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Bayesian Estimation of Heritability in Animal Breeding Experiments Under 2-way Nested Classification

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SUMMARY

Bayesian using GIBBS sampling (BUGS) algorithm to obtain numerical estimates of parameters of posterior distribution and variance components along with heritability (h^2) under 2-way nested random model has been used. Using Monte Carlo simulation, a comparison is made between the heritability estimates obtained under BUGS approach and traditional approaches like ANOVA, ML, REML for different family structures. The Bayesian approach is seen to be superior to traditional approaches for estimation of heritability under 2-way nested model.

Key words : Heritability, 2-way nested classification, BUGS, ANOVA, ML, REML.

1. Introduction

Heritability (h^2) is one of the most important genetic parameter, which measures the genetic variability, caused by differences in the genetic makeup of the individuals, out of the total variability existing in the population. Information on this parameter is a prerequisite to the planning of breeding programmes for plant and animal improvement. Such information can be obtained through sib analysis as a ratio of estimates of genetic variance to the total variance. Quite often in species like Poultry, Pig, Sheep and Goats, where a number of sires are mated to a set of dams chosen at random, produce several progeny. The data obtained from these progeny are nested first according to dams and then sires that leads to 2-way classification. While analyzing such classified data, frequently the estimates of heritability turn out to be negative. Thus to ensure that the estimates of variance components are always positive, an empirical procedure for obtaining non-negative estimate of h^2 using BUGS has been explored. Further, a comparison is made between the estimates obtained under BUGS and traditional approaches through Monte Carlo simulation.

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2. Model

The 2-way nested random linear model is given by

$$y_{ij} = s_i + d_{ij} + e_{ijk},\ i = 1, 2, \ldots, s;\ j = 1, 2, \ldots, d;\ k = 1, 2, \ldots, n$$

which can be written in matrix notation as

$$Y = (I_s \otimes 1_d \otimes 1_n)\,S + (I_s \otimes I_d \otimes 1_n)\,D + (I_s \otimes I_d \otimes I_n)\,e \qquad (2.1)$$

where, Y is a vector (sdn × 1) of the observations on the k^{th} (k = 1, 2, ..., n) progeny of j^{th} (j = 1, 2, ..., d) dam mated with i^{th} sire (i = 1, 2, ..., s), **S** is a vector (s × 1) of sire effect, $E[S] = \mu\, 1_s$, $E[SS'] = \sigma_s^2 I_s$, D is a vector (sd × 1) of effect of j^{th} dam mated with i^{th} sire, $E[D] = 0$, $E[DD'] = \sigma_d^2 I_{sd}$, e is the random term with $E[e] = 0$, $E[ee'] = \sigma_e^2 I_{sdn}$. Hence, the variance of Y is given by

$$V = \text{var}(Y) = V = (I_s \otimes J_d \otimes J_n)\sigma_s^2 + (I_s \otimes I_d \otimes J_n)\sigma_d^2 + (I_s \otimes I_d \otimes I_n)\sigma_e^2$$

1_n, I_n and J_n are n × 1 column vector of 1's, n × n identity matrix and n × n matrix of 1's respectively. σ_s^2, σ_d^2, σ_e^2 and n are scalars (>0). The estimate of heritability from sire component and (sire + dam) combined components can be obtained as a function of intra-class correlation coefficients 't_1' and 't_2' given by Fisher (1950) as

$$h_s^2 = \frac{4\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_d^2 + \hat{\sigma}_e^2} \qquad (2.2)$$

and

$$h_{s+d}^2 = \frac{2(\hat{\sigma}_s^2 + \hat{\sigma}_d^2)}{\hat{\sigma}_s^2 + \hat{\sigma}_d^2 + \hat{\sigma}_e^2} \qquad (2.3)$$

The estimate of variance components due to sire effect ($\hat{\sigma}_s^2$), dam effect ($\hat{\sigma}_d^2$) and random term ($\hat{\sigma}_e^2$) can be estimated by BUGS or traditional approaches.

3. Heritability Estimation by BUGS

Bayesian analysis of data under model (2.1) involves treating all of the parameters, including the variance components, as random. The joint distribution of the random variables $(\mu, S, D, \sigma_s^2, \sigma_d^2, \sigma_e^2))$ and data can be represented as

$$f(Y, S, D, \sigma_s^2, \sigma_d^2, \sigma_e^2) = f(Y/S, D, \sigma_e^2)\ f(S/\mu, \sigma_s^2)$$
$$f(D/\sigma_d^2) * f(\sigma_s^2) * f(\sigma_d^2) * f(\sigma_e^2)$$

Here it is assumed that

$$f(Y/\mu, S, D, \sigma_e^2) \sim N(\mu 1_{sdn}, V),\ f(S/\mu,\ \sigma_s^2) \sim N(\mu 1_s, \sigma_s^2 I_s)$$

and $$f(D/\sigma_d^2) \sim N(0, \sigma_d^2 I_d)$$

where μ, σ_s^2, σ_d^2 and σ_e^2 are again assumed as independent with prior distribution as $f(\mu) \sim N(\mu_0,\ \sigma_0^2)$, $f(\sigma_s^2) \sim IG(a_1, b_1)$, $f(\sigma_d^2) \sim IG(a_2, b_2)$, and $f(\sigma_e^2) \sim IG(a_3, b_3)$. Here, IG (.,.) denotes the Inverse Gamma distribution and μ_0, σ_0^2, a_1, b_1, a_2, b_2, a_3, b_3 are assumed known (chosen to correspond to diffuse prior). Rao and Sanjeev (2001) applied BUGS procedure to estimate heritability under one-way classification model using half-sib data. Bayesian inference of variance components, based on posterior distribution, requires ingenious numerical analysis or analytic approximation (Box and Tiao (1973)). In marked contrast to such sophisticated method, we use a Monte Carlo Markov Chain Method, Gibbs Sampling (Gelfand and Smith (1990), for summarizing the posterior distribution. For a set of k vector-valued random variables, *i. e.*, U_1, U_2, ..., U_k, the Gibbs sampler algorithm is as follows

- Start with an arbitrary set of values $U_1^{(0)}, U_2^{(0)}, ..., U_k^{(0)}$
- Draw
$$U_1^{(1)} \sim |f|(U_1/U_2^{(0)}, U_3^{(0)}, ..., U_k^{(0)})$$
$$U_2^{(1)} \sim |f|(U_2/U_1^{(1)}, U_3^{(0)}, ..., U_k^{(0)})$$
$$\vdots$$
$$U_k^{(1)} \sim |f|(U_k/U_1^{(1)}, U_2^{(1)}, ..., U_{k-1}^{(1)})$$
- Which consists of a single iteration
- Obtain $(U_1^{(i)}, U_2^{(i)}, ..., U_k^{(i)})$ after i such iterations
- m replications of the aforementioned i iterations produces m iid k tuples $(U_{1j}^{(i)}, U_{2j}^{(i)}, ..., U_{kj}^{(i)})$; (j = 1, 2, ..., m)
- From m iid k-tuples $(U_{1j}^{(i)}, U_{2j}^{(i)}, ..., U_{kj}^{(i)})$, the posterior density estimate for $f(U_s)$ is given by

$$[\hat{U}_s]_i = \frac{1}{m}\sum_{i=1}^{m} f(U_s/U_t = U_{tj}^{(i)}; t \neq s)$$

Subsequently, different statistics of interest, like posterior mean, standard deviation, etc. can be computed.

We begin with a set of starting values for $\mu, S, \sigma_s^2, \sigma_d^2, \sigma_e^2$ and then successively generate values from the conditional posterior distribution of each parameter, conditioning on the most recently generated values of the other parameters at each step.

To diagnose the convergence of the generated Gibbs sequence, we run multiple chains of Gibbs sampler from over-dispersed starting values and compute the Gelman and Rubin (1992) potential scale reduction factor ($\hat{R}^{1/2}$), which assess the between chain and within chain variation. Value of statistic $\hat{R}^{1/2}$ near one for the model parameters indicates that the Gibbs iterations are reasonably close to the stationary (posterior) distribution. From the posterior distribution of variance components, the estimates of variance components are worked out (as the posterior mean) and used to estimate the heritability using equations (2.2) and (2.3). Here, we choose the values of the parameters of the prior distributions as $\mu_0 = 0$, $\sigma_0^2 = 1 \times 10^{-10}$, $a_1 = b_1 = a_2 = b_2 = a_3 = b_3 = 0.001$. These chosen parameters of prior distribution for the variance components lead to a non-informative prior distribution and thus a proper posterior distribution. We consider three different Gibbs chains of length 2,50,000 each to obtain draws from the posterior distribution of the parameter given data with arbitrary chosen diversified starting values of μ, σ_s^2, σ_d^2 and σ_e^2. The initial 1,50,000 draws of each chain are discarded and then every 10^{th} draw is stored. So, the three chains give a posterior sample of 30,000 uncorrelated draws. It is observed that Gelman and Rubin (1992) potential scale reduction factor $\hat{R}^{1/2}$ for all the model parameters approached unity indicating the approximate convergence of Gibbs sequence. This was also confirmed by examining the plots of kernel density estimates for μ, σ_s^2, σ_d^2 and σ_e^2 based on 30,000 samples. The computations are made based on the programmes developed in WinBugs Version 1.4 (2002).

4. Simulation Study

In this section, the simulation procedure for generating data under model (2.1) is briefly described, for the purpose of comparing the Bayesian approach with traditional approaches like ANOVA, ML, REML (Searle *et al.* (1992)). Ronningen (1974) gave a general account of the use of Monte Carlo simulation techniques for statistico – biological models of interest in animal breeding. Ronningen (1974) procedure to simulate 2-way nested model is as follows

$$Y_{ijk} = \mu + \sigma_s s_i' + \sigma_d d_{ij}' + \sigma_e e_{ijk}' \qquad (4.1)$$

where s_i', d_{ij}', and e_{ijk}' are the standard random normal variates. The values of μ, σ_s, σ_d and σ_e are so chosen so as to give true heritability at levels 0.10, 0.25 and 0.50. In a 2-way nested data, if the estimation of h^2 of a trait with true value 0.10 is of interest, then to simulate data for such a population, we obtain the values of σ_s, σ_d and σ_e, from the relationship in (2.2). By considering

$h^2 = 0.10$ and $\sigma_s^2 + \sigma_d^2 + \sigma_e^2 = 1.0$, this resulted $\sigma_s = \sqrt{0.025}$, $\sigma_d = \sqrt{0.025}$ and $\sigma_e = \sqrt{1 - 0.05}$. Substituting these values in equation (4.1), data are generated for different sample sizes and family structures. Similarly data sets are simulated for medium (h^2 = 0.25) and high (h^2 = 0.50) heritability values. We also considered here a real data set, given in Narain *et al.* (1979), for comparison of h^2 estimates from BUGS and traditional approaches. The reference population is a large non-inbred flock of White Rock Chickens. Five sires are chosen at random and each sire mated to three females. The eight-week body weights of the progeny obtained was considered as the character of interest.

5. Results

The variance components are estimated from the Monte Carlo simulated data using BUGS and traditional approaches. In order to compare different approaches of heritability estimation, for a given family structure (s, d, n) and sample size, the data under 2-way nested classification are simulated, as described in Section 4.1, over 100 times. The estimate of h^2 is obtained from each simulated sample. Average of these estimates over the simulated samples is taken as the expected value of the estimator under traditional and Bayesian using Gibbs sampling approach. Deviation of the expected value from the population value provides the bias in the estimate. Variance of the estimates is determined by considering the estimates of all the simulated samples. The mean square error (MSE) is worked out from the relationship

$$\text{MSE}(h^2) = \text{Variance}(h^2) + \text{Bias}^2(h^2)$$

To compare the performance of the BUGS and traditional approaches, we used Cartesian graphs to plot the estimates obtained under different (s, d, n) combination and varying sample sizes: 50, 80, 120, 200 and 300. Separate graphs are given for sire and (sire + dam) components and also for different heritability levels. For convenience, the twelve (s, d, n) combinations (5, 5, 2), (8, 5, 2), (5, 4, 4), (10, 4, 2), (6, 10, 2), (10, 6, 2), (5, 10, 4), (10, 10, 2), (20, 5, 2), (10, 10, 3), (15, 10, 2) and (30, 5, 2) have been represented by assigning them the number codes 1 to 12 in that order. The graph depicts that for medium and high heritability (h^2 = 0.25 and 0.50), the (sire + dam) component estimates are closer to the population values, particularly, when BUGS approach is used. Whereas the performance of BUGS is comparable, in terms of bias, with the other approaches when the estimates obtained are from sire component and when the population heritability of the trait under consideration is low to medium. Further, the bias, sampling variance and MSE of h^2 estimates are presented in Tables 1 to 3. Perusal of Table 1 reveals that in the case of low heritability (h^2 = 0.1), estimates from sire component, the MSE is highest for the ANOVA method than others because of high sampling variance. The high sampling variance for ANOVA is due to the occurrence of around 40 percent of

Table 1. Bias, sampling variance (SV) and mean squared error (MSE) of heritability ($h^2 = 0.1$) under traditional and Bayesian approaches for different sample sizes and family structures

Sample Size	Structure	Herit-ability	REML		ML		ANOVA		Bayes	
			h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2
50	5×5×2	Bias	0.136	0.162	0.082	0.100	0.008	0.067	0.137	0.185
		SV	0.083	0.047	0.051	0.032	0.178	0.104	0.023	0.025
		MSE	0.102	0.073	0.058	0.042	0.178	0.108	0.042	0.059
80	8×5×2	Bias	0.102	0.068	0.070	0.026	-0.003	0.002	0.099	0.122
		SV	0.067	0.022	0.049	0.017	0.133	0.042	0.029	0.022
		MSE	0.078	0.026	0.054	0.018	0.133	0.042	0.039	0.037
	5×4×4	Bias	-0.047	-0.026	-0.075	-0.063	-0.093	-0.088	0.045	0.052
		SV	0.005	0.005	0.002	0.002	0.013	0.014	0.002	0.001
		MSE	0.008	0.006	0.008	0.006	0.022	0.021	0.004	0.004
	10×4×2	Bias	0.015	-0.025	-0.014	-0.046	-0.076	-0.117	0.029	0.101
		SV	0.023	0.013	0.017	0.009	0.067	0.036	0.005	0.012
		MSE	0.024	0.014	0.017	0.011	0.073	0.049	0.005	0.022
120	6×10×2	Bias	0.007	-0.001	-0.030	-0.029	-0.025	-0.043	0.053	0.076
		SV	0.014	0.006	0.009	0.004	0.025	0.012	0.010	0.009
		MSE	0.014	0.006	0.010	0.005	0.026	0.014	0.013	0.015
	10×6×2	Bias	0.005	-0.029	-0.020	-0.049	-0.041	-0.074	0.016	0.084
		SV	0.015	0.006	0.010	0.004	0.032	0.016	0.005	0.008
		MSE	0.015	0.007	0.011	0.006	0.034	0.022	0.005	0.015
200	5×10×4	Bias	-0.006	-0.026	-0.036	-0.046	-0.017	-0.049	0.024	0.022
		SV	0.013	0.004	0.008	0.003	0.016	0.008	0.008	0.004
		MSE	0.013	0.005	0.009	0.005	0.016	0.010	0.008	0.004
	10×10×2	Bias	-0.004	0.001	-0.025	-0.019	-0.010	-0.013	0.003	0.049
		SV	0.008	0.004	0.006	0.004	0.009	0.005	0.003	0.011
		MSE	0.008	0.004	0.007	0.004	0.009	0.005	0.003	0.014
	20×5×2	Bias	0.033	-0.006	0.020	-0.024	-0.014	-0.033	-0.013	0.038
		SV	0.046	0.010	0.040	0.009	0.067	0.015	0.008	0.006
		MSE	0.047	0.010	0.040	0.010	0.067	0.016	0.008	0.007
300	10×10×3	Bias	-0.001	-0.035	-0.021	-0.046	-0.006	-0.047	-0.002	0.032
		SV	0.006	0.003	0.005	0.003	0.007	0.004	0.003	0.007
		MSE	0.006	0.004	0.005	0.005	0.007	0.006	0.003	0.008
	15×10×2	Bias	0.003	-0.023	-0.015	-0.038	0.002	-0.028	-0.008	0.036
		SV	0.006	0.002	0.005	0.002	0.006	0.002	0.003	0.011
		MSE	0.006	0.002	0.005	0.003	0.006	0.003	0.004	0.012
	30×5×2	Bias	-0.019	-0.043	-0.029	-0.053	-0.037	-0.057	-0.021	0.037
		SV	0.012	0.003	0.011	0.002	0.017	0.003	0.004	0.002
		MSE	0.013	0.005	0.012	0.005	0.019	0.006	0.005	0.004

Table 2. Bias, sampling variance (SV) and mean squared error (MSE) of heritability ($h^2 = 0.25$) under traditional and Bayesian approaches for different sample sizes and family structures

Sample Size	Structure	Herit-ability	REML		ML		ANOVA		Bayes	
			h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2
50	5×5×2	Bias	0.032	0.050	-0.025	-0.013	-0.061	-0.028	0.087	0.119
		SV	0.102	0.060	0.070	0.044	0.181	0.122	0.054	0.039
		MSE	0.103	0.062	0.071	0.045	0.185	0.123	0.062	0.053
80	8×5×2	Bias	0.090	-0.016	0.038	-0.065	0.048	-0.055	-0.061	-0.008
		SV	0.150	0.033	0.116	0.028	0.191	0.043	0.007	0.016
		MSE	0.158	0.033	0.117	0.032	0.194	0.046	0.010	0.016
	5×4×4	Bias	-0.064	-0.098	-0.123	-0.148	-0.090	-0.149	0.004	-0.013
		SV	0.032	0.012	0.021	0.008	0.044	0.022	0.023	0.006
		MSE	0.036	0.022	0.036	0.030	0.052	0.045	0.023	0.006
	10×4×2	Bias	0.006	-0.106	-0.046	-0.138	-0.060	-0.178	-0.016	0.054
		SV	0.066	0.022	0.053	0.017	0.121	0.047	0.034	0.018
		MSE	0.066	0.033	0.056	0.036	0.125	0.078	0.034	0.021
120	6×10×2	Bias	-0.026	-0.093	-0.082	-0.128	-0.044	-0.128	-0.043	-0.012
		SV	0.049	0.014	0.035	0.011	0.059	0.023	0.017	0.016
		MSE	0.050	0.022	0.042	0.027	0.061	0.039	0.019	0.016
	10×6×2	Bias	0.009	-0.102	-0.034	-0.130	-0.014	-0.132	-0.014	0.037
		SV	0.051	0.015	0.040	0.011	0.065	0.024	0.034	0.021
		MSE	0.051	0.025	0.041	0.028	0.066	0.041	0.034	0.022
200	5×10×4	Bias	-0.030	-0.108	-0.082	-0.138	-0.036	-0.125	0.006	-0.017
		SV	0.038	0.011	0.026	0.008	0.041	0.015	0.044	0.015
		MSE	0.039	0.023	0.032	0.027	0.042	0.031	0.044	0.015
	10×10×2	Bias	-0.011	-0.079	-0.044	-0.103	-0.012	-0.092	-0.013	-0.002
		SV	0.028	0.008	0.023	0.007	0.028	0.009	0.028	0.020
		MSE	0.028	0.014	0.025	0.018	0.028	0.018	0.029	0.020
	20×5×2	Bias	0.015	-0.089	-0.007	-0.110	-0.009	-0.104	-0.030	-0.001
		SV	0.066	0.016	0.061	0.016	0.086	0.021	0.062	0.023
		MSE	0.066	0.024	0.061	0.028	0.086	0.032	0.063	0.023
300	10×10×3	Bias	0.020	-0.098	-0.014	-0.117	0.020	-0.106	0.019	0.007
		SV	0.013	0.005	0.012	0.005	0.013	0.005	0.018	0.019
		MSE	0.014	0.015	0.012	0.018	0.014	0.016	0.018	0.019
	15×10×2	Bias	0.011	-0.092	-0.014	-0.109	0.011	-0.095	-0.015	-0.015
		SV	0.015	0.003	0.013	0.003	0.015	0.004	0.018	0.022
		MSE	0.015	0.012	0.014	0.015	0.015	0.013	0.018	0.022
	30×5×2	Bias	0.014	-0.103	-0.003	-0.116	0.007	-0.113	-0.044	0.009
		SV	0.039	0.008	0.036	0.008	0.043	0.008	0.041	0.010
		MSE	0.039	0.019	0.037	0.021	0.043	0.021	0.043	0.010

Table 3. Bias, sampling variance (SV) and mean squared error (MSE) of heritability ($h^2 = 0.5$) under traditional and Bayesian approaches for different sample sizes and family structures

Sample Size	Structure	Herit-ability	REML		ML		ANOVA		Bayes	
			h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2	h_s^2	h_{s+d}^2
50	5×5×2	Bias	–0.003	–0.096	–0.093	–0.168	–0.046	–0.144	–0.006	0.042
		SV	0.176	0.079	0.126	0.059	0.237	0.129	0.134	0.084
		MSE	0.176	0.088	0.134	0.087	0.239	0.150	0.134	0.086
80	8×5×2	Bias	0.018	–0.157	–0.051	–0.212	–0.003	–0.176	–0.032	–0.054
		SV	0.140	0.035	0.117	0.033	0.167	0.045	0.144	0.071
		MSE	0.140	0.060	0.119	0.078	0.167	0.076	0.145	0.074
	5×4×4	Bias	–0.178	–0.263	–0.258	–0.323	–0.184	–0.296	–0.127	–0.093
		SV	0.051	0.019	0.034	0.014	0.054	0.027	0.046	0.022
		MSE	0.082	0.088	0.100	0.119	0.088	0.115	0.062	0.030
	10×4×2	Bias	–0.131	–0.293	–0.193	–0.332	–0.171	–0.348	–0.237	–0.084
		SV	0.070	0.024	0.059	0.019	0.111	0.044	0.031	0.050
		MSE	0.087	0.110	0.097	0.130	0.140	0.165	0.088	0.057
120	6×10×2	Bias	–0.074	–0.241	–0.151	–0.285	–0.077	–0.266	–0.086	–0.092
		SV	0.123	0.034	0.093	0.027	0.124	0.043	0.070	0.038
		MSE	0.129	0.091	0.116	0.108	0.130	0.114	0.077	0.047
	10×6×2	Bias	–0.074	–0.241	–0.151	–0.285	–0.077	–0.266	–0.086	–0.092
		SV	0.123	0.034	0.093	0.027	0.124	0.043	0.070	0.038
		MSE	0.129	0.091	0.116	0.108	0.130	0.114	0.077	0.047
200	5×10×4	Bias	–0.072	–0.248	–0.155	–0.291	–0.074	–0.254	–0.089	–0.065
		SV	0.094	0.028	0.067	0.021	0.096	0.030	0.095	0.032
		MSE	0.100	0.089	0.091	0.106	0.102	0.095	0.103	0.037
	10×10×2	Bias	–0.021	–0.211	–0.072	–0.240	–0.022	–0.224	–0.062	–0.078
		SV	0.070	0.018	0.061	0.017	0.070	0.021	0.053	0.040
		MSE	0.071	0.063	0.067	0.075	0.071	0.071	0.057	0.046
	20×5×2	Bias	0.016	–0.211	–0.012	–0.233	0.005	–0.220	–0.155	–0.069
		SV	0.102	0.026	0.094	0.025	0.116	0.030	0.056	0.045
		MSE	0.102	0.071	0.094	0.079	0.116	0.078	0.080	0.049
300	10×10×3	Bias	0.059	–0.201	0.004	–0.230	0.059	–0.206	0.080	–0.006
		SV	0.024	0.008	0.021	0.008	0.024	0.008	0.025	0.032
		MSE	0.027	0.049	0.021	0.061	0.027	0.051	0.031	0.032
	15×10×2	Bias	0.020	–0.208	–0.016	–0.230	0.020	–0.212	0.029	–0.058
		SV	0.040	0.009	0.036	0.008	0.041	0.011	0.051	0.047
		MSE	0.041	0.052	0.037	0.061	0.041	0.056	0.052	0.050
	30×5×2	Bias	0.012	–0.229	–0.010	–0.244	0.011	–0.235	–0.141	–0.024
		SV	0.049	0.010	0.047	0.010	0.049	0.010	0.033	0.020
		MSE	0.049	0.063	0.047	0.070	0.049	0.065	0.053	0.020

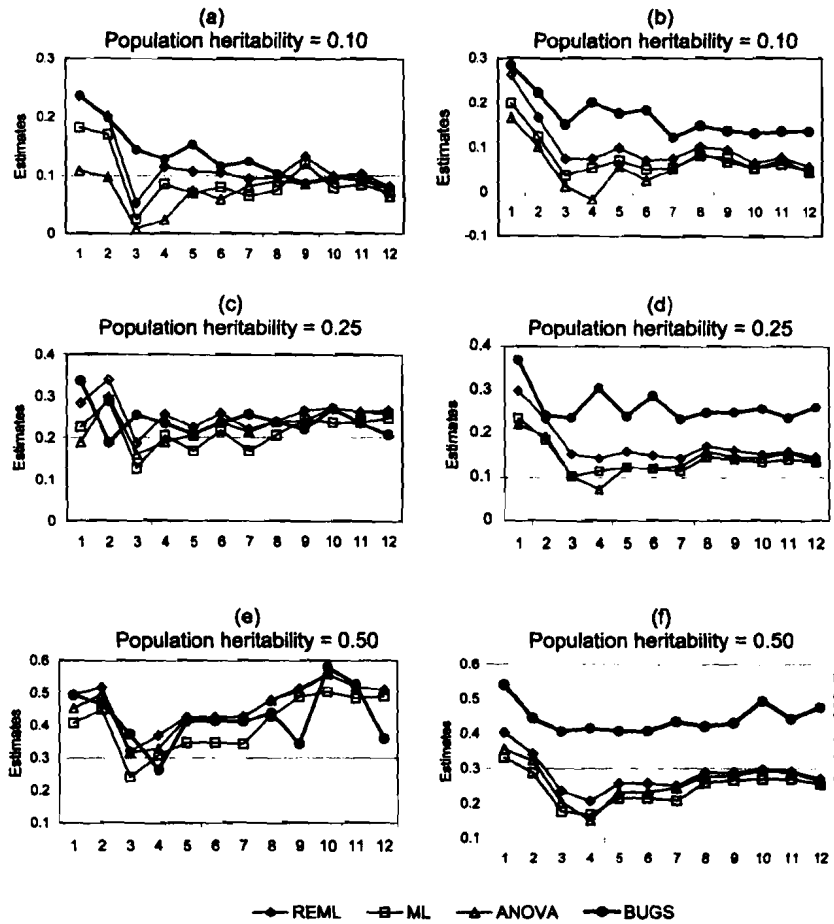

Fig 1. Graphs showing the estimates of sire component (a, c, e) and (sire + dam) component (b, d, f) heritability under different approaches and family structures at three levels of heritability (h^2).

negative estimates under all the family structures. The negative estimates of ANOVA method are truncated to zero in ML as well as REML methods, due to which the sampling variance gets reduced as compared to ANOVA, in turn reduced the MSE. Thus, the true picture of heritability is not revealed by these traditional approaches. Whereas, in case of Bayesian approach all the estimates are non-negative and the sampling variance as well as MSE is found to be minimum, irrespective of sample size and family structure. It is further observed that the MSE of the estimates, under (sire + dam) component, are found to be higher than sire component of heritability estimates. When $h^2 = 0.25$ and 0.50, a

similar trend in the performance of Bayes method over other methods is observed from Tables 2 and 3.

The estimates of variance components and h^2 obtained from real data under BUGS and traditional approaches are given in Table 4. From ANOVA method dam component of variance comes out to be highly negative and from ML and REML it is truncated to zero. Because of this the estimates of heritability under sire and (sire + dam) components comes out to be entirely different and thus becomes unreliable. As the simulation study shows that Bayesian approach is more reliable than others, the estimates of h^2 under sire and (sire + dam) components are expected to be drawn from a population with medium heritability value.

Table 4. Estimates of heritability from real data under different methods of estimation

Method of estimation	Variance Component Estimates			Heritability Estimates	
	$\hat{\sigma}_s^2$	$\hat{\sigma}_d^2$	$\hat{\sigma}_e^2$	$\hat{h}_s^2$	$\hat{h}_{s+d}^2$
ANOVA	1015.240	-425.040	6664.900	0.559	0.162
ML	699.290	0.000	6346.240	0.397	0.198
REML	1050.610	0.000	6346.140	0.568	0.284
BUGS	642.600	691.200	6777.000	0.340	0.328

Finally, we conclude that the Bayesian method of estimation is suitable for estimating h^2 under 2-way nested mating design as compared to traditional methods, particularly for small sample data. Further, for low heritability values one should go for estimating heritability from sire component whereas for medium heritability values it can be estimated by either sire or (sire + dam) component. For high heritability values it is preferable to estimate heritability from (sire + dam) components.

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