Does selection for RFI affect the sensitivity to environmental variation in pigs?

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ABSTRACT: Data were recorded in two lines divergently selected for residual feed intake (RFI) for eight generations (G0 to G7). First, an animal mixed model was applied to the full dataset to estimate least square means (LsCG) of contemporary group (CG) effects for average daily gain (ADG, 3189 pigs, 80 CG) and backfat thickness (BFT, 1668 pigs, 44 CG). Second, LsCG were used as covariates in linear models on these traits to estimate line specific regression coefficients in the later generations of selection (G6 and G7). The low RFI line showed lower regression coefficients for ADG than the high RFI line ($0.05 \leq P < 0.11$), indicating lower sensitivity to environmental variations. No difference was evidenced for BFT. Contrary to the literature, increased sensitivity to environmental variability was observed for higher RFI pigs, not for lower RFI, challenging the understanding of RFI as a buffer to face stresses.

Keywords: feed efficiency; genetics; environmental sensitivity

Introduction

Selective breeding of commercial populations is essentially carried out on animals bred in nucleus herds with high quality controlled environments. However, studies have indicated that selection for higher productivity in a non-limiting environment increases environmental sensitivity (Kolmodin et al., 2003). Results by Schinckel et al. (1999) showed significant genotype by herd-health status interactions in pigs. In their study, the pig genotypes selected for higher productivity grew faster in the high-health environment, while the less productive genotype was superior in the low-health environment. Recent studies (Li and Hermesch, 2014) have found environmental variation within nucleus herds with good health status and management practices. This variation was of similar magnitude as that observed between herds. The within-herd variation might be due to variations in daily temperatures, stocking density, feed quality, and unknown environmental factors. It has been proposed that quantifying the sensitivity of pigs to within-farm environmental variations could be a tool to explore environmental sensitivity of pigs between farms and breeding environments, with the aim to propose new selection strategies that encompass both productivity and reduced environmental sensitivity.

Feed efficiency is a major component of overall production efficiency. It is usually measured by feed conversion ratio (FCR), or residual feed intake (RFI, Koch et al. (1963)). The RFI is the difference between the observed feed intake and that predicted for growth and maintenance requirements. In growing animals, it is usually computed as the residual of a multiple linear regression of feed intake on growth rate, body composition and metabolic body weight of the animals. The main difference from FCR is the absence of correlation between RFI and growth rate or body composition (Kennedy et al., 1993). The RFI is understood to cover, among others, differences in activity, metabolism and ability to face challenges such as diseases or heat waves (Richardson and Herd, 2004). Decreasing RFI has also been interpreted as increasing animals' sensitivity to environmental variations, and reducing robustness (Knap, 2009). Two lines of pigs have been divergently selected at INRA for residual feed intake (RFI) for eight generations (Gilbert et al. 2007). Previous line comparisons have shown that the more efficient RFI line have reduced feed intake and basal metabolism compared to the less efficient line, suggesting a potential physiological advantage to face hot breeding environments (Barea et al, 2010). However, later studies showed that this advantage is offset by the higher sensitivity of the more efficient line to the reduction of feed intake in response to heat stress (Renaudeau et al. 2013). The purpose of the present study was to quantify the environmental variation in our breeding conditions, and to evaluate the environmental sensitivity in the RFI lines. Responses of environmental sensitivity for average daily gain and backfat thickness are reported, two traits which show no correlated responses to RFI selection.

Materials and Methods

Animal breeding and line management. Data comprised two lines divergently selected for RFI (highRFI for high RFI; lowRFI for low RFI) in INRA farms (GenESI, Surgères, France) for eight generations (G0 to G7) (Gilbert et al., 2012). In G7, the lines diverged by 3.1 genetic standard deviation for RFI. Contemporary groups (CG) were defined as the week of birth and were separated by at least three weeks. Sows of both lines were distributed over four of the seven batches of the herds, and generations did not overlap. Sow parities corresponded to four successive CG. In G0, five CG were tested for selecting the line founder sires (6/line). From G1 to G5, the first parity (4 CG) comprised only males candidate for selection tested from 35 kg BW to 95 kg body weight (BW) (later called candidates to selection) and the second parity (4 CG) was only females and castrated males tested from 70 days of age to 110 kg BW and slaughtered for records on meat quality and carcass composition (later called response pigs). In G6, parities 1, 2, 4 and 5 (16 CG) were response pigs, and parity 3 (4 CG) was only candidates to selection. In G7, parities 1, 2, and 3 (11 CG) were response pigs, and parity 4 (4 CG) was candidates to selection.

Data. Pigs were tested from ten weeks age to 110 kg BW. All pigs were weighed at the beginning and at the end of the test, and test average daily gain (ADG) was computed. Response pigs had records for carcass backfat thickness (BFT, average of three measurements taken on the middorsal line at the level of shoulder, last rib, and hip joint). The CG had a maximum of 48 pigs on test. Number of pigs with validated records in each CG ranged from 16 to 47 for ADG (N groups = 80; N pigs = 3189) and from 19 to 47 for BFT (N groups = 44; N pigs = 1668). Descriptive statistics for the ages, BW and traits are given in Table 1.

Table 1. Mean, standard deviations (SD), minimum (MIN) and maximum (MAX) values for the covariates[&] and traits (N=3189, except for BFT, N=1668).

Trait	MEAN	SD	MIN	MAX
BW b, kg	26.7	4.3	12.0	48.0
BW e, kg	110.1	9.0	60.0	146.0
age b, d	67.5	2.1	59.0	87.0
age e, d	176.8	13.2	137.0	229.0
ADG, kg/d	0.773	0.087	0.271	1.073
BFT, mm	22.5	4.9	10.0	38.3

[&] age and BW at the beginning of test (age b and BW b, respectively), age and BW at the end of test (age e and BW e, respectively).

Statistical analyses. First the full data set (3996 pigs; 3189 records + pedigree) was analyzed with an animal mixed model (1) using ASReml (Gilmour et al., 2009) to estimate the CG effect. The models for ADG included fixed effects of the herd of birth (2 levels), sex (3 levels) and pen (16 levels, 4 per CG), and covariates of age and/or BW at the beginning of test, plus the random effects of the animal and CG. The models for BFT included fixed effects of the herd of birth (2 levels), sex (2 levels) and pen (16 levels, 4 per CG), and covariates of age and/or BW at the end of the test, plus the random effects of the animal and CG.

Second, linear mixed models were applied on data from females and castrated males from the G6 and G7 generations (N groups= 27; N pigs = 1089 for ADG; N groups = 15; N pigs = 889 for BFT), using the least square means of the contemporary groups (LsCG) estimated with models (1) as covariates with regression coefficients depending on a line effect (proc MIXED, SAS). These linear models (2) were $y_{ijklmn} = \mu + herd_i + sex_j + line_k + a_1 \cdot BW + a_2 \cdot age + b \cdot LsCG_m + b_{line} \cdot LsCG_m + sire_l + e_{ijklmn}$, where herd, sex and line were the fixed effects, age and BW were covariates of the age and BW at beginning of test (ADG) or the age and BW at end of test (BFT), and the same covariates were fitted in both models (1) and (2), b is a general regression coefficient on LsCG, b_{line} is a regression coefficient depending on the line (2 levels) on LsCG, sire is a random effect of the sire (not structured by the parenty matrix), and e is the random residual. The b_{line} coefficient for the lowRFI line was constrained to zero.

Finally, a linear model (proc MIXED, SAS) with the fixed effects of the herd of birth (2 levels), sex (3 levels) and line (2 levels) was applied on age and BW at beginning and at end of test on the 1082 pigs from G6 and G7, to test the line effect on the covariates used in the models.

Results and Discussion

Line effect on covariates. The lowRFI pigs were older (P < 0.0028) than the highRFI pigs at beginning (0.61 ± 0.18 days) and at end of test (3.22 ± 0.70 days). The line effect was not significant on BW at beginning and at end of test (P>0.15). When adjusted for age at measurement, BW at the beginning of test was lower in the lowRFI than in the highRFI line (-770g; P=0.005), whereas the line effect was not significant on adjusted BW at end of test.

Variance components estimations. The BW at the beginning of test significantly explained variance of ADG (P < 0.001) in models (1), and the age was a tendency (P = 0.09). For BFT, both covariates in models (1) were significant (P < 0.001). The CG variance was equivalent to 39% of the genetic variance for ADG, and equivalent to the genetic variance for BFT. This suggests a large potential for improvement of the traits by reducing pigs' environmental sensitivity. Heritability estimates [(genetic variance) / (genetic variance + residual variance)] was 0.33 ± 0.05 for ADG with all models (1), and 0.35 ± 0.07 to 0.39 ± 0.07 for BFT. Standard errors (SE) of variance components estimations were larger when only the age at the end of test was used in model (1) for BFT compared to models (1) where other choices of covariates were used.

Estimation of contemporary group effects. The LsCG when age and BW at the beginning of test were used as covariates for ADG in model (1) ranged from -56g/d for most unfavorable CG to +54g/d for most favorable CG (Figure 1), with standard deviation (SD) of 25 g/d. For BFT, LsCG when age and BW at the end of test were used as covariates ranged from -3.08 to 3.80 mm (Figure 1) with SD of 2.0 mm. Largest variations were found in later generations, when more contemporary groups and more parities were available. Models (1) with other choices of covariates gave similar values, except for BFT when only the age at the end of test where the range was larger (-3.83 to 4.27 mm). The SE of LsCG ranged from 13 to 20 g/d for ADG and from 0.8 to 1.0 mm for BFT, with a limited effect of the number of pigs per contemporary group on the accuracy of the estimations (Figure 2).

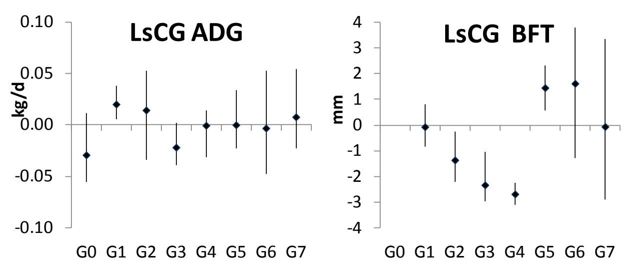

Figure 1. Distribution of mean (diamonds), max and min estimates for least square means of contemporary groups (LsCG) for ADG and BFT when both covariates were included in mixed models, depending in the generation (G0 to G7). For ADG, N groups = 5 for G0, 8 for G1 to G5, 20 for G6, and 15 for G7. For BFT, N groups = 4 for G1 to G5, 12 for G6, and 11 for G7.

Correlations between LsCG for different models (1) were higher than 0.98 for ADG and 0.91 for BFT. Correlations between LsCG for the two traits were significantly different from zero, low and negative, ranging from -0.08 to -0.24, indicating that favorable environments for ADG would also be favorable for BFT.

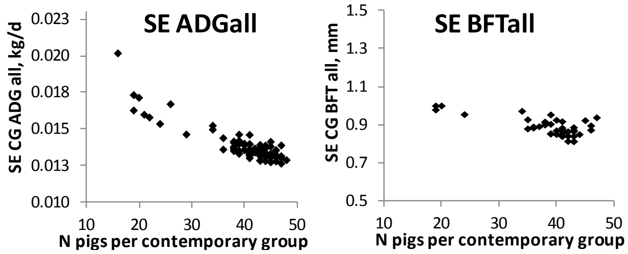

Figure 2. Standard errors of the least square means for the contemporary groups (LsCG) depending on the number of pigs measured for the trait in the group. LsCG when the two covariates are included in models (1) for ADG (left, N groups = 80, N pigs = 3189) and BFT (right, N groups = 44, N pigs = 1668). The y-axis width represents half a standard deviation of the LsCG.

Line effect on regression coefficients for contemporary groups. The fixed effect of the line was not significant in models (2) for ADG (P > 0.16) and BFT (P > 0.63). This was expected, as selection for RFI is to change the components of feed efficiency that are independent from growth rate and body composition, at least at the phenotypic level (Kennedy et al., 1993). Estimates for the general regression coefficient b were not significantly different from 1 for all models. The b_{line} estimates, representing the contrasts between regression coefficients on LsCG for the highRFI and the lowRFI line, were significantly different from zero or were a tendency ($0.05 \leq P < 0.11$) for ADG, ranging from +0.37 to +0.47 kg/d. The SE were relatively large (0.23 to 0.24), so the magnitude of the line difference in terms of regression coefficients was not accurately estimated. However, the estimations systematically indicated a positive increase of the slope for the highRFI line compared to the lowRFI line, corresponding to an increased variability of ADG depending on the quality of the environment in the highRFI line. This potentially decreased robustness in the highRFI line was unexpected and needs confirmation. However, this result, together with previous studies showing no impaired responses to immune stress in lowRFI lines (Gilbert and Dekkers, 2013), questions the role of RFI as a buffer nutrient compartment to respond to stress (Knap, 2009). The contrasts between regression coefficients for each line were not significantly different from zero for BFT (P > 0.23), showing that the environmental sensitivity for BFT was not affected by selection on RFI. Previous studies have also reported significant breed differences for environmental sensitivity for growth rate in three different breeds (Li and Hermesch, 2014), and in the same study no breed difference was found for environmental sensitivity of body composition.

Despite significant line effects on the age at the beginning and at the end of test, and on BW at the end of test adjusted for age, estimations of LsCG and b_{line} were consistent across models (1) and (2), and results were robust to the choice of covariates.

Table 2. Estimates of the general regression coefficients (b) and of the regression coefficient for the highRFI (b_{line}) on the least square means of contemporary groups (LsCG) (± SE) for ADG (kg/d) and BFT (mm).

LsCG[&]	b	b_{line}	P value
ADG all	0.95 ± 0.17	0.46 ± 0.24	0.05
ADG age b	0.97 ± 0.16	0.37 ± 0.23	0.11
ADG BW b	0.95 ± 0.16	0.45 ± 0.23	0.05
BFT all	0.99 ± 0.10	0.17 ± 0.14	0.23
BFT age e	0.99 ± 0.10	0.10 ± 0.14	0.45
BFT BW e	1.05 ± 0.10	0.08 ± 0.14	0.55

[&] Age and BW at the beginning of test (age b and BW b, respectively) for ADG or at the end of test (age e and BW e, respectively) for BFT, or both (all), included as covariates in models (1) and (2). The fixed effect of the line was not significant for these analyses (P>0.15). b_{line} for lowRFI = 0.

Conclusion

The lowRFI line showed less sensitivity to environmental variations for ADG than the highRFI line, despite no response to selection for RFI on ADG. On the other hand, no line related environmental sensitivity was evidenced for BFT. Contrary to what literature suggests increased sensitivity of the pigs to the environmental variability was observed for pigs selected for higher RFI, and not for lower RFI. This result needs confirmation, but questions the usual understanding of RFI as a buffer compartment for animals to face stresses (Knap, 2009).

Acknowledgements

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Literature Cited

Barea, R., Dubois, S. Gilbert, H. et al. (2010). J. Anim. Sci., 88:2062–2072.

Gilbert, H., Bidanel, J. P., Billon, Y. et al. (2012). J. Anim. Sci., 90:1097-1108.

Gilbert, H. and Dekkers, J. C. M. (2013). Proc of the 64th EAAP meeting, pp 589.

Gilmour, A. R., Gogel, B. J., Cullis, B. R. et al. (2009). ASReml User Guide VSN International Ltd, Hemel Hempstead, HP1 ES, UK.

Kennedy, B. W., van de Werf, J. H. J. and Meuwissen, T. H. E. (1993). J. Anim. Sci. 71:3239-3250.

Knap, P. (2009). Pp. 210-229 in Resource allocation theory applied to farm animal production.

Koch, R. M., Swiger, L. A., Chambers, D. et al. (1963). J. Anim. Sci. 22:486–494.

Kolmodin, R., Standberg, E., Jorjani, H. et al. (2003). Anim. Sci. 76:375-385.

Li, L., and Hermesch, S. (2014). Anim. Prod. Sci. submitted.

Renaudeau, D., Frances, G., Dubois, S. et al. (2013). J. Anim. Sci. 91:1162-1175.

Richardson, E. C. and Herd, R. M. (2004). Aus. J. Exp. Agri. 44:431-440.
Schinckel, A. P., Richert, B. T., Frank, J. W. at al. (1999). Purdue University 1999 Swine Day Report.