GENETIC ANALYSIS OF FLUCTUATING ASYMMETRY FOR TEAT NUMBER IN IBERIAN PIGS

A. Fernández, M.A. Toro, C. Rodríguez and L. Silió

Departamento Mejora Genética Animal, INIA, Ctra. La Coruña, km 7, 28040 Madrid, Spain

INTRODUCTION

Fluctuating asymmetry (FA) is defined as small random deviations from perfect symmetry in morphological bilateral traits. These subtle departures from identical expression of a trait across an axis of symmetry are commonly interpreted as a measure of developmental instability and is thought to reflect the ability of individuals to cope with genetic and environmental stress (Palmer and Strobeck, 1986). A meta-analysis of 34 studies of 17 species indicates that there is an additive genetic component to FA of morphological traits across the species studied (Møller and Thornhill, 1997). Despite several methodological criticisms to this kind of analysis, there is a general consensus about developmental instability does have an additive genetic component in many characters and populations. Moreover, in an other survey of 77 published reports from 29 species, Møller and Swaddle (1997) found a convincing evidence that inbreeding results in an increase in developmental instability.

Most of these results proceed from invertebrates and wild species of birds and mammals, but several papers have also been published on fluctuating asymmetry in domestic animals. Domestication of animals such as pigeons and hens has increased asymmetry, perhaps as a reflection of the decreased need for efficient flight and locomotion. A positive relationship between bilateral asymmetry and stress has been found in some poultry breeds (Campo *et al*., 2000). FA has also been negatively related to performance in some cases, as the handicap rating of thoroughbred horses (Manning and Ockenden, 1994).

Developmental instability for teat number is evidenced in pigs, where minor differences between the scores of right and left sides can be found in some individuals, but its genetic basis has not been previously analyzed. Here we present an analysis of the genetic variation and the effect of inbreeding on the fluctuating asymmetry for this important morphological trait.

MATERIAL AND METHODS

Data. The data analysed in this paper proceed from the Torbiscal strain of Iberian pigs preserved in a conservation programme. During the last 16 years, the number of teats was recorded at 21 days of age on the right (R) and left (L) sides of 13,470 piglets weaned from 2,006 litters. The mean and standard deviation of the R and L scores are 5.13 (0.36) and 5.12 (0.34), respectively. The genetic relationships among all the animals were known, the pedigree consisted of 13,959 animal-sire-dam entries.

Statistical analysis. The data analysis was performed in two steps. In the first one, the following bivariate mixed linear model was used to test the presence of asymmetry for teat number and its genetic basis:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z_1}\,\mathbf{u} + \mathbf{Z_2}\,\mathbf{c} + \mathbf{e} \qquad (1)$$

where **y** is a matrix of observations (R and L scores); **X**, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are known incidence matrices, relating location parameters **β, u** and **c**, respectively, to **y**; **β** is a matrix of systematic effects including mean, sex (2 levels) and batch (58 levels) effects; **u** is a matrix of additive genetic effects, **c** is a matrix of common litter environmental effects and **e** a matrix of random residuals. A Bayesian procedure using a Gibbs sampling algorithm (Wang *et al*., 1994; Rodriguez *et al*., 1996) was performed to obtain the marginal posterior distributions (m.p.d.) of the parameters of interest: heritabilities (h^2_R and h^2_L), common litter environmental coefficients (c^2_R and c^2_L) and genetic, common environmental and phenotypic correlations between the two scores (ρ_G, ρ_C and ρ_P). These posterior distributions were based on data information, because prior densities were assumed flat for all the parameters to represent a large *a priori* uncertainty about them.

The second step was focused on the genetic analysis of the individual values of FA. Fluctuating asymmetry on an individual *i* (FA_i) was measured as the absolute value of the differences between the measurements from each side of an individual ($|R_i - L_i|$), being the mean and standard deviation of these indices 0.17 and 0.39. A univariate animal model was used fitting the same effects as in model (1), with the F_i values being included in the incidence matrix **X** and the regression coefficient (b_{Fi}) included in the vector **β** of systematic effects. Inference about the effect of inbreeding on FA was obtained from the marginal posterior distribution of the correspondent regression coefficient (b_F). This and other m.p.d. of the remaining parameters of interest as variance components and ratios ($h^2_{|R-L|}$, $c^2_{|R-L|}$, σ^2_G, σ^2_C and σ^2_P) were achieved using a Bayesian procedure with flat priors, similar to the previously quoted one.

For each analysis, a single long Gibbs chain of 1.010,000 samples was sampled. The first 10,000 iterations were discarded and 10,000 samples of each parameter were saved each 100 iterations. Convergence was checked using coupled sample paths (García Cortés *et al*., 1998), doubling the sampling from different initial values of the additive variance and the effective numbers of independent samples were assessed using the initial positive sequential estimator proposed by Geyer (1992). The usual statistics of location (posterior mean, mode and median) and dispersion (posterior standard deviation and 95% highest posterior density interval) were calculated from saved samples.

RESULTS AND DISCUSSION

Bivariate analysis of R and L scores of number of teats. The Bayesian analysis allows to obtain the m.p.d. of systematic effects fitted in the model. No significant difference between males and females was found for the number of teats, being the posterior mean of the differences: -0.001 (PSD 0.005) for the right score and 0.003 (PSD 0.006) for the left score. The main statistics of m.p.d. of (co)variance ratios for the R and L scores of teats are summarized in the Table 1. The effective sample size for the mean of the distribution of these parameters ranged between 415 (h^2_R) and 8526 (ρ_C), with a low value of Monte-Carlo standard errors. Point estimates of heritabilities and common litter environmental coefficients for R and L scores were significantly different from zero, but the contribution of common litter environmental effects to the variation of the traits was very small. The common litter environmental effects on both scores were uncorrelated.

Table 1. Estimated statistics of m.p.d. of genetic parameters of right (R) and left (L) scores of teats in the Torbiscal line of Iberian pigs

	Mean	Mode	Median	PSD	95% HPD
h^2_R	0.146	0.147	0.147	0.014	0.117 , 0.165
h^2_L	0.151	0.152	0.151	0.013	0.125 , 0.172
c^2_R	0.015	0.014	0.014	0.004	0.007 , 0.023
c^2_L	0.015	0.018	0.016	0.006	0.001 , 0.024
ρ_G	0.985	0.987	0.986	0.005	0.973 , 0.991
ρ_C	0.011	0.012	0.011	0.032	-0.052 , 0.075
ρ_P	0.260	0.259	0.260	0.009	0.243 , 0.278

In absence of asymmetry in the population, the expected value of the phenotypic correlation between R and L scores (ρ_P) would be one. However, the results for this parameter indicate a value of the posterior mean of ρ_P significantly lower than one, that confirms the asymmetry of the trait studied. If differences between sides were purely environmental in origin, the expected genetic correlation between both scores (ρ_G) would be one. But this value is outside the limits of the 95% highest posterior density interval (95%HPD) estimated for ρ_G and the hypothesis of purely environmental asymmetry can be rejected. It was concluded that for this specific trait, additive genetic variance for FA could be detected in this population.

Genetic and environmental variance components of individual FA for teat number. The main statistics of m.p.d. of variance components and ratios of FA for teat number are summarized in Table 2. The effective sample size for the means of the distributions of these parameters ranged between 5252 (σ^2_G) and 7863 (σ^2_P), with a low value of Monte-Carlo standard errors.

Table 2. Estimated statistics of m.p.d. of genetic and environmental components of individual fluctuating asymmetry for teat number in the Torbiscal line of Iberian pigs

	Mean	Mode	Median	PSD	95% HPD
σ^2_G	0.015	0.015	0.015	0.002	0.012 , 0.019
σ^2_C	0.006	0.005	0.006	0.001	0.003 , 0.008
σ^2_P	0.150	0.150	0.150	0.002	0.146 , 0.154
$h^2_{\|R-L\|}$	0.101	0.100	0.101	0.012	0.078 , 0.124
$c^2_{\|R-L\|}$	0.037	0.036	0.037	0.008	0.022 , 0.053
b_F	-0.005	-0.005	-0.005	0.004	-0.012 , 0.003

A significant additive genetic variance for the measure of developmental instability ($|R_i - L_i|$) for teat number in Iberian pigs can be inferred from the m.p.d. of σ^2_G and $h^2_{|R-L|}$ parameters. In the quoted meta-analysis by Møller and Thornhill (1997), the overall mean effect size of the heritabilities of individual FA for different species and traits was 0.19. Because of its low level of genetic heritability, these authors suggest that FA can be related to fitness and used as an indicator of environmental conditions. A remarkable result proceeds from the m.p.d. of σ^2_C and $c^2_{|R-L|}$ parameters, that indicate a relatively small but highly significant effect of the common litter environment on the fluctuating asymmetry for teat number. It could be attributed to the developmental noise shared by the embryos of each litter or to other possible common effects as maternal or non-additive genetic effects that the model used do not discriminate.

Effect of inbreeding on individual FA for teat number. Loss of genetic variation and increase of homozygosity are the two well known main effects of inbreeding on the genomic structure of a population. Inbred individuals are expected to be more developmentally unstable, particularly if there are dominant genes that influence developmental stability. In the quoted survey of published reports by Møller and Swaddle (1997), 78% of the reviewed studies confirm this negative effect of inbreeding but a minority of studies (9%) displayed the opposite relationship.

In the present study, the relation between inbreeding coefficient (F) and individual fluctuating asymmetry has been tested from the marginal posterior distribution of the correspondent regression coefficient (b_F). The values of inbreeding coefficient (F) were expressed as percentages and the b_F values estimate the effect of a 1% of increase of inbreeding on the FA for teat number. No significant effect of inbreeding was observed, but the large values of the correspondent PSD and 95%HPD indicate that the information available in the data could be scarce to analyse accurately inbreeding effects. Although the values of the inbreeding coefficient of the scored piglets ranged from 9.34 to 33.69%, most of these values were close to the average (14.91%) being 22.64% the value of their coefficient of variation.

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