Maternal and Direct Genetic Parameters for Production Traits and Maternal Correlations among Production and Feed Efficiency Traits in Duroc Pigs

M. A. Hoque*, **H. Kadowaki**[1], **T. Shibata**[1] **and K. Suzuki**

Laboratory of Animal Breeding and Genetics, Graduate School of Agricultural Science

Tohoku University, Aoba, Sendai, Japan

ABSTRACT : Direct and maternal genetic parameters for production traits in 1,642 pigs and maternal genetic correlations among production (1,642 pigs) and feed efficiency (380 boars) traits were estimated in 7 generations of a Duroc population. Traits studied were daily gain (DG), intramuscular fat (IMF), loineye area (LEA), backfat thickness (BF), daily feed intake (FI), feed conversion ratio (FCR) and residual feed intake (RFI). The RFI was calculated as the difference between actual and predicted feed intake. The predicted feed intake was estimated by adjusting the initial test weight, DG and BF. Data for production traits were analyzed using four alternative animal models (including direct, direct+maternal permanent environmental, or direct+maternal genetic+maternal permanent environmental effects). Direct heritability estimates from the model including direct and all maternal effects were 0.41±0.04 for DG, 0.27±0.04 for IMF, 0.52±0.06 for LEA and 0.64±0.04 for BF. Estimated maternal heritabilities ranged from 0.04±0.04 to 0.15±0.05 for production traits. Antagonistic relationships were observed between direct and maternal genetic effects (r_{am}) for LEA (-0.21). Maternal genetic correlations of feed efficiency traits with FI (r_g of FI with FCR and RFI were 0.73±0.06 and 0.90±0.05, respectively) and LEA (r_g of LEA with FCR and RFI were -0.48±0.05 to -0.61±0.05, respectively) were favorable. The estimated moderate genetic correlations between direct and maternal genetic effects for IMF and LEA indicated that maternal effects has an important role in these traits, and should be accounted for in the genetic evaluation system. (**Key Words :** Genetic Parameters, Growth and Feed Efficiency, Maternal Effects)

INTRODUCTION

Accurate estimates of variance components and heritabilities depend on application of the appropriate model for traits of interest. Estimates may be biased by failure to account for appropriate genetic and environmental sources of variation, such as maternal effects. Bryner et al. (1992) reported significant maternal effects for growth rate and backfat for centrally tested Yorkshire boars. Maternal effects arise from the ability of the mother to produce the milk needed for growth and other maternal behavior. Maternal effect has been reported to have a significant influence of carcass traits (Koch et al., 1983). There is also evidence that maternal effect might affect post weaning growth as a carryover effect from weaning weight (Meyer et al., 1993). Hence, to achieve optimum progress in a selection program for many traits, both the direct and maternal component should be taken into account.

Considerable variation in individual animals has been shown in feed intake above or below that expected on the basis of size and growth rate (Hoque et al., 2006). This difference in intake is generally calculated as residual feed intake (RFI) by comparing an animal's actual and predicted feed intake, where the predicted feed intake is the amount of feed the animal is expected to consume on the basis of its body weight and growth rate. Estimations of direct and maternal genetic parameters are prerequisites for implementing sound breeding programs to improve economically important traits. The direct genetic correlations between feed efficiency and production traits in pigs have been reported (Gilbert et al., 2007; Hoque et al., 2007). However, the estimates of maternal genetic correlations between production and feed efficiency traits are, therefore, necessary to maximize selection efficiency in breeding program.

* Corresponding Author: M. A. Hoque. Department of Animal Breeding and Genetics, Bangladesh Agricultural University 2202, Bangladesh. Tel: +81-70-54702159, Fax: +81-22-717-8697, E-mail: azharhoque@yahoo.com
[1] Miyagi Prefecture Animal Industry Experiment Station, Tamatsukuri-gun, Miyagi, Japan.

Table 1. Number of parents and offspring by generation of selection

| Generation | Performance tested | | | | Parents | |
| | Candidate | | Sib-tested pig | | | |
	Boar	Gilt	Barrow	Gilt	Sire	Dam
Base	-	-	-	-	19	35
1	48	92	44	18	19	46
2	50	115	59	30	14	43
3	50	106	69	14	13	43
4	50	107	68	16	12	43
5	48	92	52	24	14	41
6	50	99	51	21	9	45
7	84	104	51	30	25	60
Total	380	715	394	153	125	356

If maternal genetic effects are important for performance traits, a model containing these effects, along with direct genetic effects, should provide more precise predictive ability of future progeny performance than a model that contains only direct genetic effects (Lykins et al., 2000). Improvement of maternal response, in addition to direct response, can lead to greater overall response (Roehe and Kennedy, 1993). Since antagonism has been observed between direct and maternal effects for many traits, information of the maternal influence on production and feed efficiency traits, and the correlation between these effects, is fundamental for achieving unbiased heritability estimates. This paper presents estimates of genetic parameters for production traits fitting four alternative animal models, attempting to separate direct genetic, maternal genetic and maternal permanent environmental effects, and maternal genetic correlations among production and feed efficiency trait in Duroc pigs.

MATERIAL AND METHODS

Animals on performance test

Duroc pigs used in this study were of a line that had been selected for daily gain (DG), intramuscular fat (IMF), loineye area (LEA) and backfat thickness (BF) through 7 generations at the Miyagi Prefecture Animal Industry Experiment Station, Japan during 1995 to 2001. A total of 1,642 pigs in 7 generations were tested, description of the data structure by generation of selection is presented in Table 1. For estimating the variance components a pedigree file was constructed and the total number of animals, including test animals, was 1,780 pigs in the pedigree. Pigs were weaned at 4 wk. At 8 wk of age, 1 to 2 male piglets (total of 50 piglets) and 2 to 4 female piglets (total of 100 piglets) from each litter were selected as candidates for breeding boars and gilts based on their individual body weight. At that time, about 80 piglets in all, composed mainly of boars and a few gilts (when boars were not available) from each litter, were selected for full-sib testing in each generation. This first stage of selection was conducted within litters based on individual body weight at 8 wk. Boars for full-sib tests were subsequently castrated. Performance tests began when the body weight reached 30 kg; testing ended at 105 kg. Pigs were provided *ad libitum* access to a specially ordered formula feed (on DM basis, 15% CP, 0.76% lysine, 3.44 DE Mcal/kg) during the testing period. The same feed was used throughout the 7 generations of selection. Pigs had free access to water. Boars were reared individually in performance testing pens. Gilts and barrows were reared in growing pens, with group feeding in a concrete-floored building with 8 pigs per pen, which allowed 1.2 m² of floor area per pig.

Selection method

The detailed procedure for selection has been described by Suzuki et al. (2005). The first and second generations of selection were performed using an index selection method based on relative desired gains. Traits used as selection criteria were DG, LEA, BF and IMF. Genetic and phenotypic parameters used to derive the selection criteria were obtained from performance test data of the first and second generation. Breeding values of DG, LEA, BF and IMF were estimated using multiple-trait animal-model BLUP from the third generation onward. The breeding values were calculated using the Prediction and Estimation (PEST) program after estimating genetic parameters using the Variance Component Estimation (VCE) program (ver. 4.2.5) (Neumaier and Groeneveld, 1998) with the models of generation and sex as fixed effects and random effects of individual additive genetic effect and error. Relative economic weights of selection traits were calculated from the relative desired gains of DG, LEA, BF and IMF, which were established from performance test data of the first generation. The aggregate breeding values were calculated by multiplying the relative economic weights by the EBV of each trait; then selection was executed. Approximately 15 boars and 50 gilts were selected at each generation.

Traits in study

The studied traits were DG, IMF, LEA and BF as

Table 2. Descriptive statistics of the studied traits

Statistics \ Traits*	DG (kg/d)	IMF (%)	LEA (cm^2)	BF (cm)	FI (kg/d)	RFI (kg/d)	FCR (feed:gain)
Mean	0.87	4.25	36.99	2.37	2.62	0.00	2.65
Observation no.	1,642	1,642	1,642	1,642	380	380	380
Minimum	0.54	0.95	21.40	1.30	1.96	-0.38	2.20
Maximum	1.20	12.32	49.50	4.25	3.32	0.42	3.14
SD	0.11	1.46	4.05	0.43	0.23	0.13	0.17

* DG, average daily gain; IMF, intramuscular fat; LEA, loineye area; BF, backfat thickness; FI, daily feed intake; RFI, residual feed intake; FCR, feed conversion ratio.

production traits, and daily feed intake (FI), feed conversion ratio (FCR) and residual feed intake (RFI) as feed efficiency traits. The weekly body weight of individual pigs during the test period was recorded, and DG for each animal was calculated. Using ultrasound (B-mode) color scanning technology (SR-100; Kaijo Corp., Tokyo, Japan), LEA and BF were measured on all live animals at 105-kg on the left side at the location of half body length. FI was measured in kilograms per day for individual boars by the difference between supplied and leftover feed. The FCR was calculated as FI divided by DG. The RFI was estimated as the difference between actual FI and that predicted from single-trait analyses of FI on initial body weight, DG and BF included as covariates. These analyses included fixed effects of litter and generation, as well as random animal effect. Regression coefficients for these covariates were used to estimate RFI. Pigs for full-sib testing (barrows and gilts) were slaughtered using manual low-voltage (200 V) electric stunning 24 h after feed removal with free access to water. Subsequently, 2 minced loin (2 thoracic vertebrae sections above the last rib) meat samples of approximately 20 g each were analyzed using the Soxhlet method to determine IMF. The descriptive statistics for studied traits are presented in Table 2. The mean value for RFI was zero, as expected by definition.

Statistical analysis

The (co)variance components and genetic parameters were estimated by the REML method using the VCE program (Neumaier and Groeneveld, 1998). The covariance structure for additive genetic effects of animals and residual effects is described below:

$$V(a) = \sigma^2_a A$$

$$V(m) = \sigma^2_m A$$

$$V(c) = \sigma^2_c I$$

$$V(e) = \sigma^2_e I$$

$$Cov(a,m) = \sigma_{am} A,$$

Where, a and m denote vectors of animals' direct and maternal additive genetic effects, respectively, and c and e vectors of maternal permanent environmental effects and residual errors. A is the numerator relationship matrix between animals and I is identity matrix. σ^2_a is the additive genetic variance, σ^2_m the maternal genetic variance, σ_{am} the direct-maternal genetic covariance, σ^2_c the maternal permanent environmental variance and σ^2_e the error variance.

The (co)variance components and genetic parameters for production traits were estimated using four different models. The first model of analysis fitted, Model 1, was a simple animal model with animals' additive genetic effects as the only random effect. Model 2 allowed for a permanent environmental effect due to dam (littermates), fitting this as an additional random effect, in the model. Model 3 attributed maternal effects to the genotype of the dam, fitting both maternal environmental and maternal genetic effects as additional effects, and allowed for a covariance between direct and maternal effects, whereas Model 4 assumed that direct and maternal effects were uncorrelated, i.e. $\sigma_{am} = 0$. The 4 models were:

$$Y_{ij} = F_i + a_j + e_{ij} \tag{1}$$

$$Y_{ijk} = F_i + a_j + c_k + e_{ijk} \tag{2}$$

$$Y_{ijk} = F_i + a_j + m_k + c_k + e_{ijk} \tag{3}$$
$$\text{with } Cov(a_j, m_k) \neq 0$$

$$Y_{ijk} = F_i + a_j + m_k + c_k + e_{ijk} \tag{4}$$
$$\text{with } Cov(a_j, m_k) = 0$$

Where, Y_{ijk} was the observation of trait i of the jth animal with the kth dam; the fixed effects, F_i, were identical for all models, including effects of generation and sex; a_j, the direct additive genetic effect of the jth animal; c_k, the permanent environmental effect due to the kth dam; m_k, the maternal additive genetic effect of the kth dam; e_{ijk}, the random residual error.

Depending on the model, the direct heritability (h^2_a), maternal heritability (h^2_m), direct-maternal genetic correlation (r_{am}), and permanent environmental variance

Table 3. Estimates (±SE) of genetic parameters for production traits using different models

Traits*	Model	Estimates**				
		h^2_a	h^2_m	r_{am}	c^2	h^2_T
DG	1	0.51±0.04	-	-	-	0.51±0.04
	2	0.48±0.03	-	-	0.04±0.03	0.48±0.03
	3	0.41±0.04	0.05±0.03	0.13±0.04	0.02±0.01	0.44±0.03
	4	0.44±0.04	0.06±0.03	-	0.04±0.02	0.47±0.03
IMF	1	0.40±0.03	-	-	-	0.40±0.03
	2	0.39±0.03	-	-	0.12±0.02	0.39±0.03
	3	0.27±0.04	0.13±0.05	0.22±0.04	0.09±0.02	0.42±0.04
	4	0.31±0.03	0.15±0.05	-	0.10±0.02	0.38±0.03
LEA	1	0.47±0.05	-	-	-	0.47±0.05
	2	0.45±0.05	-	-	0.02±0.03	0.45±0.04
	3	0.52±0.06	0.05±0.04	-0.21±0.05	0.01±0.02	0.48±0.04
	4	0.44±0.06	0.09±0.04	-	0.02±0.02	0.48±0.04
BF	1	0.72±0.04	-	-	-	0.72±0.04
	2	0.72±0.04	-	-	0.01±0.01	0.72±0.03
	3	0.64±0.04	0.03±0.04	0.17±0.05	0.00±0.00	0.71±0.04
	4	0.70±0.05	0.04±0.04	-	0.01±0.01	0.72±0.03

* DG, average daily gain; IMF, intramuscular fat; LEA, loineye area; BF, backfat thickness.
** h^2_a, direct heritability; h^2_m, maternal heritability; r_{am}, direct-maternal genetic correlation; c^2, common environmental variance as proportion of phenotypic variance; h^2_T, total heritability = $(\sigma^2_a+0.5\sigma^2_m+1.5\sigma_{am})/\sigma^2_p$, (Willham, 1972).

due to the dam as a proportion of the phenotypic variance (c^2) were estimated. Furthermore, the total heritability (h^2_T) was calculated as (Willham, 1972):

$$h^2_T = (\sigma^2_a+0.5\sigma^2_m+1.5\sigma_{am})/\sigma^2_p$$

The numerator of the equation is the covariance of the animal's phenotypic record with the sum of its genetic effects (i.e., h^2_T is the regression of an animal's total genotype (direct and maternal) on its phenotype). The standard errors (SE) for h^2_T were the averages of the estimates using different models.

The VCE program did not perform with status 1 (infinity values of log likelihood and not estimated SE) for feed efficiency traits using the Models 2, 3 and 4. Maniatis and Pollott (2002) concluded that direct by maternal genetic covariance is often difficult to estimate even in univariate analysis, and also debate surrounds the estimates performed with appropriate data structure. Hence, it was decided not to estimate such variance components for feed efficiency trait, because the size of data for feed efficiency traits was small. However, maternal genetic correlations among production and feed efficiency traits were estimated using two-trait animal model, fitting only random animal additive genetic and maternal genetic effects.

RESULTS

Estimates of genetic parameters for production traits (DG, IMF, LEA and BF) using the four alternative models are presented in Table 3. The correlation between direct and maternal genetic effects (r_{am}) was moderately positive (0.22 ±0.04) for IMF, and moderately negative (-0.21±0.05) for LEA, whereas the corresponding correlations for other production traits were low and positive (0.13±0.04 and 0.17±0.05 for DG and BF, respectively). The estimates of direct heritability were reduced about 20% for DG, 33% for IMF and 11% for BF, and increased up to 19% for LEA when maternal effects were considered in the model. The direction of the bias on the heritability estimates depends partly on the size of the maternal genetic estimates, and the size of correlation between direct additive and maternal genetic effects. The maternal heritability estimates for production traits were low (ranged from 0.03±0.04 to 0.15± 0.05). The maternal genetic and maternal environmental variances as a proportion of phenotypic variances (c^2) for each trait were similar among models 2, 3, and 4. The h^2_T estimates for each trait were close using different models.

Estimates of direct genetic correlations using sire model between feed efficiency and production traits using the same data have been reported in our previous study (Hoque et al., 2007). However, sire model assumes that sires are randomly mated to dams and that dams are not related. This might not be true in the context of the Japanese testing program, where the progeny are produced by planned mating within each testing station. Maternal genetic correlations between production traits and measures of feed efficiency are summarized in Table 4. Maternal genetic correlations of feed efficiency traits with FI were positive and high (r_g of FI with FCR and RFI were 0.73±0.06 and 0.90±0.05, respectively), and with LEA were negative and moderate to high (r_g of LEA with FCR and RFI were -0.48

Table 4. Maternal genetic correlations (±SE) among production traits and measures of feed efficiency

Traits*	IMF	LEA	BF	FI	RFI	FCR
DG	0.22±0.06	0.21±0.05	0.33±0.06	0.34±0.06	-0.05±0.03	-0.22±0.04
IMF		0.44±0.04	0.10±0.05	-0.16±0.05	0.14±0.05	0.03±0.04
LEA			0.34±0.06	0.44±0.4	-0.61±0.05	-0.48±0.05
BF				0.17±0.05	-0.19±0.04	-0.03±0.02
FI					0.90±0.05	0.73±0.06
RFI						0.95±0.04

* DG, average daily gain; IMF, intramuscular fat; LEA, loineye area; BF, backfat thickness; FI, daily feed intake; RFI, residual feed intake adjusted for initial test weight, DG and BF; FCR, feed conversion ratio.

±0.05 and -0.61±0.05, respectively). The corresponding correlations among production traits were moderate (ranged from 0.21±0.05 to 0.44±0.04), except between BF and IMF, which was low (0.10±0.05). Maternal genetic correlations of measures of feed efficiency with DG and BF were low to moderate and negative (ranged from -0.03±0.04 to -0.22± 0.04).

DISCUSSION

The low maternal heritability estimates and weak correlations between direct and maternal genetic effects for DG and BF indicate that maternal effect is relatively less important for these traits. Johnson et al. (2002) estimated maternal heritability for DG to be 0.00 for Hampshire, 0.02 for Landrace and Yorkshire, and 0.03 for Duroc pigs. With performance tested Yorkshire boars, Bryner et al. (1992) found a higher maternal heritability of 0.23; however, litter environmental effects were not included in their model. Ferraz and Johnson (1993) reported low estimates of heritability of maternal effects using different models for DG (ranged from 0.05 to 0.15). Estimated low maternal heritability for BF was also in agreement with the estimates by Ferraz and Johnson (1993) and Bryner et al. (1992), who estimated maternal heritability of BF to be 0.03 and 0.11, respectively. Ferraz and Johnson (1993) reported that, for all practical purposes, the maternal effects and the correlation between maternal and direct effects could be ignored for DG and BF, although Bryner et al. (1992) indicated that direct maternal effects were significant for both the traits in swine, accounting for 0.23 and 0.11% of the variance, respectively. Agapita et al. (2006) measured BF and LEA using two ultrasound modes (A and B) in Duroc pigs and estimated heritabilities for BF to be 0.45 and 0.39, respectively and for LEA to be 0.32 and 0.25, respectively for A and B ultrasound modes. Li and Kennedy (1994), using a model that included animal and litter effects, reported estimates of direct heritability for BF to be 0.53, 0.55, 0.51 and 0.50 for Landrace, Yorkshire, Duroc and Hampshire, respectively. Bryner et al. (1992) reported direct heritability for BF to be 0.24 for Yorkshire boars. Bereskin (1986), using performance records of purebred Duroc and Yorkshire gilts tested in littermate groups, estimated

heritability for BF to be 0.42. Ferraz and Johnson (1993), using a model that included direct additive effects and common litter environmental effects, reported estimates of 0.54 and 0.33 for two farms of Landrace pigs. Estimates of heritability with litter effects in the model for DG, LEA and BF were approximately 10% less than those obtained with only random animal effects in the model (Johnson et al., 1998).

The permanent environmental effect of dam explained 4% of the phenotypic variation in DG, which was close to the 7% reported by Ferraz and Johnson (1993) with Large White and Landrace, but slightly lower than the approximately 15% reported by Johnson et al. (2002). No relationship between direct and maternal effects (r_{am}) for DG (0.02) has been reported by Johnson et al. (2002) in Duroc and Hampshire, which supports the present result. Ferraz and Johnson (1993) reported that approximately 5% of the variation in BF of Landrace and Large White pigs was due to litter environmental effects. Li and Kennedy (1994) reported average permanent environmental effects of dam of 0.10 for BF of Yorkshire, Landrace, Duroc and Hampshire pigs.

The low maternal heritability estimates for IMF but moderate correlations between direct and maternal genetic effects for IMF and LEA indicate that maternal effect has important role in these traits. Johnson et al. (2002) reported maternal heritability for LEA to be 0.06 and 0.6, respectively, for Landrace and Yorkshire with correlation between direct and maternal effects to be -0.66 for both the breeds. Their estimates are in partial agreement with the findings of the present study. Crews and Kemp (1998) obtained estimates of maternal heritability in crossbred cattle of 0.06 and 0.09 for LEA and beef marbling, respectively. The permanent environmental effect of dam for IMF was slightly lower than that reported by Knapp et al. (1997), who estimated the permanent environmental effect of dam for IMF to be 0.14 and 0.16, respectively for Large White and Pietrain swine. A large permanent environmental effect for IMF implies that such an effect influences the IMF accumulation during the subsequent fattening period.

We are not aware of any published studies using different models for partitioning variance components for feed efficiency traits in pigs. Large number of data is

required to partition variance components for traits. Study on partitioning variance components for feed efficiency traits with sizable data needs to be focused. However, the high maternal genetic correlations between FI and measures of feed efficiency in present study suggested that maternal effects should be accounted for in a genetic evaluation system for improving efficiency of feed utilization and reducing FI. Genetic selection of individual production traits should generally be effective. However, single trait selection should be avoided. Balanced multi-trait selection should be used instead, which leads to small, but positive, gains in production and feed efficiency traits. However, most of these traits, except DG and BF, are influenced by maternal genetic effects and could be used as indicators of maternal ability. Thus, a selection program incorporating maternal effects would contribute to the improvement process not only in production, but also in feed efficiency traits. Improvement of maternal response in addition to direct response, can lead to greater overall improvement in production and feed efficiency traits.

CONCLUSION

Maternal effects appear to be important for loin eye area and intramuscular fat, and needs to be included in a genetic evaluation system to obtain unbiased estimates of direct breeding values. An antagonistic relationship existed between direct and maternal genetic effects for loin eye area, which indicates the necessity of combining both direct and maternal estimated breeding values of these traits in a selection index to increase the economic efficiency. Further research on partitioning variance components with large number of data for economically important traits, particularly for feed efficiency traits, should be focused.

ACKNOWLEDGMENT

REFERENCES

Agapita, J. S., K. S. Seo, K. H. Cho, S. D. Kim and Y. C. Lee. 2006. Genetic parameter estimation of carcass traits of Duroc predicted using ultrasound scanning modes. Asian-Aust. J. Anim. Sci. 19:1379-1383.

Bereskin, B. 1986. A genetic analysis of feed conversion efficiency and associated traits in swine. J. Anim. Sci. 62:910-917.

Bryner, S. M., J. W. Mabry, J. K. Bertrand, L. L. Benyshek and L. A. Kriese. 1992. Estimation of direct and maternal heritability and genetic correlation for backfat and growth rate in swine using data from centrally tested Yorkshire boars. J. Anim. Sci. 70:1755-1759.

Crews, D. H. and R. A. Kemp. 1998. Maternal (co)variance components for carcass traits breeding values among crossbred beef cattle. Proc. 6th Worl. Cong. Gen. Appl. Livest. Prod. 23: 177-180.

Ferraz, J. B. S. and R. K. Johnson. 1993. Animal model estimation of genetic parameters and response to selection for litter size and weight, growth, and backfat in closed seedstock populations of Large White and Landrace swine. J. Anim. Sci. 71:850-858.

Gilbert, H., J. P. Bidanel, J. Gruand, J. C. Caritez, Y. Billon, P. Guillouet, H. Lagant, J. Noblet and P. Sellier. 2007. Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. J. Anim. Sci. 85:3182-3188.

Hoque, M. A., K. Suzuki, H. Kadowaki, T. Shibata and T. Oikawa. 2007. Genetic parameters for feed efficiency and their relationships with growth and carcass traits in Duroc pigs. J. Anim. Breed. Gen. 124:108-116.

Hoque, M. A., P. F. Arthur, K. Hiramoto and T. Oikawa. 2006. Genetic relationship between different measures of feed efficiency and its component traits in Japanese Black (Wagyu) bulls. Livest. Sci. 99:111-118.

Johnson, Z. B., J. J Chewning and R. A. Nugent. 2002. Maternal effects on traits measured during postweaning performance test of swine from four breeds. J. Anim. Sci. 80:1470-1477.

Johnson, Z. B., J. J. Chewning and R. A. Nugent. 1998. Genetic parameters for performance traits of boars in a population of Large White swine with primary selection emphasis on maternal traits. J. Anim. Sci. 76(Suppl.):151(Abstr.).

Knapp, P., A. Willam and J. Solkner. 1997. Genetic parameters for lean meat content and meat quality traits in different pig breeds. Livest. Prod. Sci. 52:69-73.

Koch, R. M., M. E. Dikeman, H. Grodzki, J. D. Crouse and L. V. Candiff. 1983. Individual and maternal genetic effects for beef carcass traits of breeds representing diverse biological types (cycle 1). I. Anim. Sci. 57:1124-1132.

Li, X. and B. W. Kennedy. 1994. Genetic parameters for growth rate and backfat in Canadian Yorkshire, Landrace, Duroc, and Hampshire pigs. J. Anim. Sci. 72:1450-1454.

Lykins, L. E., J. K. Bertrand, J. F. Baker and T. E. Kiser. 2000. Maternal birth weight breeding value as an additional factor to predict calf birth weight in beef cattle. J. Anim. Sci. 78:21-26.

Maniatis, N. and G. E. Pollott. 2002. Maternal effects on weight and ultrasonically measured traits of lambs in a small closed Suffilk flock. Small Rumin. Res. 45:235-246.

Meyer, K., M. J. Carrick and B. J. P. Donnelly. 1993. Genetic parameters for growth traits of Australian beef cattle from a multibreed selection experiment. J. Anim. Sci. 71:2614-2622.

Neumaier, A. and S. L. Groeneveld. 1998. Restricted maximum likelihood estimation of covariances in sparse linear models. Genet. Sel. Evol. 30:3-26.

Roehe, R. and B. W. Kennedy. 1993. Effect of selection for maternal and direct genetic effects on genetic improvement of litter size in swine. J. Anim. Sci. 71:2891-2904.

Suzuki, K., H. Kadowaki, T. Shibata, H. Uchida and A. Nishida. 2005. Selection for daily gain, loin-eye area, backfat thickness and intramuscular fat based on desired gains over seven generations of Duroc pigs. Livest. Prod. Sci. 97:193-202.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35:1288-1293.