Bayesian Methods in Genome Association Studies

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Outline of Part I

Outline of Part II

Bayesian Regression Models

- Normal
- Student-t
- Mixture Models

Simulations

Part I

Bayesian Inference: Theory

Bayes Theorem

The conditional probability of X given Y is

$$\Pr(X|Y) = \frac{\Pr(X,Y)}{\Pr(Y)} = \frac{\Pr(Y|X)\Pr(X)}{\Pr(Y)}$$

where $\Pr(X,Y)$ is the joint probability of X and Y, $\Pr(X)$ is the probability of X, and $\Pr(Y)$ is the probability of Y.

Conditional Probability by Example

Joint distribution of smoking and lung cancer in a hypothetical population of 1,000,000:

		Smoking: Yes	Smoking: No	
Lung Cancer	Yes	42,500	7,500	50,000
	No	207,500	742,500	950,000
		250,000	750,000	

Question: What is the relative frequency of lung cancer among smokers?

Answer: $\frac{42{,}500}{250{,}000} = 0.17$

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Conditional Probability by Example

- As explained below, this relative frequency is also the conditional probability of lung cancer given smoking.
  - The frequentist definition of probability of an event is the limiting value of its relative frequency in a large number of trials.
  - Suppose we sample with replacement individuals from the 250,000 smokers and compute the relative frequency of lung cancer incidence.
  - It can be shown that as the sample size goes to infinity, this relative frequency will approach $\frac{42{,}500}{250{,}000} = 0.17$.
- This conditional probability is usually written as $\frac{42{,}500/1{,}000{,}000}{250{,}000/1{,}000{,}000} = 0.17$.
- The ratio in the numerator is joint probability of smoking and lung cancer, and the ratio in the denominator is the marginal probability of smoking.

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Meaning of Probability in Bayesian Inference

- In the frequency approach, probability is a limiting frequency
- In Bayesian inference, probabilities are used to quantify your beliefs or knowledge about possible values of parameters
  - What is the probability that $h^2 > 0.5$?
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Essentials of Bayesian Inference

- Prior probabilities quantify beliefs about parameters before the data are analyzed
- Parameters are related to the data through the model or "likelihood", which is the conditional probability density for the data given the parameters
- The prior and the likelihood are combined using Bayes theorem to obtain posterior probabilities, which are conditional probabilities for the parameters given the data
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Bayes Theorem in Bayesian Inference

- Let $f(\theta)$ denote the prior probability density for θ
- Let $f(\boldsymbol{y}|\theta)$ denote the likelihood
- Then, the posterior probability of θ is:

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\begin{aligned}
f(\theta|\boldsymbol{y}) &= \frac{f(\boldsymbol{y}|\theta)f(\theta)}{f(\boldsymbol{y})} \\
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Computing posteriors

- Often no closed form for $f(\boldsymbol{\theta}|\boldsymbol{y})$
- Further, even if computing $f(\boldsymbol{\theta}|\boldsymbol{y})$ is feasible, obtaining $f(\theta_i|\boldsymbol{y})$ would require integrating over many dimensions
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Gibbs sampler

- Want to draw samples from $f(x_1, x_2, \ldots, x_n)$
- Even though it may be possible to compute $f(x_1, x_2, \ldots, x_n)$, it is difficult to draw samples directly from $f(x_1, x_2, \ldots, x_n)$
- Gibbs:
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Inference from Markov chain

Can show that samples obtained from the Markov chain can be used to draw inferences from $f(x_1, x_2, \ldots, x_n)$ provided the chain is:

- Irreducible: can move from any state i to any other state j
- Positive recurrent: return time to any state has finite expectation
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Example

Let $f(\boldsymbol{x})$ be a bivariate normal density with means

$$\mu' = \begin{bmatrix} 1 & 2 \end{bmatrix}$$

and covariance matrix

$$\boldsymbol{V} = \begin{bmatrix} 1 & 0.5 \\ 0.5 & 2.0 \end{bmatrix}$$

Suppose we do not know how to draw samples from $f(\boldsymbol{x})$, but know how to draw samples from $f(x_i|x_j)$, which is univariate normal with mean:

$$\mu_{i.j} = \mu_i + \frac{v_{ij}}{v_{jj}}(x_j - \mu_j)$$

and variance

$$v_{i.j} = v_{ii} - \frac{v_{ij}^2}{v_{jj}}$$

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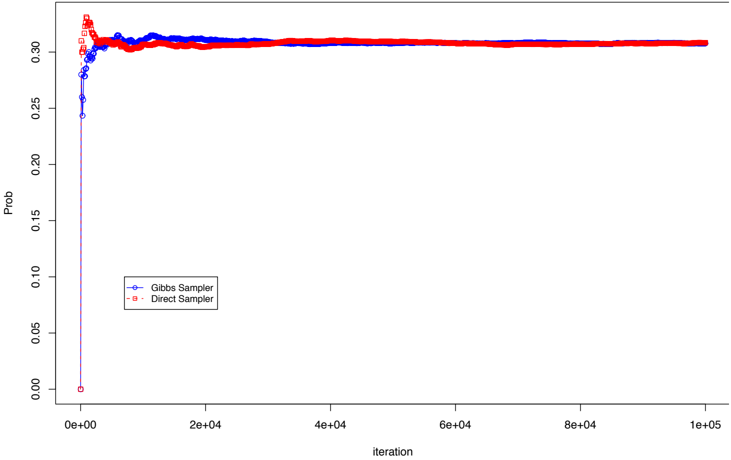

Metropolis-Hastings sampler

- Sometimes may not be able to draw samples directly from $f(x_i|\boldsymbol{x}_{i\_})$
- Convergence of the Gibbs sampler may be too slow
- Metropolis-Hastings (MH) for sampling from $f(x)$:
  - a candidate sample, y, is drawn from a proposal distribution $q(y|x^{t-1})$
  - $$x^t = \begin{cases} y & \text{with probability } \alpha \\ x^{t-1} & \text{with probability } 1-\alpha \end{cases}$$
  - $$\alpha = \min(1, \frac{f(y)q(x^{t-1}|y)}{f(x^{t-1})q(y|x^{t-1})})$$
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Proposal distributions

Two main types:

- Approximations of the target density: $f(x)$
  - Not easy to find approximation that is easy to sample from
  - High acceptance rate is good!
- Random walk type: stay close to the previous sample
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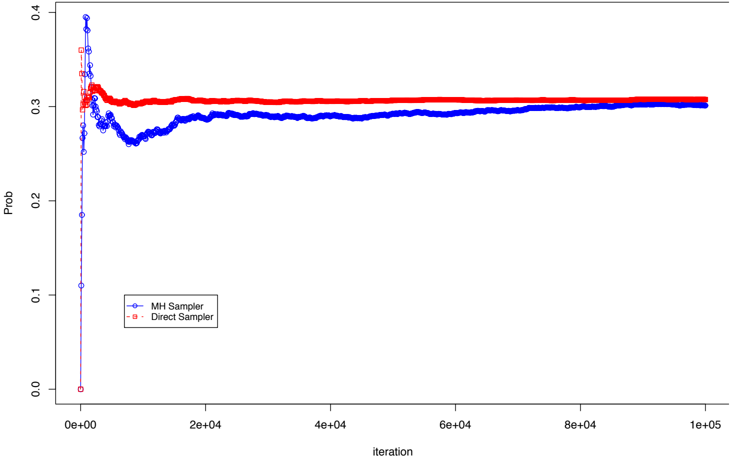
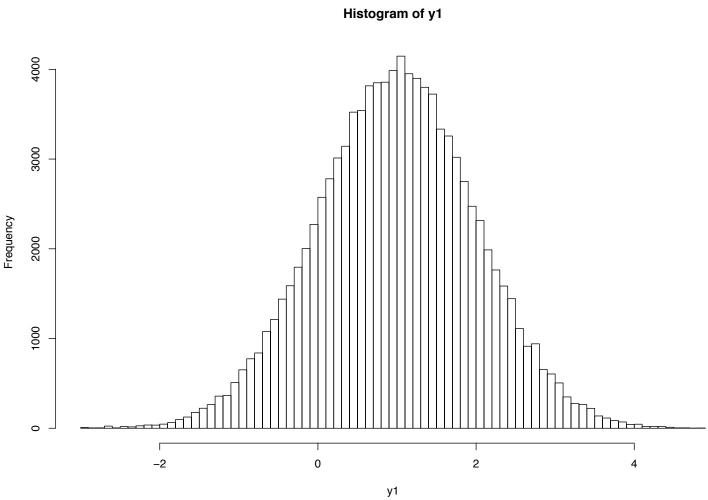


Distribution of y_1 Sampled Using MH



Part II

Bayesian Inference: Application to Whole Genome Analyses

Model

Model:

$$y_i = \mu + \sum_j X_{ij}\alpha_j + e_i$$

Priors:

- $\mu \propto$ constant (not proper, but posterior is proper)
- $(e_i|\sigma_e^2) \sim (\text{iid})\text{N}(0, \sigma_e^2)$; $\sigma_e^2 \sim \nu_e S_e^2 \chi_{\nu_e}^{-2}$
- Consider several different priors for α_j

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Normal

- Prior: $(\alpha_j|\sigma_\alpha^2) \sim$ (iid)N$(0, \sigma_\alpha^2)$; σ_α^2 is known
- What is σ_α^2?
- Assume the QTL genotypes are a subset of those available for the analysis
  - Then, the genotypic value of i can be written as:

$$g_i = \mu + \boldsymbol{x}_i' \boldsymbol{\alpha}$$

  - Note that α is common to all i
  - Thus, the variance of g_i comes from $\boldsymbol{x}_i'$ being random
- So, σ_α^2 is not the genetic variance at a locus
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Relationship of σ_α^2 to genetic variance

Assume loci with effect on trait are in linkage equilibrium. Then, the additive genetic variance is

$$V_A = \sum_j^k 2p_jq_j\alpha_j^2,$$

where $p_j = 1 - q_j$ is gene frequency at SNP locus j.
Letting $U_j = 2p_jq_j$ and $V_j = \alpha_j^2$,

$$V_A = \sum_j^k U_jV_j$$

For a randomly sampled locus, covariance between U_j and V_j is

$$C_{UV} = \frac{\sum_j U_jV_j}{k} - (\frac{\sum_j U_j}{k})(\frac{\sum_j V_j}{k})$$

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Rearranging the previous expression for C_{UV} gives

$$\sum_j U_j V_j = kC_{UV} + (\sum_j U_j)(\frac{\sum_j V_j}{k})$$

So,

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Letting $\sigma_\alpha^2 = \frac{\sum_j \alpha_j^2}{k}$ gives

$$V_A = kC_{UV} + (\sum_j 2p_j q_j)\sigma_\alpha^2$$

and,

$$\sigma_\alpha^2 = \frac{V_A - kC_{UV}}{\sum_j 2p_j q_j}$$

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Blocked Gibbs sampler

- Let $\boldsymbol{\theta}' = [\mu, \boldsymbol{\alpha}']$
- Can show that $(\theta|\boldsymbol{y}, \sigma_e^2) \sim \mathrm{N}(\hat{\theta}, \boldsymbol{C}^{-1}\sigma_e^2)$
- $$\hat{\theta} = \boldsymbol{C}^{-1}\boldsymbol{W}'\boldsymbol{y}; \quad \boldsymbol{W} = [\mathbf{1}, \boldsymbol{X}]$$
- $$\boldsymbol{C} = \begin{bmatrix} \mathbf{1}'\mathbf{1} & \mathbf{1}'\boldsymbol{X} \\ \boldsymbol{X}'\mathbf{1} & \boldsymbol{X}'\boldsymbol{X} + \boldsymbol{I}\frac{\sigma_e^2}{\sigma_\alpha^2} \end{bmatrix}$$
- Blocked Gibbs sampler
  - García-Cortés and Sorensen (1996, GSE 28:121-126)
  - *Likelihood, Bayesian and MCMC Methods* $\cdots$ (LBMMQG, Sorensen and Gianola, 2002)

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- Can show that $(\boldsymbol{\theta}|\boldsymbol{y}, \sigma_e^2) \sim \mathrm{N}(\hat{\boldsymbol{\theta}}, \boldsymbol{C}^{-1}\sigma_e^2)$
- $$\hat{\theta} = \boldsymbol{C}^{-1}\boldsymbol{W}'\boldsymbol{y}; \quad \boldsymbol{W} = [\boldsymbol{1}, \boldsymbol{X}]$$
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Full conditionals for single-site Gibbs

- $(\mu|\boldsymbol{y},\boldsymbol{\alpha},\sigma_e^2) \sim \mathrm{N}(\frac{\mathbf{1}'(\boldsymbol{y}-\boldsymbol{X\alpha})}{n},\frac{\sigma_e^2}{n})$
- $(\alpha_j|\boldsymbol{y},\mu,\boldsymbol{\alpha}_{j\_},\sigma_e^2) \sim \mathrm{N}(\hat{\alpha}_j,\frac{\sigma_e^2}{c_j})$
  - $$\hat{\alpha}_j = \frac{\boldsymbol{x}_j'\boldsymbol{w}}{c_j}$$
  - $$\boldsymbol{w} = \boldsymbol{y} - \mathbf{1}\mu - \sum_{j'\neq j} \boldsymbol{x}_{j'}\alpha_{j'}$$
  - $$c_j = (\boldsymbol{x}_j'\boldsymbol{x}_j + \frac{\sigma_e^2}{\sigma_\alpha^2})$$
- $(\sigma_e^2|\boldsymbol{y},\mu,\boldsymbol{\alpha}) \sim [(\boldsymbol{y}-\boldsymbol{W\theta})'(\boldsymbol{y}-\boldsymbol{W\theta})+\nu_e S_e^2]\chi^{-2}_{(\nu_e+n)}$

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Derive: full conditional for α_j

From Bayes' Theorem,

$$f(\alpha_j|\boldsymbol{y},\mu,\boldsymbol{\alpha}_{j\_},\sigma_e^2) = \frac{f(\alpha_j,\boldsymbol{y},\mu,\boldsymbol{\alpha}_{j\_},\sigma_e^2)}{f(\boldsymbol{y},\mu,\boldsymbol{\alpha}_{j\_},\sigma_e^2)}$$

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$$-\frac{1}{2\sigma_e^2}\{\boldsymbol{w}'\boldsymbol{w} - 2\boldsymbol{x}_j'\boldsymbol{w}\alpha_j + [\boldsymbol{x}_j'\boldsymbol{x}_j + \frac{\sigma_e^2}{\sigma_\alpha^2}]\alpha_j^2\}$$

Completing the square in this expression with respect to α_j gives

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From Bayes' theorem,

$$f(\sigma_e^2|\boldsymbol{y}, \mu, \boldsymbol{\alpha}) = \frac{f(\sigma_e^2, \boldsymbol{y}, \mu, \boldsymbol{\alpha})}{f(\boldsymbol{y}, \mu, \boldsymbol{\alpha})}$$

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So,

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Alternative view of Normal prior

Consider fixed linear model:

$$\boldsymbol{y} = \mathbf{1}\mu + \boldsymbol{X}\boldsymbol{\alpha} + \boldsymbol{e}$$

This can be also written as

$$\boldsymbol{y} = \begin{bmatrix} \mathbf{1} & \boldsymbol{X} \end{bmatrix} \begin{bmatrix} \mu \\ \alpha \end{bmatrix} + \boldsymbol{e}$$

Suppose we observe for each locus:

$$y_j^* = \alpha_j + \epsilon_j$$

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Least Squares with Additional Data

Fixed linear model with the additional data:

$$\begin{bmatrix} \boldsymbol{y} \\ \boldsymbol{y}^* \end{bmatrix} = \begin{bmatrix} \boldsymbol{1} & \boldsymbol{X} \\ \boldsymbol{0} & \boldsymbol{I} \end{bmatrix} \begin{bmatrix} \mu \\ \alpha \end{bmatrix} + \begin{bmatrix} \boldsymbol{e} \\ \epsilon \end{bmatrix}$$

OLS Equations:

$$\begin{bmatrix} \boldsymbol{1}' & \boldsymbol{0}' \\ \boldsymbol{X}' & \boldsymbol{I}' \end{bmatrix} \begin{bmatrix} \boldsymbol{I}_n \frac{1}{\sigma_e^2} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{I}_k \frac{1}{\sigma_\epsilon^2} \end{bmatrix} \begin{bmatrix} \boldsymbol{1} & \boldsymbol{X} \\ \boldsymbol{0} & \boldsymbol{I} \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{\alpha} \end{bmatrix} = \begin{bmatrix} \boldsymbol{1}' & \boldsymbol{0}' \\ \boldsymbol{X}' & \boldsymbol{I}' \end{bmatrix} \begin{bmatrix} \boldsymbol{I}_n \frac{1}{\sigma_e^2} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{I}_k \frac{1}{\sigma_\epsilon^2} \end{bmatrix} \begin{bmatrix} \boldsymbol{y} \\ \boldsymbol{y}^* \end{bmatrix}$$

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Least Squares with Additional Data

Fixed linear model with the additional data:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{y}^* \end{bmatrix} = \begin{bmatrix} \mathbf{1} & \mathbf{X} \\ \mathbf{0} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mu \\ \boldsymbol{\alpha} \end{bmatrix} + \begin{bmatrix} \mathbf{e} \\ \boldsymbol{\epsilon} \end{bmatrix}$$

OLS Equations:

$$\begin{bmatrix} \mathbf{1}' & \mathbf{0}' \\ \mathbf{X}' & \mathbf{I}' \end{bmatrix} \begin{bmatrix} \mathbf{I}_n \frac{1}{\sigma_e^2} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_k \frac{1}{\sigma_\epsilon^2} \end{bmatrix} \begin{bmatrix} \mathbf{1} & \mathbf{X} \\ \mathbf{0} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{\boldsymbol{\alpha}} \end{bmatrix} = \begin{bmatrix} \mathbf{1}' & \mathbf{0}' \\ \mathbf{X}' & \mathbf{I}' \end{bmatrix} \begin{bmatrix} \mathbf{I}_n \frac{1}{\sigma_e^2} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_k \frac{1}{\sigma_\epsilon^2} \end{bmatrix} \begin{bmatrix} \mathbf{y} \\ \mathbf{y}^* \end{bmatrix}$$

$$\begin{bmatrix} \mathbf{1}'\mathbf{1} & \mathbf{1}'\mathbf{X} \\ \mathbf{X}'\mathbf{1} & \mathbf{X}'\mathbf{X} + \mathbf{I}\frac{\sigma_e^2}{\sigma_\epsilon^2} \end{bmatrix} \begin{bmatrix} \hat{\mu} \\ \hat{\boldsymbol{\alpha}} \end{bmatrix} = \begin{bmatrix} \mathbf{1}'\mathbf{y} \\ \mathbf{X}'\mathbf{y} + \mathbf{y}^* \frac{\sigma_e^2}{\sigma_\epsilon^2} \end{bmatrix}$$

Univariate-t

Prior:

$$(\alpha_j|\sigma_j^2) \sim \text{N}(0, \sigma_j^2)$$

$$\sigma_j^2 \sim \nu_\alpha S^2_{\nu_\alpha} \chi^{-2}_{\nu_\alpha}$$

Can show that the unconditional distribution for α_j is

$$\alpha_j \sim \text{(iid)}t(0, S^2_{\nu_\alpha}, \nu_\alpha)$$

(Sorensen and Gianola, 2002, LBMMQG pages 28,60)

This is Bayes-A (Meuwissen et al., 2001; Genetics 157:1819-1829)

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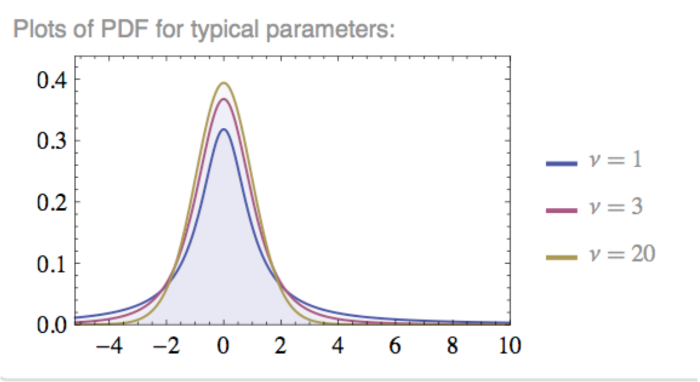

Generated by Wolfram|Alpha (www.wolframalpha.com)

Full conditional for single-site Gibbs

Full conditionals are the same as in the "Normal" model for μ, α_j, and σ_e^2. Let

$$\xi = [\sigma_1^2, \sigma_2^2, \ldots, \sigma_k^2]$$

Full conditional conditional for σ_j^2:

$$f(\sigma_j^2 | \boldsymbol{y}, \mu, \boldsymbol{\alpha}, \xi_{j\_}, \sigma_e^2) \propto f(\boldsymbol{y}, \mu, \boldsymbol{\alpha}, \xi, \sigma_e^2)$$

$$\propto f(\boldsymbol{y}|\mu, \boldsymbol{\alpha}, \xi, \sigma_e^2) f(\alpha_j|\sigma_j^2) f(\sigma_j^2) f(\mu, \boldsymbol{\alpha}_{j\_}, \xi_{j\_} \sigma_e^2)$$

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Full conditional for σ_j^2

So,

$$(\sigma_j^2|\boldsymbol{y}, \mu, \boldsymbol{\alpha}, \boldsymbol{\xi}\_, \sigma_e^2) \sim \tilde{\nu}_\alpha \tilde{S}_\alpha^2 \chi_{\nu_\alpha}^{-2}$$

where

$$\tilde{\nu}_\alpha = \nu_\alpha + 1$$

and

$$\tilde{S}_\alpha^2 = \frac{\alpha_j^2 + \nu_\alpha S_\alpha^2}{\tilde{\nu}_\alpha}$$

Multivariate-t

Prior:

$$(\alpha_j | \sigma^2_\alpha) \sim (\text{iid})\text{N}(0, \sigma^2_\alpha)$$

$$\sigma^2_\alpha \sim \nu_\alpha S^2_{\nu_\alpha} \chi^{-2}_{\nu_\alpha}$$

Can show that the unconditional distribution for α is

$$\boldsymbol{\alpha} \sim \text{multivariate-}t(\mathbf{0}, \boldsymbol{I} S^2_{\nu_\alpha}, \nu_\alpha)$$

(Sorensen and Gianola, 2002, LBMMQG page 60)

We will see later that this is Bayes-C with $\pi = 0$.

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Full conditional for σ^2_α

We will see later that

$$(\sigma^2_\alpha | \boldsymbol{y}, \mu, \boldsymbol{\alpha}, \sigma^2_e) \sim \tilde{\nu}_\alpha \tilde{S}^2_\alpha \chi^{-2}_{\nu_\alpha}$$

where

$$\tilde{\nu}_\alpha = \nu_\alpha + k$$

and

$$\tilde{S}^2_\alpha = \frac{\boldsymbol{\alpha}'\boldsymbol{\alpha} + \nu_\alpha S^2_\alpha}{\tilde{\nu}_\alpha}$$

Spike and univariate-t

Prior:

$$(\alpha_j | \pi, \sigma_j^2) \begin{cases} \sim \mathrm{N}(0, \sigma_j^2) & \text{probability } (1-\pi), \\ = 0 & \text{probability } \pi \end{cases}$$

and

$$(\sigma_j^2 | \nu_\alpha, S_\alpha^2) \sim \nu_\alpha S_\alpha^2 \chi_{\nu_\alpha}^{-2}$$

Thus,

$$(\alpha_j | \pi)(\text{iid}) \begin{cases} \sim \text{univariate-}t(0, S_\alpha^2, \nu_\alpha) & \text{probability } (1-\pi), \\ = 0 & \text{probability } \pi \end{cases}$$

This is Bayes-B (Meuwissen et al., 2001; Genetics 157:1819-1829)

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Notation for sampling from mixture

The indicator variable δ_j is defined as

$$\delta_j = 1 \Rightarrow (\alpha_j|\sigma_j^2) \sim \mathrm{N}(0, \sigma_j^2)$$

and

$$\delta_j = 0 \Rightarrow (\alpha_j|\sigma_j^2) = 0$$

Sampling strategy in MHG (2001)

- Sampling σ_e^2 and μ are as under the Normal prior.
- MHG proposed to use a Metropolis-Hastings sampler to draw samples for σ_j^2 and α_j jointly from their full-conditional distribution.
- First, σ_j^2 is sampled from

$$f(\sigma_j^2|\boldsymbol{y}, \mu, \boldsymbol{\alpha}_{j\_}, \boldsymbol{\xi}_{\_}, \sigma_e^2)$$

  using MH with prior as proposal.
- Then, α_j is sampled from its full-conditional, which is identical to that under the Normal prior

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MH acceptance probability when prior is used as proposal

Suppose we want to sample θ from $f(\theta|\boldsymbol{y})$ using the MH with its prior as proposal. Then, the MH acceptance probability becomes:

$$\alpha = min(1, \frac{f(\theta_{can}|\boldsymbol{y})f(\theta^{t-1})}{f(\theta^{t-1}|\boldsymbol{y})f(\theta_{can})}$$

where $f(\theta)$ is the prior for θ. Using Bayes' theorem, the target density can be written as:

$$f(\theta|\boldsymbol{y}) \propto f(\boldsymbol{y}|\theta)f(\theta)$$

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Thus when the prior for σ_j^2 is used as the proposal, the MH acceptance probability becomes

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where σ_{can}^2 is used to denote the candidate value for σ_j^2, and $\boldsymbol{\theta}_{j\_}$ all the other parameters. It can be shown that, α_j depends on $\boldsymbol{y}$ only through $r_j = \boldsymbol{x}_j'\boldsymbol{w}$ (page 30). Thus

$$f(\boldsymbol{y}|\sigma_j^2, \boldsymbol{\theta}_{j\_}) \propto f(r_j|\sigma_j^2, \boldsymbol{\theta}_{j\_})$$

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"Likelihood" for σ_j^2

Recall that

$$\boldsymbol{w} = \boldsymbol{y} - \boldsymbol{1}\mu - \sum_{j' \neq j} \boldsymbol{x}_{j'}\alpha_{j'} = \boldsymbol{x}_j\alpha_j + \boldsymbol{e}$$

Then,

$$\mathrm{E}(\boldsymbol{w}|\sigma_j^2, \boldsymbol{\theta}_{j\_}) = \boldsymbol{0}$$

When $\delta = 1$:

$$\mathrm{Var}(\boldsymbol{w}|\delta_j = 1, \sigma_j^2, \boldsymbol{\theta}_{j\_}) = \boldsymbol{x}_j\boldsymbol{x}_j'\sigma_j^2 + \boldsymbol{I}\sigma_e^2$$

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$$f(r_j|\delta_j, \sigma_j^2, \boldsymbol{\theta}_{j\_}) \propto (v_\delta)^{-1/2}\exp\{-\frac{r_j^2}{2v_\delta}\}$$

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Alternative View of Prior in BayesB

- How much information is being added by the prior?
- BayesB is identical to ML with additional data!
- Can “see” how much additional data in BayesB prior.

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Maximum Likelihood with Additional Data

- Suppose at locus j, $\delta_j = 1$, and we observe additional data:

$$\boldsymbol{u}_j \sim N(\boldsymbol{0}, \boldsymbol{I}_q\sigma_j^2)$$

- Assume that only unknown is σ_j^2
- So, adjust phenotypes as:

$$\boldsymbol{w} = \boldsymbol{y} - \boldsymbol{1}\mu - \sum_{j' \neq j} \boldsymbol{x}_{j'}\alpha_{j'}$$

- Likelihood:

$$L(\sigma_j^2; \boldsymbol{w}, \boldsymbol{u}_j) = L(\sigma_j^2; \hat{\alpha}_j, \boldsymbol{u}_j)$$

Likelihood with Additional Data

- $$L(\sigma_j^2; \hat{\alpha}_j, \boldsymbol{u}_j) \propto f_1(\hat{\alpha}_j|\sigma_j^2) \times f_2(\boldsymbol{u}_j|\sigma_j^2)$$

- $$f_2(\boldsymbol{u}_j|\sigma_j^2) \propto (\sigma_j^2)^{-q/2} \exp[\frac{-\boldsymbol{u}_j'\boldsymbol{u}_j}{2\sigma_j^2}]$$
  $$\propto (\sigma_j^2)^{-[\nu/2+1]} \exp[\frac{-\nu S^2}{2\sigma_j^2}]$$

- $\nu = q - 2, S^2 = \frac{\boldsymbol{u}_j'\boldsymbol{u}_j}{\nu}$

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- $$\begin{aligned} f_2(\boldsymbol{u}_j|\sigma_j^2) &\propto (\sigma_j^2)^{-q/2} \exp[\frac{-\boldsymbol{u}_j'\boldsymbol{u}_j}{2\sigma_j^2}] \\ &\propto (\sigma_j^2)^{-[\nu/2+1]} \exp[\frac{-\nu S^2}{2\sigma_j^2}] \end{aligned}$$
- $\nu = q - 2, S^2 = \frac{\boldsymbol{u}_j'\boldsymbol{u}_j}{\nu}$

Alternative algorithm for spike and univariate-t

Rather than use the prior as the proposal for sampling σ_j^2, we

- sample $\delta_j = 1$ with probability 0.5
- when $\delta = 1$, sample σ_j^2 from a scaled inverse chi-squared distribution with
  - scale parameter = $\sigma_j^{2(t-1)}/2$ and 4 degrees of freedom when $\delta_j^{(t-1)} = 1$, and
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Multivariate-t mixture

Prior:

$$(\alpha_j|\pi,\sigma_\alpha^2)\begin{cases}\sim \mathrm{N}(0,\sigma_\alpha^2) & \text{probability } (1-\pi),\\ = 0 & \text{probability } \pi\end{cases}$$

and

$$(\sigma_\alpha^2|\nu_\alpha, S_\alpha^2)\sim \nu_\alpha S_\alpha^2\chi_{\nu_\alpha}^{-2}$$

Further,

$$\pi \sim \mathrm{Uniform}(0,1)$$

- The α_j variables with their corresponding $\delta_j = 1$ will follow a multivariate-t distribution.
- This is what we have called Bayes-Cπ

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Full conditionals for single-site Gibbs

Full-conditional distributions for μ, $\boldsymbol{\alpha}$, and σ_e^2 are as with the Normal prior.

Full-conditional for δ_j:

$$\Pr(\delta_j|\mathbf{y},\mu,\boldsymbol{\alpha}_{-j},\boldsymbol{\delta}_{-j},\sigma_\alpha^2,\sigma_e^2,\pi) = \Pr(\delta_j|r_j,\boldsymbol{\theta}_{j\_})$$

$$\Pr(\delta_j|r_j,\boldsymbol{\theta}_{j\_}) = \frac{f(\delta_j, r_j|\boldsymbol{\theta}_{j\_})}{f(r_j|\boldsymbol{\theta}_{j\_})}$$

$$= \frac{f(r_j|\delta_j,\boldsymbol{\theta}_{j\_})\Pr(\delta_j|\pi)}{f(r_j|\delta_j=0,\boldsymbol{\theta}_{j\_})\pi + f(r_j|\delta_j=1,\boldsymbol{\theta}_{j\_})(1-\pi)}$$

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Full conditional for σ^2_α

This can be written as

$$f(\sigma^2_\alpha|\boldsymbol{y}, \mu, \boldsymbol{\alpha}, \boldsymbol{\delta}, \sigma^2_e) \propto f(\boldsymbol{y}|\sigma^2_\alpha, \mu, \boldsymbol{\alpha}, \boldsymbol{\delta}, \sigma^2_e) f(\sigma^2_\alpha, \mu, \boldsymbol{\alpha}, \boldsymbol{\delta}, \sigma^2_e)$$

But, can see that

$$f(\boldsymbol{y}|\sigma^2_\alpha, \mu, \boldsymbol{\alpha}, \boldsymbol{\delta}, \sigma^2_e) \propto f(\boldsymbol{y}|\mu, \boldsymbol{\alpha}, \boldsymbol{\delta}, \sigma^2_e)$$

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Note that σ^2_α appears only in $f(\boldsymbol{\alpha}|\sigma^2_\alpha)$ and $f(\sigma^2_\alpha)$:

$$f(\boldsymbol{\alpha}|\sigma^2_\alpha) \propto (\sigma^2_\alpha)^{-k/2} \exp\{-\frac{\boldsymbol{\alpha}'\boldsymbol{\alpha}}{2\sigma^2_\alpha}\}$$

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Full conditional forσ_α^2

This can be written as

$$f(\sigma_\alpha^2|\boldsymbol{y},\mu,\boldsymbol{\alpha},\boldsymbol{\delta},\sigma_e^2) \propto f(\boldsymbol{y}|\sigma_\alpha^2,\mu,\boldsymbol{\alpha},\boldsymbol{\delta},\sigma_e^2)f(\sigma_\alpha^2,\mu,\boldsymbol{\alpha},\boldsymbol{\delta},\sigma_e^2)$$

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Full conditional for σ_α^2

Combining these two densities gives:

$$f(\sigma_\alpha^2|\boldsymbol{y},\mu,\boldsymbol{\alpha},\boldsymbol{\delta},\sigma_e^2) \propto (\sigma_\alpha^2)^{-(k+\nu_\alpha+2)/2}\exp\{\frac{\boldsymbol{\alpha}'\boldsymbol{\alpha}+\nu_\alpha S_\alpha^2}{2\sigma_\alpha^2}\}$$

So,

$$(\sigma_\alpha^2|\boldsymbol{y},\mu,\boldsymbol{\alpha},\boldsymbol{\delta},\sigma_e^2) \sim \tilde{\nu}_\alpha \tilde{S}_\alpha^2 \chi_{\tilde{\nu}_\alpha}^{-2}$$

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$$\tilde{\nu}_\alpha = k + \nu_\alpha$$

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Hyper parameter: S_α^2

If σ^2 is distributed as a scaled, inverse chi-square random variable with scale parameter S^2 and degrees of freedom ν

$$E(\sigma^2) = \frac{\nu S^2}{\nu - 2}$$

Recall that under some assumptions

$$\sigma_\alpha^2 = \frac{V_a}{\sum_j 2p_jq_j}$$

So, we take

$$S_\alpha^2 = \frac{(\nu_\alpha - 2)V_a}{\nu_\alpha k(1-\pi)2\overline{pq}}$$

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Full conditional for π

Using Bayes' theorem,

$$f(\pi|\boldsymbol{\delta}, \mu, \boldsymbol{\alpha}, \sigma^2_\alpha, \sigma^2_e, \boldsymbol{y}) \propto f(\boldsymbol{y}|\pi, \boldsymbol{\delta}, \mu, \boldsymbol{\alpha}, \sigma^2_\alpha, \sigma^2_e) f(\pi, \boldsymbol{\delta}, \mu, \boldsymbol{\alpha}, \sigma^2_\alpha, \sigma^2_e)$$

But,

- Conditional on δ the likelihood is free of π
- Further, π only appears in probability of the vector of bernoulli variables: δ

Thus,

$$f(\pi|\boldsymbol{\delta}, \mu, \boldsymbol{\alpha}, \sigma^2_\alpha, \sigma^2_e, \boldsymbol{y}) = \pi^{(k-m)}(1-\pi)^m$$

where $m = \delta'\delta$, and k is the number of markers. Thus, π is sampled from a beta distribution with $a = k - m + 1$ and $b = m + 1$.

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BayesCπ with Unknown S_α^2

- Prior for S_α^2: Gamma(a,b)

$$f(S_\alpha^2|a,b) \propto b^a (S_\alpha^2)^{a-1} \exp\{-bS_\alpha^2\}$$

- Using Bayes theorem,

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- Given $\mu, \boldsymbol{\alpha}$, and σ_e^2, $f(\boldsymbol{y}|S_\alpha^2, \sigma_\alpha^2, \ldots)$ does not depend on S_α^2.
- In $f(S_\alpha^2, \sigma^2 \ldots)$, S_α^2 is only in $f(S_\alpha^2|a,b)$ and $f(\sigma_\alpha^2|S_\alpha^2, \nu_\alpha)$

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$$f(S_\alpha^2|\boldsymbol{\delta},\mu,\boldsymbol{\alpha},\sigma_\alpha^2,\sigma_e^2,\boldsymbol{y}) \propto f(\boldsymbol{y}|S_\alpha^2,\sigma_\alpha^2,\ldots)f(S_\alpha^2,\sigma^2\ldots)$$

- Given $\mu,\boldsymbol{\alpha}$, and σ_e^2, $f(\boldsymbol{y}|S_\alpha^2,\sigma_\alpha^2,\ldots)$ does not depend on S_α^2.
- In $f(S_\alpha^2,\sigma^2\ldots)$, S_α^2 is only in $f(S_\alpha^2|a,b)$ and $f(\sigma_\alpha^2|S_\alpha^2,\nu_\alpha)$

BayesCπ with Unknown S^2_α

- Prior for S^2_α: Gamma(a,b)

$$f(S^2_\alpha | a, b) \propto b^a (S^2_\alpha)^{a-1} \exp\{-bS^2_\alpha\}$$

- Prior for σ^2_α:

$$f(\sigma^2_\alpha) \propto (\sigma^2_\alpha)^{-(\nu_\alpha+2)/2} \exp\{\frac{\nu_\alpha S^2_\alpha}{2\sigma^2_\alpha}\}$$

- Combining these gives:

$$f(S^2_\alpha | \sigma^2_\alpha, \boldsymbol{y}, \ldots) \propto S^{2(a-1+\nu/2)}_\alpha \exp\{-S^2_\alpha(\frac{\nu_\alpha}{2\sigma^2_\alpha} + b)\}$$

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BayesCπ with Unknown S_α^2

- Prior for S_α^2: Gamma(a,b)

$$f(S_\alpha^2|a,b) \propto b^a (S_\alpha^2)^{a-1} \exp\{-bS_\alpha^2\}$$

- Prior for σ_α^2:

$$f(\sigma_\alpha^2) \propto (\sigma_\alpha^2)^{-(\nu_\alpha+2)/2} \exp\{\frac{\nu_\alpha S_\alpha^2}{2\sigma_\alpha^2}\}$$

- Combining these gives:

$$f(S_\alpha^2|\sigma_\alpha^2, \boldsymbol{y}, \ldots) \propto S_\alpha^{2(a-1+\nu/2)} \exp\{-S_\alpha^2(\frac{\nu_\alpha}{2\sigma_\alpha^2} + b)\}$$

BayesCπ with Unknown S^2_α

So, $f(S^2_\alpha | a, b)$ is Gamma(a*,b*), where

$$a* = a + \nu_\alpha / 2$$

and

$$b* = b + \frac{\nu_\alpha}{2\sigma^2_\alpha}$$

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- 2000 unlinked loci in LE
- 10 of these are QTL: $\pi = 0.995$
- $h^2 = 0.5$
- Locus effects estimated from 250 individuals

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Results for Bayes-B

Correlations between true and predicted additive genotypic values estimated from 32 replications

π	S^2	Correlation
0.995	0.2	0.91 (0.009)
0.8	0.2	0.86 (0.009)
0.0	0.2	0.80 (0.013)
0.995	2.0	0.90 (0.007)
0.8	2.0	0.77 (0.009)
0.0	2.0	0.35 (0.022)

Simulation II

- 2000 unlinked loci with Q loci having effect on trait
- N is the size of training data set
- Heritability = 0.5
- Validation in an independent data set with 1000 individuals
- Bayes-B and Bayes-Cπ with $\pi = 0.5$

Simulation II

- 2000 unlinked loci with *Q* loci having effect on trait
- *N* is the size of training data set
- Heritability = 0.5
- Validation in an independent data set with 1000 individuals
- Bayes-B and Bayes-Cπ with $\pi = 0.5$

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Results

Results from 15 replications

				Corr($g, \hat{g}$)	
N	Q	π	$\hat{\pi}$	Bayes-Cπ	Bayes-B
2000	10	0.995	0.994	0.995	0.937
2000	200	0.90	0.899	0.866	0.834
2000	1900	0.05	0.202	0.613	0.571
4000	1900	0.05	0.096	0.763	0.722

Simulation III

- Genotypes: 50k SNPs from 1086 Purebred Angus animals, ISU
- Phenotypes:
  - QTL simulated from 50 randomly sampled SNPs
  - substitution effect sampled from N(0,σ^2_α)
  - $\sigma^2_\alpha = \frac{\sigma^2_g}{50 2\bar{p}\bar{q}}$
  - $h^2 = 0.25$
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- Genotypes: 50k SNPs from 984 crossbred animals, CMP
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Results

Correlations between g_i and $\hat{g}_i$ estimated from 3 replications

	Correlation	
π	Bayes-B	Bayes-C
0.999	0.86	0.86
0.25	0.70	0.26

BayesCπ:

- $\hat{\pi} = 0.999$
- Correlation = 0.86

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