

The effect of selection for residual feed intake during the grow/finish phase of production on feeding behavior traits and sow reproduction and lactation efficiency in Yorkshire pigs

by

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TABLE OF CONTENTS

LIST OF FIGURES	iv
LIST OF TABLES	vi
ABSTRACT	vii
ACKNOWLEDGEMENTS	ix
CHAPTER 1. GENERAL INTRODUCTION	1
Introduction	1
Thesis Organization	2
Literature Review	3
Feeding behavior	3
Appetite regulation	20
Literature Cited	34
CHAPTER 2. EFFECT OF SELECTION FOR RESIDUAL FEED INTAKE ON FEEDING BEHAVIOR AND DAILY FEED INTAKE PATTERNS IN YORKSHIRE SWINE	41
Abstract	41
Introduction	42
Materials and Methods	43
Results and Discussion	48
Conclusion and Implications	53
Acknowledgements	54
Literature Cited	54
Figures and Tables	57
CHAPTER 3. ESTIMATION OF GENETIC PARAMETERS AND HIGH DENSITY SNP ANALYSIS OF FEEDING BEHAVIOR TRAITS IN YORKSHIRE PIGS SELECTED FOR RESIDUAL FEED INTAKE	65
Abstract	65
Introduction	66
Materials and Methods	67
Results and Discussion	72

Conclusions	82
Acknowledgements	82
Literature Cited	82
Figures and Tables	87
CHAPTER 4. EFFECT OF SELECTION FOR RESIDUAL FEED INTAKE DURING THE GROW/FINISH PHASE OF PRODUCTION IN YORKSHIRE PIGS ON SOW REPRODUCTIVE PERFORMANCE AND LACTATION EFFICIENCY	95
Abstract	95
Introduction	96
Materials and Methods	97
Results and Discussion	105
Conclusions and Implications	112
Note From Author	113
Acknowledgements	114
Literature Cited	114
Figures and Tables	120
CHAPTER 5. GENERAL CONCLUSIONS	127
General Summary	127
Implications and Future Work	131
Literature Cited	134

LIST OF FIGURES

Figure 2.1	Least square means with SE bars for the line selected for decreased residual feed intake (gray bars) and the control line (white bars) for feeding behavior traits for 3 data sets (generation by parity, G4P2, G5P1, and G5P2) over the total test period (TP) and over the first (TP1) and second (TP2) half of the test period. The <i>P</i> -value is less than 0.05 for pairs of bars marked with * and less than 0.01 for pairs of bars marked with **.	57
Figure 2.2	Least square means for feed intake per 2-h block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. No significant differences ($P > 0.1$ for all 2-hr blocks) were found between lines.	58
Figure 2.3	Least square means for occupation time per 2-hr block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. The <i>P</i> -value is less than 0.05 for differences between lines at times marked with * and less than 0.01 for **.	59
Figure 2.4	Least square means for number of visits per 2-hr block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. The <i>P</i> -value is less than 0.05 for differences between lines at times marked with *.	60
Figure 3.1	Proportion of genetic variance explained by markers for average daily feed intake. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	87
Figure 3.2	Proportion of genetic variance explained by markers for average occupation time per day. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	88
Figure 3.3	Proportion of genetic variance explained by markers for average number of visits per day. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	89
Figure 3.4	Proportion of genetic variance explained by markers for average feed intake per visit. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	90

Figure 3.5	Proportion of genetic variance explained by markers for average occupation time per visit. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	91
Figure 3.6	Proportion of genetic variance explained by markers for average feed intake rate. Each chromosome is represented in a different color, with SSC1 on the left, SSC 18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.	92
Figure 4.1	Schematic flow chart of the energy metabolism of sows during lactation (Bergsma et al., 2008, 2009).	120

LIST OF TABLES

Table 1.1	Heritabilities of feeding behavior traits in pigs, cattle, and sheep.	12
Table 1.2	Phenotypic correlations of feeding behavior traits with measures of feed efficiency in pigs, cattle, and sheep.	13
Table 1.3	Genetic correlations of feeding behavior traits with measures of feed efficiency in pigs, cattle, and sheep.	14
Table 1.4	Phenotypic correlations of feeding behavior traits with average daily gain and backfat thickness in pigs, cattle, and sheep.	15
Table 1.5	Genetic correlations of feeding behavior traits with average daily gain and backfat thickness in pigs, cattle, and sheep.	16
Table 2.1	On- and off-test characteristics for each group of pigs evaluated	61
Table 2.2	Residual correlations of feeding behavior traits with residual feed intake across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.	62
Table 2.3	Residual correlations of feeding behavior traits with ADG across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.	63
Table 2.4	Residual correlations of feeding behavior traits with backfat across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.	64
Table 3.1	Number of pigs with feeding behavior data per line, generation, and sex with number genotyped in parentheses.	93
Table 3.2	Heritabilities and correlations amongst performance and feeding behavior traits with standard errors in () below estimate.	94
Table 4.1	Number of animals available for analyses.	121
Table 4.2	Covariates used for data analysis.	122
Table 4.3	Line differences in piglet traits after 7 generations of selection for residual feed intake.	123
Table 4.4	Line differences in sow traits after 7 generations of selection for residual feed intake.	124
Table 4.5	Heritabilities of sow reproductive and efficiency traits.	125
Table 4.6	Genetic correlations of sow reproductive and efficiency traits with RFI.	126

ABSTRACT

Residual feed intake (**RFI**) is a measure of feed efficiency defined as the difference between observed and predicted feed intake based on average requirements for maintenance and production. At Iowa State University, two lines of Yorkshire pigs were developed to study the effects of selection for RFI during the grow/finish phase of production (**RFI_{G/F}**). One line was selected over 7 generations for decreased **RFI_{G/F}** (**LRFI**) to improve feed efficiency and the other line (**HRFI**) was selected randomly for 4 generations and then for increased **RFI_{G/F}**. The main objectives of this dissertation were to evaluate feeding behavior traits and sow reproductive performance and lactation efficiency. Pigs from the LRFI line had significantly lower feed intake (**FI**) per day than did HRFI pigs. After adjusting for FI per day, number of visits (**NV**) per day and per hour did not differ significantly between the two lines but the trend was for LRFI pigs to have fewer visits, particularly during peak eating times. Furthermore, pigs from the LRFI line ate faster and spent less time in the feeder per day, per visit, and per hour than HRFI pigs. Feeding behavior traits were moderately to highly heritable, with heritabilities ranging from 0.36 for FI per visit to 0.71 for occupation time (**OT**) per day. Feed intake rate was also highly heritable at 0.59. Heritabilities of NV per day, OT per visit, and FI per day were similar (0.44, 0.42, and 0.42, respectively). FI per day was strongly correlated, both phenotypically and genetically, with RFI, average daily gain (**ADG**), and backfat depth (**BF**). FI per visit was moderately correlated, both phenotypically and genetically, with ADG and BF. OT per day was moderately correlated, both phenotypically and genetically, with RFI and BF. Other correlations between feeding behavior traits and performance traits were low. For each feeding behavior trait, one or two genomic regions were identified as being important in a whole genome association study.

SNPs located adjacent to MC4R (a gene already shown to be associated with FI, fatness, and growth) were significant for FI per day. Other genes with nearby SNPs found to be associated with feeding behavior traits included several related to different transcription regulators. After 7 generations, selection for decreased $RFI_{G/F}$ has improved piglet performance and increased sow weight loss during lactation. LRFI sows had more piglets farrowed, born alive, and weaned than did HRFI sows. LRFI piglets were heavier at birth and had better litter growth than did HRFI piglets. However, this increased piglet performance came at a cost to the sow. During lactation, LRFI sows consumed less feed and lost more body weight, fat mass, and BF than did HRFI sows. LRFI sows had a greater negative energy balance but more favorable lactation efficiency and RFI during lactation than HRFI sows. Heritabilities were high ($h^2 > 0.4$) for sow weights, body composition, and maintenance requirements and piglet birth weights. Piglet growth during lactation, mobilization of the sow's body tissue, sow feed intake and total born were moderately heritable ($0.2 < h^2 < 0.4$). Correlations with $RFI_{G/F}$ were not significant for most traits. However, strong, positive genetic correlations with $RFI_{G/F}$ were found for sow weight at farrowing and weaning, sow maintenance requirements, and sow RFI and strong, negative genetic correlations with $RFI_{G/F}$ were found for sow protein mass loss and lactation efficiency. In conclusion, feed efficiency may be affected by feed intake behavior because selection for decreased $RFI_{G/F}$ has resulted in pigs which spend less time eating and eat faster. A large genetic component to feeding behavior is evident and measuring and selecting for these traits may allow for other opportunities to improve traits of economic importance. Selection for $RFI_{G/F}$ has positively affected piglet performance and lactation efficiency but has negatively affected sow body condition change and energy balance during lactation.

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CHAPTER 1. GENERAL INTRODUCTION

Introduction

As feed costs continue to rise due to competition with other industries such as ethanol for feed resources and consumers become increasingly more concerned with sustainability, feed efficiency (kg growth per kg feed) continues to grow in importance to the pig industry and is a vital component of pig breeding programs. Feed efficiency has traditionally been improved through selection for decreased feed intake and increased growth. However, only about 65% of phenotypic differences in feed intake can be accounted for by growth and performance (Cai et al., 2008). The remaining variation in feed intake can be evaluated using residual feed intake (**RFI**), which is a measure of feed efficiency defined as the difference between observed feed intake and the expected feed intake based on maintenance and performance. The impact of selecting for RFI during the grow/finish phase of production ($\text{RFI}_{\text{G/F}}$) must be evaluated so that possible detrimental effects can be assessed. At Iowa State University, two lines of Yorkshire pigs were developed to study the effects of selection for $\text{RFI}_{\text{G/F}}$. One line was selected over 7 generations for decreased $\text{RFI}_{\text{G/F}}$ (**LRFI**) to improve feed efficiency and the other line (**HRFI**) was selected randomly for 4 generations and then for increased $\text{RFI}_{\text{G/F}}$.

Therefore, the objectives of this dissertation included evaluating the effects of selection for $\text{RFI}_{\text{G/F}}$ on feeding behavior and daily feed intake patterns. Feeding behavior traits that were evaluated included average feed intake per day, visit, and 2-h block; occupation time per day, visit, and 2-h block; number of visits per day and 2-h block; and feed intake rate. To evaluate the association of feeding behavior traits with $\text{RFI}_{\text{G/F}}$, phenotypic correlations were estimated across and within lines. Phenotypic correlations of

feeding behavior traits were also estimated with average daily gain and backfat. The second objective of this study was to estimate heritabilities of feeding behavior traits, genetic correlations of feeding behavior traits with $RFI_{G/F}$, and perform a whole genome association study for feeding behavior traits in order to identify regions of the pig genome that may be associated with feeding behavior.

As the issue of sustainability becomes more important, we must also aim to have sows which produce more piglets. Because of this, it is important to evaluate the impact of selecting for more efficient finisher pigs on the reproduction and efficiency of sows. Therefore, another objective of this dissertation was to evaluate the effects of selection for $RFI_{G/F}$ on and to estimate the genetic and phenotypic correlations of $RFI_{G/F}$ with and heritabilities of sow reproductive performance and lactation efficiency. Traits pertaining to the piglets of the sow that were evaluated included number farrowed, born alive, dead at birth, mummified, weaned by litter, and weaned by sow; total and average litter weights at birth (both total farrowed and only those born alive) and weaning; farrowing and pre-weaning survival; and litter and piglet average daily gain, growth, and energy gain. Traits pertaining to the sow evaluated included sow weight, fat mass, protein mass, and backfat depth at farrowing and at weaning; weight, fat mass, protein mass, and backfat losses during lactation; sow maintenance requirements; sow feed intake; energy output and input; lactation efficiency; sow residual feed intake; and energy balance.

Thesis Organization

Three journal articles (one published, two to be submitted for publication) were written to achieve the objectives of this dissertation and are included as chapters. Some general background information and a literature review of feeding behavior and appetite regulation

are provided in the current chapter. The effects of selection for $RFI_{G/F}$ on feeding behavior traits and the phenotypic correlations of feeding behavior traits with $RFI_{G/F}$, average daily gain, and backfat thickness are reported in Chapter 2. The heritabilities of feeding behavior traits, genetic correlations of feeding behavior traits with $RFI_{G/F}$ and other performance traits, and a high density SNP analysis of feeding behavior traits are reported in Chapter 3. The effects of selection for $RFI_{G/F}$ on sow reproductive performance and lactation efficiency traits and the phenotypic and genetic correlations of $RFI_{G/F}$ with and the heritabilities of these same traits are reported in Chapter 4. General conclusions and discussion of the research are summarized in Chapter 5.

Literature Review

Feeding behavior and appetite regulation in pigs are influenced by many different factors. The objective of the below literature reviews was to better understand the many biological factors that contribute to differences in feeding behavior and appetite regulation. For the feeding behavior review, factors contributing to differences in feeding behavior are discussed. This is followed by discussion of genetic parameters of feeding behavior traits, response in feeding behavior traits to multiple selection strategies, and relationships of feeding behavior traits with RFI, average daily gain, and backfat. The appetite regulation review addresses the many biological factors that are involved in appetite regulation.

Feeding behavior

Introduction

Feeding behavior in pigs is a complex field of study with many factors contributing to differing feed intake patterns. In this dissertation, feeding behavior will refer to those traits

that pertain to the manner of feed intake including feed intake per day and per visit, occupation time per day and per visit, number of visits to the feeder per day, and feed intake rate. Group size, breed, sex, and other environmental factors contribute to feeding behavior (these areas will be discussed in more detail later in the dissertation). Prior to the development of electronic feeders, measuring individual feed intake during the grow/finish phase of production required individual housing, which is expensive and labor intensive (Nielsen et al., 1995). The development of computerized feed intake recording systems allows for the recording of individual feeding behavior while housing pigs in groups using electronic transponders (Young and Lawrence, 1994). Measures of feeding behavior that have been evaluated include number of visits or meals per day, occupation time per visit or meal, occupation time per day, feed intake rate, feed intake per visit or meal, and average daily feed intake (de Haer et al., 1993). Meals in the de Haer et al. (1993) study were classified as two or more visits within five minutes of each other without another pig occupying the feeder. Labroue et al. (1994) used a meal criterion of two minutes instead of five minutes because they found that increasing the meal criterion over two minutes did not greatly affect the number of meals per day. With feed costs rising, reducing feed consumption while maintaining production is becoming more valuable to producers. Therefore the relationship between feeding behavior traits and RFI has been evaluated in previous research (de Haer et al., 1993; Von Felde et al., 1996) but neither study selected for RFI.

Group size and feeding behavior

Previous studies have shown that group size affects feeding behavior. Walker (1991) evaluated groups of 10, 20, or 30 pigs in a pen with one single-space feeder that was the only

access to feed and water. The feeder allowed for competition at the feeder. Walker (1991) found no significant effect of group size in growing pigs on number of visits per day. However, a significant difference was found in occupation time per visit and percentage of the day that the feeder was occupied by a pig with occupation time per visit decreasing and percentage of the day that the feeder was occupied by a pig increasing as group size increased (Walker, 1991). Labroue et al. (1999) evaluated Piétrain and Large White growing boars housed in groups of eight to thirteen and collected feeding behavior data using a single-space electronic Acema 48 feeder (ACEMO, Pontivy, France). The feeder allowed for no competition at the feeder due to a full body race with a gate that shut behind the pig when it entered the feeder. Group size was not found to affect feed intake per day but number of visits per day and occupation time per day decreased and feed intake rate increased as group size increased (Labroue et al., 1999). When breeds were evaluated separately, the effect of group size on number of meals per day, occupation time per meal, and feed intake per meal were found to be breed specific with Large White boars eating a larger number of small, short meals when group size increased and Piétrain boars eating fewer and larger meals of similar length as group size increased (Labroue et al., 1999). Hyun and Ellis (2001) evaluated group sizes of 2, 4, 8, and 12 growing pigs per pen and used single-space electronic FIRE feeders (Osborne Industries, Inc., Osborne, KS) for collecting feeding behavior data. The feeder reduced competition at the feeder due to pigs being in a full body race when eating; however, the rear of the pig was still accessible by other pigs in the pen. In growing pigs, number of visits per day and occupation time per day decreased and feed intake per visit and feed intake rate increased as group size increased (Hyun and Ellis, 2001) which is what Labroue et al. (1999) found in pens of Large White and Piétrain growing boars mixed

together. Occupation time per visit was higher in groups of 8 pigs compared to the other sized groups (Hyun and Ellis, 2001). In a following study, evaluating finishing pigs, Hyun and Ellis (2002) found similar results with group size having an effect on all feeding behavior traits with the exception of occupation time per day when evaluating group sizes of 2, 4, 8, and 12 pigs per pen with a single-space electronic FIRE feeder. Hyun and Ellis (2002) found that, as group size increased, number of visits per day decreased and feed intake per visit and feed intake rate increased which is what Hyun and Ellis (2001) found in growing pigs. Also like Hyun and Ellis (2001), Hyun and Ellis (2002) found that occupation time per visit was greatest in groups of 8 pigs. Hyun and Ellis (2002) did not find a significant difference in occupation time per day like Hyun and Ellis (2001); however, the tendency was for occupation time per day to decrease as group size increased which is the same direction as Hyun and Ellis (2001).

Unlike the previous studies that used a constant pen size with differing group sizes, Nielsen et al. (1995) evaluated different group sizes of pigs in different size pens in order to maintain a space allowance of 1.06 m^2 per pig. Nielsen et al. (1995) used single-space electronic FIRE feeders for collecting feeding behavior. Nielsen et al. (1995) evaluated group sizes of 5, 10, 15, and 20 pigs per pen and found that pigs housed in groups of 20 had fewer number of visits per day, higher occupation time per visit and feed intake per visit, lower occupation time per day, and faster feed intake rate than pigs in other groups. These results are similar to those found by Labroue et al. (1999) and Hyun and Ellis (2001, 2002) although group sizes were different. Nielsen et al. (1995) found no difference in daily feed intake due to differences in group size which is also similar to Labroue et al. (1999).

Hyun et al. (1998) did not evaluate group size but rather space allowance, a trait related to group size because space allowance per pig with a constant pen size would decrease as the number of pigs per pen increases. Feeding behavior traits were compared between pigs housed in groups of eight with either 0.25 or 0.56 m² per pig of pen space (Hyun et al., 1998). With more space per pig, pigs had a higher gain to feed ratio and a higher number of visits per day but lower occupation time and feed intake per visit when compared to pigs with less space per pig (Hyun et al., 1998). These results support the results found for the effect of group size where smaller groups which have more space per pig had a greater number of visits per day and a lower feed intake per visit and occupation time per visit. However, smaller groups had a lower feed intake rate which Hyun et al. (1998) did not find with greater space allowance per pig. This shows that the number of pigs per feeder is important for feeding behavior in addition to the space allowance per pig. The results from these studies show that pigs adjust their feeding behavior based on the number of pigs per feeder space and space allowance per pig.

Other studies compared feeding behavior in group housing with individual housing. Gonyou et al. (1992) evaluated performance and behavior of pigs housed individually or in groups of five. Gonyou et al. (1992) reported that individually housed pigs ate more per day than group-housed pigs and tended to synchronize their eating schedules based on the pens next to them. If individually housed pigs were next to a pen of five, they would synchronize their eating with the pen of pigs as long as the feeder was adjacent to their individual pen (Gonyou et al., 1992). On the other hand, pigs housed in pens of five were more likely to eat by themselves rather than in pairs than would be expected by chance alone with lone eating increasing as the pig aged (Gonyou et al., 1992). In a study by de Haer and de Vries (1993a),

growing pigs housed individually or in groups of eight were evaluated for feeding behavior using single-space electronic IVOG feeders (Insentec B.V., Marknesse, The Netherlands). These feeders allowed for competition at the feeder because there was no race to protect the pig (de Haer and de Vries, 1993a). The entrance to the hopper could be adjusted based on the size of the pigs in order to allow only one pig access at a time (de Haer and de Vries, 1993a). Similar to Gonyou et al. (1992), individually housed pigs were found to eat less and spend less time eating per meal and per visit, eat slower, eat more and spend more time eating per day, and have more meals and visits to the feeder than group-housed pigs (de Haer and de Vries, 1993a). Bornett et al. (2000) also looked at the effects of group versus individual housing using three blocks of four unrelated Large White x Landrace males. Feeding behavior from grouped pigs was collected using single-space electronic FIRE feeders (Bornett et al., 2000). In blocks 1 and 3, pigs were housed individually for one period, grouped together for the second period, and then returned to individual housing while pigs in block 2 remained in individual housing for all 3 periods to serve as controls (Bornett et al., 2000). Group-housed pigs in period 2 were found to have fewer visits per day and higher occupation time per visit, feed intake per visit, and feed intake rate than in period 1 (Bornett et al., 2000). Number of visits per day was not significantly different between group-housed and individually-housed pigs (Bornett et al., 2000), which leads to the idea that the effects of group versus individually housed pigs may be confounded with age of the pig in this study.

Breed differences in feeding behavior

Previous studies have shown that breed has an effect on feeding behavior. In a study by de Haer and de Vries (1993b), Dutch Landrace and Great Yorkshire pigs differed in both growth performance and feeding behavior. Great Yorkshire pigs had higher average daily

gain and lean percentages, lower feed to gain ratios, and less backfat than Dutch Landrace pigs while also eating more frequently and faster than Dutch Landrace pigs, with a lower occupation time per day and feed intake per visit (de Haer and de Vries, 1993b). Growing Piétrain boars were found to have lower daily feed intake, number of visits per day, number of meals per day, occupation time per day, and feed intake rate than growing Large White boars with occupation time per meal not being significantly different (Labroue et al., 1999). Labroue et al. (1994) found that French Landrace pigs had fewer visits per day, higher feed intake per meal, and longer occupation time per meal than Large White pigs when penned together. When penned separately, the only feeding behavior trait that differed significantly was number of visits per day with French Landrace pigs having fewer visits to the feeder than Large White pigs (Labroue et al., 1994). The results from the above studies clearly show that breed has an effect on feeding behavior while the results from Labroue et al. (1994) suggest that breed not only affects feeding behavior but mixing breeds might also impact feeding behavior so warrants further research.

Sex differences in feeding behavior

Previous studies have found differences in feeding behavior traits between sexes. Hyun et al. (1997) found that barrows had a greater number of meals per day than boars and gilts but no differences for other feeding behavior traits. The results from Hyun et al. (1997) are similar to the findings of Hyun and Ellis (2001) who found that, in growing pigs, barrows had a greater number of visits and occupation time per day compared to gilts but no difference in other feeding behavior traits. However, this differs from the findings of Hyun and Ellis (2002) who found that, in finishing pigs, barrows had higher daily feed intake than gilts because of greater feed intake per visit rather than an increased frequency of eating. In a

study by de Haer and de Vries (1993b), gilts had greater number of visits per day and number of meals per day but consumed less feed per visit than boars which differs from Hyun et al. (1997) who found no differences in feeding behavior between boars and gilts. Labroue et al. (1994) found that barrows had higher occupation time per day, occupation time per meal, daily feed intake, and feed intake per meal than boars with no difference in number of meals per day which differs from Hyun et al. (1997) who found that barrows had a greater number of meals per day than boars but did not differ in other feeding behavior traits. Gonyou et al. (1992) showed that barrows had higher daily feed intake than gilts which differs from Hyun et al. (1997) and Hyun and Ellis (2001) who did not find a difference in daily feed intake between barrows and gilts but is similar to the study by Hyun and Ellis (2002) who found that barrows had a higher daily feed intake than gilts. Differences between sexes are inconsistent across studies which suggests that the effect of sex on feeding behavior differs depending on breed and environment evaluated.

Diet effects and feeding behavior

Hyun et al. (1997) evaluated the effect of diet on feeding behavior traits. Diet was found to affect the number of meals per day, feed intake per visit, feed intake per meal, occupation time per visit, and occupation time per meal. The diets consisted of differing concentrations of corn, soybean meal, amino acids, and calcium supplements (Hyun et al., 1997). Diets, from 1 to 4, had increasing soybean meal, DL-methionine, L-threonine, and limestone contents and decreasing corn, Lysine-HCL, L-tryptophan, and dicalcium phosphate contents, resulting in increasing dry matter, crude protein, and total lysine, with metabolizable energy being equal between the four diets (Hyun et al., 1997). Pigs on diets 1 and 2 had similar feeding behaviors as did pigs on diets 3 and 4. Pigs on diets 1 and 2 had

higher number of meals per day but lower feed intake per visit, feed intake per meal, occupation time per visit, and occupation time per meal than pigs on diets 3 and 4 (Hyun et al., 1997). Pigs on diet 1 also had lower feed intake per meal than pigs on diet 2 (Hyun et al., 1997). These results show that diet may play a significant role in the feeding behavior of pigs.

Electronic versus conventional feeders

Electronic feeders are single-spaced and provide protection from other pigs, varying from just a shoulder race to a full body race with a gate that closes behind the pig. Conventional feeders are multi-spaced and do not provide protection from other pigs. The FIRE feeders used in the following studies had a full body race but no gate so other pigs still had access to the rear of the pig in the FIRE feeder. Hyun and Ellis (2001) found that growing pigs fed on FIRE feeders had lower feed intake and a greater gain to feed ratio than pigs fed on conventional feeders. A follow up study in finishing pigs supported these results (Hyun and Ellis, 2002). However, a study by Casey (2003) found that pigs on a FIRE feeder had lower feed intake, greater feed conversion, and lower residual feed intake than pigs on a conventional feeder. Although no differences were found in boars for growth, backfat, and loin muscle area, gilts on the FIRE feeders grew slower and deposited less backfat and loin muscle than gilts on conventional feeders (Casey, 2003). Since differences were found for feed intake per day, there is the possibility that other feeding behavior traits would differ between conventional and FIRE feeders, especially since it is easier for a pig to displace another pig at a conventional feeder than at the FIRE feeder. This brings up the question of how reliable the results found using FIRE feeders, or other electronic feeders would be in a commercial setting where conventional feeders would be used.

Heritability of feeding behavior

Heritabilities of feeding behavior tended to be moderate to high regardless of breed or species evaluated and are reported in Table 1.1.

Table 1.1. Heritabilities of feeding behavior traits in pigs, cattle, and sheep			
Feeding behavior trait	Pigs ^a	Cattle ^b	Sheep ^c
Feed intake per day ^d	0.16 (0.16) ¹ , 0.22 (0.06) ⁴ , 0.42 (0.06) ² , 0.42 (0.05) ³		0.25 (0.06) ⁶
Feed intake per meal	0.47 (0.22) ¹ , 0.49 (0.06) ² , 0.53 (0.05) ³		
Feed intake per visit	0.35 (0.21) ¹ , 0.51 (0.03) ⁴		0.33 (0.07) ⁶
Occupation time per day	0.24 (0.20) ¹ , 0.36 (0.05) ³ , 0.43 (0.04) ⁴ , 0.44 (0.06) ²	0.28 (0.12) ⁵	0.36 (0.08) ⁶
Occupation time per meal	0.27 (0.17) ¹ , 0.45 (0.05) ³ , 0.54 (0.06) ²		
Occupation time per visit	0.27 (0.16) ¹ , 0.42 (0.04) ⁴		0.29 (0.06) ⁶
Number of meals per day	0.42 (0.20) ² , 0.43 (0.06) ³ , 0.45 (0.05) ¹		
Number of visits per day	0.38 (0.20) ¹ , 0.43 (0.04) ⁴	0.38 (0.13) ⁵	0.35 (0.07) ⁶
Feed intake rate	0.29 (0.24) ¹ , 0.44 (0.04) ⁴ , 0.49 (0.05) ³ , 0.50 (0.06) ²		

^a Estimates of heritabilities in pigs with standard error in ().
^b Estimates of heritabilities in cattle with standard error in ().
^c Estimates of heritabilities in sheep with standard error in ().
^d Estimates of feed intake per day as a behavior trait.
¹de Haer and de Vries, 1993b – 273 Dutch Landrace and 132 Great Yorkshire; ²Labroue et al., 1997 – 1285 French Landrace; ³Labroue et al., 1997 – 2425 Large White; ⁴Von Felde et al., 1996 – 1814 Large White and 1374 Landrace; ⁵Nkrumah et al., 2007 – 464 composites; ⁶Cammack et al., 2005 – 1239 ½ Columbia, ¼ Hampshire, and ¼ Suffolk lambs

Heritabilities found by de Haer and de Vries (1993b) tended to be lower with greater standard errors than those found by Von Felde et al. (1996) and Labroue et al. (1999) which may be due to smaller number of pigs used in the study. Even in species with different eating habits (ruminants versus non-ruminants), heritabilities of feeding behavior traits were consistent.

Predicted response to simulated selection for feeding behavior

Hall et al. (1999) predicted responses to selection when including feeding behavior traits along with average daily gain, backfat, and daily feed intake in a selection index with

the goal of improving growth rate, lean content of the carcass, and feed conversion ratio. The three traits that Hall et al. (1999) included were feed intake per visit, number of visits per day, and occupation time per visit because they had favorable correlations with performance traits and other feeding behavior traits are a function of those three traits and would therefore add no new information. Hall et al. (1999) concluded that the use of feeding behavior traits increased genetic gain potential for average daily gain, percent lean, feed conversion ratio, and daily feed intake. Hall et al. (1999) also concluded that the most effective (greatest genetic gain) and robust (less prone to error) index included average daily gain, backfat, daily feed intake, and number of visits per day. The index that also included feed intake per visit and occupation time per visit was considered to be less robust because more parameters would need to be estimated which allows for more error to be introduced into the selection index.

Relationships between feeding behavior and feed efficiency

Several studies have evaluated the relationship of feeding behavior with different measures of feed efficiency in pigs, cattle and sheep. Phenotypic and genetic correlations between feeding behavior traits and feed efficiency varied from study to study and are shown in Tables 1.2 to 1.3.

Table 1.2. Phenotypic correlations of feeding behavior traits with measures of feed efficiency in pigs, cattle, and sheep.

Feeding behavior trait	RFI ^a	FCR ^b	G:F
Feed intake per day	0.39 ⁶ , 0.47 ⁷ , 0.58 ¹¹ , 0.60 ⁹ , 0.61 ¹² , 0.98 ²	-0.01 ⁹ , 0.15 ⁴ , 0.16 ³ , 0.22 ²	-0.06 ¹¹ , 0.73 ⁵
Feed intake per meal	-0.07 ¹	-0.04 ⁴ , -0.00 ³	
Feed intake per visit	-0.20 ¹ , 0.11 ² , -0.03 ¹¹	-0.01 ²	-0.38 ⁵ , -0.12 ¹¹
Occupation time per day	0.02 ¹¹ , 0.06 ¹⁰ , 0.08 ⁶ , 0.10 ¹² , 0.15 ⁷ , 0.37 ² , 0.41 ⁹ , 0.49 ⁸ , 0.64 ¹	-0.06 ⁸ , -0.03 ^{9,10} , 0.05 ⁴ , 0.13 ³ , 0.14 ²	0.08 ^{5,11}
Occupation time per meal	0.00 ¹	-0.05 ⁴ , 0.02 ³	

Table 1.2. Phenotypic correlations of feeding behavior traits with measures of feed efficiency in pigs, cattle, and sheep.

Feeding behavior trait	RFI ^a	FCR ^b	G:F
Occupation time per visit	-0.15 ¹ , 0.03 ²	0.01 ²	-0.16 ⁵
Number of meals per day	0.45 ¹	0.07 ^{3,4}	
Number of visits per day	-0.01 ⁷ , 0.10 ¹² , 0.13 ² , 0.17 ⁶ , 0.18 ⁸ , 0.24 ¹¹ , 0.26 ⁹ , 0.45 ¹⁰ , 0.51 ¹	-0.13 ⁸ , -0.07 ⁹ , 0.02 ² , 0.14 ¹⁰	0.12 ¹¹ , 0.34 ⁵
Feed intake rate	-0.04 ¹ , -0.01 ⁷ , 0.08 ⁹ , 0.13 ² , 0.25 ¹¹ , 0.26 ¹⁰	-0.07 ² , -0.02 ³ , 0.08 ⁴ , 0.02 ⁹ , 0.54 ¹⁰	-0.15 ⁵ , -0.11 ¹¹

^a Phenotypic correlations of feeding behavior traits with residual feed intake (RFI).

^b Phenotypic correlations of feeding behavior traits with feed conversion ratio (FCR, kg feed to kg gain).

^c Phenotypic correlations of feeding behavior traits with gain to feed ration (G:F, kg gain to kg feed)

Pigs: ¹de Haer et al., 1993 – 273 Dutch Landrace and 132 Great Yorkshire; ²Von Felde et al., 1996 – 1814

Large White and 1374 Landrace; ³Labroue et al., 1997 – 1285 French Landrace; ⁴Labroue et al., 1997

– 2425 Large White; ⁵Hyun and Ellis, 2002 – 208 crossbred pigs; ⁶Rauw et al., 2006a – 104 Durocs;

⁷Rauw et al., 2006b – 200 Durocs

Cattle: ⁸Nkrumah et al., 2007 – 464 composites; ⁹Lancaster et al., 2009 – 341 Angus; ¹⁰Kelly et al., 2010a – 86

Limousin x Friesian; ¹¹Kelly et al., 2010b – 50 Limousin x Friesian

Sheep: ¹²Cammack et al., 2005 – 1239 ½ Columbia, ¼ Hampshire, and ¼ Suffolk lambs

Table 1.3. Genetic correlations of feeding behavior traits with measures of feed efficiency in pigs, cattle, and sheep.

Feeding behavior trait	RFI ^a	FCR ^b
Feed intake per day	0.61 (0.15) ⁵ , 0.97 (0.01) ¹	-0.06 (0.10) ² , 0.11 (0.06) ³ , 0.13 (0.28) ¹
Feed intake per meal		0.05 (0.06) ³ , 0.10 (0.06) ²
Feed intake per visit	0.13 (0.09) ¹	0.01 (0.13) ¹
Occupation time per day	0.22 (0.22) ⁵ , 0.44 (0.10) ¹ , 0.57 (0.28) ⁴	-0.25 (0.29) ⁴ , 0.12 (0.16) ¹ , 0.16 (0.07) ² , 0.16 (0.08) ³
Occupation time per meal		0.09 (0.04) ³ , 0.24 (0.09) ²
Occupation time per visit	-0.01 (0.12) ¹	-0.02 (0.17) ¹
Number of meals per day		-0.19 (0.10) ² , 0.03 (0.05) ³
Number of visits per day	-0.34 (0.30) ⁴ , 0.17 (0.12) ¹ , 0.20 (0.22) ⁵	-0.52 (0.21) ⁴ , 0.11 (0.16) ¹
Feed intake rate	0.25 (0.11) ¹	-0.21 (0.08) ² , -0.03 (0.05) ³ , 0.03 (0.16) ¹

^a Genetic correlations of feeding behavior traits with residual feed intake (RFI) with standard error in ().

^b Genetic correlations of feeding behavior traits with feed conversion ratio (FCR, kg feed to kg gain) with standard error in ().

Pigs: ¹Von Felde et al., 1996 – 1814 Large White and 1374 Landrace; ²Labroue et al., 1997 – 1285

French Landrace; ³Labroue et al., 1997 – 2425 Large White

Cattle: ⁴Nkrumah et al., 2007 – 464 composites

Sheep: ⁵Cammack et al., 2005 – 1239 ½ Columbia, ¼ Hampshire, and ¼ Suffolk lambs

Overall, daily feed intake was found to be strongly and positively correlated, both phenotypically and genetically, with RFI in pigs, cattle, and sheep. The relationship of other feeding behavior traits with RFI was study dependent with varying results based on breed, species, and sex of animal being evaluated. In general, feeding behavior is low to moderately correlated with RFI. In pigs, both genetic and phenotypic correlations of feeding behavior with feed conversion ratio were weaker than and in the same direction as genetic and phenotypic correlations of feeding behavior with RFI. However, this did not hold true in cattle with some correlations between feeding behavior and feed conversion ratio being in a different direction than the correlation between that feeding behavior and RFI. Although in a different direction, correlations of feeding behavior traits with feed conversion ratio were weaker than correlations of feeding behavior traits with RFI in cattle.

Relationship of feeding behavior with average daily gain and backfat thickness

Previous studies have evaluated the relationship of feeding behavior with average daily gain and backfat thickness in pigs, cattle, and sheep. Phenotypic and genetic correlations previously reported are shown in Tables 1.4 to 1.5.

Table 1.4. Phenotypic correlations of feeding behavior traits with average daily gain and backfat thickness in pigs, cattle, and sheep.

Feeding behavior trait	ADG ^a	BF ^b
Feed intake per day	0.28 ² , 0.47 ¹ , 0.50 ^{10,11} , 0.52 ³ , 0.66 ⁸ , 0.67 ^{3,4} , 0.76 ⁶	0.24 ² , 0.35 ¹ , 0.37 ⁴ , 0.43 ³ , 0.68 ⁶
Feed intake per meal	0.29 ⁴ , 0.31 ³ , 0.49 ¹	0.17 ⁴ , 0.20 ³ , 0.36 ¹
Feed intake per visit	-0.14 ¹⁰ , 0.04 ⁵ , 0.13 ² , 0.41 ¹	0.10 ² , 0.33 ¹
Occupation time per day	-0.06 ¹ , 0.09 ¹¹ , 0.10 ¹⁰ , 0.13 ³ , 0.17 ⁸ , 0.19 ^{4,6,9} , 0.20 ² , 0.25 ⁷ , 0.30 ⁵	-0.05 ¹ , 0.07 ³ , 0.08 ⁴ , 0.15 ² , 0.21 ⁶ , 0.37 ⁷
Occupation time per meal	0.14 ³ , 0.19 ¹ , 0.29 ⁴	0.17 ^{1,4} , 0.20 ³
Occupation time per visit	-0.14 ¹⁰ , 0.00 ² , 0.05 ⁵ , 0.18 ¹	0.00 ² , 0.18 ¹
Number of meals per day	-0.22 ¹ , -0.09 ⁴ , -0.07 ³	-0.19 ¹ , -0.09 ⁴ , -0.06 ³
Number of visits per day	-0.16 ⁶ , -0.14 ¹ , 0.01 ⁸ , 0.03 ² , 0.04 ⁷ , 0.16 ⁹ , 0.22 ¹¹ , 0.28 ^{5,10}	-0.20 ⁶ , -0.15 ¹ , 0.02 ² , 0.05 ⁷
Feed intake rate	-0.01 ⁵ , 0.09 ⁹ , 0.15 ¹⁰ , 0.23 ² ,	0.13 ⁴ , 0.15 ² , 0.18 ³ , 0.29 ⁶ ,

Table 1.4. Phenotypic correlations of feeding behavior traits with average daily gain and backfat thickness in pigs, cattle, and sheep.

Feeding behavior trait	ADG ^a	BF ^b
	0.25 ⁴ , 0.28 ³ , 0.32 ⁸ , 0.38 ⁶ , 0.50 ¹	0.35 ¹

^a Phenotypic correlations of feeding behavior traits with average daily gain (ADG).
^b Phenotypic correlations of feeding behavior traits with backfat thickness (BF).
Pigs: ¹de Haer et al., 1993 – 273 Dutch Landrace and 132 Great Yorkshire; ²Von Felde et al., 1996 – 1814 Large White and 1374 Landrace; ³Labroue et al., 1997 – 1285 French Landrace; ⁴Labroue et al., 1997 – 2425 Large White; ⁵Hyun and Ellis, 2002 – 208 crossbred pigs; ⁶Rauw et al., 2006b (evaluated rate of fat deposition instead of backfat thickness) – 200 Durocs
Cattle: ⁷Nkrumah et al., 2007 – 464 composites; ⁸Lancaster et al., 2009 – 341 Angus; ⁹Kelly et al., 2010a – 86 Limousin x Friesian; ¹⁰Kelly et al., 2010b – 50 Limousin x Friesian
Sheep: ¹¹Cammack et al., 2005 – 1239 ½ Columbia, ¼ Hampshire, and ¼ Suffolk lambs

Table 1.5. Genetic correlations of feeding behavior traits with average daily gain and backfat thickness in pigs, cattle, and sheep.

Feeding behavior trait	ADG ^a	BF ^b
Feed intake per day	0.68 (0.08) ¹ , 0.80 (0.10) ⁵ , 0.81 (0.03) ² , 0.87 (0.03) ³	0.35 (0.03) ³ , 0.45 (0.09) ¹ , 0.62 (0.05) ²
Feed intake per meal	0.29 (0.04) ² , 0.49 (0.05) ³	0.18 (0.02) ³ , 0.31 (0.04) ²
Feed intake per visit	0.20 (0.07) ¹	0.07 (0.05) ¹
Occupation time per day	0.02 (0.06) ³ , 0.17 (0.14) ⁵ , 0.19 (0.03) ² , 0.32 (0.08) ¹ , 0.42 (0.25) ⁴	0.07 (0.04) ³ , 0.09 (0.02) ² , 0.15 (0.07) ¹ , 0.37 (0.25) ⁴
Occupation time per meal	0.16 (0.02) ² , 0.23 (0.04) ³	0.12 (0.02) ² , 0.13 (0.02) ³
Occupation time per visit	0.07 (0.08) ¹	-0.05 (0.07) ¹
Number of meals per day	-0.19 (0.06) ³ , -0.03 (0.02) ²	-0.15 (0.06) ² , -0.10 (0.10) ³
Number of visits per day	-0.33 (0.23) ⁴ , 0.04 (0.06) ¹ , 0.31 (0.15) ⁵	-0.47 (0.22) ⁴ , 0.06 (0.07) ¹
Feed intake rate	0.27 (0.08) ¹ , 0.29 (0.04) ² , 0.48 (0.05) ³	0.11 (0.03) ³ , 0.19 (0.07) ¹ , 0.25 (0.03) ²

^a Genetic correlations of feeding behavior traits with average daily gain (ADG) with standard error in ().

^b Genetic correlations of feeding behavior traits with backfat thickness (BF) with standard error in ().

Pigs: ¹Von Felde et al., 1996 – 1814 Large White and 1374 Landrace; ²Labroue et al., 1997 – 1285 French Landrace; ³Labroue et al., 1997 – 2425 Large White

Cattle: ⁴Nkrumah et al., 2007 – 464 composites

Sheep: ⁵Cammack et al., 2005 – 1239 ½ Columbia, ¼ Hampshire, and ¼ Suffolk lambs

Overall, feed intake per day, visit, and meal were found to be highly and positively correlated, both phenotypically and genetically, with average daily gain in pigs, cattle and sheep. Daily feed intake was found to be highly and positively correlated, both phenotypically and genetically, with backfat thickness; however, feed intake per visit and meal were only lowly to moderately correlated with backfat thickness. Occupation time per day was moderately and positively correlated, both phenotypically and genetically, with average daily gain. Occupation time per day had low and positive phenotypic and genetic correlations with backfat thickness in pigs but high and positive phenotypic and genetic correlations with backfat thickness in cattle. Occupation time per visit and occupation time per meal were lowly to moderately correlated, both phenotypically and genetically, with both average daily gain and backfat thickness. The relationship of the number of visits or meals per day with average daily gain and backfat thickness varied greatly, suggesting that there is a strong influence of species, breed, and population on the phenotypic and genetic correlations. Feed intake rate was moderately to highly correlated, both phenotypically and genetically, with both average daily gain and backfat thickness.

Differences in feeding behavior based on differences in residual feed intake

A few studies have evaluated differences in beef cattle based on ranking them as low, medium, and high residual feed intake animals. Nkrumah et al. (2006, 2007) evaluated daily feeding frequency, defined as independent visits to the feed bunk, and daily feeding duration, defined as time spent at the feed bunk in feeding activities such as prehension, chewing, and socializing at the feed bunk. Nkrumah et al. (2006) evaluated 27 steers with Continental x British dams and either Angus or Charolais sires. Nkrumah et al. (2007) evaluated 464 beef composite steers. Nkrumah et al. (2006, 2007) found that low, medium, and high RFI steers

differed in both daily feeding frequency and daily feeding duration with low RFI steers having lower daily feeding frequency and daily feed duration than both medium and high RFI steers. Medium RFI steers were intermediate to low and high RFI steers for both daily feeding frequency and daily feeding duration (Nkrumah et al., 2006, 2007). Golden et al. (2008) evaluated 80 crossbred Angus steers and divided them into efficient (low RFI) and inefficient (high RFI) groups. Golden et al. (2008) evaluated eating bouts and daily eating rate. They also found that efficient (low RFI) steers had fewer eating bouts per day than did inefficient (high RFI) steers (Golden et al., 2008). They found no difference between low and high RFI steers for eating rate (Golden et al., 2008). Lancaster et al. (2009) evaluated 341 purebred Angus bulls for meal duration (defined as sum of all daily individual meal events), meal frequency (defined as number of independent meal events per day), and meal eating rate (calculated as dry matter intake divided by meal duration). Lancaster et al. (2009) found similar results to Nkrumah et al. (2006, 2007) and Golden et al. (2008) with low RFI bulls having lower meal frequency and meal duration than high RFI bulls and medium RFI bulls being intermediate to the low and high RFI bulls. Like Golden et al. (2008), they found no difference in meal eating rate between low, medium, and high RFI bulls (Lancaster et al., 2009). Bringham et al. (2009) evaluated 115 Brangus heifers for head-down duration (min/d), head-down frequency (events/d), and head-down eating rate (g/min) and only divided the heifers into low or high RFI animals and did not include a medium RFI group. Bingham et al. (2009) found that low RFI animals had a lower head-down frequency than high RFI animals but found that low RFI animals had a higher head-down duration than high RFI animals which is contrary to other studies (Nkrumah et al., 2006, 2007; Lancaster et al., 2009). This may be due to the animals in the study by Bingham et al. (2009) being heifers

while the other studies focused on steers and bulls. Unlike Lancaster et al. (2009), Bingham et al. (2009) found a difference in eating rate with low RFI animals eating slower than did high RFI animals. All studies found a decrease in dry matter intake in low RFI animals compared to high RFI animals. These studies show that there are consistent differences in feeding behavior between groups of cattle differing in RFI but these differences may be sex dependent.

Correlated response in feeding behavior to selection for feed efficiency

In laying hens, behavioral differences were evaluated in lines selected for high and low feed efficiency over 3 generations (Braastad and Katle, 1989). Feed efficiency was measured as proportional residual feed consumption (**PRFC**) which was expressed as a percentage deviation between observed and expected feed consumption. Expected feed consumption was based on weight gain, egg production, and metabolic body weight (Braastad and Katle, 1989). In the high efficiency lines, the 20 hens with the lowest PRFC were selected from 276 hens (Braastad and Katle, 1989). In the low efficiency line, the 25 hens with the highest PRFC were selected from 122 hens (Braastad and Katle, 1989). Braastad and Katle (1989) looked at eleven measures of behavior: resting (sitting inactive) or sleeping (eyes closed), standing inactive, standing with head movements, food pecking, drinking, grooming, dust-bathing, walking, extreme pacing, flight, and aggressive behavior. Food pecking was defined as time spent pecking at or eating food. Hens from the high efficiency line were found to be inactive more of the time and spent less time food pecking than hens from the low efficiency line (Braastad and Katle, 1989). They found no direct correlation between behavior and PRFC but this might be attributed to the limited individual variation within lines due to individuals selected for the study being at the extremes of PRFC

(Braastad and Katle, 1989). Food pecking was found to be negatively correlated with laying frequency, inactivity, and body weight (Braastad and Katle, 1989). This study suggests that the amount of time spent pecking at or eating food may be related to feed efficiency since more efficient hens spent less time pecking at their food than less efficient hens.

Correlated response in feeding behavior to selection for litter size

Comparing feeding behavior traits in a line selected for litter size and a randomly selected control line, Estany et al. (2002) found no differences in feed intake and feeding time. However, the number of visits per day was found to be different over the duration of the study with the select line having fewer visits to the feeder than the control line (Estany et al., 2002). Feed efficiency also differed between the lines with the select line having a higher feed efficiency up to about 100 d of age and the control line having a higher feed efficiency from approximately 100 d to 165 d of age (Estany et al., 2002).

Appetite regulation

Introduction

Understanding what controls appetite is important in the rapidly growing pig so that nutrient requirements for rapid lean growth can be met. Appetite can be defined as the desire of an animal to eat and satiety as the lack of desire to eat (Pond et al., 2005). Appetite is moderately heritable, 0.2 to 0.4, highly correlated, both phenotypically and genetically, with growth rate (positive) and percentage lean (negative) and moderately positively correlated with lean tissue growth rate (Whittemore, 1998). The relationship of appetite with feed conversion efficiency is positive as long as maintenance costs are offset by increasing lean-tissue growth rate; however, it tends towards negative when fatty tissue deposition becomes dominant (Whittemore, 1998). Appetite control usually refers to internal factors, both

physiological and psychological, which stimulate or inhibit hunger in animals (Pond et al., 1995). These various signals from the gut caused by stretch, osmo-concentration, or specific chemical stimuli must be relayed to the brain, either via the vagus nerve or the neuroendocrine system, that are then integrated with post-absorptive signals from other sites, including the brain itself, to produce a response which also accounts for the animal's previous experience (Rayner et al., 1992). The hunger and satiety centers are located in the hypothalamus (Pond et al., 1995) which is the same area where two primary regulators of growth hormone secretion, growth hormone-releasing factor and somatostatin, are produced (Barb et al., 1998). In ad libitum fed animals, individual meal size varies and influences the between meal interval that follows so that overall feed intake can be adjusted by the number of meals consumed (Le Magnen, 1983; Rayner, 1992). Pigs that weigh between 10 and 15 kg typically eat about 12 meals per day (Yen, 2001). As pigs grow, feed intake rate and feed intake per meal increase while number of meals per day decreases (Yen, 2001). As a result, 60 kg pigs typically eat about 7 meals per day and 250 kg pigs eat between 2 and 5 meals per day (Yen, 2001). In pigs that are meal-fed, long-term feed intake is a function of meal size as opposed to long-term feed intake being a function of number of meals as in ad libitum fed animals (Rayner, 1992). Long-term feed intake involves a learned anticipation of metabolic requirements (Rayner, 1992). From a management standpoint, understanding the mechanisms that regulate feed intake in the pig is of great interest because altering body composition through the repartitioning of nutrients to favor lean growth and improve production efficiency is a primary goal in the pig industry (Houseknecht et al., 1998).

Signals of hunger and satiety

Feed consumption causes both physical and chemical changes in the body. These changes create hormonal and/or neural signals that are carried to the brain in order to initiate satiety (Yen, 2001). The brain monitors these changes in order to determine when feeding should cease (Yen, 2001). Previous work has shown that recognition of gastrointestinal signaling for the learned oral control of intake from texture and taste of food is not unconditioned (Davis and Campbell, 1973). Due to the meal being completed before absorption is complete, meal size must be signaled primarily from the gastrointestinal tract (Rayner, 1992) and most of these signals will come from the stomach and small intestine (Davis and Campbell, 1973).

Central nervous system

The central nervous system has been shown to be involved in appetite regulation through a series of sophisticated neural and endocrine interactions (Whittemore, 1998). Peptides in the central nervous system have been shown to have a direct effect on feeding behavior and metabolism (Pond et al., 1995). Neuropeptide Y, agouti-related protein, melanin concentrating hormone, orexin, galanin, opioid peptides, and nitric oxide are hypothalamic neurotransmitters that strongly increase feed intake (Wilding, 2002). Neuropeptide Y is found in high concentrations in the hypothalamus where it is synthesized in the arcuate nucleus. Neuropeptide Y increases feed intake while decreasing metabolic rate (Wilding, 2002). Neuropeptide Y also inhibits LH secretion and, therefore, may be one of the signals to shut down reproduction when body fat stores decrease (Wilding, 2002). Agouti-related protein, which co-localizes with neuropeptide Y, is an endogenous antagonist of the melanocortin-4 receptor (MC4R) and is able to increase feed intake by blocking α -

melanocyte-stimulating hormone from acting at the receptor (Wilding, 2002). Melanin concentrating hormone, which is localized to the lateral hypothalamus and perifornical area, increases energy intake when administered and results in reduced body weight when absent (Wilding, 2002). Opioid peptides have been thought to play a role in appetite regulation through a reward process that increases feed intake (Wilding, 2002). Blockage of nitric oxide has been shown to decrease feed intake (Wilding, 2002). Cocaine and amphetamine-regulated transcript, α -melanocyte-stimulating hormone, neurotensin, glucagon-like peptide 1, and serotonin are hypothalamic neurotransmitters that decrease feed intake and increase energy expenditures (Wilding, 2002). Feed intake is inhibited by α -melanocyte-stimulating hormone, which acts within the hypothalamus via MC4R (Wilding, 2002). Glucagon-like peptide 1 is released from the gut in response to feed intake and stimulates insulin secretion (Wilding, 2002). Administration of glucagon-like peptide 1 results in decreased feed intake while inhibition of its action results in increased feed intake (Wilding, 2002). It is generally accepted that the ventromedial hypothalamus is responsible for satiety while the lateral hypothalamic area is responsible for hunger (Yen, 2001). Taste and smell have been shown to play important roles in central nervous system-mediated feeding behavior (Whittemore, 1998). Feed intake has been shown to increase when pigs are injected with barbiturate, a central nervous system depressant, directly into the ventromedial hypothalamus (Yen, 2001). This shows that the central nervous system clearly has a role in appetite regulation.

Glucostatic control

Glucose has been shown to have some influence on feed intake. Reduction in metabolizable brain glucose has been shown to stimulate weaned pigs to eat; however, this is not present in nursing piglets (Yen, 2001). Blood glucose concentration has been shown to be

negatively related to feed intake over a short term period and low blood glucose levels have led to contractions of the stomach (Pond et al., 1995). Glucose loading of the gastrointestinal tract has been shown to reduce meal size (Whittemore, 1998). However, it appears that the effect of glucose on feed intake is energetic as opposed to physical because feed intake is only reduced by the amount of calories that is infused in the form of glucose (Janowitz et al., 1949; Woods et al., 1984). Intestinal response to infusions of glucose seem to originate in the intestine and to be mainly neural in the pig, with osmotic action through neural elements in the wall of the duodenum that initiate inhibitory signals to the central nervous system to bring a meal to an end (Haupt et al., 1979). Glucose infusions into the small intestine have been shown to decrease feed intake in a dose dependent manner which shows that feed intake is limited physiologically by eliminating intestinal signals from the digesta (Reidelberger et al., 1983). Glucose infusion into the duodenum also slows gastric emptying in a dose dependent manner such that satiety occurs at a constant stomach fill (Rayner, 1992). However, feed intake and gastric emptying are slowed when an equivalent osmotic load of sodium chloride is infused as opposed to glucose, indicating that glucose infusions are acting on osmotic receptors and not glucoreceptors (Rayner, 1992; Yen, 2001). This was shown in a study by Haupt et al. (1979) where glucose and sodium chloride solutions covering the same range of osmoconcentrations were infused into the duodenum of pigs. The regression lines for glucose and sodium chloride impact on feed intake calculated by Haupt et al. (1979) were very similar. However, there are neurons within the dorsomedial hypothalamus, ventromedial hypothalamus, and anterior hypothalamus that are glucose-sensitive and may also respond to insulin (Wilding, 2002). High levels of insulin have been shown to stimulate feed intake in

pigs due to a depression in blood glucose concentration whereas low levels of insulin suppress feed intake (Yen, 2001).

Intestinal control

Enteroendocrine cells form part of the neuroendocrine system in the gut, producing multiple hormonally active peptides that regulate physiological functions (Bohórquez and Liddle, 2011). Some of these functions and peptides are: gastric emptying and nutrient absorption regulated by cholecystokinin and peptide tyrosine tyrosine; satiety and appetite regulated by peptide tyrosine tyrosine, cholecystokinin, ghrelin, and oxyntomodulin; and insulin release regulated by glucagon-like peptide-1 and glucose-dependent insulintropic polypeptide (Bohórquez and Liddle, 2011). Feed ingestion produces an osmotic rise in the duodenum which is sensed by the osmotic receptors and sends signals to the central nervous system to inhibit eating in pigs (Yen, 2001). Although the osmotic receptors appear to play an important role in appetite regulation, other receptors have been shown to exist in the intestine that respond to glucose, amino acids, and acidic and alkaline materials (Rayner, 1992). Intestinal receptors have been shown to regulate gastric emptying to allow a constant flow of energy into the small intestine (Rayner, 1992). This has been shown in two studies with Rhesus monkeys. McHugh and Moran (1979) infused liquid meals of saline, glucose, isocaloric casein hydrolysate, and medium-chain triglyceride oil into the stomachs of Rhesus monkeys and measured both the physical and caloric rates of emptying. Glucose solutions emptied slower than did saline solutions but at a constant caloric rate independent of glucose concentration while the casein hydrolysate and triglyceride oil solutions emptied at the same caloric rate as did glucose (McHugh and Moran, 1979). Wirth and McHugh (1983) showed that emptying the stomach of Rhesus monkeys during their first meal doubled the feed intake

over that of monkeys whose stomach contents were left alone. However, despite the large difference in feed intake, the amount of glucose that passed through the pylorus to the duodenum remained the same (Wirth and McHugh, 1983). Rayner and Miller (1990) showed that pigs may be able to regulate the amount of energy reaching the small intestine independently of gastric distension. Pigs were fed the same ration, either as a wet or dry meal, and dry matter intake and emptying was equal regardless of diet although pigs that consumed the wet diet had greater gastric distension (Rayner and Miller, 1990).

Signals generated from the stomach

Animal appetite is limited by the physical capacity of the gut which is a function of gut size and rate of throughput (Whittemore, 1998). Gastric distension has been shown to decrease feed intake (Janowitz and Grossman, 1949). Increased distension resulting from water being drawn into the gut by its hypertonic contents might result in the osmotic effect being regulated by the stretch receptors of the gut, which in turn send information to the brain via afferent fibers of the vagus in order to initiate satiety (Yen, 2001). The stomach also releases a satiety factor as evidenced when feed placed in extra transplanted stomachs reduced the overall feed intake whether or not the feed was allowed to pass from the stomach to the intestine (Koopmans, 1983). The release of this satiety factor is dependent on both the distension of the transplanted stomach and the chemical stimulation of the gastric mucosa (Koopmans, 1983).

Cholecystokinin

Cholecystokinin (CCK) is a peripheral and central satiety hormone which influences the cessation of feed intake (Rayner, 1992; Pond et al., 1995). The presence of certain amino acids and fatty acids in the duodenum has been shown to cause the release of CCK from the

intestine and cause satiety in pigs (Whittemore, 1998; Yen, 2001). In pigs, the level of CCK in the blood has been shown to be at least double after eating compared to before eating (Pond et al., 1995). Receptors for CCK exist as two subtypes in the central nervous system, CCK_a and CCK_b, with only CCK_a receptors being located peripherally (Yen, 2001).

Although there is evidence that CCK is produced and released within the brain, acting as a signal of satiety, CCK cannot enter the central nervous system and, therefore, must inhibit feed intake peripherally (Pond et al., 1995; Yen, 2001). CCK receptors are found on the muscle of the pylorus and on the vagus nerves, leading to the opinion that CCK either constricts the pylorus, which results in slower gastric emptying and greater gastric distension, or increases the sensitivity of vagal afferent receptors (Rayner, 1992; Yen, 2001). CCK stimulates the vagus nerve projecting to the nucleus tractus solitaries, where at least one of the connections is to a central CCK neurone that signals within the hypothalamus via a central CCK_b receptor (Wilding, 2002). Effects of endogenous CCK on feed intake are independent of the slowing down of gastric emptying in the pig which provides evidence that CCK has a paracrine effect in the upper small intestine and may not be mediated by circulating CCK on stomach receptors (Rayner, 1992; Yen, 2001). This is supported by CCK infusions in the pig being most effective in decreasing feed intake when they are directed toward the post-gastric mesenteric circulation (Rayner, 1992). It has been shown that pigs respond instantly to infusion of exogenous CCK although this response is short-lived (Pekas, 1991). The infusion of exogenous CCK does not significantly slow gastric emptying even when it significantly reduces feed intake (Rayner, 1992). Administration of devazepide, which is a CCK_a receptor antagonist and can cross the blood-brain barrier, results in increased feed intake as a result of a central effect rather than the antagonism of endogenous

peripheral CCK (Yen, 2001). Administration of MK-329, another CCK_a receptor antagonist, results in increased feed intake in both fasted and non-fasted animals (Rayner, 1992). In a study by Pekas (1991), feed intake increased by 8.2% and growth by 10.6% in pigs that were immunized against CCK without changing the carcass composition relative to control animals. Pekas (1991) showed that the benefit of CCK immunization is determined by the increased body and carcass weights that results from the increased feed intake.

Serotonin

Serotonin has also been shown to be involved in satiety signaling via the 5-hydroxytryptamine (5-HT) receptor (Wilding, 2002). Pharmacological studies have shown that agonists of 5-HT receptors decrease feed intake; however, injections of 8-hydroxy-2 (di-n-propylamino) tetralin (8-OH-DPAT) have been shown to increase operant feeding in satiated pigs (Ebenezer et al., 1999). Ebenezer et al. (1999) showed that administering 8-OH-DPAT (5, 10, or 20 µg doses) 15 min prior to morning feeding resulted in a dose-dependent reduction of feed intake during the first 30 minutes of feeding. When 8-OH-DPAT (25 or 50 µg doses) was administered 60 min prior to morning feeding, feed intake was reduced during the first 45 min (Ebenezer et al., 1999). These results were similar to earlier studies that showed agonists of 5-HT receptors to decrease feed intake. However, both of these experiments were in fasted pigs. After 60 min of time allotted for feeding, with pigs reaching satiety between 30 and 45 min, 8-OH-DPAT (20 µg dose) was administered and feed intake was significantly increased during the 30 min following the injection (Ebenezer et al., 1999). These results show that the effect of serotonin on feed intake may be dependent on whether the pig is faster or satiated.

Ghrelin

Ghrelin is a growth hormone-releasing peptide that has been shown to assist in the control of feed intake and long-term regulation of body weight (Vizcarra et al., 2007). The active form is a 28-amino acid peptide with an *n*-octanoyl modification at serine 3 (Jarkovská et al., 2006). The inactive form of ghrelin, or des-acyl ghrelin, lacks the substitution at serine 3 and predominates in systemic circulation (Jarkovská et al., 2006). Removing the stomach in rats decreased serum ghrelin levels, suggesting that the stomach is the main source for ghrelin synthesis (Vizcarra et al., 2007). Although the stomach is the predominant location for ghrelin production, ghrelin production has been found in the bowel, kidney, placenta, hypothalamus, and pituitary gland (Jarkovská et al., 2006). Administration of ghrelin has been shown to increase adiposity via an increase in feed intake and a decrease in fat utilization (Vizcarra et al., 2007). Ghrelin expression has been shown to be altered via ingestion of sugar and hypoglycemic and hyperglycemic states which suggests that ghrelin regulation is controlled through some of the same mechanisms that control glucose concentrations (Vizcarra et al., 2007). In pigs immunized against ghrelin, increased antibody titers, decreased feed intake, and decreased body weight gain were observed. Feed intake in immunized pigs was decreased by more than 15% while body weight was decreased by 10% (Vizcarra et al., 2007). The exact role of ghrelin in growth regulation is still unclear with a study evaluating acromegaly and growth hormone deficiency showing no difference in total or active ghrelin between acromegalics and growth hormone deficient individuals compared to controls (Jarkovská et al., 2006).

Leptin

Leptin is a 16-kDa protein that is secreted by white adipocytes into the bloodstream and has been proposed to play a role in feed intake regulation (Houseknecht et al., 1998; Ramsay et al., 1998; Yen, 2001). Leptin receptors come in long and short forms and include two cytokine domains, each containing a single copy of Trp-Ser-X-Trp-Ser motif and a fibronectin type III domain (Houseknecht et al., 1998). Although leptin production is limited to adipocytes and placenta, leptin receptors are found in most tissues with the long form being prevalent in the hypothalamus and the short form predominating in most other tissues (Houseknecht et al., 1998). The expression of leptin is highly correlated with body adipose tissue (Houseknecht et al., 1998; Yen, 2001) with leptin concentrations decreasing when animals lose weight or fall into a negative energy balance (Wilding, 2002). This is supported by obese pigs expressing higher levels of leptin mRNA and protein than non-obese pigs at the same body weight (Ramsay et al., 1998). It has been shown that as little as a 10% reduction in body weight in obese humans resulted in a 53% reduction in plasma leptin and a 10% increase in body weight resulted in a 300% increase in plasma leptin (Houseknecht et al., 1998). Leptin is actively transported into the central nervous system and binds to the long-form of its receptor, which is predominantly located in the arcuate nerve of the hypothalamus (Wilding, 2002). It is thought that leptin acts at the level of the brain through neurotransmitters such as Neuropeptide Y to reduce feed intake, body weight and fat mass, to increase energy metabolism, and to alter endocrine activity (Barb et al., 1998; Houseknecht et al., 1998). In a study by Barb et al. (1998), it was shown that leptin reduced feed intake in a dose-dependent manner in prepubescent gilts and that leptin acts directly within the central nervous system to regulate feed intake.

Leptin interactions

Neuropeptide Y, agouti-related peptide-containing neurons, and α -melanocyte stimulating hormone neurons predominantly respond to a fall in leptin, suggesting that the role of leptin in appetite regulation is to restore homeostasis when an animal falls into a negative energy balance (Wilding, 2002). Neuropeptide Y stimulates feed intake, inhibits brown fat thermogenesis, and increases plasma insulin and corticosteroid levels. Neuropeptide Y has also emerged as a major target of leptin action, most likely via the inhibition of neuropeptide Y synthesis in the hypothalamus (Houseknecht et al., 1998). Insulin has been shown to play a role in long term regulation of leptin levels with hyperinsulinemia leading to increased leptin levels (Houseknecht et al., 1998). Leptin may also affect insulin levels by affecting insulin secretion. Leptin receptors on pancreatic β -cells have been shown to inhibit β -cell secretion of insulin by changing ion channel function (Houseknecht et al., 1998). Glucocorticoids have been shown to be up-regulators of leptin expression via the in vivo administration and in vitro incubation of adipocytes with various glucocorticoids (Houseknecht et al., 1998). Leptin and cortisol are involved in a negative feedback pathway with leptin inhibiting cortisol synthesis by the adrenal cells. However, cortisol is a stimulator of leptin expression (Houseknecht et al., 1998). Expression of leptin has been shown to be inhibited by β -adrenergic agonists, cAMP, and thiazolidinediones (Houseknecht et al., 1998). Ghrelin has also been shown to be a potential inhibitor of leptin (Wilding, 2002).

Other hormones and peptides

The role of somatotrophin in appetite regulation is unclear, as it has been shown to both increase and decrease feed intake (Whittemore, 1998). Somatostatin is a peptide found

both in the central nervous system and the gastrointestinal tract. Somatostatin has been shown to peripherally reduce feed intake in both rats and baboons (Lotter et al., 1981). Bombesin is a tetradecapeptide that has been shown to inhibit feed intake when administered peripherally (Hostetler et al., 1989). Bombesin shares its terminal sequence with gastrin-releasing peptide (Rayner, 1992). Although it decreases feed intake, it does not inhibit gastric emptying and therefore must operate on something other than gastric stretch receptors to inhibit feed intake (Hostetler et al., 1998). Bombesin's reduction of feed intake is dependent on an intact gut to brain neural connection (Wilding, 2002). Gastrin is a pentapeptide that has the same terminal pentapeptide sequence as CCK (Rayner, 1992). Gastrin has been shown to slow gastric emptying without an effect on feed intake (Dozois and Kelly, 1971). Other hormones involved in the regulation of feed intake through unknown roles include glucagon, pentagastrin, vasopressin, endorphins, and satietin (Yen, 2001).

Fat

Gastrointestinal signals have shown to be important in the regulation of fat intake. Duodenal infusions of emulsified fat have been shown to be more effective than infusions of non-emulsified fat in inhibiting feed intake and slowing gastric emptying in pigs (Rayner, 1992).

Nutrient/protein balance

A balanced diet is essential in appetite regulation in pigs. Pigs are able to monitor their protein status and adjust their intake of the diet provided accordingly (Yen, 2001). If a diet is lacking in a nutrient the pig senses it needs, the pig will consume the diet to an excess of energy in order to meet its dietary requirement (Whittemore, 1998). On the other hand, a pig will also not consume enough energy if it senses that it is consuming a nutrient in excess

(Whittemore, 1998). For example, if the ratio of tryptophan to large neutral amino acids is low, competition from large neutral amino acids prevents the brain from taking up tryptophan, resulting in low brain serotonin levels, which in turn results in a reduction in feed intake (Yen, 2001). Kyriazakis and Emmans (1990), in a study using low and high protein diets, showed that pigs on the low protein diet (134 g crude protein) consumed more feed, grew slower, and had poorer feed efficiency than those pigs on the high protein diet (278 g crude protein).

Environmental temperature

Feed intake is known to increase below the thermoneutral zone and decrease above the thermoneutral zone (Yen, 2001). Avoidance of heat stress will limit feed intake when the environment fails to allow for adequate dispersal of body heat, with the limit being estimated at 1 g of feed for every 1°C of heat above the thermoneutral zone for every 1 kg of body weight (Whittemore, 1998).

Genetics

Although appetite has not been a major part of selection in pigs, there has been some manipulation of appetite through genetic selection with both high- and low-appetite pigs in current populations (Whittemore, 1998). Modern pigs breeding programs select indirectly for appetite by selecting for decreased feed intake, where decreased feed intake would be indicative of having a small appetite.

Conclusions

Appetite regulation is a complex system involving many hormones along with environmental factors. Cholecystokinin, leptin, somatostatin, bombesin, fat, and heat stress have all been shown to reduce feed intake. Neuropeptide Y, ghrelin, insulin, and low

temperatures have been shown to increase feed intake. With all the different factors affecting appetite regulation, it would be hard to identify just one as a cause in the difference between eating patterns of different pigs.

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CHAPTER 2: EFFECT OF SELECTION FOR RESIDUAL FEED INTAKE ON FEEDING BEHAVIOR AND DAILY FEED INTAKE PATTERNS IN YORKSHIRE SWINE

Modified from a paper published in the *Journal of Animal Science*¹

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Abstract

Residual feed intake (RFI) is a measure of feed efficiency defined as the difference between observed and predicted feed intake based on average requirements for growth and maintenance. The objective of this study was to evaluate the effect of selection for decreased RFI on feeding behavior traits and to estimate their relationships with RFI. Three data sets from the 4th and 5th generations of a selection experiment with a line selected for decreased RFI (LRFI) and a randomly selected control line (CTRL) were analyzed. Lines were mixed in pens of 16 and evaluated for feeding behavior traits obtained from a single-space electronic feeder over a growing period of ~3 mo before ~115 kg. The following traits were evaluated as averages over the entire test period and over the first and second half of the test period: number of visits per day and hour; occupation time per day, visit, and hour; feed intake (FI) per day, visit, and hour; and FI rate per visit. Models used included fixed effects of line and feeder, covariates of on-test age and FI per day, and random effects of pen, on-test group, sire, and litter. Repeated measures models were used to analyze feeding patterns during the day. The LRFI pigs had significantly less FI per day than CTRL pigs for all 3 data

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sets. With adjustment for FI per day, line differences of all traits were in the same direction for all 3 data sets but differed in significance and size. Feed intake per visit and hour and visits per day and hour did not differ between lines, but the trend was for LRFI pigs to have fewer visits, in particular during peak eating times. The LRFI pigs had a greater feeding rate and less occupation time per day, visit, and hour than CTRL pigs, but this was not significant for all data sets. Correlations of RFI with FI per day and visit and visits per day were positive. Average daily gain was positively correlated with FI per day and visit and occupation time per visit but negatively correlated with visits per day. Feed intake per day was positively correlated with backfat. In conclusion, feed efficiency may be affected by FI behavior because selection for decreased RFI has resulted in pigs that spend less time eating and eat faster.

Introduction

Feed is the largest variable cost in pigs production, representing 50 to 85% of production costs (McGlone and Pond, 2003). Because of this, feed intake, a component of feed efficiency (kg of product/kg of feed), is a vital component of pig breeding programs. Feed efficiency has positive genetic correlations with growth and leanness; however, only about 65% of phenotypic differences in feed intake are correlated with growth and performance (Cai et al., 2008). The remaining variation in feed intake can be evaluated using residual feed intake (RFI), which is defined as the difference between observed feed intake and the feed intake expected based on average requirements for the achieved growth and performance of the pig.

Feeding behavior of pigs housed in groups can be evaluated using data from single-space electronic feeders. Several studies have evaluated the relationship of feeding behavior

with RFI in finisher pigs (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006a, b). All these studies have found positive phenotypic or genetic correlations (or both) of RFI with feed intake per day, occupation time per day, and number of visits to the feeder per day. No study has directly evaluated the effect of selection for RFI on feeding behavior traits in pigs. Thus, the objectives of this study were to evaluate correlated responses in feeding behavior traits to selection for RFI and to establish phenotypic relationships of feed intake patterns with performance traits of RFI, ADG, and backfat. Another objective was to determine if response to selection held true across parities and generations; therefore, data from several generation and parity combinations from the selection experiment described by Cai et al. (2008) were evaluated.

Materials and Methods

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

Experimental design and data collection

Using purebred Yorkshire pigs, a selection line for decreased RFI (LRFI line) and a randomly selected control (CTRL) line were begun in 2001. In this selection experiment, each generation, 2 parities were produced, with feed intake data being collected on boars from parity 1 sows and on gilts from parity 2 sows. Beginning with random allocation of littermates from generation 0 to the LRFI and CTRL lines, the following traits were recorded for each generation on ~90 boars from first parity and ~90 gilts from second parity sows of the LRFI line: electronically measured daily feed intake, BW recorded every 2 wk, and 10th-rib backfat (BF), loin muscle area, and intramuscular fat at market weight. The latter 3 traits were evaluated by ultrasound using an Aloka 500V SSD ultrasound machine fitted with a

3.5-MHz, 12.5-cm, linear array transducer (Corometrics Medical Systems Inc., Wallingford, CT). Average daily feed intake was derived as a performance trait as described by Cai et al. (2008). Average daily gain was obtained as the slope from simple linear regression of BW on number of days on test. After evaluation of boars from first parity sows, ~12 boars and 70 gilts were selected to produce ~50 litters of ~10 piglets for the next generation. Selection decisions were based on EBV for RFI, as described by Cai et al. (2008). After selection, full- or half-sisters of selected boars were evaluated for RFI to provide additional data for the next generation. The control line was maintained by creating ~30 litters from ~10 boars, and 40 gilts were randomly selected. Full- and half-sib matings were avoided in both lines. In early generations, only LRFI pigs were evaluated for feed intake because of limited capacity to measure feed intake. Starting in generation 4 with gilts from parity 2 sows, CTRL pigs were also evaluated for feed intake to make direct line comparisons. Further details are in Cai et al. (2008) and Bunter et al. (2010).

For feed intake recording, pigs were put in pens of 16 pigs at ~90 d of age, each of which had a single-space electronic feeder, Feed Intake Recording Equipment (FIRE, Osborne Industries Inc., Osborne, KS). The FIRE feeders recorded ear transponder, entrance time, start weight of feed, exit time, and end weight of feed for each visit to the feeder. Pigs were given approximately 1 wk to acclimate to the FIRE feeders before being put on test in groups by on-test date based on age and BW (typically 2 or 3 age groups per generation and parity). In general, pigs were taken off test on an individual basis when they reached ~115 kg of BW, but were removed at a lighter BW if few pigs remained in a pen, in which case all remaining pigs were taken off test. Pigs with an off-test BW less than 102 kg did not have enough BW to estimate RFI and were also not scanned. Therefore, they were not used for

data analysis of performance traits; however, they still had feed intake data from the FIRE feeders and were included in the feeding behavior analyses.

Data for this study were from generation 4 parity 2 (G4P2) and from generation 5 parity 1 (G5P1) and parity 2 (G5P2). These were the first generations for which CTRL pigs were also placed on FIRE feeders alongside LRFI pigs in mixed pens. Data from G4P2 and G5P2 were on gilts and data from G5P1 were on boars. Pigs were placed on test in 2 groups and housed in 12 pens with 8 pigs from each line in each pen, balancing by BW. For G4P2, pens were balanced to the extent possible for genotype of the calcitonin receptor, which was used to investigate its impact on bone strength as reported by Alexander et al. (2010). Lines were mixed within a pen to maximize power at the risk of some bias from pigs from 1 line affecting the behavior of pigs from the other line. If lines are split by pen, pen would be the experimental unit, which, with only 12 pens and large feeder effects, would have severely reduced power. The pigs were housed in 1 room with fully slatted concrete flooring. Each pen was 5.6 m length x 2.3 m width (0.82 m²/pig). Pens were separated with steel rod gates and contained a 2-nipple type waterer (Edstrom, Waterford, WI), which provided ad libitum access. Collection of feeding behavior data was terminated when the first pigs were taken off from that pen due to the expectation that feeding behavior would change when stocking density and the number of pigs per feeder changed. Test lengths and average age and BW at on- and off-test are reported in Table 2.1. Only 6 of the 12 pens had feed intake recording, so pigs were switched between pens every 2 wk after being weighed in the morning. Alternate pens were in the same room and had single-space feeders of a similar design so as not to induce the need for an acclimation period. Data from days when pigs were switched between pens were not used.

Database and edit systems developed by Casey et al. (2005) were used to handle and edit the large amount of data collected by the FIRE feeders. Errors in each visit (visit defined as feeding event from the entrance of a pig into the feeder to its exit) were identified by 16 criteria. Using the edited data, feeding behavior traits were derived over the entire test period, the first half of the test period by time, and the second half of the test period by time.

Average daily feed intake as a behavior trait (DFI) was derived separately from the performance trait ADFI by summing feed intake of each pig per day and averaging across days, as recorded by the FIRE feeders. Average daily feed intake (ADFI) was calculated using a regression model as described by Cai et al. (2008). Average number of visits per day was calculated by averaging the number of visits per day by pig. Average feed intake per visit was calculated by averaging feed consumption by visits across days. Average occupation time per day and average occupation time per visit were calculated in a similar manner as DFI and feed intake per visit. Average feed intake rate was obtained by calculating a feeding rate for each visit by dividing the amount of feed consumed by the time spent in the feeder and then averaging the individual visit feeding rates. To evaluate feed intake patterns during the day, feeding behavior traits were also derived from the edited FIRE feeder data by computing traits by 2-h blocks during the day, resulting in the following traits: number of visits, feed intake, and occupation time for each 2-h block, from midnight to midnight.

Statistical analysis

Feeding behavior traits were analyzed separately for each generation and parity with the MIXED procedure (SAS Inst. Inc., Cary, NC). The following mixed linear model was used:

$$Y_{ijklmnop} = \mu + \beta_1 * A_{ijklmnop} + \beta_2 * DFI_{ijklmnop} + L_j + F_k + G_l + (LG)_{jl} + S_m + P_n + R_o + D_p + \epsilon_{ijklmnop},$$

where $Y_{ijklmnop}$ = feeding behavior trait; $A_{ijklmnop}$ = fixed regression covariate of on-test age; $DFI_{ijklmnop}$ = fixed regression covariate of DFI (not included when analyzing DFI); L_j = fixed effect for line j ; F_k = fixed effect for feeder k ($k = 1$ to 6); G_l = fixed effect of calcr genotype l ($l = 1$ to 3 , included for G4P2 only); $(LG)_{jl}$ = interaction effect of line j and calcr genotype l (for G4P2 only); S_m = random effect of sire m ; P_n = random effect of pen n ($n = 1$ to 12); R_o = random effect for on-test group o ($o = 1, 2$); D_p = random effect of litter p , and $\epsilon_{ijklmnop}$ = a random residual effect. Pigs that consume less are expected to spend less time in the feeder. Therefore, to correct for differences in feed intake so that differences in feeding behavior were independent of feed intake, DFI was included as a covariate to ensure that differences in feeding behavior were not due to differences in feed intake. Results for feed intake rate and number of visits per day were similar whether DFI was included or not. Differences for feed intake per visit and occupation time per day and visit were greater when DFI was excluded from the model. Daily feed intake over the whole, first half, or second half of the test period was used, depending on the feeding behavior trait being analyzed (whole, first, or second half). Measures of RFI for individual pigs were obtained as the residuals from analysis of ADFI using the above model but with BF and ADG included as additional covariates and DFI removed. Residual feed intake was computed over the whole test period only. Least square means were obtained from the MIXED procedure of SAS to compare line differences in feeding behavior traits.

Repeated measures models were used to analyze daily feed intake patterns, defined by 2-hr blocks. The model for analyzing daily feed intake patterns included effects for 2-h block (12 levels) and for the interaction between line and 2-h block as fixed effects to the

model above. An autoregressive covariance structure of order 1 was used in analyzing feed intake patterns.

Phenotypic correlations between behavior traits and RFI, ADG, and BF were computed based on residuals derived from the above models using the CORR procedure of SAS. Correlations were computed on combined residuals from the 3 data sets, both across and within lines, and for the whole test period and each half of the test period.

Results and Discussion

Line differences

Figure 1 shows LS means by line for feeding behavior traits for each of the 3 data sets. Pigs from the LRFI line had less ($P < 0.0001$) DFI than CTRL pigs, as expected. Pigs from the LRFI line also spent approximately 10 min less in the feeder per day than CTRL pigs, even after adjusting for differences in DFI. This difference in occupation time can be explained by differences in feeding rate and number of visits per day; LRFI pigs tended ($P = 0.40$) to visit the feeder fewer times per day and ate significantly faster ($P < 0.0001$) than CTRL pigs, even after adjusting for DFI. Line differences were consistent across the 3 data sets in direction, but results from G5P1 differed from G4P2 and G5P2 in degree and significance (Figure 2.1). These differences could be due to sex differences; G5P1 pigs were boars, whereas pigs in G4P2 and G5P2 were gilts. Differences could also be due to G4P2 and G5P2 animals coming from second parity sows, whereas G5P1 animals came from first parity sows. Season could also have an effect on differences between the 3 data sets; G4P2 was on test from November through February, G5P1 from July through November, and G5P2 from April through September. The observed differences in feeding behavior between LRFI and CTRL pigs are consistent with results found by Braastad and Katle (1989), who

selected laying hens for RFI and found that hens with low RFI spent less time food pecking than hens with high RFI. Food pecking in chickens would be equivalent to our trait of occupation time per day and the difference in time spent food pecking between greater and less RFI hens is in the same direction as the difference in occupation time per day between LRFI and CTRL pigs in our study.

Several studies have evaluated differences in feeding behavior between groups of cattle differing in RFI. Similar to our study, Nkrumah et al. (2006, 2007) found that low RFI steers had fewer visits to and spent less time at the feed bunk than did steers with medium or high RFI. Golden et al. (2008) found that low RFI Angus steers consumed less feed and had fewer eating bouts per day than high RFI steers, which is consistent with our results that low RFI pigs consume less feed and visit the feeder fewer times per day than CTRL pigs. However, Golden et al. (2008) found no difference in eating rate between low and high RFI steers, which differs from our result that low RFI pigs ate faster than CTRL pigs. Lancaster et al. (2009) found similar results in Angus bulls to Golden et al. (2008), with low RFI bulls consuming less feed and eating less often but with similar feeding rates to high RFI bulls. Lancaster et al. (2009) also evaluated time spent eating and found that low RFI bulls spent less time eating than high RFI bulls, which is what we found in pigs. However, Lancaster et al. (2009) did not adjust for DFI in evaluating time spent eating, so it cannot be determined if the difference in time spent eating is due entirely to consuming less feed. Figures 2.2, 2.3, and 2.4 show the line LS Means for feed intake pattern traits adjusted for DFI for the whole test period. Results were similar for both halves of the test period and are, therefore, not shown. The pattern of feed intake during the day was similar between the 2 lines. Occupation time was consistently less (Figure 2.3) across the entire day for LRFI compared with CTRL

pigs. Number of visits per hour also did not differ between the 2 lines for most of the day, although there was a tendency for a difference at peak eating times.

Golden et al. (2008) evaluated Angus steers for feed intake in 3-h blocks across the day. Although low RFI steers consumed less feed per time block than high RFI steers, as expected because they consumed less per day, the percentage of feed consumed did not differ between low and high RFI steers (Golden et al., 2008). This is consistent with our findings of no difference in feed intake per hour after adjusting for feed intake per day, which is equivalent to no change in the distribution of intake across the day between the 2 lines.

Residual correlations

Residual correlations of feeding behavior traits with RFI, ADG, and BF were generally low (Tables 2.2 to 2.4). However, correlations of DFI with RFI and ADG were high, positive, and very significant ($P < 0.0001$). Correlations of DFI with BF were moderate and positive. Correlations of DFI with RFI, ADG, and BF were similar across lines and within each line for the whole test period and each half of the test period. High, positive correlations of DFI with RFI are consistent with previous studies that also found high, positive correlations of DFI with RFI in pigs (Von Felde et al., 1996) and in bulls (Lancaster et al., 2009). Daily feed intake was found to be positively correlated with ADG and BF in Yorkshire and Landrace pigs by Labroue et al. (1997). Rauw et al. (2006a,b) also divided the test period into parts and found a high correlation of DFI with RFI. This supports our findings of high correlations of DFI with RFI for the first and second halves of the test period, although they were not as high as the correlation of DFI with RFI over the entire test period.

With the exception of DFI, feeding behavior traits were not significantly correlated with RFI within the LRFI line. Number of visits per day had significant positive correlations with RFI across lines and within the CTRL line for the whole test period ($P < 0.01$) and for the second half of the test period ($P < 0.05$); the correlation was in the same direction for the LRFI line. Feed intake per visit had significant negative correlations with RFI across lines and within the CTRL line for the whole test period ($P < 0.01$) and the second half of the test period ($P < 0.05$). Occupation time per visit had significant negative correlations with RFI across lines and within the CTRL line for the whole test period ($P < 0.05$) and tended to be negatively correlated with RFI across lines and within the CTRL line for the second half of the test period ($P < 0.10$). Feed intake rate tended ($P < 0.10$) to be negatively correlated within the CTRL line. Correlations of visits per day, feed intake per visit, and occupation time per visit with RFI were in the same direction as the differences that were observed between the 2 lines (Figure 2.1), although differences were not significant. Occupation time per day and feed intake rate were not significantly ($P = 0.89$ and 0.47 , respectively) correlated with RFI, although the 2 lines differed significantly ($P < 0.0001$) for these 2 traits (Figure 2.1). This could be due to line differences being genetic and correlations being phenotypic. However, the correlations were in the same direction as the line differences.

Correlations of feeding behavior with RFI can be compared with those of previous studies in pigs (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006a,b). Similar to our study, reports of phenotypic correlations of RFI with number of visits per day have been positive, although the correlations are often greater than what we found in our lines (de Haer et al., 1993; Lancaster et al., 2009). However, the correlation found by Nkrumah et al. (2007) is similar in degree to our correlations of RFI with number of visits per day. de Haer et al.

(1993) found a significant correlation of -0.20 between RFI and feed intake per visit, which is consistent with our results across lines and within the CTRL line. Lancaster et al. (2009) found a correlation of 0.41 between RFI and meal duration in Angus bulls, which is in the opposite direction from our correlation between occupation time per visit and RFI.

Correlations between occupation time per day and RFI reported in literature for pigs have been high and positive (de Haer et al., 1993; Von Felde et al., 1996; Nkrumah et al., 2007). Rauw et al. (2006a,b) found significant, positive correlations of occupation time per day with RFI after dividing the test period into parts. Although the correlation of occupation time per day with RFI was not significant ($P = 0.89$) in our study, the correlations previously reported in literature support the difference in occupation time per day we observed between the 2 lines. Von Felde et al. (1996) and Labroue et al. (1997) evaluated the relationship of feeding behavior with feed conversion ratio, another measure of feed efficiency, and found similar correlations to those previously reported with RFI. However, the correlations with feed conversion ratio were of a smaller magnitude than those with RFI and most were not significantly different from zero (Von Felde et al., 1996; Labroue et al., 1997). The observed correlations of RFI with feeding behavior traits, in both our study and previous studies, suggest that feed efficiency may be affected by the manner of feed intake.

Average daily gain was positively correlated ($P < 0.001$) with feed intake per visit and negatively correlated ($P < 0.005$) with number of visits per day across all 3 time periods (Table 2.3). This is consistent with previous reports (de Haer et al., 1993; Labroue et al., 1997). In cattle, number of visits per day was not found to be significantly correlated with ADG (Nkrumah et al., 2007; Lancaster et al., 2009). Average daily gain was positively correlated with occupation time per visit across the whole test period and the first half of the

test period (Table 2.3), consistent with results reported by de Haer et al. (1993) and Labroue et al. (1997) in pigs and in cattle by Lancaster et al. (2009). Occupation time per day was negatively correlated with ADG during the second half of the test period. This is opposite to previous reports for the correlation of occupation time per day with ADG (Labroue et al., 1997; Nkrumah et al., 2007), but these studies did not break the test period into parts and our correlations for the whole test period were not significant. The relationship of feed intake rate with ADG depended on line and part of test period but tended to be positive, which is consistent with previously reported results in pigs (de Haer et al., 1993; Labroue et al., 1997) and in cattle (Lancaster et al., 2009).

Backfat was positively correlated ($P < 0.01$) with occupation time per day and per visit across lines and within the LRFI line (Table 2.4). Previous studies in pigs have reported positive correlations of BF with occupation time per day (Labroue et al., 1997; Nkrumah et al., 2007) and per visit (de Haer et al., 1993; Labroue et al., 1997), consistent with our results. Backfat was negatively correlated with feed intake rate across lines and with the LRFI line, which was opposite to results from previous studies in pigs (de Haer et al., 1993; Labroue et al., 1997). Number of visits per day was not significantly correlated ($P > 0.10$) with BF, but all correlations were negative which is consistent with previous reports in pigs (de Haer et al., 1993; Labroue et al., 1997). Feed intake per visit was not significantly ($P = 0.36$) correlated with BF in our study, although it has been shown to be positively correlated with BF in pigs (de Haer et al., 1993; Labroue et al., 1997).

Conclusions and Implications

Differences between lines show that feeding behavior may be a factor in determining the feed efficiency of an animal. The LRFI pigs ate faster and less per day and spent less time

eating per day than the CTRL pigs, even after adjusting for difference in feed intake. These pigs also tended to visit the feeder fewer times, especially during peak eating times, and spent less time eating per visit than the CTRL pigs. This shows that feeding behavior traits have changed in response to selection for RFI. Correlations of RFI with feeding behavior traits generally supported the line differences found. However, there is still a lot to learn about the relationships of feeding behavior with feed efficiency, ADG, and backfat. These relationships also may be population dependent as shown by the varying responses found in different studies. The relationship between feed efficiency and feeding behavior traits, specifically occupation time, may lead us to review current production standards on number of pigs per feeder space. As we select for more feed efficient pigs, it appears that we are also selecting for pigs that spend less time at the feeder, meaning we would be able to have more pigs per feeder space.

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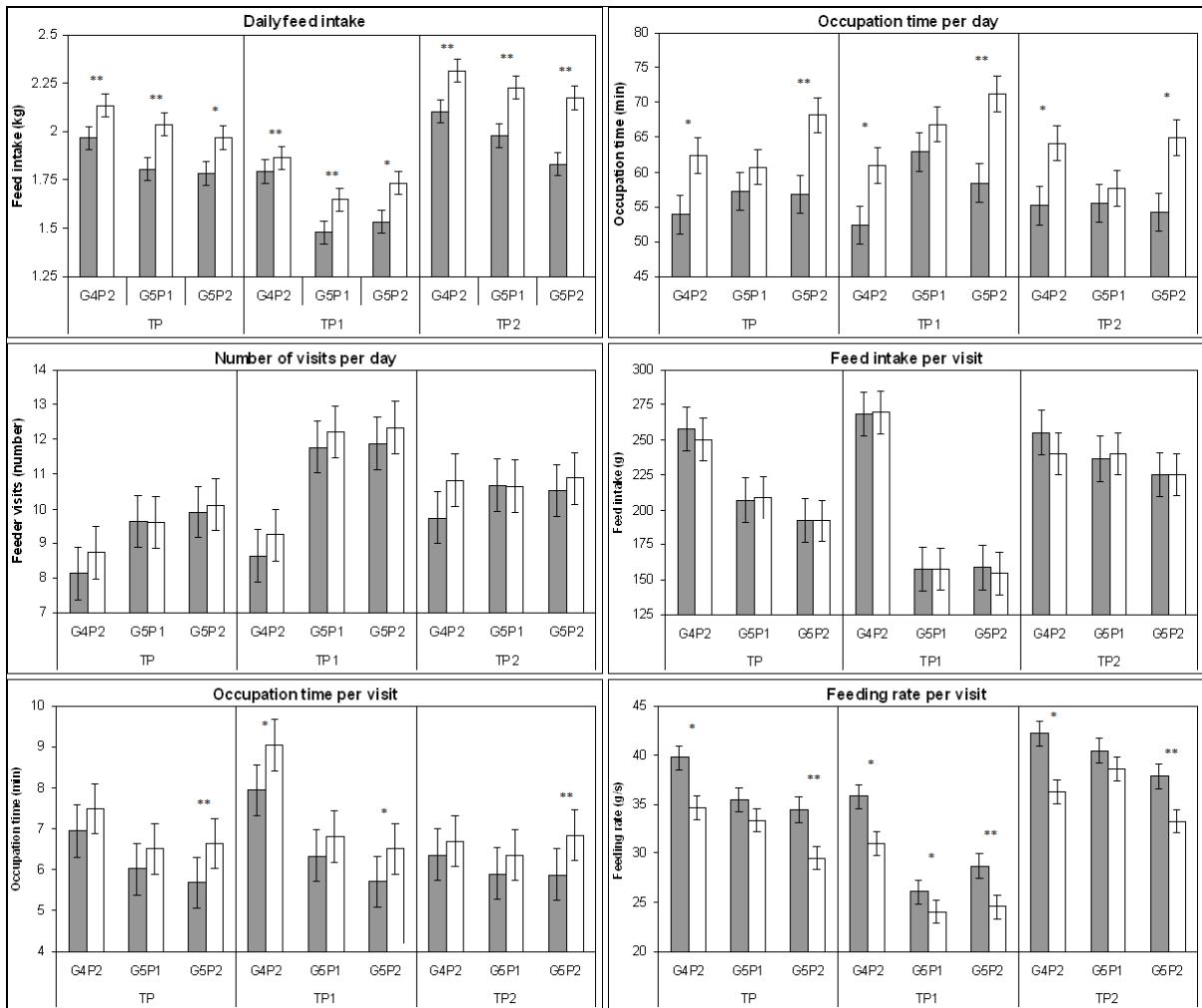


Figure 2.1. Least square means with SE bars for the line selected for decreased residual feed intake (gray bars) and the control line (white bars) for feeding behavior traits for 3 data sets (generation by parity, G4P2, G5P1, and G5P2) over the total test period (TP) and over the first (TP1) and second (TP2) half of the test period. The *P*-value is less than 0.05 for pairs of bars marked with * and less than 0.01 for pairs of bars marked with **.

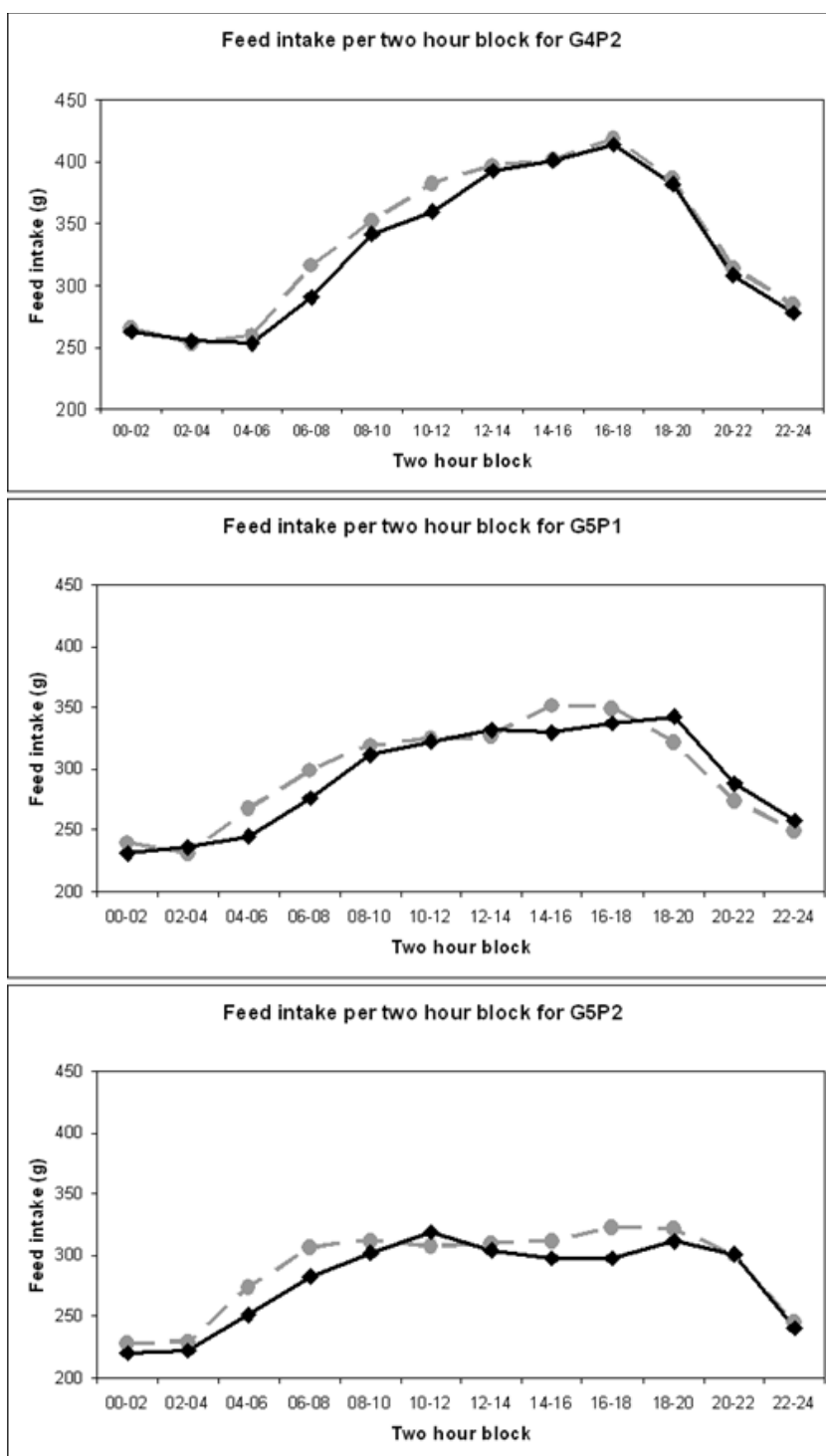


Figure 2.2. Least square means for feed intake per 2-h block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. No significant differences ($P > 0.1$ for all 2-h blocks) were found between lines.

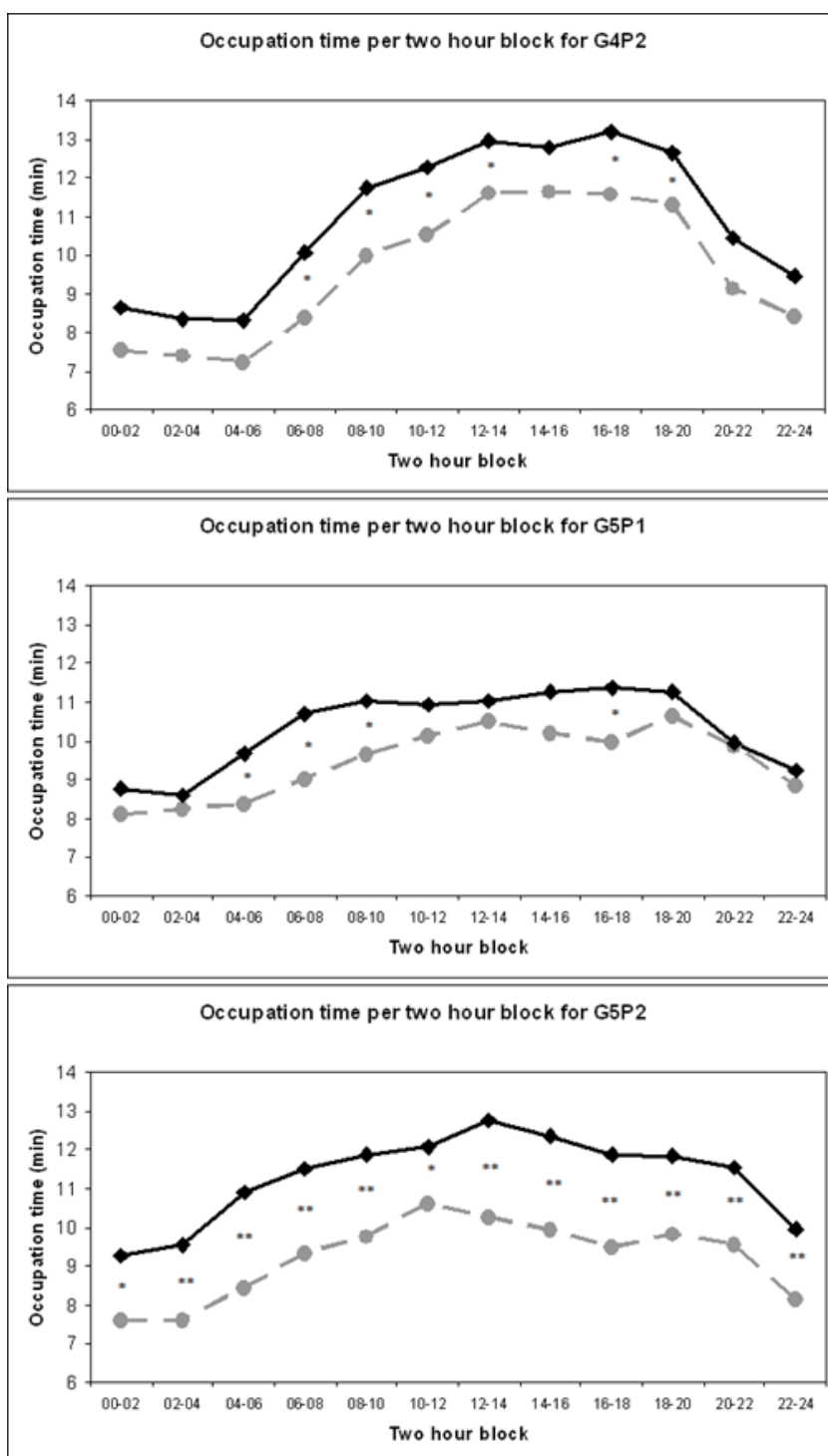


Figure 2.3. Least square means for occupation time per 2-h block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. The P -value is less than 0.05 for differences between lines at times marked with * and less than 0.01 for **.

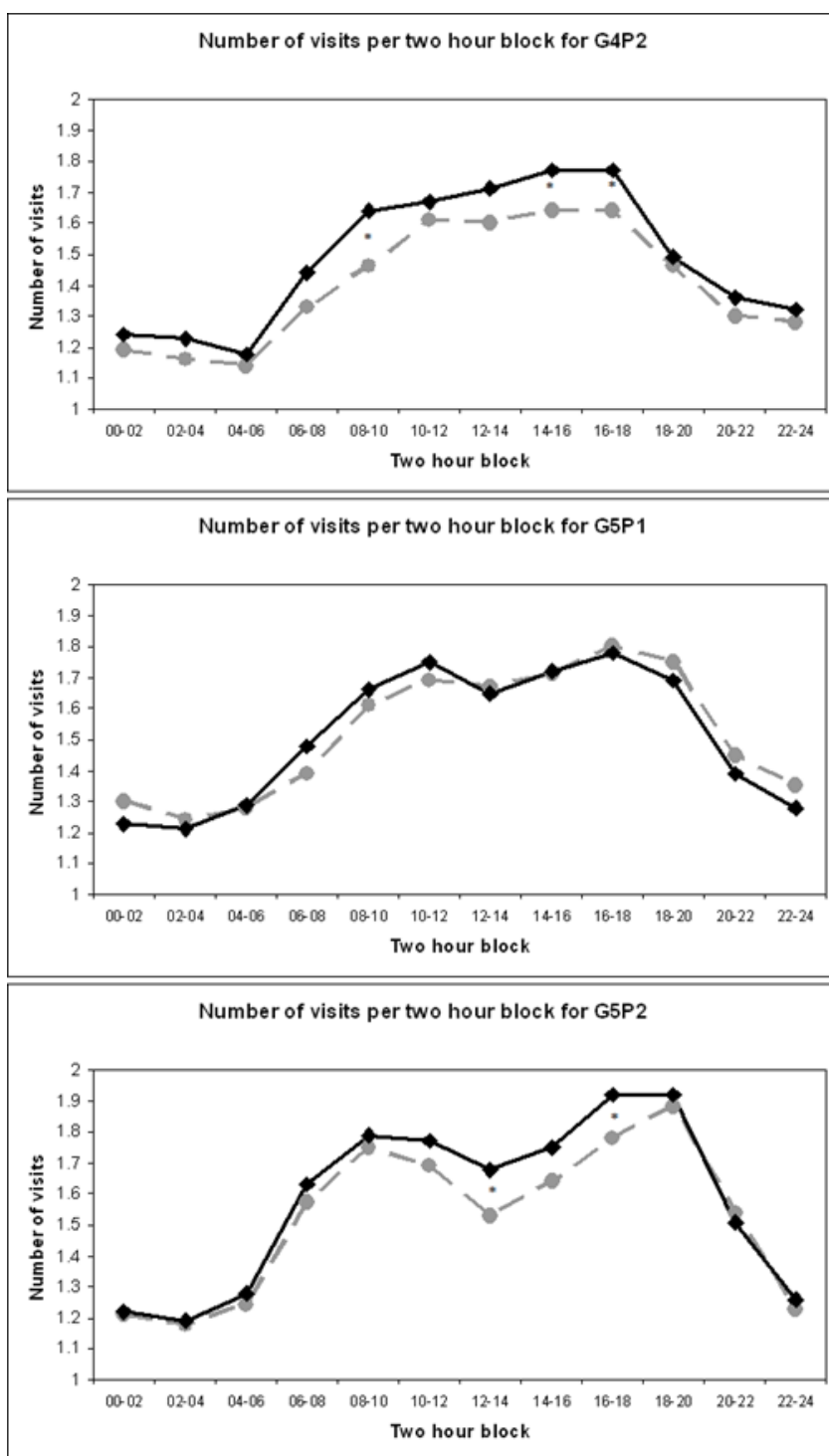


Figure 2.4. Least squares means for number of visits per 2-h block over the whole test period for the line selected for decreased residual feed intake (gray line) and the control line (black line) for 3 data sets (generation by parity, G4P2, G5P1, and G5P2), with adjustments for daily feed intake. The *P*-value is less than 0.05 for differences between lines at times marked with *.

Table 2.1. On- and off-test characteristics for each group of pigs evaluated

Generation	Parity	Group	Line	n	Test length, d	Age at on-test, d	BW at on-test, kg	Age at off-test, d	BW at off-test, kg
4	2	1	1	53	42	143.6 \pm 5.4	72.0 \pm 9.3	185.6 \pm 5.4	99.5 \pm 12.9
			2	42	42	144.8 \pm 4.9	70.5 \pm 8.2	186.8 \pm 4.9	99.5 \pm 9.2
		2	1	56	42	142.7 \pm 5.9	70.6 \pm 8.1	184.7 \pm 5.9	96.2 \pm 11.9
			2	37	42	146.0 \pm 9.6	75.7 \pm 9.2	187.2 \pm 9.6	102.4 \pm 10.9
5	1	1	1	44	92	94.8 \pm 6.0	36.5 \pm 4.8	186.8 \pm 6.0	98.6 \pm 10.9
			2	50	92	96.1 \pm 6.2	39.4 \pm 6.1	188.1 \pm 6.2	106.8 \pm 12.5
		2	1	40	106	81.4 \pm 9.3	27.6 \pm 5.4	187.4 \pm 9.3	89.5 \pm 16.3
			2	45	106	84.6 \pm 6.8	29.5 \pm 8.2	190.6 \pm 6.8	97.0 \pm 12.5
5	2	1	1	48	94	105.4 \pm 3.2	41.5 \pm 6.2	199.4 \pm 3.2	92.7 \pm 11.5
			2	47	94	103.2 \pm 2.3	40.2 \pm 4.7	197.2 \pm 2.3	103.9 \pm 11.7
		2	1	46	108	92.4 \pm 9.1	35.9 \pm 6.5	200.4 \pm 9.1	92.5 \pm 13.0
			2	47	108	92.0 \pm 7.1	37.2 \pm 4.9	200.0 \pm 7.1	102.4 \pm 12.3

Table 2.2. Residual correlations of feeding behavior traits with residual feed intake across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.

Trait	TP				TP1				TP2			
	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	LRFI	CTRL	CTRL
Daily feed intake	0.75**	0.68**	0.78**	0.47**	0.36**	0.53**	0.47**	0.45**	0.49**			
Occupation time/d	0.01	-0.07	0.05	0.06	0.01	0.09	0.01	-0.07	0.06			
No. of visits/d	0.13**	0.08	0.16*	0.07	-0.06	0.15*	0.15**	0.15**	0.15**			
Feed intake/visit	-0.13**	-0.05	-0.16**	-0.01	0.09	-0.06	-0.13**	-0.08	-0.15*			
Occupation time/visit	-0.11*	-0.09	-0.11†	0.01	0.07	-0.02	-0.12**	-0.13†	-0.11†			
Feed intake rate	-0.03	0.06	-0.10†	-0.06	0.01	-0.11†	-0.03	0.04	-0.09			

** Correlation differs from zero by $P < 0.01$.

* Correlation differs from zero by $0.01 < P < 0.05$.

† Correlation differs from zero by $0.05 < P < 0.10$.

Table 2.3. Residual correlations of feeding behavior traits with ADG across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.

Trait	TP				TP1				TP2			
	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	LRFI	CTRL	CTRL
Daily feed intake	0.59**	0.63**	0.57**	0.43**	0.44**	0.43**	0.63**	0.64**	0.64**	0.64**	0.64**	0.64**
Occupation time/d	-0.03	-0.09	0.02	0.05	-0.04	0.11†	-0.12**	-0.15**	-0.15**	-0.15**	-0.10	-0.10
No. of visits/d	-0.14**	-0.21**	-0.08	-0.15**	-0.20**	-0.11†	-0.12**	-0.19**	-0.19**	-0.19**	-0.06	-0.06
Feed intake/visit	0.15**	0.20**	0.13*	0.15**	0.17**	0.14*	0.13**	0.16*	0.16*	0.16*	0.12†	0.12†
Occupation time/visit	0.12**	0.10	0.14*	0.18**	0.16*	0.19**	0.03	0.00	0.00	0.00	0.06	0.06
Feed intake rate	0.05	0.13*	-0.02	-0.04	0.05	-0.13*	0.15**	0.21**	0.21**	0.21**	0.10	0.10

** Correlation differs from zero by $P < 0.01$.

* Correlation differs from zero by $0.01 < P < 0.05$.

† Correlation differs from zero by $0.05 < P < 0.10$.

Table 2.4. Residual correlations of feeding behavior traits with backfat across and within a line selected for decreased residual feed intake (LRFI) and a control line (CTRL), across the entire test period (TP) and in the first (TP1) and second (TP2) half of the test period.

Trait	TP				TP1				TP2			
	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	Across lines	LRFI	CTRL	LRFI	CTRL	CTRL
Daily feed intake	0.28**	0.28**	0.29**	0.20**	0.18**	0.21**	0.34**	0.29**	0.37**			
Occupation time/d	0.12**	0.27**	0.02	0.09*	0.23**	-0.01	0.13**	0.26**	0.04			
No. of visits/d	-0.05	-0.04	-0.06	-0.05	-0.02	-0.08	-0.04	-0.03	-0.04			
Feed intake/visit	0.04	-0.02	0.08	0.04	-0.03	0.10	0.02	-0.02	0.04			
Occupation time/visit	0.12**	0.19**	0.08	0.10*	0.14*	0.07	0.12**	0.20**	0.06			
Feed intake rate	-0.12*	-0.24**	0.004	-0.11*	-0.24**	0.01	-0.11*	-0.22**	-0.02			

** Correlation differs from zero by $P < 0.01$.

* Correlation differs from zero by $0.01 < P < 0.05$.

† Correlation differs from zero by $0.05 < P < 0.10$.

**CHAPTER 3: ESTIMATION OF GENETIC PARAMETERS AND HIGH DENSITY
SNP ANALYSIS OF FEEDING BEHAVIOR TRAITS IN YORKSHIRE PIGS
SELECTED FOR RESIDUAL FEED INTAKE**

To be submitted to the *Journal of Animal Science*

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Abstract

Residual feed intake (RFI) is a measure of feed efficiency defined as the difference between observed and predicted feed intake (FI) based on average requirements for growth and maintenance. Selection for RFI has been shown to be associated with changes in feeding behavior. Therefore, the objectives of this study were to investigate the genetic basis and genetic architecture of feeding behavior traits in a population of Yorkshire pigs selected for RFI (one line was selected for decreased RFI while the other was originally randomly selected and then selected for increased RFI), including estimation of trait heritabilities, of genetic and phenotypic correlations among feeding behavior traits and with performance traits, and a genome-wide association analysis using high density single nucleotide polymorphisms (SNP). Feeding behavior traits analyzed were FI per day and per visit, occupation time (OT) per day and per visit, number of visits (NV) per day, and FI rate. Feeding behavior traits were highly heritable, ranging from 0.36 for FI per visit to 0.71 for OT per day. FI per day and OT per visit had heritabilities of 0.42, NV per day had a heritability of 0.44, and FI rate had a heritability of 0.59. Phenotypic and genetic correlations

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were similar for each pair of traits. NV per day had strong, negative correlations with FI per visit and OT per visit. FI and OT per visit had strong, positive correlations. OT per day and FI rate were also strongly and positively correlated. Other correlations between feeding behavior traits were low. FI per day had strong, positive correlations with the performance traits of RFI, average daily gain (ADG), and backfat depth (BF). FI per visit was moderately and positively correlated with ADG and BF. OT per day was moderately and positively correlated with RFI and BF. Other correlations between feeding behavior traits and performance traits were low (<0.2). SNPs located adjacent to MC4R (a gene already shown to be associated with FI, growth, and leanness) were significant for FI per day. Other genes that were found to be associated with feeding behavior traits included several pertaining to transcription regulators. In conclusion, there appears to be a large genetic component to feeding behavior and measuring and selecting for these traits may allow for other opportunities to improve traits of economic importance.

Key words: residual feed intake, feeding behavior

Introduction

Feeding behavior has been shown to respond to selection for RFI in pigs (Young et al., 2011). Pigs from a line selected for decreased RFI ate faster and less per day and spent less time in the feeder per day than pigs from a randomly selected control line, even after accounting for differences in daily feed intake (Young et al., 2011). Pigs with decreased RFI also tended to visit the feeder fewer times, especially during peak eating times, and spent less time eating per visit than the control pigs (Young et al., 2011). Previous studies have also evaluated the phenotypic correlations between RFI and feeding behavior in pigs (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006a,b) but results have varied greatly. The

correlations between daily feed intake and RFI estimated by Rauw et al. (2006a, b) were much lower than the one estimated by Von Felde et al. (1996). Correlations for feed intake per visit and occupation time per visit were found to be both negative and positive depending on the study (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006a,b). The correlation between RFI and number of visits per day ranged from not significant (Rauw et al., 2006b) to positive (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006a). de Haer et al. (1993) and Rauw et al. (2006b) did not find a significant correlation between RFI and feed intake rate while Von Felde et al. (1996) estimated the correlation as 0.13.

Against this background, the objectives of this study were to investigate the genetic basis and genetic architecture of feeding behavior traits in a population of Yorkshire pigs selected for RFI (one line was selected for decreased RFI while the other was originally randomly selected and then selected for increased RFI), by estimating trait heritabilities, genetic and phenotypic correlations among feeding behavior traits and of feeding behavior traits with performance traits, and performing a genome-wide association analysis using high density single nucleotide polymorphisms (SNPs).

Materials and Methods

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

Animals and housing

Using purebred Yorkshire pigs, a selection line for decreased RFI (**LRFI** line) and a randomly selected control, which was later selected for increased RFI (**HRFI** line), were initiated in 2001. Beginning with the random allocation of littermates from generation 0 to the LRFI and HRFI lines, the following traits were recorded each generation on

approximately 90 boars from first parity sows and 90 gilts from second parity sows of the LRFI line: electronically measured daily feed intake (**FI**), BW recorded every 2 wk, and 10th-rib backfat (**BF**) and loin muscle area at market weight. Backfat and loin muscle area at market weight were evaluated by ultrasound using an Aloka 500V SSD ultrasound machine fitted with a 3.5-MHz, 12.5-cm, linear array transducer (Corometrics Medical Systems Inc., Wallingford, CT). Average daily FI was derived as a performance trait as described by Cai et al. (2008) using data collected from Feed Intake Recording Equipment (**FIRE**, Osborne Industries Inc., Osborne, KS). Average daily gain (**ADG**) was obtained as the slope from simple linear regression of BW on number of days on test. After evaluation of boars from first parity sows, approximately 12 boars and 70 gilts were selected to produce about 50 litters of 10 piglets for the next generation. Selection decisions were based on EBV for RFI, as described by Cai et al. (2008). After selection, gilts from parity 2 sows, which were full- or half-sisters of selected boars, were evaluated for RFI to provide additional data for the next generation. The HRFI line was maintained through generation 5 by creating ~30 litters from ~10 boars and 40 gilts which were randomly selected. Full- and half-sib matings were avoided in both lines. In early generations, only LRFI pigs were evaluated for RFI because of limited capacity to measure FI. Starting in generation 5 with boars from parity 1 sows, HRFI pigs were also evaluated for RFI to make direct line comparisons. This also allowed for selection within the HRFI line for increased RFI starting with the fifth generation. Further details can be found in Cai et al. (2008) and Bunter et al. (2010).

For FI recording, pigs were housed in 1 room with 12 pens with fully slatted flooring from ~90 d of age. Each pen was 5.6 m long and 2.3 m wide (0.82 m²/pig) and accommodated 16 pigs. Pens were separated by steel rod gates and contained a 2-nipple type

waterer (Edstrom, Waterford, WI) which provided ad libitum access. Six of the 12 pens had a single-space electronic FIRE feeder. The other pens had single-space feeders of a similar design so as not to induce the need for an acclimation period. Pigs were switched between pens every 2 wks after being weighed in the morning. Data from days when pigs were switched between pens were not used. The FIRE feeders recorded ear transponder, entrance time, start weight of feed, exit time, and end weight of feed for each visit to the feeder. Pigs were fitted with unique transponders at the start of the acclimation period. Lines were mixed within a pen to maximize statistical power to evaluate line differences but at the risk of some bias from pigs from one line affecting the behavior of pigs from the other line in generations when both lines were evaluated for FI. Pigs were given ~1 wk to acclimate to the FIRE feeders before being put on test in groups by on-test date based on age and BW (typically 2 or 3 age groups per generation and parity). In general, pigs were taken off test on an individual basis when they reached ~115 kg of BW but were removed at a lighter BW if few pigs remained in a pen, in which case all remaining pigs were taken off test. Pigs with an off-test BW less than 102 kg did not have enough BW to accurately estimate RFI and were not used for data analysis of performance traits but they were included in the feeding behavior analyses.

Feeding behavior traits

Feeding behavior traits were derived from data obtained from the FIRE feeders. Collection of feeding behavior data was terminated when the first pigs were taken off from that pen as feeding behavior may change when stocking density and number of pigs per feeder changes. Database and edit systems developed by Casey et al. (2005) were used to handle and edit the large amount of data collected by the FIRE feeders. Errors in each visit

(visit defined as feeding event from the entrance of a pig into the feeder to its exit) were identified by 16 criteria (Casey et al., 2005). Using the edited data, feeding behavior traits were derived. Average FI per day was derived by summing FI of each pig per day and averaging across days, as recorded by the FIRE feeders. Average number of visits per day was calculated by averaging the number of visits per day by pig. Average FI per visit was calculated by averaging feed consumption by visits across days. Average occupation time per day and per visit were calculated in a similar manner as average FI per day and per visit. Average FI rate was obtained by calculating a feeding rate for each visit by dividing the amount of feed consumed by the time spent in the feeder and then averaging the individual visit feeding rates.

Genotyping

Tail samples were collected and stored at birth from each animal. The Qiagen (Valencia, CA) DNeasy blood & tissue kit was used for DNA isolation from the tails. A total of 1042 pigs from generations 0, 4, 5, 6, and 7 of the population described above were genotyped. The number of genotyped pigs that had feeding behavior collected per line and per generation is reported in Table 3.1. A total of 1023 of the 1042 genotyped pigs had feeding behavior data. GeneSeek Inc. (Lincoln, NE) completed the genotyping with the Illumina (San Diego, CA) PorcineSNP60 BeadChip (Ramos et al., 2009). Quality control included the removal of all single nucleotide polymorphisms (SNPs) which were fixed in the entire population or had a QC score less than 0.4 in greater than 20% of the population. A total of 51,842 SNPs remained for analysis using build 10 of the pig genome.

Statistical analyses

Genetic parameters were estimated using AS-REML (Gilmour et al., 1995). All analyses included RFI as a trait to account for the effects of selection. Heritabilities and trait correlations with RFI were estimated using a two-trait animal model, fitting RFI and the trait of interest. Correlations between all other traits were estimated using a three-trait animal model, fitting RFI and the two traits of interest. The pedigree utilized included all 14,169 animals in the population, starting with generation -1 and continuing to generation 7. Fixed effects of group and sex were fitted for RFI, ADFI, ADG, and BF analyses. The interaction of generation, line, and on-test age was fitted as a covariate for RFI, ADFI, and ADG. The interaction of generation, line, and off-weight deviation was fitted as a covariate for BF. Fixed effects of generation, parity, and the interaction between generation and parity were fitted for feeding behavior traits. The interaction of generation, line, and on-age was fitted as a covariate for feeding behavior traits. Feed intake per day was also included as a covariate; however, results were the same whether feed intake per day was included as a covariate or not so feed intake per day was removed from the analysis. The concatenation of group and pen was fitted as a random effect for all traits.

The software program GenSel, developed at Iowa State University (<http://biggs.ansci.iastate.edu>), was used to perform the genome-wide association analysis using high density SNPs of feeding behavior traits. Bayes C π model averaging was used for data analyses (Habier et al., 2011). The mixed linear model used was $\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}u + e$, where \mathbf{X} is an incidence matrix for fixed effects and \mathbf{Z} is a matrix of SNP genotypes with effects fitted as random effects. Fixed effects included group, pen, parity (sex), feeder fitted within group, and on-test age as a covariate. The prior probability that a SNP in \mathbf{Z} has zero

effect was set to 0.995, which corresponds to approximately 260 non-zero SNP effects fitted in any of the Monte-Carlo Markov Chain (MCMC) used for the Bayesian analysis. Following a 1,000 iteration burn-in, 50,000 MCMC iterations were run. Results were obtained in the form of a post burn-in posterior distribution for the effect of every SNP fitted simultaneously with other informative SNPs. The posterior mean effect of each SNP across the chains was used to predict the genomic breeding value of every chromosome fragment consisting of 5 contiguous SNPs. The contribution of each chromosome fragment of 5 contiguous SNPs based on build 10 of the pig genome to the additive genetic variance in the population was then derived, a statistic that has a multi-locus analogy to the gene frequency specific contribution to genetic variance of the substitution effect of a single locus.

Results and Discussion

Heritabilities

Although heritabilities of RFI, ADG, and BF have already been estimated in this population (Cai et al., 2008), they were re-estimated in this study since it included animals in later generations than those used for previous estimates. Heritabilities for RFI, ADG, and BF were 0.20, 0.37, and 0.72, respectively, which are comparable to 0.29, 0.42, and 0.68 reported by Cai et al. (2008). Heritabilities of feeding behavior traits were moderate to high (Table 3.2). Feed intake per day had a heritability of 0.42 which is higher than previously reported heritabilities in pigs of 0.16 to 0.42 (de Haer et and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999) and much higher than the estimate of 0.25 found in sheep (Cammack et al., 2005). Heritability of occupation time per day was 0.71 which is much higher than estimates in previous studies of 0.24 to 0.44 in pigs (de Haer and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999), 0.36 in sheep (Cammack et al., 2005), and 0.28

in cattle (Nkrumah et al., 2007). Heritability for the number of visits per day was 0.44 which is high compared to previous studies in pigs (0.38 to 0.45, de Haer and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999) and sheep (0.35, Cammack et al., 2005) and cattle (0.38, Nkrumah et al., 2007). Feed intake per visit had a heritability of 0.36 which is low compared to previous studies in pigs (0.35 to 0.53, de Haer and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999) but higher than in sheep (0.33, Cammack et al., 2005). Heritability of occupation time per visit was 0.42 which is within the range of previous studies in pigs of 0.27 to 0.54 (de Haer and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999) but higher than the estimate of 0.29 found in sheep (Cammack et al., 2005). Heritability of feed intake rate was 0.59 which is higher than the range of 0.29 to 0.50 previously reported in pigs (de Haer and de Vries, 1993; Von Felde et al., 1996; Labroue et al., 1999).

Correlations among feeding behavior traits

With a few exceptions, both phenotypic and genetic correlations among feeding behavior traits were low to moderate (Table 3.2). Number of visits per day, feed intake per visit, and occupation time per visit were highly correlated with one another, both genetically and phenotypically. When number of visits per day decreases, one would expect a pig to consume more feed and spend more time in the feeder per visit which was supported by the correlations between the three traits. Occupation time per day and feed intake rate had high negative correlations, both phenotypic and genetic, which is as expected since pigs that eat faster are expected to spend less time in the feeder.

Correlations of feeding behavior traits with RFI

Feed intake per day was found to have a phenotypic correlation of 0.59 ± 0.03 and a genetic correlation of 0.65 ± 0.12 with RFI. This supports the differences between lines in FI per day previously reported (Young et al., 2011). Previous studies have reported varying values for phenotypic correlations between FI per day and RFI in pigs, ranging from 0.39 to 0.98 (Von Felde et al., 1996; Rauw et al., 2006a,b), which support our finding of 0.59. Our estimate of 0.59 also coincides with previous findings in cattle and sheep where FI per day was found to have a phenotypic correlation with RFI between 0.58 and 0.61 (Cammack et al., 2005; Kelly et al., 2010b; Lancaster et al., 2009). Our estimate of 0.65 is similar to the genetic correlation of 0.61 found by Cammack et al. (2005) between FI per day and RFI in sheep. However, our genetic correlation of 0.65 was much lower than the correlation of 0.97 reported by Von Felde et al. (1996) in pigs.

In our study, the phenotypic correlation of occupation time per day with RFI was 0.26 ± 0.06 which falls within the range of estimates reported previously in pigs of 0.64, 0.37, and 0.15 (de Haer et al., 1993; Von Felde et al., 1996; Rauw et al., 2006b). However, it is lower than reports in cattle of 0.41 and 0.49 (Nkrumah et al., 2007; Lancaster et al., 2009) but higher than that reported in sheep of 0.10 (Cammack et al., 2005). The genetic correlation between occupation time per day and RFI of 0.65 ± 0.12 found in our study is similar to that previously reported in pigs (0.44; Von Felde et al., 1996), lower than that found in cattle (0.57; Nkrumah et al., 2007), and higher than the correlation reported in sheep (0.22; Cammack et al., 2005). This suggests that the relationship between occupation time per day and RFI may be species specific. However, the strong genetic correlation supports previous

findings that low RFI animals spend approximately 10 minutes less in the feeders than high RFI animals after correcting for differences in FI per day (Young et al., 2011).

In our study, number of visits per day was not found to be significantly correlated with RFI, phenotypically or genetically. In previous studies, correlations of number of visits per day with RFI ranged from small and not significant (Rauw et al., 2006a,b) to moderate. Von Felde et al. (1996) found the phenotypic correlation between number of visits per day and RFI to be 0.13 while de Haer et al. (1993) found it to be much higher at 0.51. In cattle, phenotypic correlations of number of visits per day with RFI ranged from 0.18 to 0.45 (Nkrumah et al., 2007; Lancaster et al., 2009; Kelly et al., 2010a,b). In sheep, the phenotypic correlation was found to be 0.10 (Cammack et al., 2005). Unlike our study, previous studies reported the genetic correlation between number of visits per day and RFI to be significant. The correlations were 0.17 in pigs (Von Felde et al., 1996), -0.34 in cattle (Nkrumah et al., 2007), and 0.20 in sheep (Cammack et al., 2005). This shows that the relationship between number of visits per day and RFI is still unclear and may be population dependent.

In our study, FI per visit did not have significant phenotypic or genetic correlations with RFI. Previous studies report correlations of FI per visit with RFI to be low and both negative and positive. Phenotypic correlations of FI per visit were 0.11 (Von Felde et al., 1996) and -0.20 (de Haer et al., 1993) in pigs and -0.03 in cattle (Kelly et al., 2010b). The estimate of Von Felde et al. (1996) corresponds to our finding of 0.12 ± 0.05 for the phenotypic correlation between FI per visit and RFI. The genetic correlation of FI per visit with RFI was found to be 0.13 in pigs (Von Felde et al., 1996) which is in the opposite direction of the estimate of -0.07 ± 0.20 found in our study. However, our estimate is not significantly different from zero.

In our study, occupation time per visit did not have significant phenotypic or genetic correlations with RFI. Like our study, the two previous studies that evaluated occupation time per visit did not find a significant correlation with RFI (de Haer et al., 1993; Von Felde et al., 1996).

Despite significant line differences in FI rate (Young et al., 2011), this trait was not significantly correlated with RFI, phenotypically or genetically. The genetic correlation between FI rate and RFI was 0.07 ± 0.05 and the phenotypic correlation was -0.04 ± 0.18 . Studies by de Haer et al. (1993) and Rauw et al. (2006b) also found no significant correlations of FI rate with RFI. However, Von Felde et al. (1996) found correlations of 0.13 (phenotypic) and 0.25 (genetic) between the two traits. In cattle, studies by Kelly et al. (2010a,b) found the correlation of FI rate with RFI to be 0.25 while a study by Lancaster et al. (2009) found no significant correlation.

Overall, daily FI was found to be highly and positively correlated with RFI. The relationship of other feeding behavior traits with RFI varies in literature, depending on breed, species, and sex of the animal being evaluated. In general, feeding behavior is low to moderately correlated with RFI.

Correlations of feeding behavior traits with ADG and BF

Like previous studies, FI per day was found to be strongly and positively correlated with ADG and BF, both phenotypically and genetically. Feed intake per day was found to have a phenotypic correlation of 0.59 ± 0.03 and a genetic correlation of 0.77 ± 0.08 with ADG in our population, which falls within the ranges of 0.28 to 0.76 for phenotypic correlations (de Haer et al., 1993; Von Felde et al., 1996; Labroue et al., 1997; Hyun and Ellis, 2002; Rauw et al., 2006b; Cammack et al., 2005; Kelly et al., 2010b) and 0.68 to 0.87

for genetic correlations (Von Felde et al., 1996; Labroue et al., 1997; Cammack et al., 2005) reported in previous studies. Feed intake per day was found to have a phenotypic correlation of 0.45 ± 0.04 and a genetic correlation of 0.52 ± 0.11 with BF in our population. These values are similar to the ranges of 0.24 to 0.43 for phenotypic correlations (de Haer et al., 1993; Von Felde et al., 1996; Labroue et al., 1997) and 0.35 to 0.62 for genetic correlations (Von Felde et al., 1996; Labroue et al., 1997) reported in previous studies.

Occupation time per day was found to have a phenotypic correlation of 0.16 ± 0.04 with ADG which falls within the range of estimates previously published in pigs of 0.13 to 0.30 (Von Felde et al., 1996; Labroue et al., 1997; Hyun and Ellis, 2002; Rauw et al., 2006b) and in cattle of 0.17 to 0.25 (Nkrumah et al., 1997; Lancaster et al., 2009; Kelly et al., 2010a). Labroue et al. (1997) found occupation time per day to have a significant genetic correlation of 0.19 with ADG in French Landrace pigs but did not find a significant genetic correlation in the Large White pigs evaluated. In our population, the genetic correlation of occupation time per day with ADG was 0.13 ± 0.15 which was not significant but is in a similar direction to that found by Labroue et al. (1997) in French Landrace pigs. Other studies evaluating the genetic correlation of occupation time per day with ADG estimated the correlation to be 0.32 in pigs (Von Felde et al., 1996), 0.42 in cattle (Nkrumah et al., 2007), and 0.17 in sheep (Cammack et al., 2005). Phenotypic and genetic correlations of occupation time with BF were similar and ranged from 0.07 to 0.15 in pigs (de Haer et al., 1993; Von Felde et al., 1996; Labroue et al., 1997) and were 0.37 in cattle (Nkrumah et al., 2007). This differs from our findings where the genetic correlation (0.30 ± 0.11) was higher than the phenotypic correlation (0.19 ± 0.05) between occupation time per day and BF.

Number of visits per day was found to have a phenotypic correlation of -0.10 ± 0.04 and a genetic correlation of -0.19 ± 0.16 with ADG. These are similar to the phenotypic correlations of -0.16 and -0.14 found by Rauw et al. (2006b) and de Haer et al. (1993), respectively. The genetic correlation found in cattle by Nkrumah et al. (2007) was also in the same direction (-0.33). However, other studies found the correlation between number of visits per day and ADG to be positive. Positive phenotypic correlations were previously reported in pigs (0.28, Hyun and Ellis, 2002), in cattle (0.28, Kelly et al., 2010b), and in sheep (0.22, Cammack et al., 2005). Cammack et al. (2005) also reported a positive genetic correlation of 0.31 in sheep. Number of visits per day and BF were not found to be significantly correlated in our population. This agrees with Von Felde et al. (1996) who also found no significant phenotypic or genetic correlation between the two traits. However, a study by de Haer et al. (1993) found the phenotypic correlation of number of visits per day with BF to be -0.15. A study in cattle by Nkrumah et al. (2007) found no significant phenotypic correlation; however, they estimated the genetic correlation at -0.47.

Feed intake per visit was found to be positively correlated with ADG, both phenotypically (0.34 ± 0.04) and genetically (0.39 ± 0.15). The phenotypic correlation is similar to that found by de Haer et al. (1993) of 0.41 but much higher than correlations found by Von Felde et al. (1996) who estimated a phenotypic correlation between FI per visit and ADG of 0.13 and a genetic correlation of 0.20. In our population, correlations of FI per visit with BF were lower than those with ADG. The phenotypic correlation was 0.16 ± 0.05 which is lower than the estimate of 0.33 found by de Haer et al. (1993) but higher than the 0.10 found by Von Felde et al. (1996). The genetic correlation was 0.26 ± 0.14 which is higher than the 0.07 found by Von Felde et al. (1996).

Occupation time per visit was found to have a phenotypic correlation of 0.22 ± 0.04 and a genetic correlation of 0.20 ± 0.16 with ADG in our population. In previous studies, occupation time per visit was found to have a phenotypic correlation of 0.18 with ADG (de Haer et al., 1993) which is similar to our estimate. However, no other studies found significant correlations between occupation time per visit and ADG (Von Felde et al., 1996; Hyun and Ellis, 2002). Occupation time per visit was found to have a phenotypic correlation of 0.14 ± 0.05 and a genetic correlation of 0.32 ± 0.12 with BF in our population. In previous studies, occupation time per visit was found to have a phenotypic correlation of 0.18 (de Haer et al., 1993) with BF although Von Felde et al. (1996) found no significant correlation between the two traits.

Feed intake rate had a phenotypic correlation of 0.13 ± 0.04 with ADG which is lower than the previously reported range of 0.23 to 0.50 in pigs (de Haer et al., 1993; Von Felde et al., 1996; Labroue et al., 1997; Rauw et al., 2006b) but similar to the range of 0.09 to 0.32 previously reported in cattle (Lancaster et al., 2009; Kelly et al., 2010a,b). Feed intake rate had a genetic correlation of 0.17 ± 0.15 with ADG which is lower than the previously reported range of 0.27 to 0.48 in pigs (Von Felde et al., 1996; Labroue et al., 1997). Feed intake rate was not found to be correlated with BF, phenotypically or genetically, which contrasts with previous studies that found the phenotypic correlation of FI rate with BF to range from 0.13 to 0.35 in pigs (de Haer et al., 1993; Von Felde et al., 1996; Labroue et al., 1997) and the genetic correlation to range from 0.11 to 0.25 (Von Felde et al., 1996; Labroue et al., 1997).

Overall, daily FI was found to be highly correlated with ADG and BF. The relationship of other feeding behavior traits with ADG and BF varied between studies,

suggesting that the correlation between these traits may be dependent on the population being evaluated.

Genome-wide association analysis using high density SNPs

Results from the high density SNP analysis are shown in Figures 1 to 6. The Manhattan plots show the proportion of genetic variance explained by 5-SNP windows. Daily FI had two main regions with larger effects, the largest on pig chromosome (SSC) 11 and the second on *SSC1*. The region on *SSC11* overlaps the location of LIM domain only protein 7 (LMO7) which has been shown to regulate transcription of the nuclear membrane protein emerlin and other muscle relevant genes (Holaska et al., 2006). LMO7 was also shown to be important in the development of the heart in vertebrates (Ott et al., 2008). The region on *SSC1* is adjacent to melanocortin-4 receptor (MC4R) which has been shown to have an effect of feed intake, fatness, and growth in pigs (Kim et al., 2000). Genotypes for the MC4R mutation were not included in the panel. Occupation time per day also had two main regions, one on *SSC6* and the other on *SSCX*. The region on *SSC6* is in the same location as ZNF423 which has been shown to be important for retinoic acid-induced differentiation and for transactivation of RAR α /RXR α nuclear receptor complex in response to retinoids (Huang et al., 2009). This region was also important for FI rate which is not surprising since the two had a genetic correlation of -0.89. The region on *SSCX* is located near the short stature homeobox-containing (SHOX) gene. SHOX is a nuclear protein that acts as a transcriptional activator and deficiencies in SHOX are associated with short stature (Binder, 2011). Number of visits per day also had two main regions, one on *SSC9* and the other on *SSCX*. The region on *SSC9* is located adjacent to the jerky homolog-like (JRKL) which has not been extensively researched and has an Entrez gene function of being a

nuclear regulatory protein. The region on *SSCX* was located near the retinoic acid-induced 2 (*RAI2*) gene. *RAI2* has been shown to be involved in vertebrate anteroposterior formation and cellular differentiation (Walpole et al., 1999). This gene, along with *ZNF423*, both pertain to retinoic acid which suggests that retinoic acid may play a role in feeding behavior. Since retinoic acid is involved in growth and development, this may be explained by the moderate genetic correlations of ADG with occupation time per day, number of visits per day, and FI rate. Feed intake per visit had one main region on *SSC9* which was near the neural cellular adhesion molecule 1 (*N-CAM1*). *N-CAM1* has been shown to be involved in the response to ionic stress in the optic nerve (Carreras et al., 2009). Occupation time per visit had two main regions, one on *SSC9* at the folate receptor 4 (*FOLR4*) and the other on *SSC6* at the zinc finger Ran-binding domain-containing protein 2 (*ZRANB2*). *FOLR4* has been shown to be involved in immune response via antigen-specific regulatory T-cell expression and administration of *FOLR4* was shown to produce tumor immunity in tumor-bearing animals (Yamguchi et al., 2007). *ZRANB2* is found in the nucleus and regulates alternative splicing through its interactions with several splicing proteins (Mangs and Morris, 2008). Feed intake rate had two main regions, one on *SSC10* and one on *SSC6* as mentioned before. The region on *SSC10* is at the same location as myosin IIIA (*MYO3A*). *MYO3A* has been shown to be involved with cell structure and actin-dependent cell motility in the retina (Lin-Jones et al., 2009) as well as with progressive hearing loss in humans (Walsh et al., 2011). Since both *N-CAM1* and *MYO3* are related to the eye, it is possible that vision, or at least differences in eye development, may play a role in feeding behavior. Several of the genes mentioned above are involved in nuclear regulation and translation. More research into how these genes are involved in the multiple factors contributing to appetite regulation is

warranted. More work needs to be done to validate the above results and to better understand the connection between feeding behavior and the genes in the regions that explained the greatest amount of the genetic variation in feeding behavior traits.

Conclusions

In general, feeding behavior traits were moderately to highly heritable. Correlations with performance traits were mostly study dependent with the exception of daily FI which had high, positive correlations with RFI, ADG, and BF in most studies. Genes affecting feeding behavior traits have not been evaluated previously. Therefore, there is still more research needed to better understand the genetic basis of feeding behavior and to validate the results of this study.

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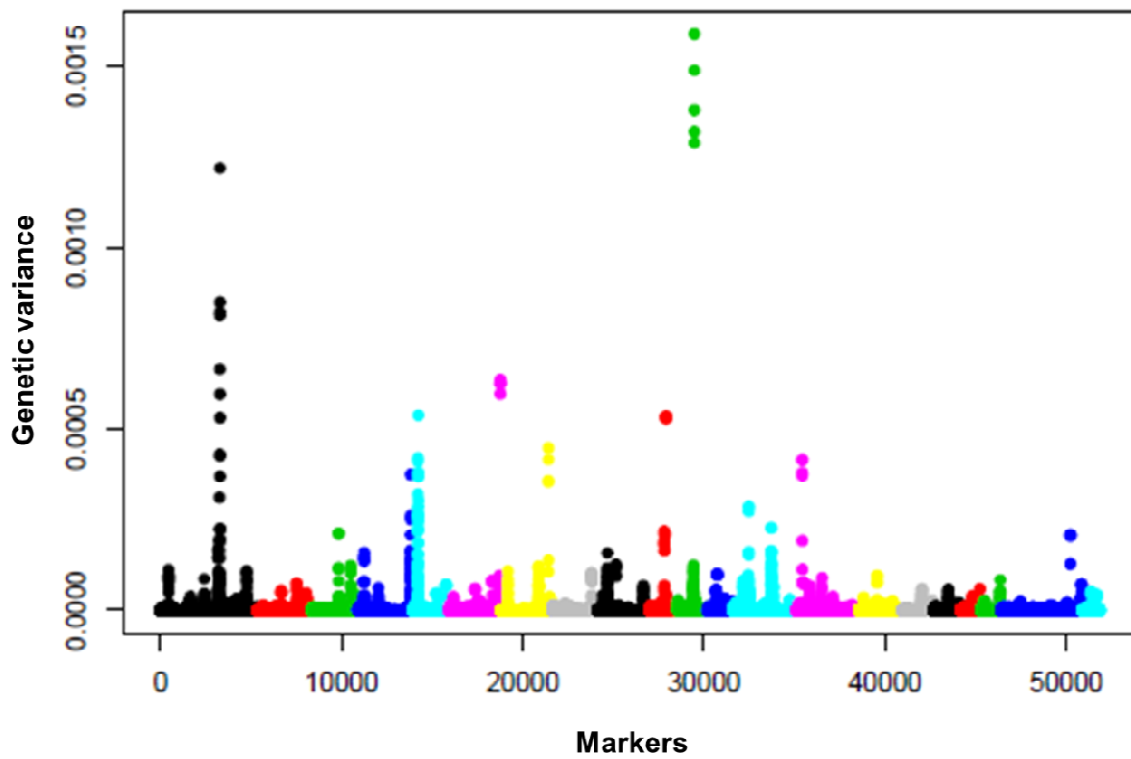


Figure 3.1. Proportion of genetic variance explained by windows of 5 SNPs for average daily feed intake. Each chromosome is represented by a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

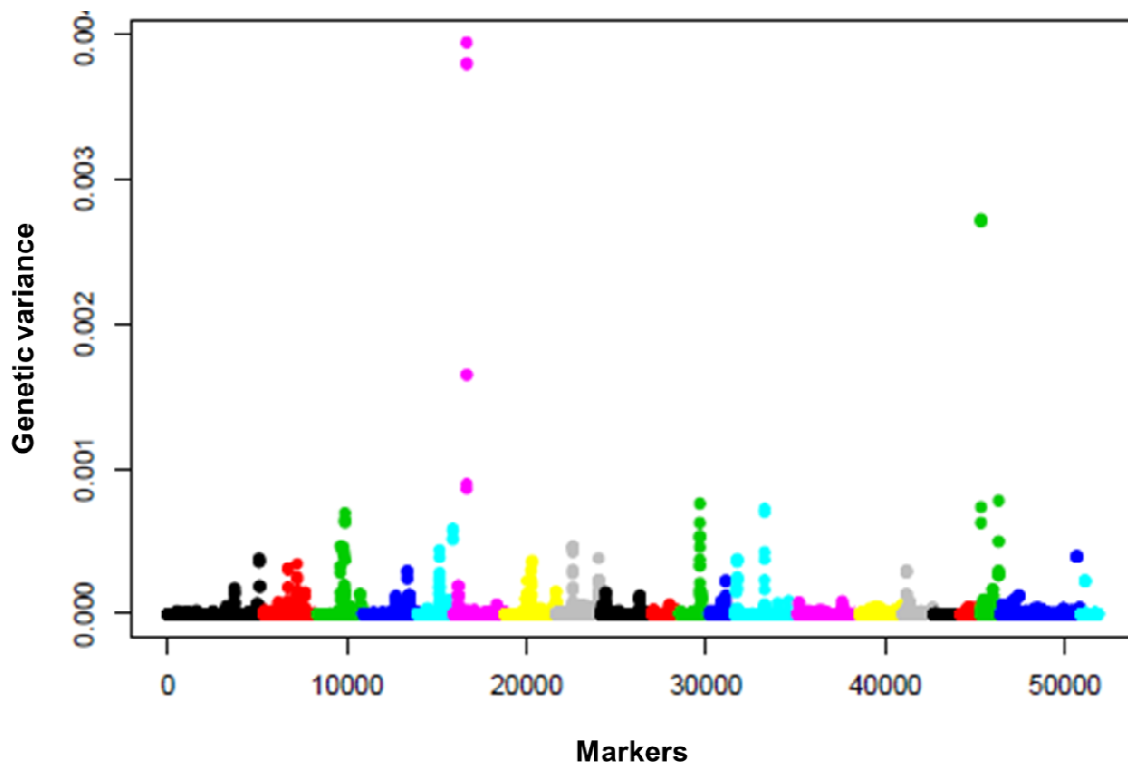


Figure 3.2. Proportion of genetic variance explained by windows of 5 SNPs for average occupation time per day. Each chromosome is represented in a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

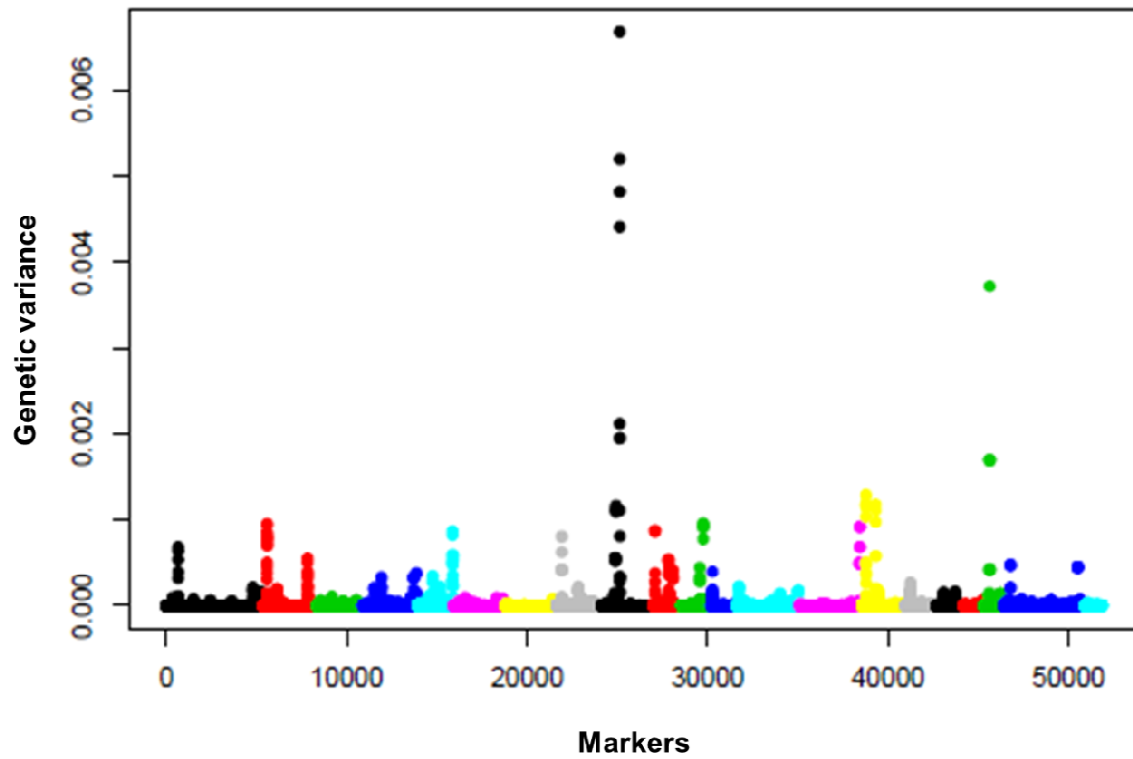


Figure 3.3. Proportion of genetic variance explained by windows of 5 SNPs for average number of visits per day. Each chromosome is represented in a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

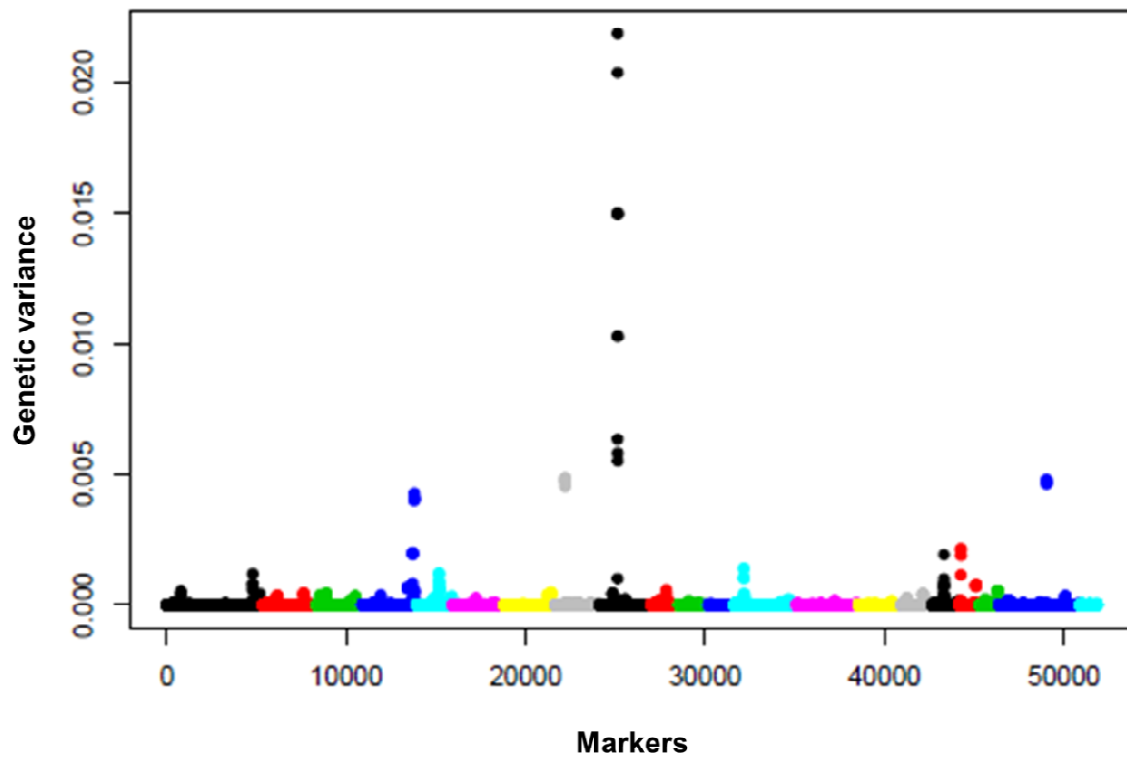


Figure 3.4. Proportion of genetic variance explained by windows of 5 SNPs for average feed intake per visit. Each chromosome is represented in a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

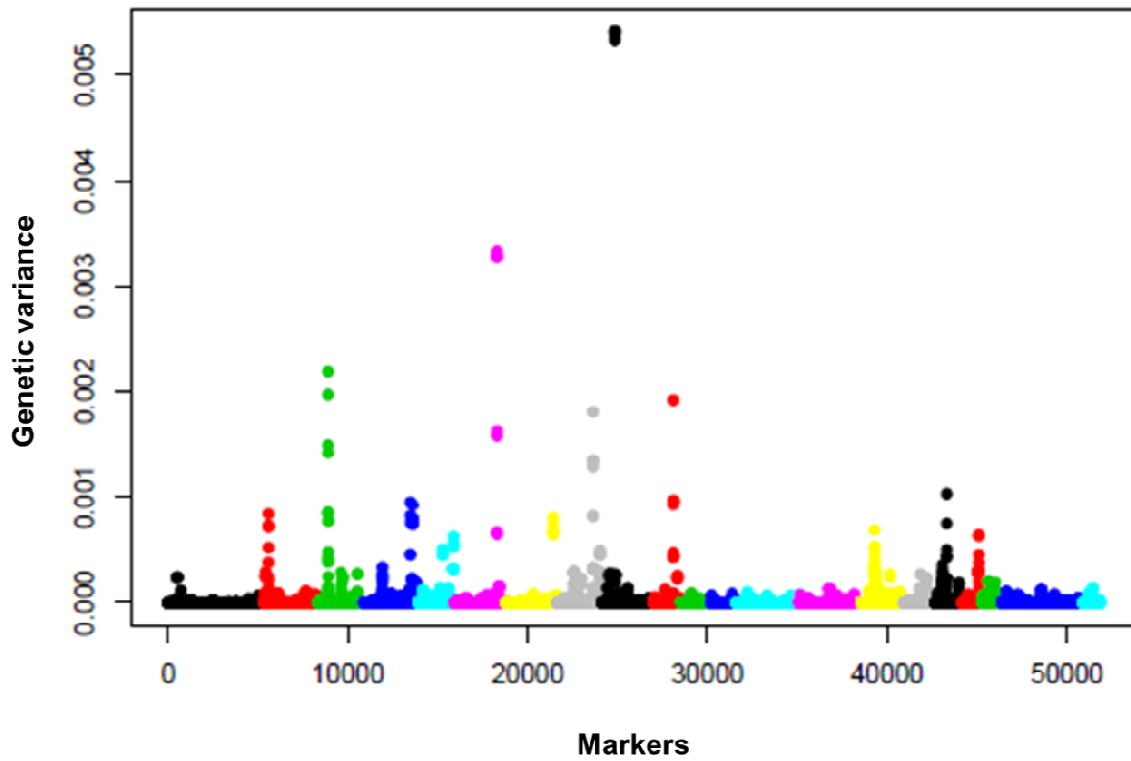


Figure 3.5. Proportion of genetic variance explained by windows of 5 SNPs for average occupation time per visit. Each chromosome is represented in a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

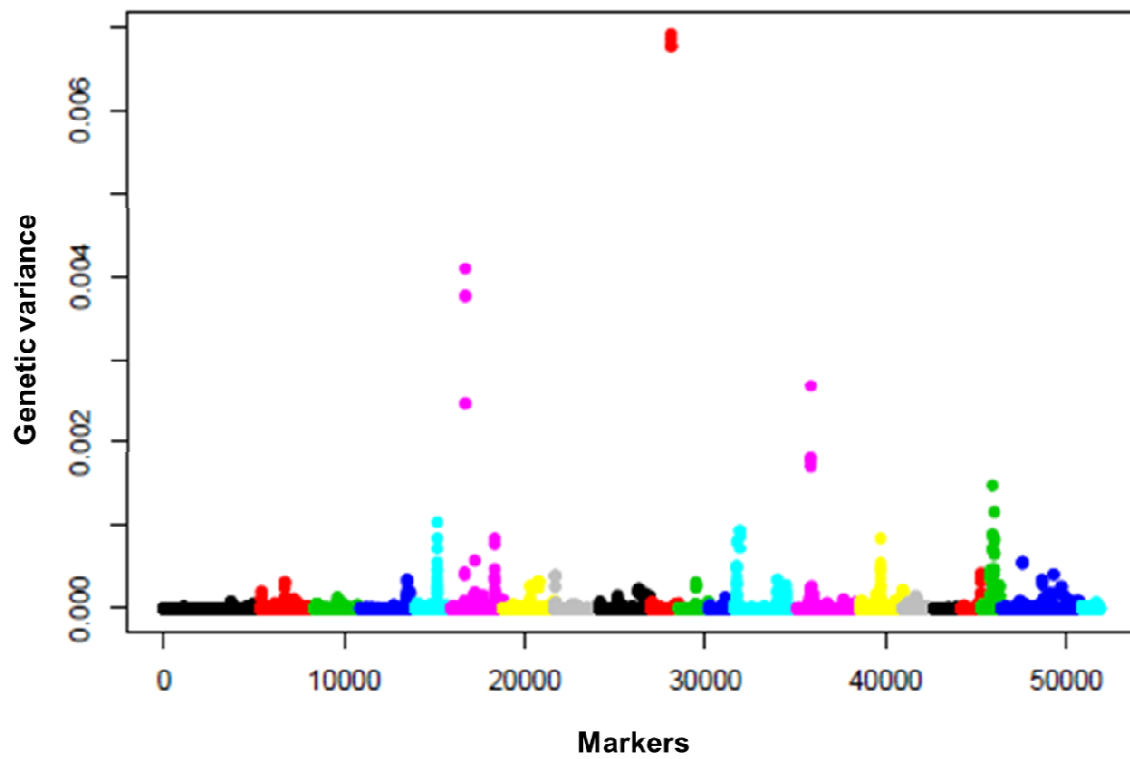


Figure 3.6. Proportion of genetic variance explained by windows of 5 SNPs for average feed intake rate. Each chromosome is represented in a different color, with SSC1 on the left, SSC18 in red on the right, SSCX in green, and unmapped markers in blue and cyan on the far right.

Table 3.1. Number of pigs with feeding behavior data per line, generation, and sex with number genotyped in parantheses.

Generation	LRFI line		HRFI line	
	Boars	Gilts	Boars	Gilts
0	87 (69)	90		
1	89	81		
2	71	86		
3	81	49		38
4	81 (31)	105 (89)		79 (73)
5	83 (62)	81 (81)	94 (85)	92 (90)
6	94 (90)		86 (83)	
7	76 (76)	61 (61)	81 (81)	52 (52)
Total	662 (328)	553 (231)	261 (249)	261 (215)

Table 3.2. Heritabilities and correlations for performance and feeding behavior traits, with standard errors in parentheses below the estimate¹.

	RFI	ADFI	ADG	BF	DFI	OTD	NVD	FIV	OTV	FIR
RFI	0.20 (0.06)				0.59 (0.03)	0.26 (0.06)	0.10 (0.06)	0.12 (0.05)	0.05 (0.05)	0.07 (0.05)
ADFI		0.37 (0.07)			0.90 (0.01)	0.29 (0.04)	-0.03 (0.05)	0.36 (0.04)	0.20 (0.05)	0.16 (0.05)
ADG			0.37 (0.08)		0.59 (0.03)	0.16 (0.04)	-0.10 (0.04)	0.34 (0.04)	0.22 (0.04)	0.13 (0.04)
BF				0.72 (0.08)	0.45 (0.04)	0.19 (0.05)	-0.05 (0.05)	0.16 (0.05)	0.14 (0.05)	0.01 (0.04)
DFI	0.65 (0.12)	0.99 (0.01)	0.77 (0.08)	0.52 (0.11)	0.42 (0.08)	0.23 (0.04)	-0.04 (0.05)	0.33 (0.04)	0.15 (0.05)	0.21 (0.04)
OTD	0.39 (0.15)	0.32 (0.13)	0.13 (0.15)	0.30 (0.11)	0.24 (0.13)	0.71 (0.09)	0.17 (0.04)	-0.05 (0.05)	0.49 (0.03)	-0.80 (0.02)
NVD	0.15 (0.18)	-0.16 (0.15)	-0.19 (0.16)	-0.16 (0.13)	-0.12 (0.15)	0.20 (0.13)	0.44 (0.08)	-0.84 (0.01)	-0.68 (0.02)	-0.09 (0.05)
FIV	-0.07 (0.20)	0.35 (0.14)	0.39 (0.15)	0.26 (0.14)	0.38 (0.14)	-0.07 (0.15)	-0.96 (0.02)	0.36 (0.08)	0.78 (0.02)	0.15 (0.04)
OTV	0.07 (0.19)	0.29 (0.15)	0.20 (0.16)	0.32 (0.12)	0.24 (0.15)	0.62 (0.09)	-0.65 (0.09)	0.71 (0.08)	0.42 (0.08)	-0.43 (0.04)
FIR	-0.04 (0.18)	0.08 (0.15)	0.17 (0.15)	0.01 (0.15)	0.15 (0.14)	-0.89 (0.03)	-0.13 (0.14)	0.12 (0.15)	-0.58 (0.11)	0.59 (0.08)

¹ Heritabilities in bold on the diagonal. Phenotypic correlations above the diagonal. Genetic correlations below the diagonal.

² Trait abbreviations: RFI = residual feed intake; ADFI = average daily feed intake (performance); ADG = average daily gain; BF = 10th rib backfat depth; DFI = average daily feed intake (behavior); OTD = average occupation time per day; NVD = average number of visits per day; FIV = average feed intake per visit; OTV = average occupation time per visit; FIR = average feed intake rate.

CHAPTER 4: EFFECT OF SELECTION FOR RESIDUAL FEED INTAKE DURING THE GROW/FINISH PHASE OF PRODUCTION IN YORKSHIRE PIGS ON SOW REPRODUCTIVE PERFORMANCE AND LACTATION EFFICIENCY

To be submitted to the *Journal of Animal Science*

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Abstract

As feed costs continue to rise and feed efficiency during finishing is emphasized, the impact of selecting for more efficient grow/finish pigs on the reproductive performance and feed efficiency of sows must be evaluated. Therefore, the objectives of this study were to evaluate correlated response to selection for residual feed intake during the grow/finish phase of production ($RFI_{G/F}$) on sow reproductive performance and feed efficiency in two lines of pigs developed at Iowa State University and to estimate heritabilities and genetic correlations of these traits with $RFI_{G/F}$. One line was selected over 7 generations for decreased $RFI_{G/F}$ (LRFI line) and the other line was randomly selected for 5 generations and then selected for increased $RFI_{G/F}$ (HRFI line). After 7 generations, LRFI sows had 1.7 more piglets farrowed ($P<0.01$) compared to HRFI sows, 1.2 more born alive ($P<0.05$), 0.4 more dead at birth ($P<0.05$), and more weaned, both by litter (9.0 vs. 7.5, $P<0.01$) and by sow (8.8 vs. 8.2, $P<0.05$). Piglets from the LRFI line were ~70 g heavier at birth ($P<0.05$) and had better litter growth (44.2 vs. 40.6 kg, $P<0.1$) than HRFI piglets. However, this increased piglet performance came at a cost to the sow as LRFI sows consumed 33 kg less feed and lost 8.5

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kg more body weight, 5.3 kg more fat mass, and 2.24 mm more backfat than HRFI sows ($P<0.01$). Although LRFI sows had a greater negative energy balance (-18.2 vs. -10.1 MJ ME/d, $P<0.01$), they had a more favorable lactation efficiency (45.9 vs. 41.0 %, $P=0.83$) and RFI during lactation (1.44 vs. 15.90 kg, $P<0.05$) than HRFI sows. Heritabilities were high ($h^2>0.4$, S.E. <0.07) for sow weights, body composition, and maintenance requirements and for piglet birth weights. Traits pertaining to piglet growth during lactation and mobilization of the sow's body tissue were moderately heritable ($0.2<h^2<0.4$, S.E. <0.07). Strong, positive genetic correlations with $RFI_{G/F}$ were found for sow weight at farrowing (0.51 ± 0.11) and at weaning (0.41 ± 0.11), for sow maintenance requirements (0.49 ± 0.11) and for lactation RFI (0.43 ± 0.20). Strong, negative genetic correlations with $RFI_{G/F}$ were found for sow protein mass loss (-0.35 ± 0.15) and for lactation efficiency (-0.55 ± 0.25). In conclusion, selection for decreased $RFI_{G/F}$ has positively affected piglet performance and lactation efficiency but has negatively affected sow body condition change and energy balance during lactation.

Key words: residual feed intake, reproduction, lactation efficiency, pigs

Introduction

Residual feed intake (**RFI**) is a measure of feed efficiency that is defined as the difference between observed feed intake and feed intake predicted from average requirements for growth and maintenance. Therefore, in theory, selection for decreased RFI in grow/finish pigs (**$RFI_{G/F}$**) should result in decreased feed intake without affecting growth. When developing strategies for genetic improvement of feed efficiency in grow/finish pigs, it is important to evaluate correlated responses to selection in other economically important traits.

Lactation is an energetically expensive process that results in the mobilization of body fat and body protein because nutrient intake often fails to meet daily requirements. This mobilization of body tissue coincides with a negative energy balance that has been shown to have negative consequences on health and reproduction in many studies involving dairy cattle, which are intensively managed (Veerkamp et al., 2001; Formigoni and Trevisi, 2003; Llewellyn et al., 2007). In pigs, the effect of a negative energy balance on the interval from weaning to first estrus has been the focus of some studies (Whittemore and Morgan, 1990; Clowes et al., 2003) which found that sows which have a greater negative energy balance have a delayed return to estrus.

Selection for decreased $RFI_{G/F}$ has resulted in market pigs that are leaner and consume less feed than pigs with higher $RFI_{G/F}$ (Cai et al., 2008; Smith et al., 2011). Selection for leanness has resulted in smaller litter sizes and birth weights (Kersey DeNise et al., 1983; Kerr and Cameron, 1996). Therefore, an objective of this study was to evaluate correlated responses in and genetic parameters of sow reproductive performance and lactation efficiency and its components in the selection lines for $RFI_{G/F}$ that have been developed at Iowa State University.

Materials and Methods

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

Selection lines and grow-finish traits

Using purebred Yorkshire pigs, a line selected for decreased RFI (**LRFI** line) and a randomly selected control (**HRFI**) line were initiated in 2001. The control line was selected for increased RFI starting generation 5. Beginning with the random allocation of littermates

from generation 0 to the LRFI and HRFI lines, the following traits were recorded for each generation on ~90 boars from first parity sows and ~90 gilts from second parity sows of the LRFI line: electronically measured daily feed intake, BW recorded every 2 wk, and 10th-rib backfat (**BF**) and loin muscle area at market weight. Backfat and loin muscle area at market weight were evaluated by ultrasound using an Aloka 500V SSD ultrasound machine fitted with a 3.5-MHz, 12.5-cm, linear array transducer (Corometrics Medical Systems Inc., Wallingford, CT). Average daily feed intake was derived as described by Cai et al. (2008) using data collected by Feed Intake Recording Equipment (FIRE[®]) stations (Osborne Industries Inc., Osborne, KS). Average daily gain was obtained as the slope from simple linear regression of BW on number of days on test. After evaluation of boars from first parity sows, each generation ~12 boars and 70 gilts were selected from the LRFI line to produce ~50 litters of ~10 piglets for the next generation. Selection decisions were based on EBV for RFI, as described by Cai et al. (2008). After selection, gilts from parity 2 sows, which were full- or half-sisters of selected boars, were evaluated for RFI to provide additional data for the next generation. The HRFI line was maintained through generation 5 by creating ~30 litters from ~10 randomly selected boars and 40 randomly selected gilts. Full- and half-sib matings were avoided in both lines. In early generations, only LRFI pigs were evaluated for feed intake because of limited capacity to measure feed intake. Starting in generation 5, with boars from parity 1 sows, HRFI pigs were also evaluated for feed intake to make direct line comparisons possible and to allow for selection within the HRFI line for increased RFI. Further details can be found in Cai et al. (2008) and Bunter et al. (2010).

Sow management and lactation traits

Sows were housed in gestation crates from breeding and fed 2.8 kg feed daily. Approximately 3 to 5 days before their due date, sows were weighed and then moved into 1 of 4 rooms in the farrowing house, with each room having 12 farrowing crates. Prior to farrowing, sows were fed 1.4 kg twice a day. After farrowing, sows were fed twice a day to appetite and the amount offered to them was recorded. If a lot of wet feed was left in the feed trough, it was removed and weighed. Piglets were processed each morning and occasionally in the afternoon if more than 5 or 6 litters were born on one day. Any cross-fostering was performed within 24 hours of birth unless a sow quit producing milk or died during lactation. At approximately 21 d post-farrowing, piglets were weaned and moved into the nursery. Sows were weighed and moved back into the gestation barn.

Traits recorded during the lactation phase that were evaluated in this study can be divided into two main categories, piglet traits and sow traits. Piglet traits pertain to the piglets while sow traits pertain only to the sow.

Piglet traits

Piglet traits included litter counts and weights. All piglets born to a sow were recorded at processing and coded for live, dead at birth, or mummy. Farrowing survival was calculated as the percent born alive out of the total number farrowed (born alive + dead at birth + mummies). Farrowing and weaning dates were recorded for all piglets, along with date of death for piglets that died during lactation. Individual weights were recorded at birth for all non-mummified piglets and at weaning for all piglets alive at weaning. Pre-weaning survival was calculated as the percent weaned out of the number of piglets the sow was nursing after cross-fostering. Cross-fostering was done within 24 hr of birth. Approximately

2% of piglets born were cross-fostered, with ~80 % of cross-fostering occurring within line. Litter weaning weight, average weaning weight, and number weaned were calculated in two ways. The first was by litter, which was based on all piglets born to a sow regardless of whether she nursed them or not. The second was by sow, which was based on all piglets nursed by a sow regardless of whether she farrowed them or not. Piglet growth was defined as the difference between weaning and birth weights. Average daily gain of piglets that survived to weaning was calculated as piglet growth divided by age at weaning. Since the weights of piglets that died were not recorded but mortality date was known, the weight of the piglets at mortality was estimated using the growth rate of their littermates and the age at mortality as:

$$\text{Mortality weight (kg)} = \text{Birth weight (kg)} + [(\text{Fraction} \times \text{ADG}_{\text{littermates}})/1000] \times \text{Age at mortality (d)}$$

where fraction refers to the relative piglet growth during each week of lactation, as defined by Bergsma et al. (2009):

$$\text{Fraction} = 0.583333 + 0.270833 \times \text{WM} - 0.058333 \times \text{WM}^2 + 0.004167 \times \text{WM}^3$$

where WM = week of mortality (1, 2, 3, 4). Piglet energy gain from birth to weaning was calculated using estimated fat and protein deposition and piglet maintenance requirements, following Bergsma et al. (2009):

$$\text{Fat deposition, } \mathbf{FD} \text{ (kg)} = (\text{Weaning weight} - \text{Birth weight}) \times (0.135 + 0.00014 \times \text{ADG})$$

$$\text{Protein deposition, } \mathbf{PD} \text{ (kg)} = (\text{Weaning weight} - \text{Birth weight}) \times 0.16$$

$$\text{Piglet maintenance (MJ ME/d)} = 0.440 \times [((\text{Weaning weight} + \text{Birth weight}) / 2) ^{0.75}]$$

$$\text{Piglet energy gain (MJ ME/d)} = [(\text{FD} \times 39.5 + \text{PD} \times 23.8) / \text{Age at weaning}] + \text{Maintenance}$$

Litter average daily gain, litter growth, and litter energy gain were calculated across piglets nursed by the sow (i.e. on a by sow basis) as the sum of piglet average daily gain, piglet growth, and piglet energy gain, respectively.

Sow traits

Sows were weighed upon entering and exiting the farrowing house. Ultrasonic backfat, using the same equipment as used on the finishing pigs, was obtained at farrowing and at weaning by averaging measurements taken at the 10th rib and the last rib. Sow weight at farrowing was calculated by adjusting the weight at entry into the farrowing house for the estimated weight of the piglets, placentas, and intra-uterine fluid, following Noblet et al. (1985):

$$\text{Total fetal weight (g), } \mathbf{TFW} = e^{(8.72962 - 4.07466 * e^{(-0.03318 * (d - 45))} + 0.000154 * f * d + 0.06774 * n)}$$

$$\text{Placental weight (g), } \mathbf{PW} = e^{(7.02746 - 0.95164 * e^{(-0.06879 * (d - 45))} + 0.000085 * f * d + 0.09335 * n)}$$

$$\text{Intra-uterine fluid weight (g), } \mathbf{IUFW} = e^{(-0.2636 + 0.18805 * d - 0.001189 * d^2 + 0.13194 * n)}$$

where d = day of pregnancy; f = energy intake during gestation (MJ ME/d); and n = number of fetuses. Parameter f was set equal to 35 MJ ME/d based on sows being fed 2.8 kg of feed each morning during gestation and the energy content of the diet being 12.5 MJ ME/kg. Total fetal weight was estimated separately for the day of pregnancy at weighing and the day of pregnancy at parturition in order to convert the observed litter birth weight to an estimated weight of the litter, placenta, and intra-uterine fluid at the time of weighing, which was used to adjust the recorded weight of the sow as follows (Noblet et al., 1985):

$$\begin{aligned} \text{Sow weight at farrowing (kg)} &= \text{Recorded weight (kg)} - \text{Litter birth weight (kg)} \times \\ &[(\text{TFW at weighing} + \text{PW at weighing} + \text{IUFW at weighing}) / \text{TFW at parturition}] \end{aligned}$$

Sow weight at weaning was adjusted for the change in water content of milk from the start to the end of lactation, using equations derived by Bergsma et al. (2009) from Kim et al. (1999a, 1999b, 2000).

$$\text{Sow weight at weaning (kg)} = \text{Recorded weight (kg)} - [(\text{water}_{\text{weaning}} - \text{water}_{\text{farrowing}}) / 1000]$$

$$\text{Water}_{\text{weaning}} (\text{g}) = (\text{NFG} - \text{NWBS}) \times 73 + (\text{NWBS} \times 146.15 + 2.17 \times \text{ADG}) \times (1 - \text{DM}_{\text{weaning}} / 100)$$

$$Water_{farrowing} (g) = NFG \times 431.5 \times (1 - DM_{farrowing}/100)$$

$$\% \text{ dry tissue } (DM) = 31.805 - 0.6027 \times DL + 0.011 \times DL^2$$

$$ADG (g) = [(Litter weaning weight of piglets / NWBS - Total birth weight of piglets to be nursed by sow / Number to be nursed by sow) \times 1000] / Lactation length$$

where NFG = number of functional glands at parturition (assumed to equal the number of piglets to be nursed + 1 with a maximum value of 15), NWBS = number of piglets weaned by sow, and DL = day of lactation.

Protein mass and fat mass of sows at farrowing and weaning were estimated using equations derived by Bergsma et al. (2009) from Everts et al. (1994):

$$Protein \text{ mass } (kg) = 1.90 + 0.1711 \times \text{Body weight } (kg) - 0.3113 \times \text{Backfat } (mm)$$

$$Fat \text{ mass } (kg) = -11.58 + 0.1027 \times \text{Body weight } (kg) + 1.904 \times \text{Backfat } (mm)$$

Weight loss, fat mass loss, protein mass loss, and backfat loss were calculated as the value at farrowing minus the value at weaning. Therefore, a positive value means there was a loss in that trait. Sow maintenance requirements were estimated using the same equation as used for piglet maintenance:

$$Sow \text{ maintenance } (MJ \text{ ME/d}) = 0.440 \times [((\text{Weight at weaning} + \text{Weight at farrowing}) / 2)^{0.75}]$$

Feed intake was recorded on sows while they were in the farrowing house. Sows were fed 1.4 kg twice a day prior to farrowing and twice a day to appetite after farrowing. The lactation diet contained 13.64 MJ ME and 172 g crude protein per kg of feed.

Lactation efficiency, sow residual feed intake, and energy balance were used to evaluate the efficiency of the sow during lactation. Lactation efficiency was defined as the ratio of energy output (in the form of piglet growth and maintenance) to energy input (energy from feed and body tissue mobilization above maintenance requirements of the sow) based on the diagram of energy flow during lactation shown in Figure 1 (Bergsma et al., 2008,

2009). Sow residual feed intake was calculated by estimating regression coefficients for sow metabolic mid-weight, litter growth, sow weight loss, and sow backfat loss using the mixed procedure in SAS (SAS Institute Inc., Cary, NC). The model used was based on the model used by Gilbert et al. (2010) which included the sow's metabolic body weight and the differences in sow body weight, sow backfat depth, and litter weight, across all line, generation, and parity combinations. Using regression coefficients estimated from our data, the equation for sow residual feed intake was:

$$\text{Sow RFI (kg)} = \text{Sow feed intake} - (84.5025 + 0.1776 \times \text{Sow metabolic mid-weight} + 4.7602 \times \text{Litter growth} - 2.1796 \times \text{Sow weight loss} - 3.5643 \times \text{Sow backfat loss})$$

Energy balance was defined as the difference between energy retained by the sow at weaning and energy retained by the sow at farrowing which were estimated using protein mass and fat mass at weaning and farrowing. The energy contents of protein and fat were set as 23.8 MJ ME/kg protein and 39.5 MJ ME/kg fat (Bergsma et al., 2009).

$$\text{Energy retained by the sow at farrowing (MJ ME)} = \text{Sow protein mass at farrowing} \times 23.8 + \text{Sow fat mass at farrowing} \times 39.5$$

$$\text{Energy retained by the sow at weaning (MJ ME)} = \text{Sow protein mass at weaning} \times 23.8 + \text{Sow fat mass at weaning} \times 39.5$$

$$\text{Energy balance (MJ ME / d)} = (\text{Energy retained by the sow at weaning} - \text{Energy retained by the sow at farrowing}) / \text{Lactation length}$$

Statistical analyses

Numbers of records available for analyses are in Table 4.1. To estimate line differences, data were analyzed using the mixed procedure of SAS. Fixed effects included in the model were line, line by generation interaction, and generation by parity interaction, where generation refers to the generation to which the piglets belong. The random effect of

sow was included for all traits to account for repeated measures on each sow. The random effect of birth litter was originally fitted for piglet traits but was small and caused problems with model convergence in SAS and, therefore, was removed from the model. Covariates depended on the trait being analyzed (Table 4.2). Heritabilities and correlations of sow traits with residual feed intake were estimated using a two trait animal model fitting a sow trait and $RFI_{G/F}$ in AS-REML (Gilmour et al., 1995), both across and within lines. The random effect of animal (=sow for piglet and sow traits and pig for $RFI_{G/F}$) was fitted as a genetic effect. The pedigree included 14,169 individuals from generation -1 through generation 8, plus the parents of generation -1. Sow was fitted as a permanent environmental effect but was removed due to it being small and not significant and causing problems with convergence in AS-REML. Fixed effects and covariates for sow traits were the same as for line differences. Fixed effects for $RFI_{G/F}$ in the two trait model were group, sex, and the concatenation of group and pen (see Cai et al., 2008 for details on model for $RFI_{G/F}$). The three-way interaction of generation, line, and on-age deviation was fitted as a covariate for $RFI_{G/F}$.

Results and Discussion

Line differences

After 7 generations, selection for $RFI_{G/F}$ impacted sow reproductive performance and lactation efficiency (Tables 4.3 and 4.4). The LRFI line had 1.7 more piglets farrowed per litter ($P < 0.01$) but only 1.2 more piglets born alive ($P < 0.05$). This was due to the LRFI line having 0.4 more piglets dead at birth per litter ($P < 0.05$). There was no difference in number of mummies between the two lines ($P = 0.76$). The LRFI line weaned more piglets both by sow (8.8 vs. 8.2, $P < 0.05$) and by litter (9.0 vs. 7.5, $P < 0.01$). Differences in number weaned by sow and by litter are due to cross-fostering across lines and a slightly higher pre-

weaning survival in the LRFI line (83.3 % vs 80.9 %, $P = 0.31$). The LRFI line had greater average birth weight than the HRFI line (1.27 vs. 1.20 kg, $P < 0.01$). Although not significantly different ($P = 0.25$), the LRFI line had a greater total birth weight (13.7 vs. 13.3 kg). Although the LRFI line still had heavier piglets when considering only piglets born alive, these differences were not significant on either an average ($P = 0.12$) or entire litter basis ($P = 0.55$). Litters nursed by LRFI sows were heavier at weaning (55.2 vs. 51.9 kg, $P < 0.1$) and grew faster during the lactation period (1824 vs. 1670 g/d, $P < 0.05$). LRFI litters were heavier at weaning than HRFI litters (53.9 vs. 50.8 kg, $P < 0.1$). However, this increased performance in terms of piglets was at a cost to the sow. The LRFI sows were 10.8 kg lighter ($P < 0.05$) at farrowing with 5.8 kg less fat mass ($P < 0.01$) than HRFI sows but 0.9 kg greater protein mass ($P < 0.01$). Sows from the LRFI line lost more weight during lactation (11.0 vs. 2.5 kg, $P < 0.01$), which was due to a greater fat mass depletion (6.9 vs. 1.6 kg, $P < 0.01$) because there was no difference in protein mass depletion (0.34 vs. -0.41 kg, $P = 0.11$). As a result, LRFI sows had lower estimated maintenance costs than HRFI sows (29.9 vs. 26.7 MJ ME/d, $P < 0.1$). Sows from the LRFI line consumed 14.9 kg less feed ($P < 0.01$) and had a greater negative energy balance (-18.2 vs. -10.1 MJ ME/d, $P < 0.01$) than sows from the HRFI line. Energy output was higher in the LRFI line than in the HRFI line (29.4 vs. 27.1 MJ ME/d, $P < 0.05$) while energy input was lower (55.2 vs. 63.4 MJ ME/d, $P < 0.05$). This resulted in the LRFI line having higher lactation efficiency (45.9 vs. 41.0 %, $P = 0.83$) than the HRFI line although it was not significantly different. Sow residual feed intake was lower in the LRFI line than in the HRFI line (1.44 vs. 15.90 kg, $P < 0.01$).

A concurrent study in France has also evaluated the effects of selection for $RFI_{G/F}$ on sow reproduction (Dekkers and Gilbert, 2010; Gilbert et al., 2010, 2011). Similar to our

study, number born alive, litter weight gain, sow weight loss during lactation, and sow backfat loss during lactation were found to be greater in their LRFI line compared to the HRFI line (Dekkers and Gilbert, 2010; Gilbert et al., 2010, 2011). Sow weight at farrowing, backfat depth at farrowing, sow feed intake, and sow residual feed intake were all found to be lower in the LRFI line compared to the HRFI line in both studies (Dekkers and Gilbert, 2010; Gilbert et al., 2010, 2011). While the French study found no difference in total born, we found that total born was greater in the LRFI line than in the HRFI line (Dekkers and Gilbert, 2010; Gilbert et al., 2010, 2011). Also contradictory to our study where we found that litter birth weight tended to be greater in the LRFI line and average birth weight was greater in the LRFI line, the French study found no difference in litter birth weight between lines (Dekkers and Gilbert, 2010; Gilbert et al., 2010; Gilbert et al., 2011).

Through selection for $RFI_{G/F}$, we have selected for leaner pigs (Cai et al., 2008; Smith et al., 2011) and results of this study show that this has resulted in sows which have less fat mass and greater protein mass than HRFI sows ($P < 0.01$). Several studies have selected for lean growth and evaluated the effects on reproduction. Correlated responses to selection for lean growth have varied and depend on the method of selection for lean growth as shown by studies that evaluated different methods of selection for lean growth (Kersey DeNise et al., 1983; Kerr and Cameron, 1996; Cameron et al., 2002). Response to selection for lean growth resulted in greater (Vangen, 1980), equal (Kerr and Cameron, 1996), or fewer (Kersey DeNise et al., 1983; Cleveland et al., 1988) piglets born. Our results of greater number of piglets farrowed agree with results by Vangen (1980) who found that number born alive also increased with selection for lean growth which is what we found when selecting for leanness by selecting for decreased $RFI_{G/F}$. However, Kersey DeNise et al. (1983) and Cleveland et al.

(1988) found that the number born alive decreased with selection for lean growth. Similar to our results, response in litter birth weight to selection for lean growth was either positive (Vangen, 1980; Cleveland et al., 1988; Kerr and Cameron, 1996) or positive but not significantly different (Kerr and Cameron, 1996; Cameron et al., 2002). Unlike our study, number weaned was lower (Kersey DeNise et al., 1983; Cleveland et al., 1988) or equal (Kerr and Cameron, 1996) in lines selected for lean growth than in control lines. Results for weaning weight varied from greater (Cleveland et al., 1988) to equal (Kerr and Cameron, 1996) to smaller (Kerr and Cameron, 1996) for lines selected for lean growth. Sow weight at farrowing was either equal or greater in lines selected for components of lean growth (Kerr and Cameron, 1996; Cameron et al., 2002) which is opposite to what we found in our study. However, like our study, sow backfat depth at farrowing was less in lines selected for components of lean growth than in control lines (Kerr and Cameron, 1996; Cameron et al., 2002). Unlike our study, weight loss and backfat loss tended to be equal between lines selected for lean growth and control lines (McKay, 1992; Kerr and Cameron, 1996; Cameron et al., 2002). Sow feed intake was less in lines selected for daily feed intake and lean food conversion but greater in lines selected for lean growth rate (Kerr and Cameron, 1996; Cameron et al., 2002). As a result, energy balance was more negative in the lines selected for daily feed intake and lean food conversion whereas the lines selected for lean growth rate had similar energy balances (Cameron et al., 2002). These results show that response to selection for lean growth will depend on which method is used. Results may also be population dependent.

Heritabilities

Heritabilities of piglet traits varied greatly, from 0.07 for average weaning weight by litter across lines to 0.51 for litter birth weight in the LRFI line (Table 4.5). Heritabilities were similar across and within lines, with the exception of weaning weight by sow and average weaning weight by sow for which heritabilities were about twice as large in the HRFI line (0.21 for both traits) than in the LRFI line (0.10 and 0.11, respectively) or across lines (0.08 for both traits). Traits pertaining to birth weight tended to be highly heritable, ranging from 0.38 for total live piglet birth weight in the HRFI line to 0.51 for litter birth weight in the LRFI line. Traits pertaining to number of piglets tended to be lowly heritable, ranging from 0.08 for number of piglets dead at birth across lines to 0.26 for total born in the HRFI line, with heritability for most traits being around 0.18. Number of mummies was not significantly heritable. Although piglet growth and litter growth were not significantly heritable across and within the LRFI line, other traits pertaining to growth of piglets during lactation were moderately heritable, ranging from 0.17 for piglet and litter growth in the HRFI line to 0.31 for piglet energy gain in the HRFI line. Heritabilities of sow traits also varied greatly, from 0.09 for lactation efficiency across lines to 0.75 for sow maintenance in the LRFI line (Table 4.5). Traits pertaining to sow weight and body composition at farrowing and at weaning were highly heritable, ranging from 0.41 for sow backfat depth at farrowing in the LRFI line to 0.73 for sow weight at weaning in the LRFI line. Sow weight loss, fat mass loss, and protein loss were moderately to highly heritable, ranging from 0.22 for fat mass loss in the HRFI line to 0.40 for sow weight loss in the LRFI line. Sow maintenance was highly heritable (0.70 in the HRFI line, 0.71 across lines, and 0.75 in the LRFI line) while sow feed intake was only moderately heritable (0.23 in the LRFI line, 0.25 across lines,

and 0.28 in the HRFI line). With the exception of energy input, traits pertaining to different measures of efficiency during lactation were lowly heritable, ranging from 0.09 for lactation efficiency across lines to 0.18 for sow residual feed intake in the HRFI line.

Heritabilities of total number born across and within lines (Table 4.5) were higher than the estimate by Bergsma et al. (2008) of 0.13. Previous reports of heritabilities for number born alive range from 0.08 to 0.16 (Tholen et al., 1996; Chen et al., 2003; Ehlers et al., 2005; Holm et al., 2005; Bunter et al., 2007) which is lower than our range of 0.18 to 0.20. Our heritabilities for litter birth weight of 0.42 to 0.51 are much higher than those previously reported by Ehlers et al. (2005) which ranged from 0.162 to 0.195. Our heritabilities for average litter birth weight were also much higher than previous reports of heritabilities by Tholen et al. (1996) which were 0.30 and 0.28 in their herd 1 and 0.15 and 0.11 in their herd 2 for first and second parity sows, respectively, and the estimate of 0.30 reported by Bunter et al. (2007). Previous reports of the heritability of number weaned by sow ranged from 0.02 to 0.09 (Chen et al., 2003; Serenius and Stalder, 2004; Serenius et al., 2008) which is lower than the heritability found across lines and in the LRFI line in our population. Although not significantly different from zero, the heritability of 0.04 for number weaned by sow in the HRFI line falls within the range of heritabilities previously reported. Our heritabilities for pre-weaning survival were much higher than the heritability of 0.04 reported by Bergsma et al. (2008). Our estimates of heritability of weaning weight by sow across lines and in the LRFI line fall within the previously reported range of 0.07 to 0.17 (Tholen et al., 1996; Chen et al., 2003), although the estimate in the HRFI line is slightly higher than the heritability of 0.17 for first parity sows found by Tholen et al. (1996). Heritability of litter growth in the HRFI line (0.17) was similar to the 0.19 reported by

Bergsma et al. (2008) and 0.16 by Bergsma (2011), although heritability of litter growth was not significantly different across lines and within the LRFI line. Heritability of sow weight at farrowing was higher in our population (0.62 to 0.66) than the 0.50 reported by Bergsma (2011). However, heritability of sow fat mass at farrowing was similar between our population (0.42 to 0.46) and the population (0.42) evaluated by Bergsma (2011). Heritability of sow weight loss was higher in our population (0.37 to 0.40) than the 0.14 reported by Bergsma (2011). However, heritability of sow feed intake was similar between our population (0.23 to 0.28) and the population evaluated by Bergsma (2011) (0.23) and estimates from both studies are greater than the 0.11 reported by Bunter et al. (2007). Heritabilities for lactation efficiency reported by Bergsma et al. (2008) of 0.12 and by Bergsma (2011) of 0.10 fall within our range of heritabilities for lactation efficiency of 0.09 to 0.15. Thus, with the exception of litter growth and lactation efficiency, heritabilities in our population appear to be greater than in previously reported studies.

Correlations with grow/finish RFI

Phenotypic correlations of reproduction traits with $RFI_{G/F}$ are not reported because they are based only on 14 sows from generation -1 which were the only sows which also had feed intake recorded during the grow/finish phase. Due to large standard errors, few genetic correlations with $RFI_{G/F}$ were significantly different from zero (Table 4.6). Although not significantly different from zero, estimates of the genetic correlation of litter growth with $RFI_{G/F}$ were -0.16 across lines and -0.14 in the HRFI line, which are in the opposite direction to the 0.18 reported by Bergsma (2011) but in the same direction as the difference in litter growth found between lines. These estimates suggest that animals with lower $RFI_{G/F}$ would have greater litter growth. Sow weight at farrowing was found to have a high genetic

correlation with $RFI_{G/F}$ (0.51 across lines and 0.55 within the LRFI line), although Bergsma (2011) found a very small, negative genetic correlation of -0.06 between sow weight at farrowing and $RFI_{G/F}$. However, the correlations found in our study support the differences found between lines where sows from the HRFI line had greater body weights at farrowing than sows from the LRFI line. Although Bergsma (2011) found a strong negative genetic correlation of -0.35 between sow fat mass at farrowing and $RFI_{G/F}$, we found no significant genetic correlation between these traits (0.04 ± 0.18). The correlation found by Bergsma (2011) is in the opposite direction as expected based on sows from the HRFI line having greater fat mass at farrowing than sows from the LRFI line. Bergsma (2011) found a genetic correlation of 0.32 between sow weight loss and $RFI_{G/F}$ which is opposite to the -0.40 found in the LRFI line in our study. Although not significantly different from zero, the genetic correlation between sow weight loss and $RFI_{G/F}$ was -0.19 across lines, which is in the same direction as the correlation estimated in the LRFI line and in the opposite direction as estimated by Bergsma et al. (2011). The correlation between sow weight loss and $RFI_{G/F}$ in the HRFI line was estimated at 0. Based on line differences where sows from the LRFI line lost more weight than sows from the HRFI line, one would expect the genetic correlation between sow weight loss and $RFI_{G/F}$ to be negative, which is what we found in our study. Although not significantly different from zero, genetic correlations of sow feed intake with $RFI_{G/F}$ in our study (0.18 across lines, 0.23 within both the LRFI and HRFI lines) are similar to the 0.18 estimated by Bergsma (2011) and agree with the difference in sow feed intake between lines where sows from the HRFI line consumed more feed during lactation than sows from the LRFI line. Lactation efficiency and $RFI_{G/F}$ were found to have a genetic correlation of -0.55 across lines in our study which is similar to the -0.51 found by Bergsma

(2011); however, the correlation in the HRFI line was much stronger (-0.97) than either the correlation across lines or the one estimated by Bergsma (2011). The genetic correlation between lactation efficiency and $RFI_{G/F}$ within the LRFI line was estimated at -0.30 which is slightly lower than that estimated across lines or by Bergsma (2011). Correlations found in our study and by Bergsma (2011) support our findings that sows from the LRFI line had a higher lactation efficiency than sows from the HRFI line. Sow residual feed intake was moderately to highly correlated with $RFI_{G/F}$ across lines (0.43 ± 0.20) and within lines (LRFI = 0.30 ± 0.22 ; HRFI = 0.64 ± 0.31). This is in a favorable direction as it indicates that sows with favorable $RFI_{G/F}$ would also have a favorable residual feed intake during lactation. The positive correlation is supported by line differences where the LRFI sows have a lower residual feed intake during lactation than the HRFI sows. However, energy balance was found to have a negative correlation with $RFI_{G/F}$ across lines (-0.25 ± 0.22) and within the LRFI line (-0.41 ± 0.25). This is also in a favorable direction being that pigs with a favorable $RFI_{G/F}$ would have a more positive energy balance. However, this correlation does not support what we found for differences between lines where the LRFI sows had a greater negative energy balance than the HRFI sows.

Conclusions and Implications

Results from this study show that selection for decreased $RFI_{G/F}$ has had no detrimental effect on sow reproductive performance and, in fact, has resulted in increased litter size and pre-weaning growth. The higher piglet performance is made possible by a greater loss of body condition for sows from the LRFI line. The greater loss of body condition for sows from the LRFI line was accounted for in part by their decreased feed intake during lactation. As a result of having increased pre-weaning growth of piglets and

decreased feed intake, sows from the LRFI line were more efficient at converting energy from feed intake and body tissue mobilization into piglet growth. The greater loss of body condition for sows from the LRFI line may have an impact on rebreeding if rebreeding was performed at first estrus post-weaning. The greater loss of body condition may also result in a greater wean to first estrus interval.

The efficiency of sows transforming feed into piglet gain is heritable, whether it is measured as lactation efficiency or sow residual feed intake. Heritability estimates were consistent across and within lines and with literature. Therefore, it would be possible to select sows which are more efficient. Efficiency during lactation appears to coincide with efficiency during the grow/finish phase. All correlations are in the favorable direction and fit with what has previously been reported. A second sign that grow/finish efficiency and sow efficiency coincide is that the LRFI line shows better efficiency regardless of how it is measured. This is particularly true in sow RFI where there is a 14.5 kg difference in residual intake when sows are only consuming ~130 kg feed during lactation. This amounts to a difference in residual feed intake of ~11% of total feed intake. With the industry moving towards more total efficiency, it is desirable that grow/finish efficiency and sow efficiency coincide which the results of this study support. Sows from the LRFI line consumed less feed and produced more (in terms of piglet growth) than sows from the HRFI line, but lost more body reserves. Therefore, when selecting for pigs that are more feed efficient during the grow/finish period, sow feed intake and body condition change during lactation must be taken into consideration.

Note from authors

Measures of longevity and rebreeding were not evaluated in this study due to the manner in which sows are bred and kept. All sows were culled after two parities; therefore, longevity cannot be evaluated. Sows were not bred at first estrus post-weaning, but to fit the farrowing and finishing schedule of the research farm. Also only sows that had offspring selected to go onto the FIRE feeders for parity 1 were rebred to produce parity 2; therefore, some sows were culled after only 1 parity.

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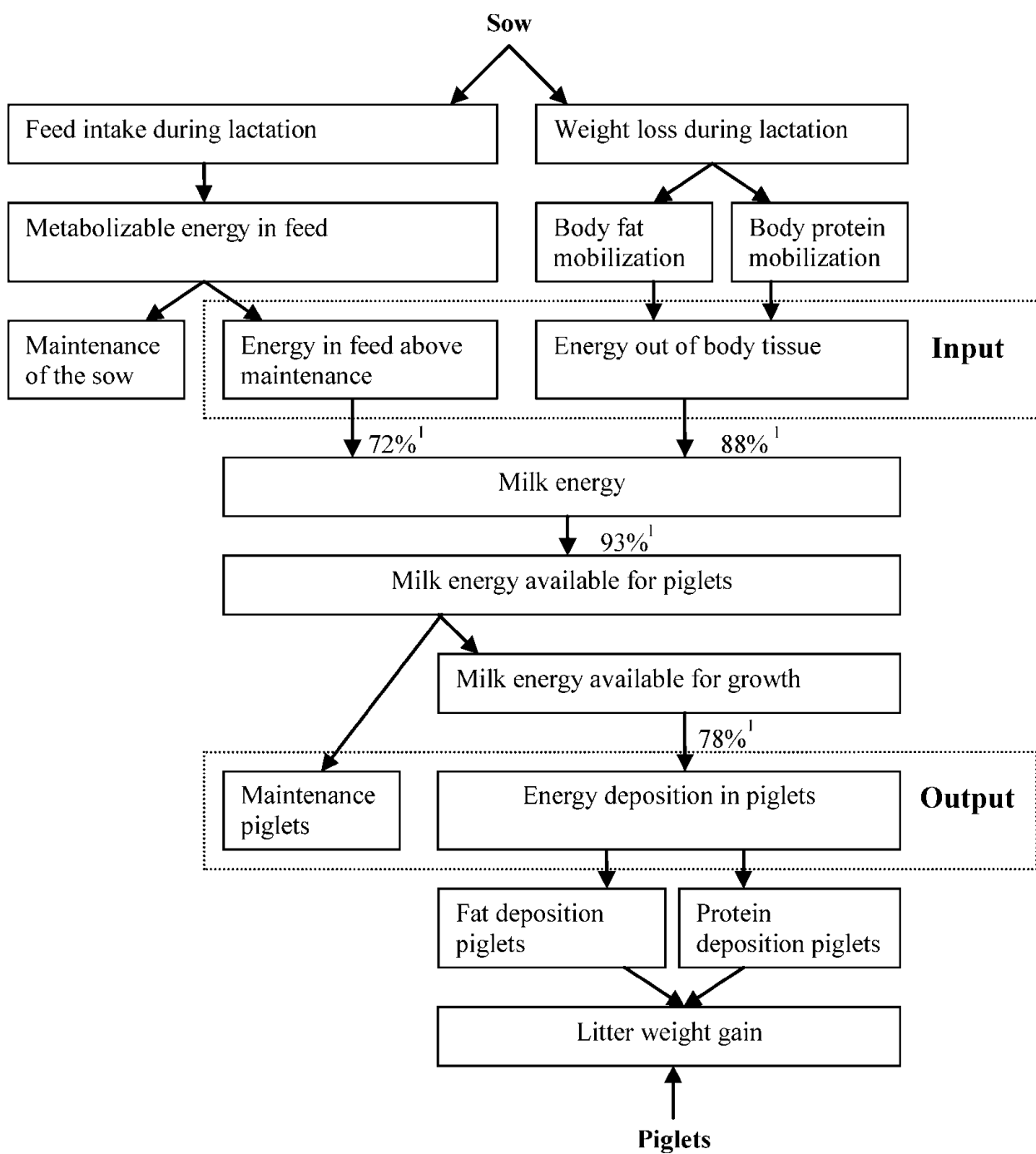


Figure 4.1. Schematic flow chart of the energy metabolism of sows during lactation (Bergsma et al., 2008, 2009).

Table 4.1: Number of animals available for analyses.

Generation	Line	Number of sows with data from ¹			Grow/finish
		Parity 1	Parity 1 & 2	Parity 2	RFI
-1		22 ³ (20 ³)	52 ⁴ (52 ⁴)	.	193 ⁵
0	LRFI	17 (14)	35 (35)	.	153
	HRFI	24 (22)	.	.	. ⁶
1	LRFI	9 (6)	36 (36)	1 (1)	139
	HRFI	17 (17)	.	.	. ⁶
2	LRFI	26 (25)	23 (23)	8 (4)	154
	HRFI	9 (7)	12 (11)	5 (5)	. ⁶
3	LRFI	16 (15)	33 (30)	.	51
	HRFI	11 (9)	17 (14)	.	. ⁶
4	LRFI	22 (17)	37 (31)	.	27
	HRFI	12 (8)	34 (22)	.	. ⁶
5	LRFI	16 (9)	41 (38)	.	64
	HRFI	24 (21)	33 (29)	.	87
6	LRFI	9 (0)	41 (1)	4 (4)	87
	HRFI	13 (2)	37 (2)	.	79
7	LRFI	.	.	.	81
	HRFI	.	.	.	85

¹ Sow counts are given as two numbers *a* (*b*) where *a* is the number of sows with reproductive data and *b* is the number of sows that have all the information necessary to calculate lactation efficiency. Also, breeding animals come from parity 1 sows; therefore, most sows do not have grow/finish RFI data since boars are on the FIRE feeders.

² Number of pigs from each generation and line with grow/finish RFI.

³ Includes 4 sows with grow/finish RFI data.

⁴ Includes 10 sows with grow/finish RFI data.

⁵ Includes 14 sows with grow/finish RFI data.

⁶ In earlier generations, only LRFI animals evaluated for RFI.

Table 4.2: Covariates used for data analysis.

Traits ¹	TB	NBA	LL	NWBL	NWBS	SFWT	SWWT	SFFM	SFPM	SFBF	IN
Litter birth weight	X										
Average litter birth weight	X										
Total live piglet birth weight		X									
Average live piglet birth weight		X									
Weaning weight by litter			X	X							
Average weaning weight by litter			X	X							
Weaning weight by sow			X		X						
Average weaning weight by sow			X		X						
Piglet average daily gain			X								
Piglet growth			X								
Piglet energy gain			X								
Litter average daily gain			X		X						
Litter growth			X		X						
Litter energy gain			X		X						
Sow fat mass at farrowing						X					
Sow protein mass at farrowing						X					
Sow weight at weaning			X				X				
Sow fat mass at weaning			X				X				
Sow protein mass at weaning			X								
Sow backfat depth at weaning			X								
Sow weight loss			X			X					
Sow fat mass loss			X					X			
Sow protein mass loss			X						X		
Sow backfat loss			X							X	
Sow feed intake			X								
Energy output			X								X
Energy input			X								
Energy balance			X								

¹ Traits down the side are the traits being analyzed, traits across the top are used as covariates. Abbreviations are TB = total born, NBA = number born alive, LL = lactation length, NWBL = number weaned by litter, NWBS = number weaned by sow, SFWT = sow weight at farrowing, SWWT = sow weight at weaning, SFFM = sow fat mass at farrowing, SFPM = sow protein mass at farrowing, SFBF = sow backfat depth at farrowing, IN = energy input.

Table 4.3: Line differences in piglet traits after 7 generations of selection for residual feed intake.

Trait	Least square means		
	LRFI	HRFI	P-value
Total born (n)	12.1	10.4	<0.01
Number born alive (n)	10.9	9.7	<0.05
Number of piglets dead at birth (n)	1.2	0.8	<0.05
Number of mummies (n)	0.24	0.21	0.76
Farrowing survival (%)	89.2	91.5	0.24
Litter birth weight (kg)	13.7	13.3	0.25
Average litter birth weight (kg)	1.27	1.20	<0.05
Total live piglet birth weight (kg)	12.8	12.6	0.55
Average live piglet birth weight (kg)	1.27	1.22	0.12
Number weaned by litter (n)	9.0	7.5	<0.01
Number weaned by sow (n)	8.8	8.2	<0.05
Pre-weaning survival by sow (%)	83.3	80.9	0.31
Weaning weight by litter (kg)	53.9	50.8	<0.1
Average weaning weight by litter (kg)	6.1	5.9	0.37
Weaning weight by sow (kg)	55.2	51.9	<0.1
Average weaning weight by sow (kg)	6.1	5.8	0.19
Piglet average daily gain (g/d)	192.1	183.3	0.14
Piglet growth (kg)	4.63	4.45	0.36
Piglet energy gain (MJ ME)	3.16	3.02	0.10
Litter average daily gain (g/d)	1824	1679	<0.05
Litter growth (kg)	44.2	40.6	<0.1
Litter energy gain (MJ ME)	30.1	27.7	<0.05

Table 4.4: Line differences in sow traits after 7 generations of selection for residual feed intake.

Traits	Least square means		
	LRFI	HRFI	P-value
Sow weight at farrowing (kg)	197.0	207.8	<0.05
Sow fat mass at farrowing (kg)	45.7	51.5	<0.01
Sow protein mass at farrowing (kg)	28.4	27.5	<0.01
Sow backfat depth at farrowing (mm)	20.5	24.9	<0.01
Sow weight at weaning (kg)	195.4	203.8	<0.1
Sow fat mass at weaning (kg)	40.2	46.8	<0.01
Sow protein mass at weaning (kg)	27.3	26.2	<0.01
Sow backfat depth at weaning (mm)	19.0	23.4	<0.01
Sow weight loss (kg)	11.0	2.5	<0.01
Sow fat mass loss (kg)	6.9	1.6	<0.01
Sow protein mass loss (kg)	0.34	-0.41	0.11
Sow backfat loss (mm)	3.02	0.78	<0.01
Sow maintenance (MJ/d)	23.2	24.0	<0.1
Sow feed intake (kg)	120.4	135.3	<0.01
Energy output (MJ ME /d)	29.4	27.1	<0.05
Energy input (MJ ME/d)	55.2	63.4	<0.05
Lactation efficiency (%)	45.9	41.0	0.83
Sow residual feed intake (kg)	1.44	15.90	<0.05
Energy balance (MJ ME/d)	-18.2	-10.1	<0.01

Table 4.5: Heritabilities¹ of piglet and sow traits.

Traits	Across lines	Within lines	
		LRFI	HRFI
Total born	0.21 ± 0.04	0.22 ± 0.05	0.26 ± 0.06
Number born alive	0.18 ± 0.04	0.19 ± 0.05	0.20 ± 0.06
Number of piglets dead at birth	0.08 ± 0.04	0.10 ± 0.05	0.18 ± 0.07
Number of mummies	0.02 ± 0.03	0.03 ± 0.04	²
Farrowing survival	0.08 ± 0.04	0.16 ± 0.05	²
Litter birth weight	0.45 ± 0.04	0.51 ± 0.05	0.42 ± 0.06
Average litter birth weight	0.46 ± 0.04	0.50 ± 0.05	0.42 ± 0.06
Total live piglet birth weight	0.40 ± 0.04	0.44 ± 0.05	0.38 ± 0.06
Average live piglet birth weight	0.42 ± 0.04	0.46 ± 0.05	0.39 ± 0.06
Number weaned by litter	0.14 ± 0.04	0.18 ± 0.05	0.15 ± 0.06
Number weaned by sow	0.12 ± 0.04	0.17 ± 0.05	0.04 ± 0.05
Pre-weaning survival by sow	0.18 ± 0.04	0.18 ± 0.06	0.15 ± 0.06
Weaning weight by litter	0.04 ± 0.03	0.06 ± 0.04	0.09 ± 0.06
Average weaning weight by litter	0.07 ± 0.03	0.10 ± 0.05	0.11 ± 0.06
Weaning weight by sow	0.08 ± 0.04	0.10 ± 0.05	0.21 ± 0.06
Average weaning weight by sow	0.08 ± 0.04	0.11 ± 0.05	0.21 ± 0.06
Piglet average daily gain	0.22 ± 0.04	0.21 ± 0.06	0.30 ± 0.06
Piglet growth	0.06 ± 0.03	0.07 ± 0.04	0.17 ± 0.06
Piglet energy gain	0.21 ± 0.04	0.20 ± 0.05	0.31 ± 0.06
Litter average daily gain	0.21 ± 0.04	0.22 ± 0.05	0.26 ± 0.06
Litter growth	0.06 ± 0.03	0.07 ± 0.04	0.17 ± 0.06
Litter energy gain	0.20 ± 0.04	0.21 ± 0.05	0.27 ± 0.06
Sow weight at farrowing	0.62 ± 0.03	0.66 ± 0.04	0.66 ± 0.05
Sow fat mass at farrowing	0.44 ± 0.05	0.46 ± 0.06	0.42 ± 0.07
Sow protein mass at farrowing	0.44 ± 0.05	0.46 ± 0.06	0.42 ± 0.07
Sow backfat depth at farrowing	0.43 ± 0.05	0.41 ± 0.06	0.47 ± 0.06
Sow weight at weaning	0.69 ± 0.03	0.73 ± 0.03	0.68 ± 0.04
Sow fat mass at weaning	0.47 ± 0.05	0.44 ± 0.06	0.46 ± 0.07
Sow protein mass at weaning	0.47 ± 0.05	0.44 ± 0.06	0.46 ± 0.07
Sow backfat depth at weaning	0.50 ± 0.04	0.46 ± 0.06	0.44 ± 0.07
Sow weight loss	0.37 ± 0.05	0.40 ± 0.06	0.38 ± 0.07
Sow fat mass loss	0.23 ± 0.06	0.28 ± 0.07	0.22 ± 0.08
Sow protein mass loss	0.36 ± 0.05	0.36 ± 0.06	0.43 ± 0.07
Sow backfat loss	0.17 ± 0.05	0.22 ± 0.06	0.18 ± 0.08
Sow maintenance	0.71 ± 0.03	0.75 ± 0.03	0.70 ± 0.04
Sow feed intake	0.25 ± 0.04	0.23 ± 0.06	0.28 ± 0.06
Energy output	0.13 ± 0.04	0.16 ± 0.05	0.09 ± 0.06
Energy input	0.23 ± 0.06	0.20 ± 0.06	0.32 ± 0.08
Lactation efficiency	0.09 ± 0.04	0.14 ± 0.06	0.15 ± 0.07
Sow residual feed intake	0.16 ± 0.05	0.17 ± 0.06	0.18 ± 0.07
Energy balance	0.12 ± 0.05	0.11 ± 0.06	0.23 ± 0.08

¹ Heritabilities in bold are significantly different from zero.² Analyses did not converge in AS-REML as a two-trait analysis with RFI; heritabilities were non-estimable when run as a single trait analysis.

Table 4.6: Genetic correlations of piglet and sow traits with $RFI_{G/F}$.

Traits	Across lines	Within lines	
		LRFI	HRFI
Total born	0.20 ± 0.17	0.47 ± 0.18	-0.37 ± 0.25
Number born alive	0.14 ± 0.18	0.44 ± 0.19	-0.40 ± 0.26
Number of piglets dead at birth	0.29 ± 0.24	0.27 ± 0.26	-0.06 ± 0.34
Number of mummies	0.53 ± 0.53	0.52 ± 0.49	¹
Farrowing survival	-0.29 ± 0.25	-0.15 ± 0.22	¹
Litter birth weight	0.16 ± 0.13	0.10 ± 0.15	0.38 ± 0.23
Average litter birth weight	0.18 ± 0.13	0.14 ± 0.15	0.43 ± 0.23
Total live piglet birth weight	0.16 ± 0.14	0.09 ± 0.15	0.40 ± 0.23
Average live piglet birth weight	0.14 ± 0.14	0.09 ± 0.15	0.43 ± 0.28
Number weaned by litter	0.16 ± 0.19	0.42 ± 0.19	-0.41 ± 0.32
Number weaned by sow	0.10 ± 0.21	-0.19 ± 0.21	0.99 ± 0.69
Pre-weaning survival by sow	0.06 ± 0.19	-0.28 ± 0.20	0.67 ± 0.31
Weaning weight by litter	-0.07 ± 0.33	0.12 ± 0.29	-0.22 ± 0.40
Average weaning weight by litter	-0.00 ± 0.25	0.14 ± 0.25	-0.27 ± 0.39
Weaning weight by sow	-0.06 ± 0.23	0.12 ± 0.31	0.03 ± 0.30
Average weaning weight by sow	-0.10 ± 0.24	0.06 ± 0.25	-0.14 ± 0.31
Piglet average daily gain	-0.13 ± 0.17	-0.01 ± 0.20	-0.54 ± 0.24
Piglet growth	-0.15 ± 0.27	0.09 ± 0.29	-0.44 ± 0.32
Piglet energy gain	-0.10 ± 0.17	0.01 ± 0.20	-0.45 ± 0.25
Litter average daily gain	-0.15 ± 0.17	-0.06 ± 0.19	-0.39 ± 0.27
Litter growth	-0.16 ± 0.27	0.04 ± 0.28	-0.14 ± 0.32
Litter energy gain	-0.12 ± 0.17	-0.03 ± 0.19	-0.30 ± 0.28
Sow weight at farrowing	0.51 ± 0.11	0.55 ± 0.12	0.26 ± 0.23
Sow fat mass at farrowing	0.01 ± 0.14	-0.04 ± 0.15	0.08 ± 0.26
Sow protein mass at farrowing	-0.01 ± 0.14	0.04 ± 0.15	-0.08 ± 0.26
Sow backfat depth at farrowing	0.29 ± 0.14	0.40 ± 0.15	0.04 ± 0.24
Sow weight at weaning	0.41 ± 0.11	0.47 ± 0.12	0.28 ± 0.21
Sow fat mass at weaning	-0.07 ± 0.14	-0.16 ± 0.15	0.02 ± 0.24
Sow protein mass at weaning	0.07 ± 0.14	0.16 ± 0.15	-0.02 ± 0.24
Sow backfat depth at weaning	0.20 ± 0.13	0.25 ± 0.15	0.09 ± 0.24
Sow weight loss	-0.19 ± 0.15	-0.40 ± 0.16	0.00 ± 0.25
Sow fat mass loss	-0.05 ± 0.18	-0.08 ± 0.19	0.13 ± 0.38
Sow protein mass loss	-0.35 ± 0.15	-0.59 ± 0.15	-0.13 ± 0.25
Sow backfat loss	0.01 ± 0.19	-0.04 ± 0.20	0.43 ± 0.39
Sow maintenance	0.49 ± 0.11	0.52 ± 0.12	0.33 ± 0.22
Sow feed intake	0.18 ± 0.16	0.23 ± 0.19	0.23 ± 0.25
Energy output	-0.05 ± 0.20	0.02 ± 0.21	-0.18 ± 0.41
Energy input	0.38 ± 0.17	0.35 ± 0.20	0.40 ± 0.28
Lactation efficiency	-0.55 ± 0.25	-0.30 ± 0.24	-0.97 ± 0.35
Sow residual feed intake	0.43 ± 0.20	0.30 ± 0.22	0.64 ± 0.31
Energy balance	-0.25 ± 0.22	-0.41 ± 0.25	0.01 ± 0.37

¹ Analyses did not converge in AS-REML.

CHAPTER 5: GENERAL CONCLUSIONS

General Summary

As shown in Chapter 2, selection for decreased residual feed intake during the grow/finish phase of production ($RFI_{G/F}$) has affected feeding behavior. Selection for decreased $RFI_{G/F}$ resulted in pigs that consume significantly less feed per day than those randomly selected. With adjustment for feed intake per day, feed intake per visit and per hour and number of visits per day and per hour did not differ significantly between the two lines but the trend was for pigs selected for decreased $RFI_{G/F}$ to have fewer visits, particularly during peak eating times. Pigs with low $RFI_{G/F}$ had a higher feed intake rate which resulted in a lower occupation time per day, per visit, and per hour than high $RFI_{G/F}$ pigs even after adjustment for feed intake per day. The decrease in occupation time per day resulted from a decrease in occupation time per hour over the course of the whole day rather than a decrease just during peak eating times like number of visits per day.

In Chapter 3, it was shown that heritabilities of feeding behavior traits were high, ranging from 0.36 for feed intake per visit to 0.71 for occupation time per day. Feed intake rate was highly heritable at 0.59. Heritabilities of number of visits per day, occupation time per visit, and feed intake per day were similar (0.44, 0.42, and 0.42, respectively). Number of visits per day, feed intake per visit, and occupation time per visit were strongly correlated with one another, both phenotypically and genetically, as expected. One would expect that pigs that visit the feeder fewer times per day would spend more time and consume more feed during each visit to the feeder than pigs that eat more frequently throughout the day and the correlations between those three traits support that expectation. Occupation time per day and feed intake rate were also strongly and positively correlated, both phenotypically and

genetically. This was expected as pigs that eat faster are expected to spend less time eating when consuming the same amount of feed. Other correlations between feeding behavior traits were low. Feed intake per day was highly correlated with the performance traits of $RFI_{G/F}$, average daily gain (ADG), and backfat depth (BF). This is as expected because animals that consume more feed have more energy to put towards growth and fat deposition than animals that consume less feed. Feed intake per visit was moderately correlated with ADG and BF but not with $RFI_{G/F}$. Occupation time per day was moderately correlated with $RFI_{G/F}$ and ADG but not BF. Other correlations between feeding behavior traits and performance traits were low.

SNPs located adjacent to MC4R, a gene already shown to be associated with feed intake, fatness, and growth (Kim et al., 2000), were significant for feed intake per day. Other genes that were located in regions associated with feeding behavior traits included several related to retinoic acid and several pertaining to transcription or nuclear regulators. ZNF423, which has been shown to be important for retinoic acid-induced differentiation (Huang et al., 2009), was located in a region associated with occupation time per day and feed intake rate. RAI2, which has been shown to be involved in cellular differentiation (Walpole et al., 1999), was located in a region associated with number of visits per day. Retinoic acid may have an association with feeding behavior. Since retinoic acid is involved in growth and development, this may be explained by the correlation of feeding behavior with average daily gain. MYO3A, which has been shown to be involved with cell structure in the retina (Lin-Jones et al., 2009), was located in a region associated with feed intake rate. N-CAM1, which has been shown to be involved in response to ionic stress in the optic nerve (Carreras et al., 2009), was located in a region associated with feed intake per visit. LMO7, which has been

shown to regulate transcription of the nuclear membrane protein emerin (Holaska et al., 2006), was located in a region associated with feed intake per day. SHOX, which is a nuclear protein that acts as a transcriptional activator (Binder, 2011), was located in a region associated with occupation time per day. JRKL, which has an Entrez gene function of being a nuclear regulatory protein, was located in a region associated with number of visits per day. ZRANB2, which is found in the nucleus and regulates alternative splicing (Mangs and Morris, 2008), was located in a region associated with occupation time per visit. These results suggest that nuclear regulation of transcription and translation may be associated with feeding behavior.

In Chapter 4, it was shown that selection for decreased $RFI_{G/F}$ has had an impact on sow reproductive performance and lactation efficiency. After 7 generations, selection for decreased $RFI_{G/F}$ has resulted in sows that have 1.7 more piglets farrowed, 1.2 more born alive, 0.4 more dead at birth, and more weaned, both by litter (9.0 versus 7.5) and by sow (8.8 versus 8.2). Piglets from the low RFI line were ~70 g heavier at birth than piglets from the high RFI line. The low RFI line also had better litter growth (44.2 versus 40.6 kg) than the high RFI line. However, this increase in piglet performance came at a cost to the sow. During lactation, sows from the low RFI line consumed 33 kg less feed and lost 8.5 kg more body weight and 5.3 kg more fat mass than high RFI sows. Sows from the low RFI line depleted 2.24 mm more of their backfat depth than did high RFI sows. Low RFI sows had a greater negative energy balance (-18.2 versus -11.4 MJ ME/d) but a higher lactation efficiency (21.6 versus 18.9%) and lower residual feed intake during lactation (1.44 versus 15.90 kg) than high RFI sows. Heritabilities were high ($h^2 > 0.4$) for sow weights, sow body composition traits, sow maintenance requirements, and piglet birth weights. Traits pertaining

to piglet growth during lactation and to tissue mobilization of the sow and sow feed intake and total born were moderately heritable ($0.2 < h^2 < 0.4$). Genetic correlations with $RFI_{G/F}$ were not significant for most traits, despite line differences for these same traits. This could be due to the large standard errors for the correlations. However, strong positive genetic correlations with $RFI_{G/F}$ were found for sow weight at farrowing and at weaning and sow maintenance requirements, suggesting that $RFI_{G/F}$ may be associated with mature body size. $RFI_{G/F}$ also had a large positive genetic correlation with sow residual feed intake, suggesting that some of the factors that result in decreased $RFI_{G/F}$ may also result in decreased residual feed intake during lactation. Strong, negative genetic correlations with $RFI_{G/F}$ were found for sow protein mass loss and lactation efficiency which is supported by line differences in those traits. Although other correlations were not significant, they were in the same direction as expected based on line differences.

In conclusion, feed efficiency has been shown to be affected by the manner of feed intake since selection for decreased $RFI_{G/F}$ has resulted in pigs that eat faster, spend less time in the feeder, and tend to visit the feeder fewer times than pigs with high $RFI_{G/F}$. There appears to be a large genetic component to feeding behavior, based on high heritabilities; therefore, measuring and selecting for feeding behavior traits may allow for other opportunities to improve traits of economic importance. Selection for decreased $RFI_{G/F}$ has positively affected piglet performance and lactation efficiency but has negatively affected sow body condition change and energy balance during lactation. Therefore, while selecting for improved feed efficiency during the growing phase, sow feed intake and change in body condition during lactation must be taken into consideration.

Implications and Further Work

As shown in Chapter 2, selection for decreased $RFI_{G/F}$, which results in more efficient pigs, resulted in pigs that spent less time in the feeder per day than pigs that were less efficient. As the pig industry continues to focus on efficient growth of pigs during the growing and finishing phases of production, feeding behavior may be changing. With that, it warrants further research into the current recommendations for number of pigs per feeder space. If pigs are spending less time at the feeder, then more pigs could utilize each feeder space, reducing the need for feeder space. Future work to investigate this could be to set up cameras to record occupancy of conventional feeders to see if the two lines differ in time spent at a conventional feeder since we know they differ in time spent occupying a single-space electronic feeder. It may also be of value to partner with a breeding company to compare time spent at the feeder between commercial lines which differ in feed efficiency to determine if current selection practices for improving feed efficiency (selection for components of efficient lean growth, feed to gain ratio, or gain to feed ratio) also result in decreased time at the feeder, similar to selection for $RFI_{G/F}$.

Labroue et al. (1997, 1999) showed that there were differences in feeding behavior between breeds when they were penned separately by breed or when breeds were mixed together, further research should be done to see if mixing selection lines affects the feeding behavior of the two lines. The question to be evaluated would be: if lines are penned separately instead of mixed, does it affect feeding behavior and the differences in feeding behavior between the two lines?

Fishermen use solar lunar calendars to determine peak fishing times. In an unpublished study at PIC-USA, day to day variation of feed intake has been shown to differ

between sire lines. Pigs have also been shown to eat in a diurnal pattern with two peaks of activity, one around 8:00 am and the other around 4:00 pm (Walker, 1991). However, when feeder space is limited, the diurnal pattern disappears due to the feeder being in almost continuous use (Walker, 1991). It would be interesting to see if the two lines that differ in $RFI_{G/F}$ also differ in their day to day variation of feed intake and if these differences in day to day variation are affected by the solar lunar calendar. However, Chapter 2 showed no differences in the pattern of feed intake over the course of the day between the two lines.

Denture irruption and its effects on feeding behavior have not been evaluated in this population. It would be interesting to see if the two lines which differ in $RFI_{G/F}$ also differ in denture irruption and if differences in denture irruption are associated with differences in feeding behavior. In Chapter 2, it was shown that feeding behavior does differ during the first and second halves of the test period, although this was not the focus of Chapter 2. It might be beneficial to evaluate the change in feeding behavior over time and see if that differs between the two lines.

In Chapter 3, a large genetic component of feeding behavior was evident. Therefore, measuring and selecting for feeding behavior traits may allow for other opportunities to improve traits of economic importance. Occupation time per day had a genetic correlation of 0.39 with $RFI_{G/F}$, suggesting that selection for decreased occupation time per day would result in pigs with decreased $RFI_{G/F}$ or more efficient pigs. Research could be done into how variable occupation time per day is. If it is lowly variable from day to day, one could potentially select for occupation time per day on conventional feeders in a commercial setting simply by videotaping the pigs for 24 hours instead of just utilizing the data obtained from FIRE feeders in a nucleus setting.

Since there is no previous research evaluating candidate genes for feeding behavior, more research to support the findings in Chapter 3 is warranted. This could be done by reanalyzing the data as newer builds and better annotation for the newer builds becomes available. Also with better annotation, all genes near a region found to be associated with a feeding behavior trait could be recorded and a network/pathway analysis could be performed to determine if there are common networks/pathways that are shared among traits. These pathways could also be compared with those that have already been found to be differently regulated in the low and high RFI lines by Lkhagvadorj et al. (2010) who evaluated gene expression differences in the adipose tissue between the low and high RFI lines. Lkhagvadorj et al. (2010) found that genes related to carbohydrate metabolic process, regulation of gene expression, potassium ion transport, response to stress, and cellular carbohydrate metabolic process were up-regulated and genes related to multiple metabolic processes, homeostatic processes, regulation of developmental process, respiratory chain complex IV assembly, protein targeting, ion transport, generation of precursor metabolites and energy, endocytosis, membrane invagination, DNA repair, membrane organization and biosynthesis, and centrosome cycle were down-regulated in the adipose tissue of low RFI pigs compared to high RFI pigs.

Chapter 4 evaluated the effects of selecting for decreased $RFI_{G/F}$ on sow reproductive performance and lactation efficiency. Although selection for decreased $RFI_{G/F}$ was not shown to have a negative impact on piglet numbers and weights, it was shown to decrease sow feed intake and increase sow weight loss, particularly fat mass loss, during lactation. With this in mind, as the pig industry continues to select for more and more efficient pigs, it will be important to consider sow feed intake and change in body condition during lactation when

making selection decisions. Typically, as litter size increases, individual birth weights of piglets decrease. In our study, both litter size and average birth weight were increased in the line selected for decreased $RFI_{G/F}$. Given that sows are fed the same amount of feed in gestation and that maintenance costs are most likely reduced in the low RFI line, then sows from the low RFI line would be able to put more nutrients towards their fetuses than sows from the high RFI line. A study that could be performed to further investigate this would be to feed sows differing amounts through lactation and compare average piglet birth weights between feeding levels within and across lines. Further research needs to be done in the areas of return to estrus post-weaning, rebreeding, and longevity to see how selection for $RFI_{G/F}$ affects these traits. Since backfat depth is measured at farrowing and at weaning, backfat depths could be measured once or twice a week post-farrowing to see if the sow returns to her farrowing backfat depth and how long it takes her to do so. Also, in our results, the line of the piglet and the line of the sow were confounded; therefore, a partial cross-fostering experiment where each sow nurses piglets from both lines could be performed to eliminate the effect of piglet line on differences in piglet performance during lactation between sow lines. Although a lot of research has been performed on the implications of selecting for decreased $RFI_{G/F}$, there is still quite a bit more needed to fully cover all potential pitfalls to selecting for decreased $RFI_{G/F}$.

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