

Genetic parameters for litter size and weight at different parities in Iberian pigs

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Abstract

Genetic progress for reproductive performance in pigs is limited by mothering ability. It is a critical aspect for dam lines, in which litter weight at weaning could be included with litter size in the selection goal. Our objective was to investigate in Iberian pigs the genetic basis of the number of alive born piglets (NBA) and the litter weight at 21 days (LW21) over the successive parities (t). Records for NBA were available from 6,775 litters born from 1,893 sows of the *Torbiscal* line, and LW21 records proceeded from 1,431 sows and 2,963 litters without crossfostering. Genetic parameters were estimated using an animal model with repeatability, a multi-trait animal model, and a random regression model. Estimated values of heritabilities for NBA and genetic correlations between parities confirm a partially different genetic control of prolificacy at parity 1 and at later parities. Results for LW21 indicate that this trait may be partially controlled by different genes at the first two parities and at the later ones. Estimated genetic parameters for NBA ($t=1$), NBA ($t\geq 2$), LW21 ($t\leq 2$) and LW21 ($t\geq 3$) were: heritability, $h^2=0.15, 0.12, 0.22$ and 0.15 , respectively, and coefficient of permanent environmental effects, $p^2=0.05, 0.02$ and 0.24 , respectively for the three last traits. The values of genetic correlations ranged from 0.44 to 0.84. A multitrait approach would be useful to estimate accurate genetic parameters, and to improve the low persistency of reproductive performance in the later parities of Iberian sows.

Additional key words: genetic correlation, maternal ability, prolificacy, random regression model.

Resumen

Evaluación genética del tamaño y peso de camada para sucesivos partos en cerdas Ibéricas

La mejora genética de la eficiencia reproductiva en cerdos está limitada por su aptitud maternal. Es éste un aspecto crítico en las líneas maternas, en las que el peso de la camada al destete podría ser incluido junto al tamaño de camada en el objetivo de selección. El objetivo del trabajo fue investigar en cerdos Ibéricos la base genética del número de lechones nacidos vivos (NBA) y el peso de camada a 21 días (LW21) a lo largo de los sucesivos partos (t). Se dispuso de registros de NBA de 6.775 camadas nacidas de 1.893 cerdas, y registros de LW21 procedentes de 1.431 cerdas y 2.963 camadas sin adopciones. Se estimaron parámetros genéticos mediante tres modelos: con repetibilidad, multicarácter y de regresión aleatoria. Los valores de las heredabilidades y las correlaciones genéticas entre NBA en diferentes partos confirman su control genético, parcialmente distinto en el parto primero y posteriores. Los resultados para LW21 indican que este carácter puede estar parcialmente controlado por diferentes genes en los dos primeros partos y en los sucesivos. Los parámetros genéticos estimados para NBA ($t=1$), NBA ($t\geq 2$), LW21 ($t\leq 2$) y LW21 ($t\geq 3$) fueron: heredabilidad, $h^2=0,15, 0,12, 0,22$ y $0,15$, respectivamente, y coeficiente de efectos de ambiente permanente, $p^2=0,05, 0,02$ y $0,24$, respectivamente para los tres últimos caracteres. El rango de las correlaciones genéticas fue de 0,44 a 0,84. Un enfoque genético multicarácter sería útil para estimar parámetros genéticos precisos y mejorar la escasa persistencia del rendimiento reproductivo en los últimos partos.

Palabras clave adicionales: aptitud maternal, correlación genética, modelo de regresión aleatoria, persistencia, prolificidad.

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Introduction¹

Selection for litter size in pig breeding schemes over the last two decades has been successful to obtain moderate genetic changes for prolificacy in dam lines (Petit *et al.*, 1988; Estany and Sorensen, 1995; Noguera *et al.*, 2002). However, the increase of litter size usually tends to decrease the piglets survival, since the maternal ability of sows to rear the extra piglets can be a limitation to the increase of reproductive efficiency (Knol *et al.*, 2002). In this case, selection for prolificacy may not be beneficial unless measures to improve the survival of low-birth-weight piglets are undertaken (Milligan *et al.*, 2002). The selection criteria for dam lines should be modified to include traits related to piglet survival and postnatal growth. A single cumulative measurement such as litter weight at weaning, treated as a trait of the sow, may be the main selection criterion under practical conditions, particularly for lines used in a wide range of management systems.

Repeated records of reproductive performance are available from each sow over different parities, and repeatability animal models (RM) are commonly used for genetic evaluation of litter size or weight (Rodríguez *et al.*, 1994; Roehe, 1999). This model assumes complete genetic correlations between parities and a constant variance along the phenotypic trajectory. But the genetic basis of reproductive performance in sows could change in different parities, and a multivariate animal model (MTM) has been proposed as more adequate to perform these analyses (Roehe and Kennedy, 1995; Noguera *et al.*, 2002). This model considers the successive records as different traits and provides a new insight into their genetic relationship. Furthermore, random regression models (RRM) have become common for the analysis of longitudinal data or repeated records on individuals over time. The main advantages of the RRM approach in comparison to MTM are the possibility to get smoother (co)variance estimates and to predict breeding values at any point along the phenotypic trajectory. In pigs, RRM have been used for analyzing feed intake or growth (Schaeffer, 2004) but, although its application for genetic evaluation of litter size has been suggested, only two papers on this topic has been published (Lukovic *et al.*, 2004; Fernández *et al.*, 2006). Both MTM and RRM allow the study of temporal changes in genetic variability and the selection of individuals to modify the

patterns of response over time. The aim of the present paper was to investigate the genetic basis of prolificacy in Iberian pigs over the successive parities using these three alternative models.

Material and Methods

Data

Litter size (number of born alive piglets, NBA) and litter weight at 21 days (LW21) were recorded on Iberian sows of the *Torbiscal* line at the experimental farm «Dehesón del Encinar» (Oropesa, Toledo). The genetic origin of this line has been previously described (Fernández *et al.*, 2002; Fabuel *et al.*, 2004). Litter size records proceeded from 6,775 litters born from 1,893 sows. The analyzed data file for litter weight included only records from 2,963 litters weaned from 1,431 sows, in which crossfostering of piglets was not performed. Although crossfostering was not systematic, it depended on extreme litter sizes among other diverse factors (useful teats of the sow, pen's availability, etc). There were two farrowing periods per year up to 1973 and since then four annual farrowing periods. Ancient farrowing buildings were substituted since 2000 by a new building with modern facilities. In this new building, piglets were provided *ad libitum* access to creep feed from seven days of age, but in the previous period no creep feed was supplied to the piglets in the first three weeks of age. The complete pedigree file contained 2,922 triads (individual-sire-dam).

Statistical analysis

Three different models were used to analyze these reproductive data. All these models can be written in a general matrix form as $\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{W}\mathbf{p} + \mathbf{e}$, but the following singularities should be remarked for each model:

a) *Repeatability animal model* (RM). In this model, \mathbf{y} represents the vector of observations for NBA or LW21; \mathbf{X} , \mathbf{Z} and \mathbf{W} are known incidence matrices relating fixed effects ($\boldsymbol{\beta}$), and random effects (\mathbf{u} and \mathbf{p}), to \mathbf{y} ; \mathbf{u} and \mathbf{p} are vectors of random additive genetic and permanent environmental effects, respectively; \mathbf{e} the vector

¹ Abbreviations used: LW21 (litter weight at 21 days), MTM, (multivariate animal model), NBA (number of piglets born alive), RM (repeatability animal model), RRM (random regression models), SB (season-building), SD (standard deviation), SE (standard error).

of random residual effects; β the vector of unknown parameters for fixed effects, including parity classes (t) and season-building (SB). Six parity classes were considered corresponding to parity numbers $t = 1$ to 5 and $t \geq 6$. All the analyzed litters were grouped in six classes of the SB effect, according to the combinations of building and season of farrowing. The assumptions for the distribution of the random effects were:

$$\mathbf{u} | \sigma_u^2, \mathbf{A} \sim N(0, \mathbf{A} \sigma_u^2), \mathbf{p} | \sigma_p^2 \sim N(0, \mathbf{I} \sigma_p^2) \\ \text{and } \mathbf{e} | \sigma_e^2 \sim N(0, \mathbf{I} \sigma_e^2)$$

being \mathbf{A} the numerator relationship matrix; \mathbf{I} the identity matrix; and σ_u^2 , σ_p^2 , and σ_e^2 the components for additive genetic, permanent environment and residual variances, respectively.

b) *Multiple trait model (MTM)*: in this approach, litter records at each one of the six parity classes ($t = 1$ to 5 and ≥ 6) were treated as a different trait. The model employed for the last parity class (≥ 6) differs from the other parities due to the inclusion of the permanent environmental effect. So, the multivariate animal model used can be written as:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \\ \cdot \\ \cdot \\ \mathbf{y}_{\geq 6} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} & \cdot & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 & \cdot & \mathbf{0} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \mathbf{0} & \mathbf{0} & \cdot & \mathbf{X}_{\geq 6} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \cdot \\ \cdot \\ \beta_{\geq 6} \end{bmatrix} + \\ + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} & \cdot & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 & \cdot & \mathbf{0} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \mathbf{0} & \mathbf{0} & \cdot & \mathbf{Z}_{\geq 6} \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \cdot \\ \cdot \\ \mathbf{u}_{\geq 6} \end{bmatrix} + \\ + \begin{bmatrix} \mathbf{0} & \mathbf{0} & \cdot & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdot & \mathbf{0} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ \mathbf{0} & \mathbf{0} & \cdot & \mathbf{W}_{\geq 6} \end{bmatrix} \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \cdot \\ \cdot \\ \mathbf{p}_{\geq 6} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \cdot \\ \cdot \\ \mathbf{e}_{\geq 6} \end{bmatrix}$$

where \mathbf{y}_1 to $\mathbf{y}_{\geq 6}$ represent different parities of each sow productivity trait (NBA or LW21). The vectors of fixed effect for the six different traits considered (β_1 to $\beta_{\geq 6}$) include only the SB effect and the vectors \mathbf{u}_1 to $\mathbf{u}_{\geq 6}$ and \mathbf{e}_1 to $\mathbf{e}_{\geq 6}$ are random additive genetics and residual effects for each trait, respectively. The incidence matrices

\mathbf{X}_1 to $\mathbf{X}_{\geq 6}$ and \mathbf{Z}_1 to $\mathbf{Z}_{\geq 6}$ associate elements of β_1 to $\beta_{\geq 6}$ and \mathbf{u}_1 to $\mathbf{u}_{\geq 6}$ with the records in \mathbf{y}_1 to $\mathbf{y}_{\geq 6}$. The vector $\mathbf{p}_{\geq 6}$ is the vector of permanent environmental effects for each sow with records in the last parity class being $\mathbf{W}_{\geq 6}$ the known incidence matrix relating the elements of this vector with the records in $\mathbf{y}_{\geq 6}$. The expectation of \mathbf{y}_i ($i = 1$ to 5 and ≥ 6) is $\mathbf{X}_i \beta_i$, and the variance-covariance structure of random effects of the multivariate animal model is as follows:

$$\mathbf{V} \begin{bmatrix} \mathbf{u}_1 \\ \cdot \\ \mathbf{u}_{\geq 6} \\ \mathbf{p}_{\geq 6} \\ \mathbf{e}_1 \\ \cdot \\ \mathbf{e}_{\geq 6} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \sigma_{u_1}^2 & \cdot & \mathbf{A} \sigma_{u_{1 \geq 6}}^2 & 0 & 0 & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \mathbf{A} \sigma_{u_{\geq 6 1}}^2 & \cdot & \mathbf{A} \sigma_{u_{\geq 6}}^2 & 0 & 0 & \cdot & 0 \\ 0 & \cdot & 0 & \mathbf{I} \sigma_{p_{\geq 6}}^2 & 0 & \cdot & 0 \\ 0 & \cdot & 0 & 0 & \mathbf{I} \sigma_{e_1}^2 & \cdot & \mathbf{I} \sigma_{e_{1 \geq 6}}^2 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & 0 & 0 & \mathbf{I} \sigma_{e_{\geq 6 1}}^2 & \cdot & \mathbf{I} \sigma_{e_{\geq 6}}^2 \end{bmatrix}$$

where $\sigma_{u_i}^2$ and $\sigma_{e_i}^2$ are direct additive genetic and residual variances for trait i , respectively; $\sigma_{u_{ij}}^2$ is the direct genetic covariance between trait i and j ($j = 1$ to 5 and ≥ 6), and their residual covariance.

c) *Random regression model (RRM)*: this model assumes the litter records as a longitudinal trait and the parity number (t) as the unit of time being observed. Legendre polynomial functions (Kirpatrick *et al.*, 1990) of increasing order (LG1 to LG3) were fitted to the average trajectory, additive genetic and permanent environmental effects (Schaeffer, 2004). Now, β is a vector of unknown parameters for fixed effects including season-building (SB), as an effect independent of the time scale for the observations, and a regression that accounts for the average trajectory over ten parity classes ($t = 1$ to 9 and ≥ 10); \mathbf{u} and \mathbf{p} are vectors comprising random regression coefficients for additive genetic effects for each animal and permanent environmental effects for each sow with records, respectively; and vector \mathbf{e} presents the random residual effects; \mathbf{X} , \mathbf{Z} and \mathbf{W} are incidences matrices relating \mathbf{y} with the new parameters in β , \mathbf{u} and \mathbf{p} , respectively, so including as covariates the corresponding terms of Legendre polynomials. Assumptions applied in the RRM analysis were:

$$\mathbf{u} | \mathbf{K}_{0u}, \mathbf{A} \sim N(0, \mathbf{A} \otimes \mathbf{K}_{0u}), \mathbf{p} | \mathbf{K}_{0p} \sim N(0, \mathbf{I} \otimes \mathbf{K}_{0p}) \\ \text{and } \mathbf{e} | \sigma_e^2 \sim N(0, \mathbf{I} \sigma_e^2)$$

where \mathbf{K}_{0u} and \mathbf{K}_{0p} are the covariance matrix for additive genetic and permanent environmental random regression coefficients, respectively.

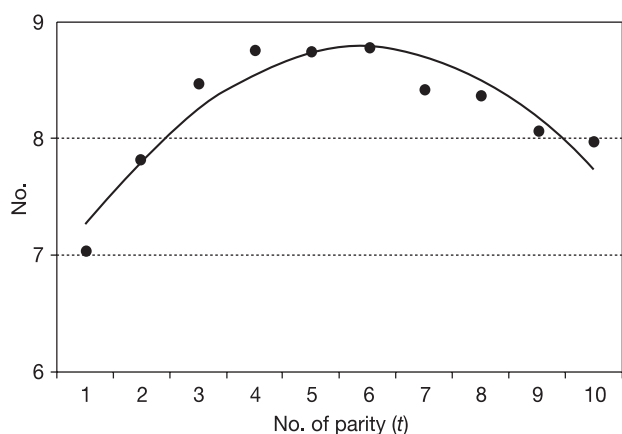


Figure 1. Phenotypic mean by parity for number of piglets born alive (NBA). Legendre polynomial LG(2) accounts for the phenotypic trajectory of averaged NBA over parities.

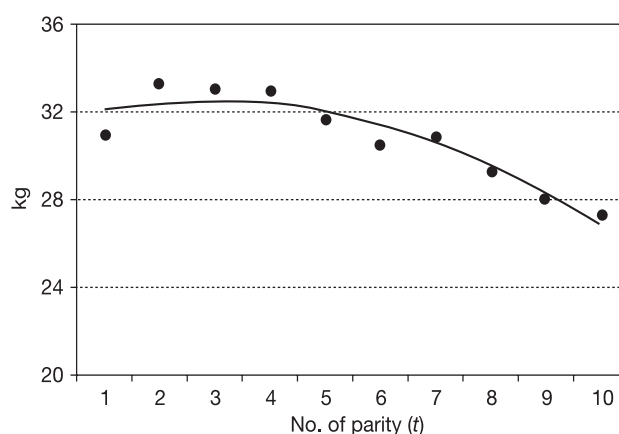


Figure 2. Phenotypic mean by parity for litter weight at 21 days (LW21). Legendre polynomial LG(2) accounts for the phenotypic trajectory of averaged LW21 over parities.

Complementary analyses were performed using repeatability and multitrait models including jointly NBA and LW21 records. Computations for all the described analyses were performed using the VCE-5 software (Kovac and Groeneveld, 2003).

Results and Discussion

Means and standard deviations of the analyzed litters for NBA and LW21 were 8.00 (SD = 2.26) piglets and 31.44 (SD = 9.20) kg, respectively. The mean values for these traits over the first ten parities are summarized in Figures 1 and 2. The increase of NBA and LW21 up to the fourth parity is evident but both traits decline later. The phenotypic trajectories of both traits describe

the low reproductive performance of Iberian sows and their low persistence.

Analysis with repeatability animal model (RM)

Estimates of parity effects on NBA and LW21 expressed as deviations from the first parity are presented in Table 1. An increase of litter size at birth up to fifth parity has been previously reported in *Torbiscal* and other Iberian pig strains by Pérez-Enciso and Gianola (1992) and Rodríguez *et al.* (1994). Mothering ability measured by LW21 may be considered as a composite trait, combining litter size and average piglet weight at 21 days, which depend on the number of piglets born and the piglets preweaning survival and growth. Milk

Table 1. Analysis of number of born alive piglets (NBA) and litter weight at 21d (LW21) under the repeatability animal model (RM): estimated parity effects, heritability (h^2) and coefficient of permanent environmental effects (p^2)

	NBA		LW21 (kg)	
	Mean	SE	Mean	SE
<i>Parity effect</i>				
2-1	0.77	0.07	2.78	0.36
3-1	1.40	0.08	1.91	0.40
4-1	1.66	0.09	1.90	0.46
5-1	1.67	0.10	0.00	0.52
≥ 6-1	1.36	0.08	-2.02	0.04
<i>Variance ratios</i>				
$h^2 = \sigma_u^2 / (\sigma_u^2 + \sigma_p^2 + \sigma_e^2)$	0.07	0.01	0.16	0.02
$p^2 = \sigma_p^2 / (\sigma_u^2 + \sigma_p^2 + \sigma_e^2)$	0.07	0.01	0.10	0.02

production in gilts may be 20% lower than in multiparous sows, as a consequence of lower feed intake and additional requirements of energy for tissue growth (Walker and Young, 1993). According to the estimated parity effects on LW21, the best mothering ability of *Torbiscal* sows is achieved at parity 2 and it slightly decreases in the later parities, being similar the maternal aptitude of sows at the parities 1 and 5. Moreover, in this Iberian line the parity effect on individual piglet weight at 21 days is also maximum at parity 2 and decreases monotonically even after the parity 6 (Rodríguez *et al.*, 1994).

The estimated values of heritability [$h^2 = \sigma_u^2 / (\sigma_u^2 + \sigma_p^2 + \sigma_e^2)$] and permanent environmental coefficient [$p^2 = \sigma_p^2 / (\sigma_u^2 + \sigma_p^2 + \sigma_e^2)$] for NBA and LW21 correspond to respective values of repeatability $r^2 = 0.14$ and 0.26 . The results of the joint analysis of all these records confirm for both traits the same values of the heritability and the coefficient of permanent environmental effects obtained in the univariate analyses. The estimated value of the genetic correlation is 0.57 ± 0.08 , and 0.26 ± 0.12 the estimated correlation between permanent environmental effects.

The estimated h^2 and p^2 values for LW21 are twice the values for NBA. With similar coefficients of variation and available information for both traits, selection for mothering ability in Iberian pigs may achieve rates of genetic change greater than those expected for litter size.

Analysis with multivariate model (MTM)

The estimated values of h^2 for NBA at each one of the six parity classes and the estimated genetic correlations between them are shown in Table 2. Homogeneous heritabilities for all parities and high values of genetic correlation would be expected if most of the genes

affecting NBA at different parities were the same. Nevertheless, some differences among heritabilities across parities are observed, with extreme values at the first and fourth parities: $h^2 = 0.13$ and 0.06 , respectively. However, only the genetic correlations between the first and the rest of the parities are lower than 0.80 , a value considered as rule of thumb to differentiate two traits as genetically different. The genetic singularity of the litter size of primiparous sows has been evidenced in other pig breeds (Hansen *et al.*, 2001; Serenius *et al.*, 2003). Moreover, Fernández *et al.* (2007) estimated significant heterosis for NBA between different strains of Iberian pigs at the second and later parities (0.65 ± 0.10 piglets per litter), but not at the first parity (0.10 ± 0.15).

The equivalent results for LW21 present some dissimilarity, being more complex the structure of the genetic parameters (Table 3). The h^2 values for this trait show a larger range of variation than those estimated for NBA. Nine out of the 15 values of genetic correlation were lower than 0.80 , and all these values correspond to genetic correlations between the first two parities and the subsequent parities. These results suggest that, in Iberian pigs, there are genetic differences for LW21 between the parities 1 and 2 and the later ones.

Permanent environmental effects may cause similitude of reproductive records in different parities of the same sow (Lukovic *et al.*, 2004). These effects are only included in the MTM model for parity numbers $t \geq 6$, and the application of a RRM model would be advisable to take into account this source of variation (Schaeffer, 2004).

Analysis with random regression model (RRM)

RRM models allow studying changes in genetic variability with time, and the time variable (t) in this

Table 2. Heritabilities over parities (diagonal), genetic correlations (above diagonal) and permanent environmental effect (p^2) for NBA estimated using a multi-trait model (MTM). Number of litters (n) and values of standard errors are presented between brackets

Parity classes	1 ($n = 1,831$)	2 ($n = 1,436$)	3 ($n = 1,029$)	4 ($n = 774$)	5 ($n = 564$)	≥ 6 ($n = 1,141$)
1	0.13 (0.02)	0.72 (0.08)	0.80 (0.08)	0.72 (0.11)	0.28 (0.12)	0.41 (0.11)
2		0.09 (0.02)	0.99 (0.01)	0.99 (0.01)	0.87 (0.05)	0.93 (0.04)
3			0.10 (0.02)	0.99 (0.01)	0.80 (0.06)	0.87 (0.05)
4				0.06 (0.02)	0.87 (0.05)	0.93 (0.05)
5					0.11 (0.03)	0.99 (0.02)
≥ 6						0.11 (0.02)
p^2						0.09 (0.01)

Table 3. Heritabilities over parities (diagonal), genetic correlations (above diagonal) and permanent environmental effect (p^2) for LW21 estimated using a multi-trait model (MTM). Number of litters (n) and values of standard errors are presented between brackets

Parity classes	1 ($n = 872$)	2 ($n = 622$)	3 ($n = 456$)	4 ($n = 319$)	5 ($n = 239$)	≥ 6 ($n = 455$)
1	0.36 (0.04)	0.80 (0.07)	0.29 (0.08)	0.33 (0.09)	0.30 (0.10)	0.64 (0.06)
2		0.18 (0.03)	0.28 (0.14)	0.20 (0.15)	0.04 (0.18)	0.58 (0.14)
3			0.29 (0.03)	0.92 (0.08)	0.84 (0.13)	0.87 (0.07)
4				0.37 (0.05)	0.97 (0.04)	0.91 (0.05)
5					0.12 (0.03)	0.83 (0.09)
≥ 6						0.25 (0.03)
p^2						0.23 (0.03)

analysis was the parity number. Orthogonal Legendre polynomials from linear (LG1) to cubic power (LG3) were fitted as covariables of random regressions to model the average phenotypic trajectory, and the genetic and permanent environmental deviations around this trajectory (Schaeffer, 2004). The quadratic Legendre polynomials (LG2), accounting for the phenotypic relationships between traits (NBA and LW21) and parities, are presented in Figures 1 and 2. The eigenvalues of the diverse genetic and environmental covariance matrices of random regression coefficients are presented in Table 4. These values show that the constant (zero) term accounts between 85 and 92% of the additive genetic variability of NBA, and between 70 and 90% of LW21. This means that approximately 8 to 15% of

the genetic variability for NBA could be explained by the individual genetic curves of the sows. For LW21, the proportion of genetic variability explained by the individual genetic curves could ascend from 10 to 30%. It must be outlined that LG2 polynomials, with three regression coefficients, are enough to model the variation for all random effects in the model.

Estimated h^2 and p^2 values for NBA were calculated at the six first parities (Table 5). Heritability increases slightly with parity number, and the coefficient of permanent environmental effects follows the same pattern, with similar values of both variance ratios. The genetic correlations are high between successive parities and decrease as the interval between parities increases, being close to unity for parities higher than 2. This

Table 4. Eigenvalues with proportion (in brackets) of estimated covariance matrices of random regression coefficients with different Legendre polynomials (LG1-LG3)

Trait		Eigenvalues			
		0 th	1 st	2 nd	e rd
<i>NBA</i>					
Additive genetic	LG1	0.84 (92.16)	0.07 (7.84)		
	LG2	0.77 (89.52)	0.09 (10.48)	0.00 (0.00)	
	LG3	0.76 (89.99)	0.10 (10.01)	0.00 (0.00)	0.00 (0.00)
Permanent environment	LG1	0.63 (99.99)	0.00 (0.00)		
	LG2	0.87 (89.34)	0.10 (10.66)	0.00 (0.00)	
	LG3	0.85 (77.84)	0.20 (18.41)	0.04 (3.74)	0.00 (0.00)
<i>LW21</i>					
Additive genetic	LG1	1,270.70 (89.99)	141.39 (10.01)		
	LG2	1,905.10 (84.77)	342.27 (15.23)	0.00 (0.00)	
	LG3	1,766.70 (78.06)	331.04 (14.63)	165.66 (7.32)	0.00 (0.00)
Permanent environment	LG1	1,764.50 (99.99)	0.01 (0.00)		
	LG2	2,132.30 (99.99)	0.18 (0.01)	0.00 (0.00)	
	LG3	2,202.40 (92.91)	168.02 (7.09)	0.01 (0.00)	0.00 (0.00)

Table 5. Heritabilities (diagonal), genetic correlations (above diagonal) and permanent environmental effect (p^2) for NBA over parities estimated using a RRM (LG2)

Parity	1	2	3	4	5	6
1	0.07	0.95	0.85	0.74	0.65	0.58
2		0.07	0.97	0.92	0.86	0.81
3			0.08	0.99	0.96	0.92
4				0.09	0.99	0.98
5					0.11	0.99
6						0.11
p^2	0.04	0.06	0.09	0.10	0.10	0.11

correlation pattern confirms that some genes controlling the prolificacy at the first parity would be different to those responsible of litter size at later parities. All the estimated values of permanent environmental correlations are close to unity (not shown results).

Estimated h^2 and p^2 values for LW21 were also calculated at the six first parities (Table 6). Heritability is remarkably higher at the parity 1 (0.28), and after then fluctuates around a value of 0.15. The estimated coefficients of permanent environmental effects follow a different pattern, with the lowest value at the parity 1 (0.05) and increasing values with the parity number with the highest value at parity 6 (0.23). Seven out of the eight genetic correlations between the first two parities and the later ones were lower than 0.75, and the genetic correlations between parities higher than 2 were greater than 0.90 (Table 6). This correlation pattern newly indicates that LW21 may be partially controlled by different genes at the first two parities and at the later parities.

Two main differences may be appreciated in the comparison between the genetic parameters estimated with both multiple-trait approaches. Using MTM, most of the h^2 estimates are greater than the correspondent values provided by the RRM, which accounts for permanent environmental effects. Moreover, the heritabilities

and genetic correlations estimated by MTM present a larger range of variation than those estimated using the RRM. Note that smoother (co)variance estimates are provided using the last method (Lukovic *et al.*, 2004).

Implications on Iberian pig breeding

In pig breeding programs, most of the genetic changes achieved for litter size have been based on the use of repeatability animal models to predict the breeding values of candidates to selection (Estany and Sorensen, 1995; Noguera *et al.*, 2002). It is necessary to improve the reproductive performance of Iberian sows in order to create an Iberian dam line to produce commercial Iberian crossbred pigs. However, this methodology has not been applied in this breed, since its traditional extensive production system makes it difficult to control the pedigree with precision and to register reproductive data. Fortunately, important modifications have been achieved in the production system of Iberian pigs that allows to overcome the old impediments. Thus, breeding nucleus of purebred Iberian sows have increased in size, and modern facilities for reproduction are used in commercial farms. Selection for litter size based on the use of the RM in breeding nucleus of 400 Iberian sows could provide annual rates of genetic progress of

Table 6. Heritabilities (diagonal), genetic correlations (above diagonal) and permanent environmental effect (p^2) for LW21 over parities estimated using a RRM (LG2)

Parity	1	2	3	4	5	6
1	0.28	0.90	0.62	0.37	0.28	0.32
2		0.16	0.90	0.73	0.66	0.70
3			0.13	0.96	0.93	0.94
4				0.14	0.99	1.0
5					0.14	1.0
6						0.13
p^2	0.05	0.11	0.17	0.21	0.22	0.23

Table 7. Heritabilities (diagonal), genetic correlations (above diagonal) and permanent environmental effect (p^2) estimated under the simplified MTM for four traits: NBA ($t=1$), NBA ($t\geq 2$), LW21 ($t\leq 2$) and LW21 ($t\geq 3$). Number of litters (n) and values of standard errors presented between brackets

Parity classes		NBA		LW21	
		$t=1$ ($n=1,831$)	$t\geq 2$ ($n=4,944$)	$t\leq 2$ ($n=1,494$)	$t\geq 3$ ($n=1,469$)
NBA	$t=1$	0.15 (0.02)	0.84 (0.05)	0.48 (0.07)	0.44 (0.08)
	$t\geq 2$		0.12 (0.01)	0.52 (0.08)	0.61 (0.09)
LW21	$t\leq 2$			0.22 (0.02)	0.73 (0.09)
	$t\geq 3$				0.15 (0.03)
p^2			0.05 (0.01)	0.02 (0.01)	0.24 (0.03)

0.15 piglets per litter (Silió *et al.*, 2001). A number of boars (35-40) higher than usual would be required to avoid an inconvenient increase of the average kinship of the breeding animals, with risks of inbreeding depression and dispersion of the expected genetic response.

Once the selection programme is started, multiple-trait genetic evaluation of animals for reproductive traits should be preferred to estimate breeding values when first and later parity records are involved. A model for litter size treating NBA records at the first parity as one trait and records at the later parities ($t\geq 2$) as one second trait could be more advisable than the repeatability model. Given the interest to include mothering ability into the selection goal, a multi-trait model for reproductive performance should incorporate traits such as litter weight at weaning or other maternal traits, taking into account their genetic basis. As a possible approach, based on the results of previous analyses, a complementary analysis of the ensemble of data was performed using a model for four traits (NBA at $t=1$ and $t\geq 2$; LW21 at $t\leq 2$ and $t\geq 3$), and its results are presented in Table 7. The breeding values for these traits could be weighted by different economic or empirical weights according the relative importance of traits and their time of expression during the sow's reproductive life (Fernández *et al.*, 2006).

Besides, a system of genetic evaluation based on MTM or RRM allow select individuals to alter the general pattern of response over time (Schaeffer, 2004). The application of these models would be useful to improve the low persistency of litter size or weight at weaning in the later parities of Iberian sows. Selection

on the shape of the production curves for these traits is possible according to the quoted remarkable proportion of genetic variability of NBA and LW21 explained by the individual genetic curves of sows. However, a multiple-trait model has a greater risk of giving wrong estimates for analyzing litter size records than a repeatability model due to the difficulty to estimate genetic correlations (Piles *et al.*, 2006). The accurate implementation of these models in breeding schemes (particularly of the RRM model) requires the availability of a large set of reproductive records over a wide range of parities for adequate fitting of the phenotypic trajectory, additive genetic and permanent environmental effects.

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