

Maternal effects on farrowing and pre-weaning traits in Line 990 pigs

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The importance was studied of the inclusion of maternal genetic effects in the animal model on genetic estimates of the following reproductive parameters of Line 990 pigs: litter size, litter weight, survival rate, age at first farrowing and farrowing interval. Additive direct genetic variance for age at first farrowing was three times smaller after fitting the model with maternal effect. The estimates of h_a^2 for the first parity litter size and litter weight appeared slightly higher than those obtained for parities 2-8 and including the maternal genetic effect. Decrease of direct heritability coefficient for age at first farrowing was observed after including maternal effect in the model (0.10 vs 0.03). The highest h_m^2 estimates were observed for age at first farrowing (0.21), number of piglets born alive and litter weight at weaning (0.09). The proportions of the sow permanent environmental variance and variance caused by service sire to total variance were small and close to those obtained for two models – with and without maternal effects. Direct-maternal correlations were high and negative for all traits. Likelihood ratio test indicated that maternal genetic effects were significant for age at first farrowing only.

KEY WORDS: genetic parameters / maternal effects / pigs / reproduction

Pig breeding programmes traditionally focus on the genetic improvement of production and reproduction traits of a clear economic value. Sow's age at first farrowing, number of live-born piglets, piglets survival rate and birth litter weight affect the economic results of a pig farm significantly, and therefore are assessed during pig performance testing. During the suckling period of mammals growth is affected by both the offspring and dam performance, the latter providing the environment for

development. These maternal effects are strictly environmental for the offspring, but can contain both genetic and environmental components [Arendonk *et al.* 1996]. Maternal environment represents mainly the dam's lactating potential and mothering ability that make a sow more or less capable of bearing, suckling and raising her litter, antibody transmitting, quality of the uterine environment and cytoplasmic heredity or genomic imprinting. The genotype of the dam, therefore, affects the phenotype of the offspring through a sample of half her direct, additive genes for growth as well as through her genotype for maternal effects on growth and fitness. Ignoring maternal effects can bias the heritability estimates for direct genetic effects. The sign and size of the bias depends on the size of the maternal genetic variance and size and sign of the direct-maternal genetic covariance [Southwood and Kennedy 1990]. Hence, to achieve optimum progress in a selection programme both the direct and maternal component should be accounted for, especially if an antagonistic relationship between them exists [Willham 1980, Robinson 1981, Meyer 1992].

Many breeding programmes focus on litter size as a selection criterion for reproduction performance, as recording live weights of piglets is both time consuming and costly. Therefore, these traits are treated as traits of the mother.

The objective of this study was to estimate genetic parameters for additive direct and maternal genetic effects on pre-weaning performance traits of Line 990 pigs. Parameters for two different models were compared to determine the influence of maternal genetic effects included.

Material and methods

The material considered was obtained over the years 1998-2005 from the single farm of Line 990 pigs managed under a batch farrowing system. Sows were housed in groups of seven. At farrowing sows were kept in individual crates. The herd had been under selection regimen for production and reproduction traits. No culling of animals showing positive reaction to the halothane test was applied. The sows were fed a restricted diet, except during lactation. Creep feed was provided to piglets at around day 7-8 of age. The piglets were weaned at 4-5 weeks of age and remained as separate litter groups for a further 4 weeks.

For each sow the following data were recorded: identity number, farrowing parity number, age at first farrowing (AFF), farrowing interval (FI), identity number of service sire, total number of piglets born/litter (TNB), numbers of piglets born alive/litter (NBA), litter size on day 21 (N21), litter size at weaning (NW), litter weight on day 21 (W21), litter weight at weaning (WW) and survival rate (%) to weaning (SV).

The data were divided into two sets: data set I comprised records from parity 1, while data set II comprised records from parities 2-8. For parity 1 (set I), a total of 915 litter records and for parities 2-8 (set II) a total of 2193 litter records were included in the analysis. Both data sets are characterized in Table 1.

Table 1. Description of the data analysed

	n	Range	Mean	Coefficient of variation
Parity 1				
Number of sows	915			
Number of service boars	119			
Number of litters per boar		1-43	7,69	97,0
Parity 2-8				
Number of records	2193			
Number of sows	816			
Number of litters per sow		1-8	2,69	41,2
Number of service boars	146			
Number of litters per boar		1-61	15,02	98,4

In step I, the statistical relevance of fixed (year-season, farrowing interval or age at first farrowing as covariate, parity number) and random (service sire) effects for examined traits were tested with the analysis of variance. Genetic parametres were estimated using four models (two for parity 1 and two for parities 2-8) in order to evaluate the consequences of ignoring maternal genetic effects:

Models for parity 1:

$$y = Xb + Z_1s + Z_2a + e;$$

$$y = Xb + Z_1s + Z_2a + Z_3m + e.$$

Models for parities 2-8:

$$y = Xb + Z_1s + Z_2a + Z_3p + e;$$

$$y = Xb + Z_1s + Z_2a + Z_3p + Z_4m + e.$$

where:

y – vector of examined traits;

b – vector of fixed (year-season, parity effect for data set II, age at first farrowing or farrowing interval); the models for the traits “age at first farrowing” and “farrowing interval” omitted the regression effects;

s – vector of random service sire effects; it was assumed that litter size is a trait expressed by the sow (ability to release ova and carry the fertilized ova through the parturition) with some influence of the service sire (ability to fertilize ova);

a – vector of direct genetic effects;

m – vector of maternal genetic effects; the maternal genetic effect was related to the of the sow’s dam, who delivered the piglets;

p – vector of permanent environmental effect for all litters of a sow;

e – vector of residual effects;

X – known design matrix for fixed effects;

Z_1, Z_2, Z_3, Z_4 – incidence matrices relating observations to random effects.

The (co)variance structure for the analysis can be described as:

$$V(a) = \sigma_a^2 A, V(s) = \sigma_s^2 I, V(m) = \sigma_m^2 A, V(p) = \sigma_p^2 I, V(e) = \sigma_e^2 I, \text{Cov}(a, m) = \sigma_{am} A$$

where:

σ_a^2 – additive genetic variance;

σ_s^2 – service sire variance;

σ_m^2 – maternal additive genetic variance;

σ_{am} – the direct-maternal genetic covariance;

σ_p^2 – the sow permanent environmental variance;

σ_e^2 – error variance;

A – numerator relationship matrix between animals;

I – identity matrix.

Vectors s, p, e were assumed to be uncorrelated with each other effects, *i.e.* all remaining covariances were assumed to be zero.

Year-season classes were composed of the data sets, the year and season (four classes per year – January-March, April-June, *etc*) of farrowing. Year-season classes with less than 10 observations were removed from the data set. Because of small number of parities larger than 5 in data set II, they were pooled.

The variance components were estimated by the REML method using Misztal's software [Misztal 1998]. The programme does not provide standard errors for estimates. All pedigree information available was included in the analysis in order to minimize bias due to selection and to increase the accuracy of estimation through additional ties between animals. The pedigrees were at least two-generations deep (animal and its parents) and included 1547 animals. Pedigrees of 86 animals were three-generations deep.

The influence of including maternal effects in the models was tested by the likelihood ratio test. The statistics of the likelihood ratio (LR_{ij}) test for sequentially reduced models [Rao 1963] are:

$$LR_{ij} = -2\log_e (L_j/L_i) = 2\log_e L_i - 2\log_e L_j;$$

where:

L_i – maximum likelihood for the complete model with maternal effect;

L_j – the maximum likelihood for the reduced model without maternal effect.

An inference about the significance of the maternal effects was based on the chi square test.

Results and discussion

Means and coefficients of variation for traits included in the analyses at different parities are presented in Table 2. A small difference was noted between the trait means at parity 1 and parities 2-8. Mean litter size (TNB, NBA, N21 and NW), mean litter weight (W21, WW) and survival rate at parity 1 were all smaller than at parities 2-8 and so were their coefficients of variation. The differences result from maturity of animals as well as from the culling of the sows.

Table 2. Range, means and coefficients of variation for traits for two data sets

Trait	Range (kg)	Mean (kg)	Coefficient of variation
Parity 1 (set I)			
Total number of piglets born/litter (TNB)	3-17	9.83	22.6
Number of piglets born alive/litter (NBA)	3-15	8.78	25.0
Litter size on day 21 (N21)	2-15	8.41	26.5
Litter size at weaning (NW)	2-15	8.40	26.7
Age at first farrowing (AFF)	314-484	354.20	7.6
Litter weight on day 21 (W21)	10-81	43.08	28.3
Litter weight at weaning (WW)	15-107.5	56.70	28.8
Survival rate (%) to weaning (SV)	30-100	85.74	16.8
Parity 2-8 (set II)			
Total number of piglets born/litter (TNB)	2-20	10.49	25.2
Number of piglets born alive/litter (NBA)	2-20	9.47	26.1
Litter size on day 21 (N21)	2-20	9.03	27.2
Litter size at weaning (NW)	2-20	8.98	27.2
Farrowing interval (FI) – days	131-322	155.20	11.7
Litter weight on day 21 (W21)	4-99	49.34	28.2
Litter weight at weaning (WW)	12.5-168.5	64.16	28.5
Survival rate (%) to weaning (SV)	18-100	86.17	16.1

To determine the effects included in the animal model preliminary analyses were carried out with the GLM procedure. The year-season effect was found highly significant for all traits except TNB at parities 2-8 and for W21 and WW as well as survival rate at parity 1. The effect of a service sire was not identified significant only for survival rate at parity 1, probably because of a small number of observations. The effect of parity in data set II (parities 2-8) was highly significant for all traits except survival rate. Linear regression on age at first farrowing in data set I was significant for TNB, W21 and WW with coefficients amounting 0.01, 0.05 and 0.06 respectively. The farrowing interval in data set II affected litter weight with the same value of regression coefficient mentioned above and litter size at weaning (0.005).

The variance components and parameters estimates obtained with or without maternal effect are shown in Table 3 for parity 1 (set I) and in Table 4 for parities 2-8 (set II).

Table 3. Estimates of (co)variance components and parameters for examined traits in parity 1 obtained with two models

Trait	σ_e^2	σ_a^2	σ_m^2	σ_{am}	s^2	h_a^2	h_m^2	r_{gam}
Model 1								
TNB	3.82	0.99			0.01	0.20		
NBA	4.12	0.55			0.03	0.11		
N21	4.24	0.56			0.03	0.11		
NW	4.34	0.51			0.03	0.10		
W21	125.10	16.25			0.03	0.11		
WW	223.20	32.12			0.02	0.12		
SV	169.80	34.05			0.02	0.16		
AFF	590.60	67.13			0.00	0.10		
Model 2								
TNB	3.78	1.09	0.15	-0.21	0.01	0.22	0.03	-0.52
NBA	3.99	0.59	0.46	-0.36	0.02	0.12	0.09	-0.68
N21	4.20	0.67	0.20	-0.27	0.03	0.14	0.04	-0.74
NW	4.28	0.60	0.25	-0.27	0.03	0.12	0.05	-0.71
W21	123.60	18.39	9.73	-10.27	0.03	0.13	0.07	-0.77
WW	217.90	34.94	24.79	-22.23	0.02	0.13	0.09	-0.75
SV	170.10	32.04	2.72	-0.99	0.02	0.15	0.01	-0.11
AFF	532.90	20.27	139.90	-34.00	0.00	0.03	0.21	-0.64

σ_e^2 – residual variance, σ_a^2 – direct additive genetic variance, σ_m^2 – maternal additive genetic variance, σ_{am} – direct-maternal genetic covariance, s^2 – proportion of variance induced by sire, h_a^2 – direct heritability, h_m^2 – maternal heritability, r_{gam} – genetic correlation between direct and maternal effects.

Symbols of traits are explained in Table 2.

The inclusion of maternal effect in the analysis for the parity 1 farrowings resulted in reduction of σ_e^2 by about 2% for litter sizes, litter weights and survival rate, and by about 10% for the age at first farrowing. For parities 2-8 fitting the model with maternal effect did not affect the σ_e^2 values significantly.

All estimates of σ_a^2 for litter size and litter weight at parity 1 were generally higher when the maternal additive and the covariance between additive direct and maternal genetic effects were fitted. A drop of approximately 6% of σ_a^2 for survival rate was observed. Direct additive genetic variance for age at first farrowing was three times smaller after including maternal effect in model 2. Differences between estimates obtained with model 1 and model 2 at parities 2-8 were much wider than for parity 1. The size of σ_m^2 component was larger at parity 1 sows than in sows at 2-8 parities. Estimates of σ_{am} were all negative and their absolute values at parity 1 were generally similar to or larger than at parities 2-8.

The estimates of h_a^2 for parity 1 litter sizes and weights were slightly higher than those obtained for parities 2-8. The lower heritabilities observed for 2-8 parity sows can be attributed to the selection applied already to young sows. Wide difference was

Table 4. Estimates of (co)variance components and parameters for examined traits in parity 2-8 obtained with two models

Trait	σ_e^2	σ_a^2	σ_m^2	σ_{am}	s^2	h_a^2	h_m^2	r_{gam}	σ_p^2	p^2
Model 1										
TNB	5.57	0.68			0.00	0.10			0.53	0.08
NBA	5.04	0.44			0.00	0.07			0.49	0.08
N21	4.78	0.43			0.00	0.07			0.71	0.12
NW	4.74	0.52			0.00	0.09			0.61	0.11
W21	147.30	14.30			0.01	0.07			24.70	0.13
WW	257.80	31.38			0.01	0.10			30.48	0.09
SV	167.80	6.23			0.02	0.03			12.79	0.07
FI	255.30	13.11			0.02	0.04			42.30	0.13
Model 2										
TNB	5.57	0.63	0.06	-0.21	0.00	0.09	0.01	-1.08	0.53	0.08
NBA	5.04	0.51	0.06	-0.11	0.00	0.08	0.01	-0.63	0.48	0.08
N21	4.78	0.65	0.14	-0.26	0.00	0.11	0.02	-0.86	0.62	0.10
NW	4.75	0.71	0.11	-0.24	0.00	0.12	0.02	-0.86	0.56	0.09
W21	147.40	20.90	2.90	-6.90	0.01	0.11	0.01	-0.88	22.10	0.12
WW	258.10	42.44	3.69	-10.65	0.01	0.13	0.01	-0.85	26.58	0.08
SV	167.70	7.56	1.72	-2.81	0.02	0.04	0.01	-0.78	12.65	0.07
FI	255.30	13.30	22.70	-14.45	0.02	0.04	0.07	-0.83	34.04	0.11

σ_e^2 – residual variance, σ_a^2 – direct additive genetic variance, σ_m^2 – maternal additive genetic variance, σ_{am} – direct-maternal genetic covariance, s^2 – proportion of variance induced by sire, h_a^2 – direct heritability, h_m^2 – maternal heritability, r_{gam} – genetic correlation between direct and maternal effects, σ_p^2 – sow permanent environmental variance, p^2 – fraction of the sow permanent environmental variance to total variance.

Symbols of traits are explained in Table 2.

found in estimates of direct heritability of survival rate between parity 1 (0.16) and 2-8 parity sows (0.03). Therefore, it can be concluded that selection for piglet survival is particularly effective at parity 1, *i.e.* when correlation between direct and maternal effects is small (-0.11). The estimates of h_a^2 were slightly higher in the presence than in the absence of maternal genetic and covariance between additive direct and maternal genetic effects. A marked decrease of direct heritability coefficient of age at first farrowing was observed after including maternal effect in the model (0.10 vs 0.03).

The heritabilities estimated in the present study are in good agreement with figures reported by Southwood and Kennedy [1990] for Landrace and Yorkshire sows and lower than those given by Tyra and Różycki [2004] for Line 990 pigs, and Jorgensen [1989], Irgang *et al.* [1994], and Torres Filho *et al.* [2005] for other breeds.

Maternal heritabilities reported here for sows at parity 1 are small for litter size, litter weight and survival rate (Tab. 3). The highest h_m^2 estimates were observed for age at first farrowing (0.21), NBA (0.09) and WW (0.09). Estimates of h_m^2 were very

small for sows at 2-8 parity (Tab. 4) and with except for farrowing interval ($h_m^2 = 0.07$) were always smaller than h_a^2 estimates. This is in accordance with Southwood and Kennedy [1990] and Kaufmann *et al.* [2000] who reported maternal heritabilities for litter size and litter weight of around 0.01 and 0.02 respectively. However, it is difficult to discuss differences when standard errors of estimates are not provided.

Correlation coefficients between additive direct and maternal genetic effects were generally high and negative reaching on average -0.66 and -0.84 for litter size and -0.76 and -0.86 for litter weight at parity 1 and parities 2-8, respectively. These coefficients increased between the first and subsequent parities. The present result is in accordance with the opinion of Riska *et al.* [1985], who suggested that there is a higher correlation between direct and maternal effect at later stages of growth. When compared with results of Irgang *et al.* (1994) the present estimates are lower for NBA and N21. The negative correlation between direct and maternal genetic effects for litter size corroborates the results of Southwood and Kennedy [1990] and Kaufmann *et al.* [2000]. The high negative covariance between direct and maternal genetic effects indicates that improvement in one effect will lead to reduction in the other. Sows born or reared in large litters seem to produce smaller litters than those born or reared in small litters.

The likelihood ratio test provided statistical evidence of a lack of maternal effects on litter size, litter weight, survival rate (in all the parities) and on the farrowing interval at parities 2-8. The inclusion of the maternal effect significantly influenced ($P < 0.01$) only the estimate of age at first farrowing at the parity 1 analysis. This result is close to those reported by Torres Filho *et al.* 2004], who concluded that genetic evaluation model including maternal effect was the most adapted for age at first farrowing, whereas inadequate for total number of piglets born, number of piglets born alive and litter weight at birth. On the other hand, Canalcante Neto *et al.* [2006] showed, that it is not necessary to include the maternal genetic effect in the animal model to estimate the first farrowing age.

The proportion of the sow permanent environmental variance to total variation (p^2) was small and close to those obtained for two models (Tab. 4). The proportion was highest for litter size, litter weight on day 21 and for farrowing interval, reaching approximately 12% of total variation for these traits. The influence of the permanent environment associated with the sow on litter size was slightly higher than the value estimated by Kaufmann *et al.* [2000].

The proportion of variation caused by service sire reached only 3% of the total phenotypic variance for litter size and litter weight at parity 1 (Tab. 3) and is in accordance with Buytels and Long [1991] and See *et al.* [1993]. With reported range of 1-3% of phenotypic variance in litter size it seems that the sire's effect is very small. Variances found for service sire in litter size may be attributable to genetic differences in semen quality or to genetic effects that influence fertilization of eggs, embryonic growth as well as foetal development and survival [Hamman *et al.* 2004]. The proportion of variance caused by service sire in litters' size at parities 2-8 (Tab. 4)

was close to zero, while for litter weight reached 2% of total variance.

It can be concluded that direct heritability and the response to selection are overestimated for age at first farrowing when maternal effects are not considered. Likelihood ratio test indicated that maternal genetic effects were significant for age at first farrowing only. However, heritability estimates for litter size and litter weight were higher as a result of including maternal effect into a model, the likelihood ratio test provided statistical evidence of a lack of maternal effects on these traits.

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Wpływ efektów matczynych na szacunki parametrów genetycznych cech reprodukcyjnych świń linii 990

Streszczenie

Oszacowano wpływ efektów matczynych na szacunki parametrów genetycznych następujących cech rozplodowych: wiek pierwszego oproszenia, długość okresu międzymiotu, liczba prosiąt urodzonych w miocie, liczba prosiąt urodzonych żywo w miocie, liczebność miotu w 21 dniu, liczebność miotu w dniu odsadzenia, masa miotu w 21 dniu, masa miotu w dniu odsadzenia i przeżywalność (%) do dnia odsadzenia. Szacunków dokonano dla danych dotyczących miotu 1 i miotów od 2 do 8 (odpowiednio 915 i 2193 obserwacje). Istotność wpływu włączenia do modelu efektów matczynych testowano za pomocą testu stosunku wiarygodności. Model statystyczny zawierał stałe wpływy roku-sezonu oproszenia, kolejnego oproszenia (*parity*), regresji na wiek pierwszego oproszenia i długości okresu międzymiotu, losowego wpływu ojca miotu (*service sire*), genetycznego addytywnego wpływu matki miotu, stałego środowiska matki oraz efektu matki. Genetyczna wariancja dla wieku pierwszego oproszenia okazała się trzykrotnie mniejsza po włączeniu do modelu wpływów matczynych. Genetyczna odziedziczalność addytywna wielkości miotu i masy miotu w oproszeniu 1 była większa niż oszacowana dla miotów 2-8. Szacunki addytywnej odziedziczalności były nieznacznie wyższe po włączeniu do modelu wpływów matczynych. Zaobserwowano znaczny spadek addytywnej odziedziczalności cechy wieku pierwszego oproszenia szacowanej modelem zawierającym wpływy matczyne w stosunku do szacowanej bez uwzględnienia tych wpływów (z 0,1 do 0,03). Najwyższe szacunki odziedziczalności matczynej uzyskano dla wieku pierwszego oproszenia (0,21), liczby prosiąt urodzonych żywo (0,09) i masy miotu przy odsadzeniu (0,09). Udział zmienności stałego środowiska lochy i ojca miotu w całej zmienności fenotypowej był niewielki i w obu modelach podobny. Uzyskano wysokie i ujemne korelacje genetyczne addytywno-matczyne dla wszystkich cech. Genetyczne efekty matczyne okazały się istotne wyłącznie dla wieku pierwszego oproszenia.