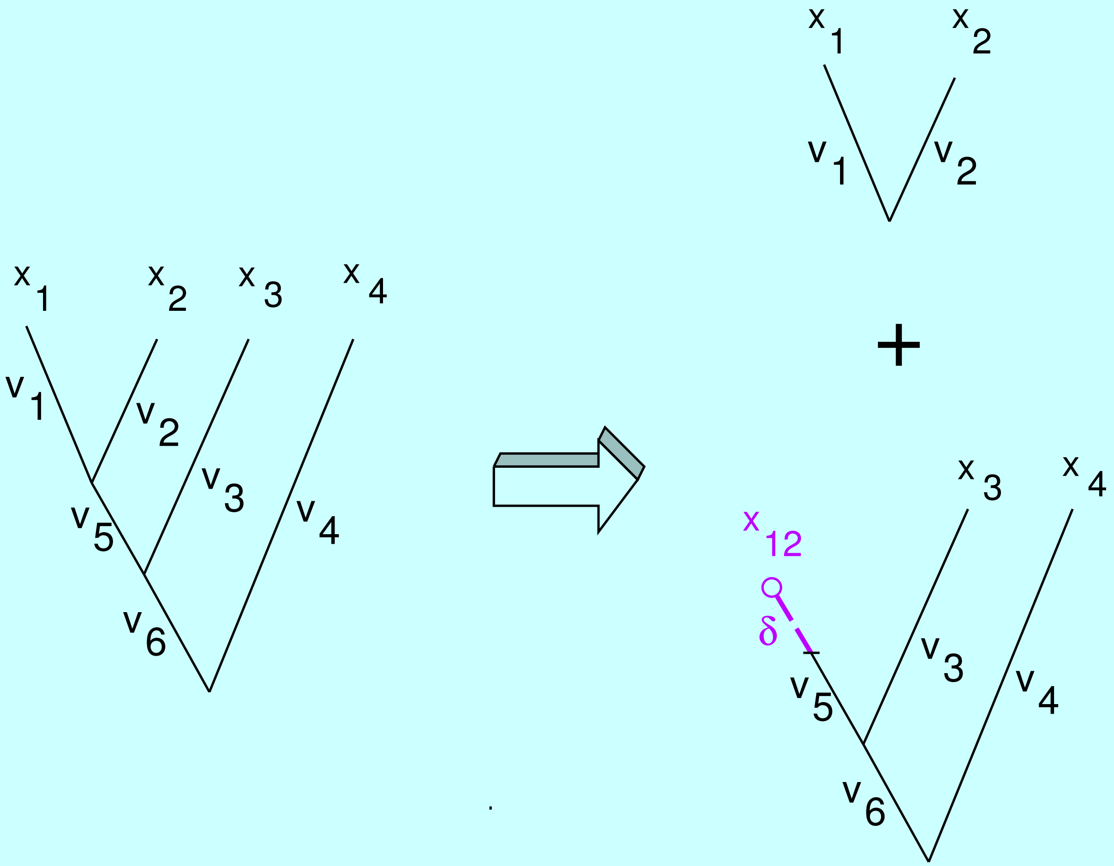
Week 9: Quantitative characters, comparative method, coalescents

Genome 570

March, 2016

“Pruning” a tree in the Brownian motion case



$$\delta = \frac{v_1 v_2}{v_1 + v_2}$$

$$x_{12} = \frac{v_2 x_1 + v_1 x_2}{v_1 + v_2}$$

What about quantitative characters?

In the classical (Fisher, 1918) model of quantitative genetics, a quantitative character is a sum of contributions from different loci, plus an independent environmental effect:

$$P = \mu + \left\{ \begin{array}{cc} \mathrm{AA} & 1.2 \\ \mathrm{Aa} & 0.8 \\ \mathrm{aa} & 0.7 \end{array} \right\} + \left\{ \begin{array}{cc} \mathrm{BB} & -0.02 \\ \mathrm{Bb} & 0.00 \\ \mathrm{bb} & 0.01 \end{array} \right\} + \ldots + \left\{ \begin{array}{cc} \mathrm{ZZ} & 0.21 \\ \mathrm{Zz} & 0.21 \\ \mathrm{zz} & -0.17 \end{array} \right\} + \varepsilon$$

In that case if locus is independently changing by (approximate) Brownian motion, the character's phenotype will also change by approximate Brownian motion.

What about quantitative characters?

For neutral mutation and genetic drift, can show that for a quantitative character with additive genetic variance V_A and population size N the variance through time of the genetic (additive) value of the population mean is:

$$\mathrm{Var}(\Delta\bar{g}) \;=\; V_A/N$$

so it is smaller the bigger the population is, as there is less genetic drift. If mutation and drift are at equilibrium:

$$E\left[V_A^{(t+1)}\right] \;=\; V_A^{(t)}\left(1-\frac{1}{2N}\right)+V_M$$

which lets us calculate what the additive genetic variance becomes, on average. This leads to a surprise ...

In neutral traits multational variance rules

so that

$$\mathsf{E}\left[\mathsf{V_A}\right] \;=\; \mathsf{2NV_M}$$

whereby

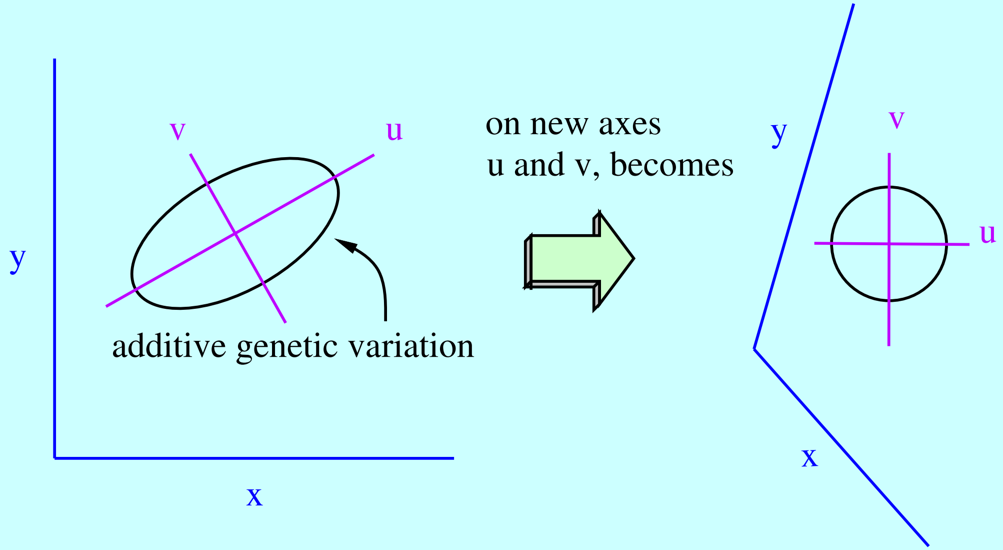
$$\mathrm{Var}[\Delta\bar{\mathsf{g}}] \;=\; \left(\mathsf{2NV_M}\right)/\mathsf{N} \;=\; \mathsf{2V_M},$$

an analogue of Kimura's result for neutral mutation.

Long-term change would mirror genetic variation

There is a precise analogue of those equations for multiple characters, using matrices instead of scalars in the equations.

Thus to transform characters to independent Brownian motions of equal evolutionary variance, we could use their current additive genetic covariances $\boldsymbol{V}_{\mathsf{A}}$,



We come up with new axes that vary independently among species. The independent Brownian Motion on these axes shows that neutral variation changes in the directions of the Principal Components of the original additive genetic covariance matrix.

With selection ... life is harder

There is the quantitative genetics formula of Wright and Fisher (1920's)

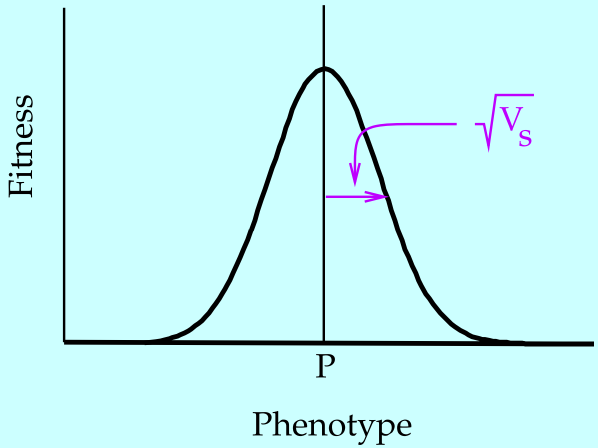
$$\Delta z \ = \ h^2 S$$

and Russ Lande's (1976) recasting of that in terms of slopes of mean fitness surfaces:

$$S \ = \ V_P \ \frac{d \log(\bar{w})}{dx}$$

$$\Delta z \ = \ (V_A / V_P) \ V_P \ \frac{d \log(\bar{w})}{dx} \ = \ V_A \ \frac{d \log(\bar{w})}{dx}$$

Selection towards an optimum



If fitness as a function of phenotype is:

$$w(x) \; = \; \exp\left[-\frac{(x-p)^2}{2V_s}\right],$$

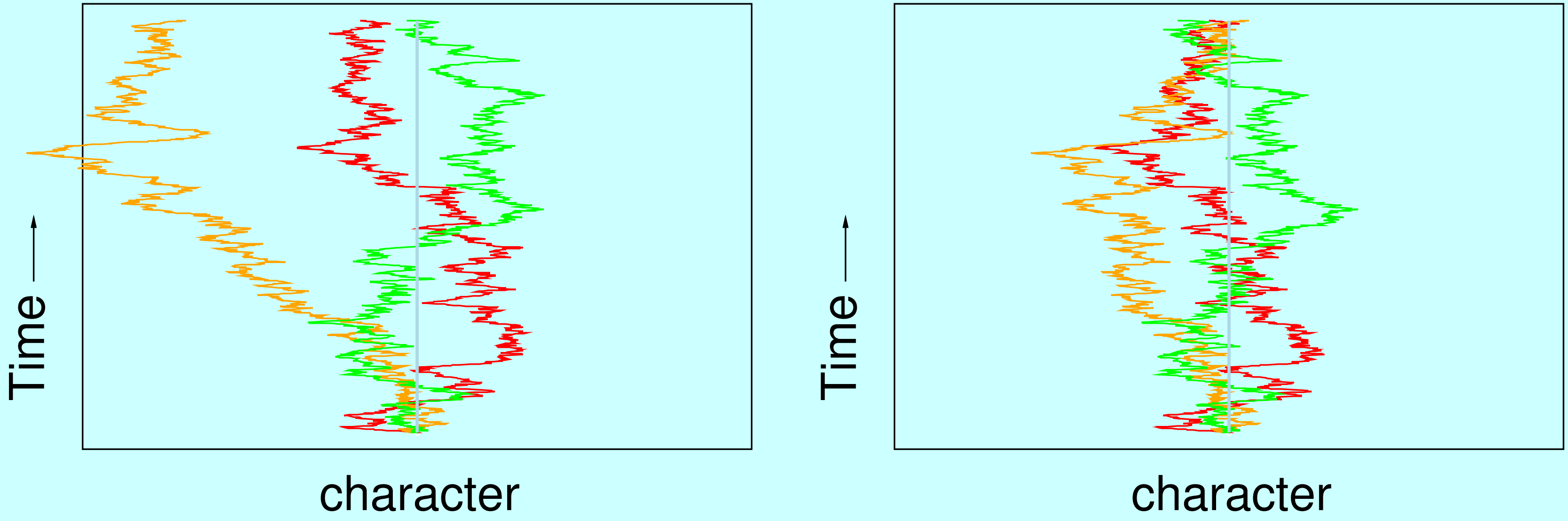
Then the change of mean phenotype “chases” the optimum:

$$m' - m \; = \; \frac{V_A}{V_s + V_P}\,(p - m),$$

in each generation moving a constant fraction of the way to the optimum.

Genetic drift, mutation and selection give an OU process

(The plots are from the same sets of random numbers)



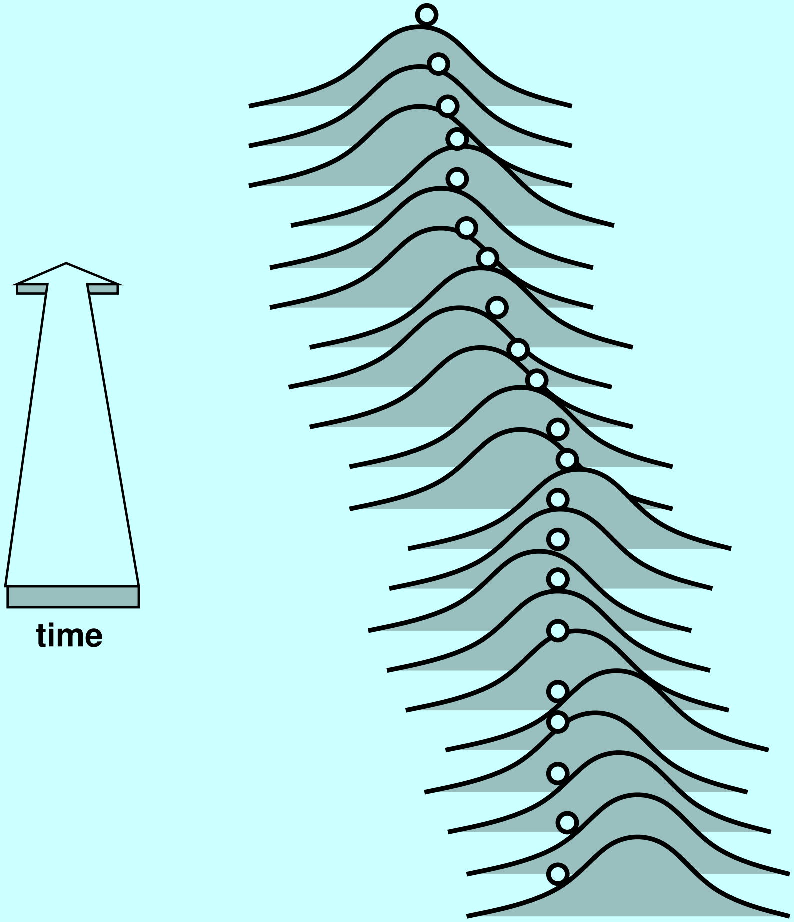
Brownian motion

an OU process

The process is approximately an Ornstein-Uhlenbeck Process, a relative of Brownian Motion in which the particle is “elastically bound” (tethered to a post by an elastic band).

In this case the OU process has the particle wandering by genetic drift, but constantly pulled toward the optimum value by natural selection.

A character changing by “chasing” an adaptive peak



The course of change of the population mean is expected to be somewhat smoother than the changes of the peak of the fitness surface.

Sources of evolutionary correlation among characters

Variation (and covariation) in change of characters occurs for two reasons:

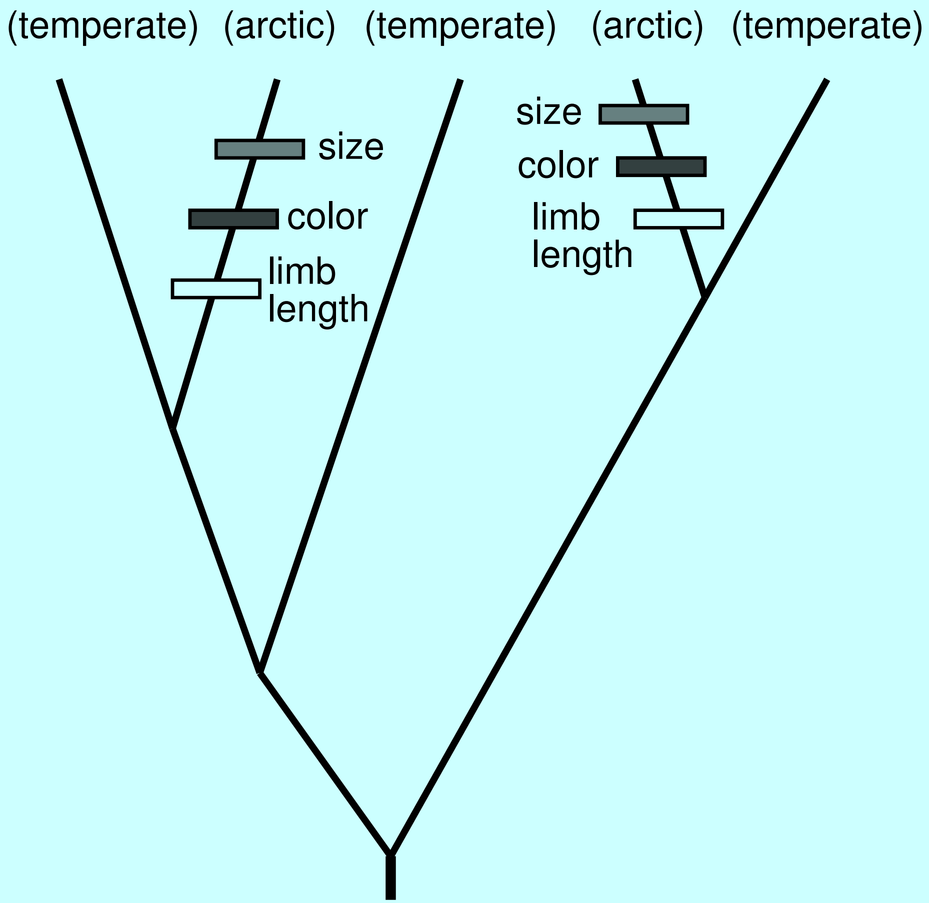
1. Genetic drift, with the covariances being proportional to the additive genetic covariances
2. Selection, with the covariances being affected by both the additive genetic covariances and the covariation of the selection pressures.

A simple example of selective covariance

covariation due not to genetic correlation
but to covariation of the selection pressure

These are Bergmann's, Allen's and Glogler's Rules
They are presumably not the result of genetic correlations
but result from patterns of selection

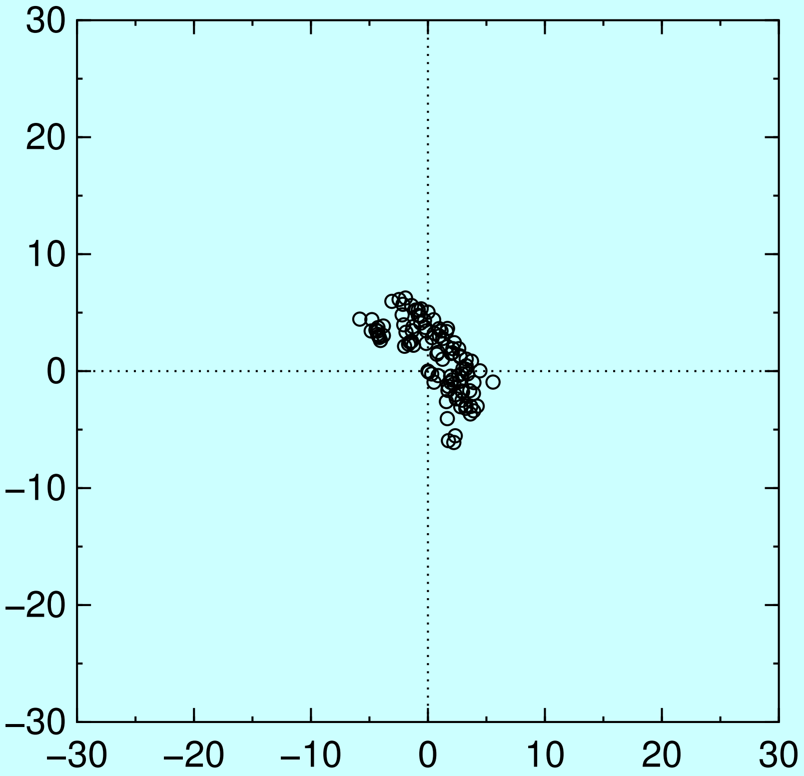
a simple example:



G. L. Stebbins. 1950. *Variation and evolution in plants.* Columbia Univ. Press, New York. page 121

A simulated example with two characters

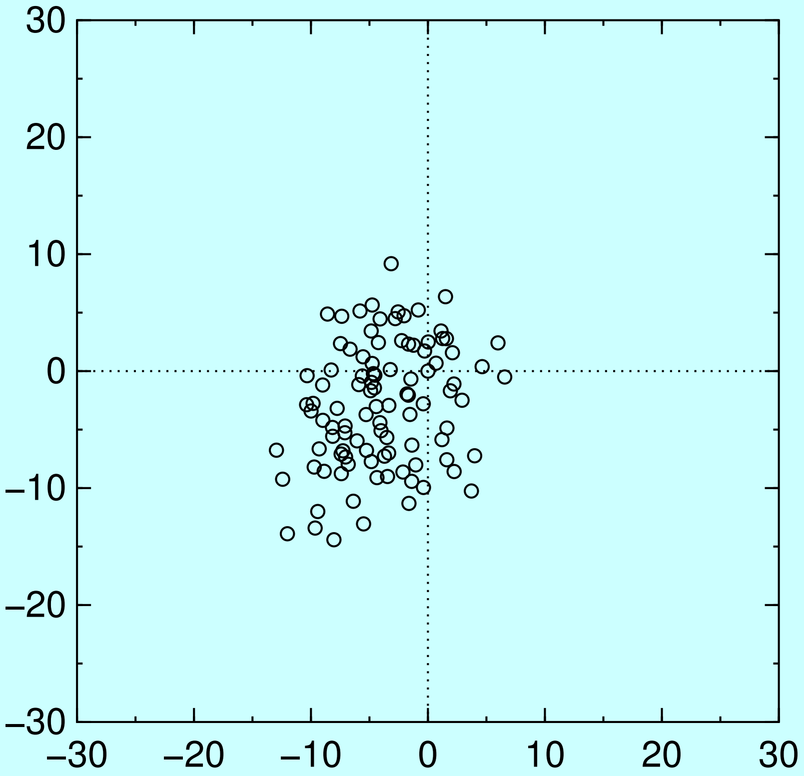
After 100 generations:



Genetic covariances are negative, but the wanderings of the adaptive peak in the two characters are positively correlated.

A simulated example with two characters

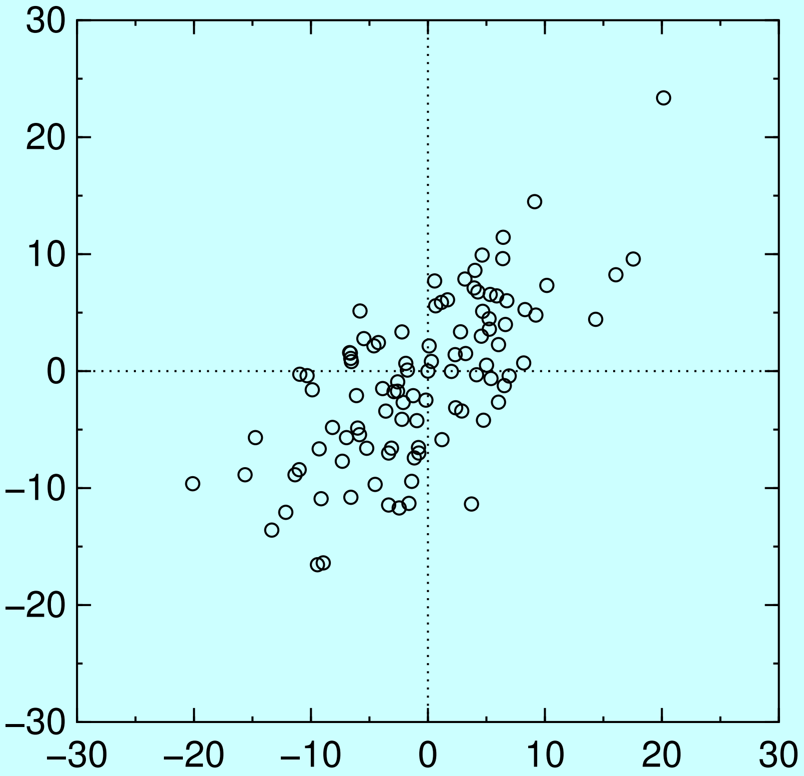
After 1000 generations:



Genetic covariances are negative, but the wanderings of the adaptive peak in the two characters is positively correlated.

A simulated example with two characters

After 10,000 generations:



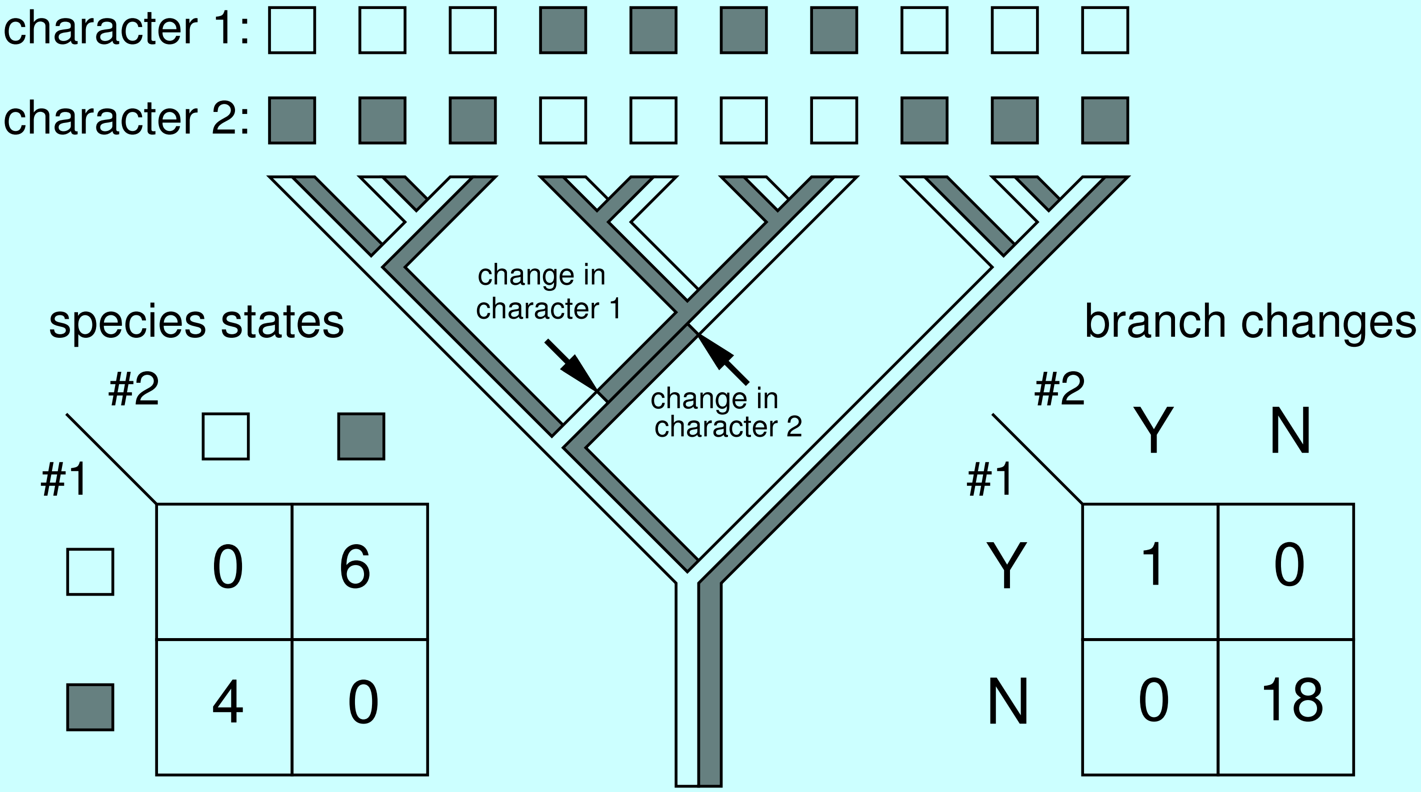
Genetic covariances are negative, but the wanderings of the adaptive peak in the two characters is positively correlated. As time goes on, the covariation of character changes is more and more dominated by the movement of the peak.

Correcting for correlations among characters

Can we transform the set of characters to remove their correlations and thus end up with independent Brownian motions of equal variance?

- We might hope to infer additive genetic covariances by doing quantitive genetics breeding experiments to infer them from covariances among relatives.
- There is little or no hope of inferring “selective correlations” without a complete understanding of the functional ecology.
- If we are given the tree from molecular data (and are willing to assume that the branch lengths are proportional to those that apply to the morphological characters), we can hope to use the tree to infer the covariation of the characters. (See the discussion of comparative methods, below).

Correlation of states in a discrete-state model



character 1: □ □ □ ■ ■ ■ ■ □ □ □

character 2: ■ ■ ■ □ □ □ □ ■ ■ ■

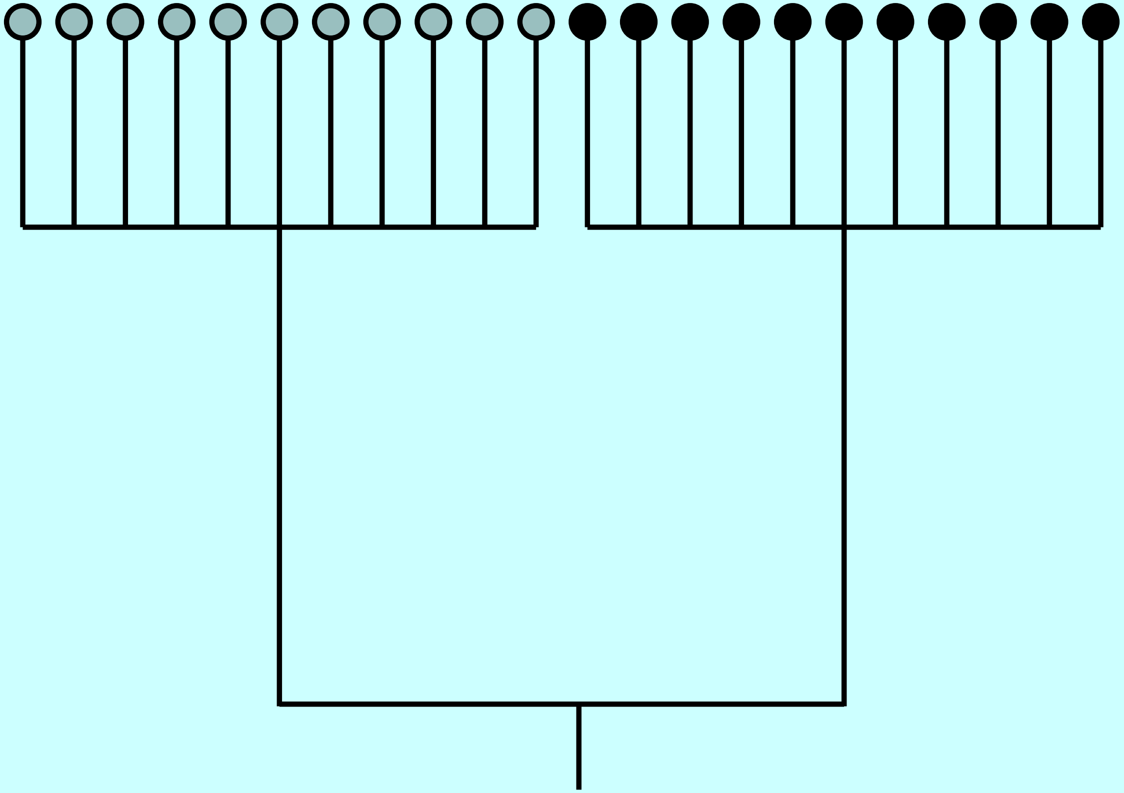
species states

#1 \ #2	□	■
□	0	6
■	4	0

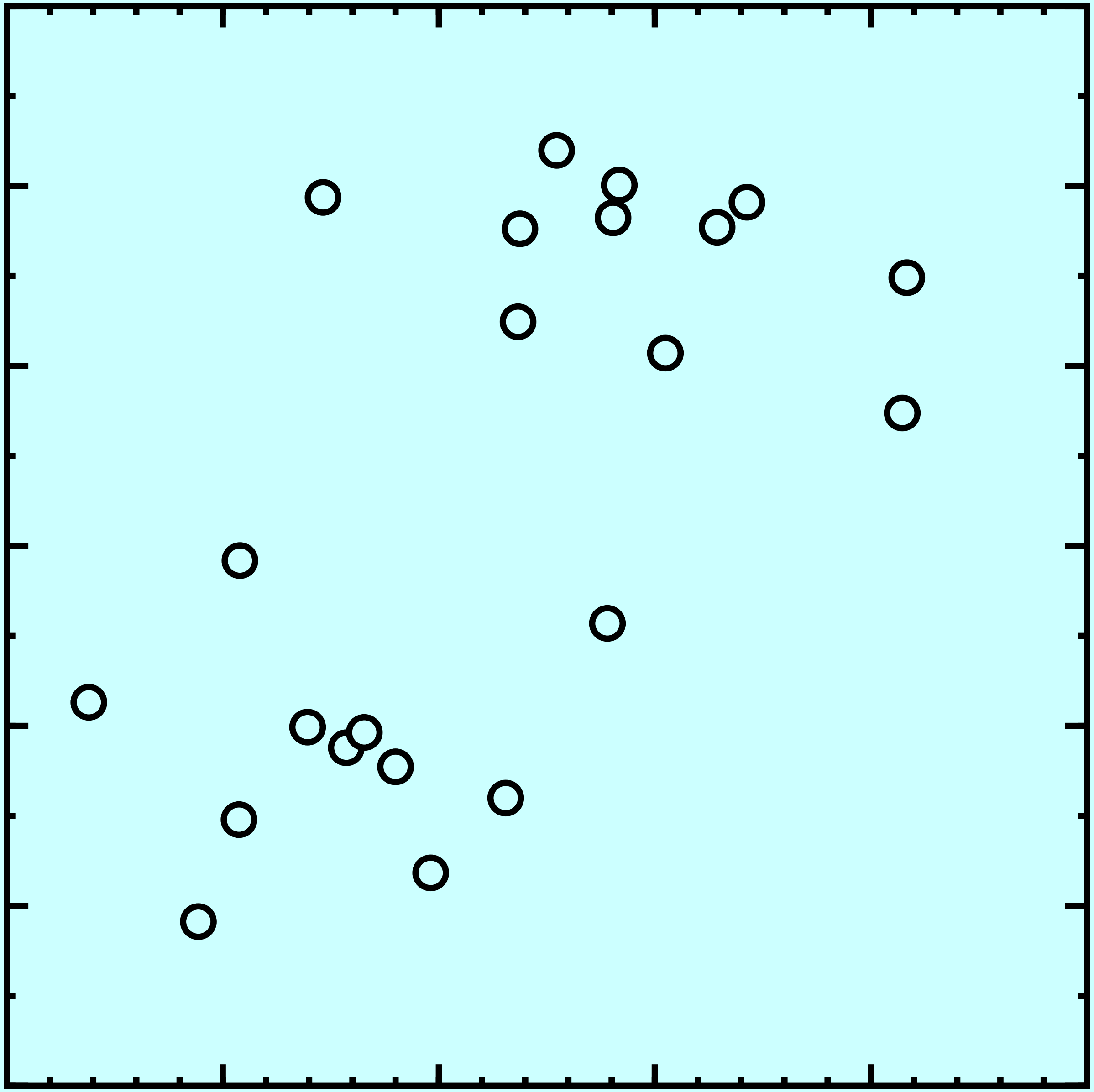
branch changes

#1 \ #2	Y	N
Y	1	0
N	0	18

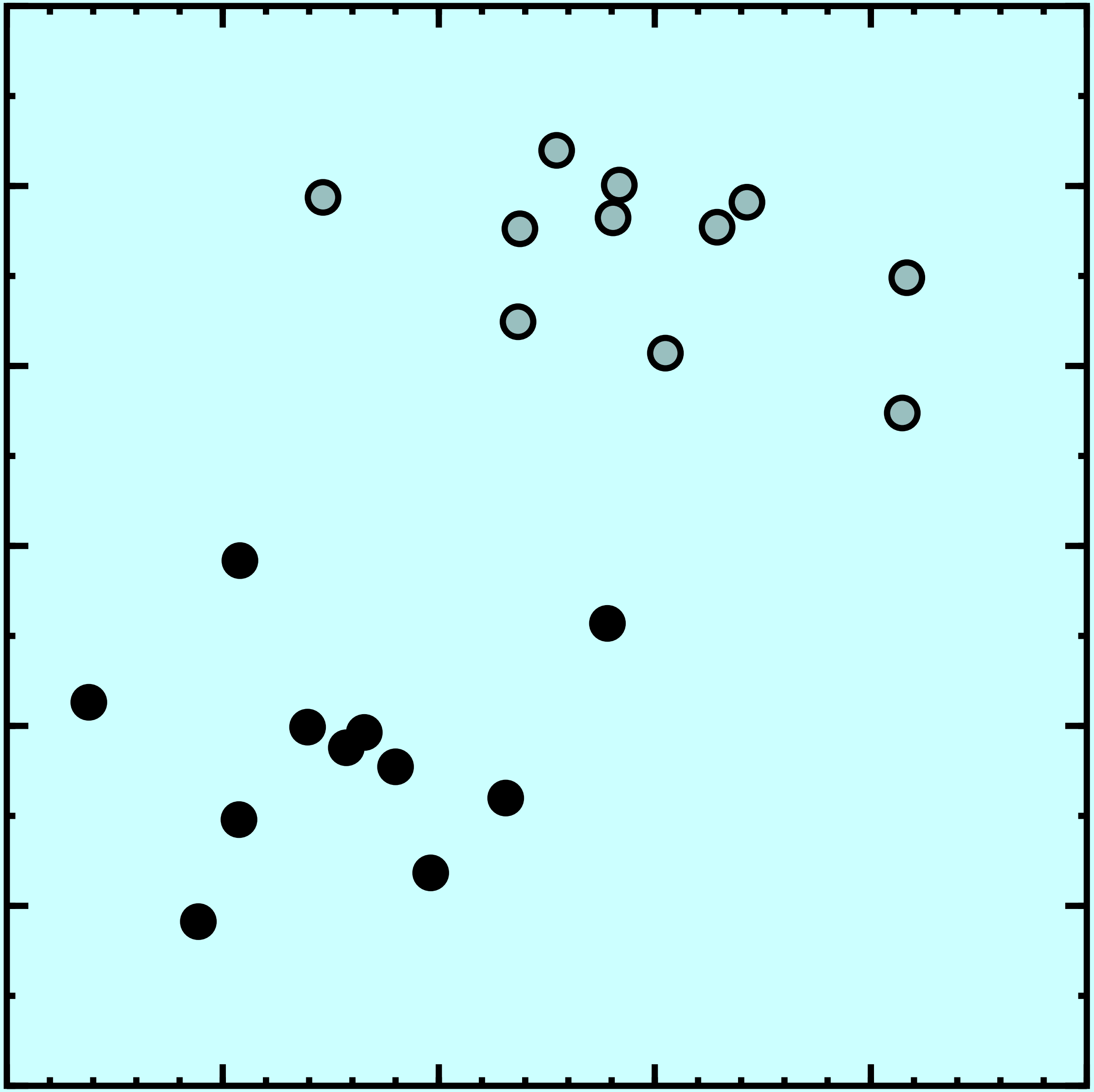
A simple case to show effects of phylogeny



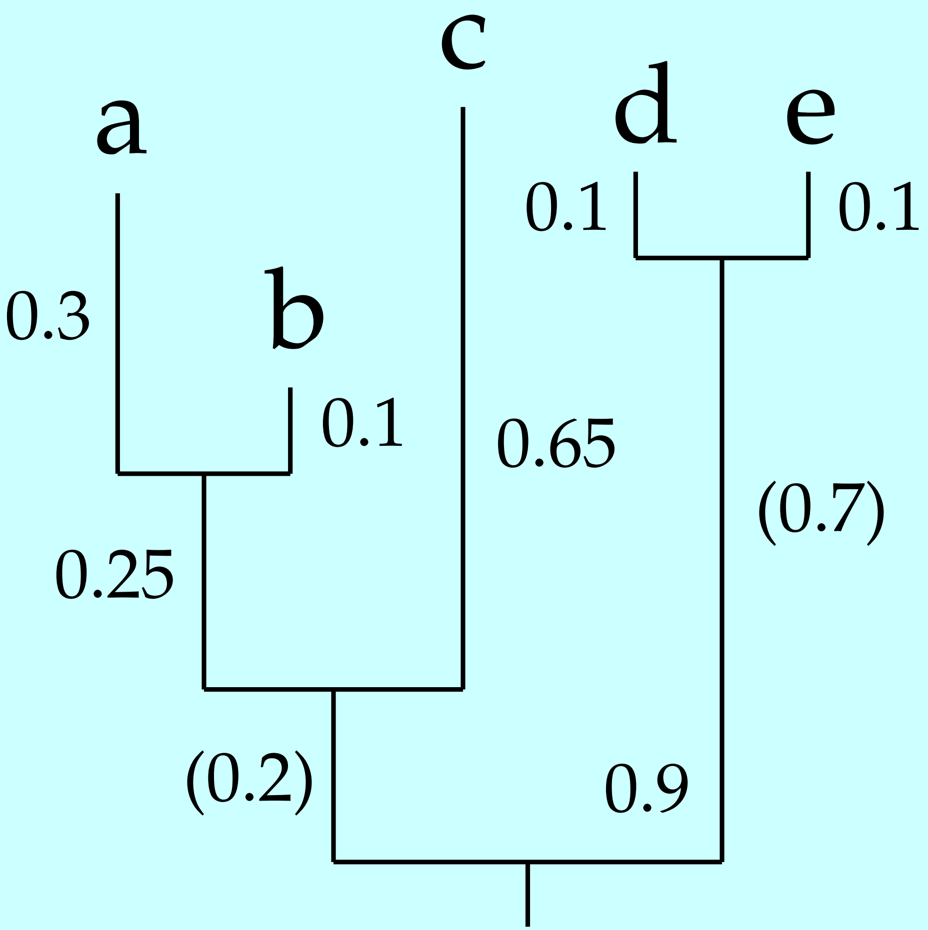
Two uncorrelated characters evolving on that tree



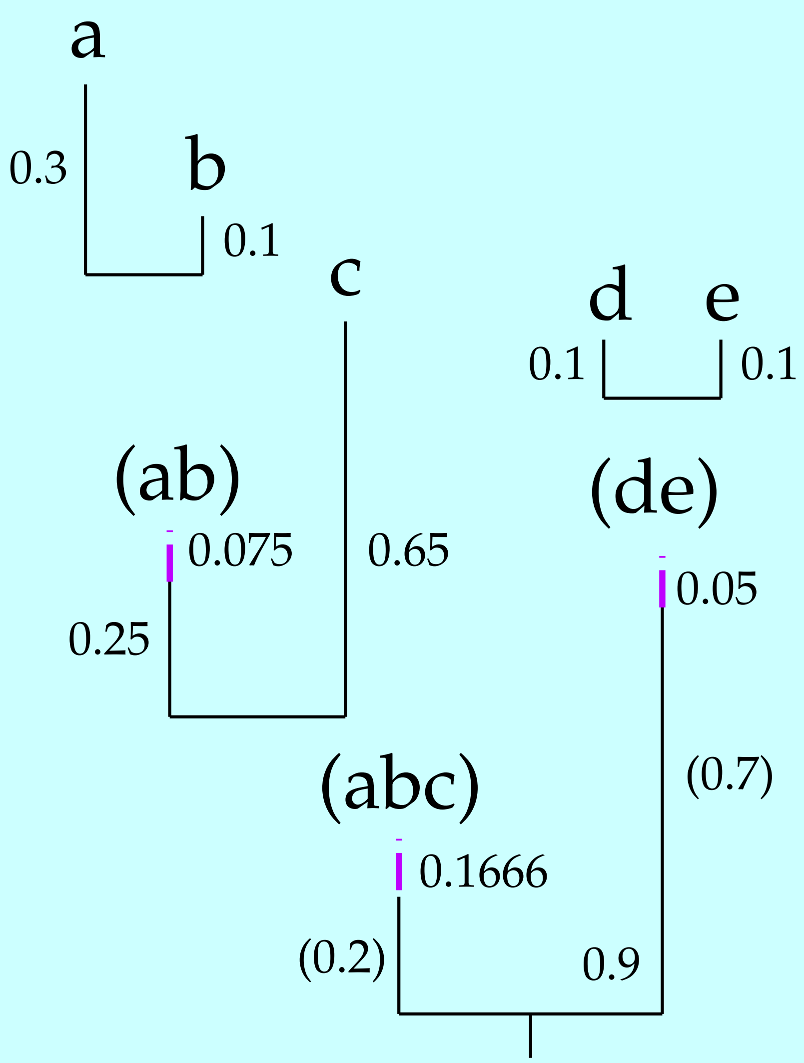
Identifying the two clades



A tree on which we are to observe two characters



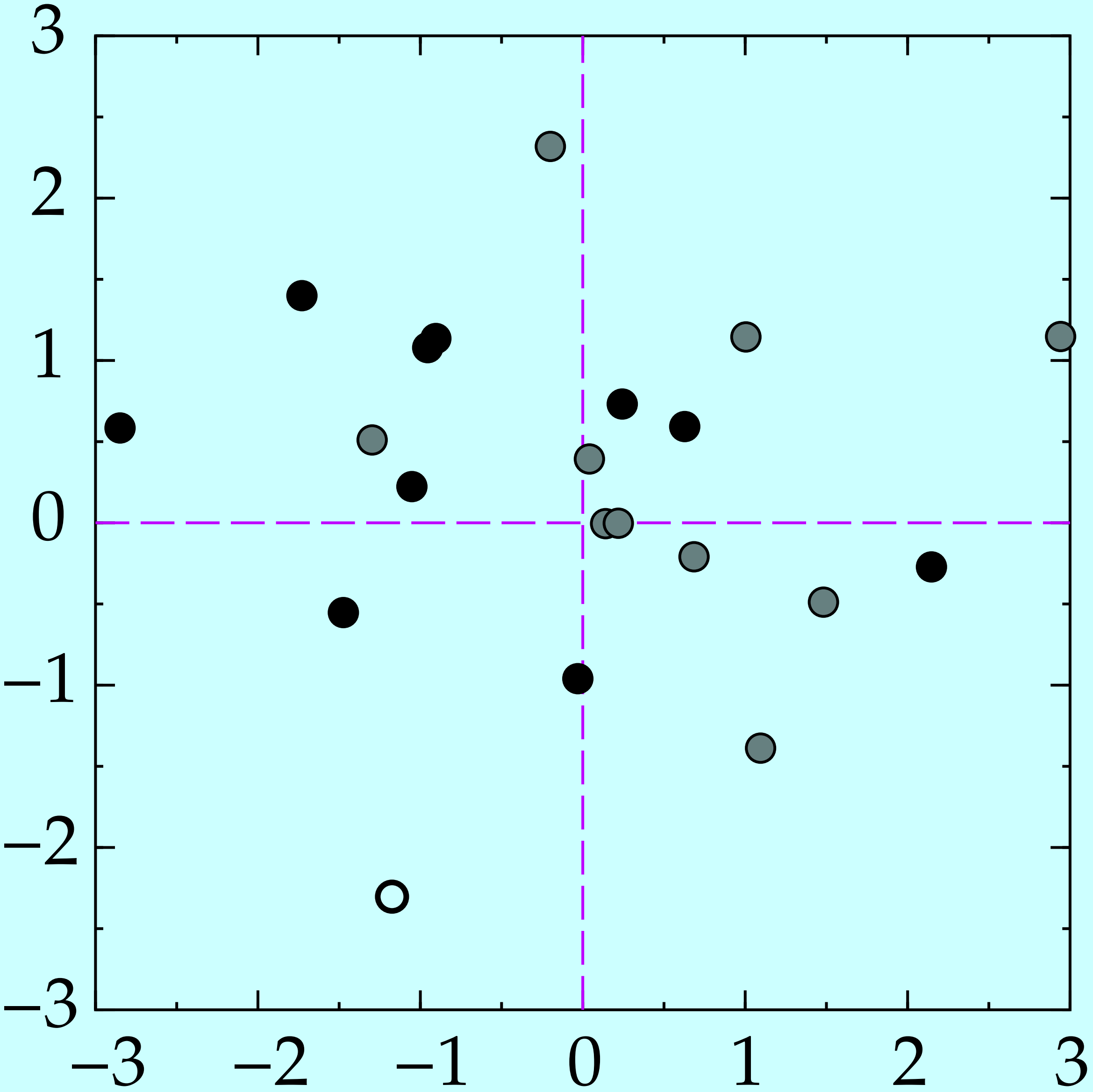
Decomposing it into two-species contrasts ...



Contrasts on that tree

Contrast	Variance proportional to
$y_1 = x_a - x_b$	0.4
$y_2 = \frac{1}{4}\,x_a + \frac{3}{4}\,x_b - x_c$	0.975
$y_3 = x_d - x_e$	0.2
$y_4 = \frac{1}{6}\,x_a + \frac{1}{2}\,x_b + \frac{1}{3}\,x_c - \frac{1}{2}\,x_d - \frac{1}{2}\,x_e$	1.11666

Contrasts for the 20-species two-clade example



An example: Smith and Cheverud 2002

Smith, R. J. and J. M. Cheverud. 2002. Scaling of sexual dimorphism in body mass: A phylogenetic analysis of Rensch's Rule in primates. *International Journal of Primatology* **23(5):** 1095-1135.

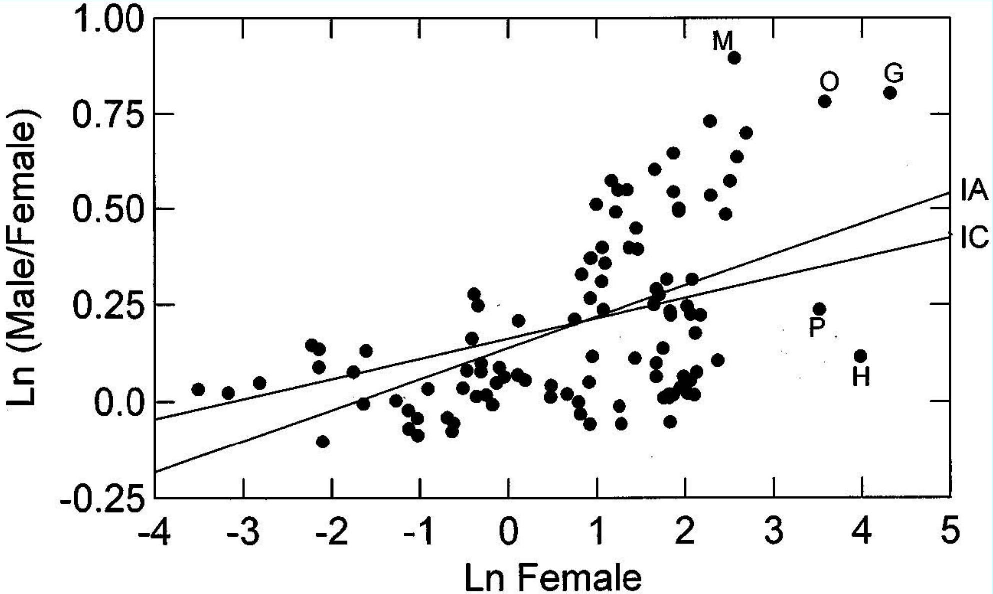
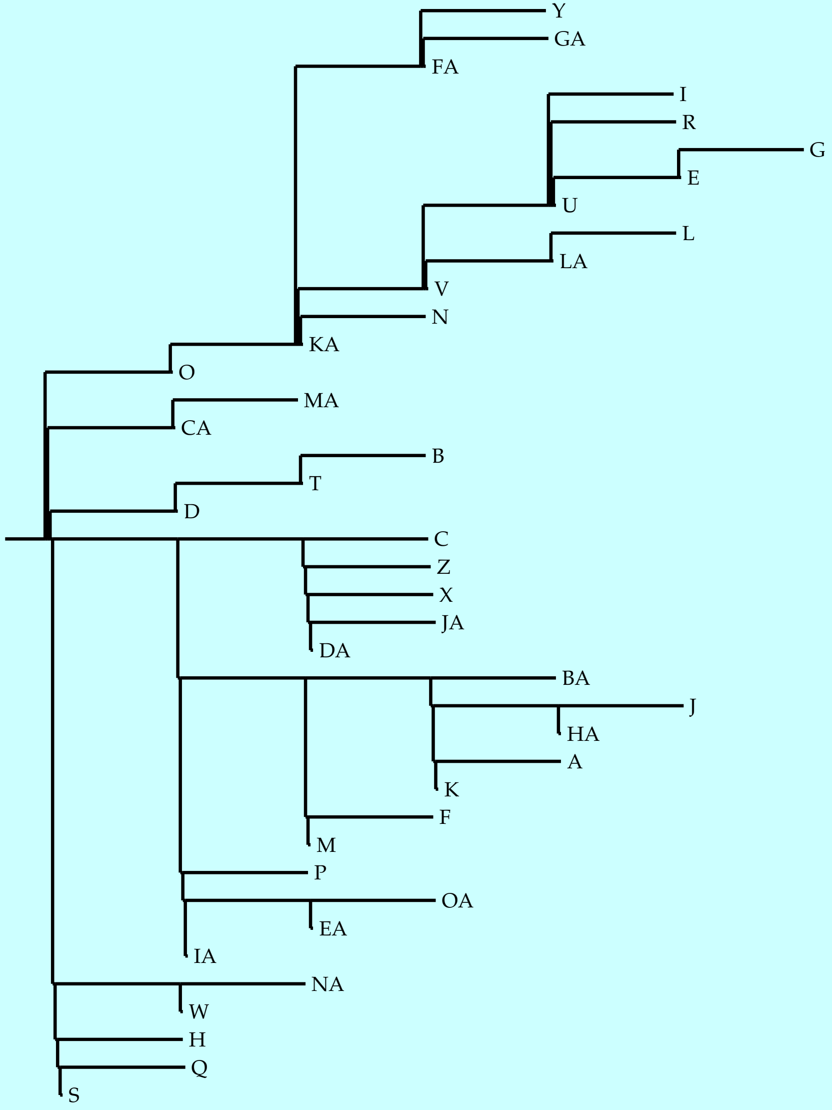
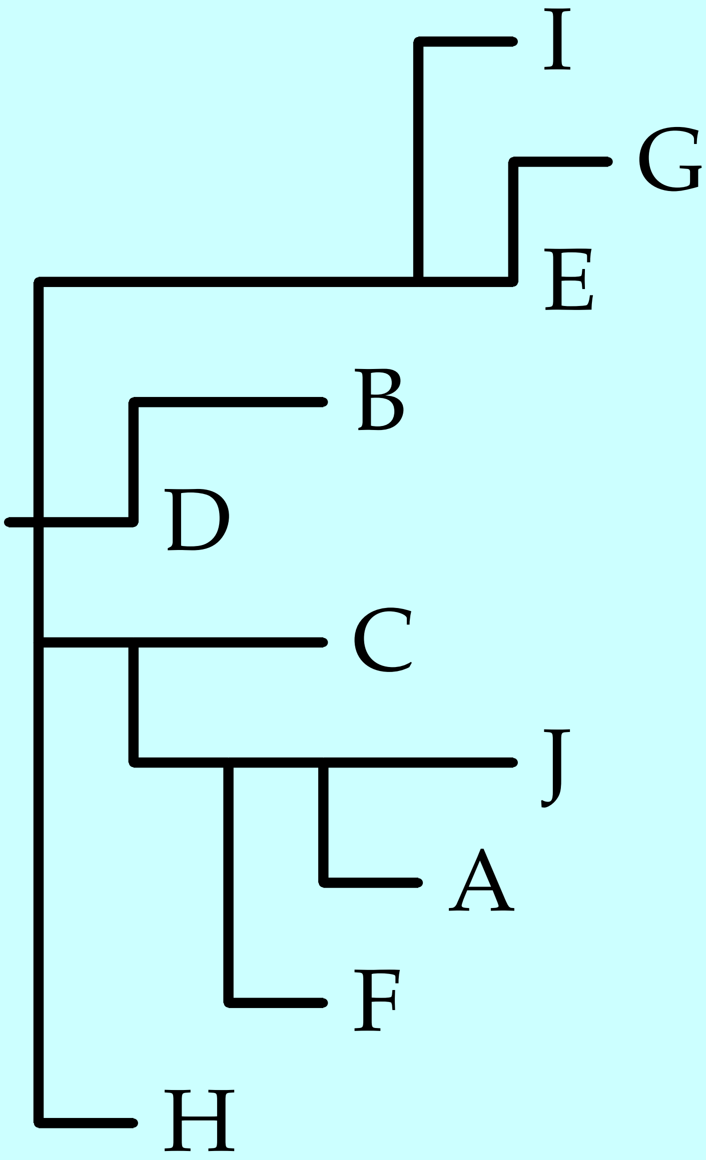


Fig. 1. The interspecific allometric equation (specific regression, identified as IA) and the independent contrasts equation (identified as IC) plotted for 105 primate species in raw data space, transformed to natural logarithms. The interspecific allometric equation is $\mathrm{ln}y = 0.139 + 0.080(\mathrm{ln}x)$, with $r = 0.53$. The phylogenetically corrected form of this equation, taken from the independent contrasts analysis, is $\mathrm{ln}y = 0.160 + 0.056(\mathrm{ln}x)$, with $r = 0.26$. The two equations are not significantly different from each other. The identified species are *Mandrillus sphinx* (M), *Pongo pygmaeus* (O), *Gorilla gorilla* (G), *Pan troglodytes* (P), and *Homo sapiens* (H).

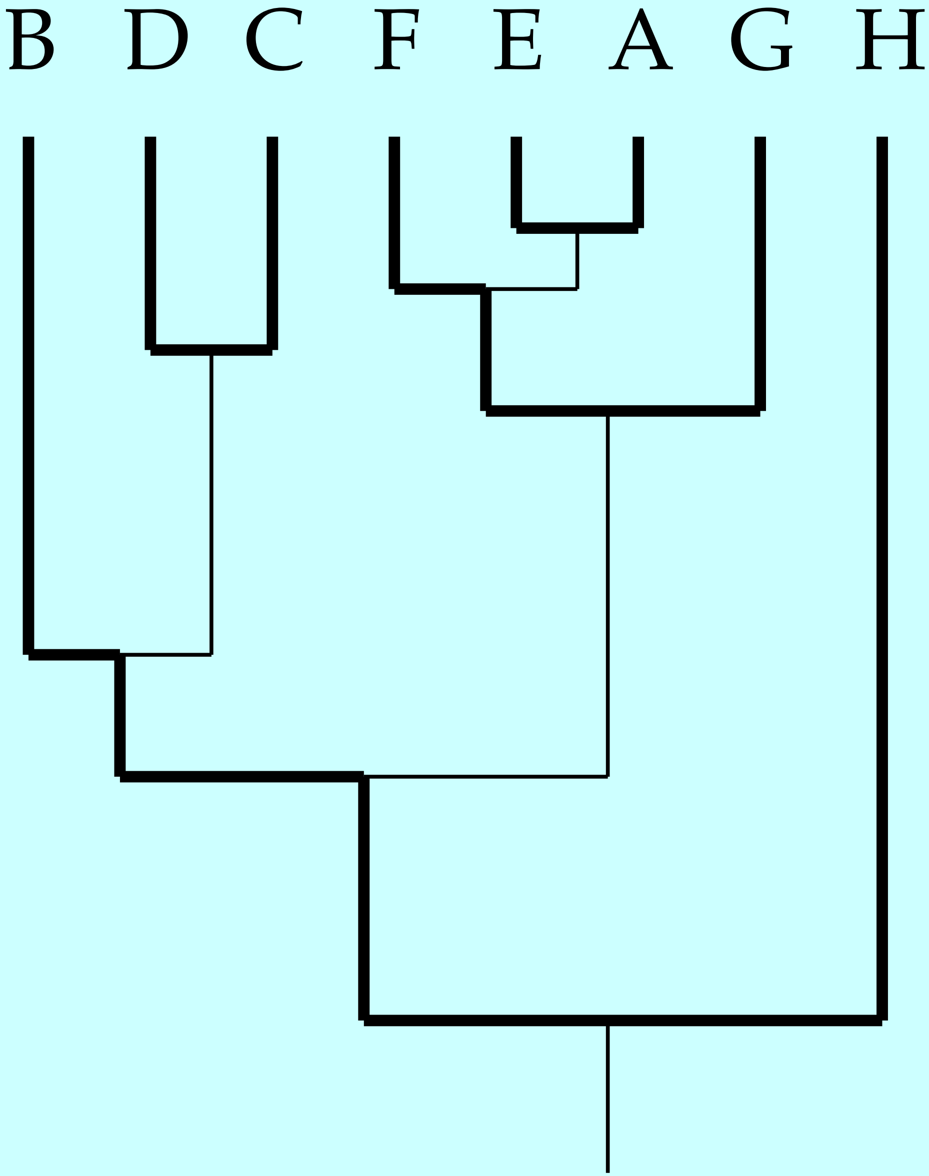
A tree with punctuated equilibrium



The punctuated tree when we sample 10 species



Two-species paired comparisons



Pagel's (1994) test for correlation with discrete 0/1 traits

When character 1 has state	**Rates of change in character 2 are:**
0	$0 \underset{\beta_0}{\overset{\alpha_0}{\rightleftarrows}} 1$
1	$0 \underset{\beta_1}{\overset{\alpha_1}{\rightleftarrows}} 1$

When character 2 has state	**Rates of change in character 1 are:**
0	$0 \underset{\delta_0}{\overset{\gamma_0}{\rightleftarrows}} 1$
1	$0 \underset{\delta_1}{\overset{\gamma_1}{\rightleftarrows}} 1$

Pagel's (1994) test for correlation with discrete 0/1 traits

To :	00	01	10	11
From :				
00	$--$	α_0	γ_0	0
01	β_0	$--$	0	γ_1
10	δ_0	0	$--$	α_1
11	0	δ_1	β_1	$--$

This can be set up as a 4 $\times$ 4 model of change with four states, 00, 01, 10, and 11, and likelihood ratio tests used.

Complete independence of the changes in the two characters involves restricting the parameters so that $\alpha_1 = \alpha_0$, $\beta_1 = \beta_0$, $\gamma_1 = \gamma_0$, and $\delta_1 = \delta_0$.