Inbreeding effects on the parameters of the growth function in three strains of Iberian pigs

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ABSTRACT: The growth performance of inbred pigs coming from full-sib matings was compared to that of contemporary animals coming from the same sires mated to control dams. The animals belong to three strains of Iberian pigs with different histories of previous inbreeding. The data consisted of 1,615 weight records between 50 and 250 d of age from 229 pigs. The statistical model assumed the two parameters that describe the linear growth function \((a = \text{intercept}, b = \text{slope})\) as different traits (weight at 120 d and daily gain) and the analysis was carried out in a Bayesian framework via Gibbs sampling. The means of the posterior distribution of heritabilities, common litter environmental coefficients, and genetic correlation were 0.328 \((h^2_a)\), 0.332 \((h^2_b)\), 0.084 \((c^2_a)\), 0.060 \((c^2_b)\) and 0.973 \((\rho_G)\). Inbreeding depression, expressed as the performance decrease relative to the mean, per 10% increase of the inbreeding coefficient, was \(-3.18\), \(-2.31\) and \(-5.37\%\) for weight at 120 d \((a)\), and \(-3.16\), \(-2.08\) and \(-6.49\%\) for daily gain \((b)\) in each of the three strains. The results indicate that the inbreeding effects are dependent on the level of previous inbreeding, the more previous inbreeding, the less inbreeding depression.

Key Words: Bayesian Theory, Coancestry, Growth, Inbreeding Depression, Pigs

Introduction

Inbreeding depression exists in some degree in all populations for essentially all characters (Falconer and Mackay, 1996). It is particularly relevant to many practical issues in conservation programs and animal husbandry. Diverse studies suggest that the level of inbreeding depression may vary among populations (Lynch and Walsh, 1998). Although inbreeding depression could compromise the immediate performance and survival of a population, it also exposes recessive deleterious harmful genes to the action of selection. Purging of deleterious genes through the inbreeding process combined with selection has been proposed as an effective strategy in conservation programs (Templeton and Read, 1983). Both simulation and empirical studies show that with intensive inbreeding, completely recessive genes of large effect, such as lethals and semilethals, can be quickly purged. However, genes of lower effect seem to be inefficiently purged and inbreeding reduces the genetic variation at other nondeleterious genes (Wang et al., 1999; Wang, 2000). Because of purging, cumulated inbreeding within an isolated population can lead to a situation in which any further inbreeding has small phenotypic consequences.

In livestock species, evidence for the inbreeding effects comes partially from data recorded in progressively inbred populations (Burrow, 1993). This procedure poses different problems that can be avoided when data are available from contemporary unselected individuals inbred to various degrees. The goal of this experiment was to analyze the effect on growth traits of a fast increase of inbreeding in three related strains of pigs with a different past level of inbreeding. To obtain accurate inferences about inbreeding effects, data were analyzed using a Bayesian procedure, which takes into account all the available information and allows a joint analysis of parameters of growth functions, (co)variance components, systematic effects, and breeding values (Varona et al., 1997).

Material and Methods

Data

Data analyzed in this paper come from three related strains of Iberian pigs maintained in a conservation program established from four Spanish and Portuguese ancient populations of this Mediterranean breed: a) Torbiscal, which is the result of blending the four an-
cient founder populations; b) Guadyerbas, which is one of these founder populations, representing the ancient earliest mature black hairless type of the Iberian breed; and c) Gamito, a hairless strain developed exclusively from Guadyerbas but showing a red coat color. These populations of different effective size have previously experienced similar mild selection pressure (Béjar et al., 1993).

An experimental trial was carried out to test the growth performance of contemporary groups of inbred and control pigs of the three strains. A combination of full-sib and minimum coancestry matings were planned for each of the available boars of each strain. Two full-sib piglets (1 male and 1 female) were sampled at weaning from each of the 116 litters born in four testing batches and each pair of full-sib pigs was separately penned and weighed monthly. Animals were fed twice daily with a diet containing 3,450 kcal of digestible energy and 186 g of crude protein per kilogram of DM. The average daily ration per pig increased from 0.75 kg up to a maximum value of 3.25 kg. The number of boars, dams, and progeny tested in the inbred and control groups of each strain are presented in Table 1. The growth data consisted of 1,615 weights recorded on 229 pigs between 50 and 250 d of age. Pigs were weighed 3 to 8 times. The average pig weight increased from 13.8 to 93.5 kg during the trial.

**Pedigree Analysis**

The genetic relationships among all the animals were known back to the founder pigs of the herd and diverse pedigree tools can monitor the loss of genetic variability throughout the history of these populations (Rodrígáñez et al., 2000; Toro et al., 2000). The basic concepts in the pedigree analysis are the coancestry (kinship) coefficient between two individuals \( f_{xy} \) (probability of identity by descent of two genes taken at random from each individual at the locus) and the inbreeding coefficient \( f_x \) of an individual (probability of identity by descent of the two genes carried by this individual at a given locus). Both concepts are closely related with the concept of genetic contribution \( c_i \) defined by James and MacBride (1958) as the proportion of all pathways leading back from descendants that pass through the individual ancestor \( i \).

Caballero and Toro (2000) have shown that in a pedigree with a total of \( M \) individuals, where \( N_0 \) are founders (animal with unknown parents), the average pairwise coancestry (including reciprocals and self-coancestries) \( f \) of a given group of individuals can be partitioned into components of coancestry due to the genetic contributions of founders:

\[
\frac{N_0}{2} \sum_{i=1}^{N_0} c_i^2
\]

and nonfounders:

\[
0.25 \sum_{i=N_0+1}^{M} c_i^2 \left(1 - \frac{F_{Si} + F_{Di}}{2}\right).
\]

Another parameter related to genetic contribution is the number of discrete generation equivalents \( \sum_i c_i \).

This parameter is equal to the number of generations in a pedigree with no overlapping generations (Woolliams and Mäntysaari, 1995). Under random mating, inbreeding is delayed with respect to coancestry for one generation. The departure from random mating can be measured with the coefficient \( \alpha \) that indicates the degree of deviation from Hardy-Weinberg proportions and it is related to the previous coefficients by \( 1 - \alpha = 1 - (1 - f)(1 - \alpha) \). A positive value of \( \alpha \) means that relatives are preferentially mated.

**The Growth Function Approach**

Varona et al. (1997) proposed a Bayesian procedure to analyze growth performance data from production functions that has been applied to these data. In the analyzed growth period, the weight of tested pigs is adequately modeled by a linear function. The two parameters of this function, \( a \) (intercept) and \( b \) (slope), correspond to productive traits: weight at 120 d of age and daily gain, respectively. The \( k \)th weight of the \( j \)th animal recorded on day \( x_{jk} \) is 120 is considered as a sample from the normal distribution:

\[
y_{jk} | a_j, b_j, \sigma^2_j \sim N \left(a_j + b_j x_{jk}, \sigma^2_j \right)
\]
where \( \sigma_2^2 \) is the variance of weight given the production function parameters. The analysis of the growth function parameters requires other variables related to genetic and environmental relationships between the growth functions of different animals. These sources of variation were represented by the following animal model:

\[
\omega = X\beta + Z_1u + Z_2c + e
\]

where \( \omega = \) matrix of values of intercept and slope (\( a \) and \( b \)) of order \( N \times 2 \); \( \beta = [\beta_a, \beta_b] \); \( u = [u_a, u_b] \); \( c = [c_a, c_b] \) and \( e = [e_a, e_b] \) are matrices of systematic, additive genetic, common litter environmental and residual effects for both parameters; \( G, C, \) and \( R \) are their respective (co)variance matrices; and \( X, Z_1, \) and \( Z_2 \) are known incidence matrices. The systematic effects considered in \( \beta \) were two sexes, four test groups, and six experimental groups (three strains \( \times \) two degrees of inbreeding).

The joint posterior distribution given the weights can be explained as their likelihood given the growth function parameters multiplied by the prior distribution of these parameters. In this application, the likelihood is equal to

\[
f(y \mid \omega, \sigma_2^2) = f(y \mid a,b,\sigma_2^2) = \prod_{j=1}^{N} \prod_{k=1}^{n_j} \frac{1}{2\sqrt{\pi} \sigma_t} \exp \left\{ -\frac{(y_{jk} - (a_j + b_kx_{jk}))^2}{2\sigma_t^2} \right\}
\]

with \( N \) being the number of pigs with records and \( n_j \) the number of weight records of the \( j^{th} \) animal.

The following prior distribution of the linear growth function parameters was assumed:

\[
f(a,b \mid \beta_a, \beta_b, u_a, u_b, c_a, c_b, R) \sim \left[ X_{\beta_a} + Z_1u_a + Z_2c_a \right] \left[ X_{\beta_b} + Z_1u_b + Z_2c_b \right] N R \otimes I
\]

The prior distributions of breeding values and common litter environmental effects given the corresponding (co)variances are, respectively, \( f(u \mid G) \sim N(0,A \otimes G) \) and \( f(e \mid C) \sim N(0,1_{116} \otimes C) \), where \( A \) is the numerator relationship matrix. The other prior distributions: \( f(\sigma_2^2), f(G), f(C), \) and \( f(\beta) \) are taken as flat, as is usual in Bayesian analysis to reflect a vague previous knowledge about these parameters.

As a consequence, the joint posterior distribution given the performances was

\[
f(a,b,\sigma_2^2,\beta,u,G,C,R \mid y) \propto f(y \mid a,b,\sigma_2^2,f(a,b \mid \beta,u,c,R) f(\sigma_2^2)
\]

Gibbs Sampler

The marginal posterior density of each unknown parameter was determined using a Gibbs sampling algorithm (Wang et al., 1994), which requires independent draws from all the full conditional posterior distributions. Conditional posterior distributions are univariate normal both for the parameters of linear function \( (a, b) \) and systematic, genetic, and common litter environmental effects \( (\beta_a, \beta_b, u_a, u_b, c_a, c_b) \). Details about all these distributions can be found in Rodriguez et al. (1996) and Varona et al. (1997). The conditional posterior distributions of the (co)variance matrices \( G, C, \) and \( R \) are bivariate inverted Wishart distributions \( W_2^{-1}(S_a, n_a - 3), W_2^{-1}(S_c, n_c - 3) \) and \( W_2^{-1}(S_r, N - 3) \), where \( N \), \( n_a \), and \( n_c \) are, respectively, the number of pigs with records, animals in the pedigree, and the number of litters and \( S_a, S_c, \) and \( S_r \) parameters are \( 2 \times 2 \) matrices with the following expressions:

\[
S_i = \begin{bmatrix} u_aA^{-1}u_a & u_aA^{-1}u_b \\ u_bA^{-1}u_a & u_bA^{-1}u_b \end{bmatrix}
\]

\[
S_c = \begin{bmatrix} c_ac_a & c_ac_b \\ c_bc_a & c_bc_b \end{bmatrix}
\]

\[
S_e = \begin{bmatrix} e_ee_a & e_ee_b \\ e_be_a & e_be_b \end{bmatrix}
\]

The convergence was assessed by the double-chain method (García Cortés et al., 1998). The length of the Gibbs sampling was 2,050,000, discarding the first 50,000 (warm-up) and saving only one sample from each 200 iterations. The effective number of samples was calculated from the estimated autocorrelations using time series methods (Geyer, 1992) and ranged from 400 to 2,700 for the different parameters resulting in low values for Monte-Carlo standard errors. Marginal densities were estimated from the Gibbs samples using nonparametric kernel estimators (Silverman, 1986) and the main statistics of the posterior distributions were computed from these densities.

Inbreeding Effects

The marginal posterior distributions of the differences between the effects of the inbred and control groups on the growth function parameters \( (a, b) \) allow inferences to be made about the inbreeding effects on growth performance in the three strains of Iberian pigs. The differences \( (a_1^S - a_0^S) \) and \( (b_1^S - b_0^S) \) were calculated for each strain \( S \) in each iteration. The following scaled expressions were also calculated:
\[
\frac{(a_{\text{INBRED}} - a_{\text{CONTROL}}) \times 10}{(F_{\text{INBRED}} - F_{\text{CONTROL}})}
\]

and

\[
\frac{(b_{\text{INBRED}} - b_{\text{CONTROL}}) \times 10}{(F_{\text{INBRED}} - F_{\text{CONTROL}})}
\]

These expressions scale the differences between average \( a \) and \( b \) of inbred and selected group of each strain \( S \) to a 10% increase in average inbreeding coefficient \( F \) [1] and additionally to the different mean value of intercept and slope of each strain [2]. Finally, the differences of the other two strains from the Torbiscal strain for the expressions [1] and [2] were also calculated.

\section*{Results and Discussion}

\textit{Pedigree Analysis}

The average values of coancestry \( f \) and inbreeding \( F \) coefficients of the pigs of the six experimental groups and of their respective parents are presented in Table 1. With an unequal number of males and females, the inbreeding and coancestry coefficients of the inbred and control groups can be calculated as an unweighted or weighted average of the two sexes. Both values were close in the analyzed cases and the unweighted coefficients are shown. The \( F \) values are dependent on the mating system. As expected, the inbred groups present positive values of \( \alpha \). The matings of breeding animals in control groups resulted in negative values for \( \alpha \), reflecting the fact that matings between close relatives were avoided, as was done in the development of these lines. The genetic diversity of a population (GD = 1 – \( f \)) can be partitioned into diversity between and within individuals. Caballero and Toro (2000) have shown that the proportion of genetic diversity between individuals can be expressed by a coefficient closely related to \( \alpha \): \( G = (1 + \alpha)/2 \). The values of \( G \) for the inbred progenies of Guadyerbas, Gamito, and Torbiscal (0.581, 0.589, and 0.598) confirm that with full-sib matings, most of the genetic diversity is between individuals. However, the values of \( G \) for the correspondent control progenies (0.471, 0.470, and 0.476) indicate a greater proportion of genetic diversity within individuals.

There are clear differences for \( f \) and \( F \) values among the three strains derived from the different effective sizes: Torbiscal, with a broader origin and higher num-

\textbf{Figure 1.} Trends in the contribution to coancestry \( f \) (□) of founder (△) and nonfounder (■) animals of the three strains of Iberian pigs: a) Guadyerbas, b) Gamito, and c) Torbiscal.
Inbreeding effects on growth parameters

Table 2. Estimated statistics of marginal posterior distributions of heritabilities \((h^2)\), common litter environmental coefficients \((c^2)\), genetic \((\rho_G)\) and common litter environmental \((\rho_C)\) correlations between \(a\) (intercept = weight at 120 d) and \(b\) (slope = rate of daily gain) and variance component \((\sigma^2_t)\) due to model fitting and the contribution of nonfounders to the respective coancestry was 0.240, 0.283, and 0.114.

<table>
<thead>
<tr>
<th>Item</th>
<th>Mean</th>
<th>Mode</th>
<th>SD</th>
<th>95% higher posterior density interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>(h^2_a)</td>
<td>0.328</td>
<td>0.303</td>
<td>0.106</td>
<td>0.128 to 0.547</td>
</tr>
<tr>
<td>(h^2_b)</td>
<td>0.332</td>
<td>0.283</td>
<td>0.112</td>
<td>0.136 to 0.561</td>
</tr>
<tr>
<td>(c^2_a)</td>
<td>0.084</td>
<td>0.080</td>
<td>0.042</td>
<td>0.006 to 0.163</td>
</tr>
<tr>
<td>(c^2_b)</td>
<td>0.060</td>
<td>0.028</td>
<td>0.038</td>
<td>0.000 to 0.130</td>
</tr>
<tr>
<td>(\rho_G)</td>
<td>0.973</td>
<td>0.990</td>
<td>0.062</td>
<td>0.824 to 0.999</td>
</tr>
<tr>
<td>(\rho_C)</td>
<td>0.038</td>
<td>0.028</td>
<td>0.133</td>
<td>−0.227 to 0.291</td>
</tr>
<tr>
<td>(\sigma^2_t)</td>
<td>10.201</td>
<td>10.209</td>
<td>0.407</td>
<td>9.405 to 10.998</td>
</tr>
</tbody>
</table>

Variance Ratios and Estimates of Linear Growth Parameters

The Bayesian procedure provides estimates of growth function parameters of each animal that take account of their own performances and, through prior distributions, the information from relatives and other unrelated animals sharing the same systematic effects (Varona et al., 1997). Moreover, this approach provides an estimation of the variance of performances given the production function parameters \((\sigma_t^2)\), that includes errors in measure or physiological variations of the animals along the fattening period. This procedure can be improved by modeling the increase of \(\sigma_t^2\) with the age of animals, as has been done in the analysis of growth data from chickens by Mignon-Grasteau et al. (2000). This more complex approach was discarded for the present analysis given its higher computational cost and the moderate value of the scale factor between the first and last weights recorded in the trial.

Table 3. Estimated statistics of marginal posterior distributions of the absolute and scaled differences between inbred and control pigs for the intercept of the linear growth function \((a = weight \text{ at } 120 \text{ d})\) in three strains of Iberian pigs

<table>
<thead>
<tr>
<th>Strain</th>
<th>differences treated as</th>
<th>Mean</th>
<th>Mode</th>
<th>SD</th>
<th>95% higher posterior density interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guadyerbas</td>
<td>(a_{INBRED} - a_{CONTROL}, \text{ kg})</td>
<td>−2.24</td>
<td>−2.62</td>
<td>0.99</td>
<td>−4.05 to −0.29</td>
</tr>
<tr>
<td></td>
<td>Scaled values, % of mean(^a)</td>
<td>−3.18</td>
<td>−3.84</td>
<td>1.39</td>
<td>−5.67 to −0.42</td>
</tr>
<tr>
<td>Gamito</td>
<td>(a_{INBRED} - a_{CONTROL}, \text{ kg})</td>
<td>−1.56</td>
<td>−1.64</td>
<td>1.05</td>
<td>−3.52 to 0.44</td>
</tr>
<tr>
<td></td>
<td>Scaled values, % of mean(^a)</td>
<td>−2.31</td>
<td>−2.45</td>
<td>1.53</td>
<td>−5.13 to 0.64</td>
</tr>
<tr>
<td>Torbiscal</td>
<td>(a_{INBRED} - a_{CONTROL}, \text{ kg})</td>
<td>−5.82</td>
<td>−5.81</td>
<td>0.94</td>
<td>−7.61 to −3.99</td>
</tr>
<tr>
<td></td>
<td>Scaled values, % of mean(^a)</td>
<td>−5.37</td>
<td>−5.54</td>
<td>0.83</td>
<td>−6.92 to −3.74</td>
</tr>
</tbody>
</table>

\(^a\) Differences scaled to the mean intercept of control group and to differences in average inbreeding according to Eq. [2].
Figure 2. Marginal posterior distributions of the differences from the Torbiscal line of the strains Guadyerbas (2a, 2b) and Gamito (2c, 2d) for the effects of 10% inbreeding on the intercept and slope scaled to the mean of control group of each strain according to Eq. [2].

The main statistics of the marginal posterior distributions (m.p.d.) of $\sigma^2_t$ and the heritabilities, common environmental coefficients for the intercept ($a$, weight at 120th d) and slope ($b$, rate of daily gain) of the growth linear functions of tested pigs are summarized in the Table 2. Point estimates of heritabilities for $a$ (0.576) and $b$ (0.547) were lower than those obtained in related strains of Iberian pigs using this Bayesian procedure, but the point estimate of genetic correlation (0.989) was very similar (Fernández et al., 2002). However, common litter environmental effects, which accounted for 6 to 8% of the variance in the present study, were not taken into account.

Differences among strains were observed for both growth parameters. The posterior means (and SD) of intercept $a$ (kg) for the control groups of Guadyerbas, Gamito, and Torbiscal were 44.32 (0.99), 43.01 (1.02), and 49.45 (0.97). The corresponding values for the slope $b$ (kg/d) were 0.422 (0.014), 0.403 (0.013), and 0.489 (0.013). Differences between sexes were also observed.
Males exceeded females by 1.91 kg (0.47) for the intercept and 0.021 kg/d (0.006) for the slope.

**Inbreeding Effects on Intercept and Slope**

The trial was designed as a comparison of the effects on growth of discrete levels of inbreeding, generated by contemporary control and full-sib matings in three populations of different previous inbreeding. The purpose was to avoid some of the problems of most of the studies of inbreeding depression based on records from mildly inbred populations of domestic animals: 1) environmental effects can be confused with inbreeding effects, when the different classes of inbreeding are assayed in different generations and environments (Lynch and Walsh, 1998) and 2) the use of pedigree-based inbreeding coefficients to estimate inbreeding depression for traits under either direct or indirect selection is potentially biased (Groen et al., 1995).

The inbreeding effects on the linear growth parameters are the main parameters of interest of this study. The m.p.d. of the effect of differences between inbred and control pigs on the \( a \) and \( b \) in the three strains are presented in Tables 3 and 4. Absolute and relative values of effects of inbreeding differences between groups have been considered, because inbreeding depression values are frequently scaled to the effect of a 10% increase in inbreeding on the mean trait of noninbred animals. The conventional techniques of animal breeding only allow approximate solutions to the scaled effects. The use of Gibbs sampling permits drawing of m.p.d. of functions of estimated parameters (as the scaled effects) expressing its uncertainty (Blasco, 2001). According to the values of 95% highest posterior density intervals (95%HPD), negative inbreeding effects on the intercept and slope of the growth function are clearly evidenced in Torbiscal but not in Guadyerbas and Gamito strains. In the last population, the 95%HPD confidence intervals of absolute or scaled inbreeding effects on growth parameters included zero and positive values. For a similar trait, Bereskin et al. (1968) have reported a decrease of 4.3% of the mean of the weight at 154 d per 10% of increase of inbreeding. This value is close to the point estimates of scaled inbreeding effect.

<table>
<thead>
<tr>
<th>Strain and differences treated as</th>
<th>Mean</th>
<th>Mode</th>
<th>SD</th>
<th>95% higher posterior density interval</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Guadyerbas</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b_{\text{INBRED}} - b_{\text{CONTROL}} ), kg/d</td>
<td>-0.021</td>
<td>-0.022</td>
<td>0.013</td>
<td>-0.046 to 0.005</td>
</tr>
<tr>
<td>Scaled values, % of mean(^a)</td>
<td>-3.16</td>
<td>-3.41</td>
<td>1.90</td>
<td>-6.74 to 0.67</td>
</tr>
<tr>
<td><strong>Gamito</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b_{\text{INBRED}} - b_{\text{CONTROL}} ), kg/d</td>
<td>-0.013</td>
<td>-0.017</td>
<td>0.014</td>
<td>-0.040 to 0.013</td>
</tr>
<tr>
<td>Scaled values, % of mean(^a)</td>
<td>-2.08</td>
<td>-2.83</td>
<td>2.12</td>
<td>-6.17 to 2.17</td>
</tr>
<tr>
<td><strong>Torbiscal</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b_{\text{INBRED}} - b_{\text{CONTROL}} ), kg/d</td>
<td>-0.070</td>
<td>-0.072</td>
<td>0.012</td>
<td>-0.094 to -0.045</td>
</tr>
<tr>
<td>Scaled values, % of mean(^a)</td>
<td>-6.49</td>
<td>-6.81</td>
<td>1.10</td>
<td>-8.53 to -4.26</td>
</tr>
</tbody>
</table>

\(^a\) Differences scaled to the mean slope of control group and to differences in average inbreeding according to Eq. [2].

<table>
<thead>
<tr>
<th>Parameter and inbreeding effects treated as</th>
<th>Guadyerbas</th>
<th>Gamito</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Intercept (a)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( (a_{\text{INBRED}} - a_{\text{CONTROL}})^{10} ) ( (F_{\text{INBRED}} - F_{\text{CONTROL}}) )</td>
<td>95.56</td>
<td>98.03</td>
</tr>
<tr>
<td>Scaled values(^a)</td>
<td>92.28</td>
<td>95.76</td>
</tr>
<tr>
<td><strong>Slope (b)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( (b_{\text{INBRED}} - b_{\text{CONTROL}})^{10} ) ( (F_{\text{INBRED}} - F_{\text{CONTROL}}) )</td>
<td>97.44</td>
<td>99.15</td>
</tr>
<tr>
<td>Scaled values(^a)</td>
<td>94.62</td>
<td>97.45</td>
</tr>
</tbody>
</table>

\(^a\) Effects of 10% inbreeding scaled to the mean of control group of each strain according to Eq. [2].
fects on weight at 120 d obtained in this study (from 2.45 to 5.54% of the mean).

The pedigree analyses of the strains show that the contribution of genetic drift to inbreeding was greater in Guayerbas and Gamito than in Torbiscal. According to the hypothesis of purging inbreeding depression, inbreeding effects of lower magnitude could be expected in the first two strains than in Torbiscal. The Bayesian techniques allowed tests of these expected differences. Table 5 shows the probability for inbreeding effects being greater in the Torbiscal line than in the other two strains. The m.p.d. of the differences from the Torbiscal line of the other two strains for the scaled effects on the linear growth parameters are presented in the Figure 2. Although differences among strains were evidenced for both growth parameters, scale effects were not the only cause of differences between strains in inbreeding depression as indicated by the probability values based on the absolute and relative measures of the inbreeding effects. These results confirm for pig growth traits that the level of inbreeding depression may vary between populations and that the inbreeding effects may be less when there has been more previous inbreeding.

The issue of purging the genetic load through inbreeding is still under dispute. More knowledge of the dynamics of the joint action of inbreeding and selection and more empirical data are needed. The theory indicates that inbreeding can purge an outbreeding population but this purging affects mainly lethal or detrimental alleles of large effect (Wang et al., 1999). Latter et al. (1995) concluded for Drosophila melanogaster that homozygous genotypes from which deleterious genes have been eliminated during slow inbreeding might show less depression than suggested by earlier studies. But Lynch (1977) in Mus musculus and Brewer et al. (1990) in Peromyscus did not find this purging effect, and Lacy and Ballou (1998) found strong, weak, or no purging effects in three subspecies of Peromyscus polionotus, perhaps due to different histories of inbreeding and selection. Our results support the hypothesis of adaptation to the genetic consequences of inbreeding by purging deleterious recessive genes through a long-term process of inbreeding along with selection. As a consequence, the relationship between inbreeding depression and inbreeding coefficient will not be linear but it will show a concave shape that could be fitted by a negative quadratic function. In livestock populations with a wide range of inbreeding values, this nonlinear relationship should be considered in the models of genetic evaluation for traits that exhibit inbreeding depression.

**Implications**

These results indicate for pig growth traits that the inbreeding effects can be dependent on the previous level of inbreeding. More previous inbreeding resulted in less inbreeding depression. This implies that in some cases, the correction for inbreeding depression fitted in models of genetic evaluation would be better described by a nonlinear, concave function. The results also support the effectiveness of purging inbreeding in populations subject to a slow process of increasing inbreeding.

**Literature Cited**


