

A study of heterogeneity of environmental variance for slaughter weight in pigs

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This work presents an analysis of heterogeneity of environmental variance for slaughter weight (175 days) in pigs. This heterogeneity is associated with systematic and additive genetic effects. The model also postulates the presence of additive genetic effects affecting the mean and environmental variance. The study reveals the presence of genetic variation at the level of the mean and the variance, but an absence of correlation, or a small negative correlation, between both types of additive genetic effects. In addition, we show that both, the additive genetic effects on the mean and those on environmental variance have an important influence upon the future economic performance of selected individuals.

Keywords: Bayesian analysis, heterogeneous environmental variance, pigs, slaughter weight

Introduction

Selection decisions in animal breeding are usually based on predicted genetic values obtained using best linear unbiased predictors (BLUP) developed by Henderson (1975). The models used often assume homogeneous environmental variances. However, in livestock populations there is some evidence for heterogeneity of environmental variance for milk yield (Jaffrezic *et al.*, 2000), beef cattle growth (Garrick *et al.*, 1989), backfat thickness in pigs (See, 1998) and body weight at slaughter in pigs (Tibau, IRTA, Monells, Spain, personal communication). The consequences of ignoring heterogeneity of environmental variance in animal breeding programmes have been studied by Hill (1984) and Garrick and Van Vleck (1987). These authors found that genetic evaluations that ignore this heterogeneity can lead to a loss of expected selection response.

Foulley and Quaas (1995) proposed a quantitative genetic model with heterogeneity of environmental variance and for other components of variance. San Cristobal-Gaudy *et al.* (1998) extended this model by including additive genetic effects affecting environmental variation. Sorensen and Waagepetersen (2003) described a Bayesian implementation of this model and applied it to analyse litter size in pigs and growth in snails (Ros *et al.*, 2004). Gutiérrez *et al.* (2006) studied litter size and weight at birth in mice.

All these investigations reported statistical evidence for additive genetic control of environmental variation.

The presence of genetic variation at the level of the environmental variance opens the possibility of modifying it by selection. Increased homogeneity facilitates the posterior processing of animal products, with a consequent reduction of costs. In particular, the homogeneity of pig carcass weight significantly reduces the cost of meat processing (Hennessy, 2005). It is therefore usual for commercial slaughterhouses to apply a price penalty for carcasses that are above or below a pre-established optimum weight.

Our research has two main objectives. First, we investigate using data from a commercial pig population, whether there is support for the presence of additive genetic effects affecting environmental variation of body weight at slaughter (175 days), and infer their genetic correlation with additive genetic effects influencing mean. Second, a commercial profit function is used as a simple illustration of how the economic performance of sires is affected by basing selection decisions on the model proposed by San Cristobal-Gaudy *et al.* (1998)

Material and methods

Field data

Data collected over a 10-year period, starting in 1988, originate from a purebred Landrace pig population

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belonging to Spanish Pig Data Bank (Noguera and Pomar, 2007). This population had a history of selection for growth performance. Pigs tested contemporaneously and in the same pen were regarded as a contemporary group (batch). Each batch had approximately the same number of individuals of each sex and the pigs were from different litters. Weight (WT) was recorded at 175 days of age. The pedigree file contained 10 930 individuals and the data file included records on 9085 animals.

Models fitted

Three models were fitted: Model 1 is the standard additive genetic model with homogeneous environmental variance

$$y|b, a, \sigma_e^2 \sim N(\mathbf{Xb} + \mathbf{Za}, \mathbf{I}\sigma_e^2), \tag{1}$$

where **b** is a vector that contains batch effects (year–season–pen: 85 levels) and sex effects (two levels); **a** is the vector of additive genetic values (10 930 levels) and σ_e^2 is the environmental variance. In (1), **X** and **Z** are known incidence matrices and **I** is the identity matrix.

The following prior assumption was made for vector **a**:

$$a|\sigma_a^2 \sim N(0, \sigma_a^2 \mathbf{A}),$$

where **A** is the additive genetic relationship matrix. The vector **b** was assigned a bounded uniform prior distribution and the variance components σ_a^2 and σ_e^2 were assigned scaled inverted chi-squared distributions. Marginal posterior distributions for all the unknown variables in Model 1 were approximated using the Gibbs sampling algorithm (Geman and Geman, 1984; Wang *et al.*, 1994).

Models 2 and 3 follow the form

$$y|b, a, (\sigma_{i,M}^2)_{i=1,\dots,n} \sim N(\mathbf{Xb} + \mathbf{Za}, \text{diag}(\sigma_{i,M}^2)_{i=1,\dots,n}), \tag{2}$$

$$M = 2, 3,$$

where *n* is the number of observations and $\sigma_{i,M}^2$ is the environmental variance for the *i*th observation under the *M*th model. Model 2 allows for heterogeneity of environmental variances due to systematic effects so that $\sigma_{i,2}^2$ is of the form

$$\sigma_{i,2}^2 = \exp(x'_i \mathbf{b}^*),$$

where x'_i is the *i*th row in a known incidence matrix **X**. Vectors **b** and **b*** contain effects associated with batch and sex. Model 3 is the model proposed by San Cristobal-Gaudy *et al.* (1998), where environmental variation is assumed to be partly under genetic control. In this case, $\sigma_{i,3}^2$ is of the form

$$\sigma_{i,3}^2 = \exp(x'_i \mathbf{b}^* + z'_i \mathbf{a}^*),$$

where **b*** contains the same effects as in Model 2, z'_i is the *i*th row of the known incidence matrix **Z** and **a*** is a column vector of additive genetic values affecting environmental

variation of slaughter weight. The distribution of genetic effects (**a**, **a***) is assumed to be Gaussian,

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{a}^* \end{pmatrix} | \mathbf{G} \sim N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \mathbf{G} \otimes \mathbf{A}\right),$$

$$\mathbf{G} = \begin{pmatrix} \sigma_a^2 & \rho\sigma_a\sigma_{a^*} \\ \rho\sigma_a\sigma_{a^*} & \sigma_{a^*}^2 \end{pmatrix},$$

where **A** is the additive genetic relationship matrix, **G** is the matrix of additive genetic (co)variances. The elements of **G** are the genetic variances associated with (**a**, **a***) and the coefficient of correlation ρ .

We used the Bayesian Markov chain Monte Carlo (MCMC) approach described in Sorensen and Waagepetersen (2003) where details are provided concerning prior assumptions and implementation. Briefly stated, the vectors **b**, **b*** were assigned a normal distribution with zero mean vector and diagonal matrix with very large diagonal elements. The variance parameters σ_a^2 , $\sigma_{a^*}^2$, σ_e^2 were assigned scaled inverted chi-squared distributions and ρ was assigned a uniform prior distribution bounded between 1 and –1. The MCMC algorithm consisted of updating vector **b** using the Gibbs sampler, while vector (**a'**, **a*'**) was reparameterised with the aim of reducing the posterior correlation, and subsequently sampled using the Metropolis–Hastings algorithm with a Langevin–Hastings proposal. The log-variance components and the correlation coefficient were sampled using the Metropolis–Hastings algorithm with random walk proposals.

Under Models 2 and 3, the variances of the conditional distribution of y_i given **b**, **b***, and ignoring inbreeding are, respectively, $\text{Var}[y_{i,2}|\mathbf{b}, \mathbf{b}^*] = \sigma_a^2 + \exp((\mathbf{Xb}^*)_i)$ and $\text{Var}[y_{i,3}|\mathbf{b}, \mathbf{b}^*] = \sigma_a^2 + \exp((\mathbf{Xb}^*)_i + \sigma_{a^*}^2/2)$, where $(\mathbf{Xb}^*)_i$ is the *i*th row of **Xb*** and the ‘heritabilities’ are

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2 + \exp((\mathbf{Xb}^*)_i)} \quad \text{and}$$

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2 + \exp((\mathbf{Xb}^*)_i + \sigma_{a^*}^2/2)}. \tag{3}$$

Details can be found in Sorensen and Waagepetersen (2003) and Ros *et al.* (2004).

The results reported from each model are based on MCMC runs consisting of 2×10^6 iterations with a burn-in period of 1×10^5 . A little experimentation revealed that this chain length resulted in satisfactory Monte Carlo standard errors. Convergence was tested using the criterion described by Gelman and Rubin (1992). For each variance, a scale parameter (‘shrink’ factor, \sqrt{R}) was computed, which involves the variance between and within chains. The shrink factor can be interpreted as the factor by which the scale of the marginal posterior distribution of each variable would be reduced if the chain were run to infinity. Values in the

vicinity of 1 indicate convergence. The shrink factor was always between 0.99 and 1.05.

Posterior predictive distributions

The use of posterior predictive distributions to check the fit of a model is reviewed in Gelman *et al.* (2004). The general idea is that if observed data y_{obs} are the realisation from a particular model, then simulated data y^{rep} under this model should resemble, in some meaningful way, the observed data. In practice, one first draws the unknown parameters θ of the model from their posterior distribution $\theta|y$ and then y^{rep} is generated, conditional on these θ 's. The distribution of y^{rep} is called the posterior predictive distribution (Gelman *et al.*, 1996) because it is a distribution of a future (predicted) value, conditional on observed data y_{obs} . Specifically, the posterior predictive distribution of a hypothetical replication of the current data set y^{rep} is:

$$\begin{aligned} p(y^{rep}|y_{obs}, M) &= \int p(y^{rep}|\theta, y_{obs}, M)p(\theta|M, y_{obs})d\theta \\ &= \int p(y^{rep}|\theta, M)p(\theta|M, y_{obs})d\theta, \end{aligned} \quad (4)$$

where θ is the parameter vector and M is a model indicator.

Model fit and comparison

Posterior predictive model checking. In the Bayesian context, one way to check the quality of fit of a model is by using the posterior predictive distribution of a discrepancy measure $T(y^{rep}, \theta)$ (Gelman *et al.*, 1996). The discrepancy measure T is chosen to diagnose failure of the model to capture a particular feature of the data that may be of scientific interest. This discrepancy measure $T(y, \theta)$ may depend on both the data and the unknown parameters θ of the model in question. The fit of the model is evaluated by comparing the posterior predictive distribution of $T(y^{rep}, \theta)$ to the posterior distribution of $T(y, \theta)$: systematic and relevant differences between the two discrepancy measures indicate a possible failure of the model with respect to the feature of the data encapsulated in the discrepancy measure.

In our particular case, we would like to diagnose whether there is residual variance heterogeneity due to effects of batch, sex and progeny of a sire family. This was assessed using the discrepancy measure proposed by Sorensen and Waagepetersen (2003):

$$T_{jk}(y, \theta_1) = \frac{1}{m_{j,k}} \sum_{K_{ij}=k} \frac{(y_i - \mu_i)^2}{\sigma_i^2} - 1, \quad (5)$$

where the vector θ_1 contains the parameters of Model 1, j is an index for the three covariates, batch, sex and offspring of a given sire, and $k = 1, \dots, n_k$ is an index for the n_k levels of the j th covariate. $K_{ij} = k$ if the i th record belongs to the k th level of the j th covariate, $m_{j,k}$ is the numbers of records with level k for the j th covariate, μ_i is the i th

element in $\mathbf{Xb} + \mathbf{Zu}$, and $(y_i - \mu_i)^2/\sigma_i^2$ is the squared standardised environmental residual associated with record i . The expected value of expression (5) is zero (see Sorensen and Waagepetersen, 2003), large or small values of T_{jk} indicate possible variance heterogeneity associated with the j th covariate. Associated with the discrepancy measure we also computed the posterior predictive P -values. The posterior predictive P -value is defined by Gelman *et al.* (2004) as the probability that the replicated data could be more extreme than the observed data. In the present work, the following posterior predictive P -values were computed:

$$\begin{aligned} p_{Bjk} &= Pr(T_{jk}(y^{rep}, \theta_1) \geq T_{jk}(y, \theta_1)|y) \\ &= \iint I_{T_{jk}(y^{rep}, \theta_1) \geq T_{jk}(y, \theta_1)} p(y^{rep}|\theta_1) p(\theta_1|y) dy^{rep} d\theta_1, \end{aligned}$$

where I is an indicator function, j is an index for the three covariates, batch, sex and offspring of sire, $k = 1, \dots, n_k$ is an index for the n_k levels of the j th covariate, $p(y^{rep}|\theta_1)$ is the posterior predictive distribution under Model 1 and $p(\theta_1|y)$ is the distribution of the parameters θ_1 under Model 1. An extreme P -value (close to 0 or 1) implies that the model fails to capture the aspect of the data defined by the discrepancy measure T (Gelman *et al.*, 2004).

Deviance information criterion. Models 1, 2 and 3 were compared using the deviance information criterion (DIC) proposed by Spiegelhalter *et al.* (2002). The DIC is defined as

$$DIC = 2\bar{D} - D(\bar{\theta}_M), \quad (6)$$

where

$$\begin{aligned} \bar{D} &= -2 \int [\log p(y|\theta_M)] p(\theta_M|y, M) d\theta_M \\ &= E_{\theta_M|y}[D(\theta_M)] \quad \text{and} \quad D(\bar{\theta}_M) = -2 \log p(y|\bar{\theta}_M). \end{aligned}$$

The DIC combines a measure of model fit (\bar{D}) and a measure of model complexity ($D(\bar{\theta}_M)$). Models with smaller DICs exhibit a better global fit after accounting for model complexity. Differences in DIC of more than 7 are considered as important by Spiegelhalter *et al.* (2002).

Predictive income using posterior predictive distributions

The economic consequences of the genetically structured heterogeneous variance model are illustrated with an example involving the computation of posterior predictive incomes. In particular, we are interested in a future phenotypic record of an offspring and the future income of a given individual, labelled y^{off} and V^{off} , respectively.

The posterior predictive income is defined as

$$p(V_i^k|y_{obs}, M) = p(y_i^k|y_{obs}, M) \cdot g, \quad (7)$$

where, $p(y_i^k|y_{obs}, M)$ is the posterior predictive distribution of y_i^k (see equation (4)), y_i^k can take the value y_i^{rep} or y_i^{off} , and g is a price function. In the present work, a price

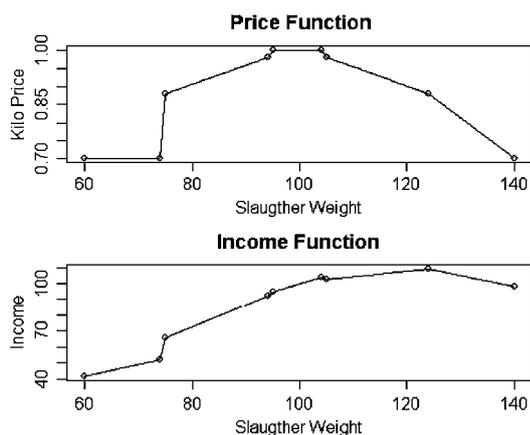


Figure 1 Commercial income function.

function provided by a commercial slaughterhouse was used (see Figure 1).

Three different predictive income distributions were analysed:

- $p(V_i^{rep} | y_{obs}, M), V_i^{rep}$, is the predictive income for animal i .
- $p(V_i^{off} | y_{obs}, M), V_i^{off}$, is the predictive income for one offspring of sire i .
- $p(V_i^{n,off} | y_{obs}, M)$, where $V_i^{n,off}$ is the sum of the predictive incomes for $n = 500$ future offspring of sire i .

Results and discussion

Inferences of model parameters

The estimate of the posterior mean of the environmental standard deviation based on Model 1 was 7.05 kg. In the case of Models 2 and 3, the estimated differences between sexes in posterior means of the environmental standard deviation were 0.44 and 0.38 kg (the larger value corresponds to males), respectively, with a posterior standard deviation of the difference equal to 0.04 kg and a posterior probability of differences greater than zero of 0.99 for both models. This confirms results previously reported for body weight in cattle (Garrick *et al.*, 1989; Kizilkaya and Tempelman, 2005). A plausible explanation could be a scale effect, because males reach a greater weight than females at age at slaughter (Wellock *et al.*, 2004). For batches, a wide range of posterior differences was observed for

Model 2 (0.06 to 4.92 kg) and for Model 3 (0.03 to 4.19 kg). Some of these differences were even greater than those associated with sexes, and their posterior probability of being greater (or smaller) than zero was more than 0.99.

Table 1 shows MCMC estimates of posterior means and 95% highest posterior density intervals for genetic (co)-variances based on Models 1, 2 and 3. The posterior mean of the additive genetic variance σ_a^2 was slightly larger for Model 1 than for Models 2 and 3. The estimated 95% posterior interval for σ_a^2 did not include zero, supporting the existence of additive genetic control of the environmental variation. This result is in agreement with other

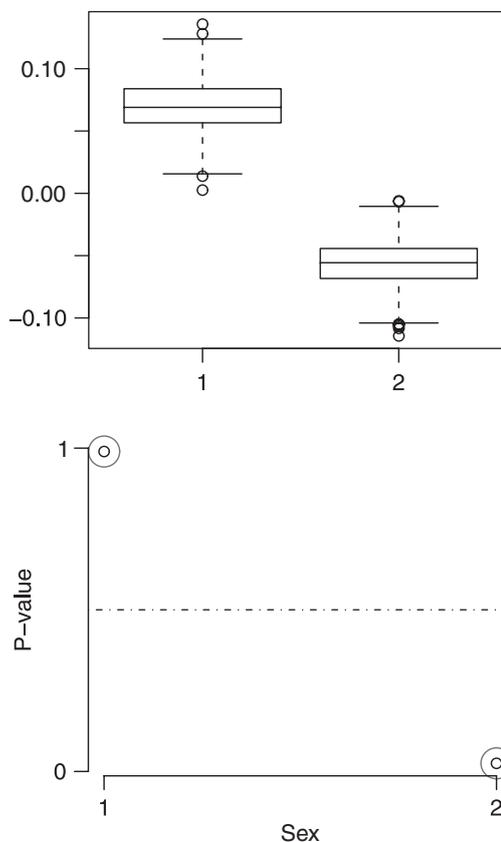


Figure 2 Upper: Boxplot for posterior predictive realisations of discrepancy measure under Model 1 designed to test environmental variance heterogeneity due to sex $T_{sk}(y, \theta_1) - T_{sk}(y^{ep}, \theta_1)$, $k=1,2$, 1: males, 2: females. Lower: Posterior predictive P-values of the discrepancy measure under Model 1 defined in expression (5).

Table 1 Monte Carlo estimates of posterior means (95% highest posterior density intervals) of genetic parameters of Models 1, 2 and 3

Model	σ_a^2	$\sigma_{a^*}^2$	ρ	h^2	h_{11}^2	h_{12}^2
1	61.10 (51.02, 70.93)	–	–	0.55 (0.48, 0.62)	–	–
2	52.66 (47.58, 57.75)	–	–	–	0.42 (0.35, 0.49)	0.53 (0.45, 0.61)
3	52.39 (46.25, 58.52)	0.11 (0.06, 0.16)	-0.07 (-0.26, 0.12)	–	0.44 (0.36, 0.51)	0.53 (0.42, 0.63)

σ_a^2 = genetic variance of the mean; $\sigma_{a^*}^2$ = genetic variance of the residual variance; ρ = correlation between genetic variances; h^2 = heritability for Model 1; h_{11}^2 = heritability for Models 2 and 3 (batch one, male sex); h_{12}^2 = heritability for Models 2 and 3 (batch one, female sex).

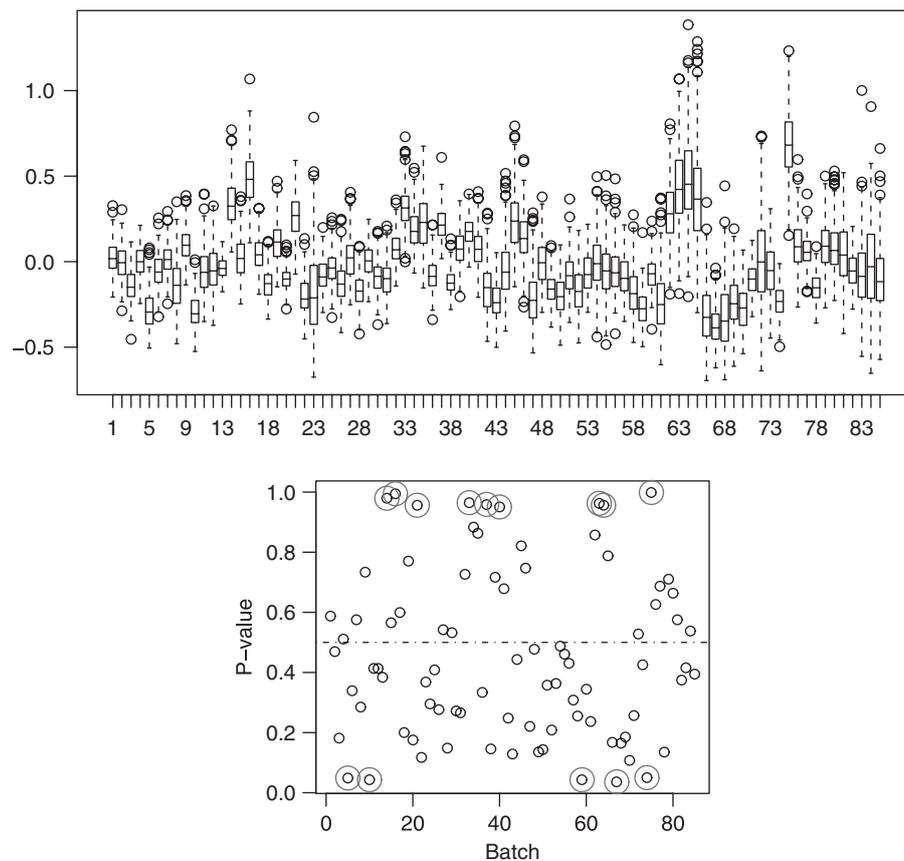


Figure 3 Upper: Boxplot for posterior predictive realisations of discrepancy measure under Model 1 designed to test environmental variance heterogeneity due to batch $T_{bk}(y, \theta_1) - T_{bk}(y^{ep}, \theta_1)$, $k=1, \dots, 85$. Lower: Posterior predictive P -values of the discrepancy measure under Model 1 defined in expression (5).

studies that provide statistical evidence for the additive genetic control of residual variation, for adult growth in snails (Ros *et al.*, 2004), weight at 35 days in poultry (Rowe *et al.*, 2006), and litter size in sheep, pigs, rabbits and mice (San Cristobal-Gaudy *et al.*, 2001; Sorensen and Waagepetersen, 2003; Gutiérrez *et al.*, 2006).

The estimate of the posterior mean of the genetic correlation (ρ) was small and the estimated 95% higher posterior density interval included the value zero. This implies a lack of (or very weak) association between the additive genes affecting the mean and those affecting environmental variance. The small negative correlation (-0.07) found between the estimated posterior means of additive values affecting mean and variance for weight in pigs is consistent with the results reported by Rowe *et al.* (2006) for body weight in broiler chickens. However, Damgaard *et al.* (2003) and Huby *et al.* (2003) found positive correlations for weight at birth in pigs, and Ros *et al.* (2004) found a high positive correlation for adult growth in snails. Nevertheless, Gutiérrez *et al.* (2006) found that correlations varied widely depending on the trait considered.

Models 2 and 3 generate a covariate-related heritability, (see equation (3)). For example, Table 1 presents the posterior means of heritability of batch one for males (h_{11}^2) and for females (h_{12}^2). Figure 6 shows the frequency distribution of heritability (posterior means) for batch and sex

combinations inferred from Model 3 (results were similar for Model 2). Differences between heritabilities were large, with a maximum value in females equal to 0.96, corresponding to batch 61, and a minimum value in males equal to 0.21, corresponding to batch 16. Heritabilities were very variable across batches, with slightly larger values in females than in males, in agreement with results reported by Garrick *et al.* (1989) for beef cattle. As previously pointed out by Hill (1984), such heterogeneity in the environmental variance can seriously affect the course of the selection process. When heterogeneity is not accounted for, for a given intensity of mass selection, a higher proportion of individuals are chosen from the highly variable groups.

Model fit and comparison

Results from the study based on posterior predictive model checking under Model 1 are shown in Figures 2–4 (see expression (7)). Figures 2–4 (upper) show the difference between the discrepancy measure evaluated using predictive (replicated) data $T_{jk}(y^{ep}, \theta_1)$ and the discrepancy measure evaluated using the observed data $T_{jk}(y, \theta_1)$. Values larger or smaller than zero indicate a possible association between heterogeneity of environmental variance and the effect (batch, sex and sire family) studied. As a measure of the discrepancy test, Figures 2–4 (lower)

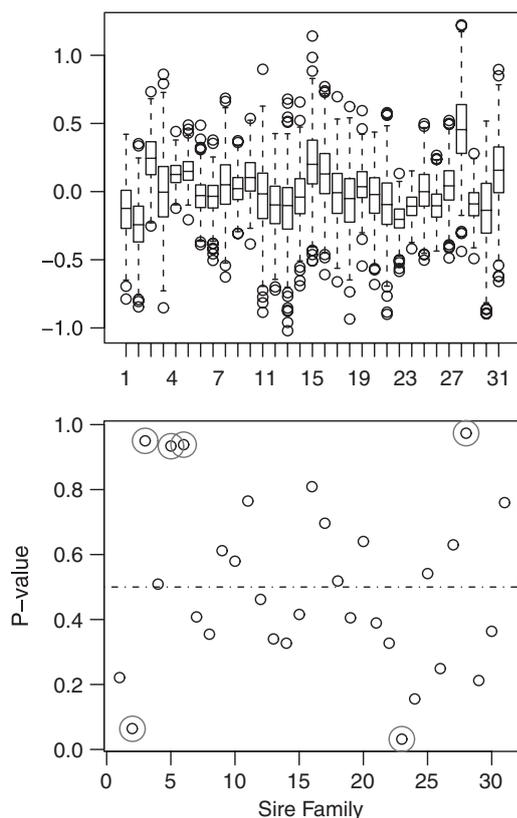


Figure 4 Upper: Boxplot for posterior predictive realisations of discrepancy measure under Model 1 designed to test environmental variance heterogeneity due to sire family $T_{sfk}(y, \theta_1) - T_{sfk}(y^{ep}, \theta_1)$, $k=1, \dots, 32$. Lower: Posterior predictive P -values of the discrepancy measure under Model 1 defined in expression (5).

show the posterior predictive P -values: the circled points indicate P -values greater than 0.95 or smaller than 0.05.

Figure 2 (upper) suggests that environmental variance is greater in males than in females. The P -values provide a little more formal support, being 0.99 for males and 0.02 for females. Heterogeneity due to batch is shown in Figure 3 (upper). Due to high posterior uncertainty, there is no clear pattern of batch effect associated with the environmental variance. However, around 17% of the posterior predictive P -values are either greater than 0.95 or smaller than 0.05 (Figure 3, lower). Moreover, these results are consistent with the wide ranges of the estimates of posterior differences between batches under Models 2 and 3. Figure 4 (upper) indicates that the association between environmental variance and sire families does not have a clear pattern. Furthermore, the posterior predictive P -values (Figure 4, lower) only demonstrate heterogeneity of environmental variance for 5 out of 31 sires. In order to explore a possible association between heterogeneity of environmental variance and an additive genetic control, Figure 5 shows a plot of the posterior predictive P -value for each sire family under Model 1 *v.* the posterior mean of the sire additive genetic values affecting environmental variation ($E(a^*|y)$). A linear regression is fitted and the estimate is 0.85, indicating that extreme values of the posterior

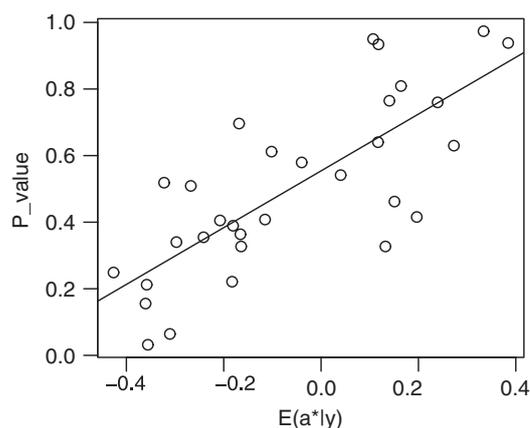


Figure 5 Association between posterior predictive P -values of the discrepancy measure for each sire family, under Model 1 defined in expression (5), *v.* posterior mean of the sire additive genetic values affecting environmental variation ($E(a^*|y)$) under Model 3.

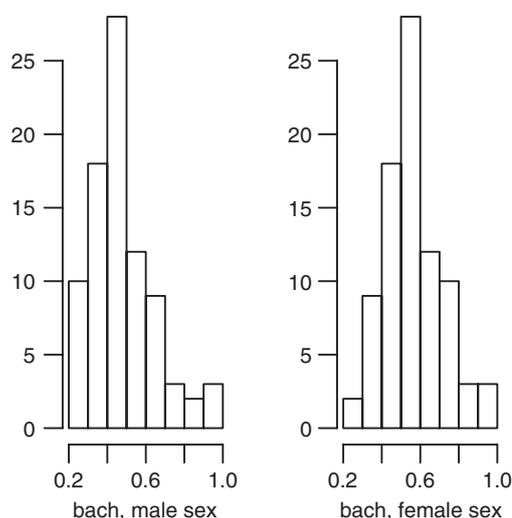


Figure 6 Histograms of heritabilities for different batches and sexes under Model 3.

Table 2 Natural logarithm of deviance information criterion (DIC) and differences in DIC expressed from Model 1

	Model 1	Model 2	Model 3
DIC	40 794	38 616	36 890
DIC _i - DIC ₁	—	-2176	-3904

predictive P -value correspond to the smallest and largest values of $E(a^*|y)$. Therefore, the heterogeneity of environmental variance associated with sire family is, to a certain degree, captured by the model that postulates that environmental variation is partly genetically controlled.

Table 2 shows the Monte Carlo estimates of the DIC for the three models, expressed as deviations from Model 1. The comparison based on DIC therefore favours Model 3

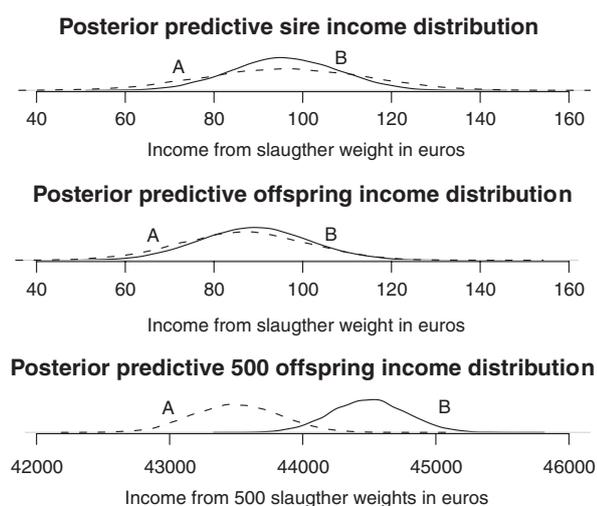


Figure 7 Posterior predictive incomes for two selected sires (A, B) with different breeding values for the environmental variance and their offspring.

followed by Model 2. This is in agreement with the posterior predictive checks.

The study of model fit based on the posterior predictive distributions, together with the model comparison study based on the DIC, and the fact that the marginal posterior distribution of $\sigma_{a^*}^2$ was clearly shifted away from zero, provide support for a genetically structured environmental variance of body weight at 175 days. This opens the possibility of controlling variation for this trait by selection.

Prediction of economic income: an illustration

One possible implication of Model 3 in an animal breeding context is illustrated below for the case of two specific sires. Figure 7 presents three different plots of the posterior predictive income distributions for these sires. The first plot shows that the posterior predictive income distributions of the two chosen sires (A and B), have almost identical posterior means of breeding values affecting the mean (2.01 kg for sire A and 2.10 kg for sire B) but different posterior means of breeding values affecting the environmental variance (0.48 kg² for sire A v. -0.50 kg² for sire B). The second plot shows posterior predictive income distributions for an offspring of the two sires. Finally, the third plot shows the distribution of the sum of the economic income of 500 offspring for each sire. These plots show that while there were no important differences between predictive incomes for one offspring (second plot), there were clear differences when 500 offspring are included. The sire with smaller breeding values affecting the environmental variance (B) generates higher incomes, with a mean difference of €2 for pig (€1000 in total), which corresponds to 2.2% increased income. This shows that genetic differences at the level of environmental variation have an important effect on the economic value of a candidate for selection.

We also compared the expected economic gain by either selecting on an index based on both breeding values

(a and a^*) or based only on breeding values affecting the mean (a). The computations were based on estimates of posterior means derived from Model 3. The expected response was calculated following Ros *et al.* (2004). We considered directional selection with a proportion selection of 10%. First, we studied selection of the highest ranking individuals based only on the posterior mean of additive genetic values controlling mean slaughter weight (i.e. $E(a|y)$). Changes in $E(a|y)$ resulted in an increase in slaughter weight of 8%, without a correlated reduction in environmental variance. Second, we considered an index $I = a^* + k \cdot a$ with $k = (\sigma_{a^*}^2 / \sigma_a^2)$ that provides the same weight to both components of the index. In this case, the change in $E(a|y)$ resulted in an increase in slaughter weight of 6% with a reduction in environmental variance of 18%. In terms of the response to selection in income ($E(V|y)$), selection based on the index results in approximately 0.7% more income than selection based on $E(a|y)$. This result must be taken with caution due to the strong influence of the price function.

In conclusion, this study provides support for a model postulating that environmental variance of slaughter weight at 175 days in pigs may be partly genetically determined. This opens the possibility of controlling variation by selection. In addition, the present study indicates that prediction of future income is influenced by genes affecting both the mean and the variance. This information could be incorporated in a selection index using a given price function.

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