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Feed efficiency effects on barrow and gilt behavioral reactivity to novel stimuli tests

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Abstract

Increasing feed efficiency is an important goal for improving sustainable pork production and profitability for producers. To study feed efficiency, genetic selection based on residual feed intake (RFI) was used to create 2 divergent lines. Low-RFI pigs consume less feed for equal weight gain compared to their less efficient, high-RFI counterparts. Therefore, our objective was to assess how a pig's behavioral reactivity toward fear-eliciting stimuli related to RFI selection and improvement of feed efficiency. In this study, behavioral reactivity of pigs divergently selected for RFI was evaluated using human approach (HAT) and novel object (NOT) tests. Forty low-RFI and 40 high-RFI barrows and gilts (n = 20 for each genetic line; 101 ± 9 d old) from ninth-generation Yorkshire RFI selection lines were randomly selected and evaluated once using HAT and once using NOT over a 2-wk period utilizing a crossover experimental design. Each pig was individually tested within a 4.9 × 2.4 m test arena for 10 min; behavior was evaluated using live and video observations. The test arena floor was divided into 4 zones; zone 1 being oral, nasal, and/or facial contact with the human (HAT) or orange traffic cone (NOT) and zone 4 being furthest from the human or cone and included the point where the pig entered the arena. During both HAT and NOT, low-RFI pigs entered zone 1 less frequently compared to high-RFI pigs ($P \leq 0.03$). During NOT, low-RFI pigs changed head orientation more frequently (P = 0.001) but attempted to escape less frequently (low-RFI = 0.97 ± 0.21 vs. high-RFI = 2.08 ± 0.38; P = 0.0002) and spent 2% less time attempting to escape compared to high-RFI pigs (P = 0.04). Different barrow and gilt responses were observed during HAT and NOT. During HAT, barrows spent 2% more time within zone 1 (P = 0.03), crossed fewer zone lines ($P < 0.0001$), changed head orientation less frequently (P = 0.002), and froze less frequently compared to gilts (P = 0.02). However, during NOT, barrows froze more frequently (P = 0.0007) and spent 2% longer freezing (P = 0.05). When the behavior and RFI relationship was examined using odds ratios, decreasing RFI by 1 kg/d decreased the odds of freezing by 4 times but increased the odds of attempting to escape by 5.26 times during NOT ($P \leq 0.04$). These results suggest that divergent selection for RFI resulted in subtle behavioral reactivity differences and did not impact swine welfare with respect to responses to fear-eliciting stimuli.

Keywords

fear, human approach, novel object, pig, residual feed intake, sex differences

Disciplines

Agriculture | Animal Sciences | Large or Food Animal and Equine Medicine | Meat Science

Comments

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Left Running Head: Colpoys et al.

Right Running Head: Effects of RFI on pig behavioral reactivity

Feed efficiency effects on barrow and gilt behavioral reactivity to novel stimuli tests[1]

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ABSTRACT: Increasing feed efficiency is an important goal for improving sustainable **pork** production and profitability for producers. To study feed efficiency, genetic selection based on residual feed intake (RFI) **was** used to create 2 divergent lines. Low-RFI pigs consume less feed for equal weight gain compared to their less efficient, high-RFI counterparts. Therefore, our objective was to assess how a pig's behavioral reactivity toward fear-eliciting stimuli related to **RFI** selection and improvement of feed efficiency. In this study, behavioral reactivity of pigs divergently selected for RFI was evaluated using human approach (HAT) and novel object (NOT) tests. Forty low-RFI and 40 high-RFI barrows and gilts (n = 20 for each genetic line; 101 ± 9 d old) from ninth generation Yorkshire RFI selection lines were randomly selected and evaluate once using HAT and once using NOT over a 2 wk period utilizing a crossover experimental design. Each pig was individually tested within a 4.9 x 2.4 m test arena for 10 min; behavior was evaluated using live and video observations. The test arena floor was divided into 4 zones; zone 1 being oral, nasal, and/or facial contact with the human (HAT) or orange traffic cone (NOT) and zone 4 being furthest from the human or cone and included the point where the pig entered the arena. During both HAT and NOT, low-RFI pigs entered zone 1 less frequently compared to high-RFI pigs ($P \leq 0.03$). During NOT, low-RFI pigs changed head orientation more frequently ($P = 0.001$), but attempted to escape less frequently (low-RFI = 0.97 ± 0.21 vs. high-RFI = 2.08 ± 0.38; $P = 0.0002$) and spent 2% less time attempting to escape compared to high-RFI pigs ($P = 0.04$). Different barrow and gilt responses were observed during HAT and NOT. During HAT, barrows spent 2% more time within zone 1 ($P = 0.03$), crossed fewer zone lines ($P < 0.0001$), changed head orientation less frequently ($P = 0.002$), and froze less frequently compared to gilts ($P = 0.02$). However, during NOT, barrows froze more frequently ($P = 0.0007$) and spent 2% longer freezing ($P = 0.05$). When the behavior and RFI relationship

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was examined using odds ratios, decreasing RFI by 1 kg/d decreased the odds of freezing by 4 times, but increased the odds of attempting to escape by 5.26 times during NOT ($P \leq 0.04$). These results suggest that **divergent selection for RFI resulted in subtle behavioral reactivity differences and did not impact swine welfare with respect to responses to fear-eliciting stimuli.**

Key words: fear, human approach, novel object, pig, residual feed intake, sex differences

INTRODUCTION

The Iowa State University (**ISU**) Yorkshire residual feed intake (**RFI**) selection project divergently selected pigs for RFI as a model to investigate the physiological and genetic differences in swine feed efficiency. This model defined RFI as the difference between the actual feed intake of a pig and its expected feed intake based on a given amount of growth and backfat (**BF**). Therefore, pigs that consume less feed than expected for maintenance and growth have a lower RFI, are more feed efficient, and are economically better for lean protein production relative to higher RFI pigs (Young et al., 2011).

It was recently suggested that breeding for improved feed efficiency may decrease the animal’s stress adaptation, thus resulting in adverse effects on livestock behavior and management (Rydhmer and Canario, 2014). Contrary to this, we reported that low-RFI (more feed efficient) barrows were less reactive to human approach (**HAT**) and novel object (**NOT**) tests compared to high-RFI barrows (Colpoys et al., 2014). However, recent research identified differences between barrows and gilts during HAT and NOT (Reimert et al., 2014) and it is unknown if barrows and gilts from this selection project have different responses to novel stimuli tests. Furthermore, the extent to which behavioral reactivity differences relate to phenotypic

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expression of feed efficiency is not well understood. In pigs, Cassady (2007) reported significant, yet inconsistent, relationships between time spent struggling during a back test and pre-weaning ADG (negative relationship) and ADG from 20 to 76 d old (positive relationship).

Using pigs from the ISU RFI selection lines, our first objective was to examine the association between long-term divergent selection for RFI and behavioral reactivity to fear-eliciting stimuli in barrows and gilts. The second objective of this study was to evaluate phenotypic relationships between behavioral responses during HAT and NOT and overall RFI during the grow-finish period.

MATERIALS AND METHODS

All experimental procedures were approved by the ISU Animal Care and Use Committee. This experiment was conducted over 2 consecutive weeks from February through March, 2013.

Animals and Housing

A total of 80 healthy Yorkshire pigs (101 ± 9 d old) divergently selected for RFI were used. Two genetic line treatments were compared: low-RFI (n=40) and high-RFI (n=40). Half were barrows (20 low-RFI, mean ± SD = 34.83 ± 6.55 kg BW; 20 high-RFI, 30.04 ± 5.21 kg BW) and half were gilts (20 low-RFI, mean ± SD = 32.33 ± 6.01 kg BW; 20 high-RFI, 28.96 ± 4.53 kg BW). Body weight was collected using a weigh scale (Electronic Weighing Systems, Rite Weigh, Robert E Spencer Enterprises, Ackley, IA, USA) three days prior to the start of testing.

This work was conducted at the Lauren Christian Swine Research Center at the ISU Bilsland Memorial Farm located near Madrid, Iowa, USA. All pigs were housed in a conventional confinement unit within 1 room containing 12 mixed-sex and mixed-line pens of 15 to 16 pigs/pen; 12 to 15 pigs from 6 pens were tested. Each pen measured 5.6 m long x 2.3 m

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wide and had a slatted concrete floor. The barn was naturally ventilated with side curtains. Each pen contained an electronic single-space feeder (FIRE®, Osborne Industries, Inc., Osborne, KS, USA) that recorded individual feed intake and was positioned at the front of the pen to provide pigs with *ad libitum* feed. All tested pigs were fed a corn-soy diet that met or exceeded NRC (1998) requirements. Water was provided *ad libitum* through 2 nipple-type waterers (Edstrom, Waterford, WI) per pen. The pigs were moved to this housing 10 d prior to the start of the experiment. One electronic recording device (HOBO Pro v2, temp / RH, U23-001, Onset Computer Corporation, Bourne, MA, USA) located in the center of the room, 2.2 m from the ground, recorded ambient temperature (°C) and relative humidity (%) every 5 min for the duration of the trial. The mean (±S.D.) ambient temperature was 22.49 (±2.74) °C and relative humidity was 50.06 (±7.00) %.

RFI Selection and Calculation

Divergent line selection criteria were based on estimated breeding values for RFI as explained by Cai et al. (2008). The low-RFI genetic line had been selected over 9 generations. The high-RFI genetic line had been randomly selected over 5 generations, and then selected for high-RFI over the next 4 generations.

Feed intake data recorded using the FIRE® feeders were edited following procedures outlined by Casey et al. (2005). Average daily feed intake was calculated as described by Cai et al. (2008). For each pig, ADG was estimated as the slope from a simple linear regression of BW that was recorded every 2 wk. Pigs identified for market had BF and loin muscle area (**LMA**) at the 10th rib 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, USA). Metabolic BW (**MBW**) was estimated as the average BW raised to the 0.75 power. Pigs entered the unit at approximately 90 d of age and 40 kg of BW; therefore, on-age deviation (**ONAGEDEV**) was calculated by subtracting 90 d from the age of the pig and on-weight deviation (**ONWTDEV**) was calculated by subtracting 40 kg from the BW of the pigs when entering the facility. Pigs were removed from the conventional confinement unit at approximately 118 kg of BW; therefore, off-weight deviation (**OFFWTDEV**) was calculated by subtracting 118 kg from the BW of the pig when removed from the facility. The mixed procedure in SAS 9.3 (SAS Institute Inc., Cary, NC, USA) was used to estimate regression coefficients for ADG, BF, MBW, ONAGEDEV, ONWTDEV, and OFFWTDEV to calculate RFI. The model used included fixed effects of sex, line, diet, and generation. Covariates included 6 three-way interactions which were the interaction of line and diet with ADG, BF, MBW, ONAGEDEV, ONWTDEV, and OFFWTDEV. Random effects fitted were dam and pen nested within generation.

Test Methodology and Facility

Pig testing occurred 5 d/wk over 2 consecutive weeks. A testing session consisted of a 10 min period during which the individual pig underwent HAT or NOT within the experimental arena. All test sessions were performed between 13:00 and 19:00 h. A total of 40 pigs (10 low-RFI barrows, 10 low-RFI gilts, 10 high-RFI barrows, and 10 high-RFI gilts) were selected using a random number generator (Microsoft Excel 2010, Microsoft Corporation, Santa Rosa, CA, USA) to be tested using HAT first and the remaining 40 pigs experienced NOT first. Pigs then experienced the opposite test 1 wk later, utilizing a crossover experimental design. Therefore, each pig was tested a total of 2 times, once in each test. Genetic line and sex were blocked by time so that within each hour each of the following types were tested in random order: low-RFI barrow, low-RFI gilt, high-RFI barrow, and high-RFI gilt. Pigs were tested in the same order for both tests and at the same time of day, and the individual pig was the experimental unit.

The HAT and NOT were conducted in a rectangular arena separate from the home pens. The arena setup followed the same procedures as previously described by Colpoys et al. (2014). The arena measured 4.9 m long x 2.4 m wide and had 1.2 m high, black corrugated plastic sides that were attached to gates. In order to hide the human observer visually during NOT, a 1.2 m wide x 2.2 m high black corrugated plastic observation hide was positioned outside the arena. Concentric curves were drawn on the slatted concrete floor using permanent marker 1 d before the start of testing to divide the arena into 4 zones in order to measure the location of the pig in proximity to the novel stimulus. Zone 1 was defined as oral, nasal, and/or facial contact with the human or the cone during HAT and NOT, respectively. For consistency with the other zones, pigs that touched the human or the cone will be referred to as entering zone 1. Zone 2 was the area nearest to the novel stimulus and zone 4 was the area where the pig entered the test arena, furthest from the novel stimulus. Zones 2-4 consisted of approximately equal area that allowed the entire body of the pig to fit within the zone. The concentric curves allowed a consistent distance from the novel stimulus to be measured in each zone (Fig. 1). Located in the center of the arena, 2.3 m from the ground, was an electronic recording device (HOBO Pro v2, temp / RH, U23-001, Onset Computer Corporation, Bourne, MA, USA) that recorded ambient temperature (°C) and relative humidity (%) every 5 min for the duration of testing. Throughout the testing period, the mean (±S.D.) ambient temperature was 13.26 (±2.16) °C and relative humidity was 69.07 (±10.23) %. This is a 9.23 °C cooler temperature and 19.01% greater relative humidity than in the home pens, due to the test room being heated only from the adjacent pig rooms rather than its own heat source.

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Three color cameras (Panasonic, Model WV-CP-484, Matsushita Co. LTD., Kadoma, Japan) were positioned 2.1 m above the test arena. Camera 1 was positioned over zone 1, camera 2 captured zones 2 and 3, and camera 3 captured zone 4. The cameras were fed into a multiplexer using Noldus Portable Lab (Noldus Information Technology, Wageningen, The Netherlands) and time-lapse video was collected onto a computer using HandyAVI (HandyAVI version 4.3 D, Anderson's AZcendant Software, Tempe, AZ, USA) at 10 frames/s.

One handler removed the pig to be tested from its home pen using a sort board. Each pig was moved down an alleyway (0.30 m to 12.47 m long x 0.79 m wide) onto a weigh scale (1.50 m long x 0.5 m wide; Electronic Weighing Systems, Rite Weigh, Robert E Spencer Enterprises, Ackley, IA, USA) adjacent to the test arena. The pig remained in the weigh scale for 1 min to create a uniform pre-test experience for every pig. Black corrugated plastic was attached to the front of the weigh scale so that pigs were not able to see into the test arena. The total number of pig urinations and defecations during handling and within the weigh scale were recorded. At the conclusion of the minute, the weigh scale door was opened and the pig was allowed to enter zone 4 of the arena. If the pig did not enter the arena within 15 s of the weigh scale door opening, the handler gently pushed the pig forward using their hands. Test time began when both front hooves entered zone 4. Following the 10 min testing period, each pig was returned to its home pen by the handler using the described methods. Feces and urine within the test arena were scraped through the slats following each testing session and the test arena was hosed down with water at the end of each testing day.

Human Approach Test

Each pig was individually assessed using HAT, which was designed to measure responses to an unfamiliar human stimulus. The human stimulus was the same woman for all

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tests, and she had never previously interacted with the pigs. This person showered into the facility using the same products at the start of each testing day. During testing, the unfamiliar human wore orange coveralls and orange boots, stood silently at the center of the opposite wall (zone 1) holding a clipboard, and did not interact with or move toward the pigs. Minimal arm movement and body shifting occurred during live observation and data collection. At the end of each testing day, coveralls were laundered and boots were hosed off with water.

Novel Object Test

Each pig was individually assessed using NOT, which was designed to measure responses to an unfamiliar object stimulus, an orange traffic cone. The traffic cone was positioned at the center of the opposite wall (zone 1) and was hosed off with water at the end of each testing day. The same woman who was the stimulus in HAT collected live observations. She was wearing blue coveralls and standing behind the black corrugated plastic observation hide outside the test arena that kept her out of pig sight (Fig. 1).

Measures

Live observations of the frequency of eliminatory behaviors were continuously collected during both tests (Dawkins et al., 2007). Video observations were continuously recorded (Dawkins et al., 2007) using the Observer software (The Observer XT version 10.5, Noldus Information Technology, Wageningen, The Netherlands) to decode approach, head orientation, freezing, and escape attempts (Table 1). All video observations were collected by the same, trained researcher who was blind to genetic line treatments. Due to technical difficulties, video of 1 high-RFI gilt during HAT was lost; therefore, video was only collected on 19 high-RFI gilts during HAT. However, live observations and latency and frequency of zone 1 entrances

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(collected live for cross-validation with video observations) were collected for all 20 high-RFI gilts during HAT.

Data Analysis

All data were evaluated for normality using the Shapiro-Wilk test and Q-Q plots using SAS (SAS version 9.3, SAS Inst. Inc., Cary, NC, USA). Data were not normally distributed; therefore, data were analyzed using the Glimmix procedure of SAS. All HAT and NOT data were analyzed separately. Latency data were analyzed with a gamma distribution; duration data were analyzed with a beta distribution; and frequency data were analyzed with a Poisson distribution. During HAT, 1 low-RFI gilt did not enter zone 1; therefore, was given a latency of 600 s. All behaviors were analyzed using a model with the fixed effects of test week, genetic line, sex, and the interaction of genetic line and sex, with the covariate of test day age, and random effect of pen. Frequency of urination and defecation models also included the random effect of total number of pre-test urinations and defecations, respectively.

Regressions were analyzed using the same models as previously described; however, linear and quadratic RFI were included as covariates in the model. Odds ratios (**OR**) were used to measure the magnitude of effect of the linear and quadratic RFI on the behavior variables. Therefore, OR indicated the multiplicative change in odds of the behavior with 1 kg/d increase in RFI. An OR of 1 indicates no effect, whereas an OR of greater than 1 indicates an increased effect and an OR less than 1 indicates a decreased effect of RFI on the behavior. For ease of interpretation, inverted OR were calculated as 1 divided by OR where necessary. The significance level was fixed at $P \leq 0.05$.

RESULTS

Human Approach Test

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Genetic Line, Barrow, and Gilt Differences. There were no line, sex, or line × sex differences in latency to enter zone 1 (*P* ≥ 0.25; Table 2). Low-RFI pigs entered zone 1 less frequently compared to high-RFI pigs (low-RFI = 7.03 ± 0.50 vs. high-RFI = 8.45 ± 0.57; *P* = 0.03; Table 2). No sex or line × sex differences were observed in zone 1 entrance frequency (*P* ≥ 0.35; Table 2). Barrows spent approximately 2% more time within zone 1 compared to gilts (barrow = 6.48 ± 0.61 vs. gilt = 4.69 ± 0.53; *P* = 0.03); however, line and line × sex did not differ in duration of time spent within zone 1 (*P* ≥ 0.53; Table 2). No line, sex, or line × sex differences were observed in duration of time spent within zone 2 (*P* ≥ 0.22), zone 3 (*P* ≥ 0.27), or zone 4 (*P* ≥ 0.60; data not presented).

Barrows crossed fewer zone lines (barrow = 49.88 ± 1.82 vs. gilt = 57.35 ± 2.05; *P* < 0.0001) and had fewer head movement frequencies than gilts (barrow = 114.24 ± 3.30 vs. gilt = 122.30 ± 3.52; *P* = 0.002). However, no line or line × sex differences were observed for zone crossing or head movement frequencies (*P* ≥ 0.26; Table 2). No line, sex, or line × sex differences were observed in duration of time spent with head in the front (*P* ≥ 0.35), side (*P* ≥ 0.17), or back (*P* ≥ 0.29) orientation relative to the human (data not presented). There were no line, sex, or line × sex differences observed in urination or defecation frequency (*P* ≥ 0.12; Table 2). No differences in total number of escape attempts were observed between lines and sexes (*P* ≥ 0.29; Table 2). However, a line × sex interaction was observed for escape attempt frequency (*P* = 0.007; Table 2), whereby low-RFI gilts attempted to escape less frequently than high-RFI gilts (*P* = 0.008) and high-RFI barrows attempted to escape less frequently than high-RFI gilts (*P* = 0.02). Low-RFI barrows did not differ from high-RFI barrows (*P* = 0.23) or gilts of both genetic lines (*P* ≥ 0.13) for this behavior. Barrows froze less frequently compared to gilts (barrow = 3.54 ± 0.47 vs. gilt = 4.64 ± 0.60; *P* = 0.02); however, no line or line × sex differences were observed

($P \geq 0.11$; Table 2). No line, sex, or line × sex differences were observed for duration of time attempting to escape or freezing ($P \geq 0.30$; Table 2).

Behavior and RFI Relationship. Residual feed intake was quadratically associated with zone crossings (OR = 1.12; $P = 0.04$) and head movement (OR = 1.08; $P \leq 0.05$); however, these variables did not show a linear relationship ($P \geq 0.34$; Supplemental Table 1). No other linear or quadratic associations were observed between behaviors and RFI (Supplemental Table 1).

Novel Object Test

Genetic Line, Barrow, and Gilt Differences. There were no line, sex, or line × sex differences in latency to enter zone 1 ($P \geq 0.15$; Table 3). Low-RFI pigs entered zone 1 less frequently compared to high-RFI pigs (low-RFI = 7.35 ± 0.64 vs. high-RFI = 9.90 ± 0.81; $P = 0.0002$); however, there was no sex difference observed in zone 1 entrance frequency ($P = 0.08$; Table 3). A line × sex interaction was observed for zone 1 entrance frequency ($P = 0.02$), where low-RFI gilts entered zone 1 less frequently than high-RFI gilts ($P < 0.0001$) and barrows of both genetic lines (P ≤ 0.009). Low-RFI barrows did not differ from high-RFI barrows ($P = 0.25$) or gilts (P = 0.12) in zone 1 entrance frequency. No line, sex, or line × sex differences were observed for duration of time spent within zone 1 ($P \geq 0.11$; Table 3), zone 2 ($P \geq 0.43$), zone 3 ($P \geq 0.22$), or zone 4 ($P \geq 0.08$; data not presented).

No sex or line × sex differences were observed in zone crossing frequency ($P \geq 0.08$; Table 3); however, low-RFI pigs had more head movements frequencies than high-RFI pigs (low-RFI = 118.68 ± 1.75 vs. high-RFI = 110.43 ± 1.68; $P = 0.001$). No sex or line × sex differences were observed in head movement frequency ($P \geq 0.29$; Table 3). No line, sex, or line × sex differences were observed for duration of time spent with head in the front ($P \geq 0.20$), side ($P \geq 0.58$), or back ($P \geq 0.11$) orientation relative to the cone (data not presented). There were no

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line, sex, or line × sex differences observed in urination or defecation frequency ($P \geq 0.24$; Table 3). Low-RFI pigs performed fewer escape attempts (low-RFI = 0.97 ± 0.21 vs. high-RFI = 2.08 ± 0.38; $P = 0.0002$) and spent approximately 2% less time attempting to escape compared to high-RFI pigs (low-RFI = 0.17 ± 0.06 vs. high-RFI = 0.41 ± 0.09; $P = 0.04$). However, no sex or line × sex differences were observed in escape attempt frequency or duration ($P \geq 0.11$; Table 3). Barrows froze more frequently (barrow = 4.73 ± 0.58 vs. gilt = 3.15 ± 0.42; $P = 0.0007$) and spent approximately 2% longer freezing compared to gilts (barrow = 3.99 ± 0.68 vs. gilt = 2.30 ± 0.52; $P = 0.05$). However, no line or line × sex differences were observed in freezing duration or frequency ($P \geq 0.27$; Table 3).

Behavior and RFI Relationship. Residual feed intake was quadratically associated with frequency of zone 1 entrances (OR = 0.65; $P = 0.004$), zone crossings (OR = 1.11; $P = 0.05$), head movement frequencies (OR = 1.15; $P = 0.0004$), and defecations (OR = 1.57; $P = 0.03$); however, there were no linear relationships between these variables ($P \geq 0.41$; Table 4). Residual feed intake was linearly associated with frequency of escape attempts (OR = 0.19; $P = 0.04$; Fig. 2A) and freezing (OR = 4.00; $P = 0.0001$; Fig. 2B); however, there were no quadratic relationships between these variables ($P \geq 0.19$; Table 4). No other linear or quadratic relationships were observed between behaviors and RFI (Table 4).

DISCUSSION

Genetic Line Differences

Low- and high-RFI pigs displayed subtle differences in behavioral reactivity in response to fear-eliciting stimuli. No differences were observed between genetic lines in latency to enter or duration of time spent in zone 1, zone crossings, elimination, or freezing during HAT or NOT. During both HAT and NOT, low-RFI pigs entered zone 1 fewer times than high-RFI pigs. A

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similar line difference was observed in eighth generation barrows but was not significant (Colpoys et al., 2014). Since the decreased zone 1 entrance frequency for the low-RFI pigs did not correspond with a difference in latency to approach or duration of time interacting with the human and cone, we reason that this difference was not related to fearfulness. Alternatively, we hypothesize that the difference observed between genetic lines for zone 1 entrance frequency may reflect appetitive exploratory behavior, such as rooting and chewing. Due to the camera angles, these detailed behaviors of interactions with the floor, human and novel object could not be reliably observed, and thus were not included in the ethogram.

In contrast to barrows from the eighth generation (Colpoys et al., 2014), during NOT, low-RFI pigs in the current study changed head orientation more frequently when compared to high-RFI pigs. It is difficult to interpret these differences in head movements, since this behavior could arise from aversive (eg. vigilance) or appetitive (eg. exploration) motivational systems. Similar to eighth generation barrows (Colpoys et al., 2014), during NOT, low-RFI pigs in the current study attempted to escape for a shorter duration and less frequently, suggesting lower fearfulness, compared to high-RFI pigs. Although the pigs had never previously interacted with the human in HAT, previous experience with humans may have reduced the genetic line differences during HAT (Hemsworth et al., 1981; Hemsworth and Barnett, 1992; Hemsworth et al., 1996). These results do not indicate greater fearfulness in one genetic line; rather, they suggest that low- and high-RFI pigs may differ in coping methods during NOT.

Barrow and Gilt Differences

Different barrow and gilt responses were observed during HAT and NOT. During HAT, barrows appeared to be less fearful than gilts. Barrows spent a longer duration of time within zone 1, crossed fewer zone lines, had fewer head movements, and froze fewer times compared to

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gilts. These results differ from Reimert et al. (2014) who reported no difference in the duration of time spent near the human but observed a tendency for a shorter latency to touch a human in gilts compared to barrows. However, it should be noted that they tested younger pigs (7 wk old) in groups within the home pen which may alter the level of fearfulness compared to older pigs (14 wk old) individually tested within a novel arena in the current study (Forkman et al., 2007; Pairis et al., 2009).

Unlike HAT, barrows spent a longer duration of time freezing and froze more often than gilts during NOT. This may indicate that barrows were more fearful than gilts during NOT, and are in line with findings of Reimert and colleagues (2014) who reached a similar conclusion following NOT. Similarly, Kranendonk et al. (2006) reported that young boars (approximately 25 d old) vocalized during NOT and struggled during a back test more often than gilts. Furthermore, physiological and hormonal differences between barrows and gilts have shown decreased stress in females (Ruis et al., 1997; Lay et al., 2002; Baxter et al., 2012), which may be reflected through NOT results of the current study.

Inconsistency of sex differences between tests was unexpected as behavior during HAT and NOT is reported to be positively correlated (van der Kooij et al., 2002; Janczak et al., 2003). Previous studies found no differences between barrows and gilts during behavioral stress tests (Hessing et al., 1994; De Jong et al., 1998; Siegford et al., 2008); however, comparison between studies is difficult as test methodology, pig ages and genetics vary. Although the human in this study was novel to these pigs, they are exposed to male and female humans during daily chores. Conversely, these pigs had never encountered an orange traffic cone before. Previous studies reported differences between males and females in coping with stressors. In rats, males had faster corticosterone habituation to chronic stress compared to females (Galea et al., 1997). To our

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knowledge, no swine studies have investigated sex differences in habituation to HAT. It could be speculated from our results that barrows may habituate quicker to humans and better generalize this to unfamiliar humans compared to their gilts counterparts. Further research on understanding the neuroendocrine and behavioral differences between males and females that could contribute to such a differential observation is warranted.

Behavior and RFI Relationships

Regardless of genetic line, RFI was not strongly related to behavior during HAT, but may reflect coping style during NOT. Decreasing RFI (increasing feed efficiency) by 1 kg/d increased the odds of attempting to escape by 5.26 times (inverted OR from Table 4), during NOT. Conversely, decreasing RFI (increasing feed efficiency) by 1 kg/d decreased the odds of freezing by 4 times. Interestingly, these phenotypic results are in contrast to genetic line differences in escape attempts described in the current study, and may explain why low-RFI pigs did not show as strong of a linear relationship between predicted escape attempts and RFI as high-RFI pigs (Fig. 2A). These results suggest that regardless of genetic line, RFI is phenotypically related to coping styles. More feed efficient (lower RFI) pigs responded to NOT more actively, or through a proactive coping style, by attempting to escape whereas less feed efficient (higher RFI) pigs responded to NOT more passively, or through a reactive coping style, by freezing (Koolhaas et al., 1999). These phenotypic relationships are unexpected as it can be assumed that escape attempts require greater energy expenditure than freezing. Therefore, these results may not reflect behavioral coping style within the home pen. We hypothesize that feed efficiency differences may be related to hypothalamic-pituitary-adrenocortical axis responsiveness to stress coping (Koolhaas et al., 1999), whereas more feed efficient pigs may secrete less cortisol in response to stress than less feed efficient pigs (Jenkins et al., 2013).

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General Discussion

Increasing swine feed efficiency is a genetic improvement and management goal to facilitate improved producer profitability, sustainability, and resource allocation. Numerous studies have been conducted to examine the physiology of feed efficiency using divergent RFI models. Specifically in pigs, RFI research has focused on feed intake patterns (Young et al, 2011), physical activity (Sadler et al., 2011), body composition (Boddicker et al., 2011a,b), nutrient digestibility (Barea et al., 2010; Harris et al., 2012), immune system activation (Rakhshandeh et al., 2012), skeletal muscle oxidative stress (Grubbs et al., 2013) and protein turnover (Cruzen et al., 2013). One aspect of swine welfare which may be influenced by altering feed efficiency is the pig's stress response (Jenkins et al., 2013), particularly to human interaction and novel stimuli.

Using RFI selection as a model to study feed efficiency, our data presented herein indicates subtle differences in grow-finish pig behavioral reactivity to fear-eliciting stimuli as it relates to feed efficiency. Moreover, sex had a larger impact on behavioral reactivity during HAT than genetic line. Therefore, overall selection for improved feed efficiency did not negatively impact swine welfare in its response to fear-eliciting stimuli compared to selection for poorer feed efficiency. Furthermore, our data suggests that regardless of genetic line, RFI may be related to coping style as more feed efficient pigs had increased odds of attempting to escape but decreased odds of freezing during NOT. In conclusion, our data supports that feed efficiency does not decrease a pig's ability to cope with a stressor as previously suggested (Rydhmer and Canario, 2014), but could relate to differences in the way pigs cope with stressors, at least for the genetic lines examined in the present study.

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Tables

Table 1. Ethogram of behaviors recorded during human approach and novel object tests. Latency in seconds (s), duration (%), and/or frequency (n) of behaviors collected[1]

Measure	**Description**
Approach	
Zone 1, s, n, %	The mouth, nose, and/or face of the pig contact any part of zone 1 (defined as the human or traffic cone).
Zone 2, 3, & 4, %	The base of both the pig's ears were within the limits of the respective zone and the pig's mouth, nose, and/or face was not touching zone 1.
Zone crossings, n	Sum of the total number of zone 2, 3, and 4 entrances.
Head orientation	
Front, Side, Back, %	The pig's snout was pointed towards, perpendicular, or in the opposite direction of zone 1, respectively.
Head movements, n	The sum of front, side, and back head orientations.
Elimination	
Urination, n	Excreting urine.
Defecation, n	Excreting feces.
Escape attempt, n, %	The front two or all four pig's hooves were off the arena floor in attempt to remove itself from the test arena. Duration was measured from the removal of the two front hooves from the floor to all four hooves returning to the floor.
Freezing, n, %	No movement of any portion of the pig's body was visible for ≥ 3 s.

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Duration was measured from the start of the freeze to any movement of the body.

[1] Ethogram adapted from Colpoys et al. (2014). Live observations were utilized to collect elimination data and video decoding was utilized to collect all other measures.

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Table 2. Latency (s), frequency (n), and duration (%) of behaviors (least square means ± SE) during the human approach test in barrows and gilts selected for low residual feed intake (**RFI**; more feed efficient) and high RFI (less feed efficient)

	Genetic line														
	Low-RFI						High-RFI						*P*-value		
Measures	Barrow			Gilt			Barrow			Gilt			Line	Sex	Line*Sex
Zone 1, s	67.13	±	16.27	101.69	±	24.61	90.76	±	21.99	103.56	±	25.05	0.50	0.25	0.55
Zone 1, n	6.68	±	0.64	7.40	±	0.68	8.67	±	0.75	8.24	±	0.72	0.03	0.76	0.35
Zone 1, %[1]	6.43	±	0.86	4.31	±	0.71	6.52	±	0.86	5.11	±	0.79	0.53	0.03	0.60
Zone crossings, n[1]	48.94	±	2.12	56.53	±	2.35	50.84	±	2.17	58.18	±	2.43	0.29	<0.0001	0.88
Head movements, n[1]	113.54	±	3.70	124.50	±	3.98	114.94	±	3.74	120.14	±	3.90	0.58	0.002	0.26
Urination, n	0.57	±	0.17	0.64	±	0.18	0.70	±	0.19	0.41	±	0.14	0.68	0.46	0.26
Defecation, n	4.04	±	0.45	3.72	±	0.43	3.46	±	0.42	3.00	±	0.38	0.12	0.34	0.80
Escape attempt, n[1]	1.31	±	0.30[ab]	0.83	±	0.22[a]	0.93	±	0.24[a]	1.80	±	0.39[b]	0.29	0.59	0.007
Escape attempt, %[1]	0. 22	±	0.08	0.18	±	0.07	0. 23	±	0.08	0. 35	±	0.10	0.30	0.73	0.34
Freeze, n[1]	4.10	±	0.62	4.48	±	0.67	3.05	±	0.50	4.81	±	0.71	0.32	0.02	0.11
Freeze, %[1]	3.57	±	0.73	3.52	±	0.73	2.52	±	0.60	3.49	±	0.74	0.38	0.45	0.40

[1] Dueto a technical problem, video of 1 high-RFI gilt was lost. Therefore, for high-RFI gilts n = 19 with regard to the noted behaviors

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Table 3. Latency (s), frequency (n), and duration (%) of behaviors (least square means ± SE) during the novel object test in barrows and gilts selected for low residual feed intake (**RFI**; more feed efficient) and high RFI (less feed efficient)

	Genetic line						
	Low-RFI		High-RFI		*P*-value		
Measures	Barrow	Gilt	Barrow	Gilt	Line	Sex	Line*Sex
Zone 1, s	78.06 ± 15.64	99.92 ± 19.98	68.55 ± 13.73	63.31 ± 12.66	0.15	0.68	0.42
Zone 1, n	8.59 ± 0.86[a]	6.28 ± 0.69[b]	9.69 ± 0.93[a]	10.11 ± 0.96[a]	0.0002	0.08	0.02
Zone 1, %	7.70 ± 1.91	5.78 ± 1.65	11.08 ± 2.28	6.68 ± 1.77	0.30	0.11	0.64
Zone crossings, n	55.01 ± 2.25	54.76 ± 2.24	53.88 ± 2.22	59.81 ± 2.38	0.27	0.10	0.08
Head movements, n	118.11 ± 2.45	119.25 ± 2.45	108.50 ± 2.34	112.40 ± 2.38	0.001	0.29	0.54
Urination, n	0.54 ± 0.17	0.44 ± 0.15	0.58 ± 0.17	0.46 ± 0.15	0.86	0.47	0.97
Defecation, n	4.04 ± 0.45	3.55 ± 0.43	3.24 ± 0.40	3.77 ± 0.44	0.49	0.93	0.24
Escape attempt, n	0.84 ± 0.24	1.13 ± 0.29	1.76 ± 0.39	2.46 ± 0.50	0.0002	0.11	0.92
Escape attempt, %	0.13 ± 0.07	0.22 ± 0.09	0.36 ± 0.12	0.47 ± 0.14	0.04	0.35	0.77
Freeze, n	4.31 ± 0.63	3.04 ± 0.49	5.19 ± 0.72	3.27 ± 0.52	0.27	0.0007	0.63
Freeze, %	3.93 ± 0.95	2.34 ± 0.73	4.04 ± 0.96	2.27 ± 0.72	0.99	0.05	0.92

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Table 4. Odds ratios of RFI and behavior regressions during the novel object test in barrows and gilts selected for low residual feed intake (more feed efficient) and high residual feed intake (less feed efficient)

	Linear		**Quadratic**	
Measures	**OR**	***P*-value**	**OR**	***P*-value**
Zone 1, s	1.05	0.93	0.87	0.71
Zone 1, n	1.02	0.94	0.65	0.004
Zone 1, %	0.53	0.50	0.50	0.18
Zone crossings, n	0.96	0.71	1.11	0.05
Head movements, n	1.01	0.84	1.15	0.0004
Urination, n	1.60	0.63	1.30	0.63
Defecation, n	0.73	0.41	1.57	0.03
Escape attempt, n	0.19	0.04	1.66	0.19
Escape attempt, %	0.17	0.21	1.53	0.58
Freeze, n	4.00	0.0001	1.04	0.84
Freeze, %	4.49	0.07	1.02	0.96

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Figures

Figure 1.

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Figure 2.

Figure Captions

Figure 1. Arena where pigs were tested using human approach (HAT) and novel object (NOT) tests.

[a]Indicates the distance of each zone from the human or cone, located in zone 1. Zones 2, 3, and 4 consisted of approximately equal area.

Figure 2. Predicted escape attempt (A) and freezing (B) frequencies across residual feed intake (**RFI**) in low-RFI (more feed efficient) and high-RFI (less feed efficient) barrows and gilts during the novel object test.

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Supplementary Material

Supplemental Table 1. Odds ratios of RFI and behavior regressions during the human approach test in barrows and gilts selected for low residual feed intake (more feed efficient) and high residual feed intake (less feed efficient)

	Linear		**Quadratic**	
Measures	**OR**	***P*-value**	**OR**	***P*-value**
Zone 1, s	2.33	0.30	1.51	0.31
Zone 1, n	0.78	0.40	1.09	0.57
Zone 1, %[1]	0.74	0.55	0.62	0.10
Zone crossings, n[1]	0.90	0.39	1.12	0.04
Head movements, n[1]	0.92	0.34	1.08	0.05
Urination, n	0.86	0.88	0.75	0.57
Defecation, n	0.64	0.25	1.21	0.38
Escape attempt, n[1]	1.32	0.69	0.55	0.11
Escape attempt, %[1]	1.61	0.65	0.45	0.19
Freeze, n[1]	0.68	0.35	0.81	0.29
Freeze, %[1]	2.08	0.24	0.78	0.51

[1] Due to a technical problem, video of 1 high-RFI gilt was lost. Therefore, for high-RFI gilts n = 19 with regard to the noted behaviors.