Abstract

The usefulness of genetic progress for litter size in pig breeding is limited by mothering ability and piglets survival. It is a critical aspect for breeds used as dam lines, in which litter weight (LW) at weaning could be an alternative selection goal. Our objective was to investigate the genetic basis of LW at 21 days for the six first parities in 1,449 Iberian sows with available records from 2,709 litters without crossfostering. REML genetic parameters were estimated using an animal model with repeatability (RM), a multitrait animal model (MTM), and a random regression model (RRM). Estimated parameters for LW21d using the RM model were: heritability, $h^2 = 0.13$ (SE = 0.02) and ratio of permanent environmental variance to total variance, $p^2 = 0.12$ (SE = 0.02). Heterogeneity of $h^2$ estimates across parities was observed using the MTM model, being the $h^2$ values for the first six parities 0.31, 0.08, 0.16, 0.13, 0.01 and 0.31 (SE from 0.01 to 0.04). The genetic correlations between parities ranged from 0.58 to 0.99, but most of them were above 0.80. The variance ratios estimated using a RRM model were $h^2 = 0.26$, 0.21, 0.19, 0.13, 0.09 and 0.19, and $p^2 = 0.08$, 0.18, 0.20, 0.20, 0.17 and 0.09. The genetic correlations between the first parity and the later ones were lower than 0.70, and the genetic correlations between parities higher than 2 were greater than 0.90. A system of genetic evaluation of LW21d based on RRM models would be useful to improve the persistency of mothering ability in the later parities.

Introduction

Selection for sow productivity in pig breeding schemes has been successful along the last two decades to obtain genetic changes for prolificacy in dam lines (Petit et al., 1988; Estany and Sorensen, 1995; Noguera et al., 2002). The introgression of genes from the hyperprolific Chinese Taihu breeds has also reinforced this genetic progress for litter size in some synthetic pig lines (Haley and Lee, 1993). However, the maternal ability of sows to rear the extra piglets could be a limitation to the increase of reproductive efficiency. Selection for increased litter size results in more live-weight-piglets per litter (Kerr and Cameron, 1995), and tends to decrease piglet survivability (Knol et al., 2002). This selection may not be beneficial unless measures are undertaken to improve the survival of low-birth-weight piglets (Milligan et al., 2002). In this sense, the selection criteria for dam lines should be modified to include traits related to piglets survival and postnatal growth, particularly for lines used in a wide range of management systems.

Combined selection for litter size and individual birth weight has been recommended as a tool to improve mothering ability or, in other words, to achieve a higher number of viable piglets with high potential for growth (Roehe, 1999). Damgaard et al. (2003)
suggested that selection for sows’ capacity to give birth to homogeneous litters, measured by within-litter variation in birth weight, may be advantageous for piglet survival, piglet growth and litter homogeneity at weaning. Moreover, maternal additive genetic effects have been reported as the main component of the variation of piglet weight at weaning, and selection for this goal may be also advisable for improving mothering ability (Rodriguez et al., 1994). But these and other approaches require a huge additional labor to collect individual piglet weights. A more single cumulative measurement such as litter weight at weaning, treated as a trait of the sow, may be the trait of interest under more practical conditions.

Repeated records of reproductive performance (litter size or litter weight) are available from each sow over different parities, and repeatability animal models (RM) are commonly used for genetic evaluation of these traits (Rodriguez et al., 1994; Roehe, 1999). But the genetic basis of sows’ reproductive performance could change in different parities, and a multivariate animal model (MTM) has been proposed as more adequate to perform these analyses (Noguera et al., 2002). Finally, the performance in previous parities could influence the reproductive performance in the current parity and a random regression model (RRM) was also applied to study these traits (Schaeffer, 2004; Lukovic et al., 2004). The aim of the present paper was to investigate the genetic basis of mothering ability in Iberian pigs over the six first parities using three alternative models (RM, MTM and RRM) for genetic evaluation.

Material and Methods

Data

Measurements of litter weight at 21 days were recorded on sows of the Torbiscal strain at the experimental farm of Iberian pigs ‘Dehesón del Encinar’ (Oropesa, Toledo). The genetic origin of this strain has been previously described (Fernández et al., 2002; Fabuel et al., 2004). Crossfostering is a common practice in the farm, large litters being reduced by transferring piglets to sows with smaller litters. Data analysed in this study correspond to 2,709 litters born from 1963 to 2004, in which crossfostering of piglets was not performed, and the parity number \((t)\) was limited to a maximum of six. The number of litters by the six parity classes was 898, 636, 468, 323, 240 and 144, respectively. There were two farrowing periods per year up to 1973 and since then four annual farrowing periods. Ancient farrowing buildings were substituted at 2000 by a new building with modern facilities. In this new building, piglets were provided ad libitum access to creep feed from 7 days of age, but in the previous period no creep feed was supplied to the piglets in the first 3 weeks of age. According to the combination of building and season of farrowing, all the analyzed litters were grouped in six classes of the effect season-building \((SB)\). The pedigree file contained 2,827 individuals, from which 390 were sires and 923 dams of 1,449 sows with analyzed litter records.

Models

The following repeatability animal model (RM) was assumed for the first analysis of litter weight at 21 days (LW21d):

\[
y_{ijk} = SB_j + t_j + u_k + pe_k + e_{ijk}
\]

where

\(y_{ijk} = \text{observation } ijk \text{ for LW21d},\)
\[ SB_i = \text{fixed effect of season-building } i \ (i = 1 \text{ to } 6), \]
\[ t_j = \text{fixed effect of } j^{\text{th}} \text{ parity number } (j = 1 \text{ to } 6), \]
\[ u_k = \text{breeding value of } k^{\text{th}} \text{ animal } (k = 1 \text{ to } 1,449), \]
\[ pe_k = \text{random permanent environmental effects common to litters farrowed by } k^{\text{th}} \text{ sow}, \]
\[ e_{ijk} = \text{random residual term.} \]

In the second analysis, LW21 recorded in each parity was considered as a different trait, and the used multivariate animal model (MTM) was as follows:
\[ y_{ik} = SB_i + u_k + e_{ik} \]

where
\[ y_{ik} = \text{observation } ik \text{ for LW21d from each one of first six parities}, \]
\[ SB_i = \text{fixed effect of season-building } i \ (i = 1 \text{ to } 6), \]
\[ u_k = \text{breeding value of } k^{\text{th}} \text{ animal } (k = 1 \text{ to } 1,449), \]
\[ e_{ik} = \text{random residual term.} \]

The random regression model (RRM) for LW21d assumes the parity number \((t)\) as the unit of time being observed, and can be written as:
\[ y_{ikj,t} = g(t_j) + r(u,t,3)_k + r( pe,t,3)_k + e_{ijk,t} \]

where
\[ y_{ikj,t} = \text{the observation for LW21d on the } k^{\text{th}} \text{ animal at } j^{\text{th}} \text{ parity number } (t) \text{ belonging to the } i^{\text{th}} \text{ building-season group} \]
\[ g(t_j) = \text{quadratic regression that account for the phenotypic trajectory of the average observations for LW21d across all animals belonging to the the } i^{\text{th}} \text{ SB group}, \]
\[ r(u,t,3)_k = \text{random regression function (Legendre polynomial of order 3) for the breeding values } (u) \text{ of the } k^{\text{th}} \text{ animal}, \]
\[ r( pe,t,3)_k = \text{random regression function (Legendre polynomial of order 3) for the permanent environmental } (pe) \text{ effects of the } k^{\text{th}} \text{ animal}, \]
\[ e_{ijk,t} = \text{random residual term.} \]

Computations for all the described analyses were performed using the VCE-5 software (Kovac and Groneveld, 2003).

**Results and Discussion**

The means and standard deviations of the analyzed litters for the number of pigs born, number of piglets alive at 21 days and litter weight at 21 days were 8.39 (SD= 1.77) and 6.65 (SD= 1.84) piglets, and 31.44 (SD= 9.20) kg, respectively. The mean values for these traits over the first six parities are summarized in Figure 1. All these values describe the low reproductive performance of Iberian pigs and outline the interest of the genetic improvement of reproductive traits in this breed.

**Analysis with repeatability model (RM)**

Estimates of mean differences between parities for LW21d are presented in Table 1. Litter weight increased up to fourth parity and then declined. LW21d may be considered as a composite trait, combining litter size and average piglet weight at 21 days, that depends on the number of piglets born and the piglets preweaning survival and growth. An increase of litter size at birth up to fifth parity has been reported in *Torbiscal* and
other strains of Iberian pigs (Pérez-Enciso and Gianola, 1992; Rodríguez et al., 1994), but large litters of later parities were associated to a lower piglet survival (Figure 1). Moreover, the parity effect on individual piglet weight at 21 days was maximum for second parity and decreased monotonically even after sixth parity (Rodríguez et al., 1994). According to Walker and Young (1993), milk production in gilts may be a 20% lower than in multiparous sows, as a consequence of lower feed intake and aditional requirements of energy for tissue growth. Our results indicate that the best mothering ability of Iberian sows is achieved between the second and fourth parities, and decreases in later parities.

The estimated values of heritability \( h^2 \) and permanent environmental coefficient \( p^2 \) for LW21d correspond to a value of repeatability \( r^2 = 0.25 \). These variance ratios double the values of the equivalent parameters for litter size at birth \( (h^2 = 0.06, p^2 = 0.06 \) and \( r^2 = 0.12 \) ) estimated in this strain of Iberian pigs (Pérez-Enciso and Gianola, 1992). With similar coefficients of variation and available information for both traits, selection for LW21d, based on schemes comparable to those used for prolificacy in European breeds, may achieve rates of genetic change greater than those expected for litter size in Iberian pigs.

**Analysis with multivariate model (MTM)**

The RM model assumes that repeated measures of the analyzed trait have a common genetic basis, while the MTM model considers these records as different traits and provides a new insight into their genetic relationship. After correction of fixed effects, total variance of LW21d in different parities ranged from 58.1 kg\(^2\) in the fifth parity to 81.3 kg\(^2\) in the second parity. The estimated values of \( h^2 \) for the six parities, and of the 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 LW21d at different parities were the same. Heterogeneity of heritabilities across parities was observed in the present analysis. However, only four out of the 15 values of genetic correlation were lower than 0.80, value assumed as rule of thumb to differentiate two traits as genetically different. The examination of the genetic correlations between adjacent parities and between non-adjacent parities did not provide a clear pattern of the correlation structure.

Permanent environmental effects may cause similitudes of reproductive records in different parities of the same sow (Lukovic et al., 2004). These effects are not included in the MTM model, and the application of a RRM model would be advisable to take account of this source of variation (Schaeffer, 2004).

**Analysis with random regression model (RRM)**

RRM models allow to study changes in genetic variability with time, and the time variable in this analysis was the parity number \( t \). The quadratic regression \( g(t) = -0.42t^2 + 2.82t + 27.9 \) fitted the data well \( (R^2 = 0.90) \), accounting for the phenotypic relationship between LW21d and parities across all the analyzed animals (Figure 1). In the performed RRM analysis, the set of quadratic regressions \( g(t) \), depicts the phenotypic trajectories of sows farrowing litters in each one of the building-season groups. Orthogonal Legendre polynomials of order 3 were fitted as covariables of random regressions to model the genetic and permanent environmental deviations around the phenotypic trajectories (Schaeffer, 2004).
Estimated heritabilities of LW21d were calculated for the six parities (Table 3). Heritability is highest at the first parity, and after that fluctuates around a value of 0.15. The estimated coefficients of permanent environmental effects also fluctuate around a value 0.15, but follow a different pattern, with the highest value at the parities third and fourth and the lowest one at the first and sixth. The genetic correlations between the first parity and the later ones were lower than 0.70, and the genetic correlations between parities higher than second were greater than 0.90 (Table 3). This correlation pattern may indicate that the genes controlling the LW21d record at the first parity would be different to those responsible of the later measures of this trait. A system of genetic evaluation based on RRM models allow selection of individuals to alter the general pattern of response over time. The application of RRM models would be useful to improve the low persistency of mothering ability in the later parities of Iberian sows.

Acknowledgements

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References


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**Figure 1.** Phenotypic means by parity for total number of piglets born (NOBT), number of live piglets at 21 days (NO21d) and litter weight at 21 days (LW21d). The quadratic regression \( g(t) \) account for the phenotypic trajectory of averaged LW21d over parities.
**Table 1.** Mean differences between parities, heritability ($h^2$), and ratio of permanent environmental effects on total variance ($p^2$) for litter weight at 21 days (LW21d) estimated using an animal model with repeatability (RM model)

<table>
<thead>
<tr>
<th>Parity effect</th>
<th>Estimate</th>
<th>Standard error</th>
<th>Variance ratio Estimate</th>
<th>Standard error</th>
</tr>
</thead>
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<tr>
<td>2-1</td>
<td>2.99</td>
<td>0.43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>2.00</td>
<td>0.47</td>
<td>$h^2$ 0.13</td>
<td>0.02</td>
</tr>
<tr>
<td>4-1</td>
<td>2.41</td>
<td>0.54</td>
<td>$p^2$ 0.12</td>
<td>0.02</td>
</tr>
<tr>
<td>5-1</td>
<td>0.64</td>
<td>0.61</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6-1</td>
<td>-0.87</td>
<td>0.76</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 2.** Heritabilities (diagonal) and genetic correlations (above diagonal) for LW21d in different parities estimated using a multivariate animal model (MTM model). Values between brackets are the corresponding standard errors

<table>
<thead>
<tr>
<th>Parity</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><strong>0.31 (0.03)</strong></td>
<td>0.72 (0.04)</td>
<td>0.75 (0.04)</td>
<td>0.90 (0.04)</td>
<td>0.96 (0.04)</td>
<td>0.90 (0.10)</td>
</tr>
<tr>
<td>2</td>
<td><strong>0.08 (0.03)</strong></td>
<td>0.85 (0.05)</td>
<td>0.94 (0.05)</td>
<td>0.58 (0.05)</td>
<td>0.94 (0.06)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td><strong>0.16 (0.04)</strong></td>
<td>0.92 (0.04)</td>
<td>0.75 (0.04)</td>
<td>0.92 (0.07)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td><strong>0.13 (0.03)</strong></td>
<td>0.82 (0.04)</td>
<td>0.99 (0.06)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td><strong>0.01 (0.01)</strong></td>
<td>0.82 (0.07)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td></td>
<td><strong>0.31 (0.05)</strong></td>
<td></td>
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</tr>
</tbody>
</table>

**Table 3.** Heritabilities ($h^2$), ratios of permanent environmental effects on total variance ($p^2$), genetic correlations (above diagonal), and correlations between permanent environmental effects (under diagonal) for LW21d in different parities estimated using a random regression model (RRM model)

<table>
<thead>
<tr>
<th>Parity</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.69</td>
<td>0.43</td>
<td>0.36</td>
<td>0.53</td>
<td>0.72</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.92</td>
<td>0.95</td>
<td>0.93</td>
<td>0.98</td>
<td>0.99</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.73</td>
<td>0.94</td>
<td>0.99</td>
<td>0.99</td>
<td>0.94</td>
<td></td>
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<tr>
<td>4</td>
<td>0.47</td>
<td>0.78</td>
<td>0.94</td>
<td>0.98</td>
<td>0.91</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.35</td>
<td>0.69</td>
<td>0.89</td>
<td>0.99</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>0.82</td>
<td>0.98</td>
<td>0.99</td>
<td>0.89</td>
<td>0.82</td>
<td></td>
</tr>
<tr>
<td>$h^2$</td>
<td><strong>0.26</strong></td>
<td><strong>0.21</strong></td>
<td><strong>0.19</strong></td>
<td><strong>0.13</strong></td>
<td><strong>0.09</strong></td>
<td><strong>0.18</strong></td>
</tr>
<tr>
<td>$p^2$</td>
<td><strong>0.08</strong></td>
<td><strong>0.18</strong></td>
<td><strong>0.20</strong></td>
<td><strong>0.20</strong></td>
<td><strong>0.17</strong></td>
<td><strong>0.09</strong></td>
</tr>
</tbody>
</table>