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BACKFAT AS AN ENVIRONMENTAL DESCRIPTOR IN DEFINING GROWTH RATE OF THE PIG: A G×E ANALYSIS

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SUMMARY

Investigations of genotype by environment (G×E) interactions may use estimates of average performance observed for contemporary groups (CGs) as environmental descriptors (ED). Data from a commercial breeding herd of Large White pigs were used to define ED based on backfat (BF) and average daily gain (ADG). The ED of BF and ADG were estimated using an animal model, with sex, month-year CG, weight (BF only), litter size and parity of birth litter as fixed effects. Estimates of CG were centred, and then used to allocate an environment for each individual in the genetic analyses of ADG. Each ED was partitioned into quartiles, allowing ADG to be defined as a separate trait in the four environments based on BF or ADG. Heritability estimates for ADG ranged from 0.12 to 0.16 for BF as ED, and 0.07 to 0.17 for ADG as ED. There was a weak relationship between the BF ED and ADG ED indicating they do not quantify the environment in the same way. Nevertheless, the use of either ED indicates re-ranking of animals in different environments, with Pearson's correlations between EBVs ranging from 0.22 to 0.55 for BF as ED, and 0.43 to 0.54 for ADG as ED.

INTRODUCTION

Genotype by environment (G×E) interactions occur when different genotypes exhibit varying responses to changes in the environment. Phenotype, in particular mean performance of a group of animals, can be seen as the result of a combination of known, plus unknown and unobservable environmental factors (Streit *et al.* 2013). Therefore, estimates of phenotypic averages of contemporary groups (CGs) at each environmental level are commonly used as an environmental descriptor (ED) in animal breeding, allowing the environment to be quantified (for example, Knap and Su (2008) in pigs). This ED can then be partitioned, and the same trait measured in the different EDs can then be considered as separate traits (Falconer 1952), with each trait having its own heritability and breeding values. This multi-trait approach of G×E analysis allows the evaluation of any genetic correlations (r_g) between the same trait expressed in different environments, and, if less than unity, this indicates a G×E interaction.

In pig breeding, an environmental variable previously used was average daily gain (ADG) (Li and Hermesch 2013).We explore the use of backfat (BF) as an alternate production trait for an ED in G×E analyses, and make comparisons with the use of ADG as the ED.

MATERIALS AND METHODS

Data. Pig identity records and production traits were obtained from a commercial herd of Large White pigs in Gatton, south east Queensland, Australia. Inclusion criteria were years of birth from 1996 to 2013 inclusive, and all traits within four standard deviations from means of the raw data. After data editing, there were a total of 40,145 individual animals, which included 19,899 entire male pigs and 20,246 female pigs. The 18 generations consisted of 2,444 dams and 568 sires. Performance traits included ADG from birth to weighing and BF at weighing. The mean age of weighing was 129.1 ± 6.79 days (mean ± SD), which gave an average weight at testing of 87.1

± 9.23 kg. CGs were defined by birth month-year, giving a total of 216 CGs, ranging from 67 to 493 pigs in each group and an average group size of 185 pigs.

Analysis. Data cleaning and analysis was conducted using R, version 3.1.3 (R Core Team 2015). Models were fitted using ASReml-R (Butler *et al.* 2009). Records were examined for duplicates and errors. The pedigree was extracted from the raw records, duplicate pigs and pedigree loops were removed, and founders identified. The analyses were conducted in two steps.

Firstly, EDs were obtained based on estimates of CGs from the following animal models. The model for BF was BF = μ + Sex + CG + βWeight + βLitterSize + BirthParity + Animal + Litter effect +ε. Fixed effects were sex, CG, weight (linear covariate), litter size of birth litter (linear covariate) and parity of birth litter. Random effects were common litter and animal effect. For ADG as the ED, the model was: ADG = μ + Sex + CG + βLitterSize + BirthParity + Animal + Litter effect + ε.

The 216 CG estimates for both EDs were centred around 0, and for maximum power to test for G×E, split into quartiles to have roughly equal number of observations within each group. Each animal was allocated an environment (E-BF1, E-BF2, E-BF3, or E-BF4; as well as E-ADG1, E-ADG2, E-ADG3, or E-ADG4) according to their CG estimate.

The second part of the analyses was to define ADG as a different trait for each environmental group. Heritabilities and estimated breeding values (EBVs) for ADG traits across environments were obtained from the animal model outlined for ADG above. Pearson's correlations between the EBVs for each of the four traits based on BF as ED, as well as ADG as ED, were calculated as a proxy measure of genetic correlations.

RESULTS AND DISCUSSION

The 40,145 animals included in analysis had a mean ADG of 675.3 ± 68.43 g/day, and a mean BF measurement of 11.6 ± 1.90 mm.

The centred CG estimates derived from the animal models in the first step of analysis ranged from -1.2 mm to 1.3 mm for the BF ED, and from -67.2 g/day to 77.5 g/day for the ADG ED. The environments E-BF1, E-BF2, E-BF3 and E-BF4 contained animals with a BF ED of < -0.38 mm, between -0.38 mm and 0.01 mm, between 0.01 mm and 0.39 mm, and > 0.39 mm, respectively; Similarly, E-ADG1, E-ADG2, E-ADG3 and E-ADG4 contained animals with an ADG ED of < -15.9 g/day, between -15.9 g/day and 1.34 g/day, between 1.34 g/day and 16 g/day, and > 16 g/day, respectively.

In an optimum environment, pigs have a higher ADG and lower BF. If the BF ED and ADG ED were able to quantify the environment in the same way, it was expected for these EDs to be highly negatively correlated. Figure 1 shows the weak relationship between the EDs based on BF and ADG (r = 0.08). This indicates that the two EDs do not describe the environment in the same way.

The partitioning of the environments appropriately described inferior and superior environments, shown in the ADG of each environment. The superior BF environments with the lowest BFs had the highest ADG performance, with ADG decreasing from 680 g/day and 681 g/day for E-BF1 and E-BF2, to 668 g/day and 671 g/day for E-BF3 and E-BF4 (Table 1). The ED derived from ADG showed an increase in ADG with quality of environment in a linear relationship, as expected. Variability in performance (CV) decreased with superior environments for ADG as ED, reflecting the results of Li and Hermesch (2013) for their seven-trait analysis. The range of heritabilities derived from the four ADG traits in each ED were 0.12 to 0.16 for ED based on BF, and 0.07 to 0.17 for ED based on ADG.

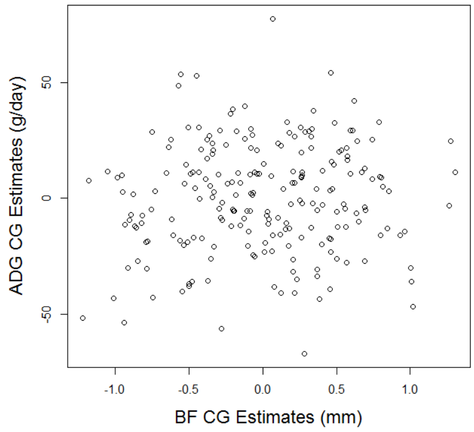

Figure 1. The relationship between centered contemporary group (CG) estimates using backfat (BF) as ED and average daily gain (ADG) as ED (*r* = 0.08).

Table 1. Number of observations (*n*), mean performance, coefficient of variation (CV), phenotypic variance (σ_p^2), heritability (h^2), standard error of heritability estimate (s.e(h^2)), fraction of variance due to common litter environment (c^2) and litter effect standard error ((s.e(c^2)) for average daily gain (ADG) defined as separate traits, using an environmental descriptor (ED) derived from backfat (E-BF1 to E-BF4) and ADG (E-ADG1 to E-ADG4).

Environment	n	ADG (g/day)	CV (%)	σ_p^2	h^2	s.e(h^2)	c^2	s.e(c^2)
E-BF1	9,767	680.0	9.97	3948.2	0.16	0.027	0.10	0.025
E-BF2	11,328	680.6	10.07	4143.7	0.16	0.025	0.09	0.026
E-BF3	9,804	668.4	10.33	4068.8	0.12	0.022	0.12	0.028
E-BF4	9,246	671.2	10.04	4110.7	0.14	0.025	0.12	0.026
E-ADG1	9,924	648.3	10.06	3941.6	0.15	0.027	0.11	0.025
E-ADG2	10,313	670.8	9.71	4034.8	0.17	0.026	0.11	0.024
E-ADG3	10,695	682.8	9.68	4158.7	0.07	0.018	0.11	0.019
E-ADG4	9,213	700.7	9.56	4133.6	0.17	0.026	0.13	0.026

Pearson's correlations between EBVs ranged from 0.22 to 0.55 for BF as ED, and from 0.43 to 0.54 for ADG as ED (Table 2). These were all significantly lower than unity, demonstrating re-ranking of animals across environments. Although Pearson's correlations indicate significant G×E interactions for both BF as ED and ADG as ED, these provisional values under-estimate genetic correlation between traits.

Table 2. Pearson's correlations between estimated breeding values (EBVs) for average daily gain (ADG) defined as separate traits in each environment, using an environmental descriptor (ED) derived from (a) backfat (BF) and (b) ADG.

(a)

	E-BF1	E-BF2	E-BF3	E-BF4
E-BF1				
E-BF2	0.35			
E-BF3	0.29	0.55		
E-BF4	0.22	0.49	0.54	

(b)

	E-ADG1	E-ADG2	E-ADG3	E-ADG4
E-ADG1				
E-ADG2	0.53			
E-ADG3	0.43	0.52		
E-ADG4	0.45	0.50	0.44	

This multi-trait approach treats the ED as a categorical variable. When the ED is treated as a continuous variable, a reaction norm (RN) approach can be used (Kolmodin 2003). There is also the option of combining both approaches, when both categorical and continuous EDs are used at the same time. Windig *et al.* (2011) explored treatment of the ED as both continuous and categorical in a combined bivariate reaction norm approach. Although there was no G×E interaction found when multi-trait, RN and combined approaches were used, the combined approach was useful for separating effects when two EDs were confounded (e.g. spring calving vs. year-round calving production system). In this example, residual variance decreased with dairy higher milk production in a RN approach, but the combined approach showed that at the same milk production level, there was higher residual variance in spring calving compared to year round calving.

The number of traits the environmental trajectory is split into is an important factor in G×E analysis. Li and Hermesch (2013) explored four different scenarios, splitting ADG as ED into one, two, three and seven traits. When treated as one and two traits, no significant G×E interaction was found, but a G×E interaction was observed when three and seven trait models were fitted. Genetic correlations also decreased as differences between environmental groups increased. Quartiles were used in the current study as it is a commonly used statistical summary. However the optimum number of traits should be further investigated.

CONCLUSIONS

This paper considers the validity and feasibility of G×E analyses when using alternative traits in defining the environmental variable. The mean performance of a production trait as ED, adjusted for by fixed and random effects, may be an appropriate variable if the environment is complex, or if there is no other available data to describe the environment. These first results indicate that BF can be used as an ED, with estimates of heritabilities and Pearson's coefficients similar to those obtained when ADG was used as the ED. Both EDs suggest re-ranking of animals across environments. However, genetic correlations between ADG defined as a separate trait in different environments are required to make a final conclusion about G×E interactions.

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