

TABLE 1  
THE FOUR CONTRASTS EXTRACTED FROM THE PHYLOGENY  
SHOWN IN FIGURE 9, EACH WITH ITS VARIANCE, ALL  
COMPUTED USING STEPS 1-4 IN THE TEXT

CONTRAST	VARIANCE
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v'_6$
$X_7 - X_8$	$v'_7 + v'_8$

where

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5}$$

$$v'_6 = v_6 + v_4 v_5 / (v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2}$$

$$v'_7 = v_7 + v_1 v_2 / (v_1 + v_2)$$

$$X_8 = \frac{v'_6 X_3 + v_3 X_6}{v_3 + v'_6}$$

$$v'_8 = v'_7 + v_3 v'_6 / (v_3 + v'_6)$$

(Felsenstein 1981)

## What are contrasts?

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

## 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

## 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

## Character correlations

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

## 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 - BM

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

# Likelihoods for Continuous Characters

March 31, 2009

# Outline

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

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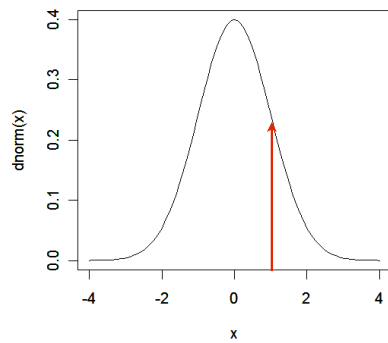
# Likelihood for a single character

Brownian motion

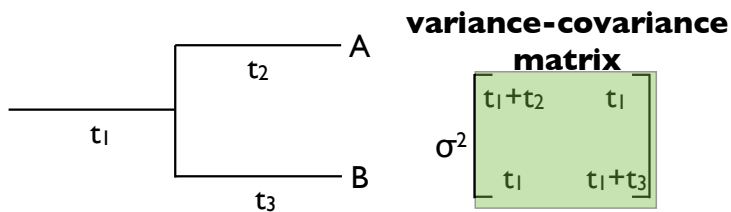
$\Theta$  —————  $y$   
t

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

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



## Multivariate Normal



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

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

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  $\sigma^2$  and mean  $\Theta$
- Calculate the phylogenetic variance-covariance matrix for the tree  $\mathbf{V}$

## Likelihood for continuous characters on trees

- $y_i \sim \text{MVN}(\Theta, \sigma^2 \mathbf{V})$
- Determine the probability of drawing the vector of  $y_i$  from the MVN distribution with mean  $\Theta$  and vcv  $\sigma^2 \mathbf{V}$

## Analytic Solution for MLE

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

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

$\mathbf{x}$  = vector of trait values,  $n$  = number of species,  
 $\mathbf{C}$  = coancestry matrix (shared path lengths)