

Bayesian Regression as an Alternative Implementation of Genomic-Enhanced Genetic Evaluation

R.L. Fernando¹ D. Garrick^{1,2}

¹Department of Animal Science
Iowa State University

²Institute of Veterinary, Animal and Biomedical Sciences
Massey University, Palmerston North, New Zealand

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Motivation

- Genotypes available only on a small subset of population
- Phenotype and pedigree information available on a much larger subset
- Single-step BLUP: optimal method to combine all information
- Bayesian regression:
 - attractive features: mixture models, richer analyses, computing time linear in n
 - approximate selection index methods used to combine the two sources
- Objective: Extend single-step idea to Bayesian regression

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Marker Effects Model

Meuwissen et al. Prediction of total genetic value using genome-wide dense marker maps. Genetics (2001)

$$y = X\beta + M\alpha + e$$

- M : Marker covariates (SNPs)
- α : random marker effects ($\mathbf{0}, I\sigma_\alpha^2$)

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Breeding Value Model

- Let $\mathbf{g} = \mathbf{M}\alpha$

- Then

$$\begin{aligned} \mathbf{y} &= \mathbf{X}\beta + \mathbf{M}\alpha + \mathbf{e} \\ &= \mathbf{X}\beta + \mathbf{g} + \mathbf{e} \end{aligned}$$

- In both models:

- $E(\mathbf{y}) = \mathbf{X}\beta$
- $Var(\mathbf{y}) = \mathbf{M}\mathbf{M}'\sigma_{\alpha}^2 + \mathbf{I}\sigma_e^2$

- So, models are equivalent (Henderson, 1984)

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Theory

- Suppose \mathbf{g} is partitioned as

$$\mathbf{g} = \begin{bmatrix} \mathbf{g}_1 \\ \mathbf{g}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{g}_1 \\ \mathbf{M}_2\alpha \end{bmatrix}$$

- \mathbf{g}_1 are BVs of the animals with missing genotypes \mathbf{M}_1
- \mathbf{g}_2 are BVs of those with observed genotypes \mathbf{M}_2 .
- Following Legarra et al. (2009) the vector \mathbf{g}_1 is written as

$$\begin{aligned} \mathbf{g}_1 &= \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{g}_2 + (\mathbf{g}_1 - \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{g}_2) \\ &= \hat{\mathbf{g}}_1 + \epsilon \end{aligned}$$

- ϵ is uncorrelated with \mathbf{g}_2
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- Conditional covariances:

- $Var(\mathbf{g}_2|\mathbf{M}_2) = \mathbf{M}_2\mathbf{M}'_2\sigma_\alpha^2$
- $Var(\mathbf{g}_1|\mathbf{M}_2) = \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{M}_2\mathbf{M}'_2\mathbf{A}_{22}^{-1}\mathbf{A}_{21}\sigma_\alpha^2 + (\mathbf{A}_{11} - \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{A}_{21})\sigma_g^2$
- $Cov(\mathbf{g}_1, \mathbf{g}_2) = \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{M}_2\mathbf{M}'_2\sigma_\alpha^2$
- σ_α^2 is the variance of marker effects
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So,

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 Var(\mathbf{g}|\mathbf{M}_2) &= \begin{bmatrix} \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{G}\mathbf{A}_{22}^{-1}\mathbf{A}_{21} + \mathbf{A}_{11} - \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{A}_{21}, & \mathbf{A}_{12}\mathbf{A}_{22}^{-1}\mathbf{G} \\ \mathbf{G}\mathbf{A}_{22}^{-1}\mathbf{A}_{21}, & \mathbf{G} \end{bmatrix} \sigma_g^2 \\
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- where $\mathbf{G} = \mathbf{M}_2\mathbf{M}'_2 \frac{\sigma_\alpha^2}{\sigma_g^2}$, or $\mathbf{G} = \frac{\mathbf{M}_2\mathbf{M}'_2}{\sum 2p_jq_j}$

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Model and MME

- Model

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{g} + \mathbf{e}$$

- MME:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{H}^{-1} \frac{\sigma_e^2}{\sigma_g^2} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{g}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix}$$

- Inverse of \mathbf{H} :

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$

Model

- Marker effects model for missing genotypes:

$$\begin{aligned}
 \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} &= \begin{bmatrix} \mathbf{X}_1 \\ \mathbf{X}_2 \end{bmatrix} \boldsymbol{\beta} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{g}_1 \\ \mathbf{g}_2 \end{bmatrix} + \mathbf{e} \\
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 &= \begin{bmatrix} \mathbf{X}_1 \\ \mathbf{X}_2 \end{bmatrix} \boldsymbol{\beta} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \hat{\mathbf{M}}_1 \boldsymbol{\alpha} + \boldsymbol{\epsilon} \\ \mathbf{M}_2 \boldsymbol{\alpha} \end{bmatrix} + \mathbf{e} \\
 &= \mathbf{X} \boldsymbol{\beta} + \mathbf{W} \boldsymbol{\alpha} + \mathbf{U} \boldsymbol{\epsilon} + \mathbf{e}
 \end{aligned}$$

$$\mathbf{U} = \begin{bmatrix} \mathbf{Z}_1 \\ \mathbf{0} \end{bmatrix}, \quad \mathbf{X} = \begin{bmatrix} \mathbf{X}_1 \\ \mathbf{X}_2 \end{bmatrix} \quad \text{and} \quad \mathbf{W} = \begin{bmatrix} \mathbf{W}_1 = \mathbf{Z}_1 \hat{\mathbf{M}}_1 \\ \mathbf{W}_2 = \mathbf{Z}_2 \mathbf{M}_2 \end{bmatrix}$$

- Impute missing genotypes in parallel:

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MME

- The MME for BayesC with $\pi = 0$ are

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{W} & \mathbf{X}'_1\mathbf{Z}_1 \\ \mathbf{W}'\mathbf{X} & \mathbf{W}'\mathbf{W} + \mathbf{I} \frac{\sigma_e^2}{\sigma_\alpha^2} & \mathbf{W}'_1\mathbf{Z}_1 \\ \mathbf{Z}'_1\mathbf{X}_1 & \mathbf{Z}'_1\mathbf{W}_1 & \mathbf{Z}'_1\mathbf{Z}_1 + \mathbf{A}^{11} \frac{\sigma_e^2}{\sigma_g^2} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\alpha} \\ \hat{\epsilon} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{W}'\mathbf{y} \\ \mathbf{Z}'_1\mathbf{y}_1 \end{bmatrix}$$

- $\tilde{\mathbf{g}} = \begin{bmatrix} \hat{\mathbf{M}}_1 \\ \mathbf{M}_2 \end{bmatrix} \hat{\alpha} + \mathbf{U}\hat{\epsilon}$

Gibbs Sampling of α_j

- Full-conditional posterior for α_j : Normal with mean $\hat{\alpha}_j$ and variance

$$\frac{\sigma_e^2}{(\mathbf{w}'_i \mathbf{w}_i + \sigma_e^2 / \sigma_\alpha^2)}$$

- solve 1×1 MME for each marker covariate
- $$\hat{\alpha}_j = \frac{\mathbf{w}'_i \tilde{\mathbf{y}}_i}{\frac{\sigma_e^2}{(\mathbf{w}'_i \mathbf{w}_i + \sigma_e^2 / \sigma_\alpha^2)}}$$
- $$\tilde{\mathbf{y}}_i = \mathbf{y} - \mathbf{X}\boldsymbol{\beta} - \sum_{j \neq i} \mathbf{w}_j \alpha_j - \mathbf{U}\boldsymbol{\epsilon}$$
- Efficient computation of $rhs_i = \mathbf{w}'_i \tilde{\mathbf{y}}_i$:
 - $\hat{\mathbf{y}} = (\mathbf{y} - \mathbf{X}\boldsymbol{\beta} - \mathbf{W}\boldsymbol{\alpha} - \mathbf{U}\boldsymbol{\epsilon})$
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 - update: $\hat{\mathbf{y}} = \hat{\mathbf{y}} + \mathbf{w}_i (\alpha_i^{[old]} - \alpha_i^{[new]})$
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 - update:
$$\hat{\mathbf{y}} = \hat{\mathbf{y}} + \mathbf{w}_i (\alpha_i^{[old]} - \alpha_i^{[new]})$$
- Use MPI to compute $\mathbf{w}'_i \hat{\mathbf{y}}$ and update $\hat{\mathbf{y}}$ in parallel

Use of MPI

- Lonestar Linux cluster: 12 cores with 24G shared memory per node (1,888 nodes)
- $n = 10$ million, $k = 500$, BayesC with $\pi = 0$, 100 samples
 - single core, took 1662 seconds
 - 192 cores across 16 nodes, took 11 seconds: speed up = 151 times
- $n = 10$ million, $k = 50K$, BayesC with $\pi = 0$, 100 samples
 - 2,400 cores across 200 nodes, took 254 seconds
 - speed up = 654
 - 40k samples will take 28 hours
- Further speed up possible by using multithreading (open MP) within nodes

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Gibbs Sampling of ϵ

- Full-conditional posterior for ϵ : Normal with
 - mean $\tilde{\epsilon}$ that is solution to:

$$(\mathbf{Z}'_1 \mathbf{Z}_1 + \mathbf{A}^{11} \frac{\sigma_e^2}{\sigma_g^2}) \tilde{\epsilon} = \mathbf{Z}'_1 (\mathbf{y}_1 - \mathbf{X}_1 \beta - \mathbf{W}_1 \alpha)$$

- covariance matrix:
$$(\mathbf{Z}'_1 \mathbf{Z}_1 + \mathbf{A}^{11} \frac{\sigma_e^2}{\sigma_g^2})^{-1} \sigma_e^2$$
- Blocking-Gibbs sampler (Garcia-Cortes and Sorensen, 1996)
 - solve MME by iteration
 - iteration can be parallelized

Alternate Sampler

- Interest is only on α and ϵ is a nuisance parameter that is eliminated from MME
- MME

$$\begin{bmatrix} \mathbf{X}'_1 \mathbf{P} \mathbf{X}_1 + \mathbf{X}'_2 \mathbf{X}_2 & \mathbf{X}'_1 \mathbf{P} \mathbf{W}_1 + \mathbf{X}'_2 \mathbf{W}_2 \\ \mathbf{W}'_1 \mathbf{P} \mathbf{X}_1 + \mathbf{W}'_2 \mathbf{X}_2 & \mathbf{W}'_1 \mathbf{P} \mathbf{W}_1 + \mathbf{W}'_2 \mathbf{W}_2 + \mathbf{I} \frac{\sigma_\epsilon^2}{\sigma_\alpha^2} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\alpha} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'_1 \mathbf{P} \mathbf{y}_1 + \mathbf{X}'_2 \mathbf{y}_2 \\ \mathbf{W}'_1 \mathbf{P} \mathbf{y}_1 + \mathbf{W}'_2 \mathbf{y}_2 \end{bmatrix}$$

- $\mathbf{P} = \mathbf{I} - \mathbf{Z}_1 (\mathbf{Z}'_1 \mathbf{Z}_1 + \mathbf{A}^{11} \frac{\sigma_\epsilon^2}{\sigma_\alpha^2})^{-1} \mathbf{Z}'_1$
- can parallelize setup of MME
- $rhs_i = r_i - \mathbf{C}'_i \theta + \mathbf{C}_{ii} \theta_i$
 - computing time independent of n
- Further efficiencies are possible when π is close to one

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Alternate Sampler with π Close to One

- Set: $\theta = \mathbf{0}$
- Recall: $rhs_i = r_i - \mathbf{C}_i' \theta + \mathbf{C}_{ii} \theta_i$
- So, initially $rhs = r$
- When non-null θ_i is sampled, update rhs as:
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Parallel Setup of MME

- Recall, MME:

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- Let $\mathbf{S} = \mathbf{W}_2$. Then,

$$\mathbf{W}'_2 \mathbf{W}_2 = \sum_i^c \mathbf{S}'_i \mathbf{S}_i$$

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Computing $W_1'PW_1$

Two steps:

- 1 Compute $B = PW_1$

- 1 $b_i = W_{1i} - Z_1(Z_1'Z_1 + A^{11}\frac{\sigma_e^2}{\sigma_g^2})^{-1}Z_1'W_{1i}$

- 2 Second term of b_i can be computed as Z_1q_i , where q_i is the solution to

$$(Z_1'Z_1 + A^{11}\frac{\sigma_e^2}{\sigma_g^2})q_i = Z_1'W_{1i}$$

- 2 Compute $W_1'PW_1 = W_1'B$ as

$$W_1'B = \sum_i^c T_i'B_i,$$

where $T = W_1$

Computing $\mathbf{W}'_1 \mathbf{P} \mathbf{W}_1$

Two steps:

- 1 Compute $\mathbf{B} = \mathbf{P} \mathbf{W}_1$

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- 2 Compute $\mathbf{W}'_1 \mathbf{P} \mathbf{W}_1 = \mathbf{W}'_1 \mathbf{B}$ as

$$\mathbf{W}'_1 \mathbf{B} = \sum_i^c \mathbf{T}'_i \mathbf{B}_i,$$

where $\mathbf{T} = \mathbf{W}_1$

Summary

- When $n > k$, marker effects model more efficient
- Missing genotypes are “imputed”
- Errors of imputation (ϵ) are included in model
- MME with ϵ eliminated
 - can be setup in parallel
 - sampling β and α are independent of n
- Do not need \mathbf{G} or its inverse!

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- NIH Grant R01GM099992
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Equivalent Models

- Breeding value model
 - Nejati-Javaremi, A. and Smith, C. and Gibson, J. P., "Effect of total allelic relationship on accuracy of evaluation and response to selection", J. Anim. Sci. 75 (1997)
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