(Felsenstein 1981)

Using and Interpreting Contrasts

$$\hat{\sigma}^2 = \frac{\sum S_i}{n-1}$$

- This provides an unbiased estimate of evolutionary rate
- The expected value of this estimate is equal to the actual rate parameter
- The maximum likelihood estimate of the rate parameter is biased

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution
- The contrasts have a close relationship with σ^2, the rate parameter from BM
- The sum of the squared contrasts divided by n gives the ML estimate of σ^2

Character correlations

- Most common use for ICs: testing for character correlations
- Are two characters evolving in a correlated fashion?

Using and Interpreting Contrasts

- Independent contrasts should be thought of as vectors
- They summarize information about the **amount** and **direction** of evolution at each node in the tree
- Standardized contrasts provide information about the **rate** of evolution

Character correlations

- Calculate independent contrasts for two characters, x and y
- Carry out a regression analysis of y on x with **no intercept** (force regression line through the origin)
- P < 0.05, then reject the null hypothesis of no evolutionary correlation

Character correlations

- Why force contrasts through the origin?
- Because, for each contrast, the direction of subtraction is arbitrary; the signs of all the contrasts could be reversed
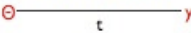- Regression through the origin treats the contrasts as vectors

Outline

- Calculating the likelihood for a single character evolving under a BM model
- Alternative models for continuous character evolution
- Multivariate character evolution

Outline - BM

- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
- Simulating Brownian motion on trees
- Independent contrasts

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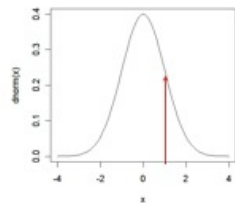
Likelihoods for Continuous Characters

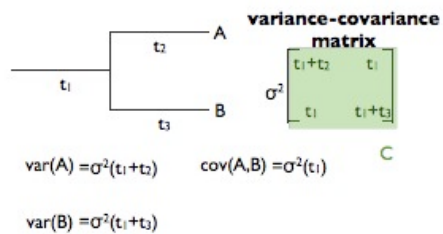March 31, 2009

Likelihood for a single character

Brownian motion

$\Theta \underset{t}{\rule{3cm}{0.4pt}} y$

$y \sim N(0, \sigma^2 * t)$

$$\Pr[y = x] = \frac{1}{\sigma\sqrt{2\pi t}} \exp\left(-\frac{(x-\theta)^2}{2\sigma^2 t}\right)$$

Multivariate Normal

variance-covariance matrix

$$\sigma^2 \begin{bmatrix} t_1+t_2 & t_1 \\ t_1 & t_1+t_3 \end{bmatrix}$$

var(A) = $\sigma^2(t_1+t_2)$ cov(A,B) = $\sigma^2(t_1)$

var(B) = $\sigma^2(t_1+t_3)$

Two dimensions (x, y) correspond to tree with n=2

$$f(x,y) = \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left(\frac{x^2}{\sigma_x^2} + \frac{y^2}{\sigma_y^2} - \frac{2\rho xy}{(\sigma_x\sigma_y)}\right)\right)$$

More dimensions gets more complicated
Easy to do with computers

Likelihood for continuous characters on trees

- Given phylogeny, measurements of character y for each tip (y_i)
- Choose a rate parameter σ^2 and mean Θ
- Calculate the phylogenetic variance-covariance matrix for the tree **V**

Likelihood for continuous characters on trees

- $y_i \sim$ MVN(Θ, σ^2**V**)
- Determine the probability of drawing the vector of y_i from the MVN distribution with mean Θ and vcv σ^2**V**

Analytic Solution for MLE

$$\hat{\sigma}^2 = \frac{(\mathbf{x}-\hat{a}\mathbf{1})'\mathbf{C}^{-1}(\mathbf{x}-\hat{a}\mathbf{1})}{n}$$

$$\hat{\mathbf{a}} = [(\mathbf{1}'\mathbf{C}^{-1}\mathbf{1})^{-1}(\mathbf{1}'\mathbf{C}^{-1}\mathbf{X})]'$$

x = vector of trait values, n = number of species,
C = coancestry matrix (shared path lengths)

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Three Models for Phenotypic Evolution

- Single Rate (SR)
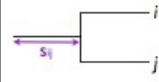- Early Burst (EB)
- Constant Constraints (CC)

Single Rate Model (SR)

- Brownian motion model with a constant rate of evolution
- Two parameters: starting value (Θ) and rate (σ^2)

Early Burst Model (EB)

- Rate of evolution slows through time
- Highest rate at the root of the tree
- Three parameters: starting value (Θ), starting rate (σ^2_0), and rate change (r)

$$r(t) = \sigma_0^2 \, e^{rt}$$

$$V_{ij} = \int_0^{s_{ij}} \sigma_0^2 \, e^{rt} \, dt = \sigma_0^2 \, \frac{e^{r s_{ij}}}{r}$$

Constant Constraints Model (CC)

- Evolution has a tendency to move towards some medial value
- "Brownian motion with a spring"
- Three parameters: starting value (Θ), rate (σ^2), and constraint parameter (α)

$$V_{ij} = \frac{\sigma^2}{\alpha} e^{-2\alpha(T - s_{ij})}(1 - e^{-2\alpha s_{ij}})$$

T = total tree depth

Why these three?

- SR (Brownian motion) is assumed by almost all phylogenetic comparative methods
- EB (early burst) corresponds to one idea of adaptive radiation
- CC (constant constraint) may capture the importance of constraints on evolution

Slide 1: BM   CC   EB

Slide 2 (top right):

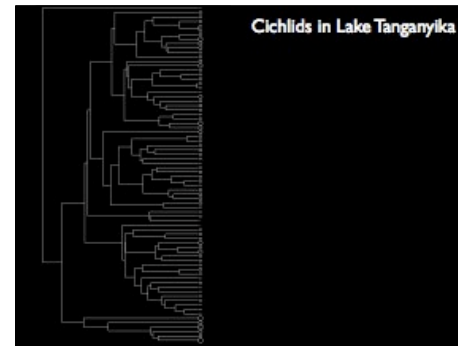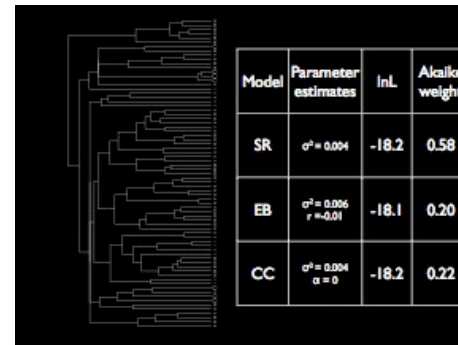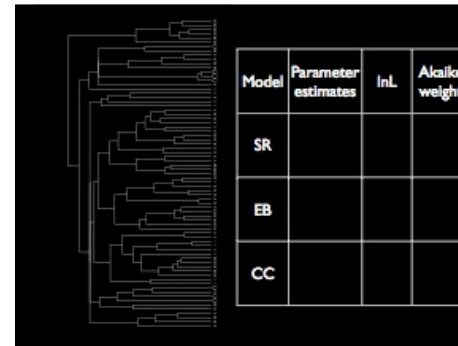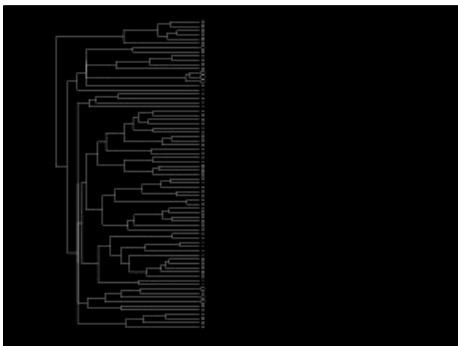| Model	Parameter estimates	lnL	Akaike weight
SR			
EB			
CC			
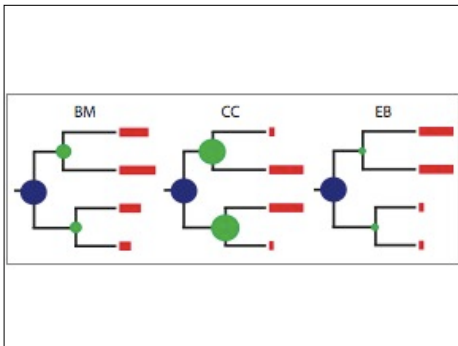
Example: *Anolis* lizards

- Lizards on Caribbean islands
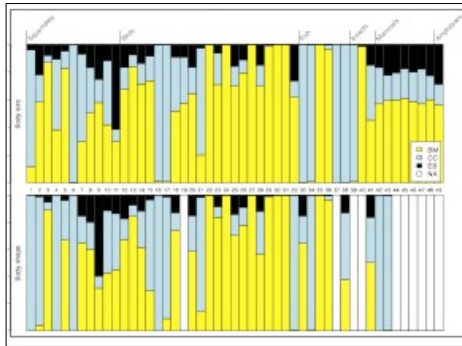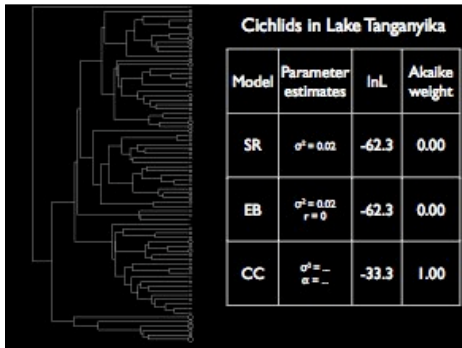- Phylogenetic and body size data for 73 species (out of ~140 total)

Anolis baleatus

Slide 4 (middle right):

Model	Parameter estimates	lnL	Akaike weight
SR	$\sigma^2 = 0.004$	-18.2	0.58
EB	$\sigma^2 = 0.006$ $r = -0.01$	-18.1	0.20
CC	$\sigma^2 = 0.004$ $\alpha = 0$	-18.2	0.22

Slide 5 (bottom left):

Slide 6 (bottom right): Cichlids in Lake Tanganyika

Cichlids in Lake Tanganyika

Model	Parameter estimates	lnL	Akaike weight
SR	$\sigma^2 = 0.02$	-62.3	0.00
EB	$\sigma^2 = 0.02$, $r = 0$	-62.3	0.00
CC	$\sigma^2 = \_$, $\alpha = \_$	-33.3	1.00

Brownian "Rates" Scale with Time

- "Adaptive radiation" pattern very rare in this data set
- Constraints dominate over long time periods
- Brownian motion is sometimes a poor fit to real data

Table 1. Number of clades and subclades showing support for each of the three models (BM, CC, EB) for body size and body shape. We count both the number of clades with the highest AICc values for a particular model ("maximum w") and those with weights greater than 0.95 ("w > 0.95").

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What if you have more than one character?

- Consider two characters evolving on a single tree
- Use a multivariate Brownian motion model
- Each character has a rate of evolution σ_i^2
- Characters also have an evolutionary covariance $\sigma_{i,j}$
- We can call this evolutionary vcv matrix R

Four taxa, two traits

What if you have more than one character?

- For each character, species covary with each other according to the coancestry matrix C
- Within species, characters covary according to the evolutionary covariance matrix R

Multiple characters

- Equations for the likelihood and analytic solutions for the mle are fairly simple, see Revell and Harmon 2008
- Easy likelihood-based tests for character correlations, etc.
- Still very similar to approaches based on contrasts

What if you have more than one character?

- All characters for all species are drawn from a multivariate normal distribution
- $V = R \otimes C$
- $\otimes$ is the *Kronecker product*

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