Genetic Parameters and Trends for Milk Production of Blond-Faced Latxa Sheep Using Bayesian Analysis

E. UGARTE,* E. URARTE,* F. ARRESE,† J. ARRANZ,* L. SILIO,‡ and C. RODRIGUEZ‡
*Departamento de Industria, Agricultura y Pesca, †Ardekin S. L. Centro Investigacion y Mejora Agraria, Granja Modelo, Apdo. 46, 01080 Vitoria-Gasteiz, Spain, ‡Area de Mejora Genetica Animal Centro Investigacion y Tecnologia, Instituto Nacional Investigaciones Agrarias, Carretera de la Coruña km 7, 28040 Madrid, Spain

ABSTRACT

The genetic progress attained with the breeding scheme of the blond-faced Latxa dairy sheep in the Spanish Basque Country was assessed by a Bayesian approach based on the marginal posterior distributions of parameters achieved via Gibbs sampling. The data file included 49,056 milk yield records of 22,363 ewes. Normal distributions were assumed for EBV and fixed effects, and scaled inverted chi-square distributions were assumed for variance components or additive, permanent environment, and residual effects. Under vague priors for variance components, the posterior means (SD) for heritability and permanent environment coefficient for milk yield at 120 d were 0.22 (0.01) and 0.20 (0.01). An important effect on the milk yield (41.6% of the mean) was evident for a genetic group of imported rams. Selection was effective for sheep that were bred by AI and that had known parents. The robustness of results for effect of genetic group and genetic trends was validated using a mildly informative prior constructed from variance components estimated with the related black-faced breed.

Key words: genetic trends, milk yield, dairy sheep, Bayesian analysis

Abbreviation key: 95% HPD = 95% highest posterior density interval.

INTRODUCTION

Recording programs for dairy sheep are widespread in the Mediterranean countries of Europe, and great efforts are being exerted to establish selection schemes for the main breeds of dairy sheep. Breeding programs based on progeny test are very comprehensive in France, particularly for the Lacaune breed. However, in other countries, such as Italy and Spain, breeding schemes still involve only a small proportion of individuals in each breed, because AI is not widely used because of the need to maintain extensive and semi-extensive production systems. Bayesian techniques were applied to analyze the genetic progress for milk yield that had been achieved with the breeding scheme of an open population of the blond-faced strain of the Latxa breed of dairy sheep. Use of the Bayesian approach for the estimation of parameters of interest in animal breeding has multiple advantages: use of prior information (when available), elimination of nuisance parameters, exact finite sample analysis, and integrated estimation, prediction, and decision (3). Markov chain Monte Carlo methods, such as Gibbs sampling, allow Bayesian inferences to be made about genetic parameters and responses (8, 11).

MATERIALS AND METHODS

The Latxa (known as Manech in France) is a breed of dairy sheep native to the Basque Country of Spain. The Latxa breed comprises two separate strains that are differentiated by skin color: black-faced, with approximately 140,000 ewes distributed over 2000 flocks, and blond-faced (Manech), with 80,000 ewes over 1300 flocks. In the Spanish Basque Country, milk recording began in 1982, and, since 1985, an a.m.-p.m. sampling method has been followed (1). Lactations are standardized to 120 d using the Fleischmann method. The number of ewes in the flocks for the milk recording scheme represent 33% of the black-faced population and 12% of the blond-faced population.

The breeding program of the blond-faced strain started in 1986 with the selection by ancestry of ram
lambs to be progeny-tested by AI, always using fresh semen (4). Since 1988, EBV for the breeding scheme have been predicted using BLUP with an animal model. Actually, male lambs to be used in the AI center were selected as lambs from the top 10% of ewes selected for EBV for milk yield.

The data analyzed in this paper (Table 1) were from 1982 to 1994 and included 49,056 lactations of 22,363 blond-faced Latxa ewes in the recording scheme. A total number of 23,776 ewes were included in pedigrees. Breeding occurred from May to September, when the ewes were moved to mountain pastures without facilities to control paternity. Only rams used for AI were recognized as sires. Genes of the related blond-faced strain of the Manech breed were imported from the French Basque Country via semen three times (1985, 1988, and 1992), and 10 Manech rams were imported from France for testing in 1991 and 1992. Forty Manech rams are included in the pedigrees.

Model

The general linear animal model used for the analysis of data can be represented in matrix notation as

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

where \( y \) is a vector of observations (milk yield records); \( X, Z_1, \) and \( Z_2 \) are known incidence matrices of the order \( n \times p, n \times q_u, \) and \( n \times q_c \) relating to location parameters \( \beta, u, \) and \( c, \) respectively, to \( y; \beta = p \times 1 \) vector of fixed effects (including effect of interaction of flock and year (1007 levels); effects of flock, age of ewe, month of lambing, and parity (2143 levels); effect of the number of lambs (3 levels); and effect of the interval between lambing and first control (8 levels]); \( u = q_u \) is a random vector of additive genetic effects; \( c = q_c \times 1 \) random vector of permanent environment effects; and \( e = n \times 1 \) vector of random residual effects. The assumptions for distribution in the model, ignoring genetic group effects, were

\[ u \mid \sigma^2_{u}, A \sim N(0, A\sigma^2_{u}), \]

\[ c \mid \sigma^2_{c} - N(0, I_c\sigma^2_{c}), \]

and

\[ e \mid \sigma^2_{e} - N(0, I_e\sigma^2_{e}) \]

where \( A = \) numerator relationship matrix; \( I_c \) and \( I_e = \) identity matrices of appropriate order; \( \sigma^2_{u}, \sigma^2_{c}, \) and \( \sigma^2_{e} = \) components for additive genetic, permanent environment, and residual variances, respectively; \( u, c, \) and \( e = \) pairs assumed to be independent. The rank of \( X \) was \( p = 3161, \) and the rank of the coefficient matrix of the mixed model equations was \( N = p + q_u + q_c = 49,300. \)

A model fitting genetic groups was also used to consider the possible differences of genetic level between the ancestors of the imported Manech rams and the unknown ancestors (base animals) of the blond-faced population. The distributional assumption regarding genetic effects in this model was

\[ u \mid \sigma^2_{u}, A, Q, g - N(Qg, A\sigma^2_{u}) \]

where \( Q = \) matrix elements \( q_{ij} = \) expected proportion of the genes of animal \( i \) derived from genetic group \( j, \) and \( g = \) matrix of the genetic group effects (5).

Grouping Strategy

For the analysis with a model that ignored genetic groups, the unknown ancestors of the 40 Manech rams as well as the remaining unknown parents in the pedigree were considered as the base animals. For the analysis with the alternative model, the unknown ancestors of the Manech animals were assigned to a genetic group (group 2) identified as a phantom parent (12), and the rest of unknown parents were assigned to genetic group 1. The groups reflected the respective genetic level of the blond-faced Manech population and of the blond-faced Latxa strain at the start of the analyzed breeding scheme.

The mean genetic contributions of the Manech group to the annual cohorts of sheep born during the period from 1986 to 1993 were obtained from the \( Q \) matrix and are presented in Figure 1 for animals bred from AI (with both parents known). The mean proportion of the genes derived from group 2 increased for the sheep with both parents identified up to a maximum of 0.237 during 1992. The lower proportion observed during 1993 (0.144) must be cautiously examined. Because most farmers delayed

<table>
<thead>
<tr>
<th>Term</th>
<th>Explanation</th>
<th>(no.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( q_u )</td>
<td>Animals in pedigrees</td>
<td>23,776</td>
</tr>
<tr>
<td>( q_{PM} )</td>
<td>Animals with known sire and dam</td>
<td>1909</td>
</tr>
<tr>
<td>( q_{OM} )</td>
<td>Animals with known dam</td>
<td>6854</td>
</tr>
<tr>
<td>( q_{U} )</td>
<td>Animals with unknown sire and dam</td>
<td>15,013</td>
</tr>
<tr>
<td>( q_c )</td>
<td>Ewes with records</td>
<td>22,363</td>
</tr>
<tr>
<td>( n )</td>
<td>Lactations recorded</td>
<td>49,056</td>
</tr>
<tr>
<td>Mean, L</td>
<td>110.0</td>
<td></td>
</tr>
<tr>
<td>SD, L</td>
<td>44.9</td>
<td></td>
</tr>
</tbody>
</table>
the first lambing of their ewes to 2 yr of age, only 98 ewes from AI and born during 1993 were included in the analyzed pedigrees (ewes with recorded lactations).

Other grouping strategies have been attempted for complementary analysis. Unknown sires or dams were assigned to different genetic groups according to the year of lambing (anterior or posterior to 1990) to consider possible genetic changes in the population.

Bayesian Analysis via Gibbs Sampling

Wang et al. (11) and Sorensen et al. (8) presented methods that are applicable to animal breeding; these methods allow inferences to be made about parameters of interest from a univariate Gaussian mixed linear model using the Gibbs sampler. The main aspect of these methods is that the inferences are based on the marginal posterior distribution of parameters, and joint posterior distribution is marginalized via the Gibbs sampler through sampling from and updating of the conditional distributions (11).

In addition to the previously mentioned assumptions about distribution, which corresponded to assumptions made about these random effects with a classic linear model, the Bayesian approach requires the assignment of prior estimates for variance components $\sigma_i^2$ ($i = u, c, e$) and for $\beta$. A flat or uniform prior was assigned to $\beta$, reflecting the lack of previous knowledge about fixed effects; thus, $p(\beta) \propto k$. For most of the analysis, the scaled and inverted chi-square distribution was used as the prior distribution of variance components. The respective densities are

$$p(\sigma_i^2 | \nu_i, s_i) \propto (\sigma_i^2)^{-\nu_i/2 - 1} \exp(-\nu_i s_i^2 / 2 \sigma_i^2)$$

where $\nu_i$ and $s_i^2$ ($i = u, c, e$) are parameters of the distribution, the expected value being of $\sigma_i^2$, $E[\sigma_i^2] = \nu_i s_i^2 / (\nu_i - 2)$, and its variance, $V[\sigma_i^2] = 2 \nu_i s_i^2 / (\nu_i - 2)^2 (\nu_i - 4)$.

Estimates of variance components obtained from a data file including 189,615 lactations of 82,269 black-faced Latxa ewes were used as values of the $s_i^2$ hyperparameters: $s' = [s_u^2, s_c^2, s_e^2] = [235.714, 274.603, 694.801]$ (Ugarte et al., 1995: unpublished results). Two types of priors were considered that had different sets of values for the $\nu_i$ parameters that describe the uncertainty of the previous knowledge of the variance components. Vague priors (prior V) were obtained setting $\nu_i = 4.000001$ ($i = u, c, e$) so that the distributions were as flat as possible with finite variances of the priors: $SD[\sigma_u^2] = 6.7 \times 10^5$, $SD[\sigma_c^2] = 7.8 \times 10^5$, and $SD[\sigma_e^2] = 19.6 \times 10^5$; this procedure allows proper posterior distributions to be obtained.

Mildly informative priors (prior I) had $\nu_i$ values specified in relation to the information from data (10), such that $\nu_i / (\nu_i + n_i) = 1/100$, where $n_u = q_u = \text{number of ewes with records} (22,363)$, $n_c = \text{number of ewes with repeated records} (12,577)$, and $n_e = n = \text{total number of lactations} (49,056)$. These $\nu_i$ values were $\nu' = [\nu_u, \nu_c, \nu_e] = [226, 127, 496]$ where the expectations of the corresponding prior distributions were $E[\sigma_i^2] = 237.8, 279.0, 679.6$, and the respective standard deviations were $SD[\sigma_i^2] = 22.6, 35.6, 44.5$.

With a proper distribution, another representation of vague prior knowledge regarding variance components, uniform bounded distributions for $\nu_i^2$ ($i = u, c, e$) on the interval $[0, \sigma_{\text{max}}^2]$, were considered for a second set of analyses (prior U). The density of $Un[\nu_i^2 | 0, \sigma_{\text{max}}^2]$ is $p(\nu_i^2) = (\sigma_{\text{max}}^2)^{-1}$, if $0 < \sigma_i^2 < \sigma_{\text{max}}^2$, and $p(\nu_i^2) = 0$ otherwise. The phenotypic variance estimated for the black-faced Latxa ewes was assumed as the maximum for each variance component $a$ priori ($\sigma_{\text{max}}^2 = 1205$); the expectation of each prior distribution $E[\sigma_i^2] = 602.5$, and the standard deviation $SD[\sigma_i^2] = 347.8$, for $i = u, c, e$. 

Figure 1. Mean genetic contribution of Manech sheep to lambs born from 1986 to 1993 with known sire and dam.

Independent sampling was used for each of the location parameters (β, u, and c). The conditional posterior distribution of each of these location parameters is normal; the mean is equal to the conditional expectation for the other parameters, and variance is equal to the inverse of the correspondent element of the diagonal of the coefficient matrix of the mixed model equations of Henderson (11).

Assuming scaled inverted chi-square distributions as priors of $\sigma_i^2$ ($i = u, c, e$), the conditional posterior distributions of variance components are in the form of the scaled inverted chi-square with parameters $V_i$ and $S_i^2$:

$$
\sigma_e^2 | y, \beta, u, c, \sigma_u^2, \sigma_c^2, s, \nu - V_e S_e^2 \chi_{re}^2
$$

$$
\sigma_u^2 | y, \beta, u, c, \sigma_c^2, \sigma_e^2, s, \nu - V_u S_u^2 \chi_{ru}^2
$$

$$
\sigma_c^2 | y, \beta, u, c, \sigma_u^2, \sigma_e^2, s, \nu - V_c S_c^2 \chi_{rc}^2
$$

where

$$
V_u = q_u + \nu_u, \quad V_c = q_c + \nu_c, \quad V_e = n + \nu_e
$$

and

$$
S_e^2 = (e^' e + \nu_e S_e^2)/V_e,
$$

$$
S_u^2 = (e^' e + \nu_u S_u^2)/V_u,
$$

and

$$
S_c^2 = (u^' A^{-1} u + \nu_u S_u^2)/V_u
$$

for the model without genetic groups, and $S_u^2 = [(u - Qg)^' A^{-1} (u - Qg) + \nu_u S_u^2]/V_u$ for the model fitting genetic groups.

Assuming uniform priors, $Un[0, \sigma_{imax}^2]$, the conditional posterior distributions of variance components are in the form of the scaled inverted chi-square truncated on the interval $0 < \sigma_i^2 < \sigma_{imax}^2$ and with parameters $V_i$ and $S_i^2$, such that $V_u = q_u - 2, V_c = q_c - 2, V_e = n - 2, S_c^2 = (c^' c)/V_c, S_e^2 = (e^' e)/V_e$, and $S_u^2 = (u^' A^{-1} u)/V_u$, for the model without genetic groups, and $S_u^2 = [(u - Qg)^' A^{-1} (u - Qg)]/V_u$ for the model fitting genetic groups. Sampling from the truncated distributions can be done by generating from the inverted chi-square distributions and rejecting those values outside the interval from 0 to $\sigma_{imax}^2$.

The specifications for Gibbs sampling conditions were based on a previous analysis of data using the techniques described by Raftery and Lewis (6). For each of the prior sets and models, the Gibbs sampler was used with a single chain of 72,288 iterations. The first 288 iterations (warm up) were discarded, and samples for each parameter of interest were saved each 9 iterations. Eight thousand Gibbs samples were saved for the variance components for additive genetic effects, permanent environment effects, and residual effects; the phenotypic variance; the usual variance ratios (coefficients for heritability and permanent environment); and, using models fitting genetic groups, the effects of genetic group. The mean EBV, by year of birth and type of pedigree information, were also calculated, and the response to selection was measured by determining the difference between the appropriate annual means (TR) or by regression of the annual means on year of birth (annual response, $b$; intercept, $a$). For each chain of Gibbs samples, the variance of the sample mean of the chain and the effective number of independent samples were estimated using the initial positive sequence estimator suggested by Geyer (2). Convergence of the Markov chains was assessed comparing the results of three attempts, using the model fitting genetic groups under vague priors, starting from different random points.

After Gibbs analysis, marginal densities were estimated from the samples for every parameter of interest using nonparametric kernel estimators in the form:

$$
f(x) = 1/mh \sum_{i=1}^{m} K [(x - x_i)/h]
$$

where $f(x) =$ estimated density at $x$, $x_i$ ($i = 1, m) =$ Gibbs samples, $h =$ window width or smoothing parameter, and $K [(x - x_i)/h] =$ Epanechnikov kernel (7).

Optimal window widths that minimized the mean integrated square error of the estimators were calculated using the subroutine CURVDAT (9); the convergence criterion for the algorithm was equal to the range of the effective domain of the parameter of interest divided by 200. Marginal densities were plotted using 1000 equally spaced pairs ($x_i, f(x_i)$). Summary statistics of the posterior distributions such as mean, mode, median, standard deviation, and 95% highest posterior density intervals ($95\%$ HPD) were computed from these estimated densities. Densities of...
any functions of the variance components could be estimated in a similar manner, provided that the needed samples were saved.

RESULTS

Variance Components
and Variance Ratios

The main statistics for distribution of variance components and variance ratios, under the different priors, are summarized in the Tables 2 and 3. The effective number of independent observations for the means of these distributions ranged from 500 to 600 for $\sigma^2_u$, $\sigma^2_c$, $h^2$, and $c^2$ because the corresponding estimate of the correlation between successive samples ranged from 0.78 to 0.86. The effective chain size for $\sigma^2_e$ was close to 7000 because the estimate of autocorrelation of the samples of this parameter was only about 0.07.

The distributions of these parameters achieved with the different priors and models were unimodal and nearly symmetrical about their modes; the estimates of posterior mean, mode, and median were very similar. The marginal posterior distributions of the variance ratios of interest, estimated with and without groups in the model, are presented in Figure 2 (a and b).

With the Bayesian approach, the knowledge of the posterior distribution of the parameters allowed the construction of proper confidence intervals. The uncertainty about the parameters (measured by the estimates of standard deviations and 95%HPD) increased when the effect of Manech genetic group was not included in the model.

Inferences About Genetic Group
Effects and Genetic Changes

The effect of Manech genetic group $(g_2 - g_1)$ was calculated as the difference in genetic worth between the corresponding phantom parents. The correlation between samples of $(g_2 - g_1)$ was about 0.32, and the effective chain size was close to 3600. A summary of the main statistics of the distribution under the different proven priors is presented in Table 4. These marginal posterior distributions of the effect of Manech genetic group are presented in Figure 2c.

The probability that a parameter lies between specified values can be easily computed and, because the 95%HPD does not include zero (Table 4), the hypothesis $g_2 - g_1 = 0$ was rejected, confirming the adequacy of fitting the Manech genetic group with the model.

Other grouping strategies were also proven with a third genetic group a) assigned to the unknown sires of ewes born after the year 1990 or b) restricted to unknown sires of ewes with a known dam. The purpose was to consider the possible increase, with time, of the genetic worth of rams used for natural service without control of paternity. The posterior means (and standard deviations) of the corresponding effects of genetic group $(g_3 - g_1)$ were 0.028 L (1.541) and 2.906 L (1.866) of milk, respectively. No differences were found between these groups and the base

---

**TABLE 2.** Estimated statistics of marginal posterior distributions, under different priors (U, V, and I), of variance components ($\sigma^2_u$, $\sigma^2_c$, $\sigma^2_e$) for milk yield (liters), using models ignoring (NG) and fitting (G) the effect of Manech genetic group.

<table>
<thead>
<tr>
<th>Variance component</th>
<th>Model</th>
<th>Prior</th>
<th>Mean</th>
<th>Mode</th>
<th>Median</th>
<th>SD</th>
<th>95% HPD</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_u$</td>
<td>NG</td>
<td>U</td>
<td>286.7</td>
<td>286.2</td>
<td>286.1</td>
<td>18.3</td>
<td>252.1, 324.0</td>
</tr>
<tr>
<td>$\sigma^2_u$</td>
<td>NG</td>
<td>V</td>
<td>285.9</td>
<td>285.4</td>
<td>285.3</td>
<td>18.1</td>
<td>251.6, 322.8</td>
</tr>
<tr>
<td>$\sigma^2_u$</td>
<td>G</td>
<td>V</td>
<td>287.8</td>
<td>267.0</td>
<td>267.6</td>
<td>14.9</td>
<td>235.7, 298.2</td>
</tr>
<tr>
<td>$\sigma^2_u$</td>
<td>G</td>
<td>I</td>
<td>255.5</td>
<td>256.7</td>
<td>255.3</td>
<td>13.3</td>
<td>229.2, 281.9</td>
</tr>
<tr>
<td>$\sigma^2_c$</td>
<td>NG</td>
<td>U</td>
<td>230.6</td>
<td>232.6</td>
<td>231.0</td>
<td>17.3</td>
<td>196.4, 263.9</td>
</tr>
<tr>
<td>$\sigma^2_c$</td>
<td>NG</td>
<td>V</td>
<td>231.4</td>
<td>233.4</td>
<td>231.8</td>
<td>17.1</td>
<td>196.6, 264.3</td>
</tr>
<tr>
<td>$\sigma^2_c$</td>
<td>G</td>
<td>V</td>
<td>246.8</td>
<td>246.8</td>
<td>247.0</td>
<td>14.2</td>
<td>219.7, 276.1</td>
</tr>
<tr>
<td>$\sigma^2_c$</td>
<td>G</td>
<td>I</td>
<td>258.0</td>
<td>257.7</td>
<td>257.9</td>
<td>13.0</td>
<td>232.5, 283.7</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>NG</td>
<td>U</td>
<td>705.1</td>
<td>705.1</td>
<td>705.1</td>
<td>6.3</td>
<td>692.7, 717.5</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>NG</td>
<td>V</td>
<td>705.1</td>
<td>705.1</td>
<td>705.1</td>
<td>6.3</td>
<td>692.7, 717.4</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>G</td>
<td>V</td>
<td>704.4</td>
<td>703.4</td>
<td>704.4</td>
<td>6.3</td>
<td>692.0, 716.5</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>G</td>
<td>I</td>
<td>704.2</td>
<td>704.2</td>
<td>704.2</td>
<td>6.3</td>
<td>692.0, 716.8</td>
</tr>
</tbody>
</table>

1The 95% highest posterior density interval.
Figure 2. Marginal posterior distributions of a) heritability, b) permanent environmental coefficient (c²), c) effect of Manech genetic group (g₂ - g₁), and d) total response for sheep with known parents (TRₚₚₚ). Results are from models ignoring genetic groups under vague priors (-----) and fitting the Manech group under vague (----) and mildly informative priors (.....).
TABLE 3. Estimated statistics of marginal posterior distributions, under different priors (U, V, and I), of heritability ($h^2 = \sigma^2_h/\sigma^2_G + \sigma^2_e$) and permanent environment coefficient ($c^2 = \sigma^2_c/\sigma^2_G + \sigma^2_e$) for milk yield (liters), using models ignoring (NG) and fitting (G) the effect of Manech genetic group.

<table>
<thead>
<tr>
<th>Model</th>
<th>Prior</th>
<th>Mean</th>
<th>Mode</th>
<th>Median</th>
<th>SD</th>
<th>95% HPD</th>
</tr>
</thead>
<tbody>
<tr>
<td>$h^2$</td>
<td>NG</td>
<td>0.235</td>
<td>0.235</td>
<td>0.234</td>
<td>0.014</td>
<td>0.206, 0.263</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>0.234</td>
<td>0.234</td>
<td>0.233</td>
<td>0.014</td>
<td>0.207, 0.263</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.210</td>
<td>0.212</td>
<td>0.210</td>
<td>0.011</td>
<td>0.189, 0.231</td>
</tr>
<tr>
<td>$c^2$</td>
<td>NG</td>
<td>0.189</td>
<td>0.191</td>
<td>0.189</td>
<td>0.014</td>
<td>0.160, 0.216</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>0.189</td>
<td>0.192</td>
<td>0.190</td>
<td>0.014</td>
<td>0.161, 0.216</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.202</td>
<td>0.203</td>
<td>0.203</td>
<td>0.011</td>
<td>0.180, 0.226</td>
</tr>
</tbody>
</table>

The 95% highest posterior density interval.

TABLE 4. Estimated statistics of marginal posterior distributions, under different priors (U, V, and I), of the effect of Manech genetic group ($g_2 - g_1$) on milk yield (liters), total response (TR), and annual ($b$) response from 1987 to 1993, using models ignoring (NG) and fitting (G) the genetic group effect.

<table>
<thead>
<tr>
<th>Model</th>
<th>Prior</th>
<th>Mean</th>
<th>Mode</th>
<th>Median</th>
<th>SD</th>
<th>95% HPD</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g_2 - g_1$</td>
<td>G</td>
<td>45.70</td>
<td>44.96</td>
<td>45.67</td>
<td>5.08</td>
<td>35.92, 55.72</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>45.70</td>
<td>44.96</td>
<td>45.67</td>
<td>5.08</td>
<td>35.93, 55.73</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>45.94</td>
<td>45.71</td>
<td>45.85</td>
<td>5.39</td>
<td>35.50, 56.62</td>
</tr>
<tr>
<td>$TR_{PM}$</td>
<td>NG</td>
<td>7.26</td>
<td>7.02</td>
<td>7.25</td>
<td>2.10</td>
<td>3.13, 11.41</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>7.25</td>
<td>7.01</td>
<td>7.23</td>
<td>2.10</td>
<td>3.12, 11.39</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>9.19</td>
<td>9.16</td>
<td>9.17</td>
<td>2.08</td>
<td>5.13, 13.20</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>8.98</td>
<td>8.97</td>
<td>8.97</td>
<td>2.02</td>
<td>4.95, 12.92</td>
</tr>
<tr>
<td>$b_{PM}$</td>
<td>NG</td>
<td>0.92</td>
<td>0.90</td>
<td>0.92</td>
<td>0.27</td>
<td>0.39, 1.46</td>
</tr>
<tr>
<td></td>
<td>V</td>
<td>0.92</td>
<td>0.90</td>
<td>0.92</td>
<td>0.27</td>
<td>0.39, 1.45</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>1.41</td>
<td>1.39</td>
<td>1.41</td>
<td>0.26</td>
<td>0.90, 1.92</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>1.36</td>
<td>1.33</td>
<td>1.36</td>
<td>0.25</td>
<td>0.86, 1.87</td>
</tr>
</tbody>
</table>

The 95% highest posterior density interval.

The PM indicates that both parents are known.

Figure 3. Annual mean EBV for milk yield of the ewes of the population born from 1987 to 1993: a) with known sire and dam (U), b) with unknown sire and known dam (O), and c) with unknown sire and dam (V). Results are from models fitting (-----) and ignoring (- - -) the effect of Manech genetic group.

The posterior distributions of total and annual responses from 1987 to 1993 indicated that selection for milk yield was effective for ewes with known parents (P[TRM > 0] = 0.999 and P[bpM > 0] = 0.999).

Influence of Priors

Under the same analytical model, the marginal posterior distributions were similar for the different parameters of interest, the uniform and vague priors for Ω² (priors U and V). As a consequence, most of the results from prior U and model G were not included in tables or figures. These distributions reflect the data information regarding these parameters and are proper because of the finite variance of the priors. The estimates of variance components from the black-faced Latxa strain, used as hyperparameters of priors V and I, had slight differences relative to those inferred from analysis of data from the blond-faced Latxa strain: lower additive variance, greater permanent environmental variance, and similar residual variance.

The influence of the external information on the point estimates of the parameters of interest was not important; the results were in basic agreement with those obtained with the uniform or vague priors. The comparison of the results obtained using the same model for variance components and variance ratios under priors I, U, and V indicated that the use of mildly informative priors reduced the variance of posterior distributions (Tables 2 and 3).

In any case, the objective of the analysis with prior I was to assess the results obtained from the data. For example, the analysis with vague priors provided the following inferences: P[g2 - g1 > 37.388] = 0.950, P[TRPM > 5.787] = 0.950, and P[bpM > 0.981] = 0.950. The analysis with mild priors provided the following results: P[g2 - g1 > 37.227] = 0.950, P[TRPM > 5.650] = 0.950 and P[bpM > 0.933] = 0.950. The main conclusion of the analysis of the breeding scheme for blond-faced Latxa is the great importance of the Manech effect on milk yield and effectiveness of selection from AI.

DISCUSSION

Although the usefulness of Bayesian methods for animal breeding is debated among animal breeders, these results and other previously published results (10, 11) show that the application of Bayesian techniques via the Gibbs sampler provide for an elegant analysis of breeding schemes based on field data that was not attainable by standard mixed model methods. The results provide evidence of a genetic group effect of the blond-faced Manech on milk yield that was equivalent to 41.6% of the phenotypic mean; consequences were important for the estimation of genetic impact of the breeding scheme and the ranking of animals for genetic merit. Only 5 of the top 15 rams ranked for EBV with the model without groups are found among the top 15 ranked with the model fitting the Manech effect. For the genetic evaluations annually provided to producers, the EBV of animals with genetic contribution from the Manech group was underestimated because of the use of a model ignoring genetic groups. This underestimation diminished the odds of animals with Manech genes being selected and reduced the applied selection differential, which was overestimated.

For example, using the model without genetic groups, the posterior means (SD) of the mean EBV of the 115 rams tested and of the 15 actually selected as breeding sires were 14.75 L (1.36) and 27.13 L (3.21); the posterior mean (SD) of the difference between the mean EBV of both sets of rams was 12.38 L (2.88). If the Manech effect was fitted in the model, the respective values were 27.50 L (1.91), 37.39 L (3.32), and 9.81 L (2.91). The corresponding posterior distributions obtained with both models are presented in Figure 4.

Several practical advantages of the Bayesian approach can be outlined. The Bayesian approach facilitates the estimation of group effects as well as the
adoption of an ad hoc grouping strategy based on the marginal posterior distributions of the genetic group effects. As a consequence, the fitting of groups without different genetic worth can be avoided. The associated measures of uncertainty also allow us to conclude that differences in genetic worth existed between classes of ewes defined by their pedigree information and that response to selection for milk yield has been greater than zero for animals resulting from AI. Other results, relative to genetic groups formed by the unknown sires of ewes born during the later years of the data indicated an inefficient diffusion of the genetic gain obtained via progeny test. The use of sons of breeding rams as sires for natural service has been recently enhanced. For future analyses that include new data, the fitting of the models for the corresponding genetic groups must be considered as described in this study.

The external information for the black-faced Latxa sheep, the other strain of the dairy breed with the same production system, has been used to contrast the results obtained from the data and to validate the inferences about the Manech effect and the effectiveness of response. If results from moderately informative priors are quite different, then the conclusions from the data should be viewed cautiously. The method of moments (10) allows other alternative uses of prior information, weighting the relevant parameters according to the information they contain for combined analysis, via Bayes theorem, of the prior with the data. This analysis could be especially useful for decision making based on the EBV of ram lambs, for which existing data are weak. The incorporation of the previous knowledge about variance components, from the diverse related populations (black-faced Latxa and the two strains of Manech), would be convenient to reduce the uncertainty of the genetic worth of candidates to be progeny tested or used as sires on farms.

ACKNOWLEDGMENTS

The authors thank D. Gianola and D. Sorensen for their information on applications of Bayesian analysis to animal breeding and L. Varona and J. M. Marín for their original software for Gibbs sampling. This work was supported by a grant from the CICYT (AGF 1017/92).

REFERENCES

3 Gianola, D., S. Im, and F. W. Macedo. 1989. A framework for