Genetic and Biological Aspect of Residual Feed Intake in Pigs

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Introduction

Improving feed efficiency is one of the major objectives in animal breeding programs, in particular in view of increasing feed costs and increasing demands on feed crops and land for biofuel production. Residual feed intake (RFI) is a measure of feed efficiency that has improved statistical properties over traditional measures of feed efficiency that are based on the ratio of feed intake and growth. During the growing period, RFI is defined as the difference between the observed feed intake and expected feed intake based on average requirements for maintenance and growth. In pigs, RFI of individuals can be estimated as the residual of a model for feed intake that includes growth rate and backfat as covariates, possibly along with metabolic body weight (Mrode and Kennedy, 1993). Variation in RFI captures differences in efficiency of digestion, efficiency of metabolic utilization of feed energy, maintenance requirements, tissue turn over rates, activity, and stress, among others. The contribution of these components to RFI has been studied in poultry (Luiting, 1990) and beef cattle (Herd and Arthur, 2009), but has not been evaluated in pigs. To this end, selection experiments for RFI were initiated at INRA and Iowa State University (ISU) in 2000, both in Large White pigs. The INRA experiment consists of a line that is selected for increased RFI and a line selected for reduced RFI. At ISU a line is selected for reduced RFI, along with a line that was randomly selected for five generations and for increased RFI in the last generation reported here. In both experiments, selection is primarily among boars from first parity sows, which are evaluated for feed intake under group-housing with single space electronic feeders. At INRA, selection is for own phenotype for RFI measured as an index of daily feed intake, growth rate, and backfat within contemporary group. At ISU, selection is for BLUP EBV for RFI from an animal model for average daily feed intake with covariates for growth rate and backfat by generation. Further details of each experiment are in Gilbert et al. (2007) and Cai et al. (2008) and Bunter et al. (2010). Both sets of lines have been the subject of investigations into the genetic and biological basis of RFI, details of which can be found elsewhere. Objectives of this paper are to summarize the major findings of these studies, focusing on consistencies and differences of findings between the two experiments. Results presented apply to data collected during the first 6 generations of both experiments.

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Genetic parameters for feed intake and growth performance

Table 1 summarizes estimated parameters for RFI and performance traits during the growing period. In both experiments, differences in growth and backfat explained approximately 65% of the phenotypic variation in feed intake, after accounting for systematic environment and pen effects, leaving 35% for RFI. RFI was moderately heritable. In both populations, RFI had moderate positive genetic correlations with growth rate and backfat, and selection for reduced RFI also reduced growth and backfat (Table 2). These non-zero genetic correlations and correlated responses are the result of the phenotypic and genetic relationships among feed intake, growth, and backfat when RFI is derived based on phenotypic adjustments for growth and backfat, as predicted by Kennedy et al. (1993).

Table 1: Parameters for feed intake and RFI. [1)]

	INRA	ISU
Phenotypic SD Feed Intake (kg/d)	0.172	0.220
Phenotypic SD RFI (kg/d)	0.116	0.125
% variation in FI due to RFI	37	33
Heritability Daily Feed Intake	0.32	0.45
Heritability RFI	0.20	0.35
Line difference in RFI (genetic SD)	-2.8	-1.3
Genetic correlations of RFI with performance traits		
Growth rate	0.18	0.24
Back fat thickness	0.24	0.20
Loin muscle depth / area	-0.16	-0.18
Daily Feed Intake	0.82	0.64
Feed conversion ratio	0.63	0.74

[1)] All parameters computed on a within-pen basis

Responses in efficiency and growth performance

Selection on RFI was successful in creating substantial differences in average RFI between the lines (Table 1). However, because of the positive genetic correlations with growth and backfat, selection for reduced RFI also resulted in reduced growth and backfat. Nevertheless, despite lower growth and backfat in the low RFI lines, these lines still consumed substantially less feed when feed intake was adjusted for growth and backfat (i.e. RFI) and had a lower feed conversion ratio. For the INRA populations, line differences in feed intake and growth were evident across the post-weaning growing period, whereas difference between the ISU lines did not emerge until the later part of the growing period. As a consequence, in the INRA experiment, daily feed intake was shown to be closely correlated to body weight in the low RFI line during the test period, whereas it tended to be high and less variable with time in the high RFI line.

Pigs from the low RFI ISU line had greater birth weight than the control line, in contrast to the INRA lines, where birth weight was lower in the low RFI line compared to the high RFI line. In both experiments, the low RFI line had greater pre-weaning growth, compared to the other line.

Table 2: Correlated responses during the growing period.
'–' indicates that the low RFI line had a lower mean than the other line

	INRA	ISU
Feed conversion ratio	–	–
Birth weight	–	+
Weaning weight	=	+
Early post weaning growth/day	–	=
Late post weaning growth/day (> 65 kg)	–	–
Early post weaning feed intake/day	–	=
Late post weaning feed intake/day (> 65 kg)	–	–
Off-test backfat thickness (95-110 kg)	–	–
Off-test loin depth / loin muscle area	+	+
Dressing %	+	+
Carcass Intra-muscular fat	–[1)]	–
Meat quality - pH, water holding capacity	–	=
Muscle fiber type	=[1,2)]	=
Energy content carcass	–[3)]	–[3)]

1) measured on 14 females per line in generation 4.
2) Type IIBW was higher in the low RFI line. Fiber diameter was also higher in the low RFI line but was not measured at ISU.
3) Based on carcass composition at INRA and based on bomb calorimetry of carcass at ISU.

Body composition and meat quality

Selection for reduced RFI resulted in leaner carcasses with less backfat, intra-muscular fat, and other fat depots, and increased loin depth and loin eye area (Table 2), which is in accordance with most reported results in growing animals (Herd and Arthur, 2009). Dressing % was greater in the low RFI line in the INRA experiment and also, but to a more limited extent, in the ISU experiment. Because of the higher metabolic cost of fat versus lean deposition, the energy content of the carcass was lower in the low RFI lines. This was confirmed by bomb calorimetry of the carcass in the ISU lines. In the ISU lines, differences in energy content of the carcass were found to explain a large part of the differences in energy consumption between the two lines (Boddicker et al. 2010).

No clear line differences in technological and sensory meat quality were observed at ISU, although there was evidence that the low RFI line had less protein degradation during aging and less marbling (Smith et al. 2009). Selection for reduced RFI did result in a decline of technological meat quality in the INRA low line, based on reduced pH, glycolytic potential, and water holding capacity. Sensory quality was not evaluated at INRA. Muscle fiber types were not different between the lines in either experiment, except for a greater fraction of Type IIBW fibers and greater fiber diameter in the INRA low RFI line. Fiber diameter was not measured in the ISU lines but this result is consistent with greater calpastatin activity in muscle post harvest that was observed in the ISU low RFI line; calpastatin inhibits the calpain system from degrading protein.

Feeding behavior, activity, and energy utilization

In both experiments, pigs from the low RFI lines ate faster when in the feeders (Table 3). The ISU low RFI line spent 10 minutes less in the feeders than the control line, even after adjusting for differences in feed intake (Young et al. 2009). The number of meals was also reduced in the INRA low RFI line, although number of visits was similar between the lines. Number of visits tended to be lower in the ISU low RFI line but the impact on number of meals was not evaluated. These findings are consistent with the positive correlation estimated by de Haer et al. (1993) between RFI and daily feeding time and total number of visits in pigs, and the generally greater levels of activity in high RFI chickens (Luiting et al. 1991) and high RFI cattle (Richardson et al. 1999).

Table 3: Correlated responses in traits related to behavior and metabolism.
'–' indicates that the low RFI line had a lower mean than the other line
'~' refers to a tendency for a difference

	INRA	ISU
Activity	–	~ –
Feeding behavior - rate	+	+
- Number of visits	=	~ –
- Number of meals	–	*NA*
Thyroid weight	+	+
Basal maintenance requirements	–	~ –
Heat from digestion	=	
Protein content of carcass	~ +	~ +
Protein metabolism	=	–
Fat content carcass	–	–
Fat metabolism	=	*NA*
Muscle glycogen	+	–
Fasting triglycerides	*NA*	~ +
Fasting non-esterified fatty acids	*NA*	~ +

Although based on small numbers of pigs, direct metabolic measurements in respiration chambers found no line differences in digestibility or retained energy per day between the INRA lines. Independence between digestibility and RFI is in accordance with results previously reported in monogastrics (pigs, de Haer et al. 1993; chicken, Luiting et al. 1994; mice, Bunger et al. 1998). On the same pigs, basal maintenance requirements were 10% lower in the low RFI line (Barea et al. 2010) and heat production related to physical activity tended to be lower. The ISU experiment provides indirect evidence for lower maintenance requirements for the low RFI line in the form of lower feed requirements to maintain constant body weight (Boddicker et al. 2010) and smaller size of visceral organs, which are energetically expensive to maintain. In both experiments, size of the thyroid was higher in the low RFI line. The thyroid axis was shown to play an important role in the differences between lines, with increased serum levels of free T3 in the low RFI lines in fasting pigs at ISU and in fed pigs at INRA, although the exact mechanisms of how this contributes to increased efficiency remains unclear.

Results also provide some evidence that low RFI pigs have reduced tissue turnover rates, which is known to be energetically expensive. This includes reduced post-mortem rates of muscle protein degradation in the ISU low RFI line, as measured by less desmin degradation during postmortem aging, and increased calpastatin activity in muscle. The ISU low RFI line also had lower levels of ATPase activity in muscle.

Both experiments showed evidence of a shift in mechanisms for use and storage of energy towards short-term storage in the low RFI lines. In both experiments, storage of energy in the form of lipids was reduced, based on lower backfat, intra-muscular fat, and other fat depots. However, glycogen levels in muscle were higher in the low RFI lines in both experiments and fasting tri-glyceride levels were increased in the ISU RFI line.

Response to stress, requiring increase in metabolic rate, energy consumption and catabolic processes, has been reported in other species as a major difference between lines selected for different levels of RFI. In pigs, no data are available but further studies are needed to investigate if low RFI animals would similarly show lower response to stress.

Sow performance

Selection for reduced RFI had no detrimental effects on sow performance (Table 4). In fact, both experiments show some evidence of improved sow performance in the low RFI lines in the form of slightly larger litters, birth weights, and pre-weaning growth, despite lower feed intake during lactation. Even though sows were lighter at farrowing in the low RFI line in the INRA experiment, these differences were not significant in the ISU experiment. Sows from the low RFI lines did lose more body weight and backfat during lactation to sustain the increased level of litter performance. Residual feed intake during lactation, evaluated by adjusting feed intake for body weight, loss of body weight and backfat, and gain of the nursed litter, was lower in the low RFI line at INRA (Gilbert et al. 2010b) but not at ISU. Rebreeding performance was not evaluated in the lines.

Table 4: Correlated responses in sow performance.
'–' indicates that the low RFI line had a lower mean than the other line
'~' refers to a tendency for a difference

	INRA	ISU
Body weight before farrowing	–	=
Body weight loss during lactation	+	+
Backfat before farrowing	~ –	–
Backfat loss during lactation	+	+
Loin depth before farrowing	=	*NA*
Loin depth loss farrowing - weaning	+	*NA*
Total born	=	+
Number born alive	+	~ +
Litter weight at birth	=	+
Weight gain to 21 days of nursed litter	+	+
Sow feed intake during lactation	–	–
RFI	–	=

Genetic markers for RFI

There was limited evidence of large differences in gene expression between extremes for RFI in the 3rd generation of the ISU RFI lines; using the Affymetrix gene expression chip, 147 and 311 genes were found to be differentially expressed at a q-value of 0.2 in liver and fat, respectively (Lkhagvadorj et al., 2010). Several of the lipid metabolic genes that were down-regulated in the low RFI line were also down-regulated in response to feed restriction in pigs from the ISU lines.

Despite having an effect on each component of RFI and on feed conversion ratio, the major mutation of halothane gene segregating in the Piétrain breed has been shown to have no effect on residual feed intake (Saintilan et al. 2010). A QTL mapping experiment involving INRA RFI lines identified only a limited number of QTL for feed intake traits and feed conversion ratio, suggesting that these traits are affected by many QTL of limited effect (Gilbert et al. 2010a). A whole genome linkage disequilibrium analysis of 750 pigs from the ISU RFI lines with genotypes from the 60k Illumina chip using genomic selection methods of analysis identified multiple regions associated with RFI, including several that contained candidate genes, among which was MC4R (Gorbach et al. 2010).

Conclusions

Residual feed intake is a trait with moderate heritability in growing pigs. Selection on RFI has shown to be effective in creating lines of pigs that differ in feed intake and in RFI in two parallel selection experiments at INRA and ISU. The direction of correlated responses was generally similar in the two experiments, indicating a similar genetic basis for RFI. In both experiments, selection for reduced RFI resulted in leaner and slower growing pigs. This was associated with a reduction in technological meat quality in the INRA experiment but not in the ISU experiment. Results from both experiments suggest that changes in body composition explain a substantial portion of line differences in RFI, even after adjusting to constant backfat. In both experiments, selection for lower RFI resulted in faster eating pigs. Both experiments suggest that low RFI pigs have reduced basal maintenance requirements, reduced tissue turnover rates, and a shift in mechanisms for use and storage of energy towards short-term storage. Selection for reduced RFI had no detrimental effects on sow performance. Low RFI sows in fact had slightly higher litter size and pre-weaning litter growth, despite lower feed intake during lactation, but this was at the expense of low RFI sows mobilizing more body reserves.

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