Genotypes differ in their response to variation in environments experienced by pigs on farm

Li Li and Susanne Hermesch

Animal Genetics and Breeding Unit (AGBU), University of New England, Armidale, NSW, 2351, AGBU is a joint venture between NSW Department of Primary Industries and the University of New England.

Genotype by environment interactions

Both animals and plants have the ability to respond to changes in their environment, which is called environmental sensitivity or phenotypic plasticity (Bradshaw, 1965). Different genotypes do not respond in the same way to different environments leading to genotype by environment interactions (GxE). There are two types of GxE: scaling effects or re-ranking for individuals. As different scaling effects for different traits can also results in re-ranking of genotypes, both are important for animal breeding and selection (Strandberg, 2006). Two traditional methods to analyse GxE are the interaction-term model and the multiple-trait model. Both methods assume that distinct environments exist. When the production environment can be described as a continuous gradient, reaction norm models are a viable alternative (Kolmodin *et al.* 2002).

The environment is quantified on a continuous scale in reaction norm models instead of being classified into groups in the traditional GxE methods. The environment is not only the space surrounding the animal; it also includes temperature, floor space, air, nutrition, feeding, vaccination etc. As the observed performance phenotype is the result of all environmental factors, it is common to use the mean performance of animals raised in the same environment as a proxy for the sum of all environmental factors affecting performance of animals (e.g. Calus and Veerkamp, 2003; Knap and Su, 2008; Hammami *et al.*, 2009).

Reliable estimates of the parameters of reaction norm models can only be obtained when there is sufficient variation in the independent parameter, a descriptor of the environment, and when progeny of sires are distributed across environments to ensure that sires have a good representation across a wide range of environments. It was the aim of this study to quantify variation in environmental descriptors within and between herds and to explore genotype by environment interactions.

Description of data

Data comprising Duroc (DU), Large White (LW) and Landrace (LR) pigs recorded from 2000 to 2010 were used. These herds are part of the across-herd genetic evaluations of the National Pig Improvement Program (NPIP) in Australia. Only herds with at least 1000 animals for each breed and at least two breeds were used for these analyses. On average, pigs were recorded for lifetime average daily gain (ADG) and backfat (BF) at a live weight of 92.8 kg. For both traits, only records that were within the range of four standard deviations from the mean of each trait within breed were considered in these analyses. After editing, the data contained 265,165 pigs belonging to nine herds, of which 130,766 were female and 134,399 were male pigs. The pedigree file was generated based on all animals with observations leading to a total of 268,989 animals from 2,394 sires and 12,363 dams.

General outline of models

The analyses were based on two steps. Firstly, estimates of environmental conditions were obtained for contemporary groups. These estimates of environments were then used as an independent variable in reaction norm models to evaluate the response of pigs from the same breed (breed by environment interactions) or progeny of sires (sire by genotype interactions) to changes in environmental conditions.

1. Models for analyses of environmental variable

Contemporary groups were based on herd by birth month (HBM) time periods. Four quantities were used to compare the properties of the two alternative environmental descriptors. These were the phenotypic mean of a contemporary group (Mean) and least squares means (LSM1, LSM2, LSM3) obtained from three linear models fitted to ADG and BF using PROC GLM in SAS (1999). Fixed effects for all three linear models were sex, birth parity and breed fitted for both traits and weight at test fitted as a linear covariate for BF only. The common litter effect was fitted as a random effect for both traits in all models. The first linear model to obtain least squares means of contemporary groups (LSM1) did not include a genetic component. Alternative models to obtain estimates of environmental conditions included sire (LSM2) or animal (LSM3) as additional random effects.

2. Statistical models used for reaction norm analyses

Reaction norms for breed were obtained by adding a fixed regression on the environmental variable for each breed, which also included the intercept for each breed. Breed was therefore not fitted as a separate fixed effect as in the models outlined above. An animal model was used fitting all other fixed effects outlined above.

Reaction norm models to investigate sire by environment interactions fitted an intercept and a slope for each sire. The estimate of the intercept represents the estimated breeding value of a sire in the average environment. The slope of a sire quantifies the response of progeny of a sire to changes in environmental conditions. Again, an overall fixed regression on the environmental variable was used to account for the overall changes of all pigs along the environmental trajectory. Differences between sires in regard to the response of their progeny to variation in different environmental variables were evaluated. The primary environmental variable was defined as the least squares means of the contemporary group for the trait of interest. For example, the primary environmental variable for ADG was the least squares means in ADG of the contemporary group. The secondary environmental variable was based on the other trait. Using the example of ADG, the secondary environmental variable was based on least squares means for BF of the contemporary group. Only sires with a minimum of 50 progeny were used in the analyses.

All reaction norm analyses were performed with the ASReml statistical software package (Gilmour *et al.*, 2009).

Data summary

Most records were available for Large White pigs while Duroc was the smallest breed with approximately 33,000 records available (Table 1). Duroc had the lowest weight and age at recording which were highest for Large White. Growth rate was similar across breeds and Landrace had a slightly lower backfat than the other two breeds.

Table 1. Descriptive statistics for weight at test (WT), age at test (AGE), average daily gain (ADG), and back fat (BF) for the three breeds Duroc (DU), Landrace (LR) and Large White (LW) as well as the total data set (All) (means; standard deviations).

Breed	N	WT (kg)	AGE (days)	ADG (g/day)	BF (mm)
DU	33,677	90.1; 12.7	139.0; 14.3	649.1; 72.7	10.5; 2.0
LR	87,987	92.9; 13.9	142.7; 16.9	652.0; 72.8	10.3; 2.0
LW	143,501	93.3; 13.5	144.5; 17.8	648.0; 73.3	10.7; 2.1
All	265,165	92.8; 13.6	143.2; 17.2	649.5; 73.1	10.5; 2.1

There were 950 herd by month groups with an average number of animals of 279 ranging from 16 to 1071 pigs per group. The distribution of the number of animals per group is shown in Figure 1. The distribution was characterized by a tail representing larger contemporary group sizes outside the normal distribution.

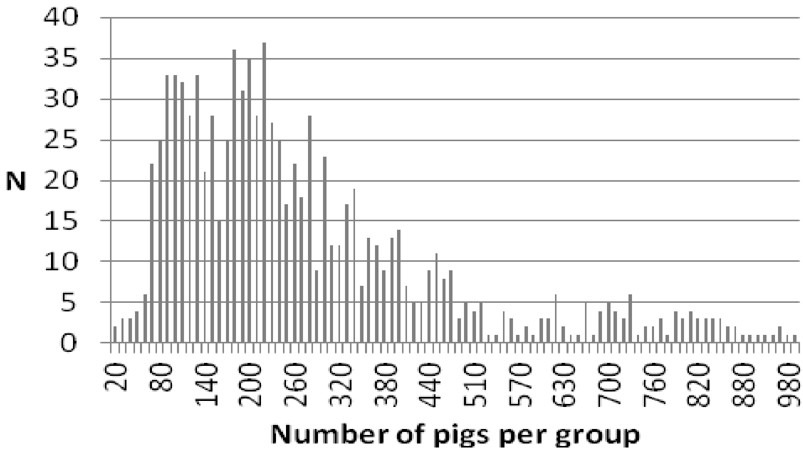


Figure 1. Frequency distribution (N) per herd by birth month group.

Distribution of mean performance of contemporary groups

The mean performance per contemporary group was normally distributed for both traits (Figure 2). The spread in mean phenotypic performance (Mean) and least squares means from different linear models were similar ranging from about 540 g/day to 720 or 740 g/day for ADG. There were less contemporary groups with higher least squares means for the animal model indicating that the higher mean for these groups obtained from alternative models may have included some additive genetic effects that were better accounted for in the animal model in comparison to the other models.

As to BF, the distribution of contemporary group predictors based on the three least squares means (LSM1, LSM2, LSM3) were similar, with means and least squares means ranging from about 8.0 mm to 14.0 mm. The mean of the mean phenotypic performance of each contemporary group (Mean) was around 0.56 mm less compared to the average of three least square means due to the adjustment for other effects fitted in models.

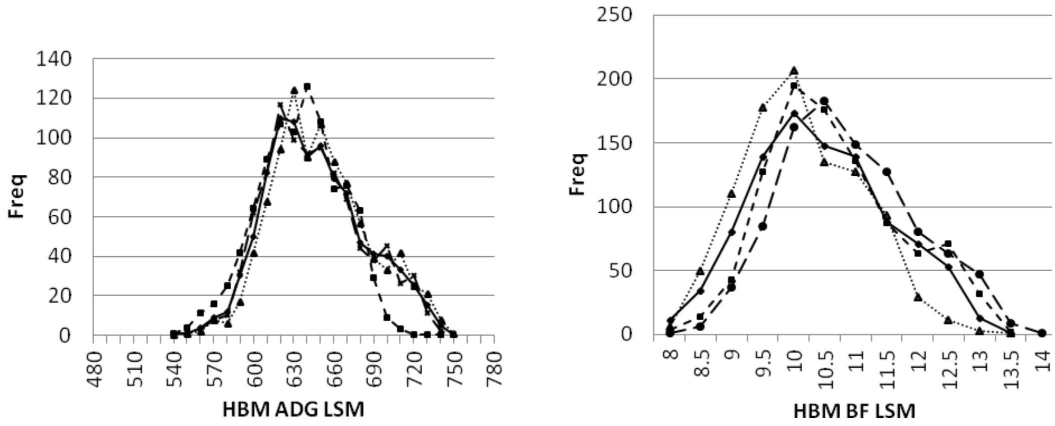


Figure 2. Distribution of means or least squares means (LSM) for average daily gain (ADG) and backfat (BF) for herd-by-month contemporary groups derived from different models (Mean: mean phenotypic performance, LSM1: least squares means from linear mixed model fitting fixed effects only; LSM2: least squares means from sire model, LSM3: least squares means from animal model).

Variation in least squares means of contemporary groups within herds and within years

In order to detect sire by environment interactions a good spread of progeny records across environmental conditions is required. In pig breeding programs in general, sires may only be used within a single herd over a relatively short time period of a few months. Therefore, variation in least squares means of contemporary groups obtained from the animal model (LSM3) was further explored by evaluating within-herd and within-year variation in least squares means. The spread of least squares means showed a range of 109 g/day to 162 g/day for ADG and 3.0 mm to 4.9 mm for BF (Figure 3) within years indicating that most variation observed in least squares means across years was also apparent within years for both traits.

There was also a considerable spread of least squares means for herd by month contemporary groups within herds for both ADG and BF. A range of 87 to 145 g/day for ADG and a range of about 1.6 mm to 3.5 mm for BF (Figure 4) were found within herds. The variation in the mean BF of contemporary groups was greater between herds than between years. This larger variation in average BF between herds was partly due to variation in weight at test and differences in selection emphasis.

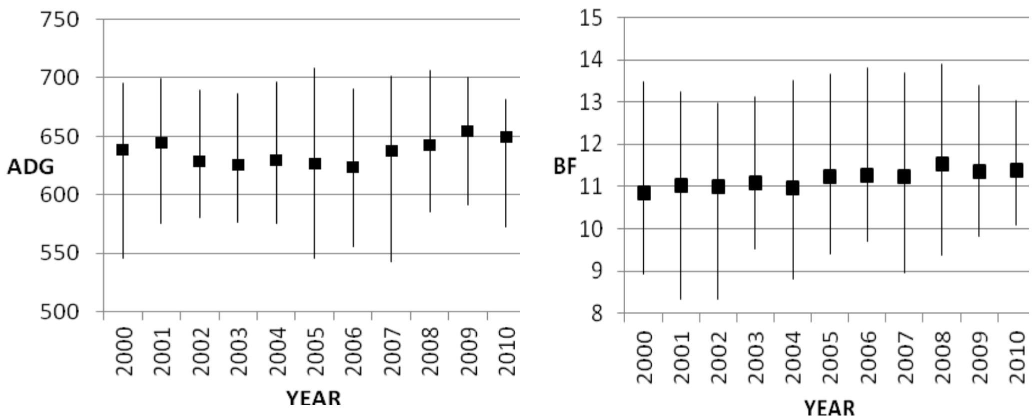
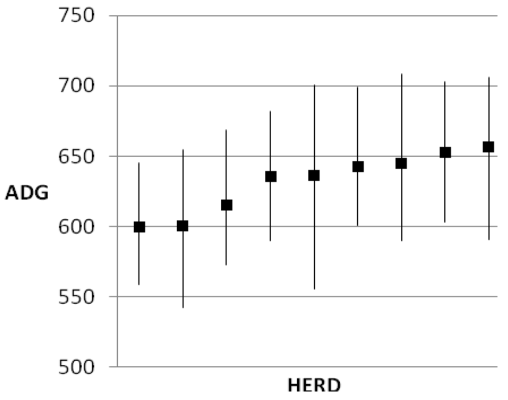


Figure 3. Mean and range of least squares means (LSM3) for average daily gain (ADG) and back fat (BF) of herd by month contemporary groups within years.



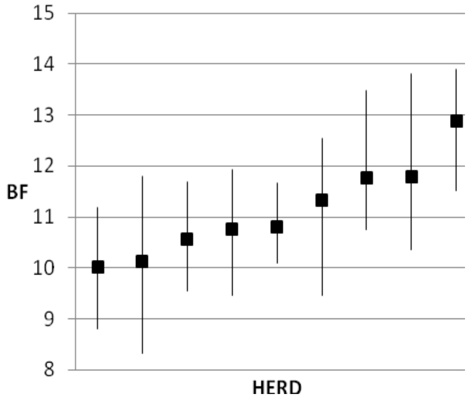


Figure 4. Mean and range of least squares means (LSM3) for average daily gain (ADG) and backfat (BF) of herd by month contemporary groups within herds.

Breed by environment interactions

Solutions for the intercept and slope of each breed are presented relative to Large White. This breed had a solution of 0 for both parameters as the reference value for comparison. Breed solutions for the intercept from the fixed regression of the observations on environmental variable showed that Landrace was the fastest growing breed with a solution for the intercept of 8.61 g/d. Large White was the leanest breed although the difference between breeds was small with solutions of 0.18 mm for Landrace and 0.33 mm for Duroc.

The fixed regression coefficients from the regression of observations on environmental variables were close to 1 with values of 1.035 g/d per g/d of LSM3 for ADG and 1.02 mm per mm of LSM3 for BF. The solutions for the fixed regression coefficients of breed on the environmental variable were 0.0 for Large White and -0.07 g/d per g/d of LSM3 for Landrace and -0.12 g/d per g/d of LSM3 for Duroc for ADG. These results indicate that Large White was more sensitive to changes in the environment than Landrace or Duroc, which were least sensitive to changes in environmental conditions for ADG.

For BF, Landrace was the least sensitive breed based on an animal model. Regression coefficients obtained for Landrace using an animal model were -0.06 mm per mm of LSM3 and differed significantly from Large White although estimates of regression coefficients did not differ significantly from Duroc which had a solution of -0.05 mm per mm of LSM3.

Reaction norms for ADG and BF predicted for three breeds are shown in Figure 6 illustrating a breed by environment interaction. Large White grew faster than Duroc in more favourable environments, while Duroc grew faster than Large White in unfavourable environments (Figure 6a). The magnitude of breed by environment interactions was lower for BF and there was no re-ranking of breeds across the environmental trajectory for BF (Figure 6b).

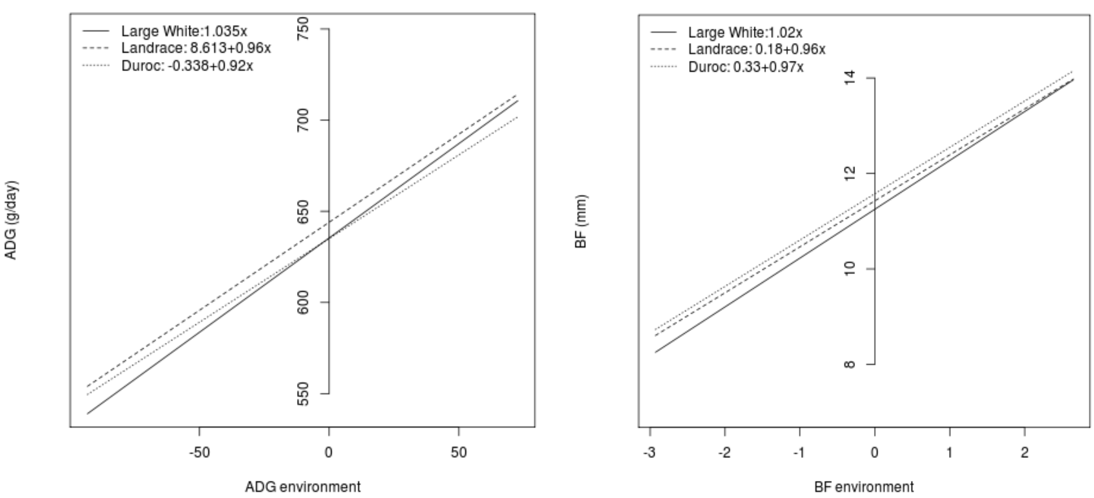


Figure 6. Reaction norms for Duroc, Landrace and Large White for average daily gain (ADG) and backfat (BF) along the environmental trajectory quantified by least squares means from an animal model (LSM3) of herd by month contemporary groups.

Sire by environment interactions

For ADG, the variance of sire slope on the primary environmental variable (least squares means for ADG of the contemporary group) was significantly different from zero indicating that sires showed different environmental sensitivity (results not shown). In contrast, sire slope variances on the primary environmental variable were not significant for BF.

The variances of sire slopes based on the second environmental variable were significant for both traits indicating that inclusion of a second different environmental variable improved the model.

The range of estimates of sire intercepts and slopes was 93.3 g/day for sire intercepts and 0.205 g/d per g/d change in the primary environmental variable (LSM3 of contemporary groups) for sire slopes for ADG (Table 2). Based on the standard errors of sire slopes, only a small proportion of sires had slopes that were significantly different from zero, although differences between extreme sires were found in regard to the response of their progeny to variation in environmental conditions.

Environmental sensitivity of sires can only be estimated for sires with progeny recorded across a wide range of environments. The average range per sire in environmental variables was about 54 g/day for ADG varying from 0 and to a maximum of 155 g/d.

Estimates of sire intercept for BF varied from -1.56 to 2.08 mm. No genotype by environment interaction was found for BF which is reflected in small estimates of sire slopes ranging from -0.076 to 0.080 mm per mm in LSM3 for contemporary groups, respectively. Therefore, progeny of sires had similar responses to changes in environmental conditions for BF. The average range in the environmental variable was 1.44 mm per sire.

Table 2. Mean, standard deviation (SD), minimum and maximum for sire intercept, sire slopes and sire environmental range for ADG and BF (number of sire: 1470).

Trait	Parameter	Mean	SD	Minimum	Maximum
ADG	Sire intercept	0.00	12.7	-41.7	51.6
	Sire slope 1	0.00	0.025	-0.102	0.103
	Sire slope 2	0.00	1.079	-5.037	6.778
	Sire environmental range	53.9	23.7	0	155.1
BF	Sire intercept	0.00	0.49	-1.56	2.08
	Sire slope 1	0.00	0.019	-0.076	0.080
	Sire slope 2	0.00	0.001	-0.004	0.004
	Sire environmental range	1.44	0.90	0	5.15

* Sire slope 1: based on primary environmental variable which was LSM3 of contemporary groups of the trait analysed; Sire slope 2: based on second environmental variable which was LSM3 of contemporary group of other traits.

Implications and outlook

These analyses demonstrated a considerable spread in environments in high-health farms with good husbandry practices. The unadjusted mean performance of a group of pigs showed a similar distribution than the more complex environmental descriptors (LSM1, LSM2 or LSM3). This simple environmental descriptor can easily be derived from standard performance records collected on farms to quantify variation in environmental conditions within herds over time. Further research will now focus on developing more precise methodology to measure variation in environmental conditions on farm making use of information about seasonal effects, air quality, disease incidence and overall performance of pigs based on multiple traits.

Breeds differed in their responsiveness to variation in environmental conditions with Large White being the most environmentally sensitive or least robust breed for growth rate and backfat. This breed was the leanest breed in comparison to Landrace and Duroc. The most robust breed was Duroc, which had a similar growth rate as Large White but was characterised by a higher backfat in comparison to the other breeds. Overall, these results support the hypothesis that leaner genotypes tend to be less robust and less able to perform consistently across a range of environmental conditions.

Extensive analyses were performed using random regression models to evaluate sire by environment interactions. For growth rate, sires differed in the response of their progeny to variation in the environment, which was less apparent for backfat. Progeny of sires differed in their response to variation in two environmental variables highlighting the need to develop methodology to combine multiple environmental variables into one overall descriptor of the environment used in genetic analyses of pig data based on reaction norm models.

Acknowledgements

This project was funded by the Pork CRC under project 2B-101.

References

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13: 115-155.

Calus, M. P. L., and R. F. Veerkamp. 2003. Estimation of environmental sensitivity of genetic merit for milk production traits using a random regression model. Journal of Dairy Science 86: 3756-3764.

Gilmour AR, Gogle BJ, Cullis BR and Thompson R 2006. ASReml User Guide Release 2.0. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK.

Hammami, H. *et al.* 2009. Environmental sensitivity for milk yield in Luxembourg and Tunisian Holsteins by herd management level. Journal of Dairy Science 92: 4604-4612.

Knap, P. W., and G. Su. 2008. Genotype by environment interaction for litter size in pigs as quantified by reaction norms analysis. Animal 2: 1742-1747.

Kolmodin, R., E. Strandberg, P. Madsen, J. Jensen, and H. Jorjani. 2002. Genotype by Environment Interaction in Nordic Dairy Cattle Studied Using Reaction Norms. Acta Agriculturae Scandinavica, Section A - Animal Science 52: 11-24.

SAS 1999. Enterprise Miner, Release 9.1. SAS Institute, Cary, NC, USA.

Strandberg, E. 2006. Analysis of genotype by environment interaction using random regression models. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Minas Gerais, Brazil, 13-18 August, 2006.