

Maternal genetic effects for lifetime growth should be considered more in pig breeding

S. Hermes¹, C.R. Parke², M.M. Bauer², H. Gilbert³

¹Animal Genetics and Breeding Unit (AGBU, joint venture of NSW Department of Primary Industries and University of New England), University of New England, Armidale, NSW, Australia, ²University of Queensland, Gatton, QLD, Australia,

³INRA, UMR1388 GenPhySE, F-31326 Castanet-Tolosan, France

ABSTRACT: Maternal genetic effects are potential breeding objective traits. Growth (LADG) and backfat (BF) at 93.9 kg body weight were recorded for 163,139 pigs in 10 herds from 2000 until 2012. Proportions of variances due to direct genetic, maternal genetic and common litter effects were 0.16, 0.03 and 0.11 for LADG and 0.28, 0.01 and 0.05 for BF, respectively. Multiple weight measurements were recorded on 896 pigs in 2013 at weaning, five, nine, 12 and 17 weeks in one herd. These individual growth traits were regressed on direct and maternal effects of LADG from the first analyses. Regression coefficients for direct or maternal genetic effects indicated that selection for these genetic effects will influence growth in a similar pattern. Whether selection for maternal genetic effects of LADG favors higher pre-weaning growth followed by a reduction in growth shortly after weaning should be explored.

Keywords: pigs; maternal genetic effects; post-weaning growth

Introduction

The genetic effect of the dam on lifetime growth (LADG) is an important breeding objective trait in pigs (Amer et al., 2014). Often this trait is ignored in pig breeding programs because low estimates of maternal genetic effects for LADG are regarded as unimportant (Solanes et al., 2004b). Estimates of maternal genetic effects are higher at birth (Hermesch et al., 2001; Solanes et al., 2004a) and decrease continuously for weights after weaning (Zhang et al., 2000). However, the genes of the dam affect all progeny in the litter. Therefore, the economic value for the direct genetic effect of growth (or backfat, BF) is multiplied by the number of pigs in a litter surviving until slaughter to derive the economic value for maternal genetic effects on LADG (or BF) (Amer et al., 2014). Further, variances are increasing over the growth trajectory, which provides opportunities for genetic improvement despite the low proportion of phenotypic variance explained by maternal genetic effects.

“Estimation of maternal genetic effects and the pertaining genetic parameters is inherently problematic.” (Meyer, 1992). Large data sets are required to disentangle direct and maternal genetic effects. These are readily available for LADG which has been routinely recorded in breeding programs for decades. These existing data allow evaluation of the correlated effects of selection for direct and maternal genetic effects of LADG on other growth traits that

may have less data available, to explore the implications of alternative selection strategies for growth.

The aim of this study was to estimate direct and maternal genetic effects for LADG and BF and to quantify the associations of direct or maternal genetic effects for LADG on pre- and post-weaning growth.

Materials and Methods

Data to estimate variance components. Data recorded on 163,139 Large White pigs that were born between January 2000 and November 2012 were used to estimate variance components for LADG and BF. This data set included 10 herds that were part of the National Pig Improvement Program (NPIP) in Australia. Both traits were recorded on females and entire males at a body weight of 93.9 kg (standard deviation, SD: 13.5) and an age of 144.2 (SD: 17.3) days. The data included 1,457 sires and 7,835 dams with 3.3 parities per dam on average.

Data to evaluate multiple growth traits. Multiple weight measurements were collected on 896 Large White pigs from January to December 2013 at the piggery of the University of Queensland in Gatton, Australia. This herd is part of the NPIP and uses sires from other members. Therefore, variance components were estimated using data across herds to ensure that pedigree information and performance records were as complete as possible across generations. The growth performances of these pigs with multiple weight records were excluded from analyses to estimate variance components. Pigs were weighed at weaning and at five, nine, 12 and 17 weeks. Pigs were 26 (SD: 2.15), 39 (SD: 2.54), 66 (SD: 2.94), 87 (SD: 2.55) and 124 (SD: 2.41) days of age at each recording. The weight measurements were used to derive five growth rate traits for the periods from birth until each weighing at weaning (ADG1), and at five (ADG2), nine (ADG3), 12 (ADG4) and 17 (ADG5) weeks. In addition, growth rate was derived from weaning until each weighing leading to further four growth traits (ADG12, ADG13, ADG14, ADG15). No other growth traits based on short time periods were considered because the accuracy of measuring growth rate decreases for shorter test periods (Arthur et al., 2008).

Statistical analyses – variance components. Variance components were estimated using ASReml (Gilmour et al. 2009) applying a univariate animal model with the addition of random maternal genetic effects and common litter effects. Fixed effects were evaluated using the GLM procedure (SAS, 2011). Significant fixed effects ($P < 0.05$)

included in the model for LADG and BF were contemporary group defined as the year by month of test within herd, sex as well as parity and litter size of the birth litter. Live weight was fitted as a linear covariable for BF.

Statistical analyses – growth traits. The pigs with multiple weight measurements were performance tested in weekly batches and week of test represented the contemporary group effect fitted for each growth trait. The sex of pigs affected early growth traits until week five (ADG1, ADG2, ADG12) and growth rate until 17 weeks (ADG5, ADG15). Parity of the birth litter was significant for all growth traits. Litter size of the birth litter was a significant linear covariable for the growth traits that included the pre-weaning period (ADG1 to ADG5). Age at recording was fitted as a linear covariable for early growth traits (ADG1, ADG12, ADG13). The mid-parent value of either direct or maternal genetic effects obtained from the first analyses to estimate variance components was then fitted as an additional linear covariable for growth traits in order to obtain regression coefficients. These analyses were conducted with the MIXED procedure (SAS, 2011) and common litter effect was fitted as a random effect. Omitting the litter effect from the model did not affect regression coefficients significantly.

Results and Discussion

Variance components. The proportions of phenotypic variance explained by maternal genetic effects were 0.03 (± 0.003) for LADG and 0.01 (± 0.002) for BF (Table 1). Inclusion of maternal genetic effects in the model reduced direct heritability for LADG from 0.21 to 0.16 and for BF from 0.30 to 0.28. Estimates of common litter effects (0.11 for LADG and 0.05 for BF) were very similar with both models. In comparison, estimates of maternal genetic effects for growth rate recorded in the tropics were 0.03 on average in a meta-analysis of genetic parameters (Akanno et al., 2013). Estimates varied from 0.0 to 0.9 for growth and from 0.00 to 0.07 for backfat recorded shortly before slaughter between breeds in studies conducted in temperate climates (Johnson et al., 2002; Solanes et al. 2004b).

Table 1. Mean, standard deviation (SD), heritability (h^2), common litter effect (c^2), maternal genetic effects (m^2) and phenotypic variance (V_p) for lifetime growth rate (LADG, g/day) and backfat (BF, mm).

Trait [§]	Mean	SD	h^2 [¶]	c^2 [¶]	m^2 [¶]	V_p
LADG	653.9	72.9	0.21	0.11		4217
			0.16	0.11	0.03	4183
BF	10.57	2.15	0.30	0.06		3.06
			0.28	0.05	0.01	3.05

[§]Two models were fitted for each trait, omitting or including (second row) maternal genetic effects.

[¶]The range of standard errors was 0.0076 to 0.0091 for h^2 , 0.0020 to 0.0025 for c^2 and 0.0021 to 0.0029 for m^2

Analyses did not converge for LADG when the covariance between direct and maternal genetic effects was fitted. However, Meyer (1992) showed that the bias intro-

duced by ignoring this component is small. Further, estimating a (co)variance when it is not present increases sampling errors for all components unnecessarily (Meyer, 1992). This was also observed in this study. Variances were inflated for BF when a covariance between direct and maternal genetic effects was fitted. The data used in this study included multiple generations and multiple litters per sow. No information, however, was available about piglets that may have been cross-fostered. The cross-fostering percentage was 28.8% in the study by Bouwman et al. (2010) who found that genetic effects due to the nurse sow was larger than genetic effects of the biological dam for piglet growth until weaning. Therefore, strategies such as systematic and documented cross-fostering may have to be used for the reliable separation of direct and maternal genetic effects.

Characterisation of growth traits. Average growth rate from birth until weighing increased as the test period was lengthened (Table 2). Despite lower means for earlier growth traits, standard deviations were largest for growth from birth until nine or 12 weeks (ADG4, ADG3) and coefficients of variation were higher for growth until five and nine weeks. For growth traits post weaning, standard deviations and consequently coefficients of variation decreased continuously as the test period post-weaning was lengthened. In particular, growth rate from weaning until five weeks (ADG12) had substantial variation which is partly due to the short test period. However, it is also an indication that variation exists in the ability of pigs to cope with the weaning process.

Table 2. Number of records (N), mean, standard deviation (SD) and coefficient of variation (CV) for growth traits.

Trait [§]	N	Mean	SD	CV
Growth from birth until weighing				
ADG1	813	328	41.6	12.7
ADG2	745	305	42.8	14.0
ADG3	771	467	66.1	14.1
ADG4	719	576	66.0	11.4
ADG5	883	687	63.5	9.2
Growth from weaning until weighing				
ADG12	678	257	103.0	39.9
ADG13	700	563	101.8	18.1
ADG14	696	687	92.0	13.4
ADG15	811	788	77.9	9.9

[§]Traits: average daily gain (g/day) from birth until weaning (ADG1), five (ADG2), nine (ADG3), 12 (ADG4) and 17 (ADG5) weeks and average daily gain (g/day) from weaning until five (ADG12), nine (ADG13), 12 (ADG14) and 17 (ADG15) weeks.

Associations of direct and maternal effects with growth traits. The expected coefficient from the regression of growth for a similar period of time (ADG5) on direct or maternal genetic effects of LADG is one. This was observed for the coefficient of direct genetic effects on ADG5 (Table 3). However, the corresponding coefficient was considerably larger (3.36 ± 0.94) for maternal genetic effects. This coefficient for maternal genetic effects was even higher for ADG15 (4.39 ± 1.26), which did not include the pre-weaning period. The standard errors illustrate the uncertain-

ty of these parameters, which may be over-estimated. However, estimates are significantly larger than one indicating a significant association between maternal genetic effects of LADG and growth at the end of the test period.

Regression coefficients for other growth traits based on lower weights at an earlier age may be affected by scaling effects. These are illustrated by the ratio of the standard deviation of each trait over the standard deviation of ADG5 in Table 3. For traits that included post-weaning growth until 12 weeks (ADG2 to ADG4; ADG12 to ADG14), regression coefficients were below expectations for direct and maternal genetic effects of LADG. The patterns of coefficients from the regression of these growth traits on genetic effects of LADG were similar for direct and maternal genetic effects. This indicates that both genetic effects influenced post-weaning growth during the growth trajectory similarly. This is further supported by a positive correlation of 0.54 between mid-parent values of direct and maternal genetic effects for the 896 pigs with multiple growth records. In comparison, genetic correlations between direct and maternal genetic effects for lifetime growth varied from -0.24 ± 0.11 to 0.05 ± 0.15 in the study by Solanes et al. (2004b). However, genetic correlations between direct or maternal genetic effects of growth until 90 kg and direct effects for growth before or after 12 weeks of age were positive in their study.

Table 3. Ratio of standard deviation (SD) of each trait over SD of lifetime growth rate (R-SD) and coefficients from the regression of growth traits on direct and maternal genetic effects of lifetime growth (LADGd, LADGm) from an animal model.

Trait ^a	R-SD	LADGd	LADGm
Growth from birth until weighing			
ADG1	0.66	0.07 ± 0.20	0.76 ± 0.72
ADG2	0.67	-0.24 ± 0.20	-0.08 ± 0.76
ADG3	1.04	0.48 ± 0.28	0.76 ± 1.03
ADG4	1.04	0.53 ± 0.27	0.80 ± 1.05
ADG5	1	1.13 ± 0.25	3.36 ± 0.94
Growth from weaning until weighing			
ADG12	1.62	-0.41 ± 0.44	-1.09 ± 1.9
ADG13	1.60	1.01 ± 0.45	0.66 ± 1.68
ADG14	1.45	1.04 ± 0.42	1.28 ± 1.59
ADG15	1.23	1.58 ± 0.33	4.39 ± 1.26

^aTraits: average daily gain (g/day) from birth until weaning (ADG1), five (ADG2), nine (ADG3), 12 (ADG4) and 17 (ADG5) weeks and average daily gain (g/day) from weaning until five (ADG12), nine (ADG13), 12 (ADG14) and 17 (ADG15) weeks.

The coefficient from the regression of pre-weaning growth (ADG1) on maternal genetic effects for LADG was positive and corresponded to the expectation. In contrast, there was no association between direct genetic effects for LADG and pre-weaning growth. This finding corresponds to higher maternal genetic effects and negligible direct genetic effects for piglet growth (e.g. Hermes et al., 2001; Solanes et al., 2000a). The positive regression coefficient of maternal genetic effects of LADG on pre-weaning growth indicates that maternal genetic effects on pre-weaning performance may be estimated indirectly based on information

available for a later growth trait. This may be of interest to pig breeding programs with limited information on birth or weaning weight of individual pigs.

There was a negative coefficient from the regression of growth shortly after weaning (ADG12) on maternal genetic effects of LADG contrary to expectation. This may indicate that selection for maternal genetic effects of LADG favors pigs with high pre-weaning growth and reduced growth shortly after weaning.

Conclusion

Both, growth and backfat recorded at 90 kg live weight had low maternal genetic effects. The economic importance of maternal genetic effects for LADG offers further opportunities for genetic improvement of growth that are currently ignored in most breeding programs. Associations between direct or maternal genetic effects with different growth traits over the growth trajectory were similar indicating that selection for direct and maternal genetic effects will influence growth in a similar pattern. This conclusion is further supported by a positive correlation between solutions of direct and maternal genetic effects. Direct and maternal genetic effects affected growth at the end of test period significantly and had lowly negative effects on growth post weaning. Whether selection for maternal genetic effects of LADG favors higher pre-weaning growth followed by a reduction in growth after weaning should be explored.

Acknowledgements

This study was funded by the Pork CRC under project 2B-103. Diligent data collection by Tanya McKenna at University of Queensland is gratefully acknowledged. The principal author thanks the breeders who kindly supplied the data.

Literature Cited

- Akanno, E. C., Schenkel, F. C., Quinton, V. M. et al. (2013). *Livest. Sci.* 152:101-113.
- Amer, P. R., Ludemann, C. I. and Hermes, S. (2014). *J. Anim. Sci.* submitted.
- Arthur, P. F., Barchia, I. M., and Giles, L. R. (2008). *J. Anim. Sci.* 86:1096-1105.
- Bouwman, A. C., Bergsma, R., Duijvesteijn, N. et al. (2010). *J. Anim. Sci.* 88:2883-2892.
- Gilmour A. R., Gogel B., Cullis B., et al. (2009). *ASReml user guide release 3.0*.
- Hermesch, S., Luxford B. G. and Graser, H.-U. (2001). *Proc. Assoc. Adv. Anim. Breed. Genet.* 14:207-210.
- Johnson, Z. B., Chewing, J. J. and Nugent III, R. A. (2002). *J. Anim. Sci.* 80:1470-1477.
- Meyer, K. (1992). *Livest. Prod. Sci.* 31:487-509.
- SAS Institute Inc (2011). *SAS/STAT 9.3 User's Guide*.
- Solanes, F. X., Grandinson, K., Rydhmer, L. et al. (2004a). *Livest. Prod. Sci.* 199-212.
- Solanes, F. X., Kihlberg, M., Andersson, K. et al. (2004b). *Acta Agric. Scand., Sect. A, Animal Sci.* 54:67-74.
- Zhang, S., Bidanel, J.-P., Burlot, T. et al. (2000). *Genet. Sel. Evol.* 32:41-56.