Residual feed intake and juvenile IGF-I

[1]Kim Bunter, [2]Weiguo Cai and [2]Jack Dekkers

[1]Animal Genetics and Breeding Unit, University of New England, Armidale, NSW 2351
[2]Department of Animal Science and Center for Animal Genomics, Iowa State University, Ames, IA, USA, 50011-3150.

Introduction

The efficiency of feed use is an important factor influencing costs of production. However, feed intake (FI) is generally difficult and costly to measure. In addition, feed intake *per se* is relatively meaningless unless taken in the context of prevailing environmental and physiological processes. For example, FI and its utilisation by animals is altered by climate, activity levels, disease and physiological status (maturity, lactation and reproductive status), dietary characteristics and delivery, along with individual animal live weight, efficiency of nutrient absorption, energetic efficiency of tissue growth and growth rate, body composition and metabolic rate. Thus, feed intake is rarely used alone; instead there are several measures of feed efficiency that combine feed intake with other measurements in an attempt to reflect production efficiency for a particular circumstance. These measures include (adapted from Archer et al, 1999; Arthur et al., 2004):

- Feed conversion ratio (FCR: kg feed/kg gain) and its European counterpart, feed efficiency (FE: kg gain/kg feed): generally measured on a time constant basis, but occasionally adapted to a weight or maturity constant basis. Correlated with aspects of production, including growth rate and mature size. Commonly used in pigs.

- Maintenance efficiency: the feed required for a zero body weight change. Not measured in practice as hard to manage for growing animals.

- Partial efficiency of growth: the ratio of weight gain to feed after the expected maintenance requirements have been subtracted.

- Efficiency of specific production attributes (eg lactation or egg production): as above but replacing weight gain with product output.

- Residual feed intake (RFI): feed intake adjusted for body weight and weight gain, plus potentially any other production trait requiring energy. Lower RFI is indicative of more efficient animals that require less feed than average for maintenance, growth and production (if production traits are included).

While phenotypic and genetic correlations among efficiency traits tend to be high, they differ from biological and/or mathematical perspectives. Thus, correlations between alternative measures of feed efficiency can be <1, and correlations between alternative efficiency measures and other traits (eg growth rate or mature size) will also differ. Feed conversion ratio is age, and therefore production level, dependent. Residual feed intake measured over different age or weight ranges may biologically differ, but be mathematically similar. Nevertheless, FI and RFI tend to be highly correlated. All other things held constant, differences between individuals in RFI are thought to be related to factors other than growth and composition: for example; feeding behaviour, nutrient digestion, maintenance requirements (activity levels), energy homeostasis and partitioning. Through a collaborative arrangement with Iowa State University (ISU), it is possible for us to examine the associations between juvenile insulin-like growth factor-I (IGF-I), feed intake, performance measures and RFI, using results from an RFI selection line.

Material and methods

Commencing in 2001, a line of Yorkshire pigs was selected for low residual feed intake (LRFI line) over three generations. Performance testing in the LRFI line consisted of recording individual feed intake in group pens fitted with FIRE electronic feeders, along with serial recording of body weight and back fat. Boars were on test between the average weights of 40 and 115 kg. At each generation, males arising from parity 1 (P1) litters in the RRFI line were selected (proportion ~10-12% of performance tested boars) on the basis of their EBVs for RFI. Gilts were selected based on EBV derived from relatives, but with a limit on the number of gilts selected per litter to reduce rates of inbreeding. In addition to RFI data for male selection candidates, information from full-sibs produced from a repeat (P2) mating was used to increase the accuracy of evaluation for RFI in the LRFI line (see Figure 1). The derivation of EBVs for RFI was described in Cai et al. (2006). Essentially RFI was feed intake adjusted for on-test gain and the change in back fat. Metabolic mid-weight was not explicitly included as a covariate in the model for RFI. The target was to produce ~50 litters from 12-15 selected boars and gilts per generation in the LRFI line. In contrast, animals for the control line were selected at random and only limited performance recording was conducted to enable the line contrast. The target was to produce about 25 litters from 9-10 boars per generation in the Control line. All pigs were raised at the ISU Bilsland Swine Breeding Farm.

Recording for IGF-I commenced in generation two. This information was not used for selection decisions so that the correlated response in IGF-I to selection for RFI could be investigated. In generation three, gilts from both the LRFI and Control lines were performance tested (between 40 to 70 kg; ie a different growth phase) for their feed intake, to estimate the change in RFI resulting from selection in the LRFI line.

The resulting data were examined using SAS. Animals were deleted from the data if their performance test period was too short (<28 days), if they were >124 days old at the completion of testing, and if their lifetime or on-test growth rates were <300 g/day. IGF-I data were only included if weaning date was known and piglets were bled at ≤42 days of age. The remaining data (~97-99% of the original data for all traits) were used to estimate heritabilities and breeding values (EBVs) in a series of single trait analyses using ASREML (Gilmour et al., 1999).

Models for estimating parameters and breeding values varied according to trait. For IGF-I, systematic effects included date of bleeding and assay batch (concatenated: 45 levels), along with sex (male: M, female: F) and age at bleeding (fitted as a linear covariate). For lifetime growth rate (LADG) and back fat (BF), models included test start date (26 levels) and sex (M, F, Barrow: B). Off test weight was a linear covariate for BF. For other performance test traits, all models included start date and sex, along with starting weight and age at finish as linear covariates. In addition, length of test was included as a linear covariate for feed intake traits or feed conversion ratio (FCR). Including or excluding further linear covariates for feed intake, such as metabolic mid-weight (MMW), gain on test (TADG), change in BF while on test (DBF), or back fat at the end of test (BF) gave rise to multiple definitions for average daily feed intake (ADFI) or residual feed intake (RFI), which are reported separately. Random effects included animal and litter effects for IGF-I, LADG and BF. However, litter effects were not significant for the remaining performance traits.

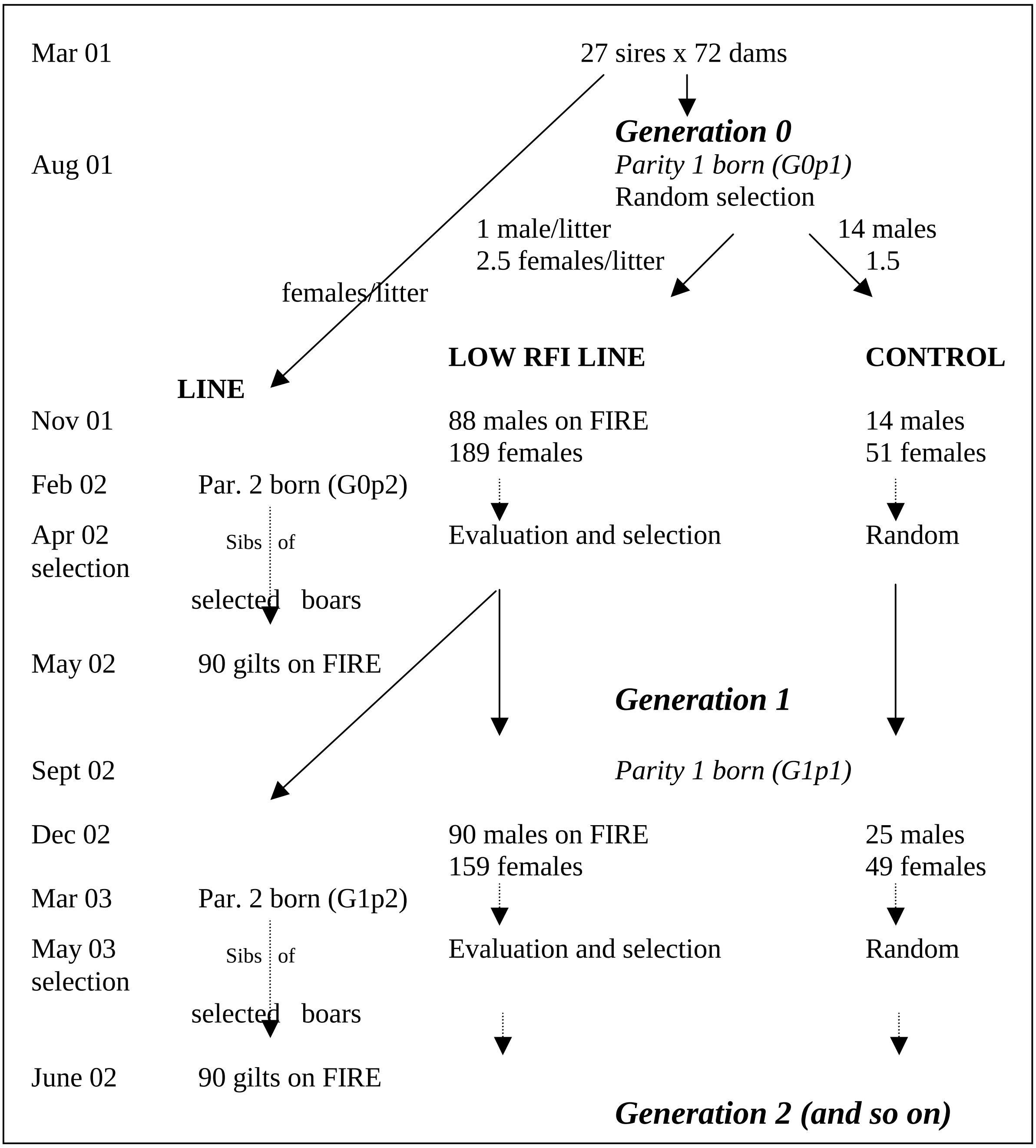

Figure 1. General structure of the ISU Yorkshire RFI selection experiment

Results and Discussion

1. Characteristics of data

Characteristics of edited performance data are presented in Table 1. Age at the start and finish of the performance testing period averaged 86 and 188 days, with coefficients of variation (CV) around 14 and 7% respectively. Corresponding weights were 36.5 and 112.5 kg, with CV of 28 and 10%. Test average daily gain for animals finished in either conventional pens or those fitted with electronic feeders was almost identical.

Table 1. Data characteristics (after editing): SD and CV are the standard deviation and the coefficient of variation

Trait	N. records	Mean (SD)	Range	CV (%)
IGF-I (ng/ml)	1240	178 (75)	6 to 536	42
LADG (g/day)	2763	601 (67)	302 to 789	11
TADG (g/day)	2763	757 (111)	306 to 1172	15
BF (mm)	2763	17.7 (5.19)	6.0 to 43.9	29
ADFI (kg/day)	813	2.00 (0.26)	1.04 to 2.87	13
FCR (kg/kg)	813	2.66 (0.28)	1.87 to 5.21	11

IGF-I: Insulin-like growth factor-I measured after weaning and before 42 days of age
LADG: lifetime average daily gain
TADG: average daily gain on test, calculated from start and end weights only
BF: 10th rib back fat measured by ultrasound
ADFI: average daily feed intake on test (average weights: start 36kg; end 112kg)
FCR: feed conversion ratio (kg feed per kg gain)

2. Estimates of genetic parameters

Parameter estimates obtained from single trait analyses are shown in Table 2.

Table 2. Genetic parameters along with the phenotypic standard deviation (σ_p) for performance traits

Trait	Covariates*	h^2 (×100)	c^2 (×100)	σ_p
IGF-I (ng/ml)		20±8	16±4	66
LADG (g/day)		44±6	9±2	63
TADG (g/day)		27±4	-	92
BF (mm)		43±5	-	3.97
ADFI_1 (kg/day)		45±9	-	0.209
ADFI_2 (kg/day)	+MMW	41±9	-	0.138
ADFI_3 (kg/day)	+MMW+TADG	41±9	-	0.135
ADFI_4 (kg/day)	+MMW+DBF	38±9	-	0.128
ADFI_5 (kg/day)	+MMW+BF	37±9	-	0.127
RFI_1 (kg/day)	+MMW+TADG+DBF	37±9	-	0.124
RFI_2 (kg/day)	+MMW+TADG+BF	36±9	-	0.122
FCR (kg/kg)		23±7	-	0.23

*MMW: metabolic mid-wt; TADG: test average daily gain; DBF: change in BF depth over test period; BF: final back fat depth.

The estimates of heritability and common litter effects for IGF-I are similar to those observed previously (Bunter et al., 2005). Parameter estimates for the remaining comparable traits are similar to those reported by Cai et al. (2006). Parameter estimates are not significantly different between these studies, although changes result from different analytical models and editing procedures. Overall, parameter estimates for performance traits are similar to those reported elsewhere (Clutter and Brascamp, 1998).

3. Line differences

Estimated breeding values for each trait were predicted using the models and parameters noted above. The average EBV in generation three for animals with records, by line, is shown in Table 3. For simplicity, results for ADG_5 and RFI_2 are not presented; these traits were almost identical to ADFI_4 and RFI_1, for which results are presented. Results clearly show that selection for low RFI was effective in generating a significant difference between lines by generation three in alternative measures of RFI (including ADG_2, ADG_3, and ADG_4). Correspondingly, correlated responses were observed in the component traits that contribute to RFI (ie daily gain, back fat and feed intake: ADG_1).

Table 3. Average EBV in generation three, by line, for animals with records only

		EBV by line	
Trait	Covariates*	Select	Control
IGF-I (ng/ml)		-9.93****	9.60
LADG (g/day)		-10.2****	3.6
TADG (g/day)		-13.4****	20.4
BF (mm)		-1.03****	0.84
ADFI_1 (kg/day)		-0.16****	-0.004
ADFI_2 (kg/day)	+MMW	-0.12****	-0.002
ADFI_3 (kg/day)	+MMW+TADG	-0.12****	-0.01
ADFI_4 (kg/day)	+MMW+DBF	-0.11****	0.009
RFI_1 (kg/day)	+MMW+TADG+DBF	-0.11****	-0.0004
FCR (kg/kg)		-0.10****	-0.009

*p<0.05; **p<0.01; *** p<0.001; ****p<0.0001

If maintenance, growth and back fat remained constant under selection for RFI, the change in ADFI_1 and RFI would be identical. However, this was not the case because production traits also changed under selection for RFI. Trends over time in the between line difference in mean EBV for a range of traits are shown in Figure 2. This difference is divided by the relevant trait phenotypic standard deviation for illustrating relative response. With respect to feed intake, trends are presented only for ADFI_1 (ie daily feed intake unadjusted for production level and body composition), ADFI_2 (ie daily feed intake accounting for assumed maintenance requirements only), and RFI_1 (ie daily feed intake adjusted for maintenance, production and composition components). Results for the excluded ADFI and RFI traits were similar.

The greatest response (approximately -0.89 SD units) was observed in feed intake traits, particularly those corrected for differences in maintenance requirements, production or composition (RFI, ADFI_2). This outcome is to be expected, as RFI was the selection criterion for the LRFI line. The change in feed intake *per se* (ADFI_1) was slightly less at –0.77 SD units, while downward trends for BF, LADG, and TADG in the LRFI line were of much lower magnitude (-0.22 for LADG to –0.47 for BF, in SD units). The trend for FCR, an alternative measure of efficiency, mirrored that for RFI but was lower (-0.39 SD units), even if standardised by the genetic standard deviation (not shown). The correlated response for IGF-I was –0.30 SD units, which was in the expected direction and of large magnitude.

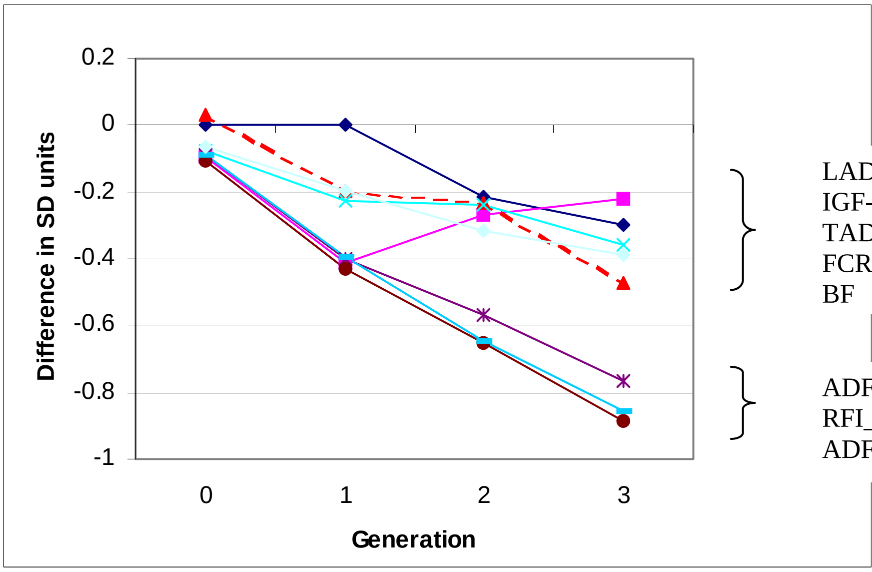

Figure 2. The differences between mean EBVs for select and control lines for each trait (rescaled to standard deviation units)

Comparison with other lines

Gilbert et al. (2006) also reported on the difference in performance of divergent LW lines selected for RFI over three generations in France. Selection for RFI was exerted on males only based on their phenotypes; thus accuracy of selection was expected to be lower than for the ISU lines. RFI was measured on group-housed LW males fed *ad-libitum* between a fixed body weight range of 35 to 95 kg using ACEMA 64 electronic feeders. The resulting ADFI and RFI were much less heritable (h^2=0.17±0.05 and 0.15±0.05) than the comparable traits of Cai et al (2006). By generation three, the divergently selected lines of Gilbert et al (2006) significantly differed by ~0.3, 0.25, and 0.23 phenotypic SD units for RFI, FCR and DFI respectively. This change is smaller than would be expected from divergently selected lines when compared to results from a single selected line at ISU. However, the lower response might reflect the lower heritability of their RFI. Further, in their study, between line differences in test average daily gain and back fat were not significant. However, they reported a consistent divergence between lines over generations for BF. With the relatively low number of animals recorded (N=625) and the lower response to selection, it is possible that lack of significance was simply due to low numbers, since correlated responses were of lesser magnitude than for RFI.

It should be noted that while both studies showed strong responses for RFI, the magnitude of correlated responses for component traits differed. This result cannot be solely attributed to differences in scaling, since the reported trait phenotypic standard deviations for component traits were similar between studies. The ISU data showed a substantially larger relative and absolute change in feed intake under selection compared to the data from France. The French selection lines demonstrated a more similar relative magnitude of response for RFI, DFI and FCR than did the ISU lines.

Factors that could influence the magnitude of change in the component performance traits include:

- Chance and population specific differences, in particular heritability of feed intake
- The age and weight range over which RFI is recorded, and therefore the relative contributions of maintenance, gain and compositional components to RFI for selection candidates **and evaluation animals**. This includes aspects of accuracy of measurements and biological changes associated with phase of growth.
- Selection on own phenotype in the French study compared to selection on EBV in the ISU lines
- Asymmetric response in the French divergent selection lines

In contrast to single trait selection for RFI, single trait selection for FCR does not by definition have to result in reduced feed intake (although reduced feed intake is frequently the outcome when selection is based on FCR and measures of leanness). For example, Hailu et al. (1995) reported an increase in both growth rate and feed intake in a dam line of Dwarf White Rocks (poultry). In contrast, Clutter and Brascamp (1998) noted that two other studies in pigs reported negligible response for single trait selection on FCR.

4. Correlations between EBVs

Correlations between trait EBVs obtained from uni-variate analyses and raw phenotypes are presented in Table 4. Please note, these correlations reflect both genetic and environmental trends, along with the underlying genetic and environmental correlations between traits. Correlations (r) between EBVs for feed intake traits (ADFI_1, ADFI_2 and RFI_1) were very high (range in r: 0.72 to 0.93). In contrast, feed intake alone was not highly correlated with FCR (r: 0.34) unless adjusted for differences in maintenance, production and body composition (r: 0.78). Lifetime and test growth rates were highly correlated (r: 0.83) due to auto-correlation, while growth on-test was highly correlated with feed intake during this period (r: 0.76), both results as expected. Correlations between EBVs for IGF-I and performance traits were in the expected directions, as were correlations between raw phenotypes.

Table 4. Pearson correlations (×100) between uni-variate EBVs (above diagonal) and raw phenotypes (below diagonal) for animals with records

Trait	IGF-I	LADG	TADG	BF	ADFI_1	ADFI_2	RFI_1	FCR
IGF-I		15	6.4	36	24	24	26	8.4
LADG	0.5		83	24	61	22	15	-21
TADG	-7.7	90		36	76	34	26	-17
BF	29	41	38		51	48	21	29
ADFI_1	14	75	49	49		80	72	34
ADFI_2	-	-	-	-	-		93	78
RFI_1	-	-	-	-	-	-		78
FCR	8.8	-37	-50	-1.6	16	-	-	

Conclusions

Results from juvenile IGF-I testing in the LRFI selection and control lines managed at Iowa State University provide supporting evidence for the previously reported genetic correlations between IGF-I and performance traits. In the LRFI line, selected solely for improved efficiency by selecting for lower RFI, a correlated response in the expected direction was observed for juvenile IGF-I.

A comparison of the ISU results with those from the French divergent selection lines showed a different pattern and magnitude of change in component traits under single trait selection for RFI. Numerous factors could have contributed to this difference, including chance. However, more generally, this trial comparison demonstrates that there are many pathways to improved efficiency, and it may be difficult to predict relative changes in component traits that contribute to the improved efficiency with variable trait definitions for efficiency, under alternative performance testing systems, and for populations that may differ in their most limiting factor with respect to efficiency.

Both selection trials have shown that lower RFI is specifically accompanied by a proportionally larger reduction in feed intake compared to a lesser reduction in growth traits. In addition, a stronger change in body composition is implicated with selection for improved RFI relative to the observed change in growth traits.

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