RESEARCHREPORT

ANIMAL SCIENCE

Title: Identification of biological factors responsible for differences in feed efficiency between selection lines for residual feed intake – **NPB #07-161**
Selection lines to enhance genetic selection for feed efficiency – **NPB 07-139**

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INDUSTRY SUMMARY

Feed for the growing phase is the largest variable cost in pork production and these costs are on the rise. Thus, research that reduces feed required for pork production can result in substantial economic benefits to pork producers. It is well known that fast-growing lean pigs require less feed to reach market weight. However, ~34% of differences in feed intake between pigs are not related to growth. Thus, although past selection for lean growth has substantially increased feed efficiency, further increases are limited by differences in feed intake that are unrelated to growth and backfat. This feed intake net of growth and backfat is called residual feed intake (RFI). RFI is a unique measure of feed efficiency because it represents true differences in the ability of pigs to use feed energy for the metabolic processes of maintenance and growth. Factors that contribute to RFI have not been quantified for the pig but can include activity, behavior, digestion, heat production, maintenance requirements, immune-response, and protein and tissue turn-over rates, some of which can be related to meat quality. Current selection for feed efficiency cannot capitalize on differences that are unrelated to growth and backfat without the expense of recording feed intake. Thus, with the ultimate aim to develop genetic tests or indicator traits to select for feed efficiency without the expense of feed intake recording, the objective of this research project was to identify the main biological factors that contribute to differences in RFI. This research capitalized on a unique line of Yorkshire pigs that has been selected for reduced RFI for 5 generations and requires 7% less feed for the same rate of growth and backfat than its randomly bred control line. Results from the experiments that were conducted demonstrated that, compared to the control line, pigs from the efficient line: 1) had different feeding behavior as the Select pigs ate faster and less often, 2) tended to be slightly less active, 3) did not differ much in other behaviors that were studied, 4) were more efficient under both ad libitum and restricted feeding, 5) required less feed to maintain a constant weight, 6) tended to have lower internal organ weights, 7) had a lower fat content of the carcass, 8) had greater dressing percentage, 9) had better carcass composition with limited effects on selected measures of meat quality such as pH and water holding capacity, 10) had decreased carcass lipid content and postmortem protein degradation, 11) had physiological parameters that indicated less protein turnover and energy expenditure in muscle. In conclusion, although a substantial part of differences in feed efficiency as measured by RFI are related to differences in body composition, part of the differences appear related to pen and feeding behavior and to lower maintenance requirements and energy expenditures. Selection for RFI does not have major negative effects on meat quality

SCIENTIFIC ABSTRACT

Understanding the biology behind genetic differences in feed efficiency is important to develop selection strategies to improve efficiency. To this end, a line of Yorkshire pigs selected for lower residual feed intake (RFI) was developed, along with a contemporary control line. The objective of this project was to evaluate the 5th generation of these two lines to identify the main biological factors that contribute to differences in RFI. Specific objectives were to evaluate differences in 1) feeding and pen behavior, 2) meat quality, 3) maintenance or static body weight requirements, 4) and body composition and energy partitioning. Three animal experiments were conducted. In experiment 1, a total of 192 gilts from generation 5 of the Select and Control lines (96 per line) were housed in 12 pens (16 gilts per pen, 8 from each line) in a conventional grow-finish unit with one single-space electronic FIRE feeder per pen. Pigs were evaluated for pen and feeding behavior and, following slaughter, for meat quality. In experiments 2 and 3, eighty young (~25 kg) and 80 older (~75 kg) barrows, with equal numbers from the two lines, were individually penned and allocated to one of four feed intake groups for six weeks: 1) ad libitum, 2) 75% of feed intake of adlib, 3) 55% of feed intake of adlib, and 4) a weight stasis group, in which intake was adjusted to maintain initial body weight. Pigs were evaluated for growth, feed intake and ultrasound, and blood sampled. Upon completion of the performance study, a total of 64 young and 64 old pigs were harvested, organ and carcass weights recorded, and tissues were collected. Chemical carcass composition was determined on one half of the carcass. In experiment 1, for pen behavior, on the day of placement there were no differences between lines for time spent at the drinker or for any postures in the home pen; however, Select gilts had lower lesion scores. Behavioral differences were identified between lines over subsequent rounds, with gilts from the Select line becoming less active compared to Control line gilts but there were no differences in lesion scores. For feeding behavior, even after correcting for differences in feed intake, pigs from the Select line were found to spend less time eating and to eat faster. This result was consistent in direction across three separate data sets. Differences in meat quality between the lines were small, but carcasses from the Select line tended to have less backfat, greater loin depth and a greater percentage fat free lean. Select line chops tended to have greater water holding capacity, less intramuscular lipid content, lower subjective marbling scores, and a greater percentage of moisture. Pigs selected for reduced RFI consumed less feed for the same rate of gain but differed in carcass composition, indicating differences in the partitioning of energy and nutrient retention, with limited changes in growth rate but some increase in dressing percentage. Select line pigs also had lower viscera weights and required less energy to maintain body weight, indicating possible differences in maintenance requirements. Selection for low RFI has also resulted in lower Na^+, K^+ -ATPase activity in the longissimus dorsi, which may contribute significantly to the observed improvements in feed efficiency and lower metabolic rates. In conclusion, although a substantial part of differences in feed efficiency as measured by RFI are related to differences in body composition, part of the differences appear related to pen and feeding behavior and to lower maintenance requirements, protein turn over rates, and ion pump expenditures in muscle. Also, selection for RFI does not have major negative effects on meat quality. However, the molecular mechanisms behind these changes are not fully understood and need to be further examined to obtain greater efficiency gains in livestock.

INTRODUCTION

Feed for the growing phase is the largest variable cost in pork production and these costs are on the rise because of increasing demands for land and crops for bio-fuel production. Thus, research that reduces feed required for pork production will result in substantial economic benefits to pork producers. Fast-growing lean pigs require less feed to reach market weight. However, ~34% of differences in feed intake between pigs are not related to growth and composition but result from differences in energy required for other processes such as maintenance, activity and digestive and metabolic efficiency. Thus, although past selection for lean growth has substantially increased feed efficiency, further increases are limited by differences in feed intake that are unrelated to growth and backfat. This feed intake net of growth and backfat is called residual feed intake (RFI). RFI is a unique measure of feed efficiency because it represents true differences in the ability of pigs to use feed energy for the metabolic processes of maintenance and growth. Differences in efficiency through RFI are not captured by selection on growth and backfat. Factors that contribute to RFI have not been quantified for the pig but can include activity, behavior, digestion, heat production, maintenance requirements, immune-response, and protein and tissue turn-over rates, some of which may be related to meat quality.

Effective selection for feed efficiency (through RFI) is limited by the high cost of recording feed intake on individual pigs and by lack of knowledge of the genetic and biological mechanisms that control efficiency in pigs. To enable research into the biological and genetic basis of feed efficiency, a selection experiment was started in 2001 in purebred Yorkshires, which after 5 generations has resulted in a low RFI line that requires less feed for the same rate of growth than its control line. Now that we have established that differences in efficiency that are unrelated to growth (i.e. RFI) are heritable and can be changed by selection, we are at a position to use these unique lines to determine the biological basis for differences in RFI and efficiency. Thus, with the ultimate aim to develop genetic tests or indicator traits to select for feed efficiency without the expense of feed intake recording, the main objective of this research was to use the RFI lines to identify the main biological factors that contribute to RFI and to identify physiological parameters that are associated with RFI.

OBJECTIVES (modified from the original as per progress report)

The overall objective was to identify the main biological factors that contribute to differences in RFI and feed efficiency that have been created by selection for RFI in the Iowa State RFI Yorkshire selection lines and to identify associated behavioral and physiological indicator traits. Specific objectives were:

Obj. 1: Determine the extent to which differences in RFI are caused by differences in behavior and activity.
Obj. 2: Determine the extent to which differences in RFI are related to changes in body composition and in biochemical mechanisms underlying meat quality traits in the longissimus dorsi (pork loin).
Obj. 3: Determine the extent to which differences in RFI are related to differences in maintenance or static body weight regulation requirements.
Obj. 4: Determine the extent to which differences in RFI are related to concentrations of hormones and metabolites in blood that are indicative of the level of energy and protein metabolism and local production of immune modulators.

MATERIALS & METHODS:

Objective 1: Determine the extent to which differences in RFI are caused by differences in behavior and activity.

Pen behavior: A total of 192 gilts from generation 5 of the Select and Control lines (96 per line) was housed in 12 pens (16 gilts per pen, 8 from each line; 0.82 m^2/gilt) in a conventional grow-finish unit with one single-space electronic FIRE$^{©}$ feeder per pen. Twelve hours of video footage was collected on the day of placement and then every 4 wk for 3 more observational periods. This 576 h of video footage was scored using a 10-min instantaneous scan sampling technique for four postures (standing, lying, sitting and locomotion) and one behavior (time at drinker). Lesion scores were collected 24-h after placement and then every 4 weeks. All analyses were done using Proc Mixed of SAS. The data were analyzed separately on the day of placement and subsequent rounds (1, 2 and 3). Analysis was performed on each behavior and posture. Lesion scores for each body region were analyzed as repeated measures.

<u>Feeding behavior:</u> Data were from 3 parities from the 4th and 5th generations were analyzed by parity. Lines were mixed in pens of 16 and evaluated for feeding behavior traits obtained from FIRE© feeders over a growing period of ~3 months prior to ~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 per hour; occupation time per day, per visit, and per hour; feed intake per day, per visit, and per hour; and feeding rate per visit. Models used included fixed effects of line and feeder, covariates of age on test and daily feed intake, and random effects of pen, on-test group, sire, and litter. Repeated measures models were used to analyze feeding patterns during the day.

Objective 2: Determine the extent to which differences in RFI are related to changes in body composition and in biochemical mechanisms underlying meat quality traits in the longissimus dorsi (pork loin).

A total of 180 gilts (90 from each line) from the fifth generation of the Iowa State RFI Select and Control lines was put in 12 pens of 16 pigs (8 per line) and evaluated for carcass and meat quality traits. Gilts (select = 80, control = 89) were harvested in three groups at ~114 kg and the boneless loins were collected at 24 h postmortem. Back fat and loin eye depth were collected off the midline at the last rib region using the Fat-O-Meater. Quality attributes were measured at 2 d postmortem. Drip loss and water holding capacity were measured in duplicate (3 d postmortem). Hunter L, a, and b values were measured in triplicate on two chops using a C10 illuminant, 10˚ observer, and 1.27cm aperture. Quality scores were assigned by a 3 member panel. Intramuscular lipid and moisture content were determined by AOAC guidelines. Desmin degradation was measured at 2 and 7 d postmortem. Purge, cook loss, sensory traits, and star probe texture were measured at 7-10 d postmortem on cooked (71˚C internal temperature) chops. The model included fixed effects of line, slaughter date, MC4R genotype, barn group, line by slaughter date, genotype by line interactions, covariate of off-test weight, and sire, pen, and litter fitted as random effects.

Objective 3: Determine the extent to which differences in RFI are related to differences in maintenance or static body weight regulation requirements.

Eighty young (~25 kg) and 80 older (~75 kg) Yorkshire barrows, with equal numbers from the Select and Control lines, were paired based on age and weight (1 pig from each line), and each pair was randomly assigned to contiguous individual pens. Following 3 days acclimation, pigs were allowed ad libitum feed intake for 7 days to establish individual feed intake. Subsequently, pairs were randomly allocated to one of four feed intake groups: 1) ad libitum (Ad), 2) 75% of feed intake of adlib (Ad75), 3) 55% of feed intake of adlib (Ad55), and a weight stasis (WS) group, in which intake was adjusted to maintain initial body weight. The duration of the test period was six weeks. Pigs were evaluated for growth, feed intake and ultrasound and blood sampled. Upon completion of the performance study, a total of 64 young and 64 old pigs was harvested and organ weights and tissues were collected. Chemical carcass composition was determined on one half of the carcass. Gross energy content of the diet and carcasses was determined in by adiabatic bomb calorimetry. The latter was completed for the older pigs only.

Objective 4: Determine the extent to which differences in RFI are related to concentrations of hormones and metabolites in blood that are indicative of the level of energy and protein metabolism and local production of immune modulators.

Pigs from the experiment described under objective 3 were blood sampled six times during the test period. Samples were evaluated for blood cell counts. Several blood parameters were evaluated, including serum glucose, insulin, free thyroxin, free triiodothyronine, IGF-1, urea nitrogen, triglycerides and non-esterified free fatty acids. In addition, Na^+, K^+ -ATPase activity was measured in the ileum and longissimus dorsi tissues.

Differences in protein turnover were investigated by evaluating differences in the amount of intact desmin and in calpastatin activity. White blood cell counts were also determined for immunological status.

RESULTS:

Objective 1: Determine the extent to which differences in RFI are caused by differences in behavior and activity.

Pen behavior:

There were no differences (*P*>0.05) between lines for all postures and time at drinker on the day of placement (Table 1). However, over subsequent rounds Select gilts spent less (*P*=0.03) time standing, more time sitting (*P*=0.05), and were less active (*P*=0.03) overall. Gilts from the Select line had lower (*P*<0.05) lesion scores on the day of placement (data not shown). However, over subsequent rounds lines did not differ (*P*>0.05). In conclusion, selection for RFI can affect some aspects of behavior and reduce activity.

Table 1: LS means for posture and behavior traits on the day of placement and during the growing period.

	Genetic Line		
	Select (n=96)	**Control (n=96)**	***P-value***[4]
Posture[1]	**On day of placement**		
Locomotion	4.25 ± 1.59	4.00 ± 1.59	0.728
Standing	10.30 ± 2.94	11.90 ± 2.94	0.113
Sitting	2.25 ± 0.37	1.98 ± 0.37	0.503
Lying	82.70 ± 5.02	81.60 ± 5.02	0.342
Active[2]	15.09 ± 5.09	16.38 ± 5.09	0.285
Inactive[3]	84.88 ± 5.02	83.54 ± 5.03	0.270
Drinking	0.46 ± 0.13	0.50 ± 0.13	0.778
	During growing period		
Locomotion	2.26 ± 0.17	2.37 ± 0.17	0.577
Standing	13.72 ± 0.88	15.21 ± 0.88	0.027
Sitting	2.50 ± 0.28	2.12 ± 0.28	0.051
Lying	80.23 ± 0.92	79.16 ± 0.92	0.179
Active[3]	16.88 ± 0.82	18.50 ± 0.82	0.028
Inactive[4]	82.70 ± 0.87	81.33 ± 0.87	0.063
Drinking	0.88 ± 0.09	0.93 ± 0.09	0.523

[1] Postures and behavior based on 10 min scan sample technique.
[2] Active is the combination of locomotion, standing and drinking
[3] Inactive is the combination of the postures sitting and lying
[4] Established using transformed data

Feeding behavior: Select line pigs had a significantly lower daily feed intake than Control pigs for all 3 data sets investigated (Figure 1). With adjustment for differences in feed intake, line differences for feeding behavior traits were in the same direction for all 3 data sets but differed in significance and size. Although not significant, Select pigs tended to have fewer visits, in particular during peak eating times. Select pigs had a higher feeding rate and lower occupation time per visit and per hour than control pigs but this was not significant for all datasets. Residuals correlations of RFI were positive with feed intake and number of visits per day, although its strength differed between datasets. In conclusion, feed efficiency may be affected by feed intake behavior because selection for RFI has resulted in pigs which spend less time eating and eat faster.

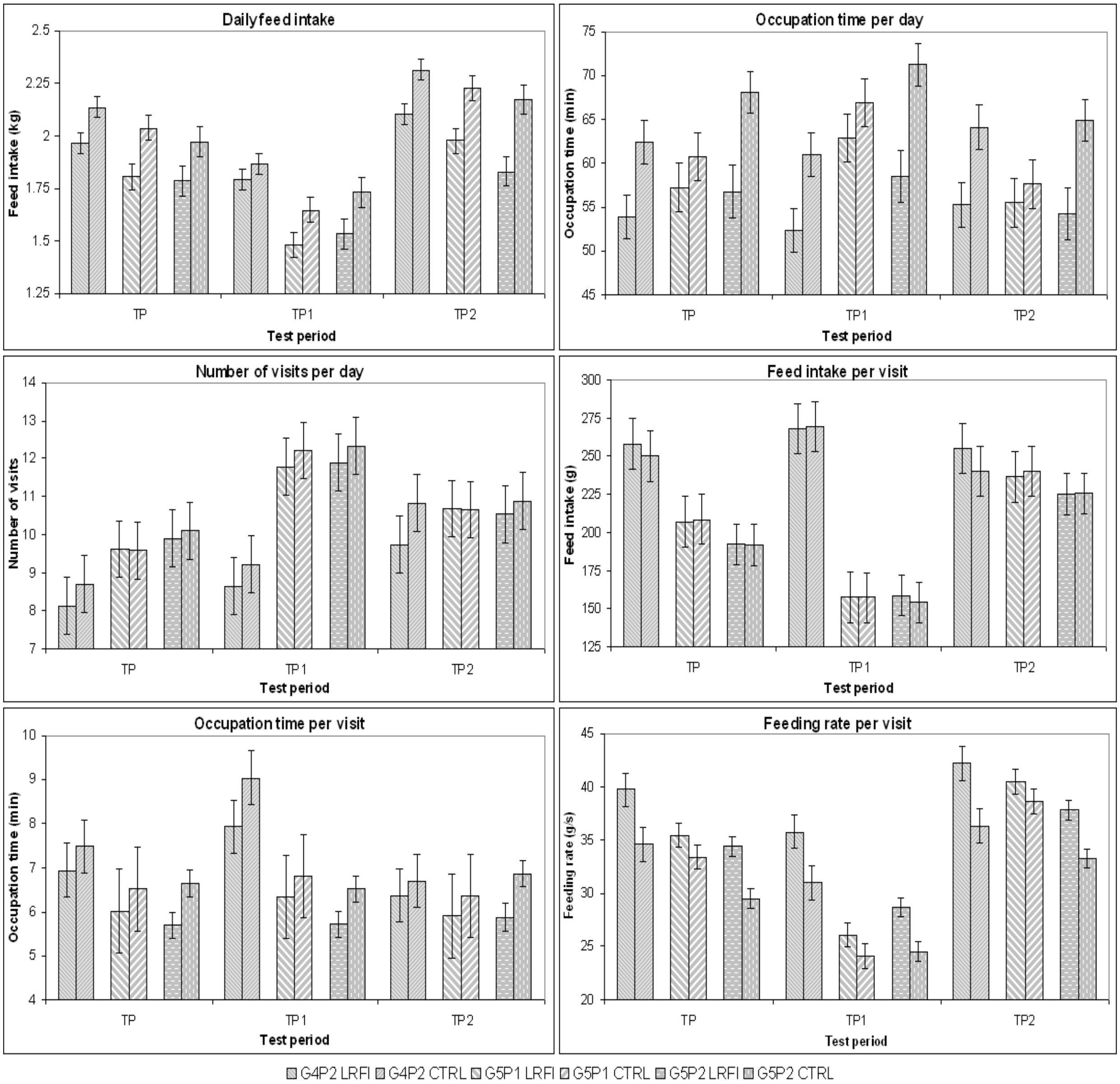

Figure 1. LS Means for feeding behavior traits for three different generation (G=4 or 5) by parity (P=1 or 2) combinations for the entire test period (TP) and for the first (TP1) and second (TP2) half of TP.

Objective 2: Determine the extent to which differences in RFI are related to changes in body composition and in biochemical mechanisms underlying meat quality traits in the longissimus dorsi (pork loin).

Compared to the Control line, carcasses from the Select line tended to have less (P=0.09) backfat (15.2 ± 0.9 vs. 17.3 ±0.7 mm), greater (P<0.05) loin depth and greater (P<0.05) calculated percentage of fat free lean (56.5% vs. 54.8%) (Table 2). Select line chops tended to have greater water holding capacity as measured by centrifugation loss (P=0.07). Loin chops from the Select line had less (P<0.01) intramuscular lipid content (1.14% vs. 1.67%), and lower subjective marbling scores (P<0.05) than control chops. Loin chops from the Select line carcasses also had a greater (P<0.01) percentage of moisture than the Control chops. There were no differences between lines for hot carcass weight, pH, drip loss, Hunter L and a values, subjective color, firmness, and wetness scores (data not shown), amount of intact desmin at 2 or 7 d, any sensory traits, or star probe values. RFI was correlated (r=0.24, P<0.01) to tenderness and negatively correlated (r= -0.26, P<0.01) to star probe. The residual correlation of intact desmin at 2 d postmortem was not significant, but RFI was correlated (r= -0.18, P=0.02) to the amount of intact desmin at 7 d postmortem. RFI was also correlated (r= -0.15, P<0.05) to chewiness. RFI tended to be correlated (r=0.15, P=0.06) to the percentage of intramuscular lipid.

Table 2: LS Means for carcass, meat, sensory, and biochemical measurements of pork quality

Trait	Select (n=80)	Control (n=89)	P-value
Hot carcass weight, kg	87.0 ± 1.3	85.9 ± 1.1	0.15
Loin eye depth, mm	57.5 ± 1.1	54.7 ± 0.8	<0.05
Backfat depth, mm	15.2 ± 0.9	17.3 ± 0.7	0.09
Percentage lean	56.48 ± 0.60	54.85 ± 0.45	<0.05
pH, 48 h	5.55 ± 0.02	5.54 ± 0.01	0.71
Drip Loss	1.41 ± 0.13	1.39 ± 0.12	0.91
Centrifugation Loss	6.28 ± 0.30	6.95 ± 0.25	0.07
Purge Loss	1.99 ± 0.17	2.01 ± 0.14	0.34
Cook Loss	17.19 ± 0.48	16.98 ± 0.41	0.31
Hunter L	45.83 ± 0.30	45.97 ± 0.26	0.74
Hunter a	2.37 ± 0.15	2.67 ± 0.12	0.13
Hunter b	7.41 ± 0.11	7.67 ± 0.08	0.08
% Lipid	1.14 ± 0.09	1.67 ± 0.08	<0.01
% Moisture	74.35 ± 0.07	73.78 ± 0.06	<0.01
Juiciness	9.87 ± 0.21	9.93 ± 0.18	0.51
Tenderness	10.09 ± 0.22	9.99 ± 0.19	0.15
Chewiness	2.97 ± 0.16	3.09 ± 0.14	0.21
Pork Flavor	2.49 ± 0.14	2.66 ± 0.12	0.91
Off Flavor	2.19 ± 0.24	2.02 ± 0.20	0.99
Star Probe	5.19 ± 0.11	5.29 ± 0.09	0.54
Intact Desmin D2	1.01 ± 0.04	0.97 ± 0.03	0.42
Intact Desmin D7	0.79 ± 0.03	0.78 ± 0.03	0.66

Objective 3: Determine the extent to which differences in RFI are related to differences in maintenance or static body weight regulation requirements.

Under ad libitum feeding, Select line pigs consumed 8% less feed (P=0.15) with no difference in growth rate versus the control line. However, the Select line pigs under 55% of ad lib feeding gained 10% more (P<0.01) than the Control pigs on the same amount of feed. Despite attempts to hold pigs on the weight stasis treatment at constant body weight for six weeks, the Select line

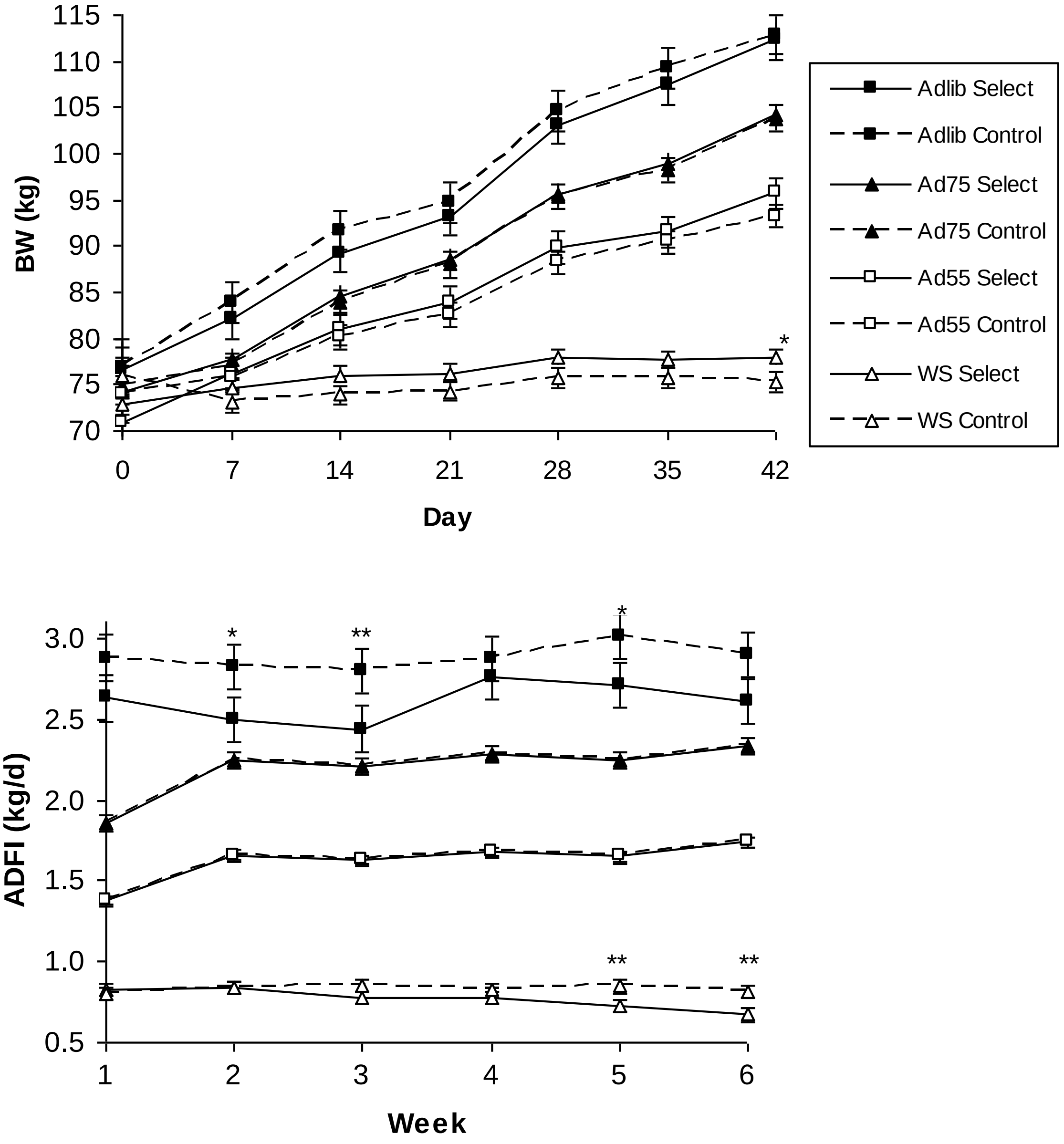

Figure 2. Effects of diet restriction on BW (A) and ADFI (B) of control and low residual feed intake finisher barrows. Top panel A represents weekly body weight. Bottom panel B represents weekly feed intake

pigs gained body weight while consuming 11% less feed than the control pigs (P=0.05). The Select line also had a higher dressing percentage (P<0.03) than the Control pigs (Table 3), but this was significant only for the Ad75% level (P<0.02). Select line pigs also had lower viscera weights and required less energy to maintain body weight, indicating possible differences in maintenance requirements. Further analysis will focus on differences between retained and consumed energy. Analyses of chemical composition of the carcasses (Table 3) indicated significant differences in energy partition between the two lines. While protein contents were the same between the lines, we observed a significant increase in overall carcass water content in the Select pigs compared to the Controls. At present, we have no explanation for this, as water and protein content are usually tightly correlated. Nevertheless, these results translate into greater lean mass in the Select versus the Control pigs. These findings were confirmed by loin eye muscle area ultrasound scan results. We observed no detectable differences in bone content between the lines, as measured by mineral ash. Genetic selection for low RFI significantly reduced carcass fat, compared to the control pig line (Table 3). Altogether, these results indicate that selection for low RFI has altered carcass energy partitioning and nutrient retention, with limited changes in growth rate but some increase in dressing percentage.

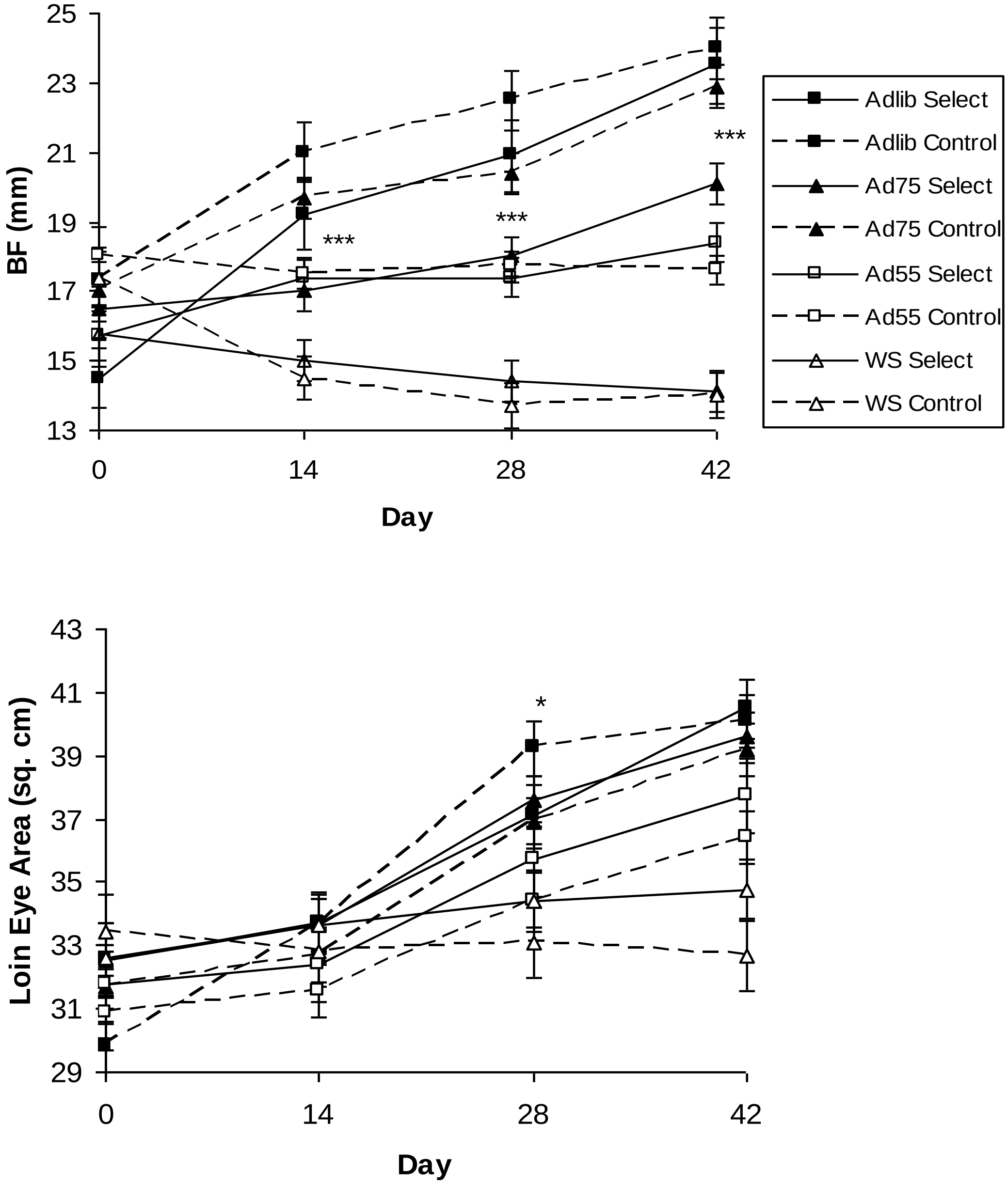

Figure 3. Effects of diet restriction on backfat (bottom panel) and loin eye area (top panel, both measured by ultrasound, pigs from the control and low RFI lines.

Table 3: Least square means for young and older pigs for the Select and Control lines on four feeding treatments.

YOUNG PIGS	**Genetic Line and Treatment**											
Carcass	Adlib		75% of Adlib		55% of Adlib		Weight Stasis		Line difference^{2}	Main Effect p -value		
Item	Select	Control	Select	Control	Select	Control	Select	Control		L	T	L*T^{3}
BW, kg ^{7}	55.0±1.0^{d}	59.1±1.1^{e}	49.3±1.1^{c}	48.1±1.0^{c}	42.7±1.0^{b}	41.3±1.1^{b}	24.4±1.1^{a}	24.1±1.0^{a}	0.33±0.72	0.65	0.01	0.02
BF, mm ^{9}	12.4±0.33^{d}	13.7±0.34^{e}	11.2±0.36^{c}	11.0±0.33^{c}	10.0±0.34^{b}	9.5±0.34^{b}	6.3±0.29^{a}	5.5±0.28^{a}	0.0±0.23	0.90	0.01	0.01
LEA, cm^{2} ^{10}	22.7±0.54^{d}	23.0±0.56^{d}	20.0±0.58^{c}	19.3±0.56^{bc}	18.3±0.55^{b}	17.8±0.56^{b}	12.8±0.48^{a}	12.2±0.48^{a}	-0.40±0.36	0.27	0.01	0.78
Carc.wt kg$^{4, 8}$	46.3±0.39^{d}	45.5±0.38^{d}	37.8±0.40^{c}	37.6±0.36^{c}	32.9±0.36^{b}	33.3±0.39^{b}	19.8±0.37^{a}	18.8±0.36^{a}	-0.40±0.29	0.19	0.01	0.20
Viscera, kg$^{5, 8}$	9.7±0.26^{cd}	10.3±0.26^{c}	9.6±0.27^{cd}	10.0±0.24^{c}	8.4±0.24^{b}	9.0±0.26^{bd}	5.2±0.25^{a}	5.7±0.24^{a}	0.55±0.19	0.01	0.01	0.95
Dress % $^{6, 7}$	0.80±0.01^{a}	0.79±0.01^{a}	0.78±0.01^{a}	0.78±0.01^{a}	0.78±0.01^{a}	0.80±0.01^{a}	0.83±0.01^{b}	0.79±0.01^{a}	-0.01±0.01	0.40	0.08	0.01
Chemical Composition, % of Carcass												
Water, % ^{7}	60.8±0.66^{e}	58.8±0.67^{f}	62.6±0.69^{cd}	62.1±0.65^{de}	64.1±0.65^{bc}	64.1±0.69^{b}	72.4±0.66^{a}	72.6±0.64^{a}	-0.57±0.64	0.39	0.01	0.13
Protein, % ^{7}	18.2±0.23^{bc}	17.8±0.24^{c}	18.5±0.25^{bc}	17.9±0.23^{c}	18.0±0.23^{bc}	18.7±0.25^{b}	20.4±0.24^{a}	19.7±0.23^{a}	-0.24±0.22	0.29	0.01	0.01
Fat, % ^{7}	18.8±0.70^{d}	21.0±0.71^{e}	16.4±0.74^{bc}	17.6±0.68^{cd}	15.4±0.68^{b}	14.9±0.74^{b}	4.2±0.70^{a}	4.7±0.68^{a}	0.83±0.65	0.21	0.01	0.16
Ash, % ^{7}	3.1±0.11^{ab}	3.0±0.11^{b}	3.1±0.11^{ab}	2.9±0.11^{b}	2.9±0.11^{b}	3.2±0.11^{ab}	3.4±0.11^{a}	3.4±0.10^{a}	0.00±0.08	0.96	0.01	0.19
Carcass Energy, Mcal/pig												
BCE ^{11}	55.4±1.9^{d}	57.0±2.1^{d}	42.7±2.0^{c}	42.3±2.0^{c}	35.3±2.0^{b}	33.5±2.0^{b}	13.6±2.0^{a}	12.2±2.0^{a}	-0.52±1.5	0.72	0.01	0.79
GEC^{12}	292.8±13.8	318.4±13.8	204.1±0.0	204.7±0.0	150.8±0.0	150.8±0.0	54.0±1.0	56.4±1.0	--	--	--	--
OLDER PIGS												
BW, kg ^{7}	114.6±1.3^{d}	115.2±1.3^{d}	106.0±1.3^{c}	108.2±1.2^{c}	97.3±1.3^{b}	97.8±1.3^{b}	77.5±1.3^{a}	78.4±1.3^{a}	1.03±0.88	0.25	0.01	0.89
BF, mm ^{9}	23.3±0.67^{de}	24.8±0.63^{e}	20.3±0.61^{c}	22.6±0.61^{d}	17.9±0.65^{b}	17.7±0.64^{b}	14.2±0.62^{a}	14.7±0.63^{a}	0.10±0.04	0.03	0.01	0.16
LEA, cm^{2} ^{10}	41.2±0.86^{d}	40.2±0.85^{cd}	39.3±0.80^{bcd}	39.1±0.80^{bcd}	38.4±0.86^{bc}	37.6±0.83^{b}	32.8±0.80^{a}	31.3±0.84^{a}	-0.88±0.55	0.12	0.01	0.84
Carc.wt kg$^{4, 8}$	98.0±0.41^{d}	97.3±0.41^{d}	90.3±0.41^{c}	89.6±0.40^{c}	82.7±0.43^{b}	82.2±0.40^{b}	66.3±0.41^{a}	65.8±0.41^{a}	-0.57±0.29	0.07	0.01	0.99
Viscera, kg$^{5, 8}$	13.8±0.32^{c}	14.2±0.30^{cd}	13.8±0.32^{c}	14.5±0.30^{d}	12.4±0.31^{b}	12.7±0.30^{b}	9.9±0.30^{a}	10.0±0.30^{a}	0.36±0.17	0.05	0.01	0.46
Dress % $^{6, 7}$	85.3±0.39^{b}	84.8±0.39^{ab}	84.4±0.39^{ab}	83.7±0.38^{a}	84.8±0.42^{ab}	84.2±0.39^{ab}	85.1±0.41^{b}	84.5±0.40^{ab}	-0.62±0.62	0.03	0.11	0.99
Chemical Composition, % of Carcass												
Water, % ^{7}	55.3±1.1	51.2±1.0	54.6±0.98	53.8±1.0	57.4±1.1	55.1±1.0	60.7±1.0	59.1±1.0	-2.18±0.64	0.18	0.01	0.56
Protein, % ^{7}	17.6±0.57^{ab}	17.2±0.56^{a}	17.5±0.52^{ab}	17.8±0.54^{abc}	18.7±0.58^{abc}	17.5±0.55^{ab}	18.8±0.54^{bc}	19.3±0.54^{bc}	-0.20±0.38	0.60	0.03	0.40
Fat, % ^{7}	24.1±1.4	29.6±1.4	25.6±1.3	25.9±1.4	21.6±1.5	24.7±1.4	16.8±1.4	18.9±1.4	2.72±0.95	0.21	0.01	0.53
Ash, % ^{7}	2.9±0.13	2.7±0.13	2.9±0.12	2.7±0.12	2.9±0.13	2.7±0.12	3.1±0.13	3.0±0.12	-0.15±0.10	0.37	0.13	0.95
Carcass Energy, Mcal/pig												
BCE ^{11}	302.8±7.0^{e}	322.0±7.0^{f}	263.0±6.7^{c}	282.2±6.7^{d}	232.6±6.9^{b}	231.4±6.9^{b}	163.3±6.8^{a}	164.2±6.9^{a}	9.50±4.2	0.04	0.01	0.13
GEC^{12}	464.3±18.4	487.1±18.4	360.3±3.3	356.0±3.3	264.4±0.0	264.4±0.0	141.1±1.9	142.4±1.9	--	--	--	--

Footnotes for for Table 3

[a,b,c,d,e,f] ,different letters in a row represent significant differences at $p < 0.05$

[1] values are least square means based on 8 pigs per line per treatment

[2] difference of control minus select

[3] interaction of line by treatment

[4] carcass equals empty body weight, including head and hair

[5] viscera includes entire intestinal tract with contents, kidney, heart, and lungs

[6] dressing percentage is carcass weight as a percent of slaughter weight

[7] analysis included week 0 body weight as a covariate

[8] analysis included week 0 body weight and adjusted slaughter weight (average slaughter body weight within each treatment minus individual pig's slaughter body weight) as covariates

[9] analysis included day 0 body weight and day 0 backfat

[10] analysis included day 0 body weight and day 0 loin eye area

[11] carcass energy determined from protein and lipid values of 5.6 and 9.4 kcal/g, resp.

[12] gross energy consumed over the 6 week test period (analyzed per treatment)

Objective 4: Determine the extent to which differences in RFI are related to concentrations of hormones and metabolites in blood that are indicative of the level of energy and protein metabolism and local production of immune modulators.

Fasting blood measures taken from individually penned pigs from the control and low RFI lines at approximately 115 kg body weight indicated differences in metabolism. Compared to the Control pigs, serum urea nitrogen concentrations were 13% lower ($P<0.05$) in pigs from the Select line, indicating less protein catabolism. In contrast, fasting serum triglycerides and non-esterified free fatty acids concentrations were 25% higher in the Select pigs relative to pigs from the Control line ($P<0.05$). Further, compared to the Control pigs, serum glucose concentrations were 10% lower ($P<0.05$) in the Select pigs, while insulin, free thyroxin, free triiodothyronine and IGF-1 concentrations were not detectably different between the lines.

Ion pumps are another energy expensive process in livestock. Active pumping of ions across the plasma membrane is catalyzed by ATPase at the cost of ATP hydrolysis. Thus, in excess of 20% of the energy expenditure in skeletal muscle, liver and intestines of livestock is attributed to Na^+/K^+ transport and 10% to Ca^{2+} transport. Additionally, this energy cost will vary with the physiological status of the animal. Furthermore, Na^+, K^+ -ATPase dependent respiration has been correlated in pigs with protein synthesis rates. However, the contribution of ATPase pumps in relation to efficiency gains is not known. To investigate this, the activity of Na^+, K^+ -ATPase activity was measured in the ileum and longissimus dorsi tissues of the low RFI and control pigs (Figure 4). Interestingly, there were no differences in the ileiac Na^+, K^+ -ATPase activity. However, a 30% reduction in the Na^+, K^+ -ATPase activity in the longissimus dorsi was observed. This finding is of great significance, as the energetic cost to support these pumps is high and appears to be a substantial component of the maintenance energy expenditure of tissues.

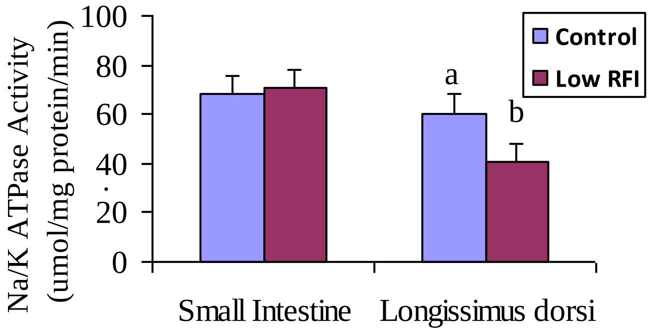

Figure 4. Na/K ATPase activity in ad libitum fed finisher pigs (n=6/line) from the control and low RFI selection lines. Different letters (a,b) represent significant differences at P<0.05.

Protein turnover in animals is also an energetically expensive process. Several indicators were investigated that suggest that selection for low RFI may alter protein degradation and thus protein turnover. First, the amount of intact desmin was correlated with RFI (r= -0.18, P=0.02) in the Select and Control lines. Desmin is an intermediate filament that links adjacent myofibrils and it can undergo rapid proteolysis catalyzed by µ-calpain. Therefore, the higher amount of intact desmin in low RFI pigs indicates less protein degradation. Secondly, pigs from the Select line also had higher skeletal muscle calpastatin activity, compared to the Control pigs (2.09 vs 1.65 units/g tissue, P<0.05). Calpastatin is a competitive inhibitor of the proteinases µ-calpain and m-calpain. These proteinases (specifically µ-calpain) are considered the "initiators" of protein turnover by degrading structural proteins like desmin. Calpastatin thus regulates the initiation of skeletal muscle protein turnover by regulating the calpains. The results of the described experiments show that more calpastatin is expressed in response to selection for low RFI. It therefore follows that less desmin degradation would be detected. Thirdly, blood urea nitrogen was significantly lower in the Select line compared to Control pigs (11.9 vs 13.7 mg/dL, (P<0.05). Together, these results indicate lower rates of muscle protein degradation in pigs selected for low RFI than in the Control pigs. The molecular explanation for this result is not known and must be determined if the mechanism for decreased protein degradation is to be understood in relation to efficiency.

To evaluate the potential impact of selection for RFI on immune-related parameters, complete blood counts were evaluated on all pigs at week 3 and week 6 of treatment. Although treatment effects were significant (P<0.05) at week 6 for white blood cell count and red blood cell count, with counts being higher for the weight stasis treatment, differences between the two lines for blood cell numbers were not found to be significant.

DISCUSSION.

This research has given insight into the biological basis of differences in RFI that were established by selection in the ISU RFI lines. In addition to providing knowledge on the biological and genetic basis of feed efficiency, results can be used to enhance feed efficiency in pork production in several ways: 1) by developing genetic tests and physiological or behavioral indicator traits for feed efficiency, individual breeders can select for feed efficiency without recording intake, and 2) resulting tests and traits can also be useful for sorting pigs at an early age on their potential for lean growth and efficiency, which allows management and feeding to be tailored to each pig's potential. Both these and other uses have the potential to substantially reduce the largest variable cost in pork production, i.e. feed.