INTRODUCTION

Because of the economic importance of growth rate and carcass lean (McPhee and MacBeth, 2000), it is necessary to evaluate in a production environment the responses in these traits when selection of parental stock takes place in a performance testing environment. Production environments for pigs usually provide group housing and ad libitum feeding from weaning to slaughter. On the other hand, where selection is for growth, feed efficiency and carcass lean, performance testing has often been carried out on pigs penned separately over a limited post-weaning period and fed either ad libitum or on a restricted amount (e.g., McPhee et al., 1988). It is important to see if the genetic gains suggested in the selected generation are realised in the generation exposed to a commercial production environment. No published reports were found of correlated responses in a production environment to selection in a different environment. In this study, after four years of selection for high and low post-weaning daily gain on a fixed but restricted ration, the divergence in genetic response between the lines was 81.25 g/d or 2.78 genetic standard deviations for average daily gain on test. Pigs from the selection lines were also subject to different performance methods on either ad libitum or group feeding. As reported by Nguyen (2002), genetic gains (measured as average differences between the high and low growth lines on ad libitum feeding) were 37.7 g/d for test daily gain, -0.79 mm for ultrasonic backfat and -0.21 unit for food conversion ratio.

The current study examines genetic changes in growth and carcass traits in lines of Large White pigs selected divergently (high and low) for post-weaning growth in individual pens and fed on a restricted scale (80% of ad libitum) (Nguyen, 2002). Testing of the lines occurred under commercial production conditions of group housing and ad libitum feeding. Genetic correlations between and genetic responses in growth and carcass traits under these conditions are presented.

MATERIALS AND METHODS

The genetic lines and measurements

Details of the development of the two selection lines were fully described by Nguyen and McPhee (2005). Briefly, the lines, each of 36 sows and 6 boars were initially formed by sampling within Large White litters. They were divergently selected for high and for low post-weaning gain on a restricted scale (80% ad libitum) over a 6-week period.
starting at 50 kg. Pigs were also sampled from the same litters for growth testing on either individual or group ad libitum feeding. In this study, pigs of similar weight and sex were intermingled in group pens and fed ad libitum to an average live weight of 100 kg. All animals were fed a diet containing 14 mega-joules of digestible energy (MJ DE) and 0.65 g available lysine per MJ DE. End weight was measured before sending the pigs to the abattoir. Lifetime daily liveweight gain (LDG) was the ratio of end weight to days from birth to final liveweight.

At the end of the trial, pigs were deprived of food for approximately 20 h before slaughter. In this period, they were trucked 800 km by road and rested overnight. After lairage, pigs were stunned electrically in a V-restrainer and exsanguinated within 10 s of stunning. Hot carcass weight (HCW) including fore and hind trotters, and flare fat but not fat. Carcass fat depth (CFT) was made at the last rib position, using an Hennessy Grading Probe (Hennessy Grading Systems, Auckland, New Zealand). Average daily carcass gain (CDG) was calculated as the hot carcass weight over days from birth to slaughter.

**Data structure**

Of the total of 5,324 animals measured on all feeding regimes, for which pedigrees were available, 1728 heads were group housed and ad libitum fed (Table 1). They were progeny of 110 sires and 363 dams from 740 litters.

**Co-variance components**

A preliminary general linear model (GLM) analysis was carried out to determine the significance of fixed effects. Genetic and environmental variance components for all traits were estimated with the animal model restricted maximum likelihood method using the average information algorithm (ASREML, Gilmour et al., 1999). A series of univariate analyses was carried out to obtain estimates of heritability. Genetic and phenotypic correlations among the traits were derived from multivariate model analyses, using bivariate analysis starting values. The fixed effects of batch (33 classes) and sex (males and females), and the random effect of the individual animal were included in the equation for statistical analytic models. Litter effect was found to be insignificant for carcass traits but significant for LDG. The ratio of the common litter variance component for LDG to its standard error was 4.10 and the -2LogL (logarithmic likelihood) after dropping common litters from the full model was 23.2. A Chi-squared test with one degree of freedom verified that the effect of common litter was significant (p<0.001) only for LDG and thus it was included as an additional random effect for that trait in the models. Lifetime age from birth to slaughter (AGE) and hot carcass weight (HCW) were fitted as linear covariates for carcass fat.

**Breeding values**

Breeding values (EBVs) for all the traits were estimated using the Best Linear Unbiased Prediction (BLUP) analysis of the PEST package (Groeneveld, 1990). The additive genetic and residual (co) variances used in the multi-trait model included the same fixed and random effects as described in estimation of genetic parameters. Selection line means of EBVs for all traits were derived for each year of birth (GenStat 6, 2002).

**Realised genetic correlations**

Following Falconer (1954) the realised genetic correlations were estimated from $\Delta G_X$, the difference between the high and low selection lines in the selected trait (TDG) on restricted feeding and the correlated genetic changes ($\Delta G_Y$) in traits measured on ad libitum group feeding

$$ r_g = \frac{\Delta G_Y \sigma_{AX}}{\Delta G_X \sigma_{AY}} = \frac{\Delta G_Y h_X \sigma_{PX}}{\Delta G_X h_Y \sigma_{PY}} $$

where $h_X^2$ and $h_Y^2$ are heritabilities and $\sigma_{AX}$ and $\sigma_{AY}$ the genetic and phenotypic standard deviations ($\sigma_{PX}$ and $\sigma_{PY}$) for TDG on restricted (X) and ad libitum (Y) feeding, respectively. All parameters on restricted and ad libitum group feeding were taken from Nguyen and McPhee (2005) and the current estimates.

**Means and standard deviations**

Descriptive statistics for lifetime daily gain (LDG), carcass weight daily gain (CDG) and carcass fat (CFT) are given in Table 1. Estimate of heritability for CFT was moderate while those for LDG and CDG were relatively low (Table 1), but generally fell within the literature ranges reviewed by Sellier (1998). Common litter effect for LDG to its standard error was 4.10 and the -2LogL (logarithmic likelihood) after dropping common litters from the full model was 23.2. A Chi-squared test with one degree of freedom verified that the effect of common litter was significant (p<0.001) only for LDG and thus it was included as an additional random effect for that trait in the models. Lifetime age from birth to slaughter (AGE) and hot carcass weight (HCW) were fitted as linear covariates for carcass fat.

**Genetic correlations**

Genetic correlations between growth rate and carcass traits, and among carcass traits are generally favourable

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**Table 1. Number of records (N), means, standard deviations (SD) of the means, heritabilities ($h^2$) and common litters effects ($\sigma^2$) in italicics) and genetic standard deviations ($\sigma_A$) of measured traits**

<table>
<thead>
<tr>
<th>Traits</th>
<th>Unit</th>
<th>N</th>
<th>Means</th>
<th>SD</th>
<th>$h^2$ and $c^2$</th>
<th>$\sigma_A$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDG</td>
<td>g/d</td>
<td>1,728</td>
<td>582.8</td>
<td>67.2</td>
<td>0.11±0.05</td>
<td>21.51</td>
</tr>
<tr>
<td>CDG</td>
<td>g/d</td>
<td>1,728</td>
<td>435.7</td>
<td>56.5</td>
<td>0.13±0.04</td>
<td>18.63</td>
</tr>
<tr>
<td>CFT</td>
<td>mm</td>
<td>1,728</td>
<td>16.2</td>
<td>4.2</td>
<td>0.28±0.06</td>
<td>2.57</td>
</tr>
</tbody>
</table>
Table 2. Heritabilities (bold on the diagonal) and phenotypic and genetic (above and below the diagonal, respectively) correlations (±standard errors) for carcass and production traits in ad libitum fed group housed pigs

<table>
<thead>
<tr>
<th>Traits</th>
<th>LDG</th>
<th>CDG</th>
<th>CFT</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDG</td>
<td>0.11±0.05</td>
<td>0.89±0.01</td>
<td>-0.15±0.03</td>
</tr>
<tr>
<td>CDG</td>
<td>0.98±0.01</td>
<td>0.13±0.05</td>
<td>-0.01±0.03</td>
</tr>
<tr>
<td>CFT</td>
<td>-0.26±0.21</td>
<td>-0.16±0.21</td>
<td>0.28±0.06</td>
</tr>
</tbody>
</table>

Table 3. Phenotypic means for growth rate and carcass traits over the course of selection in ad libitum fed group housed pigs

<table>
<thead>
<tr>
<th>Traits</th>
<th>High line</th>
<th>Low line</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDG (g/d)</td>
<td>556.2</td>
<td>538.2</td>
<td>2.58</td>
<td>***</td>
</tr>
<tr>
<td>CDG (g/d)</td>
<td>409.4</td>
<td>399.4</td>
<td>2.59</td>
<td>***</td>
</tr>
<tr>
<td>CFT (mm)</td>
<td>15.26</td>
<td>16.58</td>
<td>0.24</td>
<td>***</td>
</tr>
</tbody>
</table>

SED: Standard error of difference between the high and low growth line. *** p<0.001.

DISCUSSION

Group housing and performance

The growth rate of pigs raised under commercial conditions of group housing with ad libitum feeding was below that of their counterparts from the same selection lines fed ad libitum in individual pens (583 vs. 625 g/d). Differences in growth rate between individual and group penned pigs are reported in the literature ranging from 5 to 17% (Black et al., 2001). In this study, all pigs were kept in the same post-weaning conditions before allocation to the growth test on either ad libitum individual or group feeding at 50 kg. Hence the differences in their growth rates were attributed due to social and environmental stressors of mixing unfamiliar pigs in groups. In a review, Black et al. (2001) pointed out that multiple stressors such as group size, stocking rate, housing and climatic environments, and disease and microbial load, had negative additive effects on the performance of pigs held under common commercial practices. Pigs of the present study were penned in groups of 15-20 but provided with a generous space allowance both for lying and feeding. Thus social interaction is the most likely cause of the growth depression of the group-housed pigs relative to their individually housed sibs. As the number of pigs in a pen increased from one to three or five there was a significant linear reduction in the growth rate and food intake, although difference in these traits of pigs housed in groups ranging from 5 to 20 or even to a larger size was negligible (Wolter et al., 2001). Social interaction related to dominance hierarchy may occur, even when the animals had been acquainted previously with each other before mixing (Black et al., 2001).

Genetic parameters

The current estimates of heritability for performance and carcass traits were in line with literature results previously reported (e.g., Hofer et al., 1992; Skorupski et al.,...
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1996; Kim et al., 2004) in group housed, *ad libitum* fed pigs under commercial conditions, but were somewhat lower than estimates obtained from group housed pigs with a well controlled environment of automatic feeder systems (Von Felde et al., 1996; Labroue et al., 1997; Hall et al., 1999). The high values in the literature could be partly explained by the absence of a common litter effect in the analytical models. Only Hall et al. (1999) found negligible litter effects for both performance and feeding pattern behaviour traits. In the present study when using a model without common litter as a random effect, the heritability for LDG was of moderate magnitude (0.20). The common litter effect for LDG accounted for 13% of total phenotypic variance, indicating that a large proportion of resemblance between sibs was due to shared family environments, rather than shared genes. This reflects differences in mothering ability among dams, i.e. variation in milk yield that caused differences between litters in growth rate.

The directions of the genetic correlations between the traits measured in group housed, *ad libitum* fed pigs were generally consistent with the reviewed results of Sellier (1998). Lifetime daily weight gain had a highly positive genetic correlation with daily carcass gain and moderately negative correlation with carcass backfat, indicating that if selection for growth rate had been carried out under group housed, *ad libitum* feeding conditions, favourable improvements in these important traits would have occurred.

**Genetic correlated responses**

Genetic responses realised in the production environment were favourable for all traits although the changes were variable, particularly for LDG and CDG in the early years of selection. Over four years of selection the genetic changes, especially for carcass fat, were considerable and differences between the selection lines were all statistically significant. This indicates that the selection of breeding stock for increased post-weaning growth rate on individual restricted feeding will result in an economically beneficial increase in the rate of lean growth in their descendants raised in a production environment of group housing and *ad libitum* feeding. The magnitudes of genetic changes in growth rate and carcass traits in the production environment were comparable to those in the selection environment of restricted feeding (Nguyen, 2002). This supports the conclusion of Clutter and Brascamp (1998) that restricted feeding is an effective performance testing approach for seedstock lines supplying commercial systems that use either *ad libitum* or restricted feeding.

Even though food conversion efficiency was not measured in this study, an economically beneficial change in this trait would have been expected in the high growth line due to its decreased carcass fatness and from feed efficiency measurements on the same line fed *ad libitum* in individual pens (Nguyen, 2002). Using the genetic standard deviation for FCR of 0.50 and the genetic correlation with LDG of -0.40 estimated in individually housed *ad libitum* fed pigs, an annual improvement in FCR by -0.126 unit is expected to result from selection for LDG. A reduction in residual food intake and thus maintenance requirement is also likely to have occurred.

**Pedigree information and model validation**

REML estimates of (co)-variance components and BLUP estimation of breeding values are unbiased if the usual assumptions of the animal model are satisfied and if all animals used for selection are included in analyses (Kennedy, 1990; van der Werf and De Boer 1990). When the analysis of the present data was carried out using only the pedigrees of animals fed *ad libitum* in groups, changes in EBVs, especially for LDG and CDG fluctuated erratically over the years of selection. The magnitudes of genetic responses tended also to be greater in the high than the low line for all traits. For example, genetic gains in CFT estimated using the shorter pedigrees in the high growth line at the end of selection were -3.44 mm compared with -1.42 mm when a full pedigree was applied.

EBVs for LDG were also biased if common litter effects were ignored in the genetic models, leading to overestimation by approximately 12.7% and 9.7%, the EBVs for LDG in the high and low growth lines in the final year of selection. This supported the hypothesis that the addition of common litter to the analytical model was able to account for non-additive genetic effects such as dominance associated with inbreeding. Results from simulation studies showed that the prediction of additive effects was biased in presence of dominance (Johansson et al., 1993) or maternal genetic effects (e.g. Roehe and Kennedy, 1993b). The maternal genetic effects tested by the likelihood ratio were not significant for any trait in this study. Further, multiple trait BLUP analysis increased the accuracy and precision of EBVs for all traits, even though the differences from those using simple trait models were small. It is concluded that predictions of random effects in selected populations are unbiased if the relationship information on selected animals is included and the models are tested for goodness of fit.

**IMPLICATIONS**

The descendants of breeding pigs selected for high post-weaning daily gain on restricted feeding have increased growth rate, slaughter weight and reduced fatness in their carcasses when grown under commercial condition of group housing with *ad libitum* feeding. It is concluded that performance testing on restricted feeding is suitable for the selection of pig lines to perform well under commercial housing and feeding systems.
REFERENCES


