Bayesian Interval Mapping

- multiple QTL likelihood
  - compare CIM, MIM, imputation, BIM
  - *Drosophila* shape example
- Bayesian idea
  - Who was Bayes? What is Bayes theorem?
  - Bayesian
  - Bayes factors and marginal posteriors
  - Markov chain sampling to search model space

multiple QTL likelihood

- likelihood is mixture over unknown QTL
  - likelihood = product of sum of products
  - now have multiple QTL
    - $Q = (Q_1, Q_2, \ldots, Q_m)$
    - $\lambda = (\lambda_1, \lambda_2, \ldots, \lambda_m)$
    - $\theta = (\mu, \theta_1, \theta_2, \ldots, \theta_m, \sigma^2)$ plus interactions…

$$
\begin{aligned}
L(\theta, \lambda \mid Y, X) &= \text{pr}(Y \mid X, \theta, \lambda) \\
&= \text{prod}_i \ \text{pr}(Y_i \mid X_i, \theta, \lambda) \\
&= \text{prod}_i \ \text{sum}_Q \ \text{pr}(Q \mid X_i, \lambda)\text{pr}(Y_i \mid Q, \theta)
\end{aligned}
$$

Bayesian model posterior

- augment data (Y,X) with unknowns Q
  - study unknowns (θ,λ,Q) given data (Y,X)
  - $Q \sim \text{pr}(Q \mid Y_i, X_i, \theta, \lambda)$
  - sample genotypes Q for every individual at m QTL
- study properties of posterior $\text{pr}(\theta,\lambda,Q \mid Y, X)$
  - sample from posterior in some clever way
    - multiple imputation or MCMC

$$\text{pr}(\theta,\lambda,Q \mid Y,X) = \frac{\text{pr}(Q \mid X,\lambda)\text{pr}(Y \mid Q,\theta)\text{pr}(\lambda \mid X)\text{pr}(\theta)}{\text{pr}(Y \mid X)}$$

$$\text{pr}(\theta,\lambda \mid Y,X) = \text{sum}_Q \ \text{pr}(\theta,\lambda,Q \mid Y,X)$$

shape phenotype in BC study indexed by PC1

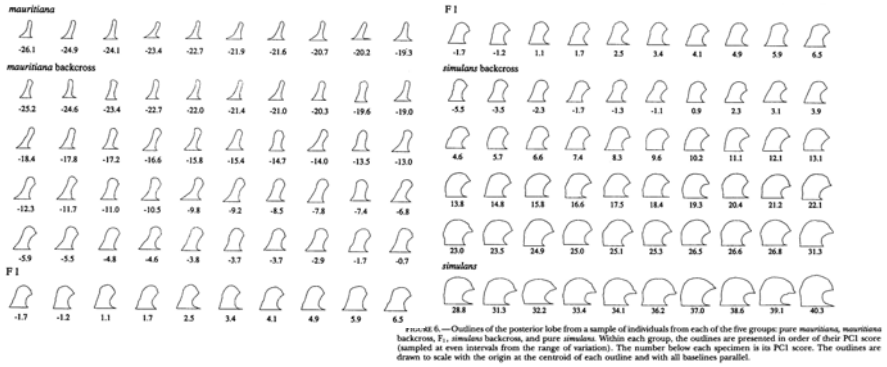


FIGURE 6.—Outlines of the posterior lobe from a sample of individuals from each of the five groups: pure *mauritiana*, *mauritiana* backcross, F_1, *simulans* backcross, and pure *simulans*. Within each group, the outlines are presented in order of their PC1 score (sampled at even intervals from the range of variation). The number below each specimen is its PC1 score. The outlines are drawn to scale with the origin at the centroid of each outline and with all baselines parallel.

Liu et al. (1996) *Genetics*

shape phenotype via PC

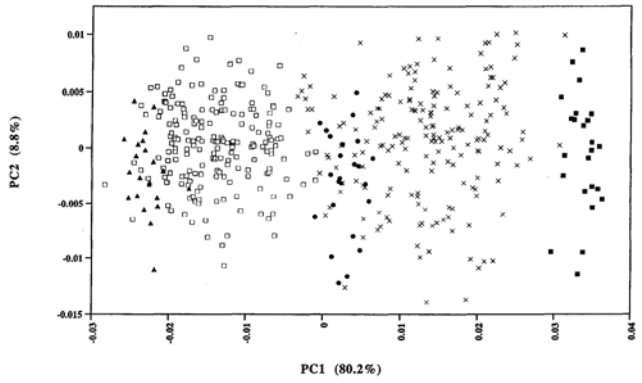


FIGURE 5.—A plot of the first two principal components of the Fourier coefficients from posterior lobe outlines. Many individuals from each of five genotypic classes are represented. Each point represents an average of scores from the left and right sides of an individual (with a few exceptions for which the score is from one side only). The percentage of variation in the Fourier coefficients accounted for by each principal component is given in parentheses. Liu et al. (1996) *Genetics*

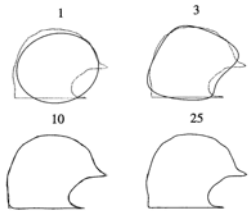


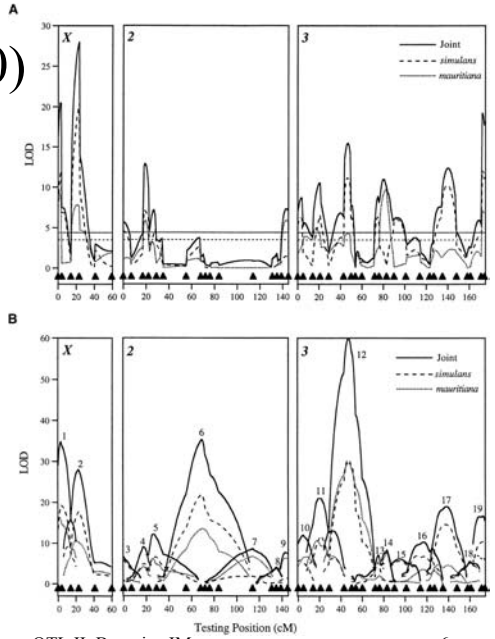
FIGURE 2.—The effect of harmonic number on the accuracy of reconstruction of a posterior lobe outline by elliptical Fourier analysis.

Zeng et al. (2000) CIM vs. MIM

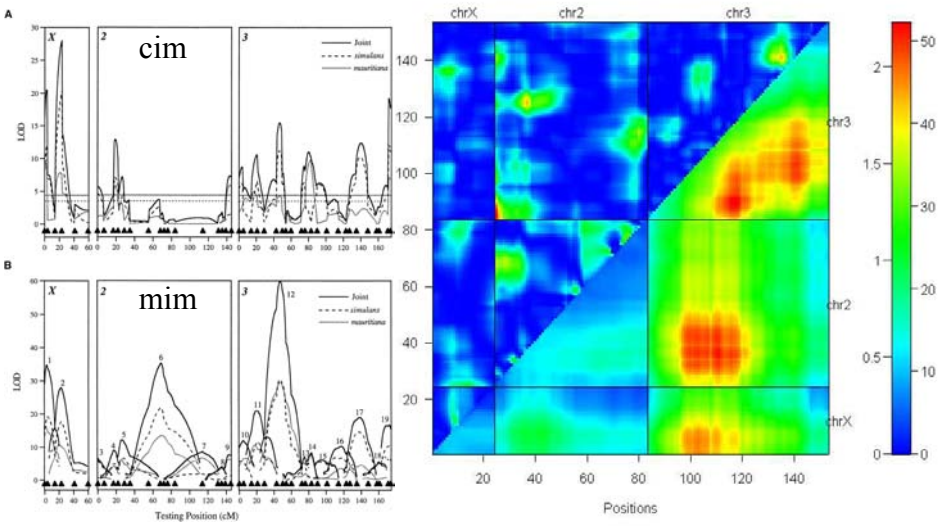
composite interval mapping
- (Liu et al. 1996)
- narrow peaks
- miss some QTL

multiple interval mapping
- (Zeng et al. 2000)
- triangular peaks

both conditional 1-D scans
- fixing all other "QTL"



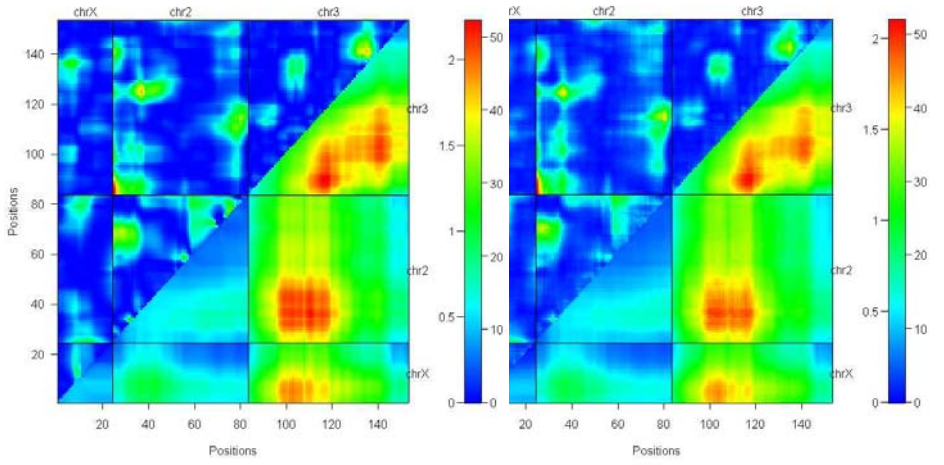
CIM, MIM and IM pairscan



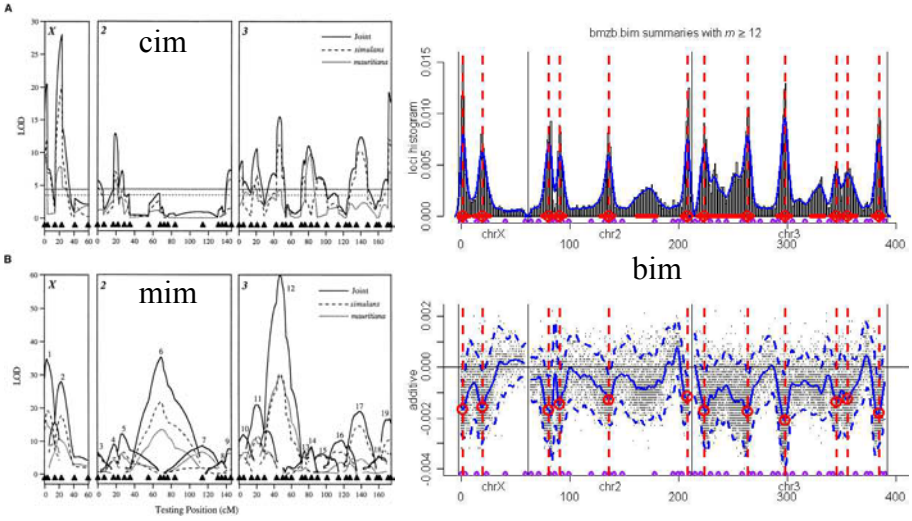
2 QTL + epistasis: IM versus multiple imputation

IM pairscan

multiple imputation

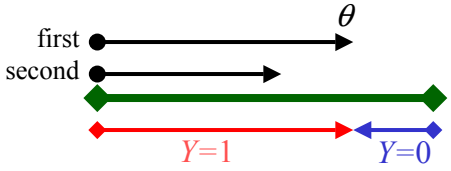


multiple QTL: CIM, MIM and BIM



who was Bayes?

- Reverend Thomas Bayes (1702-1761)
  - part-time mathematician
  - buried in Bunhill Cemetary, Moongate, London
  - famous paper in 1763 *Phil Trans Roy Soc London*
  - was Bayes the first with this idea? (Laplace)
- billiard balls on rectangular table
  - two balls tossed at random (uniform) on table
  - where is first ball if the second is to its left (right)?

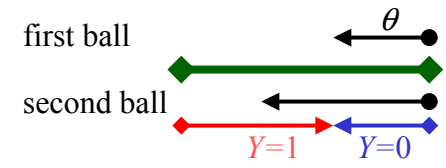


prior $\quad \Pr(\theta) \quad = 1$

likelihood $\quad \Pr(Y|\theta) = \theta^{Y}(1-\theta)^{1-Y}$

posterior $\quad \Pr(\theta|Y) = ?$

where is the first ball?



prior $\quad \text{pr}(\theta) \quad = 1$

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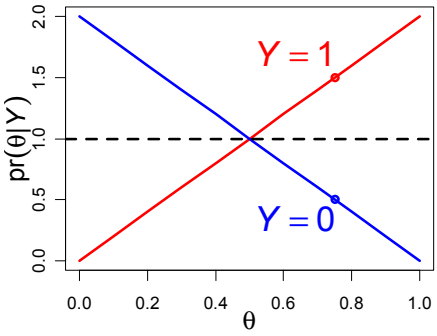
posterior $\quad \text{pr}(\theta|Y) = ?$



$$\text{pr}(\theta|Y) = \frac{\text{pr}(Y|\theta)\text{pr}(\theta)}{\text{pr}(Y)}$$

$$\text{pr}(Y) = \int_0^1 \theta^{Y}(1-\theta)^{1-Y}\,d\theta = \frac{1}{2}$$

$$\text{pr}(\theta|Y) = \begin{cases} 2\theta & Y = 1 \\ 2(1-\theta) & Y = 0 \end{cases}$$

(now throw second ball *n* times)

what is Bayes theorem?

- before and after observing data
  - prior: $\text{pr}(\theta)$ = pr(parameters)
  - posterior: $\text{pr}(\theta|Y)$ = pr(parameters|data)
- posterior = likelihood * prior / constant
  - usual likelihood of parameters given data
  - normalizing constant pr(Y) depends only on data
    - constant often drops out of calculation

$$\text{pr}(\theta|Y) = \frac{\text{pr}(\theta,Y)}{\text{pr}(Y)} = \frac{\text{pr}(Y|\theta)\times\text{pr}(\theta)}{\text{pr}(Y)}$$

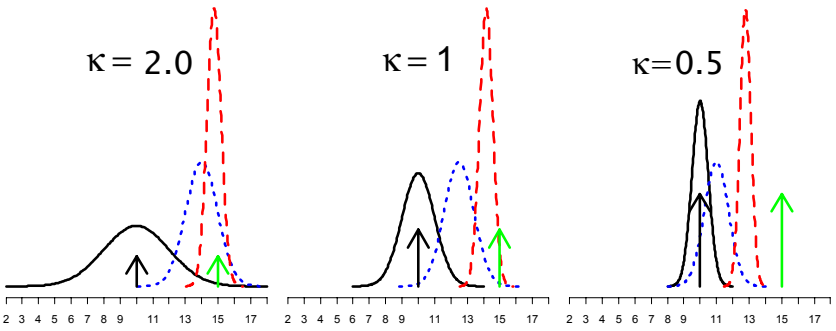
Bayes for normal data

$Y = \mu + E$	posterior for single individual
environ	$E \sim N(0, \sigma^2)$, σ^2 known
likelihood	$pr(Y \mid \mu, \sigma^2) = N(Y \mid \mu, \sigma^2)$
prior	$pr(\mu \mid \mu_0, \sigma^2, \kappa) = N(\mu \mid \mu_0, \kappa\sigma^2)$
posterior	$N(\mu \mid \mu_0 + B_1(Y - \mu_0),\ B_1\sigma^2)$
$Y_i = \mu + E_i$	posterior for sample of n individuals
	shrinkage weights B_n go to 1

$$pr(\mu \mid Y, \mu_0, \sigma^2, \kappa) = N\left(G \middle| \mu_0 + B_n(\overline{Y}_\bullet - \mu_0), B_n \frac{\sigma^2}{n}\right)$$

$$\text{with } \overline{Y}_\bullet = \text{sum}\frac{Y_i}{n}, B_n = \frac{\kappa n}{\kappa n + 1} \to 1$$

effect of prior variance on posterior



normal prior, posterior for $n = 1$, posterior for $n = 5$, true mean
(solid black) (dotted blue) (dashed red) (green arrow)

Bayesian priors for QTL

- locus λ may be uniform over genome
  - pr($\lambda \mid X$) = 1 / length of genome
- missing genotypes Q
  - pr($Q \mid X, \lambda$)
  - recombination model is formally a prior
- effects $\theta = (\mu, G, \sigma^2)$, $G = (G_{QQ}, G_{Qq}, G_{qq})$
  - conjugate priors for normal phenotype
  - $\mu \sim N(0, \kappa_0\sigma^2)$
  - $G_Q \sim N(0, \kappa\sigma^2)$
  - $\sigma^2 \sim$ inverse-$\chi^2(\nu,\tau^2)$, or $\nu\tau^2 / \sigma^2 \sim \chi^2$

details of phenotype priors

- priors depend on "hyper-parameters"
- $\mu \sim N(\mu_0, \kappa_0\sigma^2)$ grand mean
- $G_Q \sim N(0, \kappa\sigma^2)$
  - $\kappa\sigma^2 \approx \sigma_G^2$ = genetic variance
  - $\kappa \approx \sigma_G^2 / \sigma^2 = h^2 / (1-h^2)$
  - $h^2 = \sigma_G^2 / (\sigma_G^2 + \sigma^2)$ = heritability
- $\sigma^2 \sim$ inverse-$\chi^2(\nu,\tau^2)$, or $\nu\tau^2 / \sigma^2 \sim \chi^2$
  - $\tau^2 \approx s^2$ = total sample variance
  - ν = prior degrees of freedom = small integer

posterior by QT genetic value

$Y = \mu + G_Q + E$ genetics Q = qq,Qq,QQ

environment $E \sim N(0,\sigma^2)$, σ^2 known

parameters $\theta = (\mu, G, \sigma^2)$

likelihood $\text{pr}(Y \mid Q, G, \sigma^2) = N(Y \mid G_Q, \sigma^2)$

prior $\text{pr}(G_Q \mid \sigma^2, \kappa) = N(G_Q \mid 0, \kappa\sigma^2)$

posterior:

$$\text{pr}(G_Q \mid Y, Q, \sigma^2, \mu, \kappa) = N\left(G_Q \middle| B_Q(\bar{Y}_Q - \mu), B_Q \frac{\sigma^2}{n_Q}\right)$$

$$n_Q = \text{count}\{Q_i = Q\}, \bar{Y}_Q = \underset{\{i:Q_i=Q\}}{\text{sum}} \frac{Y_i}{n_Q}, B_Q = \frac{\kappa n_Q}{\kappa n_Q + 1} \to 1$$

Empirical Bayes: choosing hyper-parameters

How do we choose hyper-parameters μ, κ?

Empirical Bayes: marginalize over prior

estimate μ, κ from marginal posterior

likelihood $\text{pr}(Y_i \mid Q_i, G, \sigma^2) = N(Y_i \mid G(Q_i), \sigma^2)$

prior $\text{pr}(G_Q \mid \sigma^2, \kappa) = N(G_Q \mid 0, \kappa\sigma^2)$

marginal $\text{pr}(Y_i \mid \sigma^2, \mu, \kappa_0, \kappa) = N(Y_i \mid \mu, (\kappa_0 + \kappa + 1)\sigma^2)$

estimates $\hat{\mu}_0 = \bar{Y}_\bullet, \; s^2 = \text{sum}_i (Y_i - \bar{Y}_\bullet)^2 / n$

$\hat{\sigma}^2 = s^2/(\kappa + 1) \approx s^2/(1 - h^2)$

EB posterior $$\text{pr}(G_Q \mid Y) = N\left(G_Q \middle| B_Q(\bar{Y}_Q - \bar{Y}_\bullet), B_Q \frac{\hat{\sigma}^2}{n_Q}\right)$$

What if variance σ^2 is unknown?

- recall that sample variance is proportional to chi-square
  - $\text{pr}(s^2 \mid \sigma^2) = \chi^2(ns^2/\sigma^2 \mid n)$
  - or equivalently, $ns^2/\sigma^2 \mid \sigma^2 \sim \chi_n^2$
- conjugate prior is inverse chi-square
  - $\text{pr}(\sigma^2 \mid \nu,\tau^2) = \text{inv-}\chi^2(\sigma^2 \mid \nu,\tau^2)$
  - or equivalently, $\nu\tau^2/\sigma^2 \mid \nu,\tau^2 \sim \chi_\nu^2$
  - empirical choice: $\tau^2 = s^2/3$, $\nu = 6$
    - $E(\sigma^2 \mid \nu,\tau^2) = s^2/2$, $\text{Var}(\sigma^2 \mid \nu,\tau^2) = s^4/4$
- posterior given data
  - $\text{pr}(\sigma^2 \mid Y,\nu,\tau^2) = \text{inv-}\chi^2(\sigma^2 \mid \nu+n, (\nu\tau^2+ns^2)/(\nu+n))$
  - weighted average of prior and data

joint effects posterior details

$Y_i = \mu + G(Q_i) + E_i$ genetic Q_i = qq,Qq,QQ
environ $E \sim N(0,\sigma^2)$
parameters $\theta = (\mu, G, \sigma^2)$

likelihood $\text{pr}(Y_i \mid Q_i, G, \sigma^2) = N(Y_i \mid G(Q_i), \sigma^2)$

prior $\text{pr}(G_Q \mid \sigma^2, \kappa) = N(G_Q \mid 0, \sigma^2/\kappa)$
$\text{pr}(\sigma^2 \mid \nu,\tau^2) = \text{inv-}\chi^2(\sigma^2 \mid \nu,\tau^2)$

posterior:

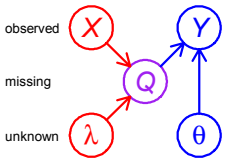
$$\text{pr}(G_Q \mid Y, Q, \sigma^2, \kappa) = N\left(G_Q \middle| B_Q(\bar{Y}_Q - \bar{Y}_\cdot), B_Q\frac{\sigma^2}{n_Q}\right)$$

$$\text{pr}(\sigma^2 \mid Y, Q, G_Q, \nu, \tau^2) = \text{inv-}\chi^2\left(\sigma^2 \middle| \nu+n, \frac{\nu\tau^2+ns_Q^2}{\nu+n}\right)$$

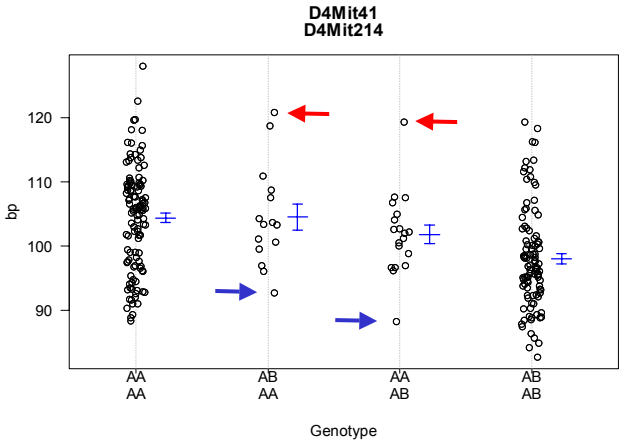
$$\text{with } B_Q = \frac{n_Q}{\kappa+n_Q}, s_Q^2 = \text{sum}_i\left(Y_i - G(Q_i)\right)^2/n$$

uncertainty in QTL genotype *Q*

- how to improve guess on *Q* with data, parameters?
  - prior recombination: pr($Q \mid X_i, \lambda$)
  - posterior recombination: pr($Q \mid Y_i, X_i, \theta, \lambda$)
- main philosophies for assessing likelihood
  - maximum likelihood: study peak(s)
  - Bayesian analysis: study whole shape
- implementation methodologies
  - Expectation-Maximization (EM)
  - Markov chain Monte Carlo (MCMC)
  - multiple imputation
  - genetic algorithms, GEE, …



how does phenotype *Y* affect *Q*?



what are probabilities for genotype *Q* between markers?

recombinants AA:AB

all 1:1 if ignore *Y* and if we use *Y*?

posterior on QTL genotypes

- full conditional of Q given data, parameters
  - proportional to prior $\text{pr}(Q \mid X_i, \lambda)$
    - weight toward Q that agrees with flanking markers
  - proportional to likelihood $\text{pr}(Y_i \mid Q, \theta)$
    - weight toward Q so that group mean $G_Q \approx Y_i$
- phenotype and flanking markers may conflict
  - posterior recombination balances these two weights

$$\text{pr}(Q \mid Y_i, X_i, \theta, \lambda) = \frac{\text{pr}(Q \mid X_i, \lambda)\text{pr}(Y_i \mid Q, \theta)}{\text{pr}(Y_i \mid X_i, \theta, \lambda)}$$

MCMC idea for QTLs

- construct Markov chain around posterior
  - want posterior as stable distribution of Markov chain
  - in practice, the chain tends toward stable distribution
    - initial values may have low posterior probability
    - burn-in period to get chain mixing well
- hard to sample (λ, Q, θ, m) from joint posterior
  - update (λ, Q, θ) from full conditionals for m-QTL model
  - update m using reversible jump technology

$$(\lambda, Q, \theta, m) \sim \text{pr}(\lambda, Q, \theta, m \mid Y, X)$$

$$(\lambda, Q, \theta, m)_1 \rightarrow (\lambda, Q, \theta, m)_2 \rightarrow \cdots \rightarrow (\lambda, Q, \theta, m)_N$$

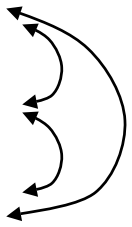
MCMC sampling of (λ, Q, θ)

- sample missing genotypes Q
  - decouples effects θ from QTL λ
  - but Q depends on (θ,λ) and vice versa
- cycle updates using full conditionals:

$$\lambda \sim \frac{\text{pr}(Q \mid X, \lambda)\text{pr}(\lambda \mid X)}{\text{pr}(Q \mid X)}$$

$$Q \sim \text{pr}(Q \mid Y_i, X_i, \theta, \lambda)$$

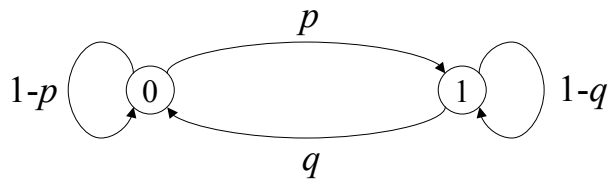
$$\theta \sim \frac{\text{pr}(Y \mid Q, \theta)\text{pr}(\theta)}{\text{pr}(Y \mid Q)}$$



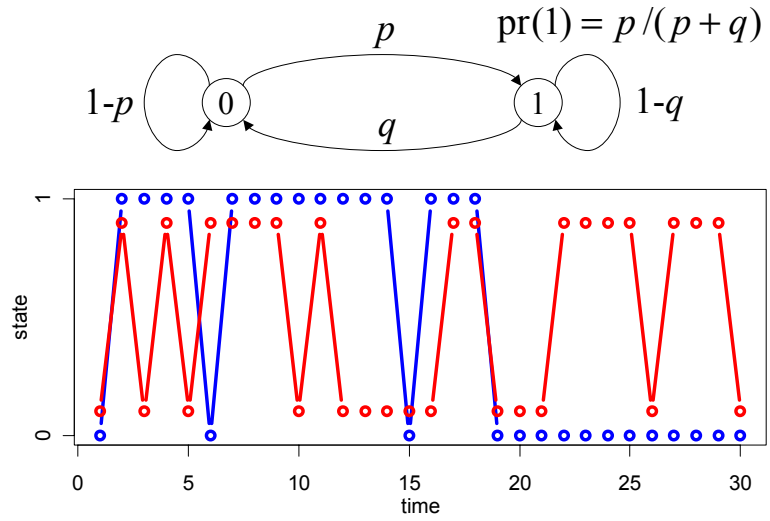
What is a Markov chain?

- future given present is independent of past
- update chain based on current value
  - can make chain arbitrarily complicated
  - chain converges to stable pattern $\pi()$ we wish to study

$$\text{pr}(1) = p/(p+q)$$



Markov chain idea



Gibbs sampler idea

- want to study two correlated normals
- could sample directly from bivariate normal
- Gibbs sampler:
  - sample each from its full conditional
  - pick order of sampling at random
  - repeat *N* times

$$\begin{pmatrix}\theta_1\\ \theta_2\end{pmatrix}\Big|\,\mu,\rho \sim N\left(\begin{pmatrix}\mu_1\\ \mu_2\end{pmatrix},\begin{pmatrix}1 & \rho\\ \rho & 1\end{pmatrix}\right)$$

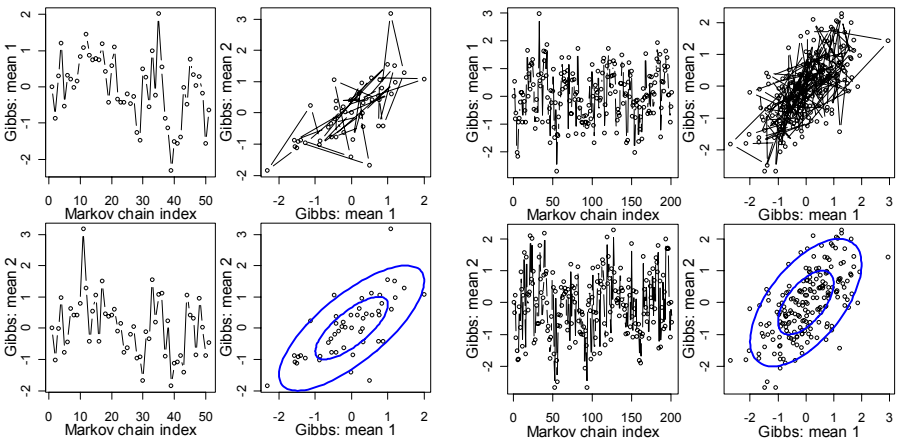
$$\theta_1 \mid \theta_2,\mu,\rho \sim N\left(\mu_1+\rho(\theta_2-\mu_2),1-\rho^2\right)$$

$$\theta_2 \mid \theta_1,\mu,\rho \sim N\left(\mu_2+\rho(\theta_1-\mu_1),1-\rho^2\right)$$

Gibbs sampler samples: $\rho = 0.6$

$N = 50$ samples

$N = 200$ samples



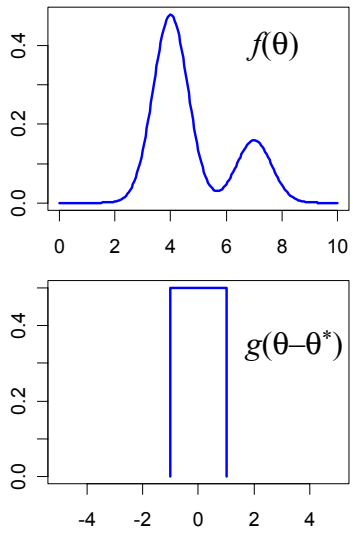
Gibbs Sampler: effects & genotypes

- for given locus λ, can sample effects θ and genotypes Q
  - effects parameter vector $\theta = (G, \sigma^2)$ with $G = (G_{qq}, G_{Qq}, G_{QQ})$
  - missing genotype vector $Q = (Q_1, Q_2, \ldots, Q_n)$
- Gibbs sampler: update one at a time via full conditionals
  - randomly select order of unknowns
  - update each given current values of all others, locus λ and data (Y,X)
    - sample variance σ^2 given Y,Q and genetic values G
    - sample genotype Q_i given markers X_i and locus λ
  - can do block updates if more efficient
    - sample all genetic values G given Y,Q and variance σ^2

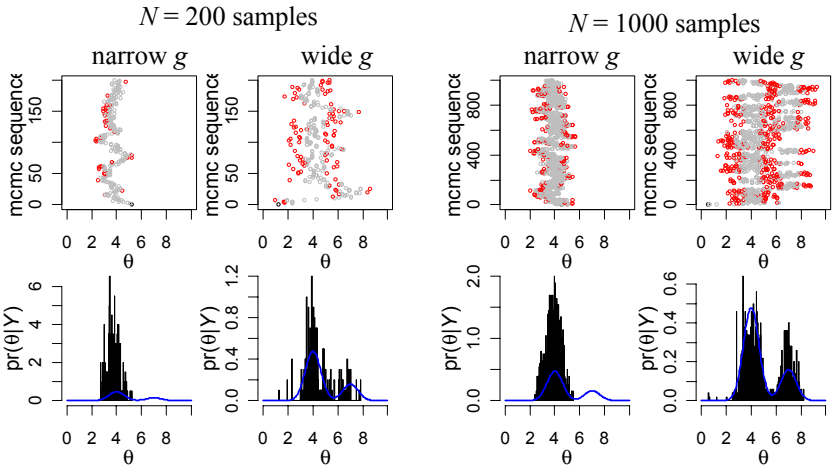
Metropolis-Hastings idea

- want to study distribution $f(\theta)$
- take Monte Carlo samples
  - unless too complicated
- Metropolis-Hastings samples:
  - current sample value θ
  - propose new value θ^*
    - from some distribution $g(\theta,\theta^*)$
    - Gibbs sampler: $g(\theta,\theta^*) = f(\theta^*)$
  - accept new value with prob A
    - Gibbs sampler: $A = 1$

$$A = \min\left(1, \frac{f(\theta^*)g(\theta^*,\theta)}{f(\theta)g(\theta,\theta^*)}\right)$$



Metropolis-Hastings samples



full conditional for locus

- cannot easily sample from locus full conditional

$$\begin{aligned} \Pr(\lambda \mid Y, X, \theta, Q) &= \Pr(\lambda \mid X, Q) \\ &= \Pr(\lambda)\ \Pr(Q \mid X, \lambda)\ / \text{constant} \end{aligned}$$

- cannot explicitly determine full conditional
  - difficult to normalize
  - need to average over all possible genotypes over entire map
- Gibbs sampler will not work
  - but can use method based on ratios of probabilities…

Metropolis-Hastings Step

- pick new locus based upon current locus
  - propose new locus from distribution $q(\ )$
    - pick value near current one?
    - pick uniformly across genome?
  - accept new locus with probability $a()$
- Gibbs sampler is special case of M-H
  - always accept new proposal
- acceptance insures right stable distribution
  - accept new proposal with probability A
  - otherwise stick with current value

$$A(\lambda_{old}, \lambda_{new}) = \min\left(1, \frac{\pi(\lambda_{new} \mid \mathbf{x}^*) q(\lambda_{new}, \lambda_{old})}{\pi(\lambda_{old} \mid \mathbf{x}^*) q(\lambda_{old}, \lambda_{new})}\right)$$

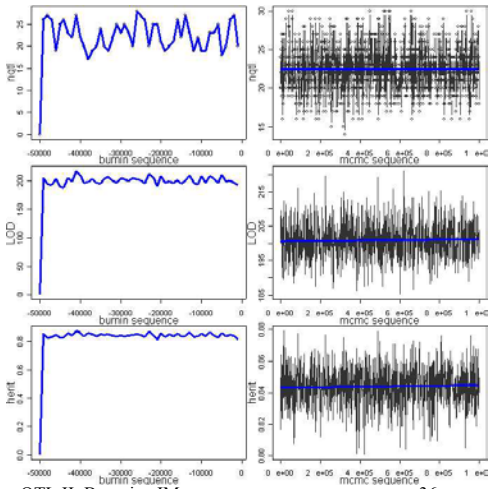
Markov chain Monte Carlo

- can study arbitrarily complex models
  - need only specify how parameters affect each other
  - can reduce to specifying full conditionals
- construct Markov chain with "right" model
  - joint posterior of unknowns as limiting "stable" distribution
  - update unknowns given data and all other unknowns
    - sample from full conditionals
    - cycle at random through all parameters
  - next step depends only on current values
- nice Markov chains have nice properties
  - sample summaries make sense
  - consider almost as random sample from distribution
  - ergodic theorem and all that stuff

MCMC diagnostics for *Dm* shape

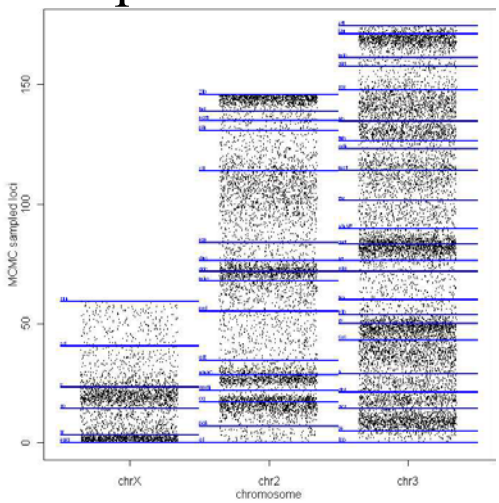
- *m* ~ Poisson(15) prior on number of QTL
- Bayesian LOD (log posterior density)
- Heritability

- 5% burnin
- 1,000,000 samples
  - every 1000th recorded
- note stable mean



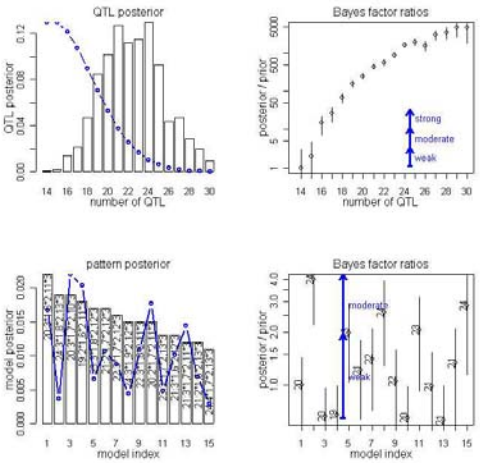
MCMC sampled loci

- markers as blue lines
  - horizontal jittering
- note denser regions
  - 10-11 broad regions
- jointly sampling
  - 15-30 QTL at once



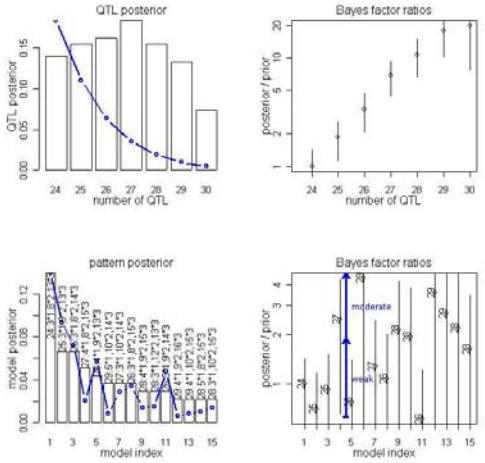
MCMC model selection

- m = number of QTL
  - prior: Poisson(15)
    - rescaled in blue
  - posterior: mean 22.4
  - Bayes factor increases
- pattern across genome
  - prior depends on m and length of chromosomes
  - posterior mode: m=20
  - Bayes factor favors
    - m = 24
    - 3*1, 8*2, 13*3



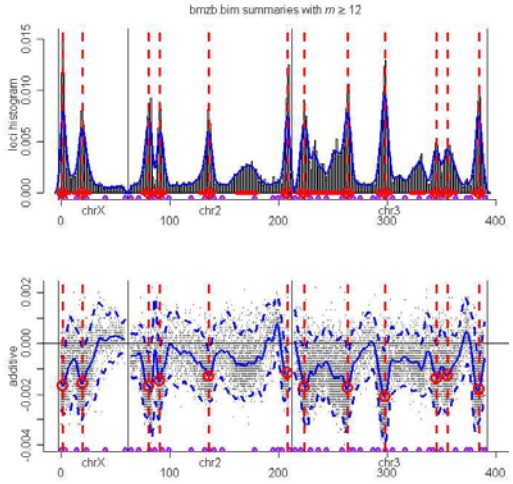
MCMC model selection restricted to "better models"

- models with minimum
  - $m \geq 24$
  - pattern ≥ 3*1, 8*2, 13*3
- note uncertainty in BF
  - estimate ± 2 SE
- mode is chosen pattern
  - ~14% of samples
- BF similar to more complicated patterns
  - parsimony: simpler model
  - 2SE intervals overlap



MCMC loci and effects

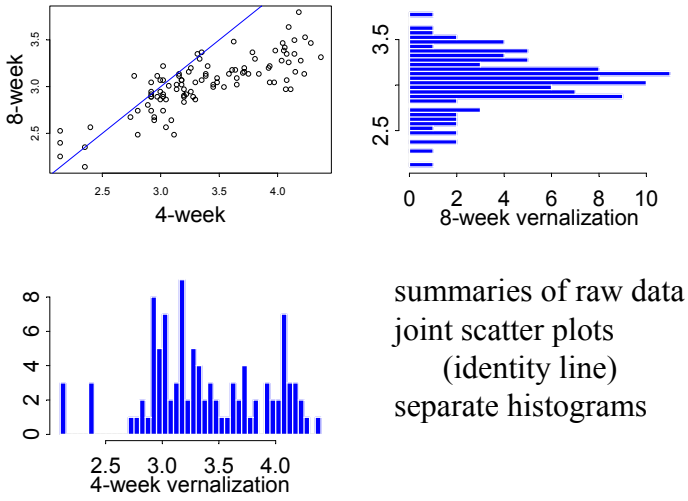
- model averaging
  - over all models
  - 1000 samples
- histogram of loci
  - marginal posteriors
  - superimposed on genome
  - 12 peaks identified
- scatterplot: loci & effects
  - smoothed mean ± 2 SE



Brassica napus data

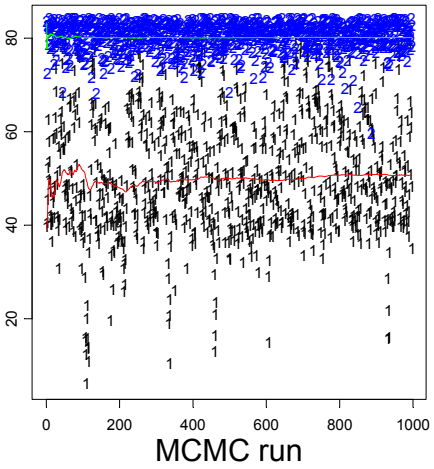
- 4-week & 8-week vernalization effect
  - log(days to flower)
- genetic cross of
  - Stellar (annual canola)
  - Major (biennial rapeseed)
- 105 F1-derived double haploid (DH) lines
  - homozygous at every locus (*QQ* or *qq*)
- 10 molecular markers (RFLPs) on LG9
  - two QTLs inferred on LG9 (now chromosome N2)
  - corroborated by Butruille (1998)
  - exploiting synteny with *Arabidopsis thaliana*

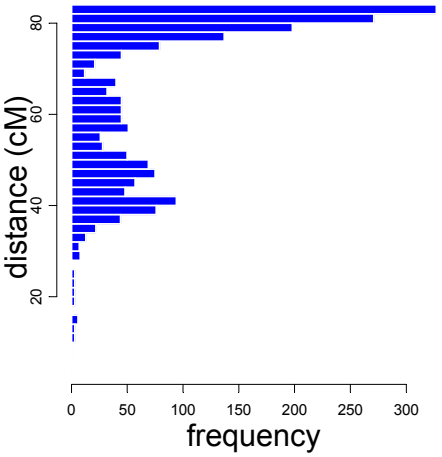
Brassica 4- & 8-week data



summaries of raw data
joint scatter plots
(identity line)
separate histograms

Brassica 8-week data locus MCMC with m=2





4-week vs 8-week vernalization

4-week vernalization

- longer time to flower
- larger LOD at 40cM
- modest LOD at 80cM
- loci well determined

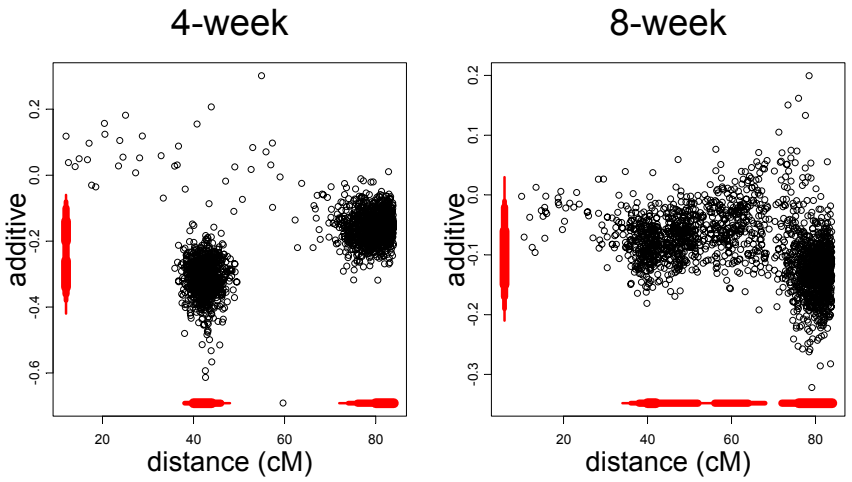
cM	add
40	.30
80	.16

8-week vernalization

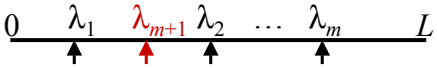
- shorter time to flower
- larger LOD at 80cM
- modest LOD at 40cM
- loci poorly determined

cM	add
40	.06
80	.13

Brassica credible regions



reversible jump MCMC



action steps: draw one of three choices

- update m-QTL model with probability 1-$b(m+1)$-$d(m)$
  - update current model using full conditionals
  - sample m QTL loci, effects, and genotypes
- add a locus with probability $b(m+1)$
  - propose a new locus along genome
  - innovate new genotypes at locus and phenotype effect
  - decide whether to accept the "birth" of new locus
- drop a locus with probability $d(m)$
  - propose dropping one of existing loci
  - decide whether to accept the "death" of locus

sampling the number of QTL

- use reversible jump MCMC to change *m*
  - bookkeeping helps in comparing models
  - adjust to change of variables between models
  - Green (1995); Richardson Green (1997)
  - other approaches out there these days…
- think model selection in multiple regression
  - but regressors (QT genotypes) are unknown
  - linked loci = collinear regressors = correlated effects
  - consider additive effects with coding Q_{ij}= -1,0,1

$$\theta_{ijQ} = \alpha_j (Q_{ij} - \overline{Q}_j)$$

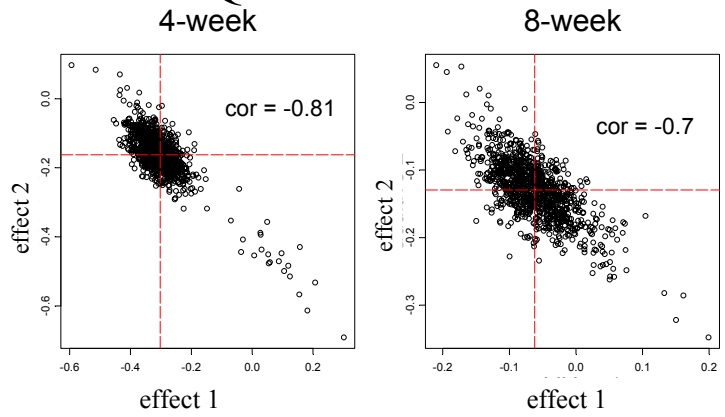
model selection in regression

- consider known genotypes (*Q*)
  - models with 1 or 2 QTL at known loci
- jump between 1-QTL and 2-QTL models
  - adjust posteriors when model changes
  - due to collinearity of QTL genotypes

$$m = 1 : Y_i = \mu + \alpha(Q_{i1} - \overline{Q}_1) + e_i$$

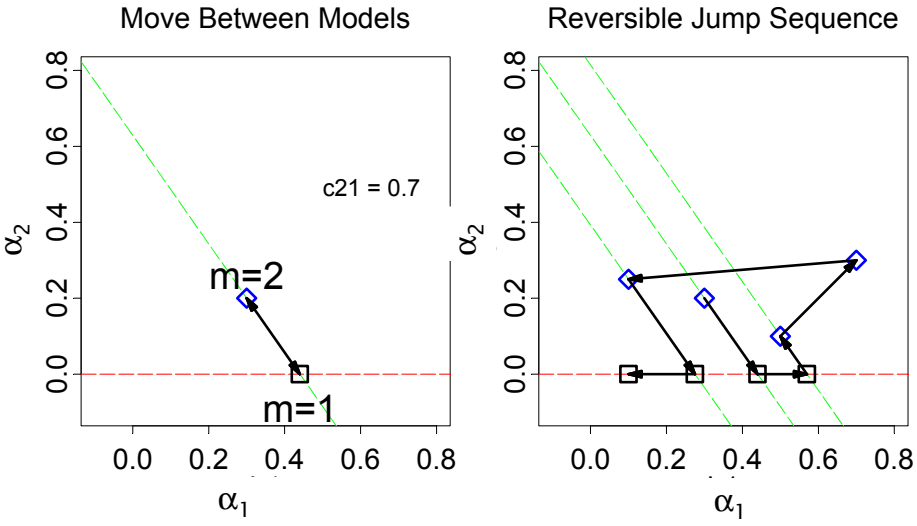
$$m = 2 : Y_i = \mu + \alpha_1(Q_{i1} - \overline{Q}_1) + \alpha_2(Q_{i1} - \overline{Q}_1) + e_i$$

collinear QTL = correlated effects

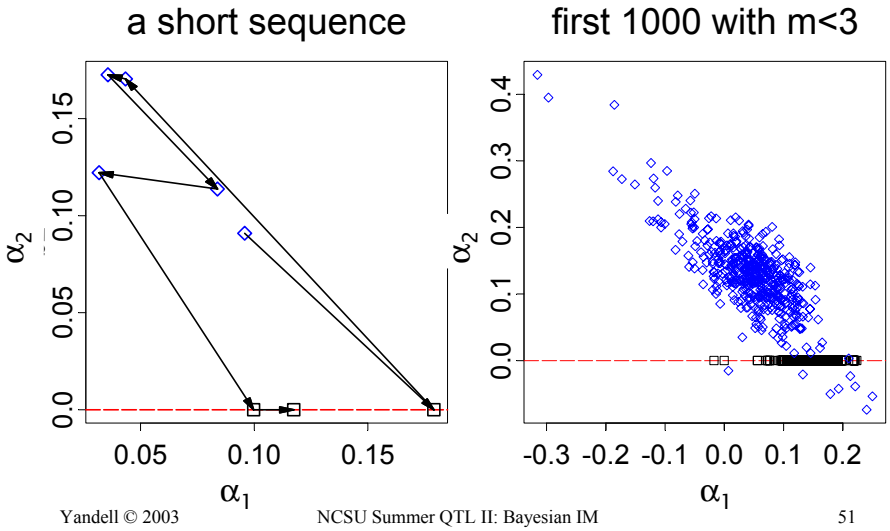


- linked QTL: collinear genotypes & correlated effect estimates
  - –sum of linked effects usually well determined
- which QTL to go after in breeding, genome walking?

Geometry of Reversible Jump



QT additive Reversible Jump



Bmapqtl: our RJ-MCMC software

- www.stat.wisc.edu/~yandell/qtl/software/Bmapqtl
  - module using QtlCart format
  - compiled in C for Windows/NT
  - extensions in progress
  - R post-processing graphics
    - library(bim) is cross-compatible with library(qtl)
- Bayes factor and reversible jump MCMC computation
- enhances MCMCQTL and revjump software
  - initially designed by JM Satagopan (1996)
  - major revision and extension by PJ Gaffney (2001)
    - whole genome
    - multivariate update of effects; long range position updates
    - substantial improvements in speed, efficiency
    - pre-burnin: initial prior number of QTL very large