

The relationship between different measures of feed efficiency and feeding behavior traits in Duroc pigs¹

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ABSTRACT: Utilization of feed in livestock species consists of a wide range of biological processes, and therefore, its efficiency can be expressed in various ways, including direct measurement, such as daily feed intake, as well as indicator measures, such as feeding behavior. Measuring feed efficiency is important to the swine industry, and its accuracy can be enhanced by using automated feeding systems, which record feed intake and associated feeding behavior of individual animals. Each automated feeder space is often shared among several pigs and therefore raises concerns about social interactions among pen mates with regard to feeding behavior. The study herein used a data set of 14,901 Duroc boars with individual records on feed intake, feeding behavior, and other off-test traits. These traits were modeled with and without the random spatial effect of Pen_Room, a concatenation of room and pen, or random social interaction among pen mates. The nonheritable spatial effect of common Pen-Room was observed for traits directly measuring feed intake and accounted for up to 13% of the total phenotypic variance in the average daily feeding rate. The social

interaction effect explained larger proportions of phenotypic variation in all the traits studied, with the highest being 59% for ADFI in the group of feeding behaviors, 73% for residual feed intake (RFI; RFI4 and RFI6) in the feed efficiency traits, and 69% for intramuscular fat percentage in the off-test traits. After accounting for the social interaction effect, residual BW gain and RFI and BW gain (RIG) were found to have the heritability of 0.38 and 0.18, respectively, and had strong genetic correlations with growth and off-test traits. Feeding behavior traits were found to be moderately heritable, ranging from 0.14 (ADFI) to 0.52 (average daily occupation time), and some of them were strongly correlated with feed efficiency measures; for example, there was a genetic correlation of 0.88 between ADFI and RFI6. Our work suggested that accounting for the social common pen effect was important for estimating genetic parameters of traits recorded by the automated feeding system. Residual BW gain and RIG appeared to be two robust measures of feed efficiency. Feeding behavior measures are worth further investigation as indicators of feed efficiency.

Key words: feed efficiency, feeding behavior, social interaction, variance components

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J. Anim. Sci. 2017.95:3370–3380
doi:10.2527/jas2017.1509

INTRODUCTION

Feed efficiency (FE) is a complex and important trait in the pork industry and is commonly measured by the feed conversion ratio (FCR), a feed-to-gain ratio.

Animals with similar FCR may greatly differ in growth rate and feed intake (Smith et al., 2010). Selection against FCR might cause 1) large size animals that have high energy requirements for maintenance (Smith et al., 2010) and 2) problems in predicting changes in component traits in future generations (Gunsett, 1984). Alternatively, FE can be measured by residual feed intake (RFI; Koch et al., 1963), which, however, has not been the focus of FE research until recently and has been computed in different ways in the current literature (e.g., Johnson et al., 1999; Hoque et al., 2009; Do et al., 2013), potentially causing difficulty in comparing results among published research.

¹We would like to thank I. Misztal and S. Tsuruta for comments and help during the analysis of data. The project was funded by the National Pork Board, the North Carolina Pork Council, and the National Swine Genome Coordinator NSRP8.

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Received February 24, 2017.

Accepted June 9, 2017.

Alternative measures of efficiency are residual BW gain (**RG**) and RFI and BW gain (**RIG**; Berry and Crowley, 2012). Although RG should be associated with faster growth and independent of feed intake, RIG combines RFI and RG to identify efficient and fast-growing individuals independent of BW (Berry and Crowley, 2012). However, RG and RIG have not been used in swine research (MacNeil and Kemp, 2015). Additionally, relationships between efficiency measures and feeding behavior have not been well documented in the current literature.

Feed intake in the calculation of FE is partially influenced by other factors, including spatial competition for feed, group size, space allowance, and social mixing (Manteca and Edwards, 2009). These effects create social interactions between animals, yet differences among animal groups are often overlooked in pig research.

The study presented herein aimed at 1) estimating the genetic parameters of different measures of FE, feeding behavior, and other production traits as well as the relationship among them and 2) quantifying the effect of social common pens on all the traits.

MATERIALS AND METHODS

Field Data

Animal care approval was not required for the present study because all records came from field data. The data provided by Smithfield Premium Genetics (Rose Hill, NC) were collected from June 2004 through May 2013 for Duroc purebred boars on a nucleus farm, including 14,901 boars from 4,801 litters parented by 3,084 dams and 329 sires. Distribution of sires, dams, and litters over number of progeny included in the data set is presented in Fig. 1. Briefly, the majority of the sires (30.09%) had 21 to 50 progeny in the data set and 2.13 and 6.69% of sires had 1 and more than 100 progeny in the data set, respectively. Approximately 22% of the dams had 2 progeny, whereas only 2 dams (0.06%) had 21 to 50 progeny in the data set. Roughly 30% of the litters were represented by 1 progeny each in the data set. There were only 36 litters (0.75%) that were represented by 7 to 10 littermates each in the current data.

This data set had records on birth date and birth weight all pigs in the data set. They were weaned at approximately 25 d of age and had records on weaning weight. Pigs weaned within the same week were grouped into same contemporary groups (**CG**; concatenation of year and week; $n = 223$) and moved to a finishing barn at approximately 49 d of age. Pigs were randomly chosen to enter the feeding test, which began when the animals were approximately 93 d old and ended when they were roughly 170 d old. During that time, animals were

kept in groups of an average size of 12 (between 6 and 19) in single-space Feed Intake Recording Equipment (**FIRE**) feeder pens (Osborne Industries, Inc., Osborne, KS). Each FIRE feeder was equipped with a weighing scale (ACCU-ARM Weigh Race; Osborne Industries Inc., Osborne, KS) to measure the BW of the pig accessing the feeder. There were 240 such pens located in 14 rooms. Animal identification, feed intake, and feeding time were recorded every time a pig visited the feeder. The feeding system recorded 4,958,077 visits to the feeders from all of the tested boars. Data cleaning was performed and potential errors (Casey et al., 2005; Zumbach et al., 2010) were corrected using a multiple imputation technique described by Jiao et al. (2016) and a robust regression detailed by Zumbach et al. (2010).

This study analyzed 2 groups of traits, behavior and production. Seven feeding behavior traits were recorded and included 1) ADFI, measured as the average amount of feed (g) consumed daily during the test period; 2) average daily occupation time (**AOTD**), the average amount of time (s) an animal spent daily at the feeder; 3) average daily feeding rate (**ADFR**), the average amount of feed an animal consumed per minute spent at the feeder (g/m), computed as the total amount of feed the animal consumed across the testing period divided by the total amount of time they spent at the feeder; 4) average daily number of visits to feeder (**ANVD**), the average number of visits an animal made to the feeder; 5) average feed intake per visit across testing period (**AFIV**), the average amount of feed an animal consumed per visit to the feeder; 6) average occupation time per visit across testing period (**AOTV**), the average time length (s) of each visit an animal made to the feeder; and 7) average feeding rate per visit across testing period (**AFRV**), the average amount of feed an animal consumed per minute of each visit to the feeder, computed as the total amount of feed the animal consumed across the test period divided by the total number of visits they had to the feeder.

Production traits included 3 growth and 9 FE traits measured during the test period as well as 4 off-test traits. Growth rates for each tested boar were computed in 3 different ways: ADG from birth to off-test period, ADG from postweaning to off-test, and ADG across the testing period using FIRE (**ADG_FIRE**). Additionally, the metabolic midtest BW (**MMW**) was computed using the estimates of intercept from a robust regression described by Nguyen et al. (2005).

Nine FE measures were used in this study, including G:F during the test period, 6 RFI (RFI1 through RFI6), RG, and RIG. The 6 RFI traits were calculated as the residuals of 6 different regression models described in Table 1. The models differed with respect to the inclusion of different components of FE. Briefly, RFI1 was modeled on ADG_FIRE; RFI2 was modeled

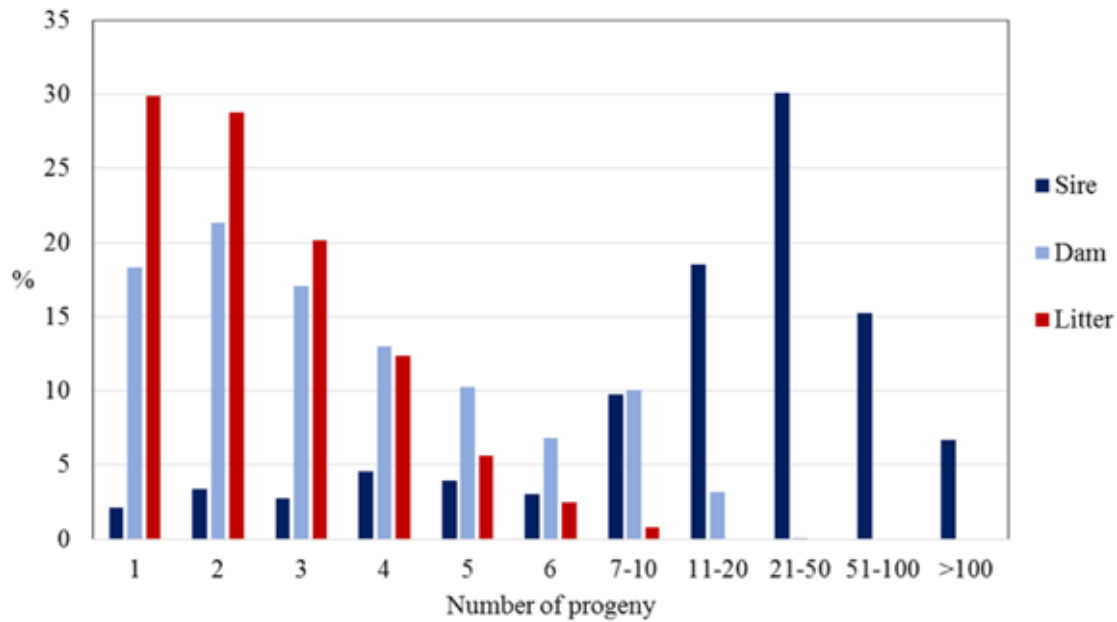


Figure 1. Distribution of sires, dams, and litters over number of progeny in the data set.

on ADG_FIRE and MMW; RFI3 was modeled on ADG_FIRE and ultrasound backfat thickness at off-test (BF); RFI4 was modeled on ADG_FIRE, MMW, and BF; RFI5 was modeled on ADG_FIRE, BF, and ultrasound muscle depth at off-test (MD); and RFI6 was modeled on ADG_FIRE, MMW, BF, and MD.

Residual growth ($\bar{R}G$) was determined as follows:

$$y_i = \beta_0 + CG_{ij} + \beta_1 MMW_i + \beta_2 ADFI_i + \beta_3 BF_i + \beta_4 MD_i e_i$$

in which y_i was ADG_FIRE of the i th boar; CG_{ij} was the j th CG of the i th boar; MMW_i , $ADFI_i$, BF_i , and MD_i were MMW, ADFI, BF, and MD for the i th boar, respectively, as covariates in the model; β_0 was the intercept; β_1 to β_4 were regression coefficients for the corresponding covariates; and e_i was the residual. Residual gain represented the difference between recorded growth (ADG_FIRE) and predicted growth (Crowley et al., 2010; Willems et al., 2013). Residual feed intake and BW gain

was the difference between RG and RFI6 (Crowley et al., 2010; Willems et al., 2013).

The off-test traits included off-test BW at 155 to 160 d of age (BW_Off), BF, MD, and ultrasound intramuscular fat percentage (IMF). Ultrasound images were captured over the last 3 ribs, using an Aloka 500 system (Corometrics Medical Systems, Inc., Wallingford, CT), and were analyzed for IMF using the Swine Image Analysis Software (Designer Genes Technologies, Inc., Harrison, AR).

Descriptive statistics of all the traits are presented in Table 2, including the number of observations, minimums, maximums, means, and SD for all the phenotypes.

Statistical Analysis

Variance components were estimated using AIREMLF90 in the BLUPF90 family of programs (Misztal et al., 2002). All analyses were completed with either univariate or bivariate animal models using pedigree information. To estimate heritability for

Table 1. Different measures (1–6) of residual feed intake (RFI; g)

Trait	Model ¹	b_1 (SE)	b_2 (SE)	b_3 (SE)	b_4 (SE)	r^2
RFI1	$CG_j + b_1 ADG_i + e_i$	2.74 (0.09)**				0.38
RFI2	$CG_j + b_1 ADG_i + b_2 MMW_i + e_i$	2.21 (0.09)**	4.87 (0.30)**			0.45
RFI3	$CG_j + b_1 ADG_i + b_3 BF_i + e_i$	1.97 (0.11)**		35.75 (2.77)**		0.43
RFI4	$CG_j + b_1 ADG_i + b_2 MMW_i + b_3 BF_i + e_i$	1.54 (0.11)**	4.57 (0.30)**	32.24 (2.73)**		0.47
RFI5	$CG_j + b_1 ADG_i + b_3 BF_i + b_4 MD_i + e_i$	1.93 (0.11)**		36.13 (2.79)**	1.35 (1.23)	0.44
RFI6	$CG_j + b_1 ADG_i + b_2 MMW_i + b_3 BF_i + b_4 MD_i + e_i$	1.49 (0.11)**	4.57 (0.30)**	32.68 (2.75)**	1.51 (1.21)	0.48

¹Models differed on the left hand side with different production traits such as ADG (ADG during testing period; on-test ADG), metabolic midtest BW (MMW), ultrasound backfat thickness at off-test (BF), and ultrasound muscle depth at off-test (MD) as covariates. CG_j was the j th contemporary group. The regression coefficients b_1 , b_2 , b_3 , and b_4 were estimated for ADG (g), MMW (kg), BF (mm), and MD (mm), respectively.

** P -value of t test for regression coefficient < 0.01.

Table 2. Descriptive statistics for feeding behavior measures, growth, feed efficiency, and off-test traits

Category	Trait ¹	No. of observations	Minimum	Mean	Maximum	SD
Behavior	ADFI, g	11,798	78.68	2,154.60	8,250.63	609.84
	AOTD, s	11,798	155.00	3,715.00	11,494.00	840.24
	ANVD	11,798	1.19	5.77	20.86	1.78
	ADFR, g/min	11,798	1.58	36.72	288.57	12.64
	AFIV, g	11,798	21.98	471.62	1,259.73	181.66
	AOTV, s	11,798	48.92	778.39	2,025.41	233.22
	AFRV, g/min	11,798	1.58	36.72	288.86	12.65
Growth	ADG_Life, g/d	15,221	307.00	656.80	976.00	76.32
	ADG_FIRE, g/d	6,500	351.00	886.10	1,450.00	222.87
	ADG_PostWean, g/d	14,254	344.40	733.80	1,115.20	86.99
Efficiency	G:F, %	6,485	7.60	41.86	65.80	16.04
	RFI1, g	6,464	-2,207.74	0.00	5,644.27	459.35
	RFI2, g	6,464	-2,225.27	0.00	5,644.75	456.52
	RFI3, g	6,464	-2,172.20	0.00	5,778.53	453.42
	RFI4, g	6,464	-2,189.72	0.00	5,777.60	450.68
	RFI5, g	6,464	-2,169.33	0.00	5,776.80	453.38
	RFI6, g	6,464	-2,187.05	0.00	5,776.00	450.65
	RG, g	6,464	-191.80	0.00	134.10	40.56
	RIG, g	6,464	-6.23	0.00	12.97	1.49
Off-test	BW_Off, kg	15,209	68.04	114.58	168.74	12.94
	BF, mm	15,218	4.32	11.03	25.23	5.68
	MD, mm	15,216	23.37	42.19	70.70	2.81
	IMF, 100%	11,351	1.41	3.64	7.01	0.49

¹AOTD = average daily occupation time; ANVD = average daily number of visits to feeder; ADFR = average daily feeding rate; AFIV = average feed intake per visit across testing period; AOTV = average occupation time per visit across testing period; AFRV = average feeding rate per visit across testing period; ADG_Life = ADG from birth to off-test period; ADG_FIRE = ADG across the testing period using Feed Intake Recording Equipment (Osborne Industries, Inc., Osborne, KS); ADG_PostWean = ADG from postweaning to off-test; RFI = residual feed intake (RFI1 through RFI6 are measures of RFI); RG = residual BW gain; RIG = RFI and BW gain, measured as difference of residual growth and RFI; BW_Off = off-test BW at 155 to 160 d of age; BF = ultrasound backfat thickness at off-test; MD = ultrasound muscle depth at off-test; IMF = intramuscular fat percentage.

each of RFI1 through RFI6, 3 univariate animal models were used. The first statistical model was

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{e}, \quad [1]$$

in which \mathbf{y} was the vector of observations (behavior, growth, FE, and off-test traits); \mathbf{b} was the vector of fixed effects including CG ($n = 223$), parity of dam (1, 2, and 3+), and fitted covariates for corresponding trait; \mathbf{a} was the vector of additive genetic effects of the animal; \mathbf{e} was the vector of random residuals; and \mathbf{X} and \mathbf{Z} were the corresponding incidence matrices. On-test age and test duration were fitted as covariates for behavior traits, ADG_FIRE, and FE traits; off-test age was fitted as a covariate for BW_Off, which, in turn, was fitted as a covariate for BF, MD, and IMF. The additive effect was assumed $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$, in which \mathbf{A} was the numerator relationship matrix. A pedigree of the phenotyped pigs was traced back 3 generations to construct the numerator relationship matrix.

The effect of individual grouping was investigated using a univariate animal model to reduce computational burden by reducing the models' complexities and allowing easier interpretation of the models tested.

To account for the possible effect of the pen, the following univariate animal model was used:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{p} + \mathbf{e}, \quad [2]$$

This model was identical to model [1], except for the extra term \mathbf{p} , which was the vector of the Pen_Room effect (concatenation of pen and room; $n = 240$), treated as a random effect, and \mathbf{Z}_2 , which was the incidence matrix of \mathbf{p} . The assumptions for random effects of this model in pedigree analysis were as follows:

$$\begin{pmatrix} a \\ p \\ e \end{pmatrix} \sim N \begin{pmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I_p\sigma_p^2 & 0 \\ 0 & 0 & I_e\sigma_e^2 \end{pmatrix},$$

in which σ_a^2 , σ_p^2 , and σ_e^2 were variance components for additive, spatial Pen_Room, and residual effects, respectively, and \mathbf{A} was the numerator relationship matrix derived from pedigree information.

A third univariate animal model was fitted to take into account the interactions among pen mates, a social common pen effect, instead of the spatial Pen_Room effect. The statistical model was

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_3\mathbf{s} + \mathbf{e},$$

in which \mathbf{s} was a vector of social common pen effect ($n = 921$) and \mathbf{Z}_3 was the incidence matrix of \mathbf{s} . All other terms of model [3] remained the same as in model [1]. The assumptions for model [3] were similar to those for model [2], except for replacing $\mathbf{I}_p\sigma_p^2$ in the variance or covariance structure in model [2] with $\mathbf{I}_p\sigma_s^2$ in model [3].

Bivariate animal models used in this study were identical to model [1], except for the added covariance among additive effects of the 2 traits in the model. For simplicity and easier convergence, only model [1] was used to obtain genetic variance or covariance among behavior traits and other traits.

The estimates of variance components from univariate and bivariate models were obtained by using the AIREMLF90 program. Estimates of heritability and genetic correlations and their SE were computed using the approach suggested by Klei and Tsuruta (2015).

RESULTS

Table 1 presents 6 different regression models used to compute RFI1 through RFI6 in this study. They were different by the components of FE, including ADG_FIRE, MMW, BF, and MD. Nearly all of the regression coefficients were significant, except for MD in the formulae for RFI5 and RFI6. The residuals from each of those 6 models represented the corresponding RFI.

Figure 2 shows the average relationship among pen mates in each pen, which ranged from 0 to 0.08, which is consistent with the fact that there were only 3 littermates per pen, on average. Consequently, we excluded the litter effect, which was proven not to improve model fitness, in all analyses in this study.

Table 3 shows the variance components and heritability estimates for 7 feeding behavior traits, 3 growth traits, 9 FE traits, and 4 off-test traits derived from 3 different univariate animal models with pedigree information. With the simplest model, model [1], the estimates of heritability for all the traits of interest were moderate to high: estimates of heritability for feeding behavior traits ranged from 0.18 ± 0.03 for ADFI to 0.68 ± 0.02 for ANVD, estimates of heritability for growth traits during the testing period were 0.35 ± 0.03 (ADG_FIRE) and were slightly higher for ADG from birth to off-test period (0.48 ± 0.02) and ADG from postweaning to off-test (0.47 ± 0.03), the estimated heritabilities for FE traits ranged from 0.44 ± 0.04 for G:F to 0.57 ± 0.03 for RIG, and the heritability estimates for IMF was 0.11 ± 0.02 , which was the least heritable of the off-test traits, whereas BF's heritability was the highest, 0.56 ± 0.04 . Compared with results derived from model [1], estimates of additive ge-

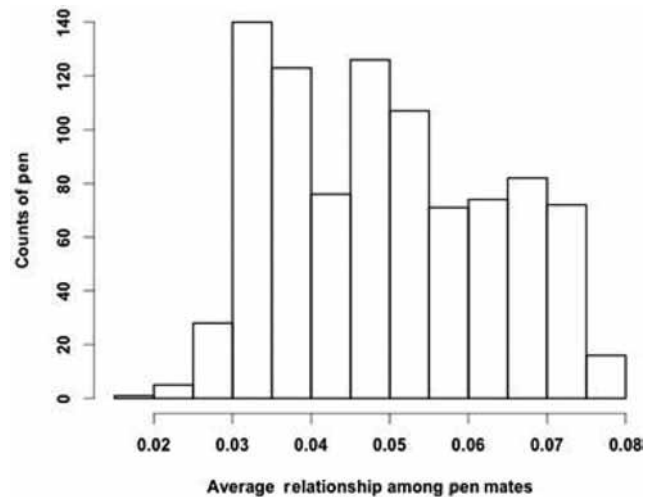


Figure 2. The average relationship among pigs sharing the same pen as pen mates. The average relationship for each pen was computed by taking the mean of the off-diagonal elements of the \mathbf{A} matrix for pigs living in the same pen.

netic variance for all the traits in model [2] were slightly reduced, except those for ADFI, ADFR, and BW_Off. The magnitudes of the additional estimated variance components capturing the Pen_Room effect were smaller compared with the additive genetic variance, leading to slightly decreased estimates of heritability for most of traits, and the ratio of Pen_Room variance to the total phenotypic variance ranged from 0.01 to 0.18. When the additional social common pen effect was fitted to model [3], variances associated with the social common pen effect mostly came from the residual variances in model [1], whereas the estimates of additive genetic variance were slightly reduced or increased in comparison with those in model [1]. The estimates of social common pen variances in model [3] were larger than the spatial variances in model [2], which was reflected in the variance ratios. The estimates of heritability using model [3] were substantially reduced for all feeding behavior traits, growth rate on test (ADG_FIRE), and FE traits compared with model [1] and model [2]. However, they still remained moderate to high for 4 of the feeding behavior traits, growth traits, efficiency trait RG, and off-test traits except IMF. The proportions of trait variances explained by model [3] were always higher than those derived from model [2]. The largest differences were 0.44 and 0.58, observed in ADFI and IMF, respectively. In terms of model fitness, the Akaike information criteria derived from model [3] were always lower than those derived from model [2], showing that fitting the social effect of pens resulted in model fitness improvement compared with fitting the spatial effect of Pen_Room.

Table 4 shows the estimates of additive genetic correlation between the FE traits and the production traits (both growth and off-test traits) using model [1] on pairs of traits and pedigree information. The G:F was

Table 3. Estimates of variance components¹ and heritability (h^2) for behavior, growth, efficiency, and off-test traits with pedigree information

Category	Trait ²	Model [1] ³					Model [2] ⁴					Model [3] ⁵				
		σ_a^2	h^2 (SE)	AIC ⁶	σ_a^2	σ_p^2	h^2 (SE)	$\sigma_a^2/\sigma_{\text{phe}}^{2.7}$	$(\sigma_a^2 + \sigma_p^2)/\sigma_{\text{phe}}^2$	AIC	σ_a^2	σ_s^2	h^2 (SE)	$\sigma_a^2/\sigma_{\text{phe}}^{2.8}$	$(\sigma_a^2 + \sigma_s^2)/\sigma_{\text{phe}}^2$	AIC
Behavior	ADFI, g	4.30×10^4	0.18 (0.03)	184,277	4.75×10^4	2.72×10^4	0.19 (0.03)	0.11	0.29	183,797	4.53×10^4	1.91×10^5	0.14 (0.01)	0.59	178,885	
	AOTD, s	3.53×10^5	0.71 (0.03)	193,666	2.27×10^5	5.74×10^3	0.50 (0.04)	0.01	0.62	193,643	3.22×10^5	9.27×10^4	0.52 (0.04)	0.15	193,041	
	ANVD	1.46	0.68 (0.02)	50,384	0.984	7.69×10^{-2}	0.42 (0.03)	0.03	0.53	50,327	0.883	0.452	0.36 (0.03)	0.18	49,458	
	ADFR, g/min	89.90	0.35 (0.03)	95,055	90.90	32.30	0.35 (0.01)	0.13	0.58	94,854	65.80	1.69×10^2	0.19 (0.03)	0.48	91,597	
	AFIV, g	1.10×10^4	0.49 (0.01)	155,305	1.06×10^4	1.88×10^3	0.45 (0.02)	0.08	0.51	155,060	8.65×10^3	6.86×10^3	0.37 (0.03)	0.29	153,244	
	AOTV, s	2.75×10^4	0.58 (0.04)	164,002	2.66×10^4	1.56×10^3	0.57 (0.04)	0.03	0.62	163,949	2.52×10^4	7.59×10^3	0.51 (0.04)	0.15	163,124	
Growth	AFRV, g/min	2.25×10^4	0.48 (0.03)	95,074	2.06×10^4	5.49×10^3	0.43 (0.05)	0.11	0.58	94,874	9.98×10^3	3.06×10^4	0.18 (0.03)	0.56	91,620	
	ADG_FIRE, g/d	1.35×10^4	0.35 (0.03)	101,800	1.35×10^4	7.82×10^3	0.31 (0.01)	0.18	0.49	101,500	1.22×10^4	2.91×10^4	0.23 (0.01)	0.55	99,451	
	ADG_Life, g/d	2.38×10^3	0.48 (0.02)	169,922	2.36×10^3	80.00	0.47 (0.02)	0.02	0.49	169,888	2.23×10^3	3.84×10^2	0.44 (0.01)	0.08	169,662	
Efficiency	ADG_PostWean, g/d	2.94×10^3	0.47 (0.03)	164,170	2.91×10^3	1.36×10^2	0.46 (0.04)	0.02	0.48	164,127	2.73×10^3	5.31×10^2	0.42 (0.03)	0.08	163,921	
	G:F, %	85.50	0.44 (0.04)	68,238	81.20	30.20	0.39 (0.03)	0.14	0.53	67,903	16.30	1.79×10^2	0.06 (0.04)	0.69	64,704	
	RF11, g	1.25×10^5	0.54 (0.04)	113,960	1.09×10^5	4.03×10^4	0.45 (0.03)	0.16	0.61	113,353	2.35×10^4	1.94×10^5	0.08 (0.03)	0.69	110,183	
Off-test	RF12, g	1.28×10^5	0.55 (0.03)	114,136	1.15×10^5	3.86×10^4	0.47 (0.04)	0.16	0.63	113,462	1.67×10^4	2.10×10^5	0.06 (0.04)	0.71	110,310	
	RF13, g	1.21×10^5	0.53 (0.04)	113,819	1.06×10^5	3.94×10^4	0.44 (0.02)	0.17	0.61	113,207	1.57×10^4	1.99×10^5	0.06 (0.03)	0.71	109,876	
	RF14, g	1.23×10^5	0.54 (0.04)	114,003	1.12×10^5	3.85×10^4	0.47 (0.03)	0.16	0.63	113,319	1.12×10^4	2.17×10^5	0.04 (0.04)	0.73	110,045	
	RF15, g	1.20×10^5	0.53 (0.03)	113,816	1.06×10^5	3.93×10^4	0.44 (0.04)	0.16	0.61	113,207	1.60×10^4	1.99×10^5	0.06 (0.04)	0.71	109,880	
	RF16, g	1.23×10^5	0.54 (0.03)	113,999	1.11×10^5	3.84×10^4	0.46 (0.05)	0.16	0.63	113,318	1.15×10^4	2.16×10^5	0.04 (0.03)	0.73	110,051	
	RG, g	1.15×10^3	0.46 (0.04)	85,266	1.13×10^3	37.90	0.45 (0.03)	0.02	0.47	85,240	9.37×10^2	2.60×10^2	0.38 (0.04)	0.11	85,067	
	RIG, g	1.49	0.57 (0.03)	41,144	1.42	0.262	0.53 (0.02)	0.10	0.62	40,764	0.497	1.35	0.18 (0.01)	0.48	39,229	
	BW_Off, kg	7.99	0.37 (0.02)	89,110	8.00	0.243	0.37 (0.01)	0.01	0.38	89,089	6.87	2.49	0.31 (0.01)	0.11	88,696	
	BF, mm	2.64	0.56 (0.04)	65,199	2.64	7.82×10^{-2}	0.55 (0.03)	0.02	0.57	65,160	2.56	0.241	0.53 (0.03)	0.05	65,066	
	MD, mm	6.88×10^{-2}	0.41 (0.03)	19,777	6.86×10^{-2}	1.46×10^{-3}	0.41 (0.03)	0.01	0.42	19,769	6.54×10^{-2}	1.01×10^{-2}	0.38 (0.04)	0.06	19,700	
IME, %	3.56×10^{-3}	0.11 (0.02)	3,864	3.78×10^{-3}	3.46×10^{-4}	0.11 (0.01)	0.01	0.12	3,844	4.58×10^{-4}	2.80×10^{-2}	0.01 (0.03)	0.69	-4,219		

¹Variance components include additive genetic variance (σ_a^2), spatial Pen_Room (a concatenation of room and pen) effect (σ_p^2), social common pen effect (σ_s^2), and phenotype variance (σ_{phe}^2).

²Traits analyzed: AOTD = average daily occupation time; ANVD = average daily number of visits to feeder; ADFR = average feed intake per visit across testing period; AOTV = average occupation time per visit across testing period; AFRV = average feeding rate per visit across testing period; ADG_FIRE = ADG across the testing period using Feed Intake Recording Equipment (Osborne Industries, Inc., Osborne, KS); ADG_Life = ADG from birth to off-test period; ADG_PostWean = ADG from postweaning to off-test; RFI = residual feed intake (RFI) through RFI6 are measures of RFI); RG = residual BW gain; RIG = RFI and BW gain, measured as difference of residual growth and RFI; BW_Off = off-test BW at 155 to 160 d of age; BF = ultrasound backfat thickness at off-test; MD = ultrasound muscle depth at off-test; IMF = intramuscular fat percentage.

³Model [1]: $y = Xb + Za + e$, in which additive effect $a \sim N(0, A\sigma_a^2)$, A was the numeric relationship matrix, and residual $e \sim N(0, I\sigma_e^2)$. The vector of fixed effects b included contemporary groups (257 levels of concatenation of year and week), sow parity (1, 2, and 3+), and age start testing and length of testing period as covariates.

⁴Model [2]: $y = Xb + Z_1a + Z_2p + e$, in which additive genetic effect $a \sim N(0, A\sigma_a^2)$, A was the numeric relationship matrix, p was the Pen_Room effect ($n = 240$ levels) effect as $p \sim N(0, I\sigma_{\text{pen}}^2)$, and $e \sim N(0, I\sigma_e^2)$. The room_pen represented the physical position of pens equipped with Feed Intake Recording Equipment.

⁵Model [3]: $y = Xb + Z_1a + Z_2s + e$, in which additive genetic effect a followed $a \sim N(0, A\sigma_a^2)$, A was the numeric relationship matrix, s is the social common pen ($n = 921$ levels) effect as $s \sim N(0, I\sigma_{\text{pen}}^2)$, and $e \sim N(0, I\sigma_e^2)$. The pen group included only boars living together as pen mates.

⁶AIC = Akaike information criterion.

⁷ $\sigma_p^2/\sigma_{\text{phe}}^2$ is the variance ratio for spatial Pen_Room effect against phenotype variance.

⁸ $\sigma_s^2/\sigma_{\text{phe}}^2$ is the variance ratio for social common pen effect against phenotype variance.

Table 4. Estimates of additive genetic correlation (SE) between feed efficiency and other production traits using a bivariate animal model with pedigree information

Trait ¹	Feed efficiency ²								
	G:F	RFI1	RFI2	RFI3	RFI4	RFI5	RFI6	RG	RIG
ADG_FIRE	0.29 (0.13)	0.13 (0.07)	0.21 (0.15)	0.19 (0.05)	0.20 (0.13)	0.11 (0.04)	0.15 (0.08)	0.30 (0.05)	0.46 (0.02)
ADG_Life	0.17 (0.05)	0.22 (0.05)	0.24 (0.07)	0.19 (0.05)	0.24 (0.02)	0.17 (0.03)	0.12 (0.04)	0.45 (0.08)	0.38 (0.03)
ADG_PostWean	0.17 (0.03)	0.19 (0.03)	0.24 (0.06)	0.10 (0.04)	0.12 (0.05)	0.19 (0.06)	0.16 (0.04)	0.44 (0.03)	0.38 (0.04)
BW_Off	0.18 (0.03)	0.17 (0.03)	0.15 (0.04)	0.18 (0.02)	-0.20 (0.16)	0.14 (0.07)	0.10 (0.11)	0.27 (0.03)	0.25 (0.05)
BF	-0.17 (0.09)	-0.21 (0.05)	-0.27 (0.13)	-0.14 (0.02)	-0.11 (0.03)	-0.10 (0.02)	-0.14 (0.03)	0.21 (0.11)	0.19 (0.07)
MD	0.22 (0.13)	0.22 (0.06)	0.13 (0.04)	0.11 (0.04)	0.20 (0.08)	-0.14 (0.09)	-0.10 (0.08)	0.26 (0.04)	0.31 (0.14)
IMF	0.12 (0.07)	0.09 (0.03)	0.11 (0.04)	0.08 (0.05)	0.14 (0.05)	0.13 (0.10)	0.21 (0.09)	0.13 (0.09)	-0.11 (0.03)

¹ADG_FIRE = ADG across the testing period using Feed Intake Recording Equipment (Osborne Industries, Inc., Osborne, KS; g/d); ADG_Life = ADG from birth to off-test period (g/d); ADG_PostWean = ADG from postweaning to off-test (g/d); BW_Off = off-test BW at 155 to 160 d of age (kg); BF = ultrasound backfat thickness at off-test (mm); MD = ultrasound muscle depth at off-test (mm); IMF = intramuscular fat percentage (%).

²RFI = residual feed intake (RFI1 through RFI6 are measures of RFI; g); RG = residual BW gain (g); RIG = RFI and BW gain, measured as difference of residual growth and RFI (g).

positively correlated with all the production traits but BF, for which a negative correlation (-0.17 ± 0.09) was observed. All these correlations were between weak and moderate. Its strongest correlation was 0.29 ± 0.13 with ADG_FIRE, and its weakest was 0.12 ± 0.07 with IMF. Slightly negative genetic correlations were found between BF and RFI1 through RFI6. Moderate to strong genetic correlations were observed between RG, RIG, and the 3 growth traits, from 0.30 ± 0.05 to 0.46 ± 0.02 . However, genetic correlations between RG and BF, as well as RIG and BF were also positive, 0.21 ± 0.11 and 0.19 ± 0.07 , respectively. Alternative forms of RFI, RFI1 through RFI6, were strongly positively correlated to each other, averaging 0.98 ± 0.01 , whereas RG and RIG were strongly negatively correlated (-0.89).

Table 5 shows the estimates of additive genetic correlations between feeding behavior traits and all other traits analyzed. A wide range of genetic correlations was found among the feeding behavior traits as well as between them and other production traits. Strong positive genetic correlations were found between ADFI and other behavior traits (ranging from 0.42 ± 0.04 for ADFI and AOTV to 0.83 ± 0.12 for ADFI and AFIV); between AOTD and other behavior traits, ranging from 0.31 ± 0.03 to 0.77 ± 0.05 , except for AFIV (0.08 ± 0.02); and between ADFR and AFIV (0.63 ± 0.30), between AFIV and AOTV (0.89 ± 0.01), and between AFIV and AFRV (0.63 ± 0.02). Strong negative genetic correlations were found between ANVD and AFIV (-0.78 ± 0.06) and between ANVD and AOTV (-0.72 ± 0.03). Except for AOTD, all other behavior traits showed moderate to high genetic correlations with growth traits, ranging from -0.28 ± 0.03 for ANVD and ADG_FIRE to above 0.80 for ADFI and growth traits. The additive genetic correlations between behavior traits and RFI6 were found to be positive, ranging from 0.03 ± 0.01 (AOTV and RFI6)

to 0.88 ± 0.10 (ADFI and RFI6). The genetic correlation between behavior traits and other RFI measures are not provided in Table 5 due to the high similarity in genetic correlation between behavior traits and all RFI measures. In contrast, the additive genetic correlation between feeding behavior traits and other FE measures (G:F, RG, and RIG) were found to be negative, ranging from -0.10 ± 0.03 between AOTV and G:F to -0.65 ± 0.04 between AOTD and G:F. There was no clear trend for genetic correlations between the feeding behavior traits and the off-test traits, except for the trivial correlations between MD and the feeding behavior measures.

DISCUSSIONS

Feeding Behavior Traits

Given the recording system available on farm and the recorded data, the focus of the feeding behavior section of this study was to analyze activities of pigs during their feeder visits rather than meals as defined by Forbes (1995). Analyses based on feeder visits have been documented in the current literature, for example, Hyun et al. (1997) and Do et al. (2013). In our analysis, feeding behavior traits were moderately to highly heritable and were in agreement with findings reported in pig research by Labroue et al. (1997), Do et al. (2013), and Rohrer et al. (2013). Our results showed that some of the feeding behavior measures were strongly genetically correlated with growth and off-test traits, especially those highly correlated with FE traits, such as AOTD and ANVD. The findings herein suggested that feeding behavior measures could be used as a selection criterion to improve FE traits, because some feeding behavior traits can be recorded without measuring individual feed in-

Table 5. Estimates of additive genetic correlation¹ from a 2-trait animal model between behavior and other traits with pedigree information

Category	Trait ²	Feeding behavior						
		ADFI	AOTD	ANVD	ADFR	AFIV	AOTV	AFRV
Behavior	AOTD	0.75 (0.04)						
	ANVD	0.47 (0.03)	0.77 (0.05)					
	ADFR	0.67 (0.02)	0.42 (0.03)	-0.28 (0.07)				
	AFIV	0.83 (0.12)	0.08 (0.02)	-0.78 (0.06)	0.63 (0.30)			
	AOTV	0.42 (0.04)	0.68 (0.02)	-0.72 (0.03)	-0.43 (0.06)	0.89 (0.01)		
	AFRV	0.71 (0.04)	0.31 (0.03)	-0.33 (0.05)	NaN ³	0.63 (0.02)	-0.43 (0.02)	
Growth	ADG_FIRE	0.82 (0.04)	0.11 (0.04)	-0.28 (0.03)	0.57 (0.09)	0.54 (0.06)	0.22 (0.05)	0.23 (0.04)
	ADG_Life	0.88 (0.05)	0.06 (0.02)	-0.56 (0.03)	0.60 (0.06)	0.78 (0.02)	0.42 (0.02)	0.60 (0.16)
	ADG_PostWean	0.87 (0.06)	0.06 (0.02)	-0.56 (0.05)	0.59 (0.09)	0.78 (0.02)	0.42 (0.02)	0.59 (0.19)
Efficiency	G:F	-0.42 (0.03)	-0.65 (0.04)	-0.37 (0.03)	-0.48 (0.03)	-0.34 (0.03)	-0.10 (0.03)	-0.48 (0.03)
	RFI6	0.88 (0.10)	0.72 (0.06)	0.23 (0.05)	0.78 (0.04)	0.57 (0.12)	0.03 (0.01)	0.78 (0.13)
	RG	-0.39 (0.03)	-0.29 (0.03)	-0.50 (0.03)	-0.41 (0.06)	-0.56 (0.03)	-0.35 (0.03)	-0.41 (0.16)
	RIG	-0.39 (0.06)	-0.61 (0.02)	-0.50 (0.05)	-0.52 (0.03)	-0.14 (0.03)	-0.20 (0.03)	-0.52 (0.03)
Off-test	BW_Off	0.53 (0.03)	0.06 (0.02)	-0.50 (0.08)	0.58 (0.03)	0.10 (0.02)	0.42 (0.02)	0.60 (0.13)
	BF	0.61 (0.04)	0.17 (0.02)	-0.25 (0.08)	0.10 (0.02)	0.15 (0.03)	-0.02 (0.02)	0.12 (0.02)
	MD	-0.02 (0.05)	-0.08 (0.03)	-0.14 (0.10)	0.02 (0.02)	0.11 (0.03)	0.05 (0.03)	0.04 (0.03)
	IMF	0.34 (0.05)	0.10 (0.03)	0.01 (0.03)	-0.08 (0.02)	0.18 (0.03)	0.08 (0.03)	0.04 (0.03)

¹Estimates of additive genetic correlation and their SE (in parentheses) are provided.

²AOTD = average daily occupation time (s); ANVD = average daily number of visits to feeder; ADFR = average daily feeding rate (g/min); AFIV = average feed intake per visit across testing period (g); AOTV = average occupation time per visit across testing period (s); AFRV = average feeding rate per visit across testing period (g/min); ADG_FIRE = ADG across the testing period using Feed Intake Recording Equipment (Osborne Industries, Inc., Osborne, KS; g/d); ADG_Life = ADG from birth to off-test period (g/d); ADG_PostWean = ADG from postweaning to off-test (g/d); RFI = residual feed intake (RFI6 is a measure of RFI; g); RG = residual BW gain (g); RIG = RFI and BW gain, measured as difference of residual growth and RFI (g); BW_Off = off-test BW at 155 to 160 d of age (kg); BF = ultrasound backfat thickness at off-test (mm); MD = ultrasound muscle depth at off-test (mm); IMF = intramuscular fat percentage (%).

³NaN = Not available; the model did not converge.

take (Maselyne et al., 2014, 2015), implying less equipment required, lower costs, and easier maintenance.

Estimated Genetic Parameters and Spatial Environmental Effect

In the present study, 9 FE measures were evaluated, including G:F, RFI1 through RFI6, RG, and RIG. The estimates for G:F and RFI were higher than the literature averages for pigs (Hoque et al., 2009; Rothschild and Ruvinsky, 2011) but only slightly higher when using the model with animal effect as the only random effect. Nevertheless, an overly high estimate of heritability might indicate that the additive genetic variance was overestimated or the residual variance was small or a combination of both. Reasons for the upward bias of the additive genetic variance might include the limited pedigree depth and/or related individuals being exposed to environmental heterogeneity. The former might be resolved by using genetic markers to link the animals together via identity-by-state or identity-by-descent. In fact, we performed a parallel analysis (results were not reported in this paper) that used a relationship matrix blending the numerator relationship matrix with a genomic relationship matrix. However, heritability estimates were similar to the results from using only

the numerator relationship matrix. There were 3,699 animals genotyped with the Illumina PorcineSNP60 BeadChip (Illumina Inc., San Diego, CA) and 4,621 animals genotyped with the 10K GeneSeek Genomic Profiler Porcine SNP chip (GeneSeek, Inc., Lincoln, NE) and imputed up to the Illumina PorcineSNP60 BeadChip. The number of genotyped animals and the imputation might have affected our results.

The additive genetic variance could also be biased upward when relatives, or litter mates in this study, do not share a similar living environment (for example, litter mates were split up and mixed with nonrelatives in different pens as observed in this study), but the statistical model does not properly account for spatial heterogeneity (Kruuk and Hadfield, 2007; Stopher et al., 2012). Fitting a common litter effect was suggested by Johnson et al. (1999), Hoque and Suzuki (2008), and Hoque et al. (2009) to further partition the additive genetic variance of G:F and RFI. However, it explained less than 5% of the variation of the traits in our preliminary analysis and, therefore, was removed as suggested by MacNeil and Kemp (2015). The very small proportion of variance accounted for by the common litter effect was expected because the number of observations per common litter was small, approximately 80% of the litters had between

1 and 3 observations each, and therefore, the estimated variance might have been shrunk aggressively toward 0.

The animals in this study were placed in groups of 6 to 19 individuals based on their size (BW) when entering the test. In a sense, faster growing pigs from different families were more likely to assemble together, and slower growing ones were together in other groups. This is a common practice in real production situations, and this group effect should be accounted for in genetic analyses of farm data. The common litter effect did not represent the spatial heterogeneity experienced by family members.

The proportions of total variation in G:F and RFI explained by the random spatial effect of Pen_Room in this study were approximately 10 to 17%, much larger than the 3% reported by Do et al. (2013) for FCR and RFI. However, it was unclear whether the “pen” effect reported by Do et al. (2013) was a common space shared by all pen mates (social common pen as defined in our analysis) or a physical space (pen) longitudinally shared by different groups of pigs (Pen_Room as defined in the present study).

Large proportions of phenotypic variation due to social group effects have been reported for feed intake and growth rate in pigs, with estimates of 27.5 and 42.2%, respectively, reported by Bergsma et al. (2008). Similar results have been found in feeding behavior traits in pigs reported by Chen et al. (2010). However, the large reduction in trait heritability found in the current study has not been reported in the current literature for FE traits in pigs. That could be because social common pen effects have not been fitted in linear mixed models when evaluating FE traits. Nevertheless, a drop in heritability with similar magnitude has been observed in deer research when a spatial environmental effect was fitted in a linear mixed animal model (Stopher et al., 2012).

The social common pen effect, a nonheritable social effect, in our study was used to simplify correlated residuals within pens (Bijma et al., 2007; Bergsma et al., 2008) and to capture variation among the groups. The importance of this spatial environmental effect on ADFI, ADG_FIRE, G:F, RFI, and RIG was larger than it was on most of other traits. The variation captured between groups perhaps reflected the variation in food accessibility, space availability, and social interactions of pigs between groups. Faster growing pigs might have had higher BW and were therefore placed in a smaller group size, leading to less space and food competition. Faster growing individuals might also have better temperament (Reinhardt et al., 2009; Cafe et al., 2011; Sant’Anna et al., 2012), meaning less fight and higher FE. Traits that were directly related to feed intake, which might have been the main reason for within-group competition or fighting, experienced the largest reduction in

estimated additive genetic variance. Residual BW gain was designed to be independent of feed intake (Berry and Crowley, 2012) and therefore less affected by the inclusion of the spatial group effect in the model.

Additive genetic correlations between various measures of FE and other traits, especially growth and off-test traits in the present study, may provide new insight into the relationships between those measures and other economically important traits. The weak but positive genetic correlations between measures of G:F and growth and BF indicate that selection for G:F may lead to a small favorable indirect response for growth as well as the undesirable increase in BF. Those results differ from previously reported estimates (Jiao et al., 2014) using data collected from a similar population. This could be because the previous study used a smaller number of animals. Our estimates agreed well with the findings in other studies. Do et al. (2013) reported a similar genetic correlation between FCR and growth as well as between FCR and BF in a Danish Duroc and Yorkshire population. Similar results were also observed by Hoque and Suzuki (2008) in a Duroc and Landrace population. Measures of RFI were not genetically independent of growth (weak positive correlation) and BF (weak negative genetic correlation) in the present population, consistent with results reported by Kennedy et al. (1993), Mrode and Kennedy (1993), Johnson et al. (1999), and Do et al. (2013). However, Hoque et al. (2009) reported lower estimates of genetic correlation for BF and RFI (adjusted for both growth and BF) but significant higher estimates for BF and another measure of RFI (adjusted only for growth). Given the genetic correlation in this Duroc population, selection against RFI (using formulae provided in this study) may lead to slightly slower growth and a slight increase in BF. The moderate genetic correlation found between RG and growth as well as a weak correlation between RG and BF indicates that RG might be a more robust FE measure. Selection for RG would result in faster growing pigs with only a negligible increase in BF. Selection for RIG may achieve a similar goal, given the similar genetic correlations to RG. Our finding agreed well with the report by Berry and Crowley (2012). Given the very low estimated heritability of RFI from the model that accounted for the spatial common pen effect in this study, RG and RIG might be the traits of choice for selection programs that aim at increasing growth rate while maintaining feed intake.

Conclusions

The present study was designed to characterize the genetic components of different measures of FE and the relationships between feeding behavior traits and

production traits as well as to quantify the nonheritable spatial effect of pens. After accounting for the common social effect of pens, RG and RIG have been found to be 2 most robust measures of FE in the study population. They also had moderate heritability and genetic correlations with other economically important traits, such as growth and off-test traits. Feeding behavior traits were found to be moderately heritable, and some of them were highly correlated with FE traits and therefore worth further investigation into their use as selection criteria. The inclusion of the common social effect of pens in mixed animal models is necessary to improve the estimation of genetic parameters.

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