Effect of lower-energy, higher-fiber diets on pigs divergently selected for residual feed intake when fed higher-energy, lower-fiber diets¹

E. D. Mauch,^{*} J. M. Young,[†] N. V. L. Serão,^{*} W. L. Hsu,[‡] J. F. Patience,^{*} B. J. Kerr,[§] T. E. Weber,[#] N. K. Gabler,^{*} and J. C. M. Dekkers^{*,2}

^{*}Department of Animal Science, Iowa State University, Ames, IA 50011; [†]Department of Animal Sciences, North Dakota State University, Fargo, ND 58108; [‡]Department of Biostatistics, School of Public Health, University of Washington, Seattle, WA 98195; [§]USDA-ARS National Laboratory for Agriculture and the Environment, Ames, IA 50011; and [#]Kalmbach Feeds Inc., Upper Sandusky, OH 43351

ABSTRACT: Residual feed intake (RFI) is the difference between observed and predicted feed intake of an animal, based on growth and maintenance requirements. In Yorkshire pigs, divergent selection for increased (**Low RFI**) and decreased (**High RFI**) RFI was carried out over 10 generations (**G**) while feeding a corn- and soybean-meal-based, higher-energy, lower-fiber (**HELF**) diet. In G8 to G10, representing 4 replicates, barrows and gilts ($n = 649$) of the RFI lines were fed the HELF diet and a diet incorporating coproducts that were lower in energy and higher in dietary fiber (**LEHF**). The diets differed in ME, 3.32 vs. 2.87 Mcal/kg, and in neutral detergent fiber (**NDF**), 9.4% vs. 25.9%, respectively. The impact of the LEHF diet on 1) performance and growth, 2) diet digestibility, 3) genetic parameter estimates, and 4) responses to selection for RFI, when fed the HELF, was assessed. In general, the LEHF diet reduced the performance of both lines. When fed the HELF diet, the Low RFI pigs had lower ($P < 0.05$) ADFI (−12%), energy intake (−12%), ADG (−6%), and backfat depth (−12%); similar ($P > 0.05$) loin muscle area (**LMA**; +5%); and greater ($P < 0.05$) feed efficiency (i.e., 8% higher G:F and 7% lower RFI) than the High RFI line. These patterns of line differences were still present

under the LEHF diet but differences for ADFI (−11%), energy intake (−10%), G:F (+2%), and RFI (−6%) were reduced compared to the HELF diet. Apparent total tract digestibility (**ATTD**) of the HELF and LEHF diets was assessed using 116 barrows and gilts from G8. When fed the HELF diet, ATTD of DM, GE, N, and NDF were similar between lines ($P \geq 0.27$), but when fed the LEHF diet, the Low RFI pigs had greater digestibility (7%, 7%, 10%, and 32%) than the High RFI line ($P \leq 0.04$). To measure responses to selection for RFI and estimate genetic parameters, data from all 10 generations were used (HELF; $n = 2,310$; LEHF, $n = 317$). Heritability estimates of performance traits ranged from 0.19 to 0.63, and genetic correlations of traits between diets were high and positive, ranging from 0.87 (RFI) to 0.99 (LMA). By G10, RFI in the Low RFI line was 3.86 and 1.50 genetic SD lower than in the High RFI line when fed the HELF and LEHF diets, respectively. Taken together, the results of this study demonstrate that responses to selection for RFI when fed a HELF diet are not fully realized when pigs are fed an extremely LEHF diet. Thus, feeding diets that differ from those used for selection may not maximize genetic potential for feed efficiency.

Keywords: digestibility, feed efficiency, genetic parameters, genotype-by-diet interaction, low-quality feedstuffs, response to selection

¹This article was supported by a USDA-NIFA grant (no. 2011-6800430336). Gratitude is expressed to past and present employees of the Iowa State University Lauren Christian Swine Research Center (Madrid, IA), along with the past and present members of the Dekker Lab. Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by Iowa State University,

North Dakota State University, or the USDA and does not imply approval to the exclusion of other products that may be suitable. The USDA is an equal opportunity provider and employer.

²Corresponding author: jdekkers@iastate.edu

Received February 16, 2018.

Accepted April 11, 2018.

© The Author(s) 2018. Published by Oxford University Press on behalf of American Society of Animal Science. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com.

J. Anim. Sci. 2018.96:1221–1236
doi: 10.1093/jas/sky065

INTRODUCTION

In the US swine industry, feed costs account for over half of total production costs (Giamalva, 2014). Periods of high feed prices have resulted in interest in reducing feed costs and improving feed efficiency (FE). A common approach to mitigate high feed costs is to substitute corn and soybean-meal with less costly ingredients. However, high inclusion rates of alternative feedstuffs, which are often lower in energy and higher in dietary fiber content, may reduce performance. Genetic selection for FE is another approach to reduce feed costs. Since 2001, selection for increased and decreased FE, measured as residual feed intake (RFI), has occurred over 10 generations in Yorkshire swine at Iowa State University (ISU). Residual feed intake is defined as the difference between observed feed intake (FI) and predicted FI, given expected growth and maintenance requirements (Koch et al., 1963). Residual feed intake is a moderately heritable trait, with estimates in growing pigs ranging from 0.14 to 0.45 (Nguyen et al., 2004). Understanding the effect of combining alternative feedstuffs and RFI is pertinent for the swine industry. Interestingly, the influence of genetic background on dietary fiber utilization has been controversial (Pond et al., 1988; Kemp et al., 1991; Yen et al., 2004). Little is known about the impact of nutrition on genetic progress because genetic selection is primarily carried out in high-health facilities while feeding high-quality diets, yet producers feed a wide range of diets. Therefore, the aim of this study was to assess the effect of lower-quality feedstuffs, particularly those lower in energy and higher in dietary fiber, on pigs that have been divergently selected for RFI when fed a standard high-energy (corn and soybean-meal based) diet. Specific objectives were to assess this effect on 1) production performance, 2) feed digestibility, 3) genetic parameter estimates, and 4) responses to selection.

MATERIALS AND METHODS

Experimental procedures for this study were approved by the Iowa State University Animal Care and Use Committee (IACUC #11-1-4996S).

Experimental Design and Data Collection

ISU RFI Selection Experiment. Since 2001 at ISU, selection for increased (Low RFI) and decreased

(High RFI) FE, measured as RFI, has taken place in Yorkshire pigs (Cai et al., 2008; Bunter et al., 2010; Young et al., 2011; Young and Dekkers, 2012). In brief, single-trait selection for Low RFI was continued for 10 generations (G) based on EBV for RFI. In parallel, a randomly mated control line was maintained from the base generation (G0) through G4; selection for High RFI began in G5 and was continued through G10. During this period of selection, pigs were fed a high-energy, low-dietary fiber (corn and soybean-meal based) diet that met NRC (1998) requirements. In each generation, ~12 out of ~125 boars and ~70 out of ~125 gilts were selected per line for breeding from first parity litters, while gilts from parity 2 litters were utilized to generate additional data, except in G10 when first and second parity pigs were utilized for other purposes (detailed later). Selection and breeding occurred within line and were constructed to limit inbreeding and avoid full- and half-sibling matings.

Individual FI, as-fed, was recorded with single-space electronic FIRE feeders (Osborne Industries Inc., Osborne, KS) in pens housing 14 to 16 pigs. The targeted test period was from ~40 to 115 kg or greater BW. Through G4, BW measurements were collected every week and every other week in subsequent generations. At the end of the test period, 10th-rib ultrasonic loin muscle area (LMA) and backfat depth (BF) were measured 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). Feed intake data were edited as detailed by Casey et al. (2005), and ADFI was calculated as the average of all FI records as described by Cai et al. (2008). Phenotypic records were recorded on a total of 1,978 pigs from G0 through G7 and on the first parities of G8 and G9, while remaining generations and parities were utilized for other studies (detailed later). Standard phenotypic traits recorded over the test period were ADFI (kg/d), ADG (kg/d), G:F, feed conversion ratio (FCR = ADFI/ADG), LMA (cm²), BF (mm), and RFI (kg/d).

Line-by-Diet Performance. Barrows and gilts ($n = 649$) from the second parity litters of G8 through G10 and from the first parity of G10 of the ISU RFI lines (Low RFI, $n = 331$; High RFI, $n = 318$) were used to determine the effect of lower-quality feedstuffs on swine divergently selected

for RFI. This was accomplished utilizing a 2×2 factorial treatment design with 2 genetic lines (Low and High RFI, herein referred to as lines or RFI lines) and 2 diets in 4 replicates from October 2011 to January 2015, although these were not true genetic replicates because of the ongoing selection. Pigs came from 46 sires, 144 dams, and 170 litters, where 26 dams had 2 litters represented. As described by [Arkfeld et al. \(2015\)](#), pigs were fed 1 of 2 diets in

3 growth phases from ~40 to 118 kg BW, either a commercial standard high(er)-energy, low(er)-fiber diet (**HELF**; $n = 332$) or a low(er)-energy, high(er)-fiber diet (**LEHF**, $n = 317$) for the entirety of the test period. Both diets met or exceeded NRC (1998) requirements throughout the growing-finishing phase ([Table 1](#)). Across grow-finish phases, diets had differences in average ME content (3.32 vs. 2.87 ME Mcal/kg) and average neutral detergent fiber

Table 1. Diet formulations (as-fed basis) for grow-finish¹

	Phase 1 ²		Phase 2 ³		Phase 3 ⁴	
	HELF ⁵	LEHF ⁶	HELF ⁵	LEHF ⁶	HELF ⁵	LEHF ⁶
Ingredients (%)						
Corn	73.83	36.39	80.18	42.34	82.42	44.59
Soybean-meal, 46.5% CP	22.90	13.76	16.72	7.99	14.65	5.92
Soybean hulls	—	20.00	—	20.00	—	20.00
Corn bran	—	7.00	—	7.00	—	7.00
Wheat middlings, <9.5% CP	—	20.00	—	20.00	—	20.00
L-lysine HCl	0.25	0.25	0.25	0.25	0.25	0.25
DL-methionine	0.04	0.03	0.01	0.01	—	0.01
L-threonine	0.07	0.07	0.05	0.06	0.05	0.05
Monocalcium phosphate	1.14	0.83	1.06	0.71	0.97	0.62
Limestone	0.98	0.86	0.93	0.83	0.85	0.76
Salt	0.50	0.50	0.50	0.50	0.50	0.50
Vitamin premix ⁷	0.15	0.15	0.15	0.15	0.15	0.15
Trace mineral premix ⁸	0.15	0.15	0.15	0.15	0.15	0.15
Nutrients						
Calculated composition						
DM, %	89.50	89.40	89.40	89.30	89.40	89.30
DE, Mcal/kg	3.46	2.99	3.45	2.98	3.46	2.99
ME, Mcal/kg	3.31	2.86	3.32	2.87	3.33	2.88
NE, Mcal/kg	2.42	1.99	2.47	2.03	2.48	2.05
CP, %	17.10	16.00	14.70	13.80	13.90	13.00
ADF, %	3.50	12.50	3.30	12.30	3.20	12.20
NDF, %	9.40	25.90	9.40	25.90	9.40	25.90
Crude fiber, %	2.70	10.60	2.60	10.50	2.50	10.40
Crude fat, %	3.60	3.50	3.60	3.50	3.70	3.50
SID lysine ⁹ , %	0.95	0.84	0.80	0.70	0.75	0.65
SID lysine ⁹ :ME, g/Mcal ME	2.87	2.94	2.41	2.44	2.25	2.26
Analyzed composition¹⁰						
DM, %	92.38	93.06	—	—	90.63	91.60
GE, Mcal/kg	3.74	3.76	—	—	3.80	3.77
CP, %	16.13	15.13	—	—	12.86	11.91
NDF, %	7.89	29.49	—	—	7.75	29.32

¹Diets in G9 and G10 had 1% corn replaced with oil on an as-fed basis.

²Pigs of BW from 30 to 60 kg.

³Pigs of BW from 60 to 90 kg.

⁴Pigs of BW from 90 to 118 or greater kg.

⁵HELF = higher-energy, lower-fiber diet.

⁶LEHF = lower-energy, higher-fiber diet.

⁷Provided per kg: 459,375 IU vitamin A; 52,500 IU vitamin D; 3,750 IU vitamin E; 225 mg Vitamin K; 825 mg Riboflavin; 4,200 mg niacin; 2,025 mg Pantothenic acid; 3.75 mg Vitamin B₁₂.

⁸Provided per kg: 900-mg copper; 21-mg iodine; 12,000-mg iron; 675-mg manganese; 22.5-mg selenium; 12,000-mg zinc.

⁹SID = standardized ileal digestible.

¹⁰Feed sample collected and analyzed per diet during phases 1 and 3 of G8, parity 2.

(NDF) content (9.40 vs. 25.90% NDF) but were balanced for standardized ileal digestible (SID) lysine to ME ratio (2.5 g SID Lys/Mcal). Corn bran, soybean hulls, and wheat middlings were used to replace corn and soybean-meal to achieve ME and NDF differences. To mitigate barn dust, both diets (HELF and LEHF) were adjusted in G9 and G10 by substituting 1% corn with oil on an as-fed basis. Further details of sample distributions across replicates, lines, diet, and sex are presented in [Supplementary Table S1](#).

Prior to the start of the study, all pigs were raised using standard protocols and diets, as described by [Young et al. \(2011\)](#). In each of the 4 replicates, pigs were housed in 12 pens in the same barn and grown, on average ($\pm$ SD), from 102 ($\pm$ 11) d of age and 43.4 ($\pm$ 8.9) kg BW to 232 ($\pm$ 20) d of age and 125.6 ($\pm$ 8.8) kg BW ([Supplementary Table S1](#)). Each pen housed 14 to 16 pigs, a single-space electronic feeder, 2 nipple-type waterers, and measured 5.6×2.3 m, resulting in a minimum space of 0.82 m²/pig and ad libitum access to feed and water ([Young et al., 2011](#)). Pens were balanced, as much as possible, with even numbers of pigs from each RFI line, sex, and littermates, and were randomly assigned the HELF or LEHF diet. Prior to data collection, a 1-wk acclimation period was given for pigs to adjust to feeders, feed, and contemporary groups. Performance data were collected in a similar manner as during selection experiment; BW was measured every other week and individual FI data were recorded electronically with FIRE equipment and edited in accordance with [Cai et al. \(2008\)](#) methodology. Pigs were taken off-test in 2 or 3 groups per replicate, depending on BW. At the end of this period, two ultrasonic 10th-rib images were captured, analyzed, and averaged to determine off-test LMA and BF. Performance data included ADFI (kg/d), average daily ME intake ($\text{ADI_ME} = \text{ADFI} \times \text{average formulated ME concentration in the diet}$, Mcal/d), ADG (kg/d), G:F (kg gain/kg feed), ME efficiency ($\text{G:F_ME} = \text{ADG}/\text{ADI_ME}$, g gain/Mcal), FCR (kg feed/kg gain), FCR on ME basis ($\text{FCR_ME} = \text{ADI_ME}/\text{ADG}$, Mcal/kg gain), RFI (the residual of ADFI linear model described in Statistical Analyses, kg/d), RFI on a ME basis ($\text{RFI_ME} = \text{the residual of ADI_ME linear model described in Statistical Analyses}$, Mcal/d), LMA (cm²), and BF (mm).

Line-by-Diet Digestibility. Pigs from G8 parity 2 of the line-by-diet study were utilized to evaluate apparent total tract digestibility (ATTD) of the HELF and LEHF diets fed to pigs divergently

selected for RFI. In addition to the pigs described above for the line-by-diet performance study, additional contemporary pigs ($n = 192$) were put on-test in the same barn as line-by-diet performance pigs in 8 pens of 24 pigs with conventional 5-space feeders (Smidley Mfg. Inc., Britt, IA). These pens were balanced for RFI line, sex, and littermates. Half of then pens were fed each diet (HELF or LEHF).

All G8 parity 2 pigs (i.e., contemporary pigs plus previously mentioned line-by-diet performance pigs) were fed diets ([Table 1](#)) in meal form with 0.5% titanium dioxide (TiO₂) added as an indigestible marker during the first growth phase from ~40 to 60 kg BW. In total, 116 ($n = 36$ line-by-diet, $n = 80$ contemporary pigs) randomly sampled pigs were utilized to evaluate the ATTD of the HELF and LEHF diets fed to pigs divergently selected for RFI.

Feed samples from the first growth phase were collected from both HELF and LEHF diets prior to administration into the individual feeders. Fresh fecal grab samples were obtained from a total of 116 pigs when they weighed between ~40 and 60 kg BW and between 19 and 21 d after the initiation of diet treatments (Low RFI-HELF, $n = 23$; Low RFI-LEHF, $n = 35$; High RFI-HELF, $n = 24$; High RFI-LEHF, $n = 34$). All fecal and feed samples were stored at -20°C until further processing. Feed and fecal samples were dried at 70°C in a forced-air oven to constant weight in order to determine DM and then ground through a 1-mm screen prior to further analyses. Feed and fecal samples were analyzed for GE using an isoperibol bomb calorimeter (Model 1282, Parr Instrument Company, Moline, IL) with benzoic acid used as a standard, nitrogen (N) using thermocombustion (VarioMax, Elementar Analysensysteme GmbH, Hanau, Germany), NDF using filter-bag technology (Ankom2000, method #8-ADF, method #9-NDF, Ankom Technology, Macedon, NY), and TiO₂ by digesting the samples in sulfuric acid and hydrogen peroxide with subsequent absorbance measured using a ultraviolet spectrophotometer (Method 988.05; [AOAC, 1978](#)). Apparent total tract digestibility was determined indirectly by indigestible marker methodology for DM, GE, N, and NDF using the following equation ([Oresanya et al., 2008](#)):

ATTD of x =

$$\left[1 - \left(\frac{\text{Fecal amount of x}}{\text{Feed amount of x}} \right) * \left(\frac{\text{Feed TiO}_2}{\text{Fecal TiO}_2} \right) \right]$$

* 100, where x = DM, GE, N or NDF.

Statistical Analyses

Line-by-Diet Performance. Linear mixed models were fit in SAS v. 9.4 (SAS Institute Inc., Cary, NC) utilizing the GLIMMIX procedure, using pen as the experimental unit and pig as the observational unit. Outliers were removed for each trait individually using the UNIVARIATE procedure in SAS for studentized residuals exceeding ± 3 SD. Pigs that did not reach an off-test BW greater than 102 kg were also removed from the analysis. For all traits, fixed class effects of replicate, line, diet, sex, and line-by-diet interaction were fitted, along with random effects of sire, dam, and pen nested within replicate. An additional fixed covariate of on-test age was fitted for ADFI, ADI_ME, ADG, G:F, G:F_ME, FCR, and FCR_ME, as well as off-test BW for BF and LMA. Ultrasound technician within replicate was fit as an additional fixed effect of for BF and LMA. To calculate RFI and RFI_ME, additional fixed covariates were fit for ADFI and ADI_ME of ADG, BF, on-test age, on-test BW, off-test BW, and metabolic BW (calculated as $BW^{0.75}$), all deviated from the mean within each replicate. These covariates were fitted within diet because partial regression coefficients differed between diets ($P < 0.1$ for 5 out of 6 covariates), as expected based on the different composition of the diets. Significant ($P < 0.1$) interactions of fixed effects were retained in the model for each trait. Models for each trait are shown in [Supplementary Tables S2 and S3](#).

Line-by-Diet Digestibility. Utilizing the GLIMMIX procedure in SAS v. 9.4, linear mixed models were fit for each ATTD trait. Fixed effects included line, diet, sex, feeder type, on-test BW, line-by-diet interaction, and other significant ($P < 0.1$) interactions between fixed effects. Random effects included sire, dam, and pen. Outlier removal was performed as previously outlined. Models for traits are shown in [Supplementary Table S4](#).

Genetic Parameters and Responses to Selection. Phenotypic records ($n = 2,627$) for ADG, ADFI, FCR, LMA, BF, and RFI from both the RFI selection ($n = 1,978$) and line-by-diet performance ($n = 649$) studies were utilized to estimate genetic parameters and to quantify direct and correlated responses to selection for RFI. Pigs were produced from 258 sires, 813 dams, and 1,138 litters. Phenotypic records from pigs fed the HELF ($n = 2,310$) or LEHF ($n = 317$) diet were analyzed for (in)direct and correlated response to single-trait selection on RFI when fed the HELF diet.

After removal of outliers (as described previously) and animals with the end of test BW less than

102 kg, bivariate (for RFI) and trivariate (for all other traits) animal models that treated phenotypes as separate traits for the HELF and LEHF diets were fit in ASReml v.4 ([Gilmour et al., 2015](#)). For all trivariate models, the calculation of **RFI*** was included as the third trait to account for selection. Fixed class effects of line, sex, and pen-cohort were fit for all traits, along with random effects of litter and animal. On-test age was fit as a fixed covariate for ADFI, FCR, RFI, and ADG; off-test BW was fit for BF and LMA. To calculate RFI, the additional fixed covariates were fit for ADFI, including on-test BW, metabolic BW, ADG within generation, and off-test BF. From the RFI model, the main effect of line, additive genetic component, and residual were summed to calculate RFI*. For all models, residual and litter covariances were constrained to 0. The numerator relationship matrix was constructed from a pedigree containing 18,227 individuals. Models for each trait are shown in [Supplementary Table S5](#). Responses to selection were quantified based on the average EBV of phenotyped individuals within line, generation, and diet plus the effect of line, and deviated from the average EBV of the base population, which was computed as the average EBV of all pigs in the pedigree ($n = 1,522$) plus half of the line effect to account for approximately half of the base population being from each RFI line. Recall that line was fit in all models as a fixed class effect, capturing part of the genetic component, which was why this effect must be added back to represent the entire genetic response to selection.

RESULTS

Line-by-Diet Performance

The effects of line, diet, and their interaction on performance traits are shown in [Table 2](#).

For ADG, both line ($P < 0.0001$) and diet ($P < 0.0001$) were significant, but there was no significant line-by-diet interaction ($P = 0.32$). Averaged across lines, ADG was significantly lower when pigs were fed the LEHF diet at $0.59 (\pm 0.01)$ kg/d compared to $0.70 (\pm 0.01)$ kg/d for the HELF diet. Regardless of diet, the Low RFI line was slower growing at $0.62 (\pm 0.01)$ kg/d compared to $0.67 (\pm 0.01)$ kg/d for the High RFI line.

For ADFI, line ($P < 0.0001$) and diet ($P = 0.003$) were significant, and there was no significant line-by-diet interaction ($P = 0.45$). Regardless of line, pigs fed the HELF diet consumed significantly less feed, $2.36 (\pm 0.03)$ kg/d, than the LEHF diet fed pigs, $2.48 (\pm 0.03)$ kg/d. Regardless of diet, Low

Table 2. Least squares means (SE) of performance traits for the line-by-diet study

Trait ¹	N	Low RFI		High RFI		P-values		
		HELF ²	LEHF ³	HELF ²	LEHF ³	Line	Diet	Line × Diet
ADG, kg/d	640	0.68 ^b (0.01)	0.56 ^d (0.01)	0.72 ^a (0.01)	0.62 ^c (0.01)	<0.0001	<0.0001	0.32
ADFI, kg/d	636	2.21 ^d (0.04)	2.34 ^c (0.04)	2.51 ^b (0.04)	2.62 ^a (0.04)	<0.0001	0.003	0.45
ADI_ME, Mcal/d	638	7.32 ^b (0.11)	6.74 ^c (0.11)	8.33 ^a (0.11)	7.51 ^b (0.11)	<0.0001	<0.0001	0.02
G:F, kg gain/kg feed	635	0.309 ^a (0.004)	0.241 ^c (0.004)	0.287 ^b (0.004)	0.236 ^c (0.004)	<0.0001	<0.0001	<0.0001
G:F_ME, g gain/Mcal	635	93.12 ^a (1.32)	83.98 ^{b,c} (1.34)	86.32 ^b (1.34)	82.15 ^c (1.35)	0.0002	0.0001	<0.0001
FCR, kg feed/kg gain	626	3.36 ^c (0.08)	4.29 ^a (0.08)	3.61 ^b (0.08)	4.38 ^a (0.08)	0.0003	<0.0001	0.003
FCR_ME, kg gain/Mcal	628	10.82 ^c (0.18)	12.05 ^{a,b} (0.19)	11.63 ^b (0.19)	12.31 ^a (0.19)	0.0003	0.0001	0.001
LMA, cm ²	629	46.46 ^a (0.57)	45.05 ^b (0.58)	44.20 ^b (0.59)	43.74 ^b (0.59)	0.02	0.01	0.13 ⁴
BF, mm	634	21.41 ^b (0.59)	17.93 ^c (0.60)	24.24 ^a (0.62)	20.87 ^b (0.61)	0.004	<0.0001	0.85 ⁴
RFI, kg/d	633	2.15 ^b (0.03)	—	2.31 ^a (0.03)	—	<0.0001	NA ⁵	NA ⁵
		—	2.53 ^b (0.03)	—	2.69 ^a (0.03)			
RFI_ME, Mcal/d	635	7.13 ^b (0.09)	—	7.67 ^a (0.10)	—	<0.0001	NA ⁵	NA ⁵
		—	7.25 ^b (0.10)	—	7.70 ^a (0.09)			

^{a-d}Letters represent statistical differences between estimates within each row ($P < 0.05$).

¹ADI_ME = average daily metabolizable energy intake, G:F_ME = gain to feed ratio on metabolizable energy basis, FCR = feed conversion ratio, FCR_ME = feed conversion ratio on metabolizable energy basis, LMA = off-test loin muscle area, BF = off-test backfat depth, RFI = residual feed intake, RFI_ME = residual feed intake on metabolizable energy basis.

²HELF = higher-energy, lower-fiber diet.

³LEHF = lower-energy, higher-fiber diet.

⁴LMA and BF had significant ($P < 0.05$) line × diet × generation–parity interaction.

⁵RFI and RFI_ME were calculated as adjusted ADFI within diet thus the difference between lines cannot be compared across diets.

RFI line pigs consumed less feed, 2.27 (± 0.03) kg/d, than High RFI line pigs, 2.57 (± 0.03) kg/d.

Considering ADFI on the basis of ME, ADI_ME, accounts for differences in ME content of the HELF and LEHF diets (3.32 vs. 2.87 Mcal/kg, respectively). This resulted in a significant line-by-diet interaction ($P = 0.02$) for ADI_ME that was not observed for ADFI on a weight basis. The Low RFI line consumed 1.01 Mcal/d less ME than the High RFI line when fed the HELF diet and 0.77 Mcal/d ME less when fed the LEHF diet ($P = 0.02$). As a consequence, the reduction in ADI_ME when feeding the LEHF compared to the HELF diet was smaller for the Low RFI line (0.58 Mcal/d) than for the High RFI line (0.82 Mcal/d).

A significant line-by-diet interaction was also observed for G:F ($P < 0.0001$). The Low RFI line fed the HELF diet had the highest feed efficiency compared to each of the other treatments ($P < 0.05$) and gained 0.309 kg BW/kg of feed consumed. High RFI line pigs fed the HELF were more efficient than pigs from either RFI line fed the LEHF diet ($P < 0.05$). On the LEHF diet, G:F was not significantly different between the RFI lines ($P = 0.21$), although, numerically, the Low RFI was more efficient than the High RFI line (0.241 vs. 0.236 kg BW gain/kg feed, respectively). Line differences (High minus Low RFI) on the HELF diet (-0.023 kg BW gain/kg feed) were significantly

($P < 0.0001$) different from the line differences on the LEHF diet (-0.005 kg BW gain/kg feed).

There was a significant line-by-diet interaction for G:F_ME ($P < 0.0001$). Similar to results for G:F, pigs from the Low RFI line fed the HELF diet had the highest efficiency, with an average gain of 93.12 g BW/Mcal of ME consumed ($P < 0.05$). For the HELF diet, the line difference (High minus Low RFI) was -6.80 g BW gain/Mcal, with the High RFI line having significantly less gain per unit energy consumed than the Low RFI line ($P < 0.0001$). For the LEHF diet, the line difference (High minus Low RFI) was smaller, -1.83 g BW gain/Mcal, which resulted in nonsignificant differences in ME efficiency between the RFI lines ($P = 0.14$). The line difference observed on the HELF diet (-6.80 g/Mcal) was significantly different from the line difference on the LEHF diet (-1.83 g/Mcal) and thus a line-by-diet interaction was observed ($P < 0.0001$). FCR and FCR_ME results reflected the similar differences in efficiencies between lines and diets as G:F and G:F_ME.

Since RFI was computed within diet, using separate regression coefficients for growth- and maintenance-related covariates, estimates of effects and contrasts that include diet comparisons are not interpretable. Thus, only within-diet comparisons will be considered. For both diets, there was a significant line difference for RFI, with the High

RFI consuming 0.16 kg/d more than the Low RFI line after adjusting for expected growth and maintenance requirements ($P < 0.0001$). Thus, for both diets, the Low RFI line was more feed efficient compared to the High RFI line, when measured as RFI.

When considering RFI on an energy basis, RFI_ME, similar results were observed as for RFI. The High RFI line consumed significantly more ME per day than the Low RFI line at 0.54 Mcal/d for the HELF diet ($P < 0.0001$) and 0.45 Mcal/d for the LEHF diet ($P < 0.0001$). For both diets, the Low RFI line was more efficient than the High RFI line, when measured as RFI_ME.

In general, off-test LMA was lower when the LEHF diet was fed for both RFI lines, and, within diet, LMA was not significantly different between the RFI lines. However, a significant 3-way interaction of line-by-diet-by-replicate was observed for LMA ($P < 0.0001$). Line-by-diet results are presented in Table 2, and line-by-diet-by-replicate results are presented in Supplementary Figure S1. Except for G8, feeding the LEHF diet decreased LMA ($P < 0.01$). On the LEHF diet, the Low RFI line had greater LMA than the High RFI line in G8 ($P < 0.05$); this pattern was also observed in G9 and G10, but these differences were not statistically significant ($P > 0.05$). On the HELF diet, line differences for LMA were more variable across replicates. Specifically, in G8, the High RFI line had significantly lower LMA than the Low RFI line fed the HELF diet ($P < 0.05$), whereas, in G9 and G10, the High RFI line had numerically higher LMA than the Low RFI line, but these differences were not statistically significant ($P > 0.05$).

Across all replicates and diets, the Low RFI line had numerically lower BF depth at off-test, but this was not always statistically significant. Moreover, a significant line-by-diet-by-replicate interaction was observed for BF ($P = 0.03$). Line-by-diet results are presented in Table 2, while line-by-diet-by-replicate results are presented in Supplementary Figure S1.

Across replicates, the trends for BF were similar for each line-by-diet combination, but the magnitude of those trends varied, thus resulting in a 3-way interaction. Feeding the LEHF diet significantly reduced BF depth compared to the HELF diet ($P < 0.01$). In G8, the effect of the LEHF diet compared to the HELF diet, across RFI lines, was the most pronounced ($P < 0.0001$). Lines had significantly different BF when fed the LEHF diet in G9 and G10 parity 2 ($P < 0.05$) but not in G8 and G10 parity 1. For the HELF diet, the RFI lines were only significantly different in G8 ($P < 0.05$), yet all generations had the same numerical pattern.

Line-by-Diet Digestibility

Results for ATTD traits are shown in Table 3. All ATTD coefficients had significant line-by-diet interactions ($P < 0.10$), with the exception of the ATTD of NDF ($P = 0.24$). Similar patterns of ATTD were observed between line-by-diet combinations for DM, GE, N, and NDF. In general, pigs fed the HELF diet had higher digestibility coefficients than the LEHF fed pigs. Additionally, digestibility coefficients were not significantly different between the RFI lines when fed the HELF diet ($P \geq 0.27$), although, numerically, the Low RFI line had greater digestibility coefficients than the High RFI line. When the LEHF diet was fed, the Low RFI line had significantly higher ATTD coefficient estimates than the High RFI line ($P \leq 0.04$).

For DM, a significant line-by-diet interaction ($P = 0.03$) was observed since the High RFI line had a more severe decrease (-29.41%) in ATTD of DM from the HELF to the LEHF diet compared to the Low RFI line (-26.27%).

For ATTD of GE, on the LEHF diet, the Low RFI line had a significantly higher digestibility than the High RFI ($P = 0.001$). There was a trend for a line-by-diet interaction ($P = 0.06$), which was driven by the decrease in ATTD of GE from the HELF to

Table 3. Apparent total tract digestibility least squares means (SE) for the line-by-diet digestibility study

ATTD ¹ , %	N	Low RFI		High RFI		P-values		
		HELF ²	LEHF ³	HELF ²	LEHF ³	Line	Diet	Line × Diet
DM	116	85.74 ^a (1.24)	59.47 ^b (1.08)	84.94 ^a (1.21)	55.53 ^c (1.10)	0.04	<0.0001	0.03
GE	116	84.91 ^a (1.32)	58.49 ^b (1.15)	84.02 ^a (1.29)	54.69 ^c (1.17)	0.06	<0.0001	0.06
Nitrogen	116	80.13 ^a (1.24)	61.94 ^b (1.04)	78.81 ^a (1.22)	56.12 ^c (1.05)	0.002	<0.0001	0.004
Neutral detergent fiber	114	47.99 ^a (2.75)	20.19 ^b (2.19)	47.31 ^a (2.67)	15.28 ^c (2.28)	0.02	<0.0001	0.24

^{a-c}Letters represent statistical differences between estimates within each trait ($P < 0.05$).

¹ATTD = apparent total tract digestibility.

²HELF = higher-energy, lower-fiber diet.

³LEHF = lower-energy, higher-fiber diet.

the LEHF in the High RFI line (-29.33%) compared to the Low RFI line (-26.42%).

As observed for ATTD of DM and GE, the significant line-by-diet interaction ($P = 0.004$) for ATTD of N was the result of a larger decrease in digestibility for the High RFI (-22.69%) than the Low RFI (-18.19%) line when switching from the HELF to the LEHF diet.

As expected, the ATTD of NDF was lower than that of DM, GE, or N. The effects of both line ($P = 0.02$) and diet ($P < 0.0001$) were significant, but the interaction was not significant ($P = 0.24$). Digestibility of NDF was significantly higher for the HELF diet, 47.65% , than the LEHF diet, 17.73% ($P < 0.0001$). For the HELF diet, ATTD of NDF was similar for the RFI lines at $\sim 48\%$ ($P = 0.81$). However, the Low RFI line did have significantly higher digestibility than the High RFI line when fed the LEHF diet ($P = 0.04$). A significant line-by-diet interaction was not observed for ATTD of NDF because differences in digestibility between the 2 diets were not significantly different for the Low and High RFI lines (-27.80% and -32.03% , respectively), as a result of the higher SE of the estimates than for the other ATTD traits.

Genetic Parameters and Responses to Selection

Genetic parameter estimates from the bivariate animal model fit for RFI and the trivariate models fit for all other traits are reported in Table 4. Heritability estimates for ADG, ADFI, FCR, LMA, BF, and RFI ranged from moderate to high

across diets and traits. The selection trait, RFI, was estimated to be moderately heritable at $0.24 (\pm 0.05)$ for the HELF diet and $0.35 (\pm 0.17)$ for the LEHF diet. For the other traits, heritability estimates were similar between diets, except for BF. Common litter effects ranged from 0 to 0.18, with SE ranging from 0 to 0.10.

Within a trait, the phenotypic and genetic SD were similar between diets, with the largest differences observed for FCR. Across traits, the HELF diet usually had lower phenotypic and genetic SD than the LEHF diet; furthermore, the SE was larger for the LEHF diet than the HELF diet. Phenotypic SD differences between HELF and LEHF diet were in part due to energy differences in the diets, although not completely. For example, the phenotypic SD for ADFI was 0.20 kg/d for the HELF diet, compared to 0.27 kg/d for the LEHF diet, but on an energy basis, the phenotypic SD were more similar (0.66 and 0.77 Mcal/d, respectively).

Environmental and, therefore, phenotypic correlations could not be estimated between the 2 diets because no pig was fed both diets. For all traits, estimates of genetic correlations between diets were high and positive and ranged from 0.87 to 0.99 , with SE ranging from 0.17 to 0.52 . Genetic correlations between diets for ADG, LMA, and BF were high, with estimates greater than or equal to 0.95 . Other traits had genetic correlation estimates further from 1, particularly RFI and ADFI, which had estimates between the diets of 0.87 ± 0.28 and 0.89 ± 0.17 , respectively. Due to limited observations for the LEHF diet, the power to estimate

Table 4. Genetic parameter estimates¹ (SE) from bi- and tri-variate² analyses for performance traits for 2 diets

Trait ³	Diet ⁴	h^2 (SE)	c^2 (SE)	Phenotypic SD (SE)	Genetic SD (SE)	r_g (SE)
ADG, kg/d	HELF	0.39 (0.05)	0.03 (0.03)	0.09 (0.02)	0.05 (0.02)	0.95 (0.17)
	LEHF	0.41 (0.13)	0.00 (0.00)	0.07 (0.02)	0.05 (0.03)	
ADFI, kg/d	HELF	0.43 (0.05)	0.01 (0.02)	0.20 (0.04)	0.13 (0.05)	0.89 (0.17)
	LEHF	0.41 (0.14)	0.00 (0.00)	0.27 (0.08)	0.17 (0.11)	
FCR, kg/kg	HELF	0.31 (0.05)	0.04 (0.02)	0.26 (0.05)	0.14 (0.06)	0.90 (0.31)
	LEHF	0.22 (0.13)	0.00 (0.00)	0.51 (0.16)	0.24 (0.19)	
LMA, cm ²	HELF	0.51 (0.06)	0.07 (0.03)	4.63 (0.94)	3.30 (1.27)	0.99 (0.23)
	LEHF	0.45 (0.21)	0.12 (0.10)	4.91 (1.64)	3.31 (2.42)	
BF, mm	HELF	0.63 (0.06)	0.07 (0.03)	3.64 (0.77)	2.88 (1.04)	0.95 (0.52)
	LEHF	0.19 (0.18)	0.18 (0.10)	3.90 (1.19)	1.69 (1.68)	
RFI, kg/d	HELF	0.24 (0.05)	0.09 (0.03)	0.13 (0.02)	0.06 (0.03)	0.87 (0.28)
	LEHF	0.35 (0.17)	0.00 (0.00)	0.22 (0.07)	0.13 (0.10)	

¹Genetic parameters: h^2 = narrow-sense heritability, c^2 = common litter effect, r_g = genetic correlation between the trait on the HELF and LEHF diets.

²Trivariate models fit for ADG, ADFI, FCR, LMA, and BF; bivariate model fits for RFI.

³FCR = feed conversion ratio, LMA = off-test loin muscle area, BF = off-test backfat depth, RFI = residual feed intake.

⁴HELF = higher-energy, lower-fiber diet; LEHF = lower-energy, higher-fiber diet.

Figure 1. Direct and correlated responses to selection for divergent residual feed intake (RFI) while feeding a higher-energy, lower-fiber diet (HELHF, left panel) and correlated responses to selection for RFI and component traits given a lower-energy, higher-fiber diet (LEHF, right panel). BF, off-test backfat depth; FCR, feed conversion ratio; LMA, off-test loin muscle area; RFI, residual feed intake.

genetic correlations between diets was low and the SE were large. Therefore, none of the genetic correlations were significantly different from 1.

Figure 1 depicts estimates of responses to selection from G0 to G10 for pigs fed the HELHF diet (left panel) and the LEHF diet (right panel), while Table 5 reports the line differences in average EBV (High minus Low RFI) for G8 through G10. Recall that selection for High RFI began in G5 and that pigs were only fed the LEHF diet in G8 through G10. In Figure 1, for the HELHF diet, a general trend was observed of decreasing genetic means for traits in the Low RFI line as selection progressed, except for LMA, which had a positive response to selection. For the High RFI line, genetic means were positive from G6 onward for all traits, except for LMA, which had a mostly negative response to selection. Consistent with these results, correlated responses to selection on the LEHF diet observed negative genetic means for the Low RFI line for all traits, except for LMA. For the LEHF diet, the High RFI line was estimated to have negative genetic means in G8 and G9, but they were positive by G10 for ADFI, RFI, and LMA, while ADG and BF had positive genetic means throughout. However, the negative genetic means of the High RFI line fed the LEHF diet were greater than (i.e., closer to zero) those of the Low RFI line, which agreed with line differences expected based on the HELHF results. By G10, the difference in the genetic means of the Low

and High RFI lines for the selection trait, RFI, was 3.86 genetic SD for the HELHF diet and 1.50 genetic SD for the correlated response to selection on the LEHF diet. For ADFI, line differences in G10 were 3.50 genetic SD for the HELHF and 2.32 genetic SD for the LEHF diet. In G10, all remaining traits, for both diets, had line differences lower than 2 genetic SD. When averaging G8 through G10 (Table 5), smaller line differences were observed for the LEHF diet than for the HELHF diet, in agreement with the Figure 1 results. Interestingly, line differences for ADI_ME, RFI, and RFI_ME when fed the LEHF diet were nearly half of the HELHF line differences, while LMA and BF had larger line differences for the LEHF diet than the HELHF diet.

DISCUSSION

The objectives of this study were to investigate the effect of a lower-energy, higher-fiber diet on 1) production performance, 2) feed digestibility, 3) the genetic relationships, and 4) selection responses in pigs divergently selected for RFI when fed a higher-energy, lower-fiber diet.

Line-by-Diet Performance

In agreement with previous studies on the ISU RFI lines when fed standard corn- and soybean-meal-based diets (Cai et al., 2008; Bunter et al., 2010), the Low RFI line had reduced FI, lower

Table 5. RFI line differences (High RFI minus Low RFI) from phenotypic and genetic models for 2 diets

Trait ¹	HELF ²		LEHF ³	
	Phenotypic ⁴	Genetic ⁵	Phenotypic ⁴	Genetic ⁵
ADG, kg/d	0.04	0.05	0.05	0.04
ADFI, kg/d	0.31	0.33	0.28	0.22
ADI_ME, Mcal/d	1.01	1.11	0.77	0.64
G:F, kg gain/kg feed	-0.023	—	-0.005	—
G:F_ME, g gain/Mcal	-6.80	—	-1.83	—
FCR, kg feed/kg gain	—	0.23	—	0.05
FCR_ME, Mcal/kg gain	—	0.76	—	0.15
LMA, cm ²	-2.27	-1.67	-1.31	-2.25
BF, mm	2.82	2.50	2.93	3.01
RFI, kg/d	0.16	0.21	0.16	0.12
RFI_ME, Mcal/d	0.54	0.69	0.45	0.34

¹ADI_ME = average daily metabolizable energy intake, G:F_ME = gain to feed ratio on metabolizable energy basis, FCR = feed conversion ratio, FCR_ME = feed conversion ratio on metabolizable energy basis, LMA = off-test loin muscle area, BF = off-test backfat depth, RFI = residual feed intake, RFI_ME = residual feed intake on metabolizable energy basis.

²HELF = higher-energy, lower-fiber diet.

³LEHF = lower-energy, higher-fiber diet.

⁴Phenotypic results from line-by-diet performance analyses.

⁵Genetic results from line-by-diet bi- and tri-variate, animal model analyses, averaged across G8 to G10.

growth, less BF, greater FE (i.e., lower RFI and greater G:F), and similar LMA compared to the High RFI line. In independent, but similar, divergent RFI lines from INRA in France, similar line differences were reported, although differences in ADG were smaller (Gilbert et al., 2017). The decreased growth rate observed in the ISU Low RFI line was less than expected given the large decrease in FI. These findings support that selection for RFI when feeding commercially, standard diets have been successful and that line differences on such diets were similar in this study to previous studies.

Previous studies have been conducted to understand the effects of higher dietary fiber or higher-energy diets on pig performance. High-fiber diets, incorporating 35% and 80% dehydrated alfalfa meal (respectively), have been reported to reduce growth, G:F, BF, and LMA, while reducing or not affecting FI (Varel et al., 1984; Pond et al., 1988). Diets lower in energy concentrations, with energy contents ranging from 3.30 to 3.48 ME Mcal/kg, 3.09 to 3.58 DE Mcal/kg, and 3.32 to 3.54 ME Mcal/kg tested (respectively), have been reported to have variable effects, but they have often been observed to result in reduced growth, energy intake, G:F, and BF; similar LMA; and increased FI (Apple et al., 2004; Beaulieu et al., 2009; Hinson et al., 2011). Baird et al. (1975) studied the interaction of crude fiber (2.09% vs. 8.87%) and energy (3.50 vs. 2.94 ME Mcal/kg), but did not observe a significant interaction between fiber and energy content. In the

present study, the LEHF diet resulted in reduced ADG, energy intake, G:F, G:F_ME, BF, LMA (in most replicates), and increased FI compared to the HELF diet. Interestingly, both RFI lines increased ADFI in order to compensate for the extreme reduction in energy provided by the LEHF diet, yet both lines failed to achieve the same energy intake as obtained when fed the HELF diet. In general, the results of this study align well with previous effects reported for high-fiber diets on ADG, G:F, BF, and LMA, while changes in energy intake and FI observed in this study also agree well with previously observed effects of lower-energy diets. However, analyzing the effect of diet alone is not appropriate for many traits in this study because line-by-diet interactions were observed.

For the LEHF diet, the Low RFI line had reduced FI, energy intake, growth, and BF (numerically); similar LMA and FE based on G:F and G:F_ME; and increased FE based on RFI and RFI_ME compared to the High RFI line. The line differences were in the same direction but generally smaller for the LEHF diet than those observed for the HELF diet, particularly for G:F and G:F_ME. In a similar line-by-diet study carried out with the INRA RFI lines (Montagne et al., 2014), pigs were fed a lower-energy, higher-fiber diet (1.79 vs. 2.31 NE Mcal/kg and 31.14% vs. 15.80% NDF than a control diet) that incorporated wheat bran, dehydrated sugar beet pulp, and soybean hulls to increase the dietary fiber content and reduce the NE. In the study by Montagne et al. (2014), the Low RFI line ate

less (-0.04 kg/d), grew faster (0.29 kg/d), and had greater G:F (0.13 kg gain/kg feed) compared to the High RFI line when fed a LEHF diet. These line differences were in the same direction, yet smaller than those observed for the INRA RFI lines fed a control diet, which agrees with the results observed in the current study. Both the ISU and INRA studies observed that the Low RFI line continued to be more feed efficient and eat less than the High RFI line when given a lower-quality feed than was fed during selection. Differences observed in ISU and INRA RFI lines for growth response to lower-quality feeds were likely due to a combination of diet composition differences, genetic background, and age of pigs during the experiments.

In the current study, line-by-diet interactions were observed for ADI_ME, G:F, and G:F_ME. Unlike the current study, [Fix et al. \(2010\)](#) did not observe a genetic by feeding program interaction for G:F at any stage of production when comparing 1980 vs. 2005 genetics and feeding programs (3.30 vs. 3.55 ME Mcal/kg average, respectively). A possible reason why an interaction was observed in the current study but not by [Fix et al. \(2010\)](#) may be because both feeding programs used by [Fix et al. \(2010\)](#) had higher-energy contents than the LEHF diet fed in this present study or because genetic lines from 1980 to 2005 were not selected solely for improved FE.

Interestingly, the line-by-diet interaction was significant for ADFI on an energy basis but not on a weight basis. In order to confirm this interaction, models fitting 2 additional pigs that differed after quality control between ADFI and ADI_ME were assessed, with no significant differences in results (data not shown). Models fitting heterogeneous variances for each diet were also tested for ADI_ME, but they gave a similar fit based on Akaike information criterion as the model utilized here (data not shown). The High RFI line increased its feed consumption by 4.5% on a weight basis when switching from the HELF to the LEHF diet but, due to the lower energy density of the LEHF diet, had a 9.8% decrease in energy intake. The Low RFI line was better able to accommodate the reduction in energy density provided by the diet and increased feed consumption by 6.3% on a weight basis when switching from the HELF to the LEHF diet, although this was not significantly different from the 4.5% increase in ADFI observed for the High RFI line ($P = 0.45$). However, this did result in a significantly smaller decrease in energy intake for the Low RFI line (-8.0%) than for the High RFI line (-9.8%). If one assumes that the RFI lines were eating to meet energy requirements for maximum growth potential

when fed a nonlimiting diet (i.e., the HELF diet), then it may stand to reason that when fed a limiting diet (i.e., the LEHF diet) the RFI lines were no longer able to consume enough feed to meet energy requirements for their maximum growth potential and they were, therefore, eating to maximum gastrointestinal tract capacity ([Patience, 2012](#)). Based on this logic, the Low RFI line was able to meet a larger proportion of its energy requirements for maximum growth on the LEHF diet than the High RFI line (92.0% vs. 90.2% , respectively, based on ADI_ME results in [Table 2](#)). In addition, the Low RFI line was able to increase FI to a higher degree than the High RFI line when switching from the HELF to LEHF diet, which suggests the Low RFI was utilizing less of its maximum FI capacity when fed the HELF diet than the High RFI line. This suggests that selection for Low RFI resulted in lower-energy requirements for the Low RFI line without altering the maximum FI capacity. Taking this one step further, the significant line-by-diet interactions observed for G:F and G:F_ME suggest that the Low RFI line had a greater decrease in these measures of FE than the High RFI line when comparing the HELF and LEHF diets. This resulted in more non-significant differences in G:F and G:F_ME between RFI lines when fed the LEHF diet, although the Low RFI line remained numerically more efficient. If the Low RFI line was able to meet 1.8% more of its energy requirements for maximum growth on the LEHF diet, this could biologically explain the slight advantage in G:F and G:F_ME that was observed for the Low RFI line compared to the High RFI line when fed the LEHF diet.

Feeding a lower-quality diet negatively impacted most performance traits, such as reducing ADG and increasing ADFI. The observed differences between RFI lines when fed the HELF diet were also observed when pigs were fed the LEHF, although they were smaller and not always statistically significant. These results suggest that not all genetic progress made when selection is performed while feeding high-quality diets will carry over if pigs are subsequently fed lower-quality feedstuff. It should be noted, however, that the LEHF diet used in this study was more extreme than typical diets that include coproducts in the US, which suggests that the negative impacts of the LEHF diet observed in this study may be more extreme than expected from a typical coproduct US swine diet. In the end, selecting for RFI when feeding a high-quality diet resulted in some responses in FE when feeding a lower-quality diet but these responses for RFI and RFI_ME were

reduced, and the full genetic potential was not realized for RFI.

Line-by-Diet Digestibility

Apparent total tract digestibility coefficients were greater for the HELF diet than the LEHF diet, which was expected based on the extreme increase in dietary fiber in the LEHF diet. [Moore et al. \(1988\)](#) found that higher-fiber diets (14.3% to 17.3% NDF) resulted in reduced ATTD of GE, DM, and N in growing pigs, which supports the findings of this study. In addition, the current study found the higher-fiber diet to have lower NDF digestibility. This is not surprising since the digestibility of dietary fiber has been found by many researchers to be lower and more variable than that of other nutrients, such as starch ([Jha and Berrocso, 2015](#)). In the previously mentioned INRA RFI line-by-diet study ([Montagne et al., 2014](#)), the high-fiber diet also had lower ATTD of GE, DM, and N, but had greater digestibility of NDF, which is opposite of the results presented here. This is possibly due to differences in the source of dietary fiber, which in the INRA high-fiber diet was primarily contributed by increased inclusion of wheat bran, dehydrated sugar beet pulp, and soybean hulls in comparison to the use of corn bran, wheat middlings, and soybean hulls in this study. In addition, standard European swine diets, such as those used in the INRA experiment, tend to have greater dietary fiber content compared to commercial US diets, which corresponded to a smaller increase in fiber between the INRA control (i.e., the diet fed during INRA RFI selection) and the high-fiber diet compared to the diets used in the current study (97% vs. 194% NDF increase on a DM basis, respectively).

In general, significant differences in ATTD of key nutrients and GE between the RFI lines were not observed when the HELF diet was fed, which fails to validate previous findings within the ISU RFI lines. [Harris et al. \(2012\)](#) found that when a corn- and soybean-meal-based diet was fed, Low RFI gilts had significantly greater ATTD of GE (+1.5%), DM (+1.4%), and N (+2.2%) compared to the High RFI line. Numerically, the Low RFI line also had higher GE, DM, and N digestibility in the current study (+0.89%, +0.80%, and +1.32%, respectively), but none of these increases were significant ($P > 0.27$). These differences in results could be due to differences in age and initial BW (~50 vs. 62 kg BW), housing (group-penned vs. individual metabolism crates), or sex differences (barrows and gilts vs. gilts only) between the current study and the

study by [Harris et al. \(2012\)](#), respectively. In addition, the level of digestibility observed in the current study for the HELF were lower for DM, GE, and N than those observed by [Harris et al. \(2012\)](#). On the LEHF diet, however, the Low RFI line did have significantly greater ATTD of GE (+3.8%), DM (+3.9%), N (+5.8%), and NDF (+4.9%) than the High RFI line, which were in the same direction with greater digestibility differences than those observed by [Harris et al. \(2012\)](#).

In comparison to the INRA RFI lines, [Barea et al. \(2010\)](#) did not observe significantly greater ATTD for the Low RFI line of DM (−0.1%), N (+0.6%), and energy (+0.1%) compared to the High RFI line on a standard European diet (i.e., control diet). The levels of digestibility observed in the current study were lower than those observed by [Barea et al. \(2010\)](#). Furthermore, [Montagne et al. \(2014\)](#) analyzed diet digestibility in the INRA RFI lines during their line-by-diet study and, in agreement with [Barea et al. \(2010\)](#), observed no significant ATTD differences between the INRA RFI lines fed the control diet (similar to HELF). Yet, [Montagne et al. \(2014\)](#) observed numerically lower digestibility coefficients of the control diet for the INRA Low RFI line compared to the INRA High RFI line for DM (−2.1%), N (−1.3%), and energy (−1.8%), which was opposite to the direction of numerical differences observed by [Harris et al. \(2012\)](#), [Barea et al. \(2010\)](#), and in the current study. Additionally, [Montagne et al. \(2014\)](#) observed that the INRA Low RFI pigs had reduced ATTD of NDF (−9.4%) compared to the INRA High RFI pigs, which is opposite to results observed in the current study (+0.68%). This could be due to different dietary fiber sources used to formulate the diets, housing (group-penned vs. individual metabolism crates), or sexes (barrows and gilts vs. barrows only), respectively. [Montagne et al. \(2014\)](#) did not observe significant differences in ATTD between the INRA RFI lines when a high-fiber diet was fed, except for ATTD of NDF. Although the opposite numerical trend from this study was observed by [Montagne et al. \(2014\)](#) in that the INRA Low RFI line had lower digestibility of GE (−0.9%), DM (−1.0%), N (−0.1%), and NDF (−5.9%) compared to the High RFI line. Again, these differences may be due to differences in dietary fiber sources between the high-fiber diets fed in the current study and by [Montagne et al. \(2014\)](#).

Overall, digestibility has been shown to play a major role (10%) in FE differences in beef cattle divergently selected for RFI ([Herd and Arthur, 2009](#)). [Harris et al. \(2012\)](#) suggested that nutrient

and energy digestibility also play a key role in different feed efficiencies between the ISU RFI lines. That conclusion has been partially validated here. Although no statistically significant digestibility differences were observed between the RFI lines when given the HELF diet in the current study, the direction of the line differences observed in this study were in the same direction as those reported by [Harris et al. \(2012\)](#). In addition, the results of the current study suggest that the Low RFI line was better able to utilize nutrients from the LEHF diet than the High RFI line, at least in the early grow-finish phase. [Noblet et al. \(2013\)](#) suggested that genetic differences observed in energy digestibility of growing pigs were not dependent on BW or age; thus, it is likely that the observed differences in the RFI lines in the early grow-finish phase would persist throughout the finishing period. This provides additional evidence that selection for low RFI has resulted in favorable correlated responses to selection. A limitation to the digestibility coefficient estimates presented in this study was the inability to adjust for feed consumed on the day of sample collection. [Harris et al. \(2012\)](#) reported that adjusting for ADFI did not alter line differences, and [Montagne et al. \(2014\)](#) reported that adjusting for the ADFI for the week of sample collection did affect digestibility values but that the effect of selection for RFI on ATTD of key nutrients and energy did not change regardless of accounting for ADFI or not. Therefore, if ATTD estimates could be adjusted for ADFI in this study, it is likely that similar results to those reported here would be found. In addition, this and previous studies conducted at ISU and INRA were limited to the early grow-finish phase. Thus, no studies have been conducted on digestibility differences in the later grow-finish phases of pigs divergently selected for RFI.

Genetic Parameter Estimation and Responses to Selection

To understand the genetic relationships of performance traits when diet is altered drastically, genetic parameters and responses to selection were estimated for the HELF and LEHF diets. Heritability estimates for production traits in this study were similar to those reported previously for the ISU ([Cai et al., 2008](#); [Bunter et al., 2010](#)) and INRA RFI lines, although the heritability estimate for RFI in the INRA lines was lower at 0.13 ± 0.05 ([Gilbert et al., 2017](#)). Heritability estimates for the LEHF diet had larger SE due to smaller sample sizes compared to the HELF diet. For RFI, the heritability estimate was greater for the LEHF diet

than for the HELF diet, although these differences were not significant as a result of the high SE of the estimates. The larger heritability estimate for the LEHF diet could also be due to confounding between the additive genetic and common litter effects (i.e., c^2 was 0.09 for HELF and 0 for LEHF), particularly for the smaller LEHF data set. Similar, but larger, differences were observed for BF heritability estimates between diets; these differences were likely due to confounding between the additive genetic and common litter effects, which were twice as large for LEHF than for the HELF diet (0.18 vs. 0.07, respectively).

Genetic correlations for the same trait between diets were high and positive, in general. For LMA and ADG, similar heritability estimates, in addition to genetic correlations near 1, between the HELF and LEHF diets indicated that these traits were genetically the same regardless of the diet fed. For traits such as ADFI and RFI that had lower genetic correlation estimates between the diets, it was less clear if these traits should be considered genetically the same or different depending on the diet fed. Further work should be done to understand these correlations.

Predicted direct and correlated responses to selection for divergent RFI when given the HELF diet were similar to those previously reported for the ISU RFI lines by [Cai et al. \(2008\)](#) and [Bunter et al. \(2010\)](#). [Cai et al. \(2008\)](#) reported that by G4 the average RFI EBV of the Low RFI line was more than 1.6 genetic SD lower than in G0, which is greater than the estimate for G4 in this study (-1.50 genetic SD). This is likely due to differences in samples of animals used in these studies. The line differences in G5 estimated by [Bunter et al. \(2010\)](#) in trait units were similar to those estimated in this study for that same generation (data not shown), with all estimates differing less than 0.5 genetic SD and less than 0.1 genetic SD for RFI. Any differences are likely due to differences in genetic SD estimates.

The response to selection for RFI, in G10, was 3.86 genetic SD for the HELF diet and 1.50 genetic SD for the LEHF diet. The latter of which is 55% less than predicted based on the estimate of the genetic correlation ($r_g = 0.87$) between the diets for RFI. For the LEHF diet, the High RFI line was estimated to have a negative genetic mean for some traits, compared to 0 in G0. This is likely due to use of all G0 pigs in the pedigree as a base population, which was an extrapolation for the High RFI line fed the LEHF diet since no data for either group were available in G0. For the purpose of estimating line differences, this assumption is acceptable, and the results show

that the High RFI line had greater genetic means than the Low RFI line when given the LEHF, with the exception of LMA.

As expected, the average line difference in RFI increased from the G5 [Bunter et al. \(2010\)](#) estimate (0.09 kg/d), with the High RFI line having greater RFI (+0.21 kg/d) than the Low RFI line for G8 through G10 on the HELF diet ([Table 5](#)). For the HELF diet, line differences indicated that the High RFI line had a greater mean for all traits, except for LMA. This was also true for the LEHF diet, but line differences were lower than for the HELF diet, except for LMA and BF. This is of particular interest because the advantage of the Low RFI line in terms of lower RFI and RFI_ME over the High RFI line were nearly cut in half by the change from the HELF to LEHF diet, while, for FCR and FCR_ME, the advantage of the Low RFI line requiring less feed per unit of gain was reduced by more than half from the HELF to LEHF diet.

All in all, genetic parameter estimates, direct and correlated responses to selection estimates, and line differences were similar to those previously reported for the ISU RFI lines. However, a genetic correlation lower than 0.9, lower correlated responses to selection for the LEHF diet than predicted, and a line difference for the LEHF diet that was half of the HELF diet line difference suggest that RFI may be a different genetic trait on the LEHF diet than on the HELF diet. Thus, if the breeding objective is to maximize genetic response for FE then, based on these results, it may be necessary to feed a diet very similar to the diet fed during selection or for breeders to select for FE while feeding a diet similar to those used in commercial production.

CONCLUSIONS AND IMPLICATIONS

The previous body of work reported with the ISU RFI lines has been generated when feeding HELF diets. The results of this study have shown that feeding lower-energy, higher-fiber diets to pigs divergently selected for FE when fed a corn- and soybean-meal-based diet (i.e., higher in energy and lower in dietary fiber) decreased performance (ADG, G:F, G:F_ME, LMA, BF, and energy intake) and RFI line differences, while increasing feed consumption. In addition, feeding a lower-quality diet reduced the digestibility of GE, DM, N, and NDF, although the more FE pigs (i.e., Low RFI) had increased digestibility of these nutrients and energy compared to the less-efficient pigs when given this diet. Feeding lower-quality feedstuffs also reduced the responses to selection for performance

traits. Thus, feeding lower-quality diets may reduce input costs upfront, but might not be economically beneficial in the long term due to reduced growth rate, increased FI, and lower responses to selection for performance traits.

At ISU, selection for increased FE, based on RFI, when given a high-quality feed resulted in pigs that eat less ([Cai et al., 2008](#); [Bunter et al., 2010](#); [Young et al., 2011](#)), eat faster ([Young et al., 2011](#)), and tend to be leaner ([Cai et al., 2008](#); [Smith et al., 2011](#); [Young et al., 2011](#); [Arkfeld et al., 2015](#)), with no evidence of negative impacts on meat quality ([Cai et al., 2008](#); [Smith et al., 2011](#); [Arkfeld et al., 2015](#)) or reproduction ([Young et al., 2016](#)). Collectively, these results suggest that selection for increased FE is primarily beneficial and has limited negative impacts. When switching from the diet fed during selection to an extremely lower-quality feed during the grow-finish phase, we observed that many of these advantages remained, albeit at a lower level, in the more feed efficient line (i.e., Low RFI) compared to their counterparts (i.e., High RFI), suggesting pigs that are selected for increased efficiency based on RFI on a standard diet will perform better or the same as less feed efficient pigs when given a much lower-quality diet.

For swine producers to capitalize on the genetic gain made by breeding companies in terms of FE, it appears a similar diet to that fed during selection should be fed to pigs, but also that even with an extreme reduction in diet quality some of the selective advantage in RFI may be realized. With this in mind, extreme diet alterations are not suggested if maximal FE is the primary goal of a swine operation. On the other hand, breeding companies may want to alter the diet fed during selection to a diet more similar to that fed in commercial production to maximize the genetic gain achieved at the production level. Unfortunately, a wide range of diets are fed in commercial swine production and determining the best diet to feed during selection to maximize commercial production remains a challenge. However, the results of this study suggest genotype-by-diet interactions should be considered when making those decisions.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Animal Frontiers* online.

LITERATURE CITED

AOAC. 1978. Official methods of analysis. 9th ed. Assoc. Off. Anal. Chem., Washington, DC.

- Apple, J. K., C. V. Maxwell, D. C. Brown, K. G. Friesen, R. E. Musser, Z. B. Johnson, and T. A. Armstrong. 2004. Effects of dietary lysine and energy density on performance and carcass characteristics of finishing pigs fed ractopamine. *J. Anim. Sci.* 82:3277–3287. doi:10.2527/2004.82113277x
- Arkfeld, E. K., J. M. Young, R. C. Johnson, C. A. Fedler, K. Prusa, J. F. Patience, J. C. M. Dekkers, N. K. Gabler, S. M. Lonergan, and E. Huff-Lonergan. 2015. Composition and quality characteristics of carcasses from pigs divergently selected for residual feed intake on high- or low-energy diets. *J. Anim. Sci.* 93:2530–2545. doi:10.2527/jas2014-8546
- Baird, D. M., H. C. McCampbell, and J. R. Allison. 1975. Effect of levels of crude fiber, protein and bulk in diets for finishing hogs. *J. Anim. Sci.* 41:1039–1047. doi:10.2527/jas1975.4141039x
- Barea, R., S. Dubois, H. Gilbert, P. Sellier, J. van Milgen, and J. Noblet. 2010. Energy utilization in pigs selected for high and low residual feed intake. *J. Anim. Sci.* 88:2062–2072. doi:10.2527/jas.2009-2395
- Beaulieu, A. D., N. H. Williams, and J. F. Patience. 2009. Response to dietary digestible energy concentration in growing pigs fed cereal grain-based diets. *J. Anim. Sci.* 87:965–976. doi:10.2527/jas.2007-0834
- Bunter, K. L., W. Cai, D. J. Johnston, and J. C. Dekkers. 2010. Selection to reduce residual feed intake in pigs produces a correlated response in juvenile insulin-like growth factor-I concentration. *J. Anim. Sci.* 88:1973–1981. doi:10.2527/jas.2009-2445
- Cai, W., D. S. Casey, and J. C. Dekkers. 2008. Selection response and genetic parameters for residual feed intake in Yorkshire swine. *J. Anim. Sci.* 86:287–298. doi:10.2527/jas.2007-0396
- Casey, D. S., H. S. Stern, and J. C. Dekkers. 2005. Identification of errors and factors associated with errors in data from electronic swine feeders. *J. Anim. Sci.* 83:969–982. doi:10.2527/2005.835969x
- Fix, J. S., J. P. Cassady, E. Van Heugten, D. J. Hanson, and M. T. See. 2010. Differences in lean growth performance of pigs sampled from 1980 and 2005 commercial swine fed 1980 and 2005 representative feeding programs. *Livest. Sci.* 128:108–114. doi:10.1016/j.livsci.2009.11.006
- Giamalva, J. 2014. Pork and swine: Industry and trade summary. International Trade Commission. Washington, DC.
- Gilbert, H., Y. Billon, L. Brossard, J. Faure, P. Gatellier, F. Gondret, E. Labussière, B. Lebret, L. Lefaucheur, N. Le Floch, et al. 2017. Review: Divergent selection for residual feed intake in the growing pig. *Animal*. 11:1427–1439. doi:10.1017/S175173111600286X
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2015. ASReml User Guide. Release 4.1. Functional Specification, VSN International Ltd, Hemel Hempstead, HPI 1ES, UK.
- Harris, A. J., J. F. Patience, S. M. Lonergan, C. J. M. Dekkers, and N. K. Gabler. 2012. Improved nutrient digestibility and retention partially explains feed efficiency gains in pigs selected for low residual feed intake. *J. Anim. Sci.* 90:164–166. doi:10.2527/jas.53855
- Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. *J. Anim. Sci.* 87:E64–E71. doi:10.2527/jas.2008-1345
- Hinson, R. B., B. R. Wiegand, M. J. Ritter, G. L. Allee, and S. N. Carr. 2011. Impact of dietary energy level and ractopamine on growth performance, carcass characteristics, and meat quality of finishing pigs. *J. Anim. Sci.* 89:3572–3579. doi:10.2527/jas.2010-3302
- Jha, R., and J. D. Berrocoso. 2015. Review: Dietary fiber utilization and its effects on physiological functions and gut health of swine. *Animal*. 9:1441–1452. doi:10.1017/S1751731115000919
- Kemp, B., L. den Hartog, J. Klok, and T. Zandstra. 1991. The digestibility of nutrient, energy and nitrogen in the Meishan and Dutch Landrace pig. *J. Anim. Physiol. Anim. Nutr. (Berl)*. 65:263–266. doi:10.1111/j.1439-0396.1991.tb00265.x
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486–494. doi:10.2527/jas1963.222486x
- Montagne, L., F. Loisel, T. Le Naou, F. Gondret, H. Gilbert, and M. Le Gall. 2014. Difference in short-term responses to a high-fiber diet in pigs divergently selected for residual feed intake. *J. Anim. Sci.* 92:1512–1523. doi:10.2527/jas.2013-6623
- Moore, R. J., E. T. Kornegay, R. L. Grayson, and M. D. Lindemann. 1988. Growth, nutrient utilization and intestinal morphology of pigs fed high-fiber diets. *J. Anim. Sci.* 66:1570–1579.
- Nguyen, N. H., C. P. McPhee, and C. M. Wade. 2004. Genetic selection strategies for efficient lean growth in pigs. *Pig News Inf.* 25:149N–163N.
- Noblet, J., H. Gilbert, Y. Jaguelin-Peyraud, and T. Lebrun. 2013. Evidence of genetic variability for digestive efficiency in the growing pig fed a fibrous diet. *Animal*. 7:1259–1264. doi:10.1017/S1751731113000463
- NRC. 1998. Nutrient requirements of swine. 10th revised edition. National Academic Press, Washington, DC.
- Oresanya, T. F., A. D. Beaulieu, and J. F. Patience. 2008. Investigations of energy metabolism in weanling barrows: The interaction of dietary energy concentration and daily feed (energy) intake. *J. Anim. Sci.* 86:348–363. doi:10.2527/jas.2007-0009
- Patience, J. F. 2012. The influence of dietary energy on feed efficiency in grow-finish. In: J. F. Patience, editor. *Feed efficiency in swine*. Wageningen Acad. Publ., The Netherlands. p. 101–129.
- Pond, W. G., H. G. Jung, and V. H. Varel. 1988. Effect of dietary fiber on young adult genetically lean, obese and contemporary pigs: Body weight, carcass measurements, organ weights and digesta content. *J. Anim. Sci.* 66:699–706.
- Smith, R. M., N. K. Gabler, J. M. Young, W. Cai, N. J. Boddicker, M. J. Anderson, E. Huff-Lonergan, J. C. Dekkers, and S. M. Lonergan. 2011. Effects of selection for decreased residual feed intake on composition and quality of fresh pork. *J. Anim. Sci.* 89:192–200. doi:10.2527/jas.2010-2861
- Varel, V. H., W. G. Pond, and J. T. Yen. 1984. Influence of dietary fiber on the performance and cellulase activity of growing-finishing swine. *J. Anim. Sci.* 59:388–393.
- Yen, J. T., V. H. Varel, and J. A. Nienaber. 2004. Metabolic and microbial responses in western crossbred and Meishan growing pigs fed a high-fiber diet. *J. Anim. Sci.* 82:1740–1755. doi:10.2527/2004.8261740x
- Young, J. M., R. Bergsma, E. F. Knol, J. F. Patience, and J. C. Dekkers. 2016. Effect of selection for residual feed intake during the grow/finish phase of production on sow reproductive performance and lactation efficiency. *J. Anim. Sci.* 94:4120–4132. doi:10.2527/jas.2015-0130

- Young, J. M., W. Cai, and J. C. Dekkers. 2011. Effect of selection for residual feed intake on feeding behavior and daily feed intake patterns in Yorkshire swine. *J. Anim. Sci.* 89:639–647. doi:10.2527/jas.2010-2892
- Young, J. M., and J. C. M. Dekkers. 2012. The genetic and biological basis of residual feed intake as a measure of feed efficiency. In: J. F. Patience, editor. *Feed efficiency in swine*. Wageningen Acad. Publ., The Netherlands. p. 153–166.