

Bayesian Inference on Variance Components Using Gibbs Sampling with Various Priors

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ABSTRACT : Data for teat number for Landrace (L), Yorkshire (Y), crossbred of Landrace and Yorkshire (LY), and crossbred of Landrace, Yorkshire and Chinese indigenous Min Pig (LYM) were analyzed using Gibbs sampling. In Bayesian inference, flat priors and some informative priors were used to examine their influence on posterior estimates. The posterior mean estimates of heritabilities with flat priors were 0.661 ± 0.035 for L, 0.540 ± 0.072 for Y, 0.789 ± 0.074 for LY, and 0.577 ± 0.058 for LYM, and they did not differ ($p > 0.05$) from their corresponding estimates of REML. When inverse Gamma densities for variance components were used as priors with the shape parameter of 4, the posterior estimates were still corresponding ($p > 0.05$) to REML estimates and mean estimates using Gibbs sampling with flat priors. However, when the inverse Gamma densities with the shape parameter of 10 were utilized, some posterior estimates differed ($p < 0.10$) from REML estimates and/or from other Gibbs mean estimates. The use of moderate degree of belief was influential to the posterior estimates, especially for Y and for LY where data sizes were small. When the data size is small, REML estimates of variance components have unknown distributions. On the other hand, Bayesian approach gives exact posterior densities of variance components. However, when the data size is small and prior knowledge is lacked, researchers should be careful with even moderate priors. (*Asian-Aust. J. Anim. Sci.* 2001. Vol 14, No. 8 : 1051-1056)

Key Words : Teat Number, Variance Component, REML, Bayesian Inference

INTRODUCTION

Teat number of sow is a concern to swine breeders because of the importance for its mothering ability. Swine breeders usually pay considerable attention to the teat number when selecting breeding stock, especially in herds where teat number is less than litter size. (Enfield and Rempel, 1961; McKay and Rahnefeld, 1990). Accurate estimation of variance components is important for selection because prediction error variance for breeding value increases by the difference between estimate and true value of genetic parameter (Schaeffer, 1984).

Previous estimation of heritability for teat number was predominantly based on conventional methods such as regression and analysis of sire or dam variance (Enfield and Rempel, 1961; Pumfrey et al., 1980; Clayton et al., 1981; Jungst and Kuhlert, 1983; Toro et al., 1986; McKay and Rahnefeld, 1990). However, the practical mating system in the breeding herds is not designed to optimize the estimation of genetic parameters. Thus the irregular mating system with unequal family size and overlapping generations often decreases the accuracy of heritability estimates with these methods. Recently, the teat number was analyzed using the class of mixed models and more complex ones by Lee and Wang (2001). Since teat number was a count trait, they compared a Poisson error model (a hierarchical Poisson generalized linear mixed model) to a

normal error model (a mixed model). However, the latter fit the field data better than the former, and it seemed that the mean and variance of the observations were not equal. Their study suggested that the teat numbers did not have Poisson distribution.

Selection of appropriate estimation methods for variance components has always been an important issue for animal breeders (Lee, 2000). Lee and Wang (2001) obtained variance component estimates for mixed linear model using REML that is now considered as a standard method. The use of REML has become increasingly popular due to easy access to general purpose programs such as MTDFREML (Boldman et al., 1995) or ASREML (Gilmour et al., 1995). Meanwhile, a sample of parameter values can be easily obtained from a posterior density in a Bayesian approach using Gibbs sampling and then be used to estimate a moment of a lower dimensional marginal of the posterior. While BLUP of breeding values cannot be obtained from REML estimation of variance components, Bayesian analysis via Gibbs sampling overcomes the problem. Furthermore, Bayesian approach always gives exact posterior densities while REML estimates of variance components have unknown distributions for small data sets (Gianola and Fernando, 1986). Bayesian inference provides a rich inferential framework that can be strengthened by considering relevant external information. Van Tassell and Van Vleck (1995) developed a multiple-trait Gibbs sampler for animal models (MTGSAM) to implement the Gibbs sampling algorithm for Bayesian analysis of a broad range of animal models.

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The objective of this study was to compare different priors for variance components using Gibbs sampling in porcine teat numbers. The posterior estimates were also compared with REML estimates obtained by Lee and Wang (2001).

MATERIALS AND METHODS

Data

The data structure of swine utilized in the current study were explained in detail in Lee and Wang (2001). The data were collected from 1993 to 1997 on Tianjin Ninhe swine breeding farm managed by Chinese government. As explained in Lee and Wang (2001), 16,255 records were finally utilized; 9,898 records for Landrace, 1,748 records for Yorkshire, 1,924 records for crossbred of Landrace and Yorkshire, and 2,685 records for crossbred of Landrace, Yorkshire, and Chinese indigenous Min pig. Toro et al. (1986) reported that 90 percent of teat number in Iberian pig had 10 teats. Yet, the data in the current study showed a sound normal distribution where roughly 40 percent of individuals have 14 teats. The distribution of teat number is shown in table 1. Lee and Wang (2001) showed the statistical differences ($p < 0.05$) among means of teat number for the four breeds. Teat number of Yorkshire (14.42 ± 0.03) was larger ($p < 0.05$) than that of Landrace (14.03 ± 0.01). The crossbreds (14.64 ± 0.03 for LY and 14.58 ± 0.02 for LYM) had more teats ($p < 0.05$) than the purebreds. Heterogeneity of parameters for the breeds was suspected, which led the current study to analyze the data by breeds.

Analytical model

For each breed, variance components were estimated using a mixed linear model. The analytical model used in this study was:

$$y = X\beta + Za + e$$

where y represents a vector of observations (teat number recorded within 12 hours after birth), β is a vector of sex fixed effects, a is a vector of additive direct genetic random

effects with the assumption of $a \sim N(0, A\sigma_a^2)$ where A is a numerator relationship matrix, e is a random vector of residuals with the assumption of $e \sim N(0, I\sigma_e^2)$. And σ_a^2 and σ_e^2 are additive genetic and residual variance components, respectively. The X and Z are known incidence matrices relating the fixed and random effects to their corresponding observations.

Parameter estimation

Inferences about unknown variance components in Bayesian approach were based on their marginal posterior distribution, and the marginalization of the joint posterior distribution is attained through Gibbs sampling. The Gibbs sampling is a numerical integration method based on Markov chain Monte Carlo. The joint posterior distribution of all parameters in the model given the data can be expressed by Bayes theorem:

$$f(\beta, a, \sigma_a^2, \sigma_e^2 | y) \propto f(y | \beta, a, \sigma_a^2, \sigma_e^2) f(a | \sigma_a^2) \pi(\beta) \pi(\sigma_a^2) \pi(\sigma_e^2)$$

$$\text{where } f(y | \beta, a, \sigma_a^2, \sigma_e^2) \sim N(X\beta + Za, I\sigma_e^2),$$

$$f(a | \sigma_a^2) \sim N(0, A\sigma_a^2), \pi(\beta), \pi(\sigma_a^2), \text{ and}$$

$\pi(\sigma_e^2)$ are the priors for β , σ_a^2 , and σ_e^2 . For the priors, a Uniform distribution was assumed for the fixed effects, and five different sets of prior distributions were assumed for the variance components:

G1: Uniform distribution;

G2: Inverse Gamma (IG) distribution with mean $\sigma_a^2 = 0.5$, $\sigma_e^2 = 1.0$ and shape parameter=4;

G3: IG distribution with mean $\sigma_a^2 = 1.0$, $\sigma_e^2 = .5$ and shape parameter=4;

G4: IG distribution with mean $\sigma_a^2 = 0.5$, $\sigma_e^2 = 1.0$ and shape parameter=10;

G5: IG distribution with mean $\sigma_a^2 = 1.0$, $\sigma_e^2 = .5$ and shape parameter=10.

Then the joint posterior density was:

Table 1. Teat number distributions by breeds

Breed	10	11	12	13	14	15	16	17	18
L ¹	38 0.4%	170 1.7%	1074 10.9%	1261 12.7%	4383 44.3%	1754 17.7%	1038 10.5%	150 1.5%	30 0.3%
Y	1 0.1%	12 0.7%	89 5.1%	170 9.7%	725 41.5%	435 24.9%	270 15.4%	38 2.2%	8 0.5%
LY	5 0.3%	5 0.3%	66 3.4%	127 6.6%	766 39.8%	482 25.1%	394 20.5%	54 2.8%	25 1.3%
LYM	4 0.1%	12 0.4%	121 4.5%	213 7.9%	1034 38.5%	660 24.6%	546 20.3%	75 2.8%	20 0.7%

¹ L: Landrace, Y: Yorkshire, and M: Chinese indigenous Min pig.

$$f(\beta, a, \sigma_a^2, \sigma_e^2 | y) \propto (\sigma_a^2)^{-\frac{n}{2}} \exp\left\{-\frac{1}{2\sigma_a^2}(y-X\beta-Za)'(y-X\beta-Za)\right\} \\ \times (\sigma_a^2)^{-\frac{p}{2}} \exp\left\{-\frac{1}{2\sigma_a^2}a'A^{-1}a\right\} \\ \times (\sigma_e^2)^{-\frac{1}{2}(v_e+2)} \exp\left\{-\frac{1}{2\sigma_e^2}(v_e-2)S_e^2\right\} \\ \times (\sigma_e^2)^{-\frac{1}{2}(v_e+2)} \exp\left\{-\frac{1}{2\sigma_e^2}(v_e-2)S_e^2\right\} \\ \propto (\sigma_a^2)^{-\frac{1}{2}(p+v_a+2)} (\sigma_e^2)^{-\frac{1}{2}(p+v_e+2)} \\ \times \exp\left[-\frac{1}{2\sigma_a^2}\{(y-X\beta-Za)'(y-X\beta-Za)+(v_e-2)S_e^2\}\right] \\ \times \exp\left[-\frac{1}{2\sigma_e^2}\{(a'A^{-1}a)+(v_a-2)S_a^2\}\right]$$

where S_a^2 and v_a were scale and shape parameters for genetic variance component respectively, and S_e^2 and v_e were for environmental variance component. In order to implement Gibbs sampling, full conditional posterior distributions were obtained by deriving the posterior distribution of each parameter given the data and all other parameters in the model. Let $s=[\beta' \ a']$ and $W=[X \ Z]$. Then, the conditional distribution of s was derived from the joint density.

$$f(s | \sigma_a^2, \sigma_e^2, y) \propto \exp\left\{-\frac{1}{2}\left(s-\frac{1}{\sigma_e^2}C^{-1}W'y\right)'C\left(s-\frac{1}{\sigma_e^2}C^{-1}W'y\right)\right\}$$

where C was the coefficient matrix of the Henderson's mixed model equation, $Cs = r$. This is the kernel of a normal density, i.e.

$$s | \sigma_a^2, \sigma_e^2, y \sim N\left(\frac{1}{\sigma_e^2}C^{-1}W'y, C^{-1}\right)$$

Furthermore, full conditional distribution can be derived for a scalar or subvector s_1 of the solution vector, s , where $s = [s_1' \ s_2']'$;

$$s_1 | s_2, \sigma_a^2, \sigma_e^2, y \sim N(C_{11}^{-1}(r_1 - C_{12}s_2), C_{11}^{-1})$$

where $C = \begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}$ and $r = [r_1' \ r_2']'$

The full conditional distribution of the genetic variance component was

$$f(\sigma_a^2 | \beta, a, \sigma_e^2, y) \propto \sigma_a^2^{-\frac{1}{2}(p+v_a+2)} \times \exp\left[-\frac{1}{2}tr\left\{\frac{1}{\sigma_a^2}(v_a S_a^2 + a'A^{-1}a)\right\}\right]$$

This is the kernel of an inverse Gamma distribution, that is

$$\sigma_a^2 | \beta, a, \sigma_e^2, y \sim IG((v_a S_a^2 + a'A^{-1}a)^{-1}, p + v_a)$$

The full conditional distribution of the environmental

variance component was

$$f(\sigma_e^2 | \beta, a, \sigma_a^2, y) \propto \sigma_e^2^{-\frac{1}{2}(n+v_e+2)} \times \exp\left[-\frac{1}{2}tr\left\{\frac{1}{\sigma_e^2}(v_e S_e^2 + e'e)\right\}\right]$$

This is the kernel of an inverse Gamma distribution, that is

$$\sigma_e^2 | \beta, a, \sigma_a^2, y \sim IG((v_e S_e^2 + e'e)^{-1}, n + v_e)$$

Then iterative sampling was required from the consecutively updated full conditional posterior distributions (Van Tassell and Van Vleck, 1996). Then iterative sampling was required from the consecutively updated full conditional posterior distributions. The MTGSAM programs (Van Tassell and Van Vleck, 1995) were used to generate the samples, and Gibbsit programs (Raftery and Lewis, 1995) were used to determine burn-in periods and thinning intervals. The Gibbs sampler was run 202,000 rounds, and the first 2000 rounds were discarded as a warming-up period, and a thinning interval of 100 rounds were used to retain sampled values which reduced lag correlation among thinned samples. The posterior means, modes, and medians of the expected values for variance components and those of observed values for heritabilities were calculated. The expected values for genetic and environmental variance components were calculated as follows:

$$E(\sigma_a^2 | a, S_a^2, v_a) = \frac{v_a S_a^2 + a'A^{-1}a}{p + v_a - 2}$$

$$\text{and } E(\sigma_e^2 | e, S_e^2, v_e) = \frac{v_e S_e^2 + e'e}{n + v_e - 2}$$

RESULTS AND DISCUSSION

Posterior estimates with flat priors for variance components were obtained (table 2) and compared with estimates using REML in Lee and Wang (2001). Posterior mean, mode, and median estimates were all corresponding ($p>0.05$) to the REML estimates. Since flat priors were used for the variance components, the posterior densities were supposed not to differ from the likelihood function. The standard deviations of the posterior distribution were used as equivalent estimates for the frequentist standard error. Although they were similar, the standard deviations for all the parameters were somewhat larger than their corresponding standard errors of REML estimates.

It was reported that teat number is moderately heritable (Pumfrey et al., 1980; Clayton et al., 1981). However, the genetic parameter estimates of teat number in the present study were large, especially for the crossbred between

Table 2. Marginal posterior means, medians, modes, and standard deviations (SD) of, σ_a^2 , σ_e^2 and h^2 using Gibbs sampling with flat priors

Breed ¹	Parameter	REML ²		Gibbs Sampling			
		Mean	SE	Mean	SD	Median	Mode
L	σ_a^2	1.011	0.074	1.046	0.081	1.039	0.991
	σ_e^2	0.548	0.041	0.534	0.043	0.537	0.525
	h^2	0.649	0.033	0.661	0.035	0.662	0.664
Y	σ_a^2	0.722	0.126	0.759	0.130	0.755	0.770
	σ_e^2	0.658	0.076	0.639	0.081	0.623	0.647
	h^2	0.532	0.070	0.540	0.072	0.539	0.551
LY	σ_a^2	1.348	0.178	1.336	0.205	1.311	1.269
	σ_e^2	0.338	0.097	0.349	0.105	0.350	0.353
	h^2	0.800	0.066	0.789	0.074	0.787	0.787
LYM	σ_a^2	0.868	0.111	0.878	0.117	0.874	0.925
	σ_e^2	0.642	0.066	0.638	0.072	0.638	0.610
	h^2	0.575	0.055	0.577	0.058	0.579	0.588

¹ L: Landrace, Y: Yorkshire, and M: Chinese indigenous Min pig. ² Lee and Wang (2001)

Landrace and Yorkshire (table 2). It had been suspected that the large estimates were due to the inflation from the model excluding maternal genetic effects. Yet, when the maternal genetic effects were included in the model, likelihood ratio tests showed that maternal genetic variance and direct-maternal genetic covariance were not significant ($p > 0.05$, data are not shown). As expected, the heterogeneity of variance components for the four breeds was found. Furthermore, the heterogeneity of heritabilities was also obviously shown (table 2). When the crossbred data were analyzed, exclusion of nonadditive genetic effects such as dominance in the analytical model may have inflated additive direct genetic variance.

The mean, mode, and median of variance component estimates were different, although the differences were not statistically significant at the level of $\alpha = 0.05$. The differences implied the unsymmetric posterior densities. The optimum Bayes decision rule under quadratic loss is the posterior mean rather than the posterior mode.

Although the posterior estimates with the assumption of flat priors empirically did not differ from REML estimates, applications of the Gibbs sampling with flat priors for variance components may yield a theoretically improper posterior distribution, which means the inferences would be based on nonexistent posterior distributions (Hobert and Casella, 1996). In practice, there have been many cases where flat priors for variance components were used, and reasonable posterior estimates were obtained empirically (Van Tassell and Van Vleck, 1996; Janss et al., 1997; Blasco et al., 1998). Wang et al. (1994) used the method of moment fit to derive priors for variance components from experimental data in order to avoid improper posterior. Hobert and Casella (1996) recommended very small parameter values for variance components. Roehle (1999)

used .01% of the phenotypic variance for each variance component. Use of the priors with the low probability mass led the marginal posterior distribution to be almost entirely determined by the data. Therefore, several sets of informative priors other than flat prior (G1) were constructed to examine their influence on the posterior means of parameters, and the parameter estimates were presented in table 3. Priors with the very small degree of belief (G2 and G3) led to posterior means close to G1 estimates without a significant difference ($p > 0.05$). However, when the degree of belief increased up to 10 from 3, the priors showed a significant influence on the posterior mean estimates. This impact was more clearly pronounced in the data for Y and LY where data sizes were smaller than those for L and LYM. There was no statistical significance ($p > 0.10$) for L data where data size was the most. The Bayesian treatment highlights the fact that prior knowledge as well as data become weighted contribution to posterior estimates. The prior tends to be overwhelmed or dominated by the likelihood as the size of data increase. In other words, the contribution from knowledge about priors is more important when the data information is scant than when it is plentiful (Gianola and Fernando, 1986). Although moderate degree of belief was used, the prior was influential to posterior estimate due to the relatively small-sized data in the current study.

IMPLICATIONS

Bayesian inference overcomes the problem on non-BLUP of breeding values when using REML variance component estimates. The Bayesian approach gives exact posterior densities of variance components while REML estimates of the variance components have unknown distributions for small data sets in this study. However,

Table 3. Marginal posterior means and standard deviations for parameters using Gibbs sampling with five sets of priors (G1-G5)¹

Breed ²	Parameter	G1	G2	G3	G4	G5
L	σ_a^2	1.046±.081 ^a	1.031±.083 ^a	1.041±0.084 ^a	1.008±0.076 ^a	1.049±.080 ^a
	σ_e^2	0.543±0.043 ^a	0.547±0.042 ^a	0.539±0.041 ^a	0.556±0.040 ^a	0.531±0.044 ^a
	h^2	0.661±0.035 ^a	0.653±0.034 ^a	0.659±0.036 ^a	0.644±0.034 ^a	0.663±0.036 ^a
Y	σ_a^2	0.759±0.130 ^{ab}	0.753±0.108 ^{ab}	0.761±0.117 ^{ab}	0.617±0.057 ^a	0.803±0.059 ^b
	σ_e^2	0.639±0.081 ^{ab}	0.646±0.077 ^{ab}	0.629±0.076 ^{ab}	0.738±0.056 ^a	0.615±0.071 ^b
	h^2	0.540±0.072 ^{ab}	0.538±0.065 ^{ab}	0.547±0.065 ^{ab}	0.453±0.059 ^a	0.564±0.061 ^b
LY	σ_a^2	1.336±0.205 ^a	1.327±0.182 ^a	1.340±0.189 ^a	0.933±0.158 ^b	1.244±0.173 ^a
	σ_e^2	0.349±0.105 ^a	0.359±0.080 ^a	0.370±0.090 ^a	0.579±0.076 ^b	0.396±0.086 ^a
	h^2	0.789±0.074 ^a	0.787±0.069 ^a	0.784±0.070 ^a	0.615±0.061 ^b	0.755±0.063 ^a
LYM	σ_a^2	0.878±0.117 ^a	0.902±0.120 ^a	0.909±0.115 ^a	0.768±0.124 ^a	0.911±0.100 ^a
	σ_e^2	0.638±0.072 ^{ab}	0.634±0.062 ^{ab}	0.628±0.058 ^{ab}	0.722±0.060 ^a	0.618±0.060 ^b
	h^2	0.577±0.058 ^a	0.587±0.056 ^a	0.591±0.050 ^a	0.513±0.052 ^a	0.594±0.047 ^a

¹ G1: flat prior (table 2); G2: IG prior with $\sigma_a^2=0.5$, $\sigma_e^2=1.0$ and shape parameter=4; G3: IG prior with $\sigma_a^2=1.0$, $\sigma_e^2=0.5$ and shape parameter=4; G4: IG prior with $\sigma_a^2=0.5$, $\sigma_e^2=1.0$ and shape parameter=10; G5: IG prior with $\sigma_a^2=1.0$, $\sigma_e^2=0.5$ and shape parameter=10. The numbers in the same row without the same suffix differ significantly ($p<0.10$).

² L: Landrace, Y: Yorkshire, and M: Chinese indigenous Min pig.

improper prior leads to improper posterior (Hobert and Casella, 1996). Especially, animal breeders often use flat priors for variance components because the mode of the marginal posterior density with the prior corresponds to REML estimator (Harville, 1977). Posterior estimates are sensitive to the priors with small size data, thus caution should be given with those priors. Without convinced prior information, a weak prior close to a flat one, i.e. a really small degree of belief was recommended.

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