Correlated Evolution

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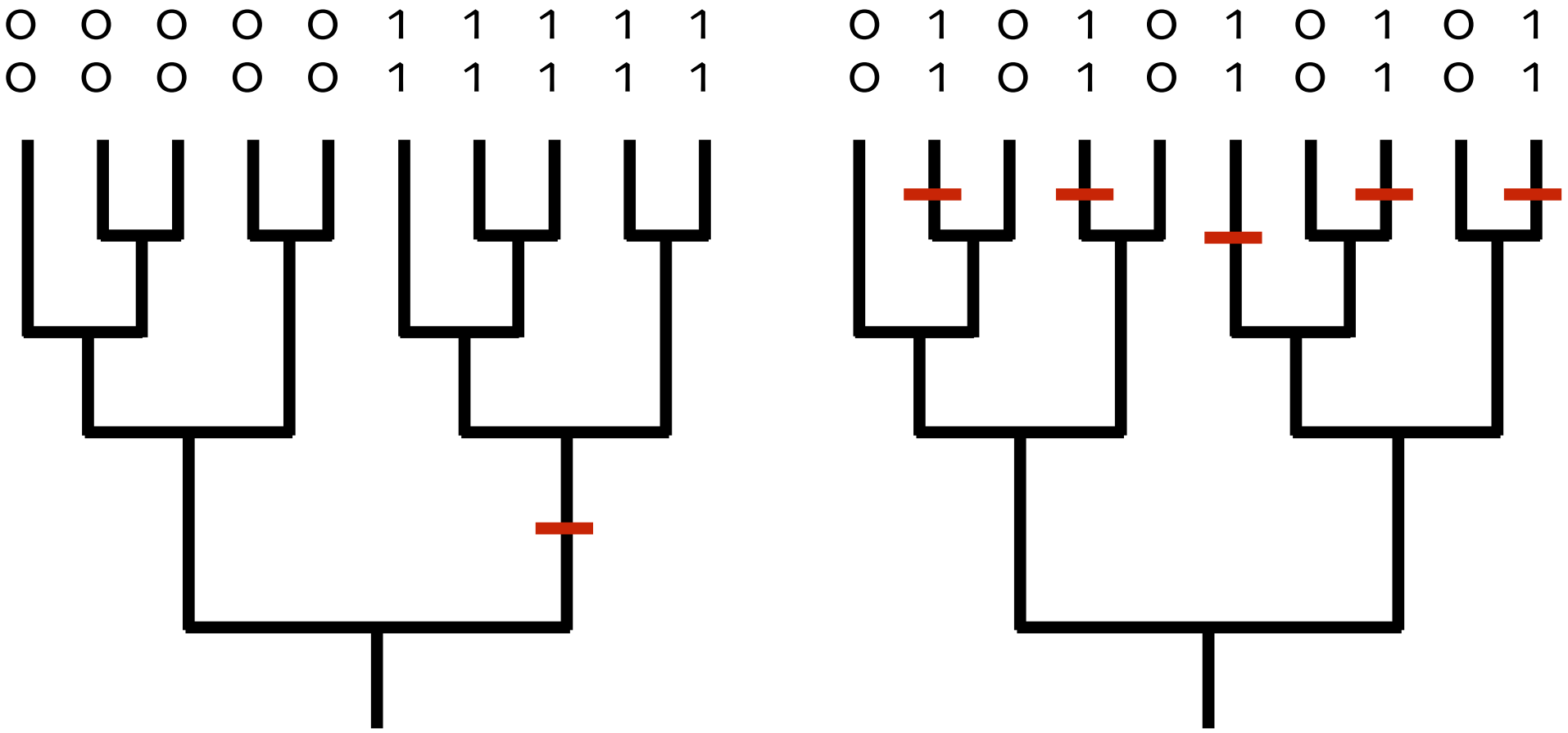
coincidence?

definitely not
independently evolving



Pagel (1994) Example

http://anthro.palomar.edu/primate/prim_4.htm

- Phylogeny of 8 primates
- Character **X** is "mating system":
  - 0 = mate with one male during estrus
  - 1 = mate with multiple males during estrus
- Character **Y** is "perineum swelling and reddening":
  - 0 = no swellings at estrus
  - 1 = reddening and swelling at estrus

Pagel 1994

Independence (I) Model

- Same as asymmetric 2-state model
- α and β allowed to differ for the two characters (4 parameters total):

Character X

		uni	multi
		0	1
uni	0	$-\alpha_X$	α_X
multi	1	β_X	$-\beta_X$

Character Y

		no	red
		0	1
no	0	$-\alpha_Y$	α_Y
red	1	β_Y	$-\beta_Y$

Pagel 1994

Independence (I) Model

$$\begin{array}{cc} & \begin{array}{cc} \text{uni} & \text{multi} \\ 0 & 1 \end{array} \\ \begin{array}{c} \text{uni} \\ \text{multi} \end{array} & \begin{array}{c} 0 \\ 1 \end{array} \begin{pmatrix} -\alpha_X & \alpha_X \\ \beta_X & -\beta_X \end{pmatrix} \end{array}$$

$$\begin{array}{cc} & \begin{array}{cc} \text{no} & \text{red} \\ 0 & 1 \end{array} \\ \begin{array}{c} \text{no} \\ \text{red} \end{array} & \begin{array}{c} 0 \\ 1 \end{array} \begin{pmatrix} -\alpha_Y & \alpha_Y \\ \beta_Y & -\beta_Y \end{pmatrix} \end{array}$$

	0,0	0,1	1,0	1,1
0,0	---			0
0,1		---	0	
1,0		0	---	
1,1	0			---

Dependence (D) Model

- Pagel and Meade's 2006 correlated evolution model

	0,0	0,1	1,0	1,1
0,0	---	q_{12}	q_{13}	0
0,1	q_{21}	---	0	q_{24}
1,0	q_{31}	0	---	q_{34}
1,1	0	q_{42}	q_{43}	---

state for character 1

state for character 2

q_{34} (for example) is the rate at which character 2 changes from state 0 to state 1 while character 1 remains unchanged in state 1

Pagel 1994

Dependence (D) Model

This notation may be easier to understand

		uni, no	uni, red	multi, no	multi, red
		$0,0$	$0,1$	$1,0$	$1,1$
uni, no	$0,0$	—	$q^{\text{no}\rightarrow\text{red}}_{\text{uni}}$	$q^{\text{no}}_{\text{uni}\rightarrow\text{multi}}$	0
uni, red	$0,1$	$q^{\text{red}\rightarrow\text{no}}_{\text{uni}}$	—	0	$q^{\text{red}}_{\text{uni}\rightarrow\text{multi}}$
multi, no	$1,0$	$q^{\text{no}}_{\text{multi}\rightarrow\text{uni}}$	0	—	$q^{\text{no}\rightarrow\text{red}}_{\text{multi}}$
multi, red	$1,1$	0	$q^{\text{red}}_{\text{multi}\rightarrow\text{uni}}$	$q^{\text{no}\rightarrow\text{red}}_{\text{multi}}$	—

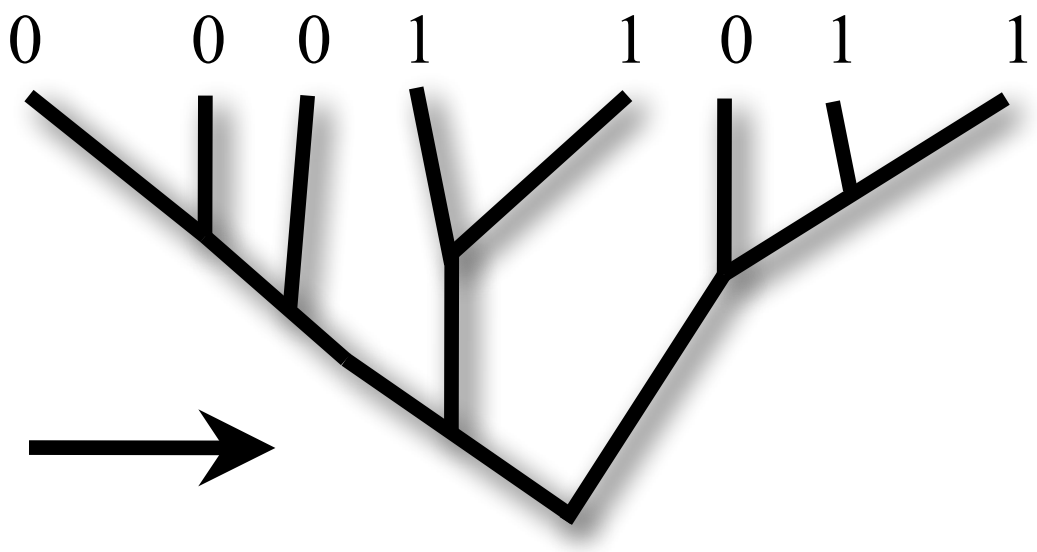
8 parameters total

Estrus Advertisement Example

- maximum log-likelihood under I model = -11.9
- maximum log-likelihood under D model = -8.43
- Likelihood ratio test statistic = 6.94
- Small amount of data, so chi-squared distribution may be misleading
- $p > 0.12$ (not significant) determined by **parametric bootstrapping**

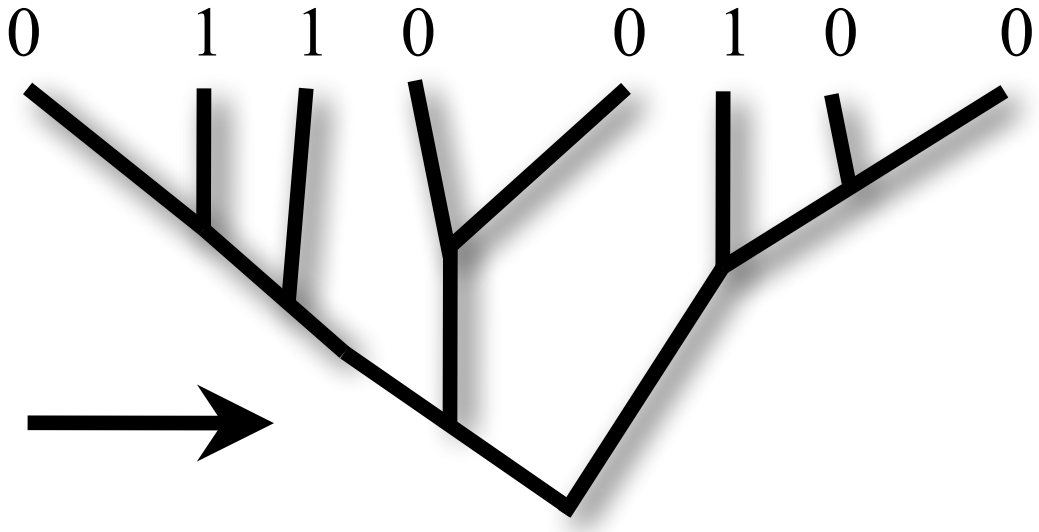
Parametric bootstrapping

Character X:



Use independence model with estimated parameters α_X, β_X to simulate data on tree

Character Y:



Use independence model with estimated parameters α_Y, β_Y to simulate data on tree

Parametric bootstrapping

Character X:	0	0	0	1	1	0	1	1
Character Y:	0	1	1	0	0	1	0	0

Maximize log-likelihood under I model: -10.49
Maximize log-likelihood under D model: -9.23
LRT statistic = 2.52

This particular simulated dataset yielded a value less than the 6.94, need to do more replicates to build a histogram.

Is estrus advertisement more likely to evolve in the presence of a multi-male mating system?

Advertisement (Y: 0→1) evolves in the evolutionary context of a **monogamous** mating system (X: 0→0)

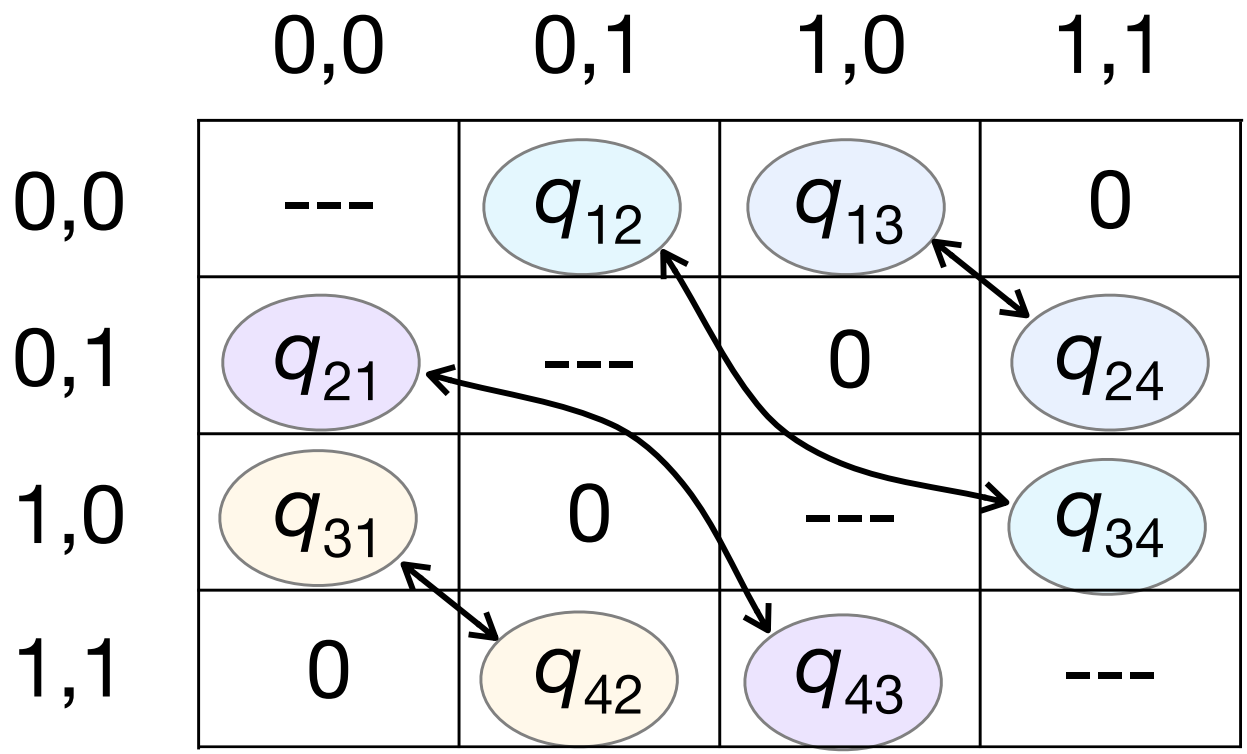
		1-male no swellings	1-male red swellings	multi-male no swellings	multi-male red swellings
		0,0	0,1	1,0	1,1
1-male no swellings	0,0	—	$q_{12} = 0.29$	q_{13}	0
1-male red swellings	0,1	q_{21}	—	0	q_{24}
multi-male no swellings	1,0	q_{31}	0	—	$q_{34} = 3.45$
multi-male red swellings	1,1	0	q_{42}	q_{43}	—

Advertisement evolves about 12 times faster in multi-male systems than in single-male systems (q_{34}/q_{12}=11.9)

Advertisement (Y: 0→1) evolves in the evolutionary context of a **multi-male** mating system (X: 1→1)

Pagel-Meade 2006 rjMCMC correlated evolution model

Independent evolution of two characters is implied when all of the pairs of rates tied together by arrows are identical



Here are three examples of rate matrices that imply *independent* character evolution

	0,0	0,1	1,0	1,1
0,0	---	***a***	***a***	0
0,1	***a***	---	0	***a***
1,0	***a***	0	---	***a***
1,1	0	***a***	***a***	---

	0,0	0,1	1,0	1,1
0,0	---	***a***	***a***	0
0,1	***b***	---	0	***a***
1,0	***b***	0	---	***a***
1,1	0	***b***	***b***	---

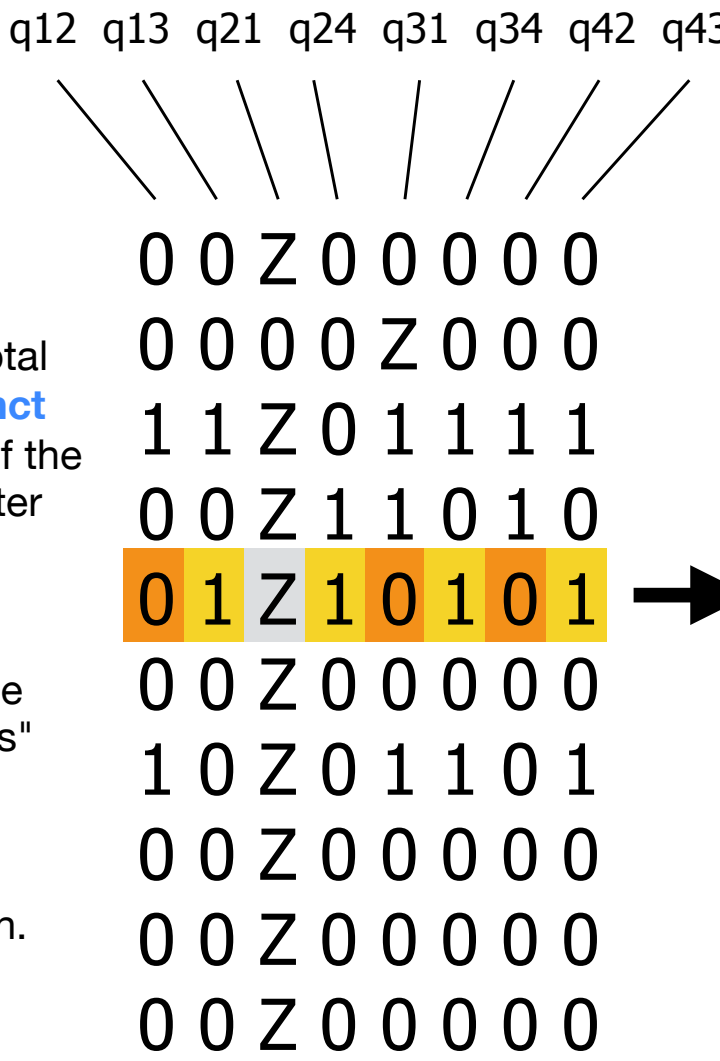
	0,0	0,1	1,0	1,1
0,0	---	***a***	***b***	0
0,1	***c***	---	0	***b***
1,0	***d***	0	---	***a***
1,1	0	***d***	***c***	---

Pagel and Meade (2006)

Sampling models in BayesTraits

There are a total of **4140 distinct submodels** of the full 8-parameter model.

This is an example of the "model strings" saved in BayesTraits' output when rjMCMC is run.



This model has 2 estimated parameters (a, b) and q21 is fixed at 0

q21 \ q12, q13	0,0	0,1	1,0	1,1
0,0	---	*a*	*b*	0
0,1	**0**	---	0	*b*
1,0	*a*	0	---	*b*
1,1	0	*a*	*b*	---

q24 q34 q42 q43

(BayesTraits software at http://www.evolution.reading.ac.uk/SoftwareMain.html)