofuel production. Although intense selection for lean growth has significantly improved feed efficiency in pork production, further improvements require direct selection on FI and, specifically, on components of FI that are independent of lean growth. This is, however, prohibited by the difficulty and expense of recording FI on large numbers of animals, but possible if the genes responsible for differences in FI and efficiency are known. A thorough understanding of mechanisms that control FI and energy metabolism will be needed to discover such genes and to utilize genetic information on FI in a manner that will enhance production efficiency. The Yorkshire selection lines described here can be an important resource for such research into the physiological and genetic (genomic) basis of feed efficiency.

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