GENOTYPE BY ENVIRONMENT INTERACTIONS FOR AVERAGE DAILY GAIN USING MULTIPLE-TRAIT ANALYSES IN AUSTRALIAN PIGS

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SUMMARY

Data comprised of 265,103 records on pigs from nine herds collected from 2000 to 2010 were used to investigate whether genotype by environment interactions (GxE) existed for average daily gain (ADG) of pigs. Least squares means for herd by birth month from an animal model were used to quantify environmental conditions of contemporary groups. The environmental trajectory was divided into two, three or seven groups for alternative trait definitions of ADG considered to be a distinct trait for each environmental group. A multi-trait approach was used to investigate GxE. Heterogeneity of additive genetic variance and heritabilities were found for ADG between environmental groups when the environmental trajectory was divided into three or seven groups. Heritability estimates were highest for the intermediate environmental group (0.22±0.01) and reduced continuously to 0.15±0.02 for lower environmental groups. Estimated common litter effect did not differ significantly between trait definitions of ADG. Genetic correlations between ADG observed in different environments varied from 0.61±0.16 to 0.99±0.02. Genetic correlations were less than 0.80 when ADG was observed in two environments that differed by more than about 60 g/day indicating existence of significant GxE for ADG in pigs. At least 200 common sires were required to achieve statistical significance of these genetic correlations, demonstrating that large data sets with good data structures are required to detect GxE.

INTRODUCTION

Genotype by environment interactions (GxE) reduce the efficiency of a selection programme, as the ranking of animals differs between environments. Selecting the right genotypes for specific environments will increase genetic response across environments. Genotype by environment interactions can be analyzed using a multi-trait model in which traits records in different environments are considered separate traits (Falconer, 1952). Genetic correlations among separate traits quantify the extent of GxE, a value significantly less than unity demonstrates GxE. Further, a value of less than 0.8 was suggested to have biological importance (Robertson, 1959). This approach has been widely adopted to account for GxE in animal breeding.

Previous analyses (Li and Hermesch, 2012) showed that genotypes (breed or sire) had different sensitivities across the environmental trajectory defined by least squares means of herd by birth month contemporary groups (LSG). This study used multi-trait models to evaluate GxE for lifetime average daily gain (ADG) treated as a different trait for diverse environments classified according to LSG.

MATERIALS AND METHODS

Data. Records for 265,103 pigs from nine herds collected from 2000 to 2010 were available from the across-herd genetic evaluations of the National Pig Improvement Program database in Australia. Pigs were from three breeds: Large White (143,485), Landrace (87,946) and Duroc (33,672). Average daily gain was derived from live weight recorded shortly before slaughter on farms divided by age at recording. Mean (SD) for live weight, age at slaughter and ADG were 92.8 (13.6) kg, 143 (17.2) days and 649 (73.1) g/day, respectively. Based on previous analyses by Li

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Industry 2

and Hermesch (2012), herd by birth month (HBM) was used as the contemporary group. There were 950 HBM groups with an average size of 279, ranging from 16 to 1071 pigs.

Analysis. Average daily gain based on all data was analyzed fitting the linear model: $ADG = \mu + \sec + birth parity + breed + HBM + litter + animal + error, where <math>\mu$ is the overall mean. Fixed effects were sex, birth parity, breed and HBM contemporary group. Random effects were litter and animal effects. Genetic correlations were estimated using information from the numerator relationship matrix fitted in the animal model. The pedigree file contained 268,989 animals with 2,394 sires and 12,363 dams.

LSG from the model were used as an environmental descriptor to define environmental groups. LSG were normally distributed with mean (SD) of 644 (32.4) g/day and range of 534 to 738 g/day. Based on the distribution of LSG, three scenarios were considered to define ADG as a separate trait for different environments: 1) two environmental groups below and above the mean (644 g/day) of LSG; 2) three environmental groups for LSG <620 g/day, 620 to 660 g/day and >660 g/day; 3) seven environmental groups with increments of 20 g/day for LSG from <600 to >700 g/day. Genetic parameters were estimated fitting univariate and all pairs of bivariate analyses (3 and 21 pairs for three and seven trait definition respectively) using ASReml (Gilmour et al., 2009). Residual and phenotypic correlations were not estimated as each animal had only one observation.

RESULTS AND DISCUSSION

As expected, average phenotypic performance increased as environmental conditions improved as expected (Table 1). Coefficients of variation (CV) decreased from the inferior to superior environments for all trait definitions of growth rate. For the seven-trait analyses CV decreased from 11.3% to 8.7% indicating that pigs with higher growth rate had less observed variation relative to the mean. For all scenarios, all breeds had records across all traits.

Heritabilities. The heritability estimate for ADG defined as one trait across environments was 0.22 ± 0.01 (Table 1). When ADG was treated as two traits, heritabilities did not differ significantly between these two traits. In contrast, heterogeneity of additive genetic and total variances as well as heritabilities existed for different environmental groups of the three- and seven-trait analyses. Highest estimates were found for the intermediate environmental group. In the seven-trait analyses, heritabilities and additive genetic variances decreased from 0.22 ± 0.01 to 0.15 ± 0.02 and from 964±61 to 622 ± 88 g/day for ADG in the intermediate group (ADG4) to ADG in the lowest environmental group (ADG1). Zumbach *et al.* (2007) studied two purebred Duroc pig populations (P1 and P2) and their terminal crossbreds (C1 and C2) raised in different production environments in comparison to the heritability estimate (0.16 ± 0.01) obtained for C1 raised in inferior environments. However, no differences in heritability estimates between P2 and C2 was found. Common litter effect estimates did not differ significantly between trait definitions in our study.

Genetic correlations. Genetic correlations between ADG1 and ADG2 for two-trait definition and between ADG1 and ADG2 as well as ADG2 and ADG3 for three-trait definition were 0.98 ± 0.01 , 0.97 ± 0.02 and 0.96 ± 0.02 , respectively. For three-trait definition, genetic correlation (0.78 ± 0.06) between ADG1 and ADG3 differed significantly from unity with observed phenotypic mean difference of 76.8 g/day. The additive genetic (co)variance matrix among the seven traits was not positive definite, indicating that defining ADG as separate traits for less than seven environmental groups might be better for genetic evaluations. However, seven traits were defined in this study to see better the trend for change of genetic correlations along the environmental trajectory.

Scenario Trait		Ν	Mean	CV(%)	σ^2_{a}	σ^2_{e}	σ^2_p	h^2	c^2	
1 trait	ADG	265,103	650	11.3	955	2,845	4,314	0.22	0.1	
2 traits	ADG1	136,641	625	10.9	834	2,885	4,268	0.20	0.1	
2 (1016)	ADG2	128,462	675	10.3	977	2,851	4,317	0.23	0.1	
3 traits	ADG1	63,269	610	10.9	714	2,908	4,182	0.17	0.1	
	ADG2	122,081	645	10.4	936	2,909	4,378	0.21	0.1	
	ADG3	79,753	687	9.9	840	2,853	4,179	0.20	0.1	
	ADG1	19,118	593	11.3	622	2,999	4,206	0.15	0.1	
	ADG2	44,151	618	10.6	727	2,879	4,165	0.17	0.1	
	ADG3	56,459	635	10.4	815	2,925	4,278	0.19	0.1	
7 traits	ADG4	65,622	654	10.2	964	2,932	4,434	0.22	0.1	
	ADG5	44,518	672	9.9	737	3,111	4,368	0.17	0.1	
	ADG6	19,245	695	9.3	648	2,864	4,066	0.16	0.1	
	ADG7	15,990	721	8.7	731	2,403	3,593	0.20	0.1	
ange of s.e.*		-	-	-	29-94	17-57	17-54	1-2	0-	

Table 1. Number of records (N), means and coefficients of variation (CV) along with additive genetic (σ_a^2), residual (σ_e^2) and phenotypic (σ_p^2) variances as well as heritability (h^2) and common litter effect (c^2) as a proportion of phenotypic variance for average daily gain (ADG) observed in inferior (i.e. ADG1) to superior (i.e. ADG7) environments

*Note: s.e. for h^2 and c^2 have been multiplied by 100.

Genetic correlations between ADG*i* and ADG*i*+1 along with ADG*i* and ADG*i*+2 (0< *i* <6) were not significantly different from unity indicating that no GxE existed for ADG expressed in similar environmental conditions (Table 2). Genetic correlations decreased as differences between environmental groups increased ranging from 0.61 ± 0.16 to 0.99 ± 0.02 . Differences between phenotypic means of pairs (ADG*i* – ADG*j*, absolute value) ranged from 17 g/day (ADG2 versus ADG3) to 127 g/day (ADG1 versus ADG7) in the seven-trait definition. Genetic correlations were below 0.8 and of statistical significance when environmental groups differed by about 60 g/day (Figure 1a). Zumbach *et al.* (2007) found genetic correlations of 0.60 ± 0.07 (P1 and C1) and 0.79 ± 0.07 (P2 and C2) between growth rate recorded in purebred and crossbred populations that were raised in environments with different health status leading to superior performances of 60 and 100 g/day of the purebred populations in the two examples presented. Standard errors (s.e.) of genetic correlations were affected by the number of common sires shared between environmental groups (Figure 1b), decreasing from 0.27 to below 0.10. This indicates at least 200 common sires between two groups were required to detect GxE of biological significance. This threshold may vary for data sets with different data structures.

CONCLUSIONS

Genotype by environment interactions were found for growth rate based on variation in environmental conditions prevalent in herds with good health and management practices. Heritability estimates were highest for the intermediate environment and lowest for the most inferior environment. Genetic correlations decreased as differences between environmental groups increased. Estimates differed significantly from unity for ADG recorded in two environments that

Industry 2

varied in mean performance by about 60 g/day. This multi-trait methodology offers a practical approach to consider genotype by environment interactions for growth rate in pig breeding programs. However, large data sets with good data structures are required for genetic analyses.

Table 2. (a) Genetic correlations (above diagonal) and differences of phenotypic mean (below diagonal) of average daily gain (A); (b) Standard errors of genetic correlations (above diagonal) and number of common sires (below diagonal) observed between pairs of A for the seven-trait definition^{*}

(a)							(0)								
	A1	A2	A3	A4	A5	A6	A7		A1	A2	A3	A4	A5	A6	A7
A1		92	92	<u>77</u>	<u>61</u>	65	70	A1		5	5	8	16	19	27
A2	24		99	92	<u>80</u>	<u>79</u>	73	A2	527		2	4	7	10	17
A3	42	17		97	96	88	67	A3	437	889		2	3	8	14
A4	61	36	19		96	96	<u>70</u>	A4	294	697	1100		2	5	10
A5	78	54	37	18		97	98	A5	157	387	669	864		5	6
A6	101	77	60	41	23		92	A6	46	142	245	362	410		7
A7	127	103	86	67	49	26		A7	11	40	68	82	85	62	

^{*}Note: Both above diagonal elements have been multiplied by 100; Estimates with underscore are significantly different from one (p<0.05).

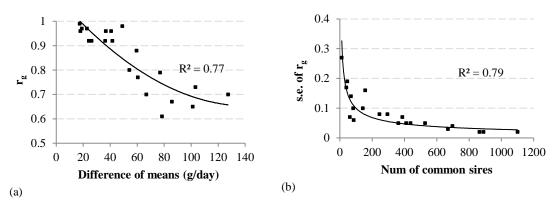


Figure 1. Association between genetic correlations (r_g) and differences in means between two envrionments (a) and standard errors (s.e.) of r_g and number of common sires between two environments (b) based on seven-trait analyses.

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