Outline

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

Three Models for Phenotypic Evolution

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

Single Rate Model (SR)

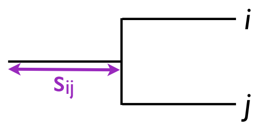
- Brownian motion model with a constant rate of evolution
- Two parameters: starting value (Θ) and rate (σ^2)

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_o), and rate change (r)

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

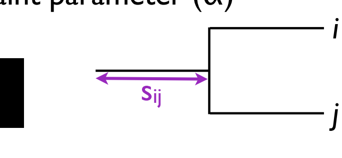
$$V_{ij} = \int_0^{s_{ij}} \sigma_0^2\, e^{rt}\, dt = \sigma_0^2\, \frac{e^{r s_{ij}}}{r}$$



Constant Constraints Model (CC)

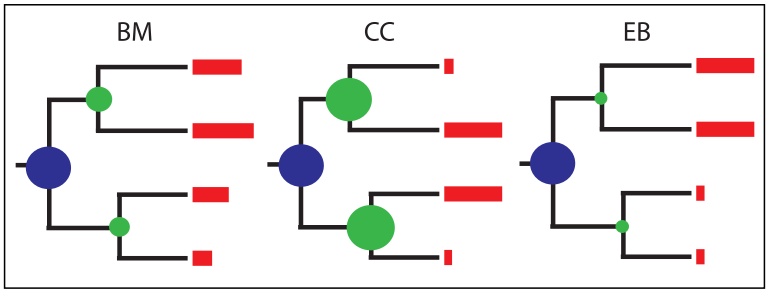
- Evolution has a tendency to move towards some medial value
- “Brownian motion with a spring”
- Three parameters: starting value (Θ), rate (σ^2), and constraint parameter (α)

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



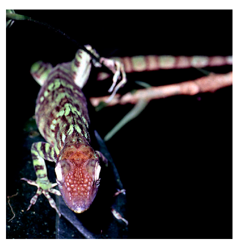
Why these three?

- 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

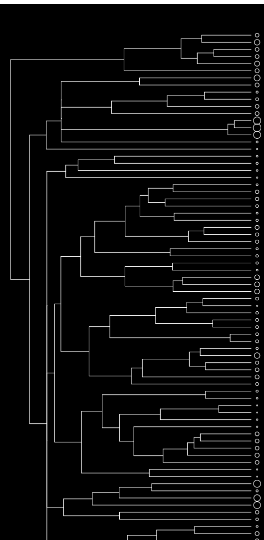


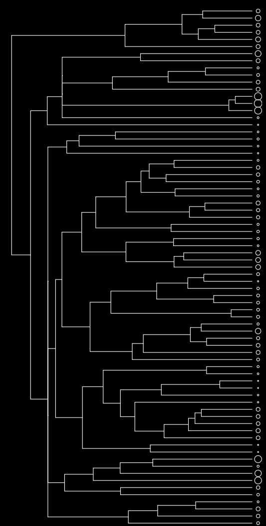
Example: *Anolis* lizards

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

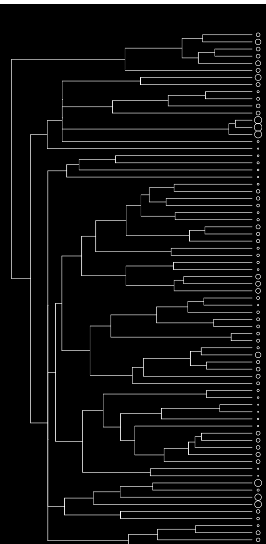


Anolis baleatus



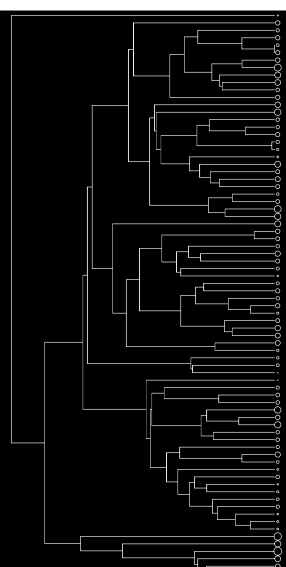


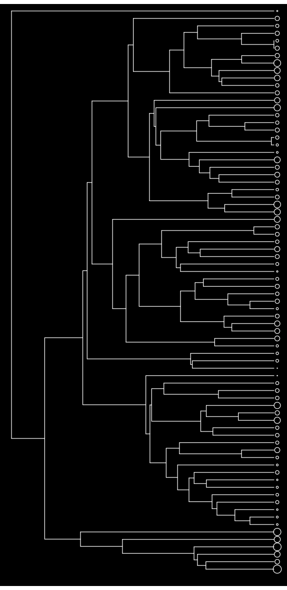
Model	Parameter estimates	lnL	Akaike weight
SR			
EB			
CC			



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

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

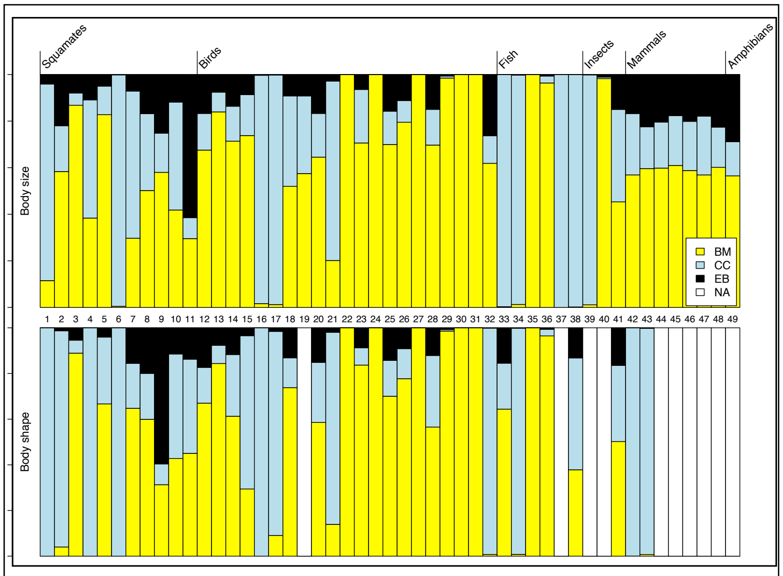
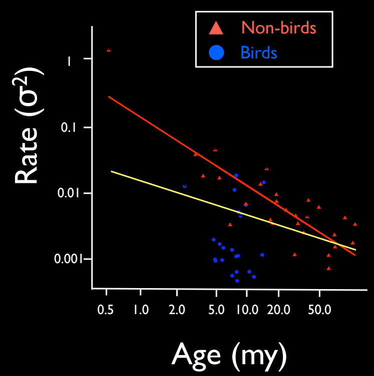


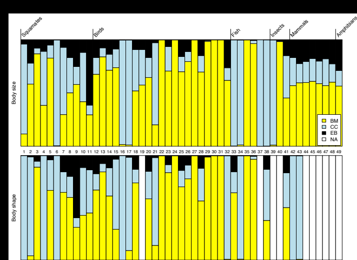
Table 1. Number of clades and subclades showing support for each of the three models (BM, CC, EB) for body size and body shape. We count both the number of clades with the highest AICc values for a particular model ("maximum w") and those with weights greater than 0.95 ("w > 0.95").

Clades	Data set	n	Criterion	BM	CC	EB
All full clades	Body size	49	Maximum w	35	13	1
			w > 0.95	9	8	0
	Body shape	39	Maximum w	24	14	1
			w > 0.95	8	8	1
All subclades	Body size	284	Maximum w	200	74	10
			w > 0.95	0	22	0
	Body shape	205	Maximum w	99	101	5
			w > 0.95	0	41	0

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



Outline

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

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

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

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*

If A is an m-by-n matrix and B is a p-by-q matrix, then the Kronecker product $\mathbf{A} \otimes \mathbf{B}$ is the mp-by-nq block matrix $\mathbf{A} \otimes \mathbf{B} = \begin{bmatrix} a_{11}B & \cdots & a_{1n}B \\ \vdots & \ddots & \vdots \\ a_{m1}B & \cdots & a_{mn}B \end{bmatrix}$.

More explicitly, we have

$$\mathbf{A}\otimes\mathbf{B} = \begin{bmatrix} a_{11}b_{11} & a_{11}b_{12} & \cdots & a_{11}b_{1q} & \cdots & \cdots & a_{1n}b_{11} & a_{1n}b_{12} & \cdots & a_{1n}b_{1q} \\ a_{11}b_{21} & a_{11}b_{22} & \cdots & a_{11}b_{2q} & \cdots & \cdots & a_{1n}b_{21} & a_{1n}b_{22} & \cdots & a_{1n}b_{2q} \\ \vdots & \vdots & \ddots & \vdots & & & \vdots & \vdots & \ddots & \vdots \\ a_{11}b_{p1} & a_{11}b_{p2} & \cdots & a_{11}b_{pq} & \cdots & \cdots & a_{1n}b_{p1} & a_{1n}b_{p2} & \cdots & a_{1n}b_{pq} \\ \vdots & \vdots & & \vdots & \ddots & & \vdots & \vdots & & \vdots \\ \vdots & \vdots & & \vdots & & \ddots & \vdots & \vdots & & \vdots \\ a_{m1}b_{11} & a_{m1}b_{12} & \cdots & a_{m1}b_{1q} & \cdots & \cdots & a_{mn}b_{11} & a_{mn}b_{12} & \cdots & a_{mn}b_{1q} \\ a_{m1}b_{21} & a_{m1}b_{22} & \cdots & a_{m1}b_{2q} & \cdots & \cdots & a_{mn}b_{21} & a_{mn}b_{22} & \cdots & a_{mn}b_{2q} \\ \vdots & \vdots & \ddots & \vdots & & & \vdots & \vdots & \ddots & \vdots \\ a_{m1}b_{p1} & a_{m1}b_{p2} & \cdots & a_{m1}b_{pq} & \cdots & \cdots & a_{mn}b_{p1} & a_{mn}b_{p2} & \cdots & a_{mn}b_{pq} \end{bmatrix}.$$

Examples [ec

$$\begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} \otimes \begin{bmatrix} 0 & 5 \\ 6 & 7 \end{bmatrix} = \begin{bmatrix} 1\cdot 0 & 1\cdot 5 & 2\cdot 0 & 2\cdot 5 \\ 1\cdot 6 & 1\cdot 7 & 2\cdot 6 & 2\cdot 7 \\ 3\cdot 0 & 3\cdot 5 & 4\cdot 0 & 4\cdot 5 \\ 3\cdot 6 & 3\cdot 7 & 4\cdot 6 & 4\cdot 7 \end{bmatrix} = \begin{bmatrix} 0 & 5 & 0 & 10 \\ 6 & 7 & 12 & 14 \\ 0 & 15 & 0 & 20 \\ 18 & 21 & 24 & 28 \end{bmatrix}.$$

$$\mathbf{V} = \left[\begin{array}{cccc:cccc} R_{11}C_{11} & R_{11}C_{12} & R_{11}C_{13} & R_{11}C_{14} & R_{12}C_{11} & R_{12}C_{12} & R_{12}C_{13} & R_{12}C_{14} \\ R_{11}C_{21} & R_{11}C_{22} & R_{11}C_{23} & R_{11}C_{24} & R_{12}C_{21} & R_{12}C_{22} & R_{12}C_{23} & R_{12}C_{24} \\ R_{11}C_{31} & R_{11}C_{32} & R_{11}C_{33} & R_{11}C_{34} & R_{12}C_{31} & R_{12}C_{32} & R_{12}C_{33} & R_{12}C_{34} \\ R_{11}C_{41} & R_{11}C_{42} & R_{11}C_{43} & R_{11}C_{44} & R_{12}C_{41} & R_{12}C_{42} & R_{12}C_{43} & R_{12}C_{44} \\ \hdashline R_{21}C_{11} & R_{21}C_{12} & R_{21}C_{13} & R_{21}C_{14} & R_{22}C_{11} & R_{22}C_{12} & R_{22}C_{13} & R_{22}C_{14} \\ R_{21}C_{21} & R_{21}C_{22} & R_{21}C_{23} & R_{21}C_{24} & R_{22}C_{21} & R_{22}C_{22} & R_{22}C_{23} & R_{22}C_{24} \\ R_{21}C_{31} & R_{21}C_{32} & R_{21}C_{33} & R_{21}C_{34} & R_{22}C_{31} & R_{22}C_{32} & R_{22}C_{33} & R_{22}C_{34} \\ R_{21}C_{41} & R_{21}C_{42} & R_{21}C_{43} & R_{21}C_{44} & R_{22}C_{41} & R_{22}C_{42} & R_{22}C_{43} & R_{22}C_{44} \end{array}\right].$$

Four taxa, two traits

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

Outline

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