WHAT DRIVES BIOLOGICAL DIVERSIFICATION?

DETECTING TRAITS UNDER SPECIES SELECTION

RICHARD G. FITZJOHN

University of British Columbia
Macquarie University








Gould 1839

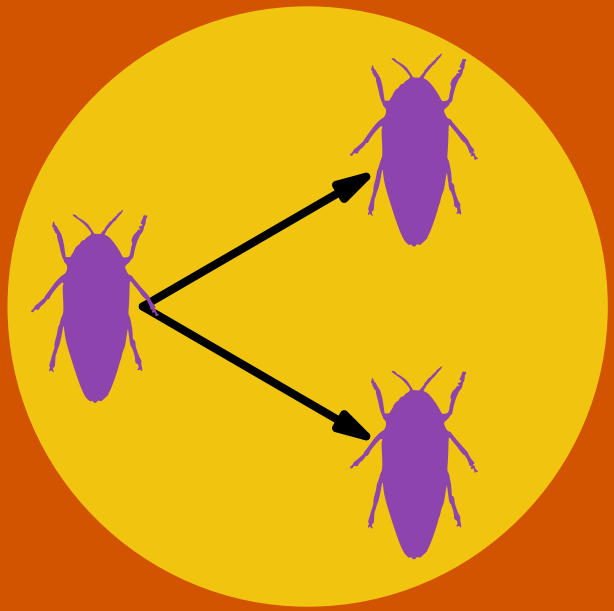
Gould 1839

Gould 1839

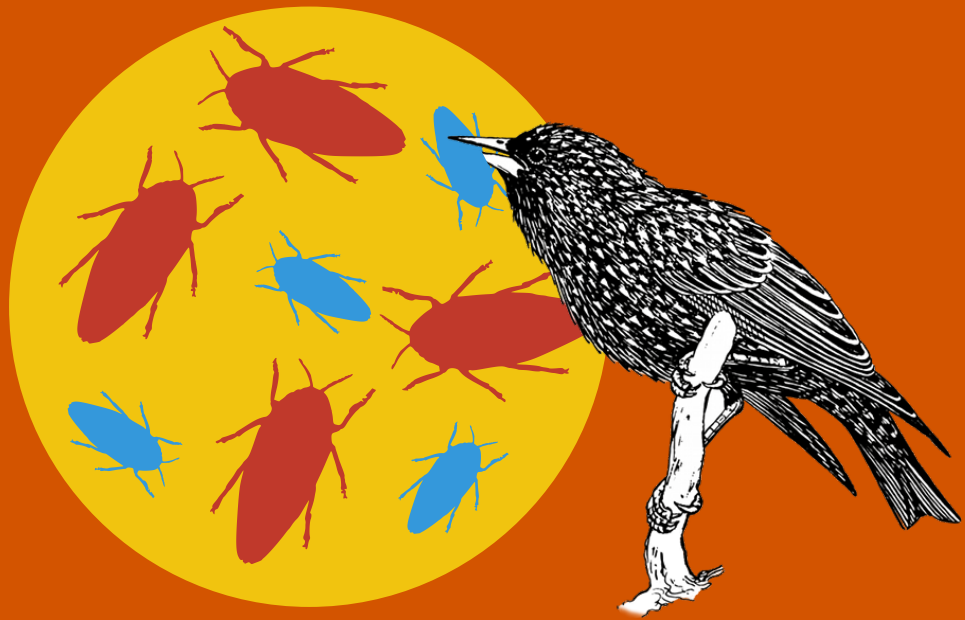
Gould 1839

SPECIES SELECTION

Variation



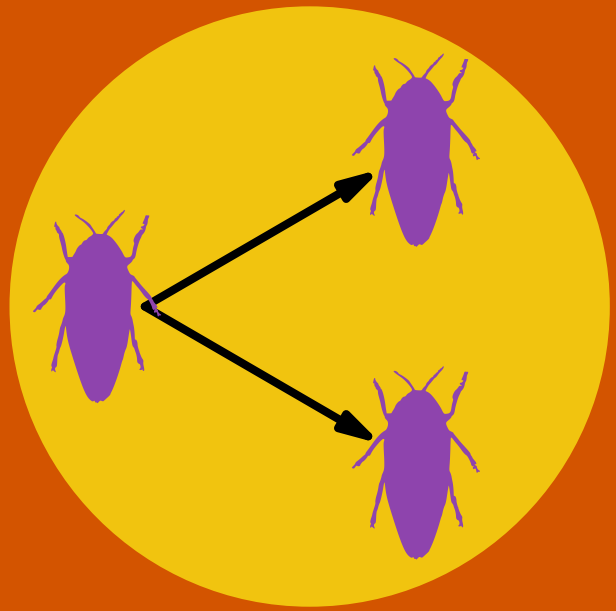
Heritability



Differential fitness

Lewontin 1970

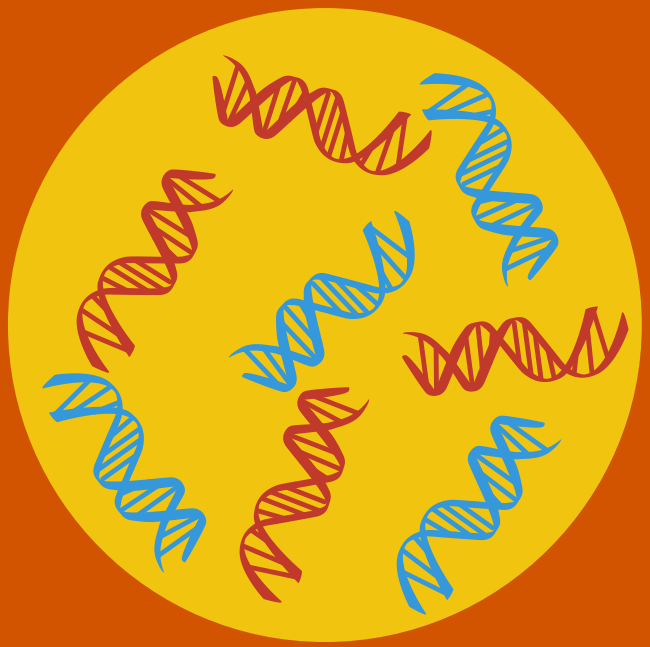
Variation



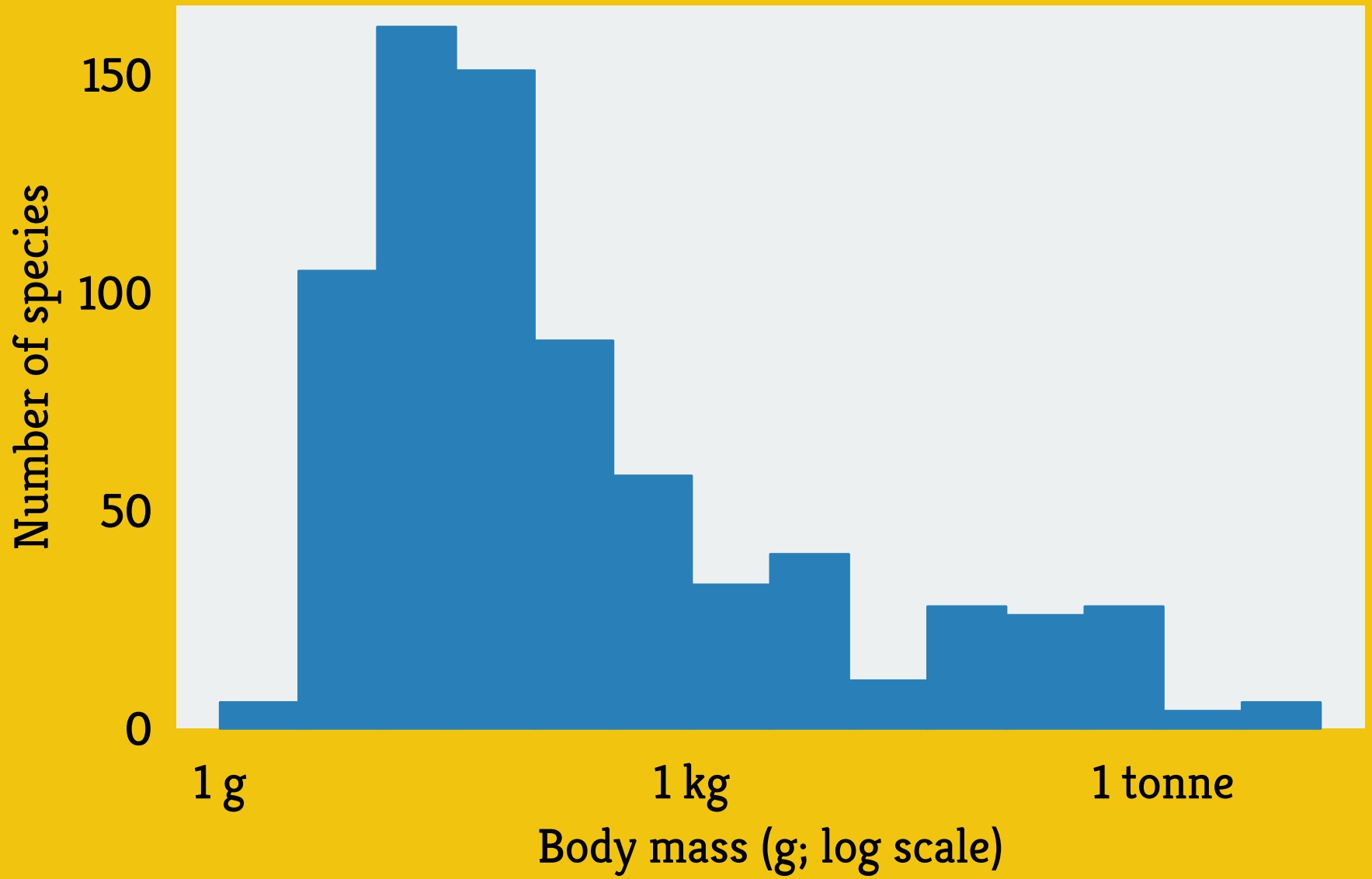
Heritability

Differential fitness

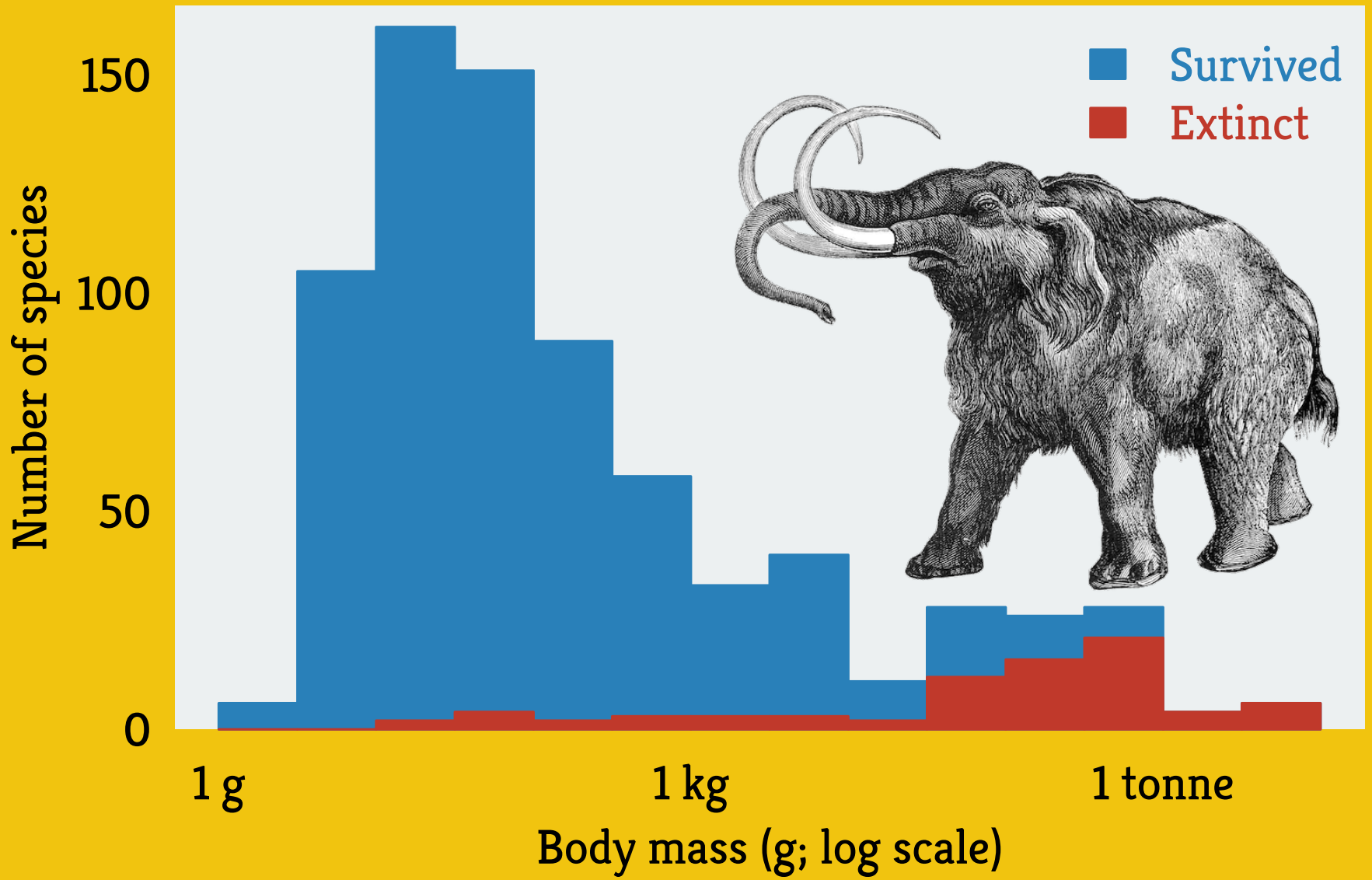
Lewontin 1970



SPECIES SELECTION
HAS NOT BEEN POPULAR

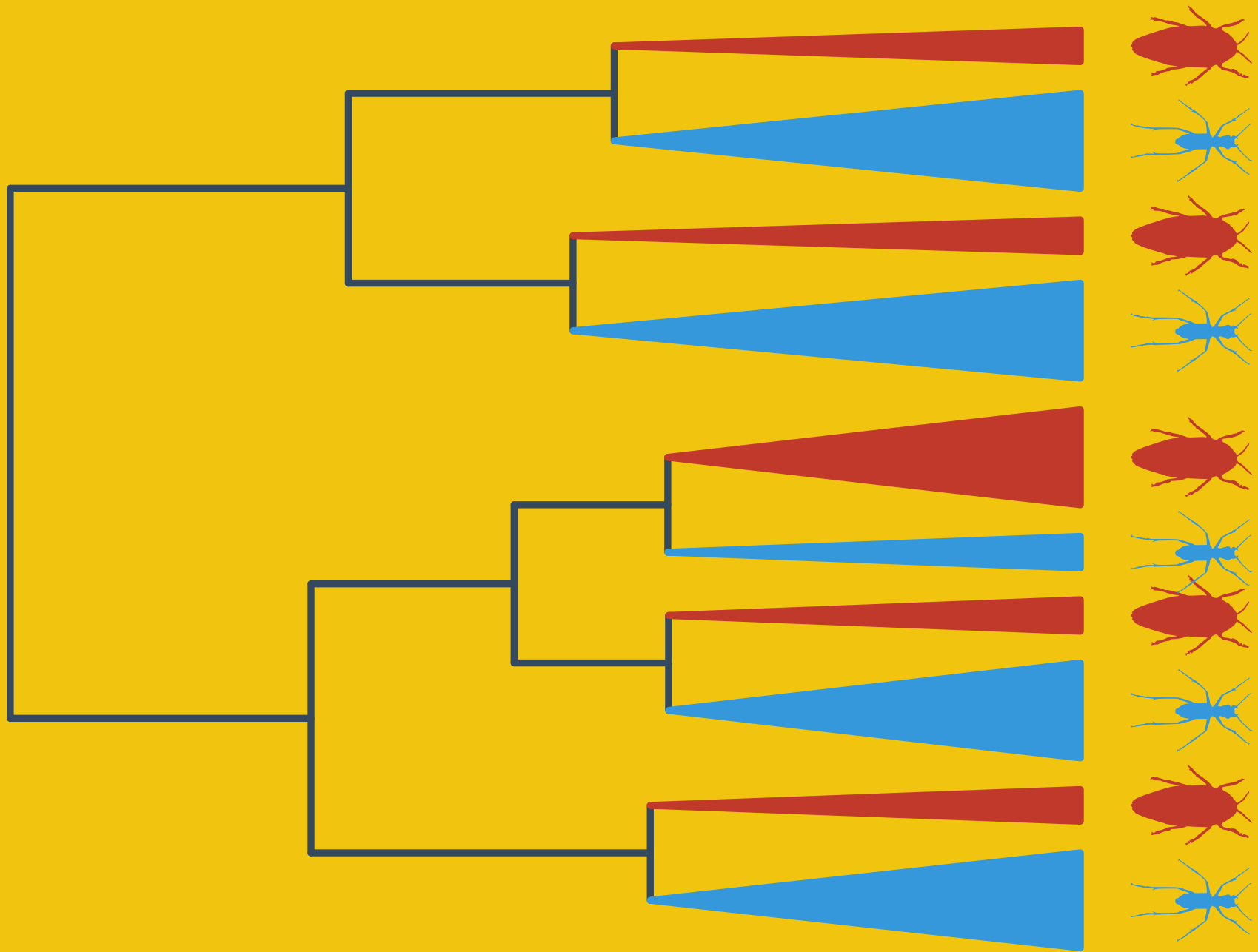


Data: Lyons et al. 2004

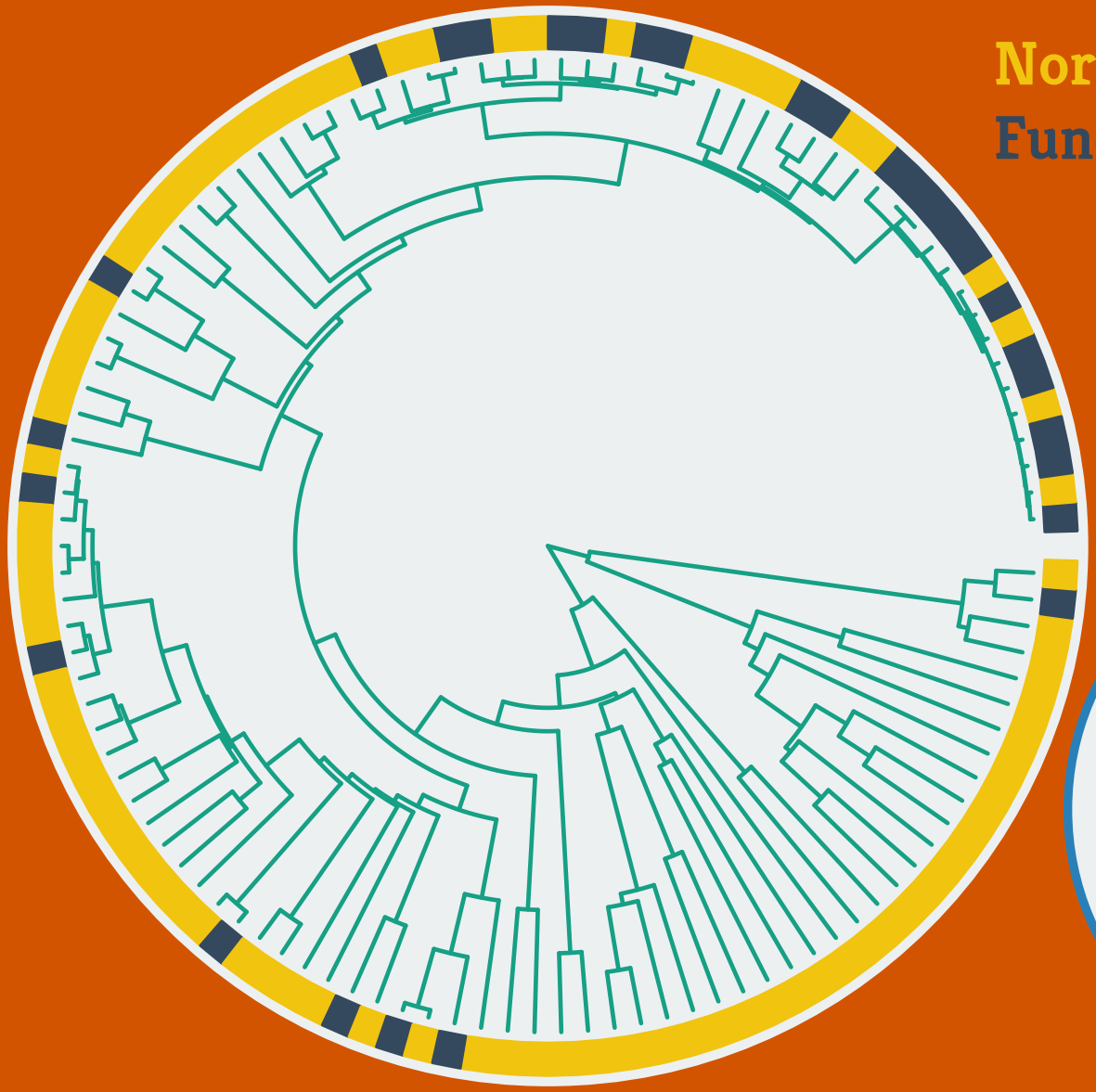


Data: Lyons et al. 2004

HOW TO DETECT SPECIES SELECTION?



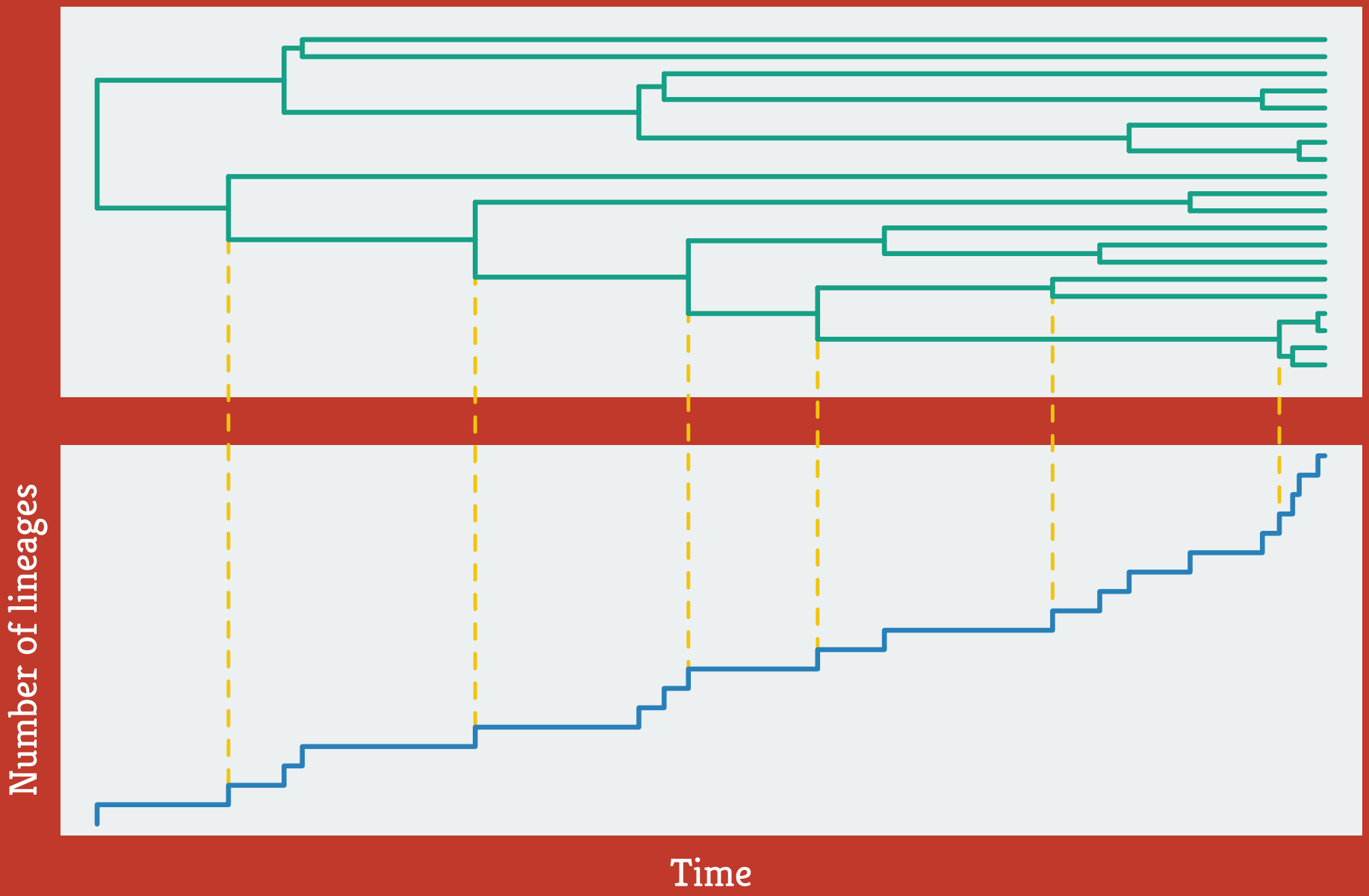
Mitter 1988



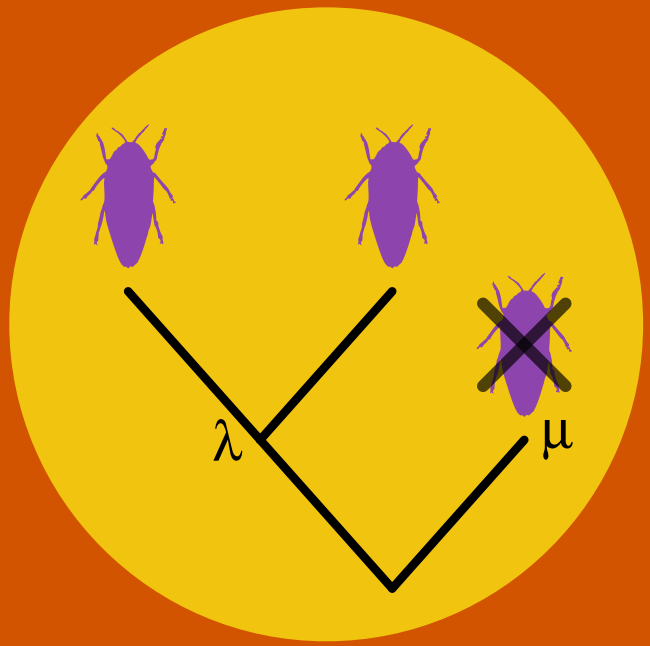
Normal

Functionally asexual

Johnson et al. 2011

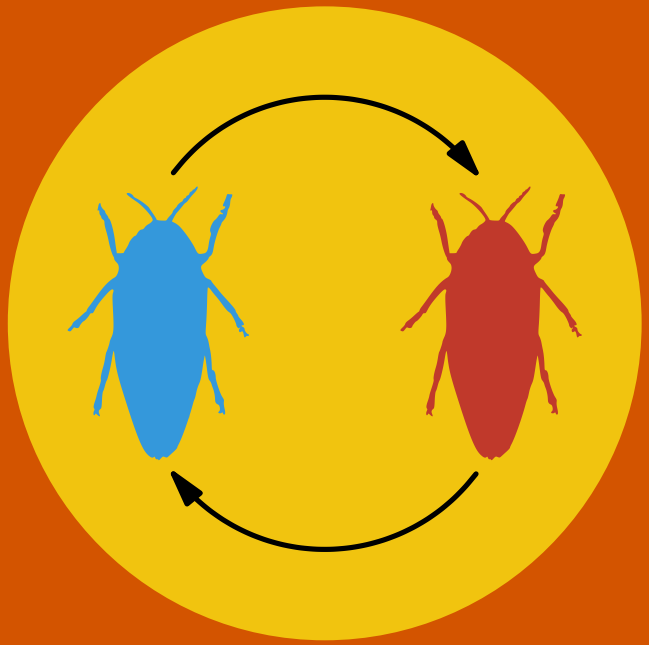


Nee et al. 1994



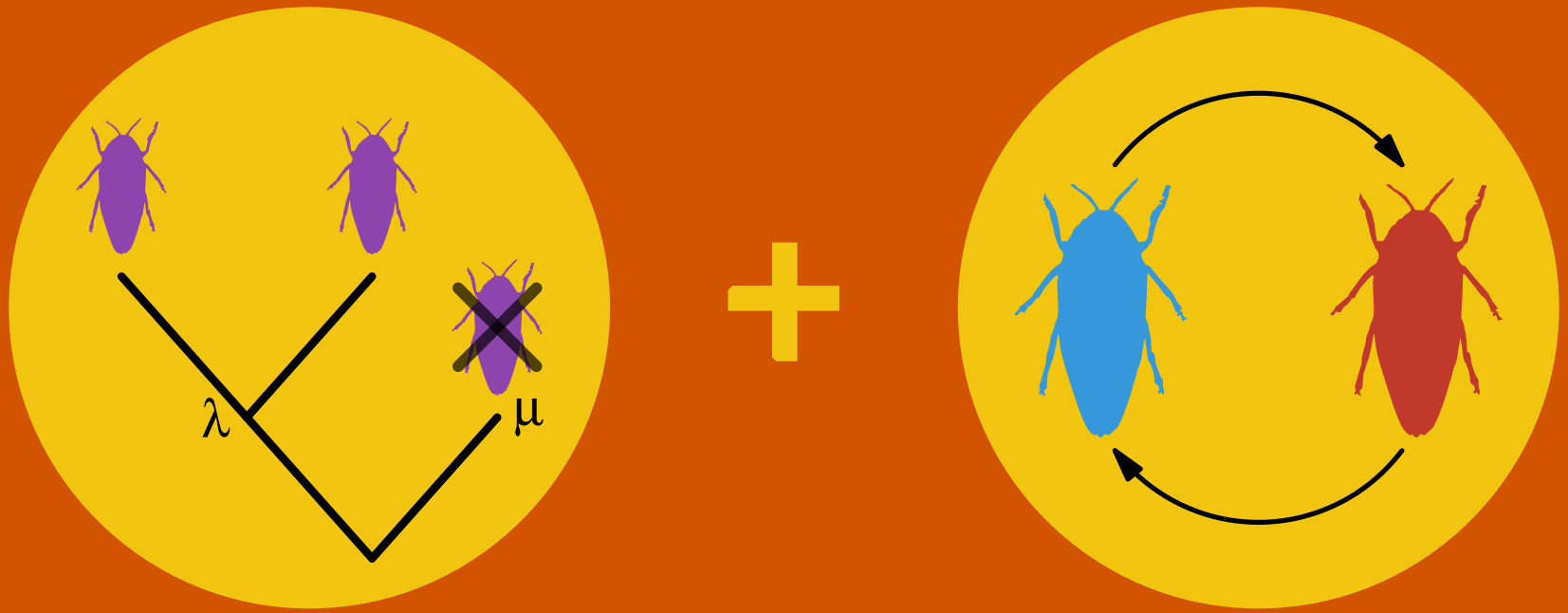
Speciation / extinction: birth death model

Nee et al. 1994



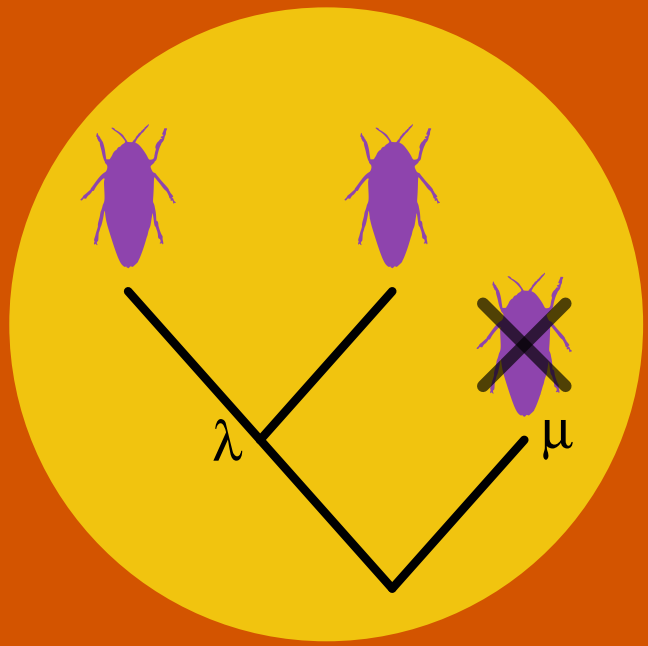
Trait evolution: Markov model

Pagel 1994, Lewis 2001



BiSSE: Binary State Speciation & Extinction

Maddison, Midford & Otto 2007



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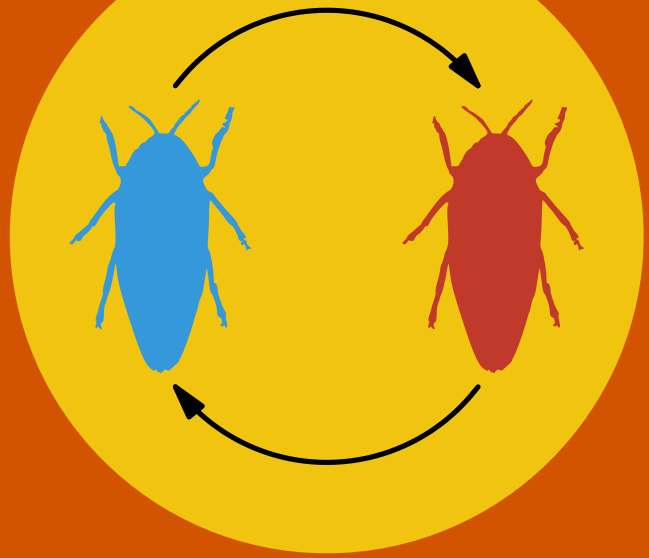

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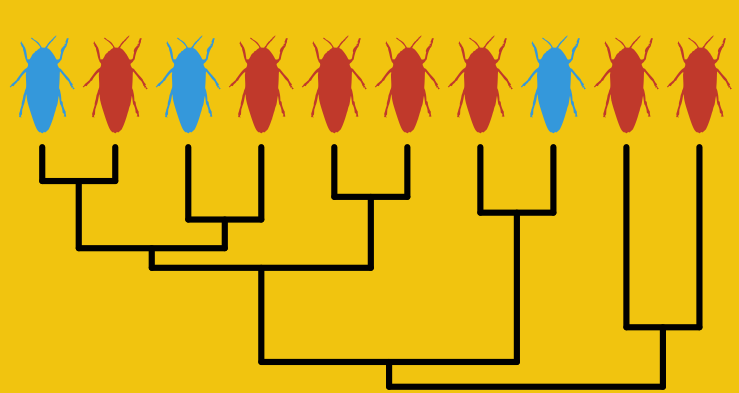
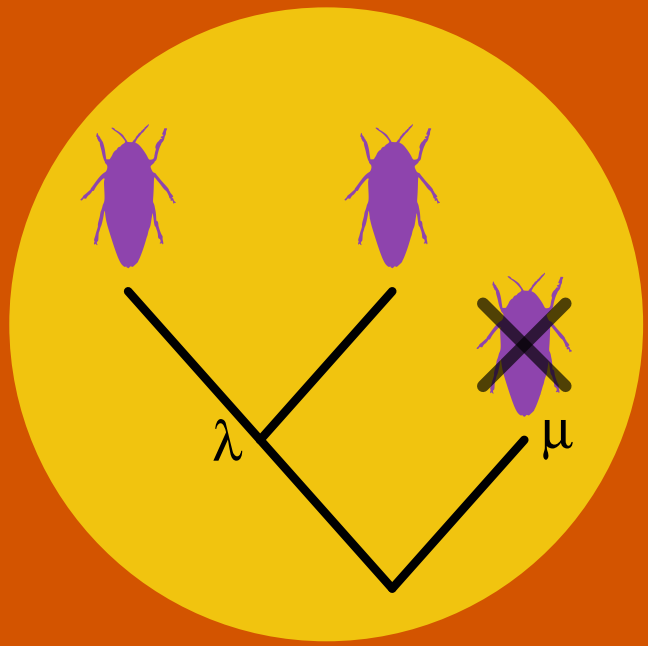
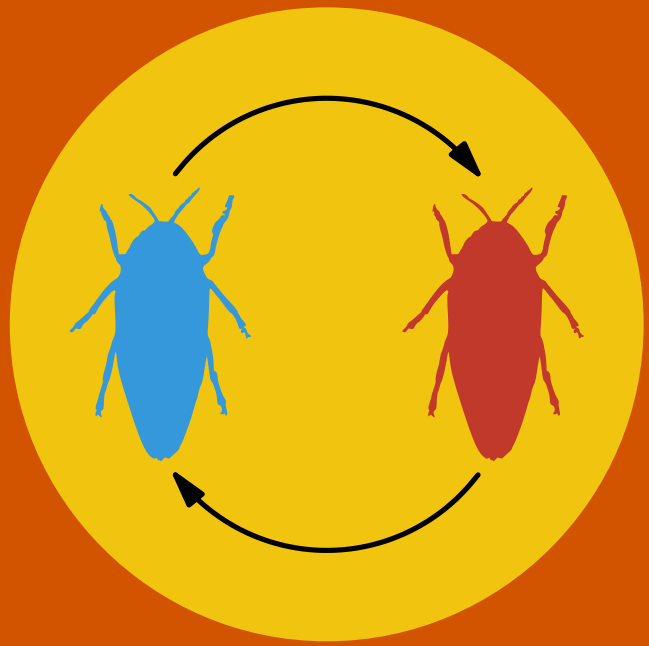


Maddison, Midford & Otto 2007



+

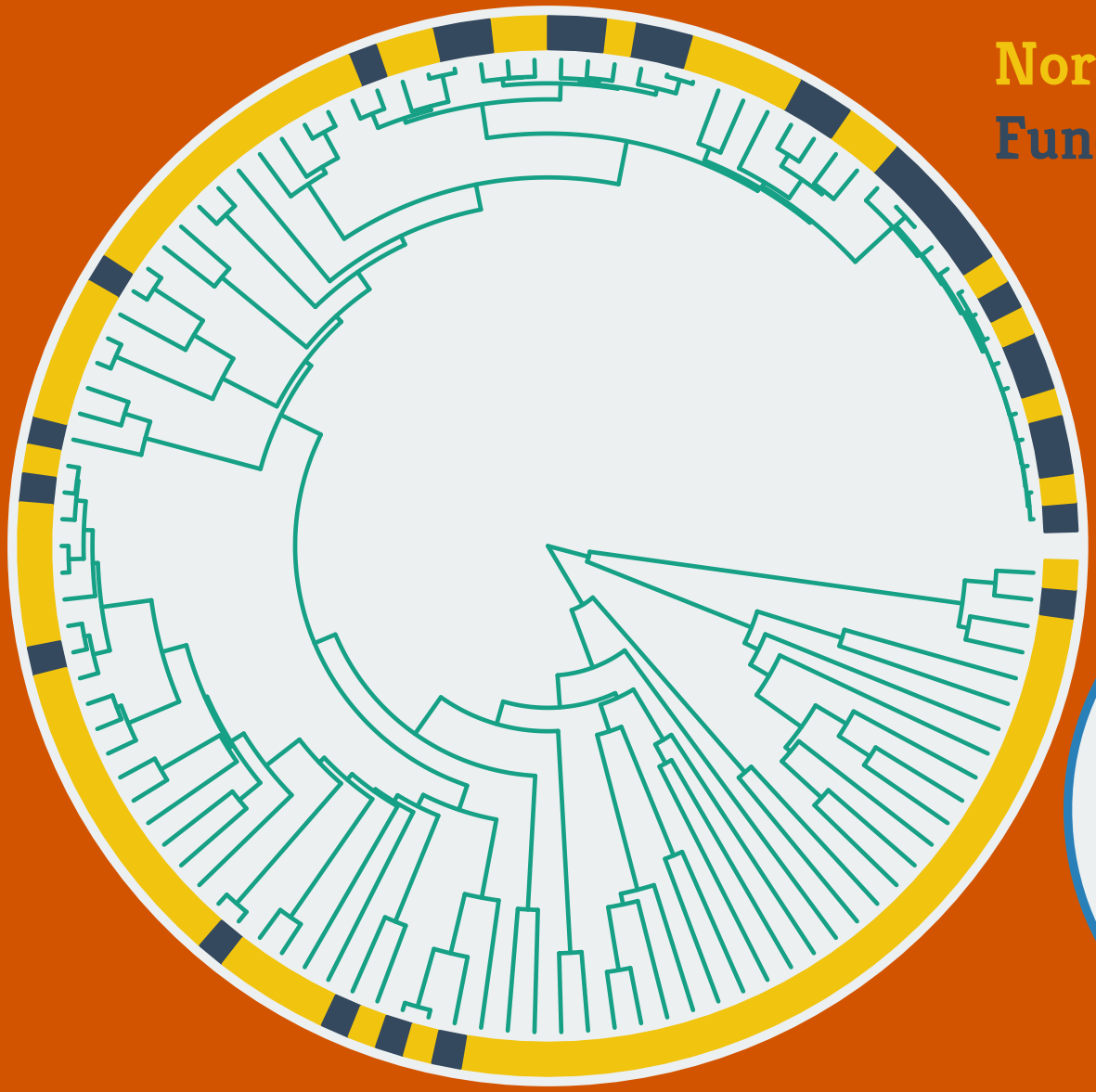


λ μ q

λ μ q

Maddison, Midford & Otto 2007

COPING WITH PHYLOGENETIC INCOMPLETENESS



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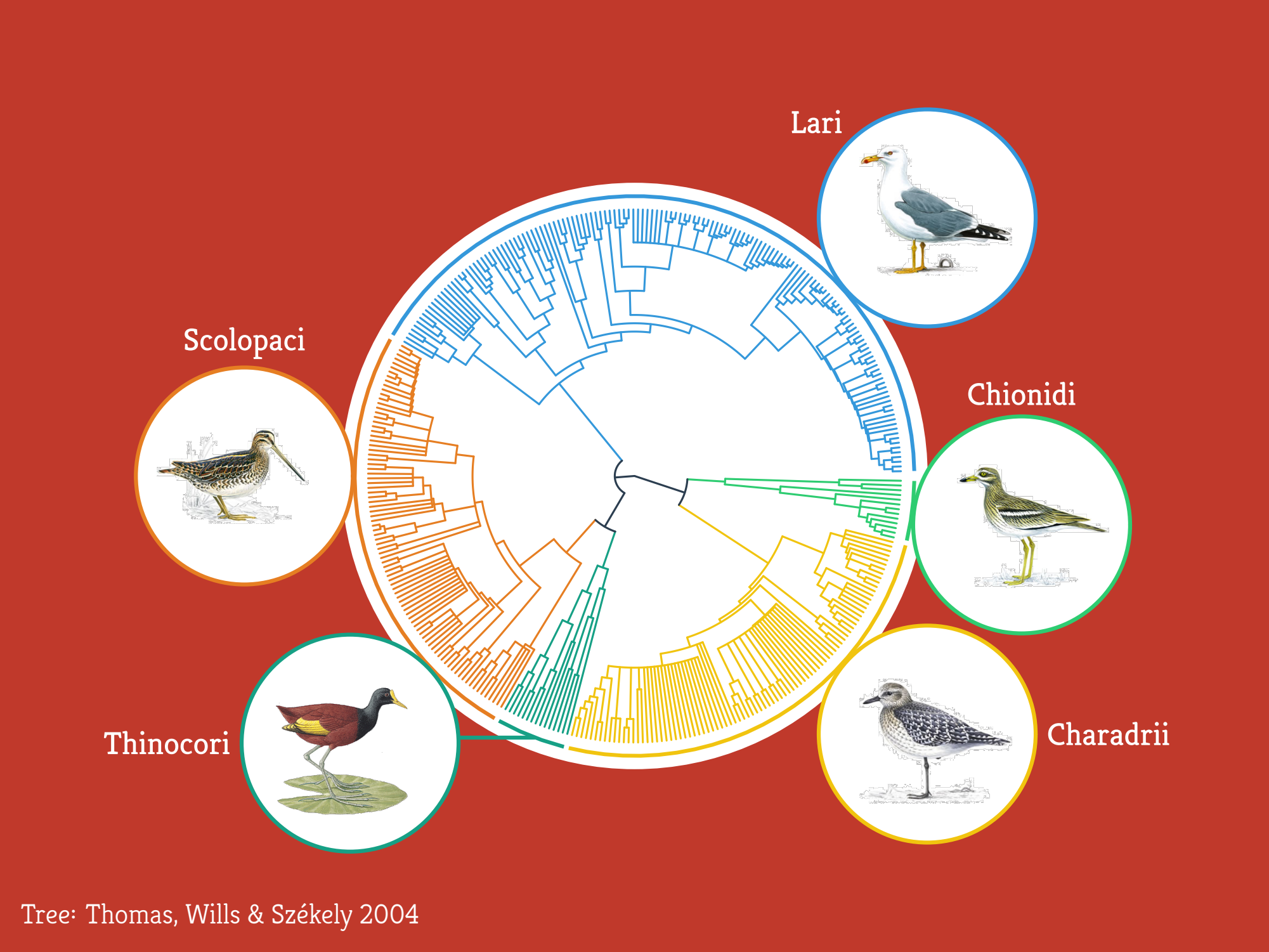
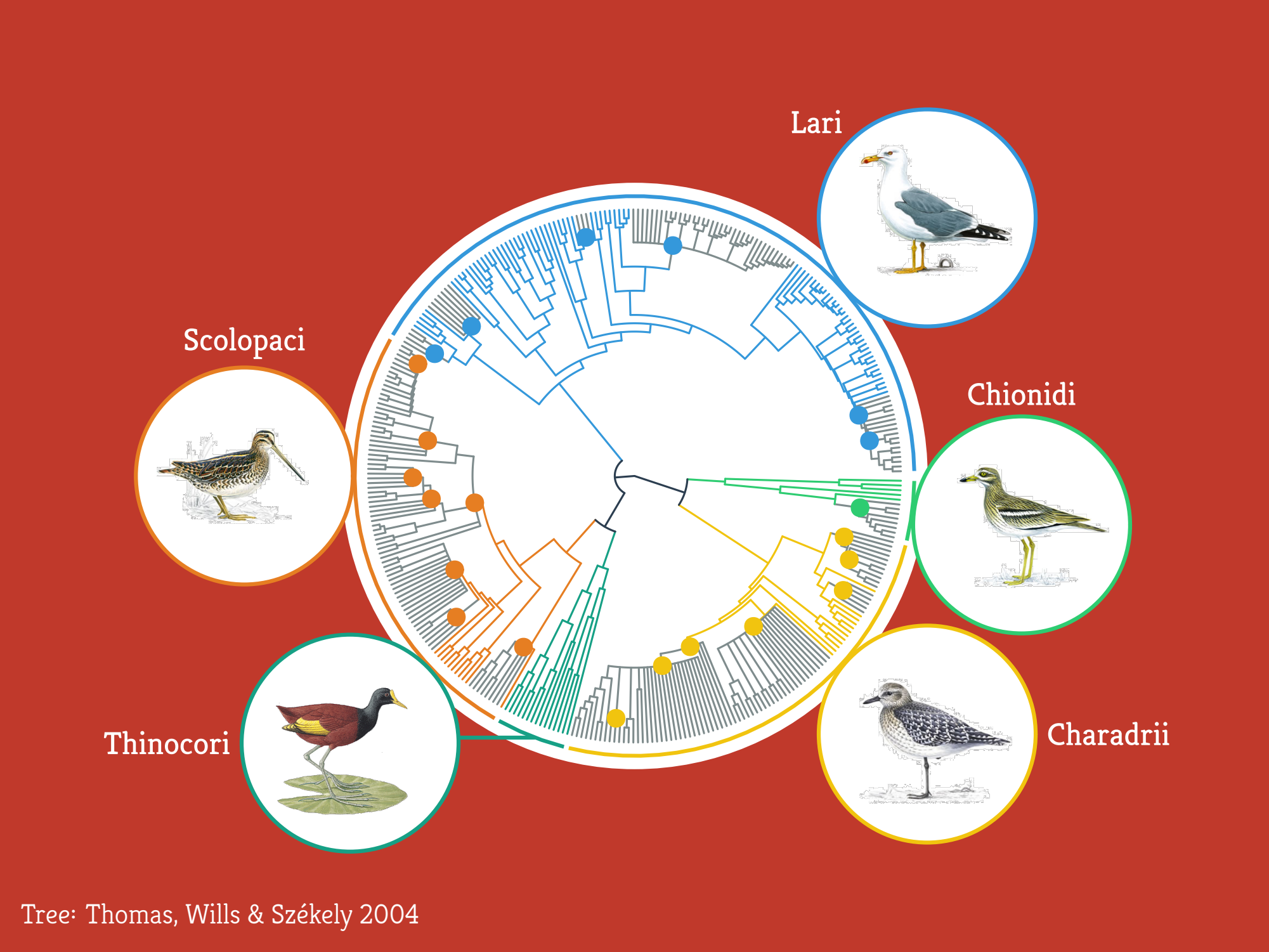
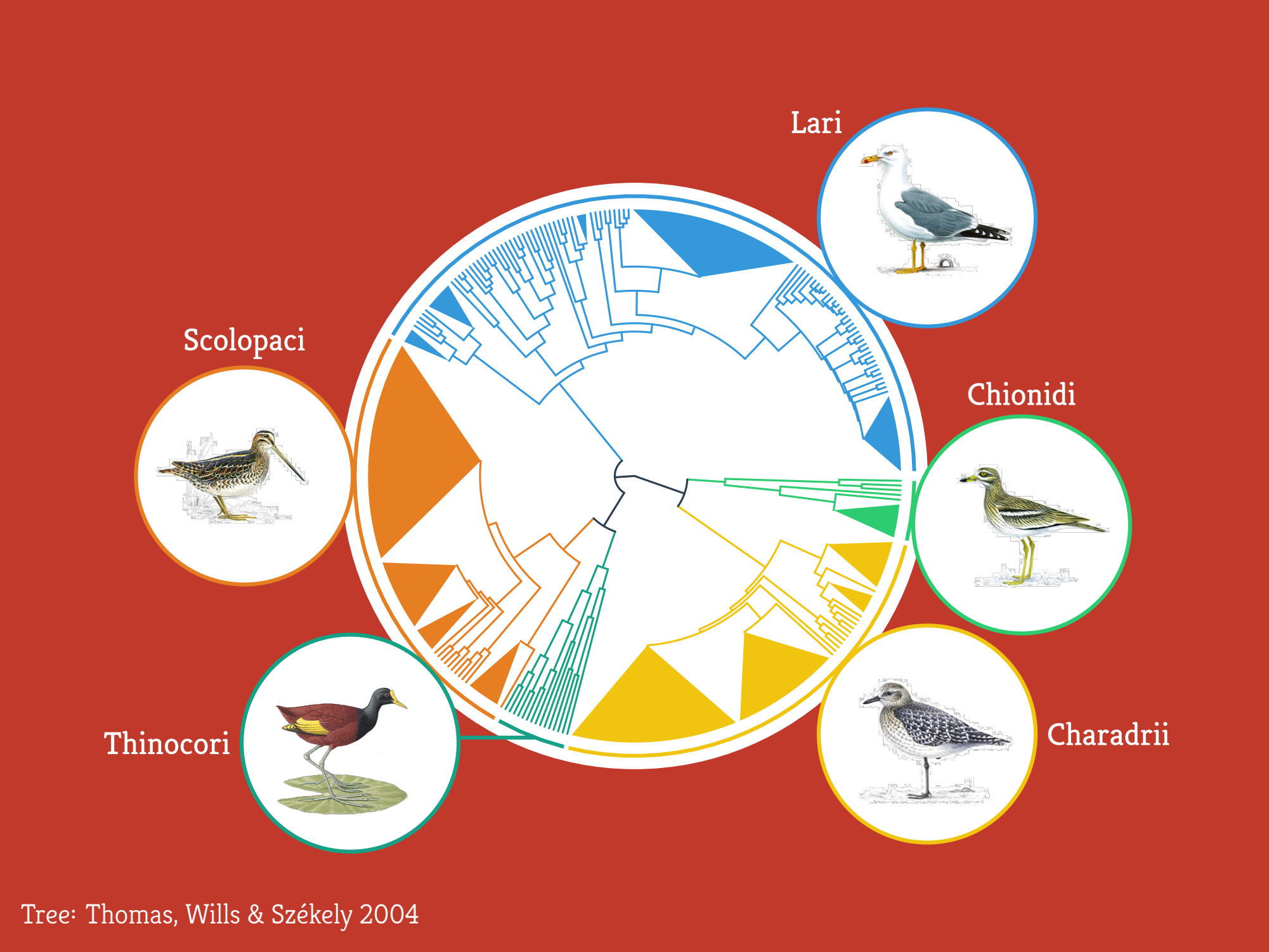


Tree: Thomas, Wills & Székely 2004

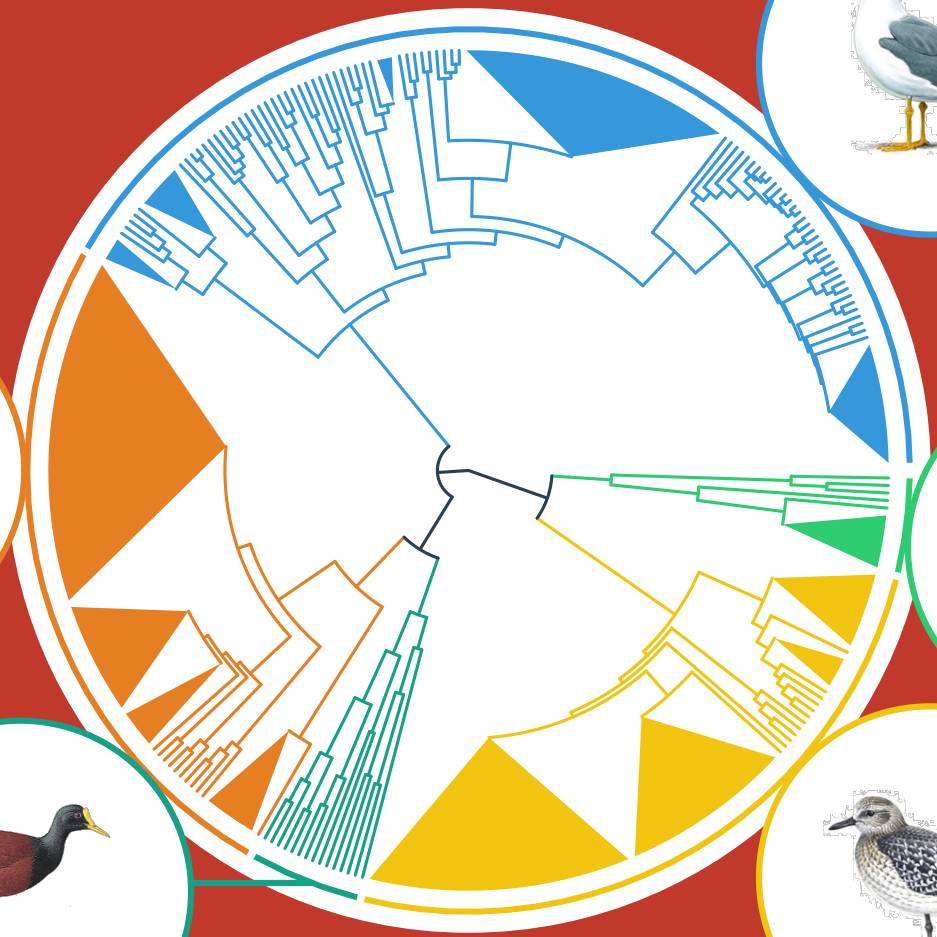


Tree: Thomas, Wills & Székely 2004



Tree: Thomas, Wills & Székely 2004

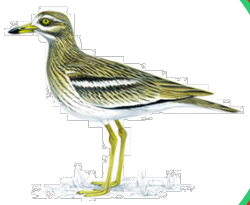
diversitree



Lari

Scolopaci

Chionidi



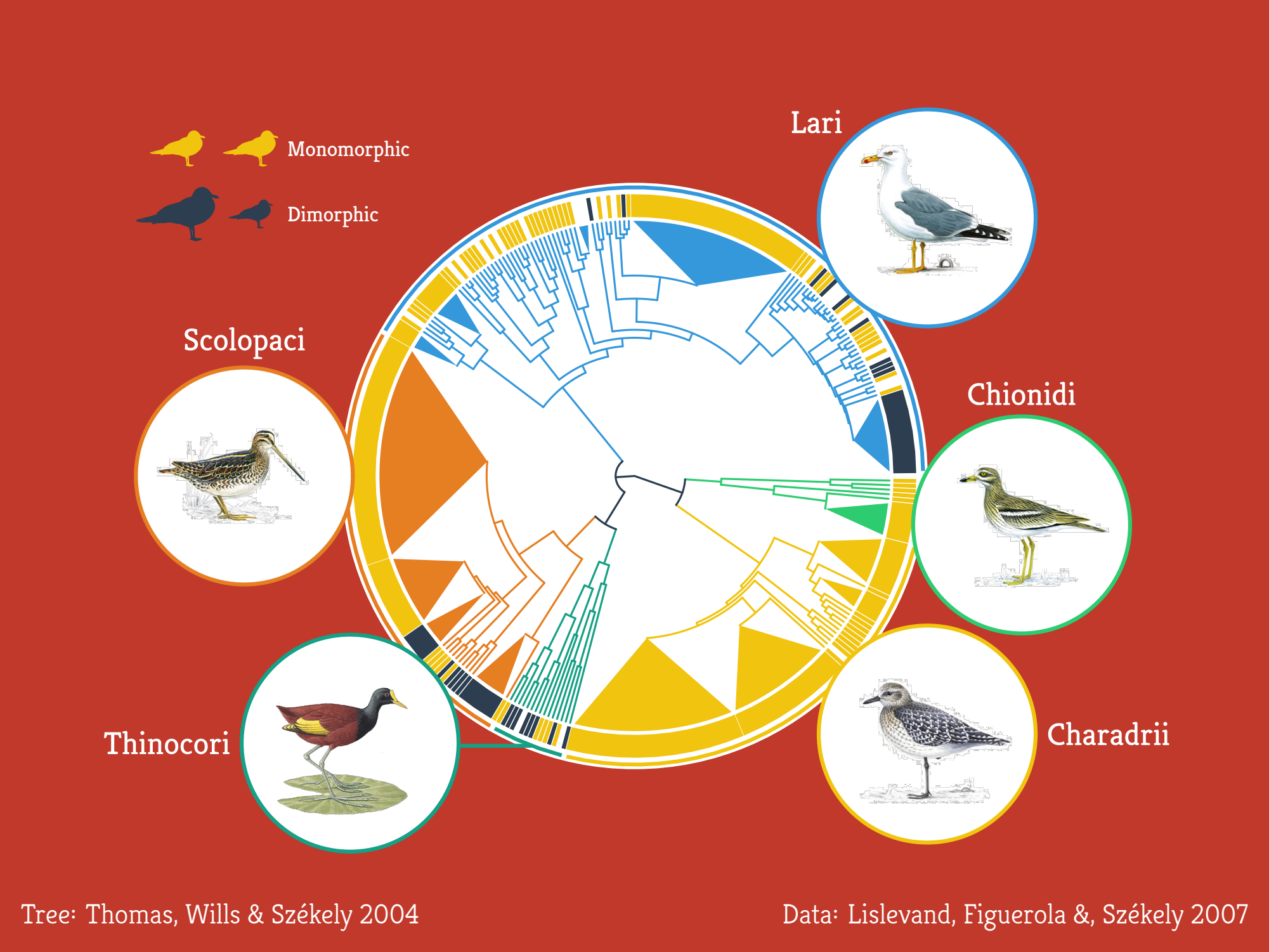
Thinocori

Charadrii

www.zoology.ubc.ca/prog/diversitree

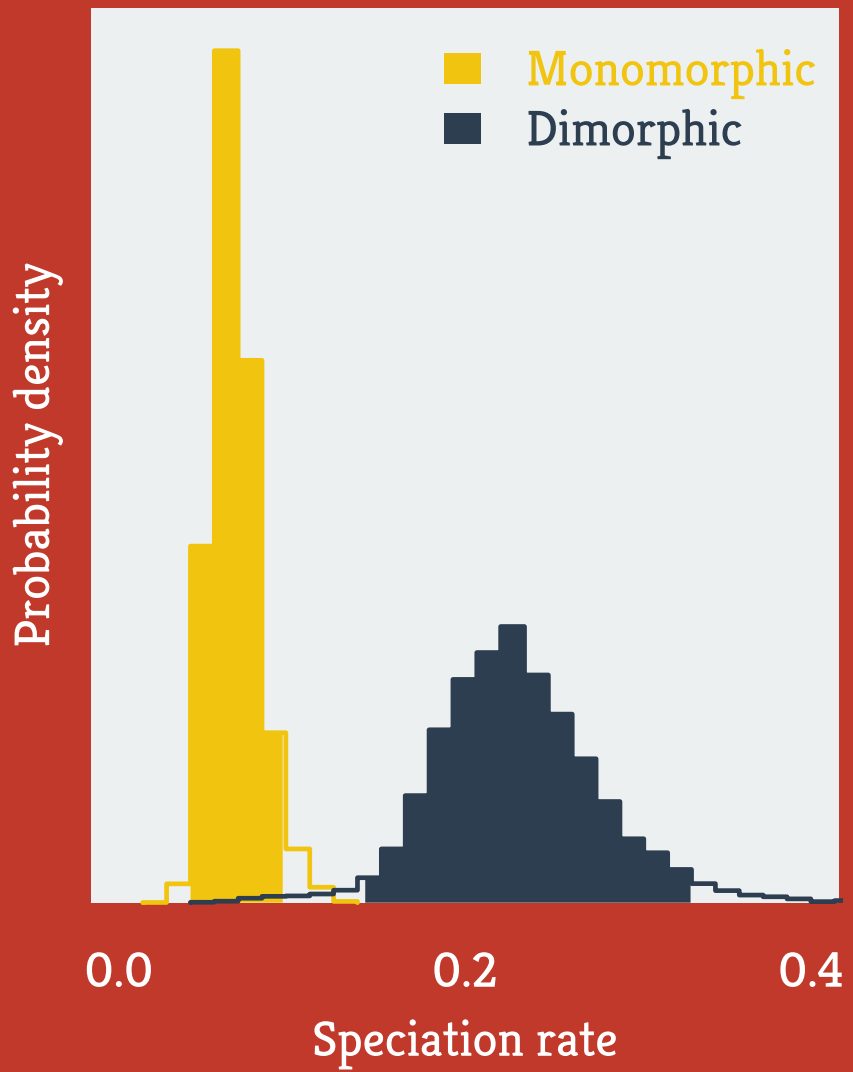
Photo: Thor Veen

Is
sexual size dimorphism
under species selection?

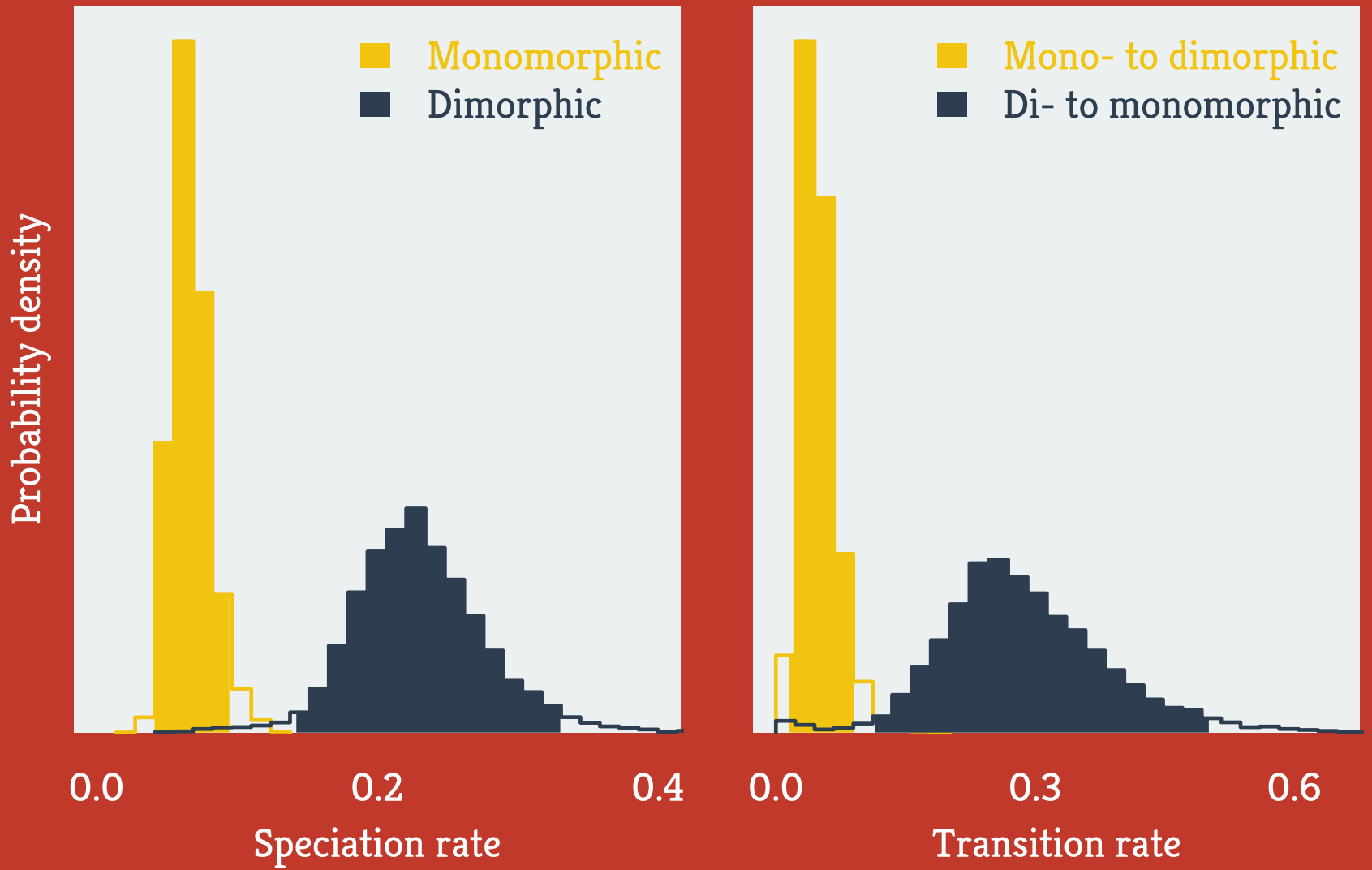


Tree: Thomas, Wills & Székely 2004

Data: Lislevand, Figuerola &, Székely 2007



FitzJohn, Maddison & Otto 2009

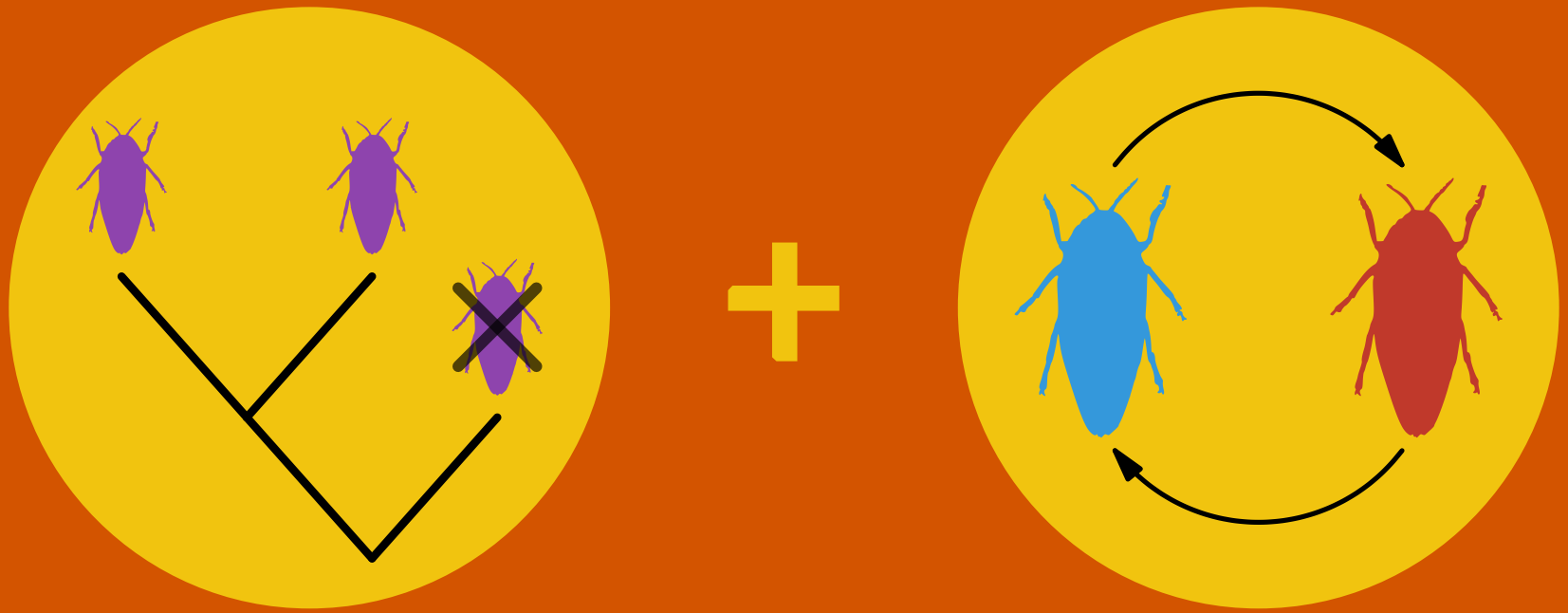


FitzJohn, Maddison & Otto 2009

Is
sexual size dimorphism
under species selection?

Perhaps briefly

DEALING WITH MULTIPLE TRAITS



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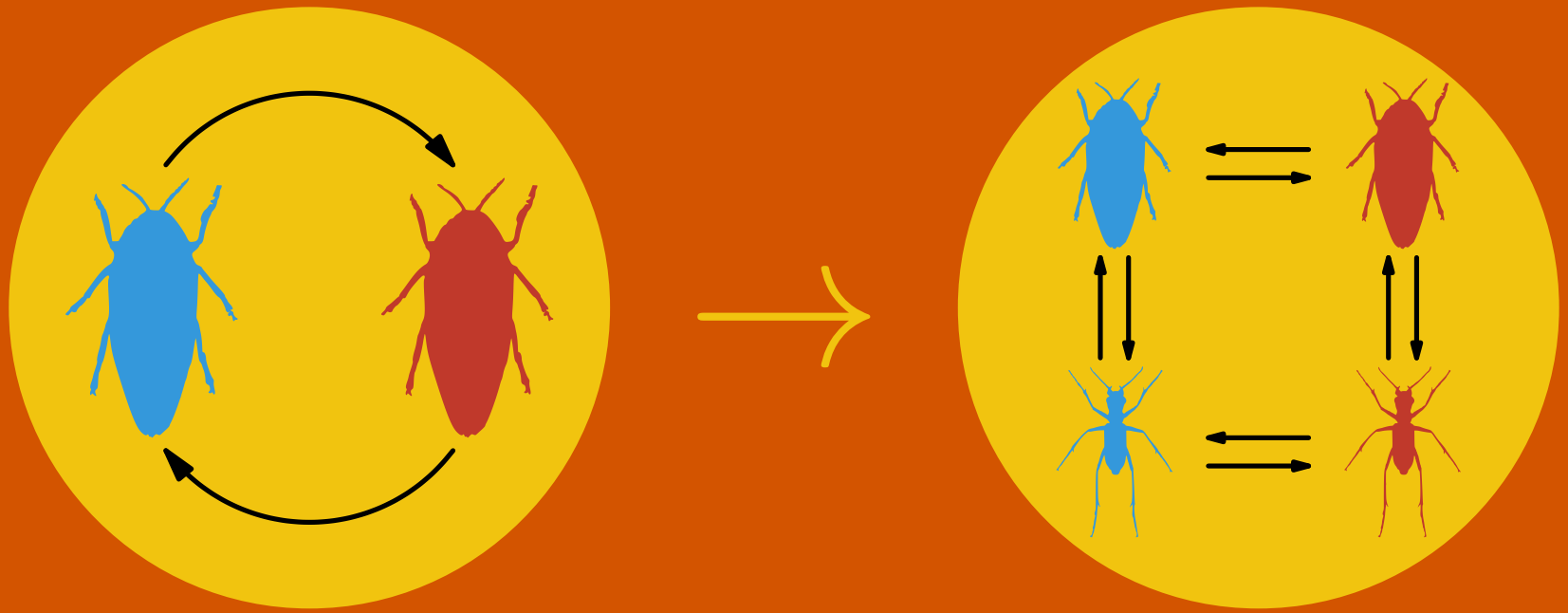

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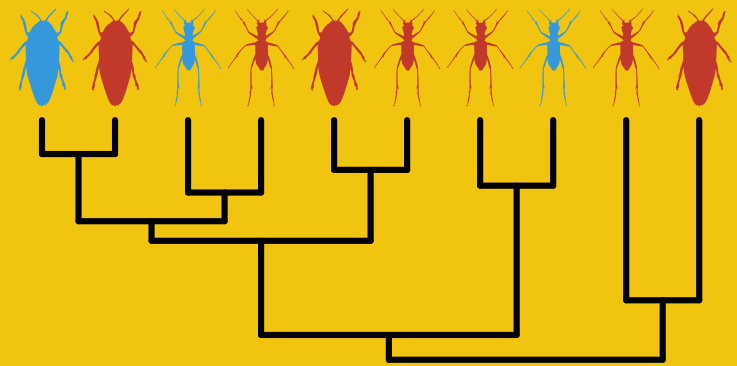
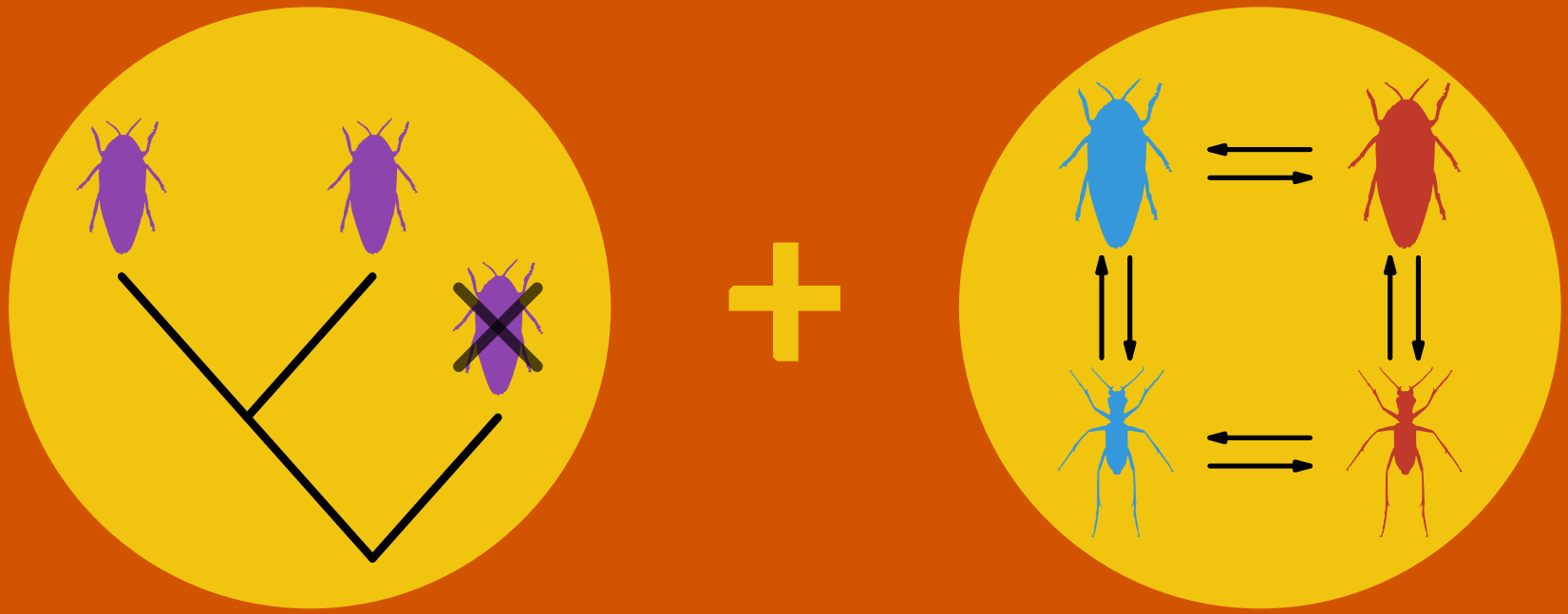


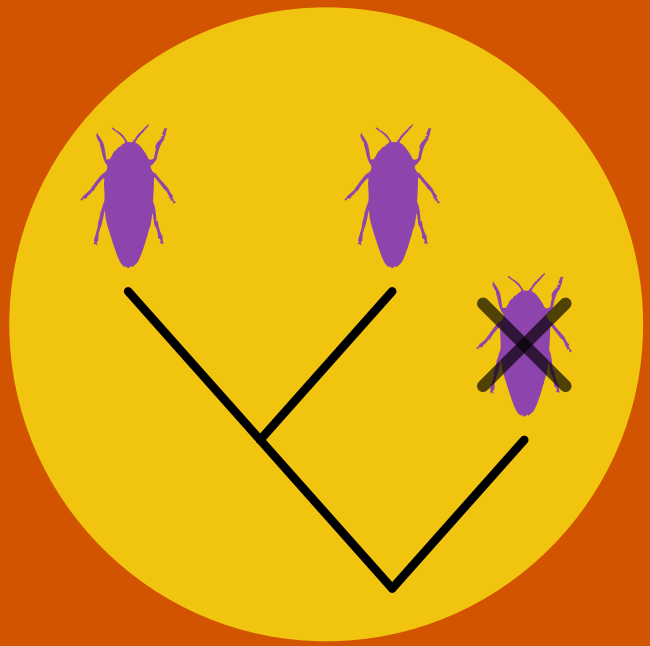
FitzJohn 2012

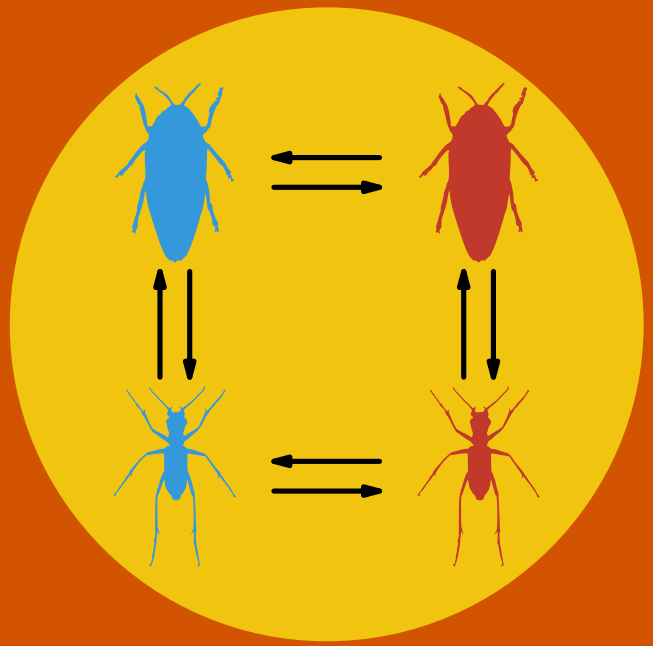


MuSSE: Multi State Speciation & Extinction

FitzJohn 2012

diversitree





Speciation rate:

$$\lambda = \lambda_0 + \lambda_{\bullet} + \lambda_{\text{ant}} + \lambda_{\bullet} \times$$ 

FitzJohn 2012

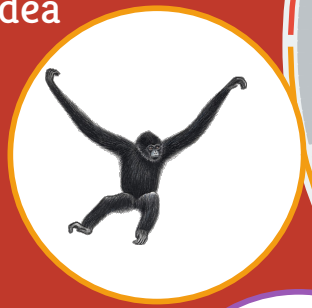
Monogamous:
Solitary:

Cercopithecoidea

Lorisiformes

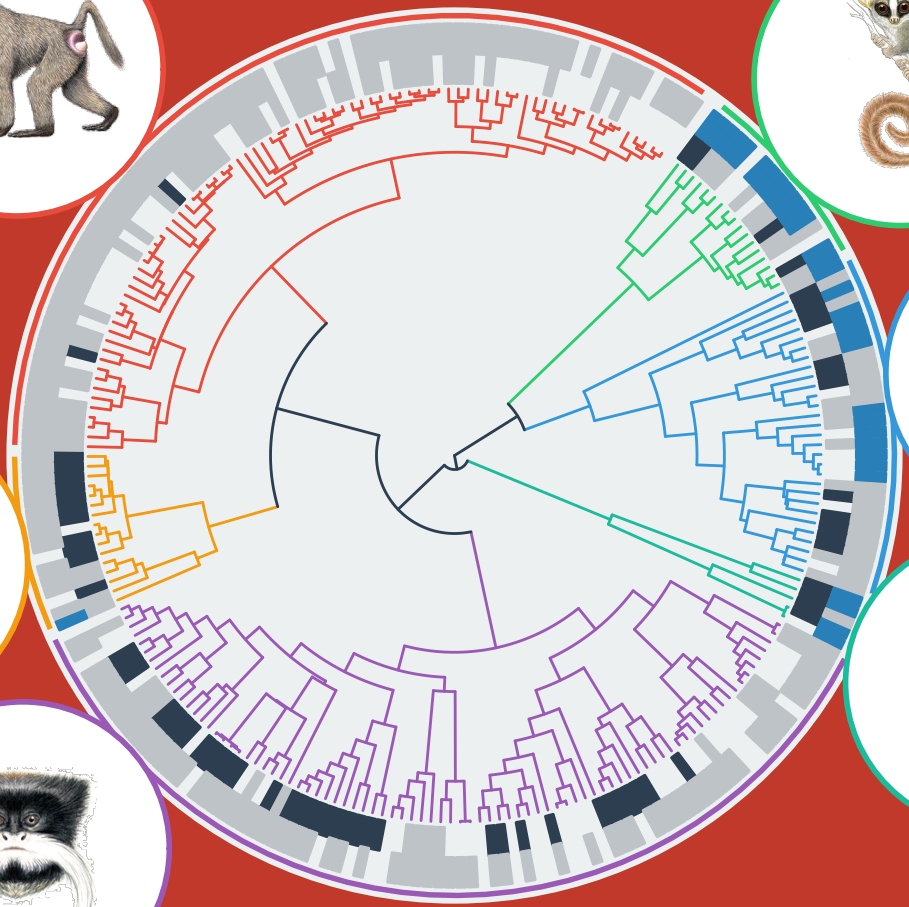
Lemuriformes

Hominoidea



Tarsiformes

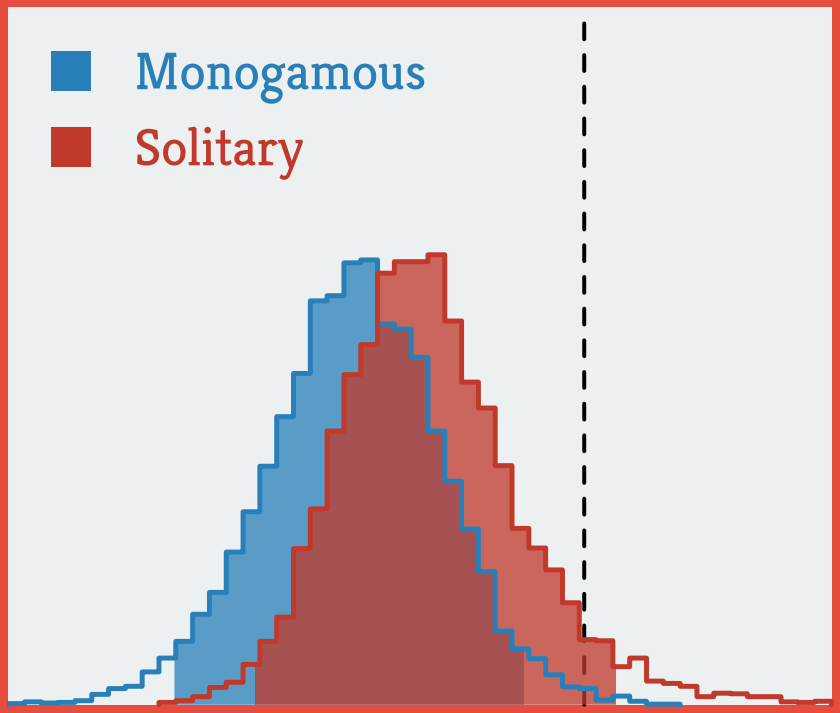
Platyrrhini



Tree: Vos & Mooers unpublished

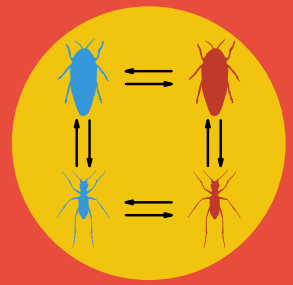
Data: Redding & Mooers 2006

BiSSE (independent)

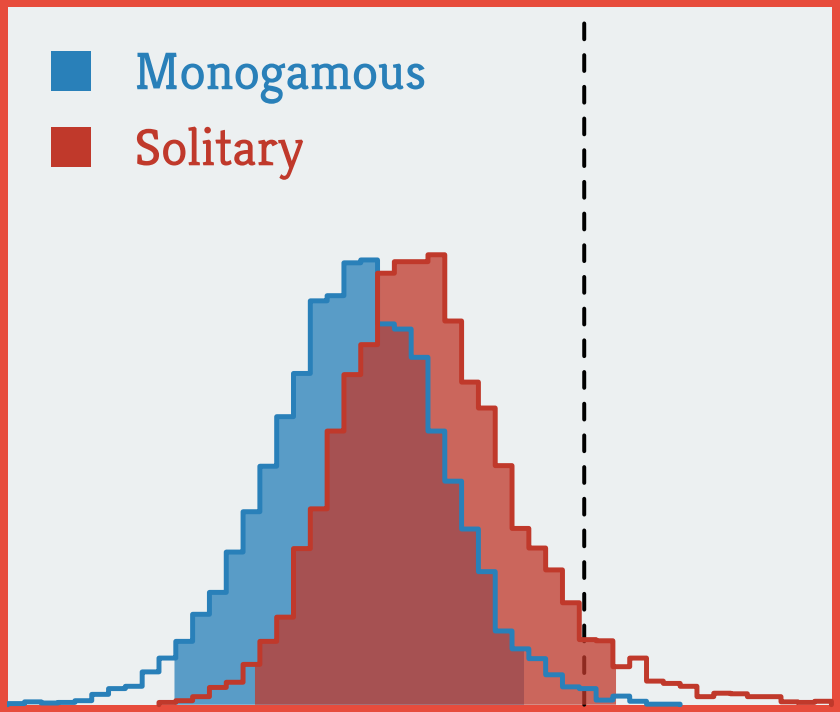


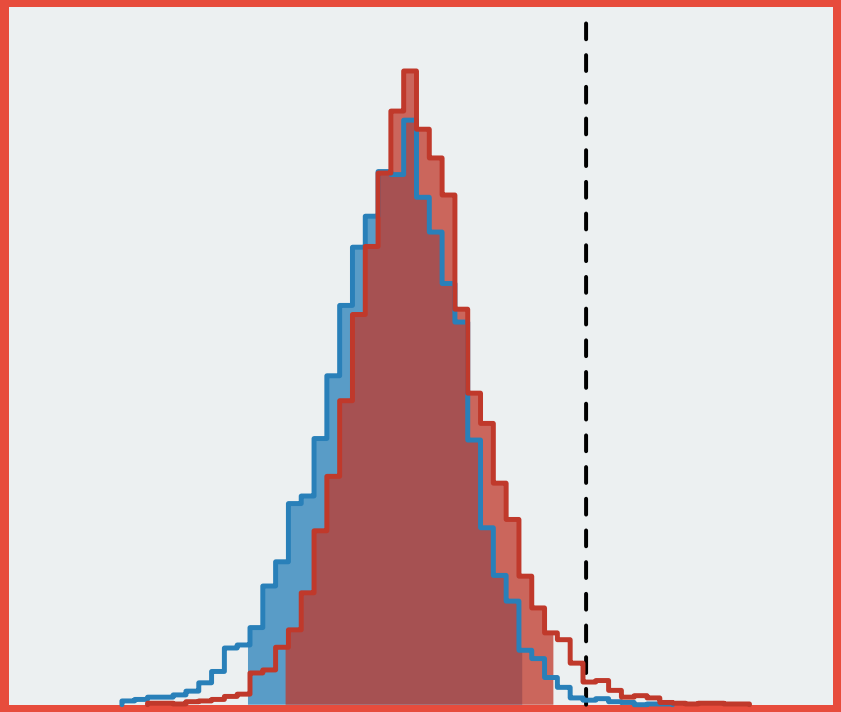
Magnusson Ford & Otto 2011

BiSSE (independent)



MuSSE (simultaneous)

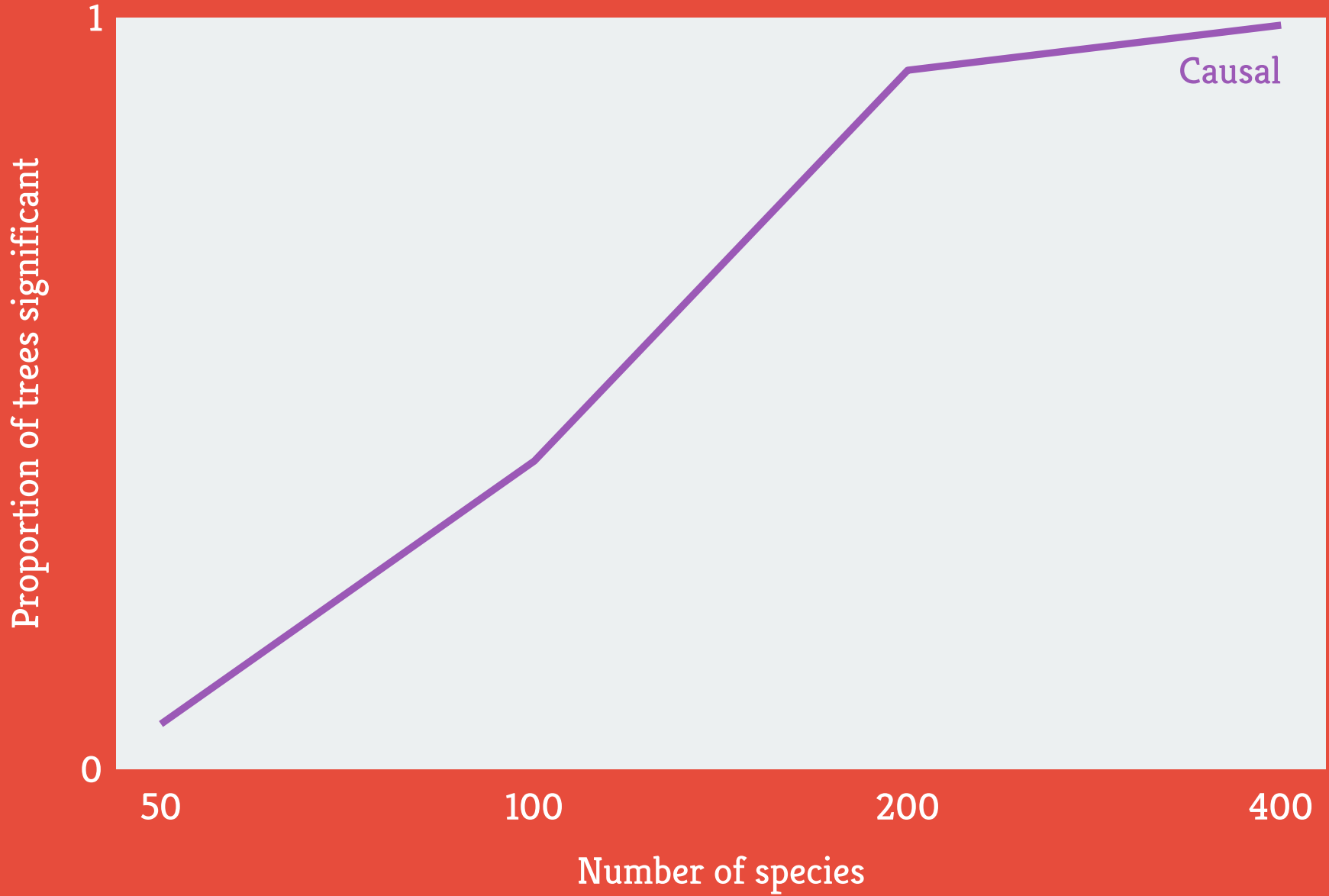


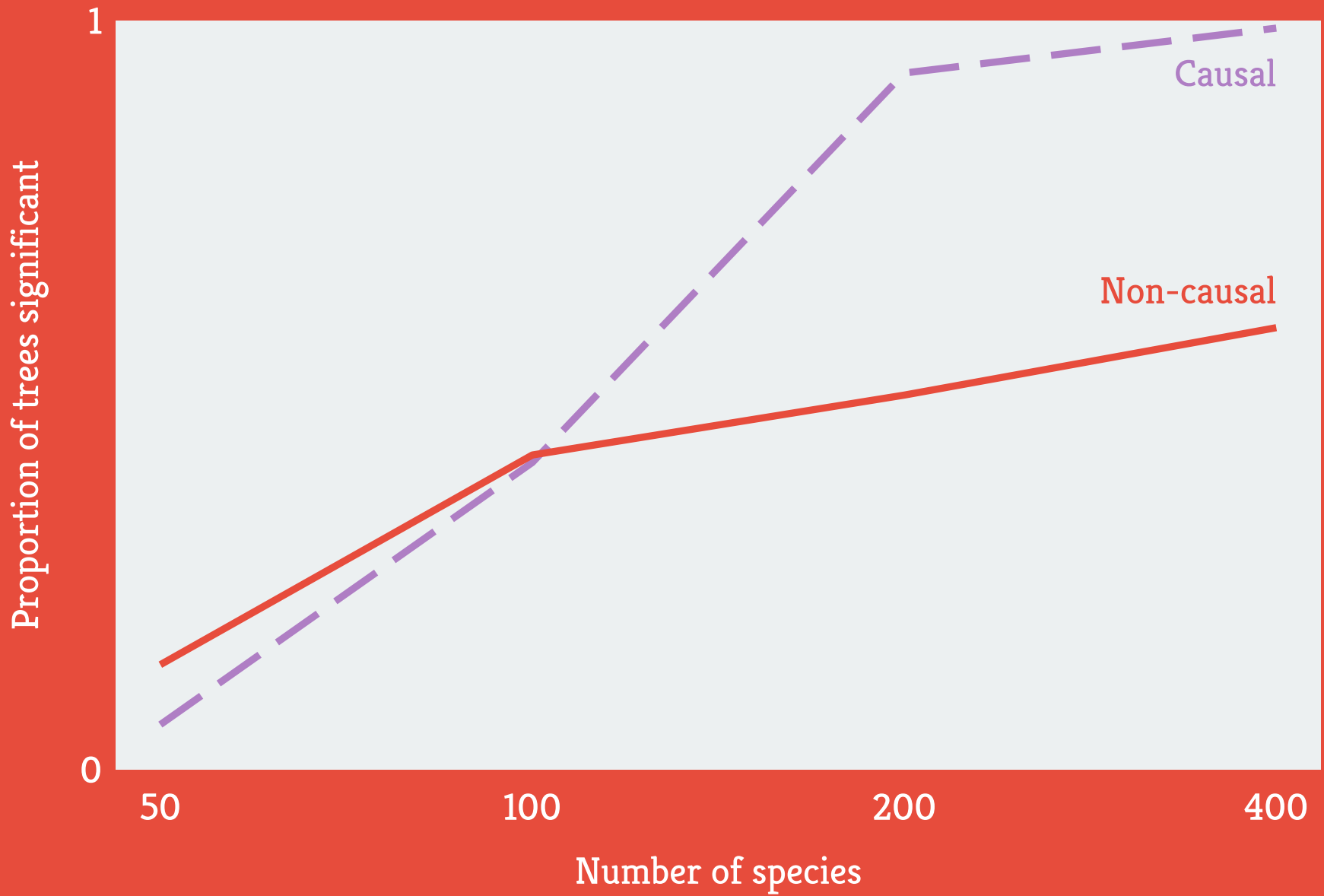


-0.2 0.0 -0.2 0.0

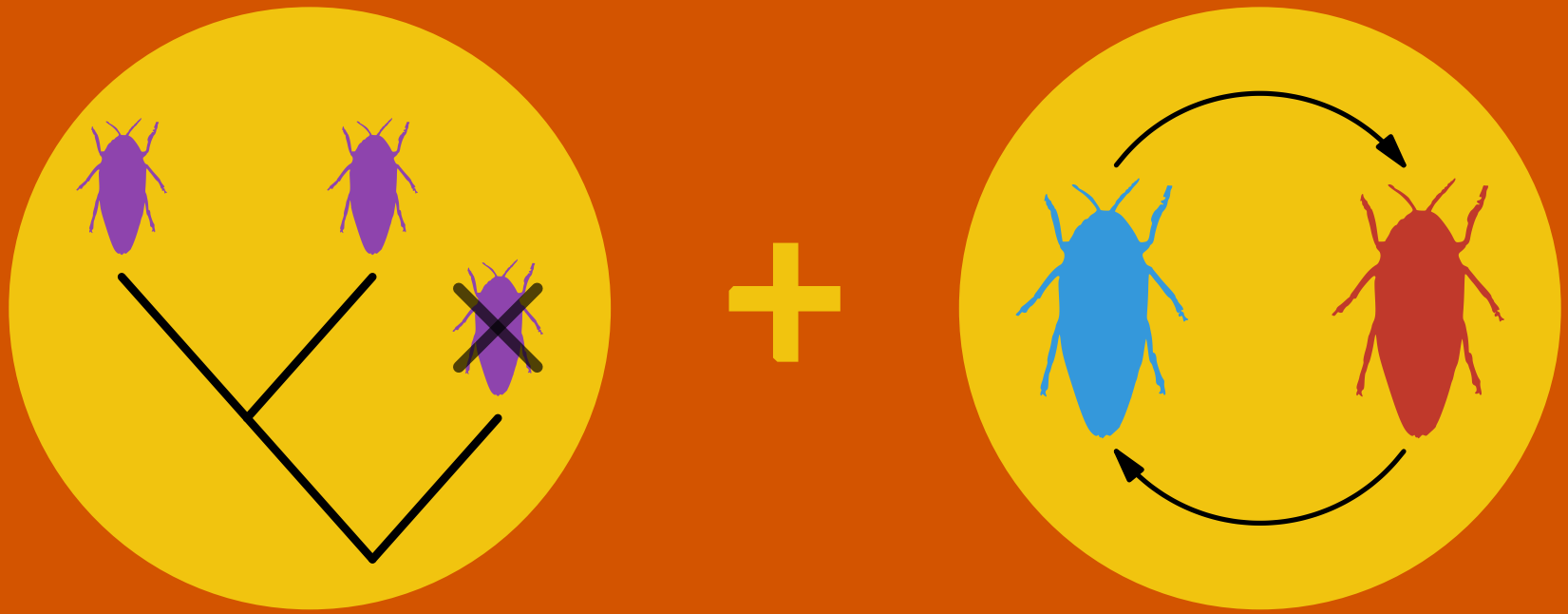
Trait effect on speciation

FitzJohn 2012


1
0
Proportion of trees significant
Causal
50
100
200
400
Number of species


1
0
Proportion of trees significant
Causal
Non-causal
50
100
200
400
Number of species

QUANTITATIVE TRAITS



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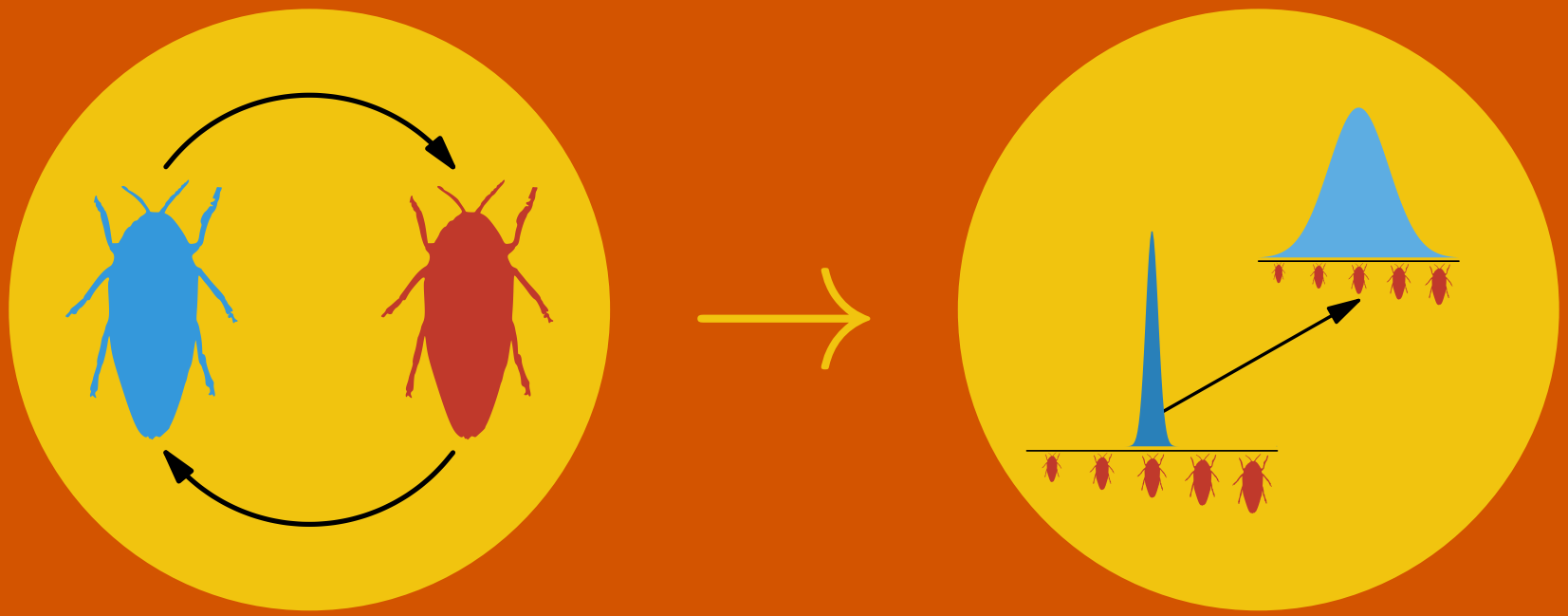
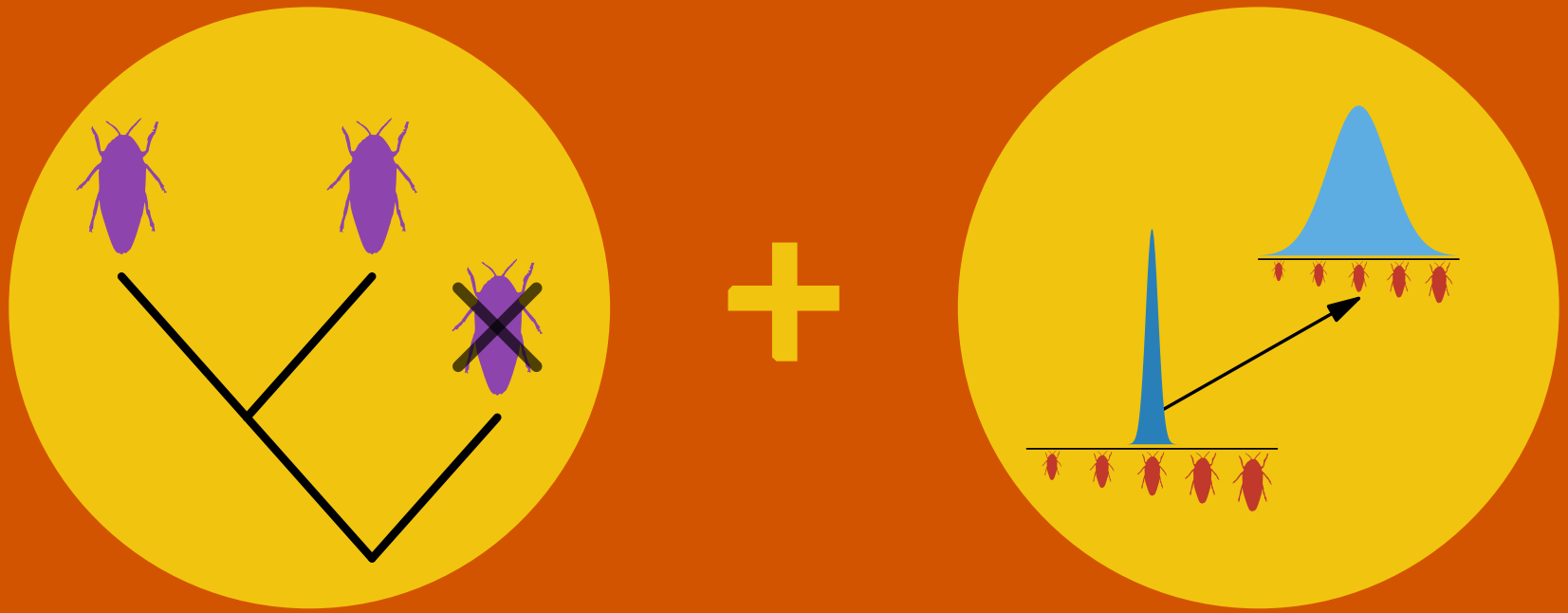
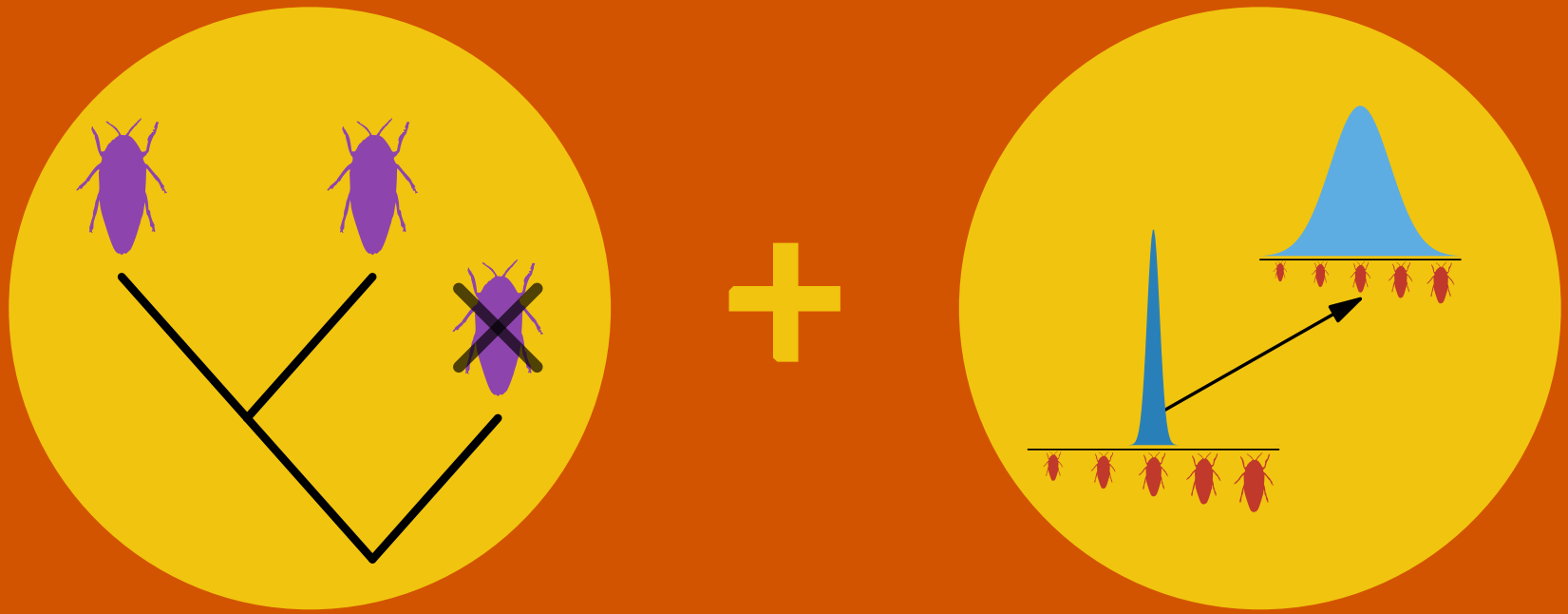


Trait evolution: Brownian Motion



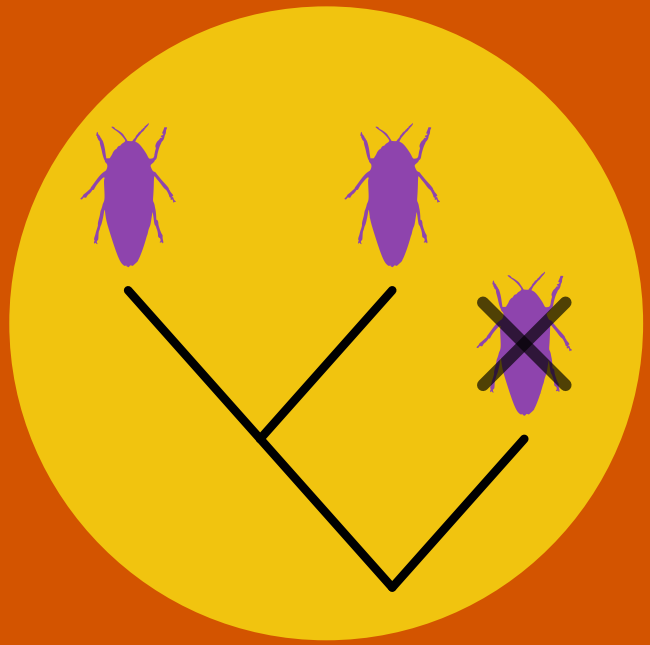
QuaSSE:
Quantitative State Speciation & Extinction

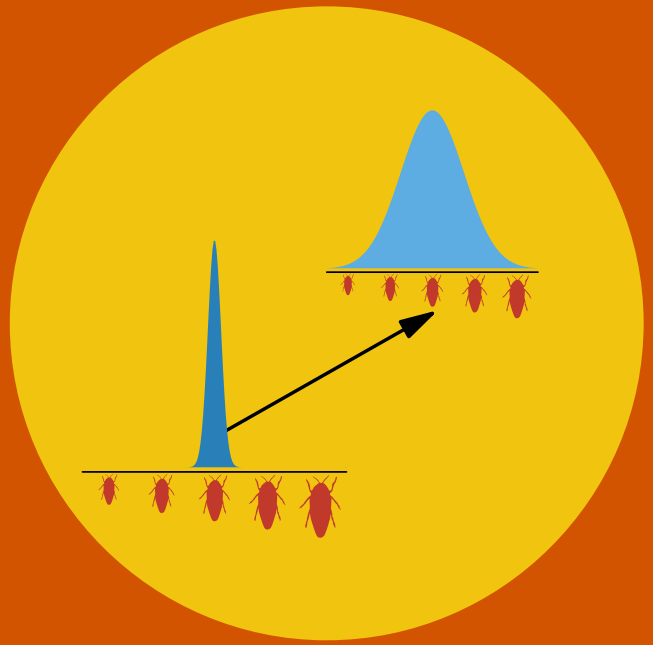
FitzJohn 2010



$$\Pr\left[\ \right]$$

FitzJohn 2010





$$\text{speciation rate} = \text{function}\left[\ \right]$$

FitzJohn 2010

Why are there

so many small

mammal species?

1.8g

> 170 tonnes

Data: Jones et al. 2009

1 g 1 kg 1 tonne 100 tonnes

Body mass (g; log scale)

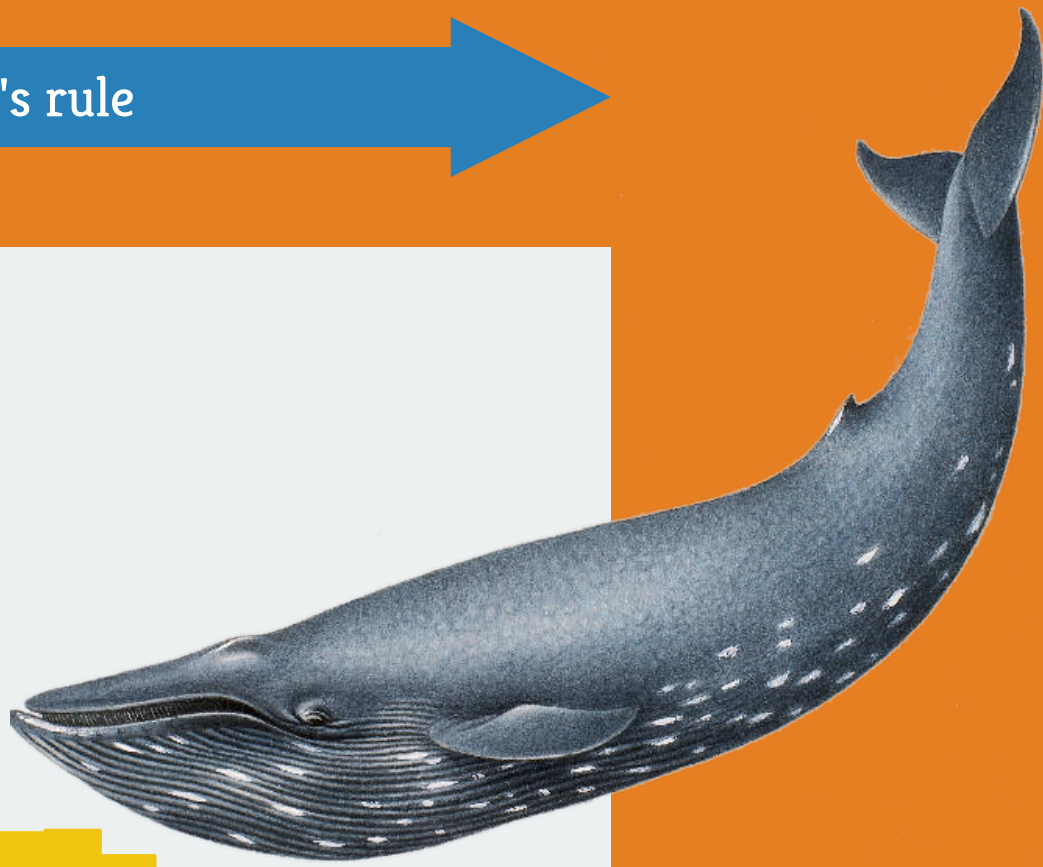
Data: Jones et al. 2009

1 g 1 kg 1 tonne 100 tonnes

Body mass (g; log scale)

Data: Jones et al. 2009

Cope's rule

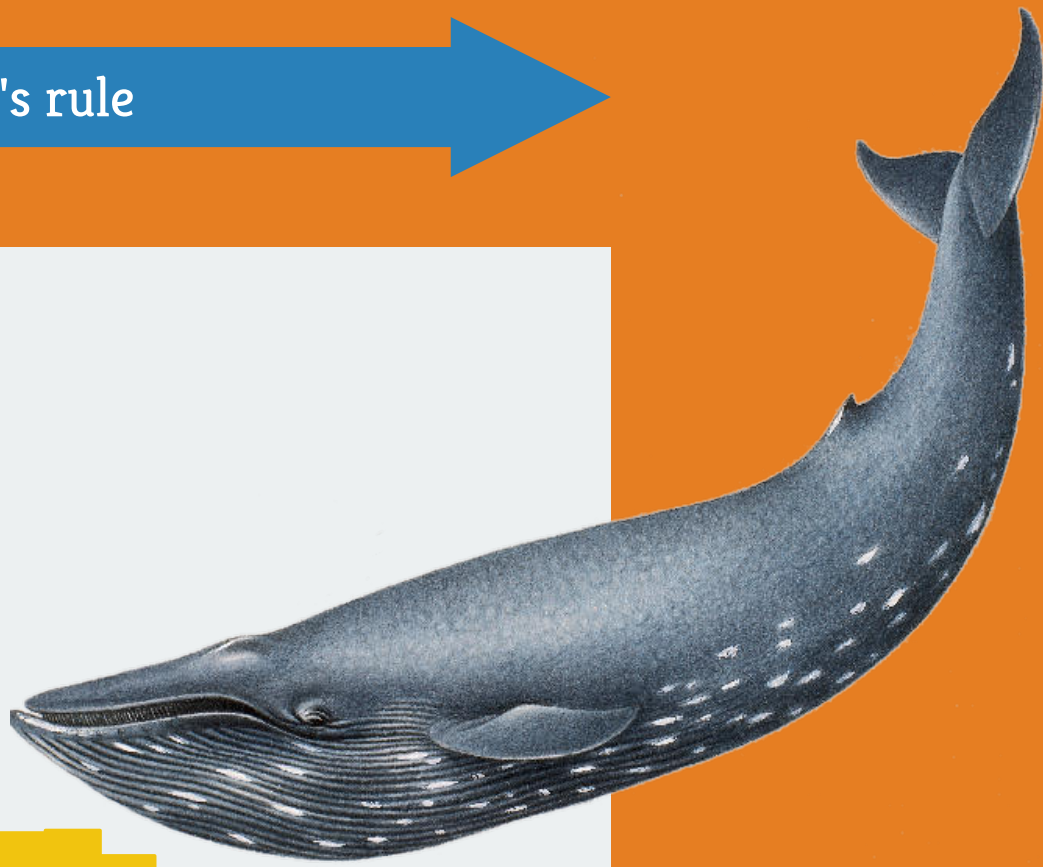


1 g 1 kg 1 tonne 100 tonnes

Body mass (g; log scale)

Data: Jones et al. 2009

Cope's rule

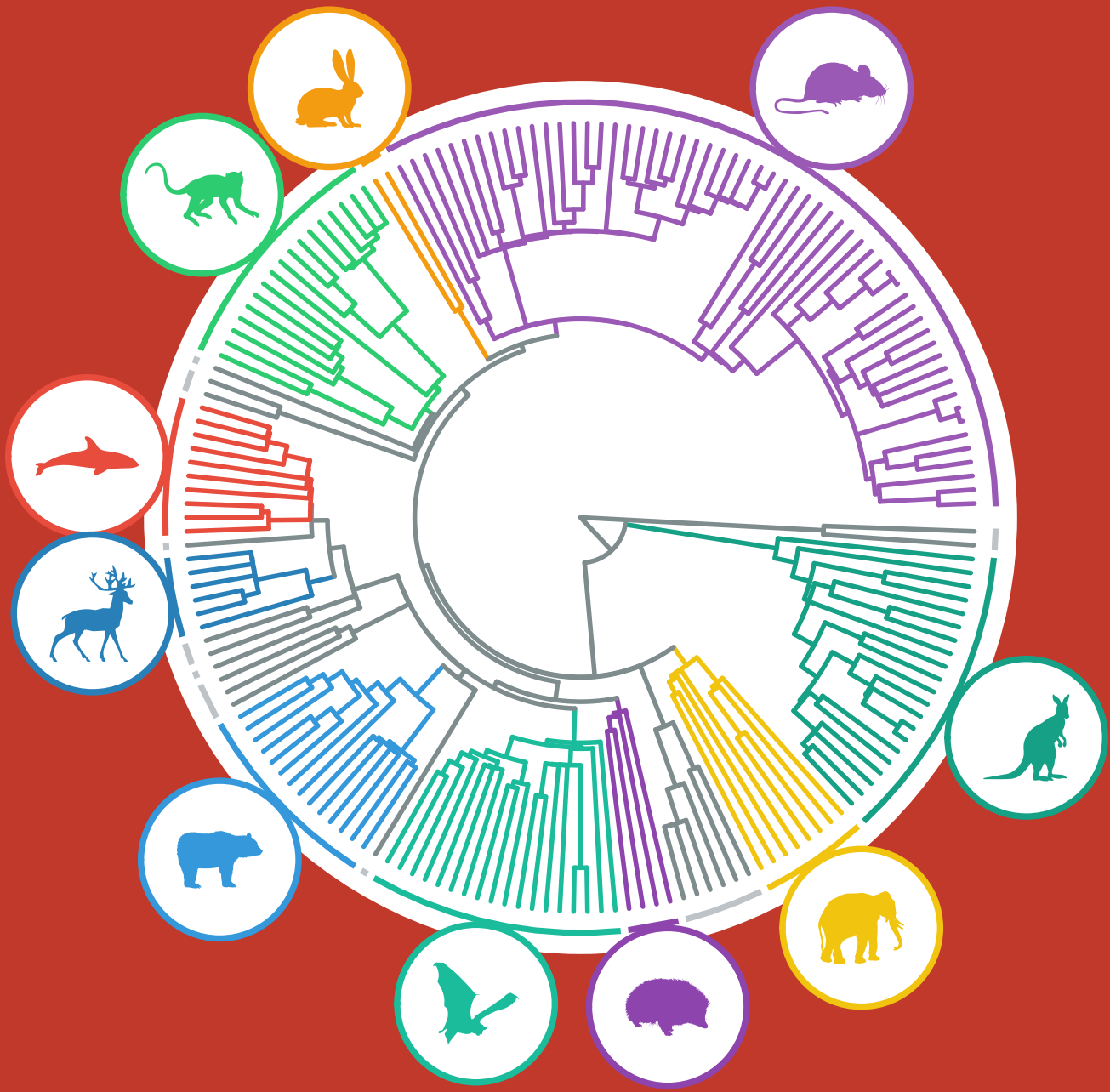


1 g 1 kg 1 tonne 100 tonnes

Body mass (g; log scale)

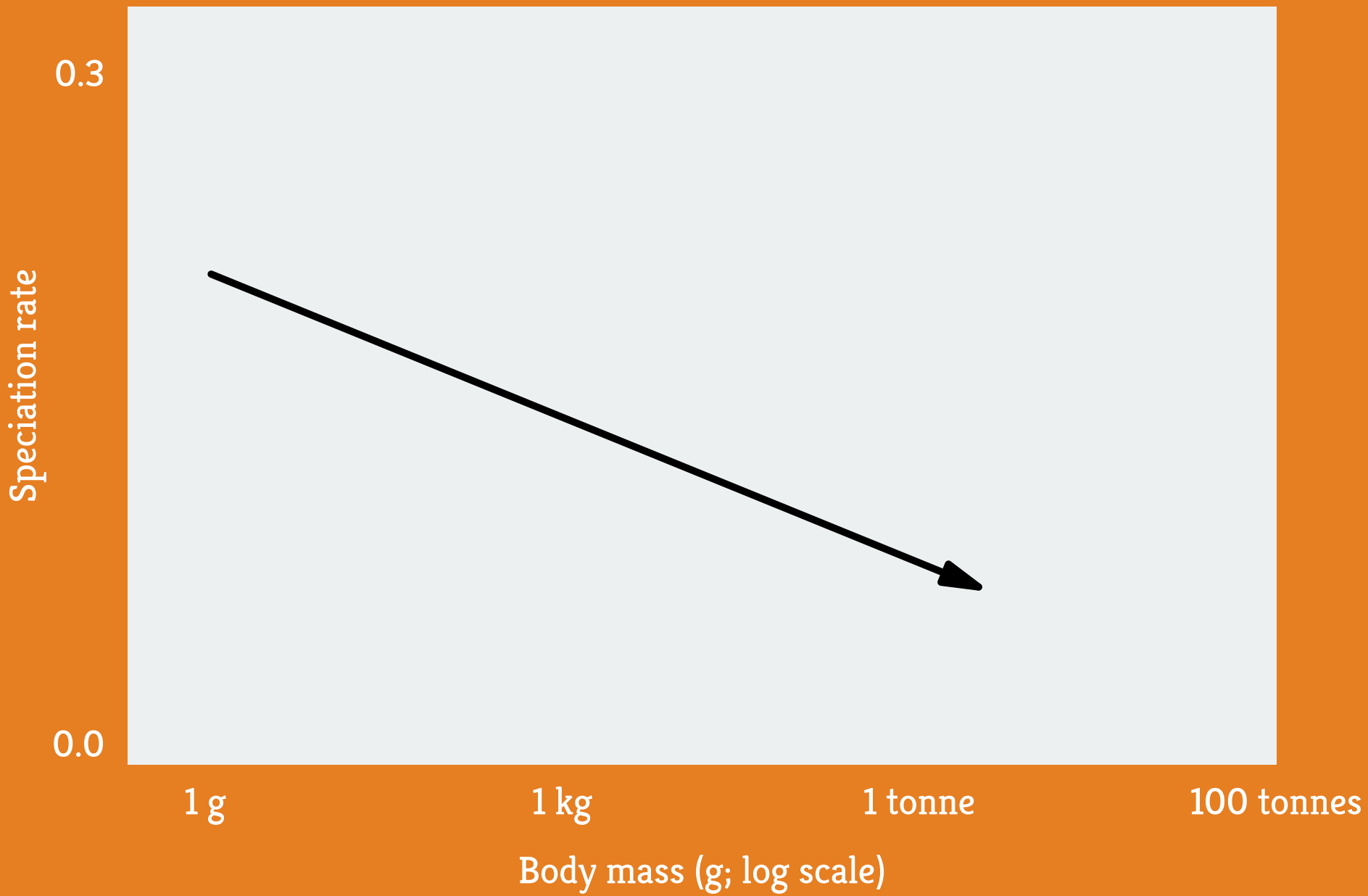
Species selection

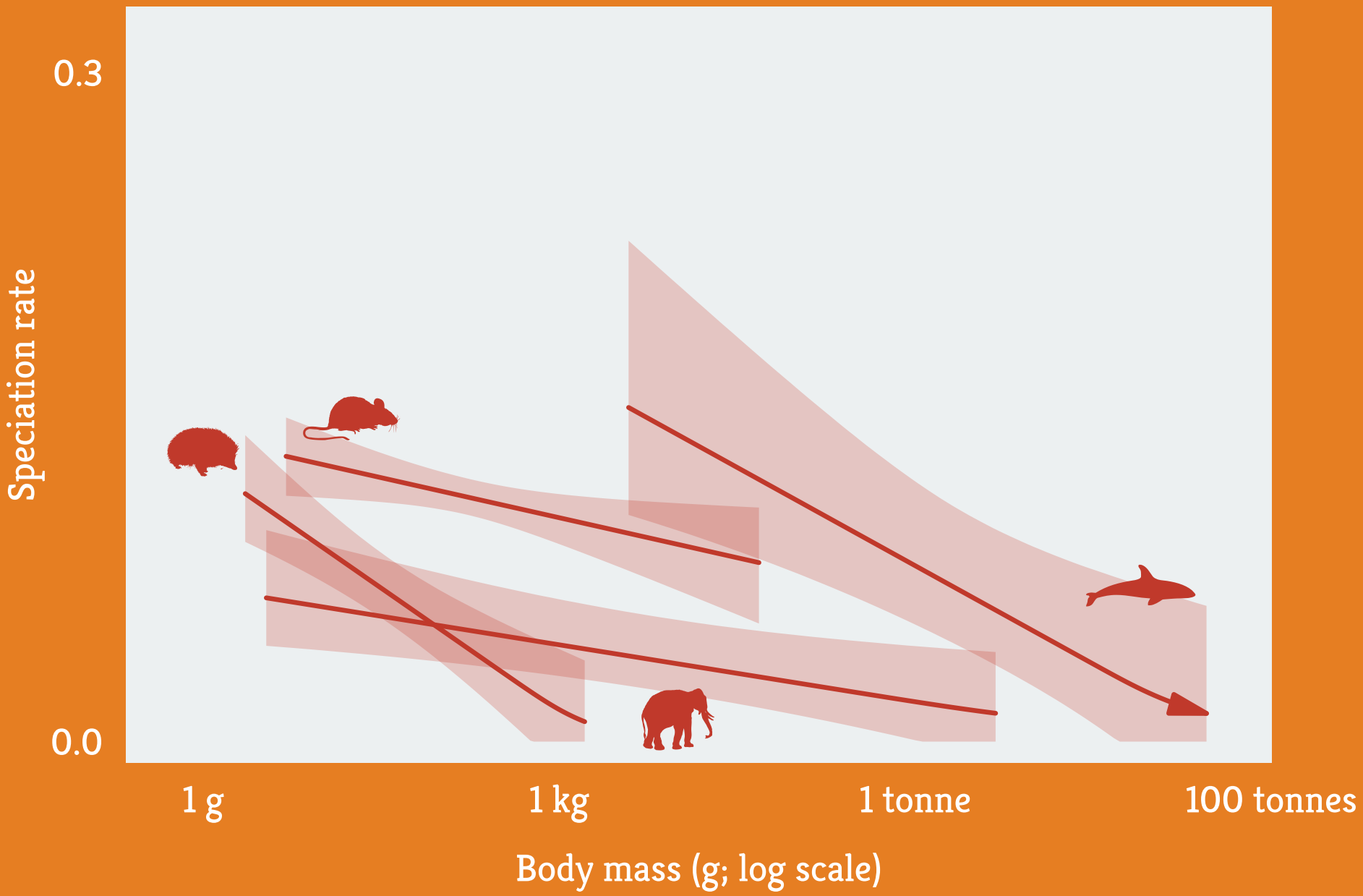
Data: Jones et al. 2009

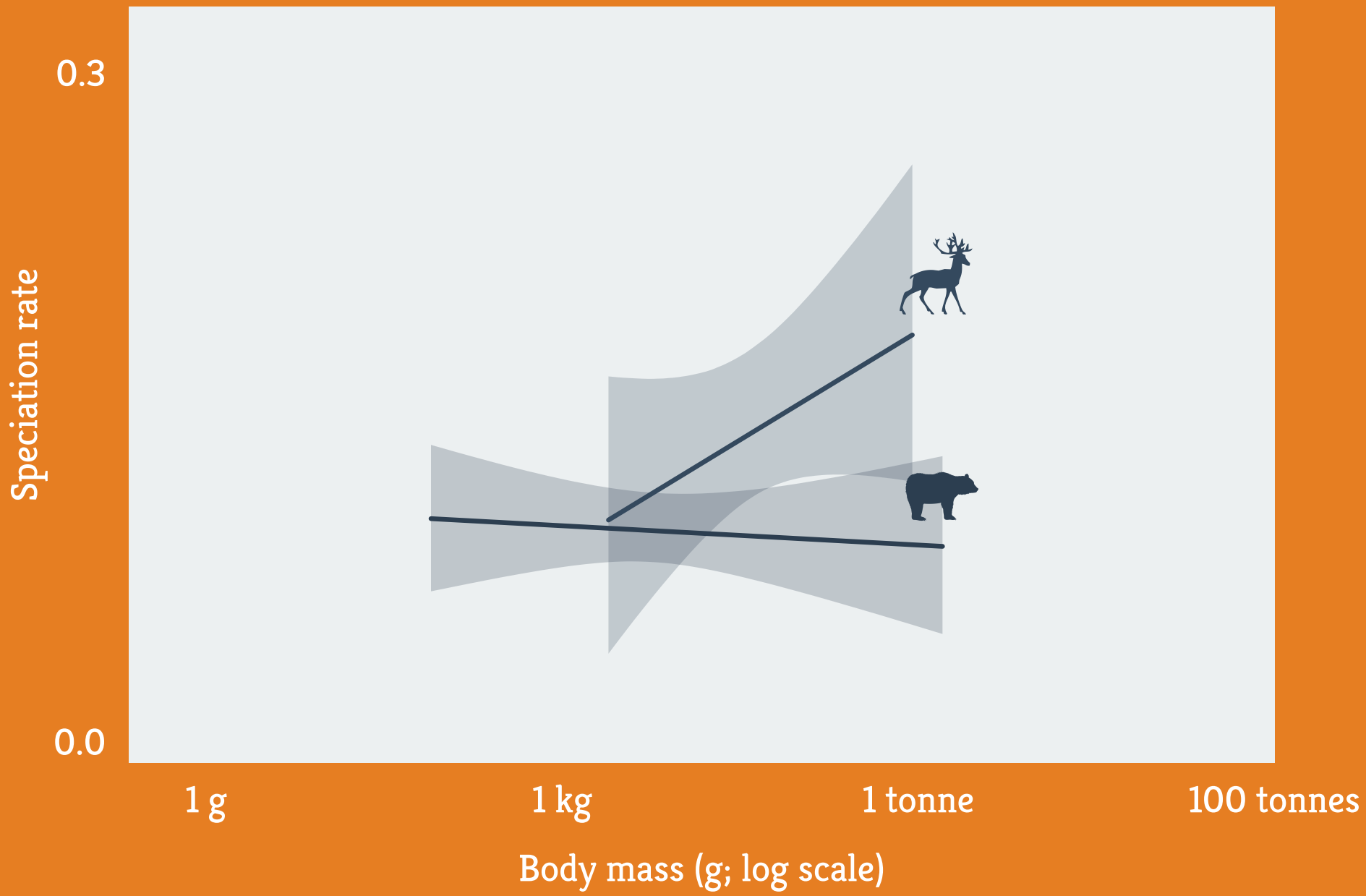


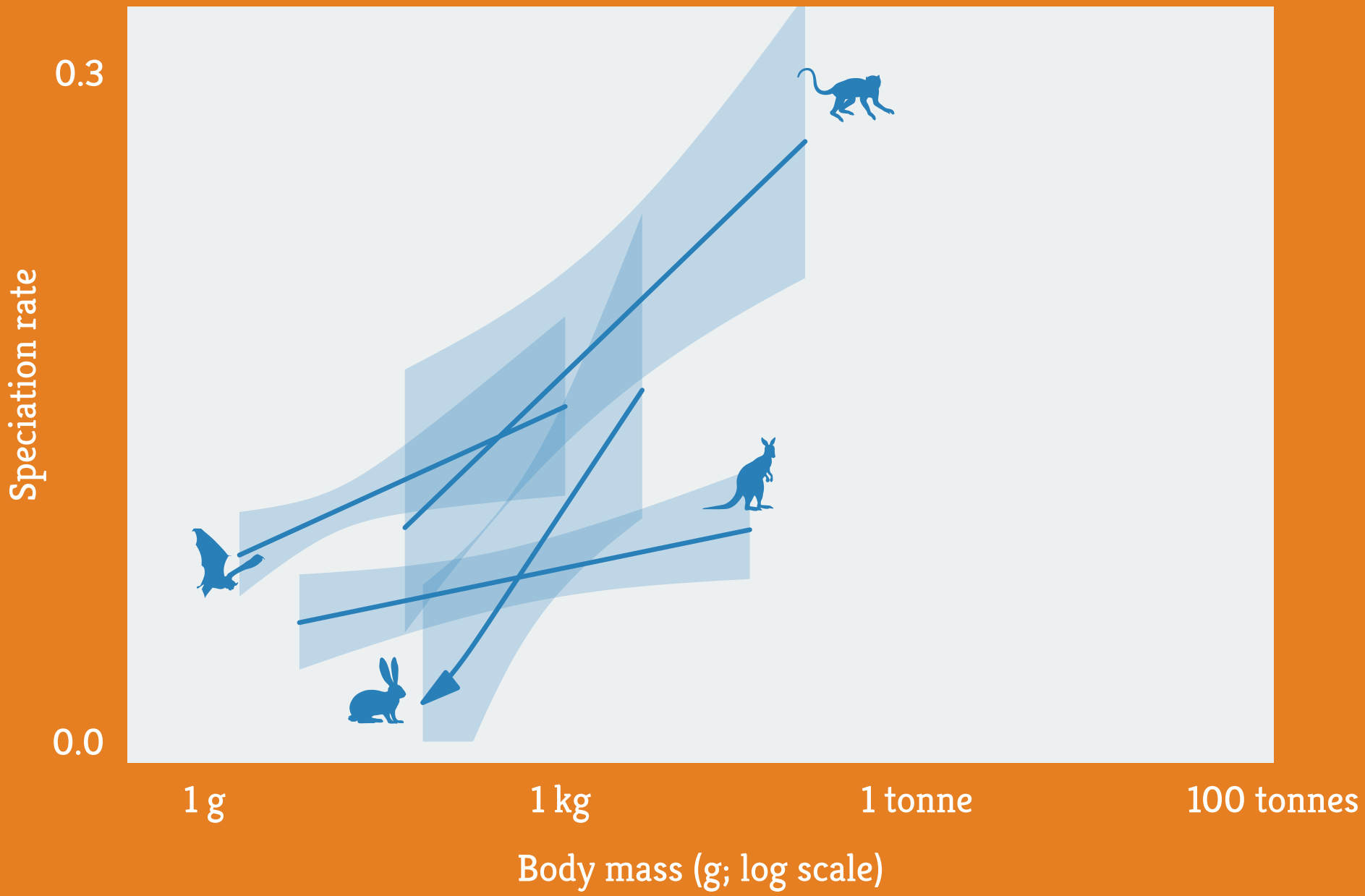
Tree: Bininda-Emonds et al. 2007

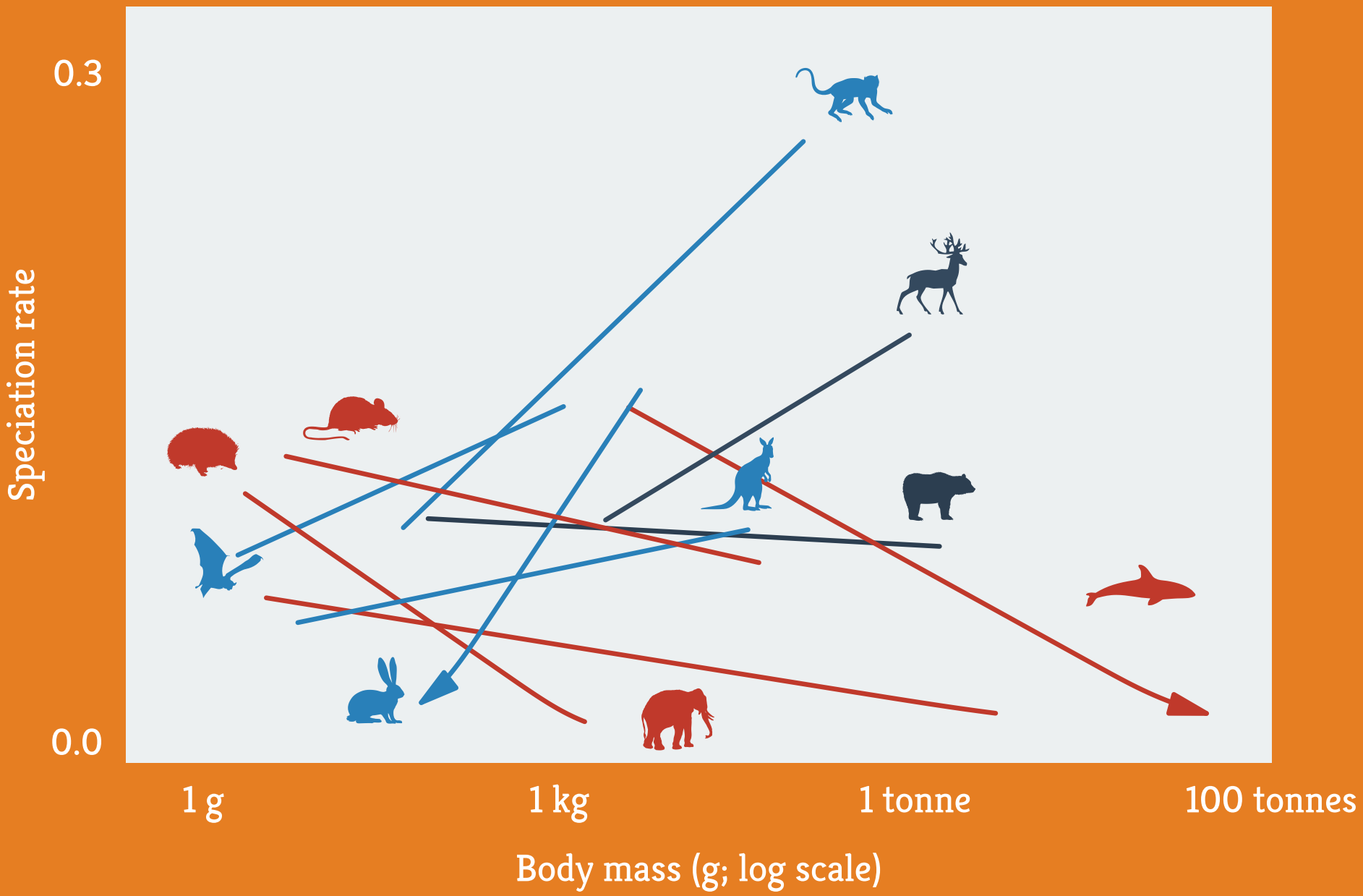
Data: Jones et al. 2009


0.3
0.0
Speciation rate
1 g
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)


0.3
0.0
Speciation rate
1 g
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)


0.3
0.0
Speciation rate
1 g
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)


0.3
0.0
Speciation rate
1 g
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)


0.3
0.0
Speciation rate
1 g
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)

Why are there

so many small

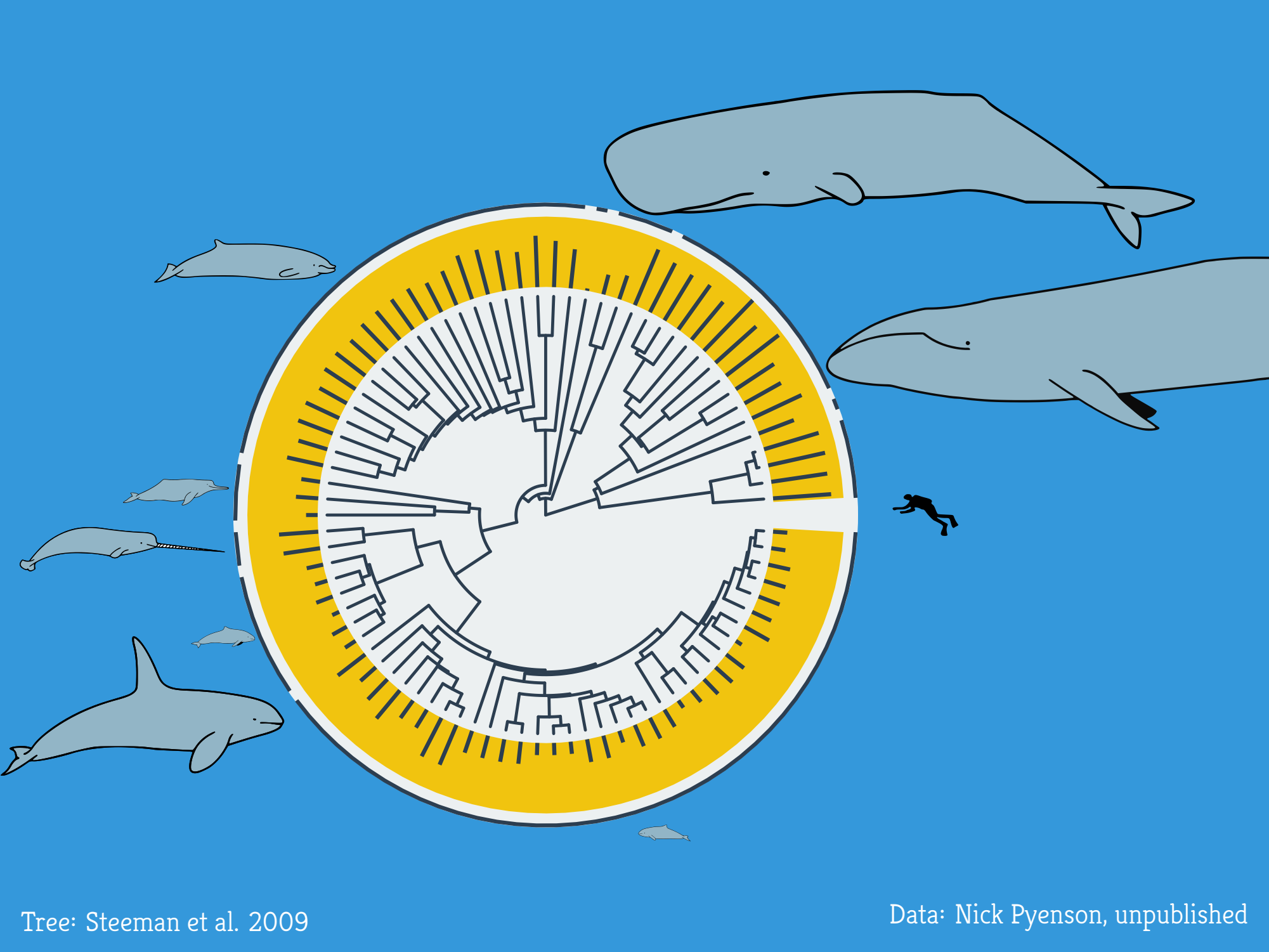
mammal species?

Probably not species selection

LIMITATIONS

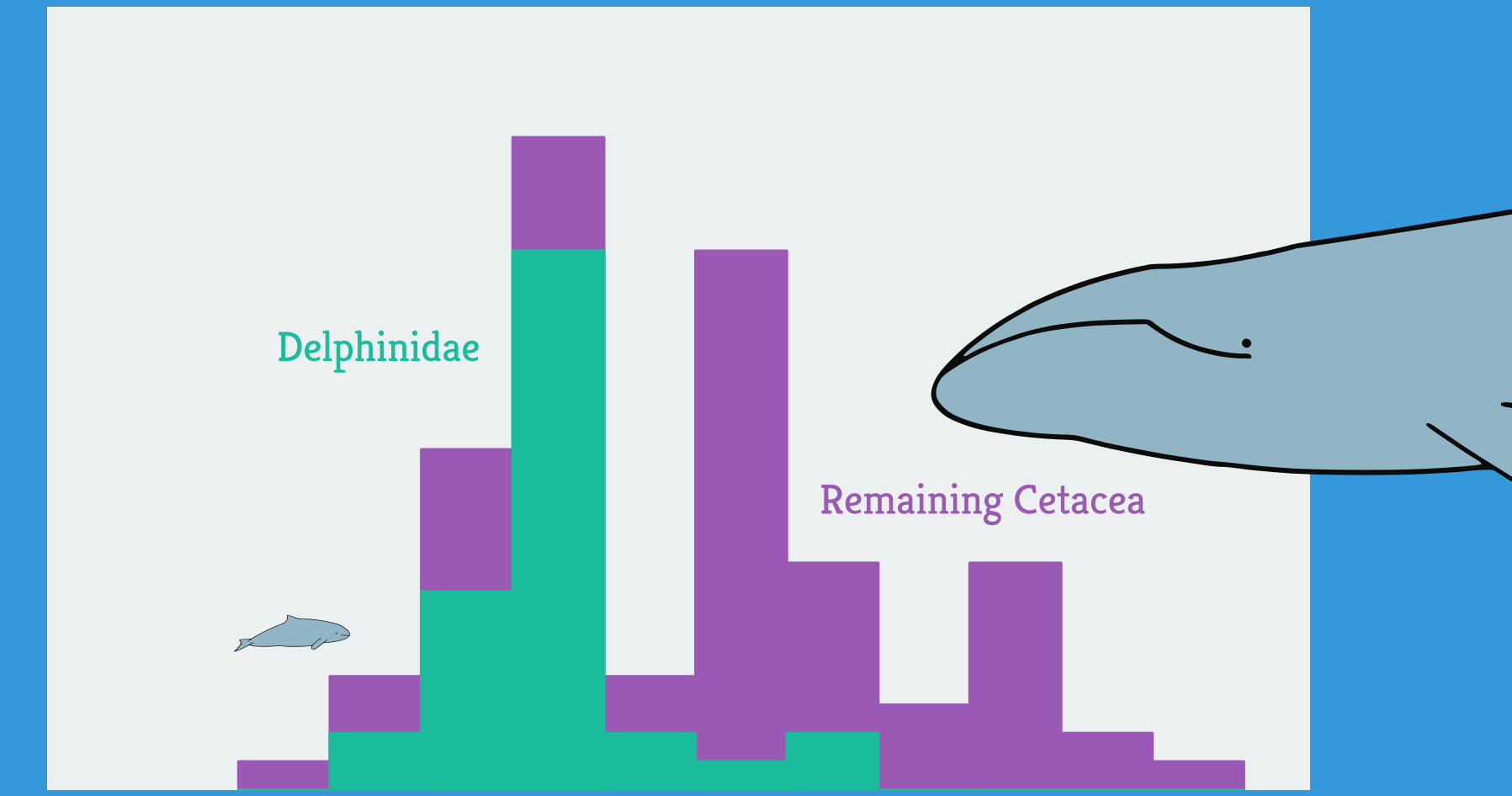
OF THESE METHODS

SIGNIFICANT
VS
REPLICATED

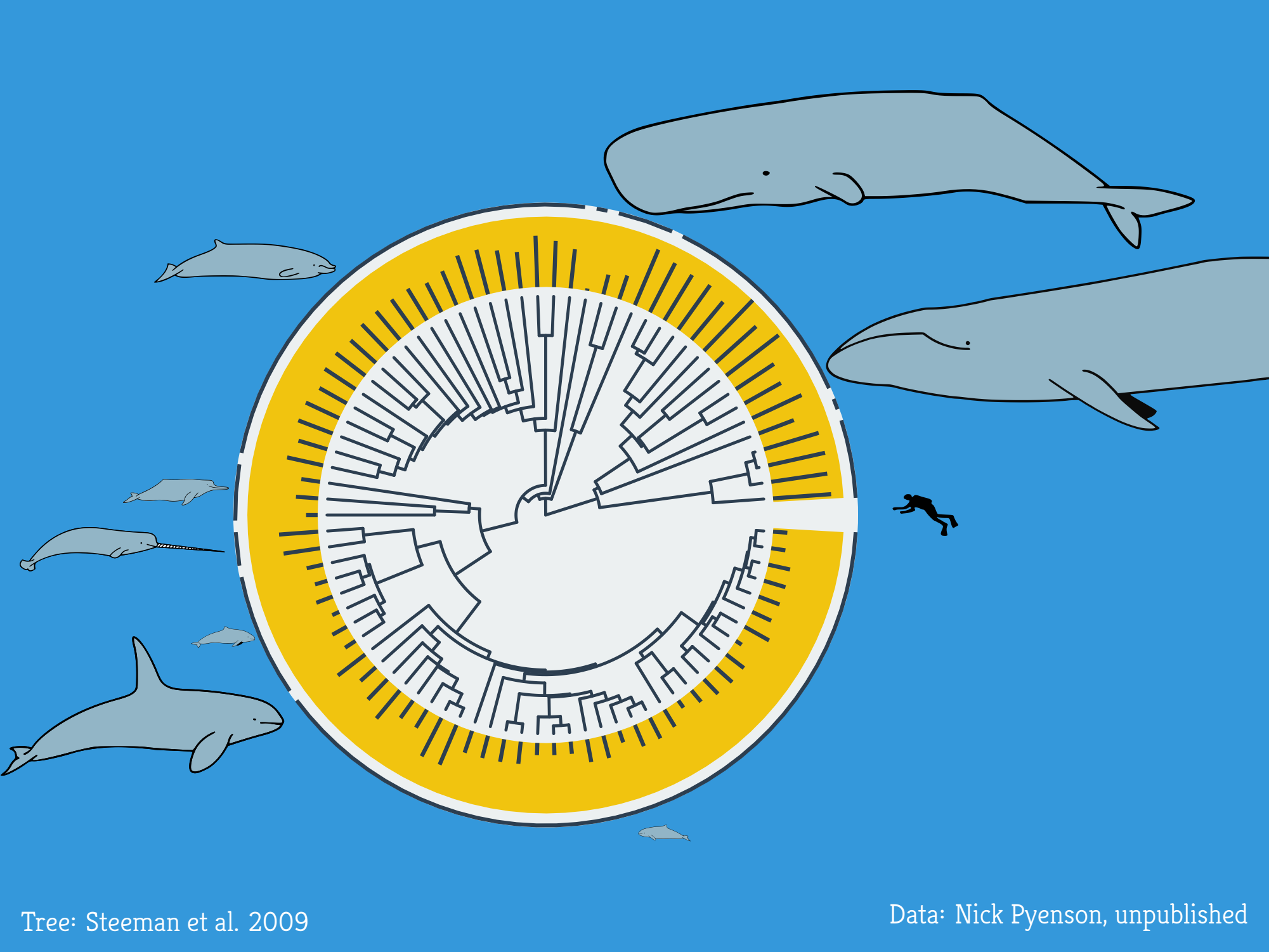


Tree: Steeman et al. 2009

Data: Nick Pyenson, unpublished



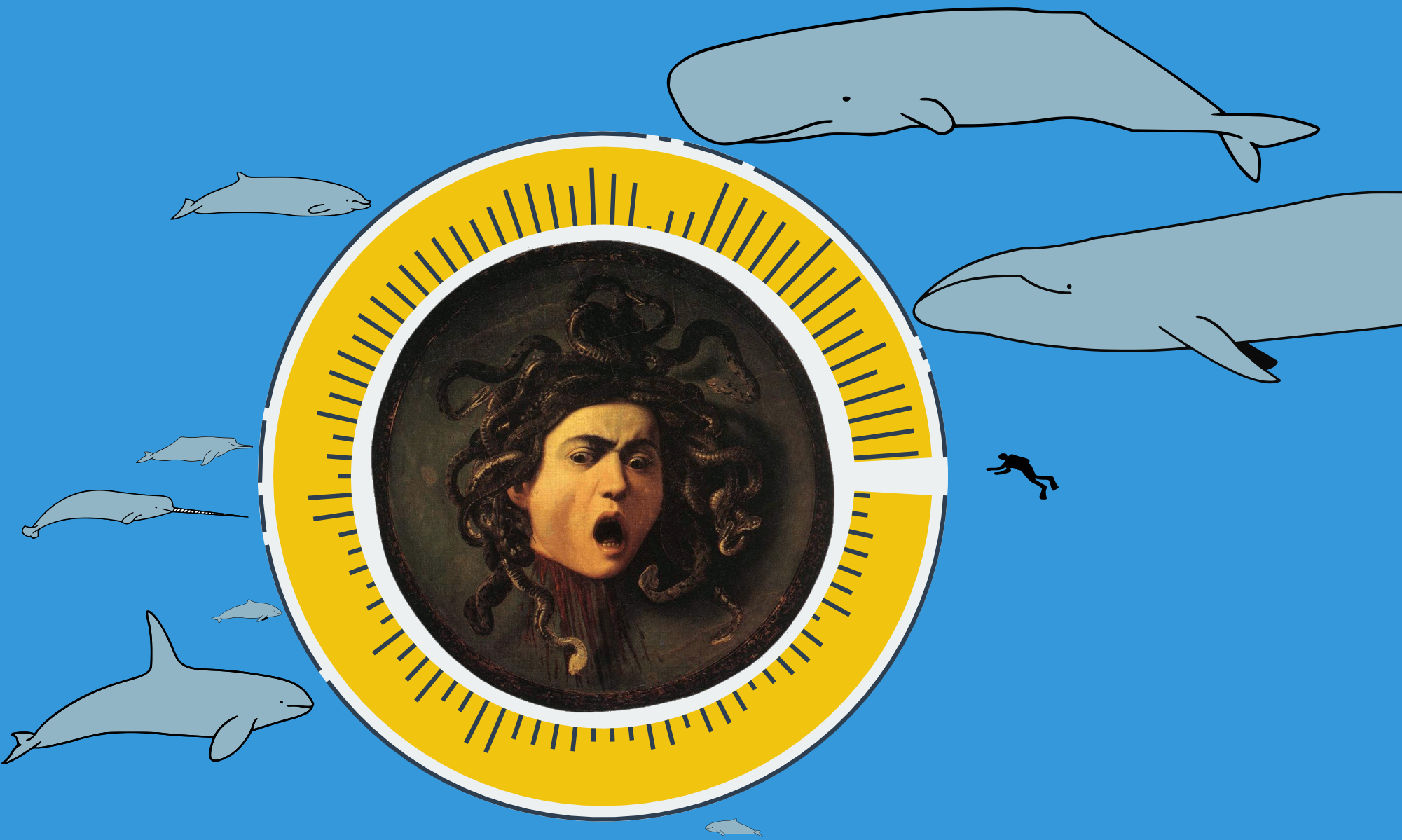
Data: Nick Pyenson, unpublished



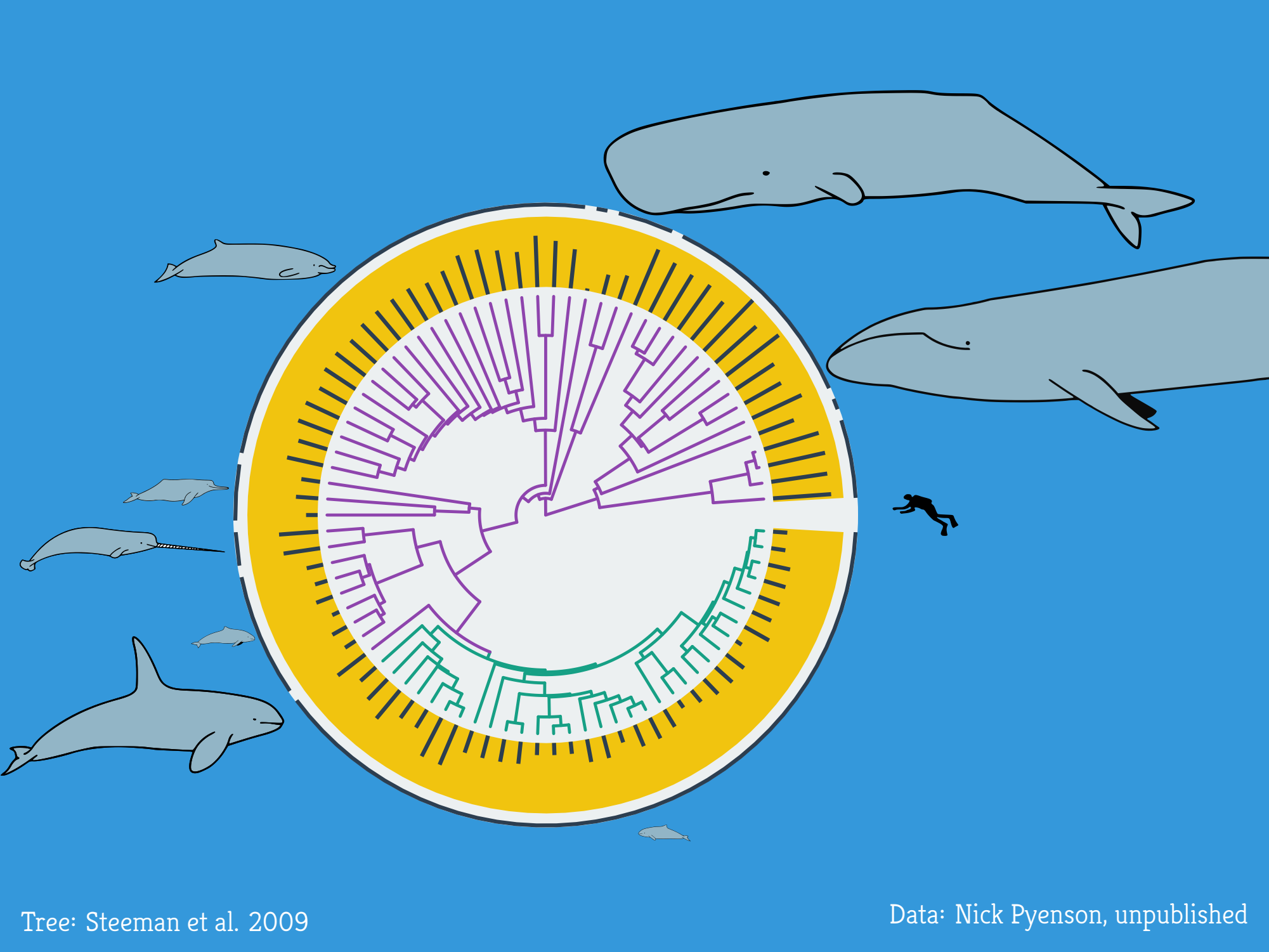
Tree: Steeman et al. 2009

Data: Nick Pyenson, unpublished

MEDUSA

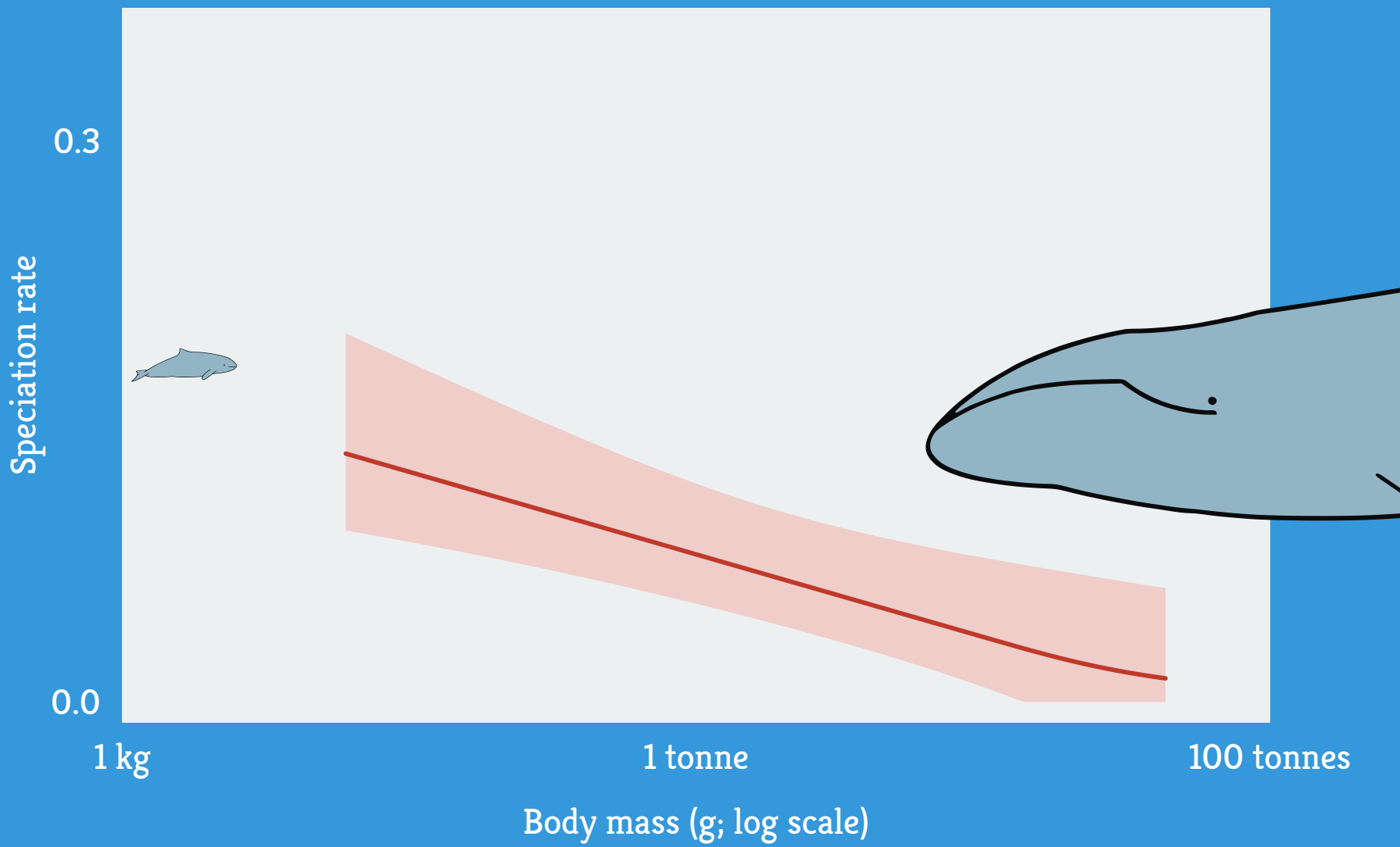


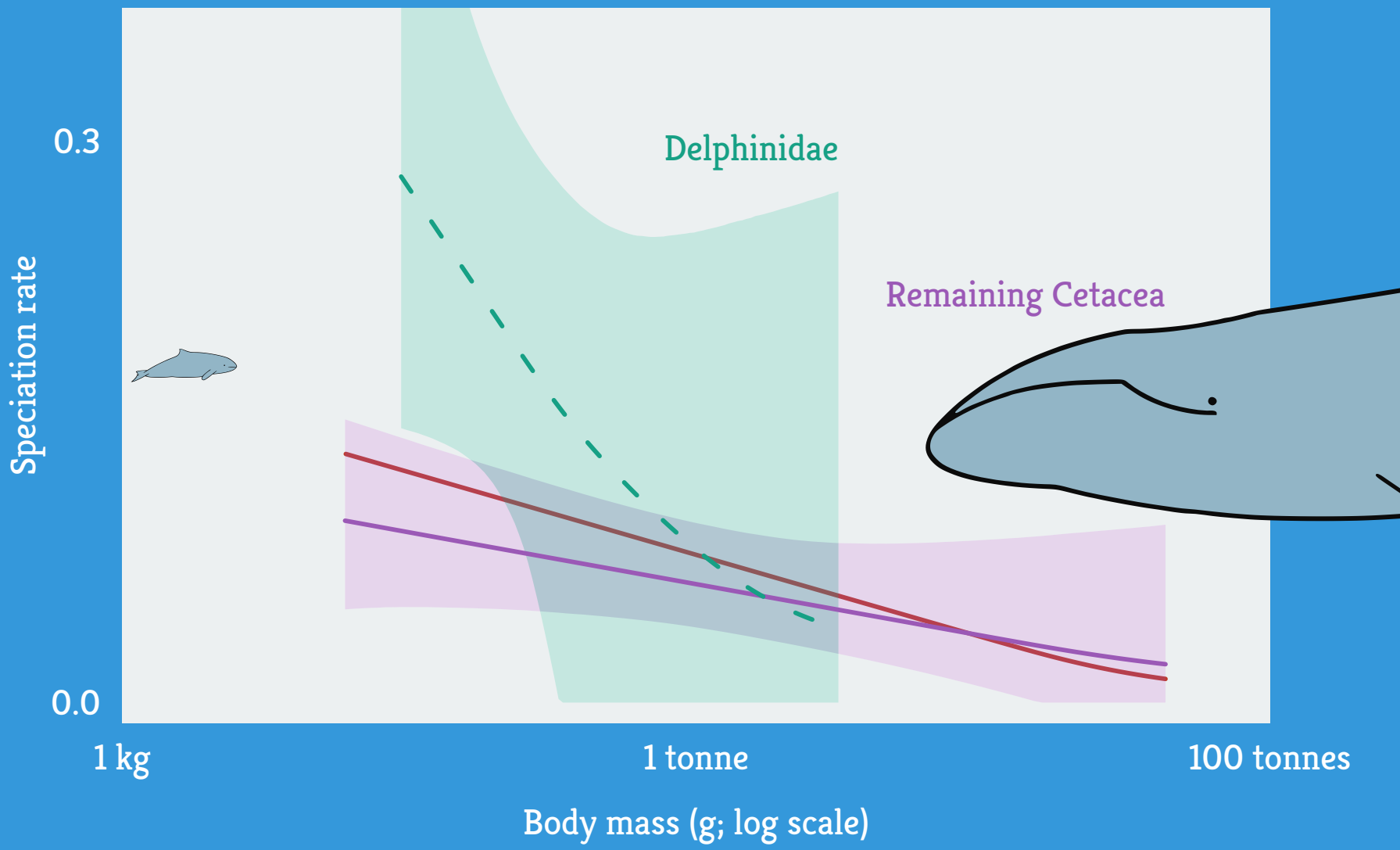
Medusa: Alfaro et al. 2009

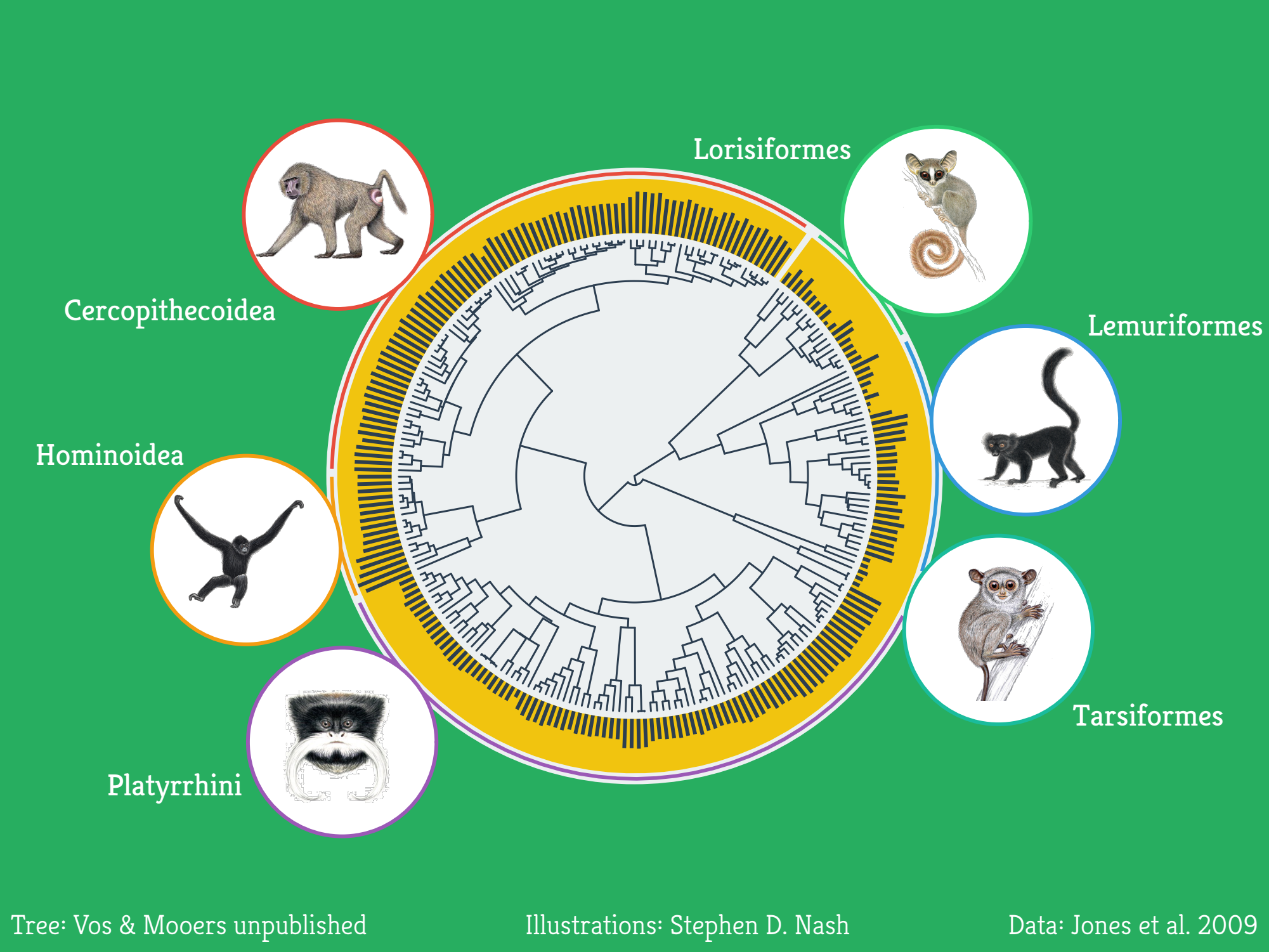


Tree: Steeman et al. 2009

Data: Nick Pyenson, unpublished


0.3
0.0
Speciation rate
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)

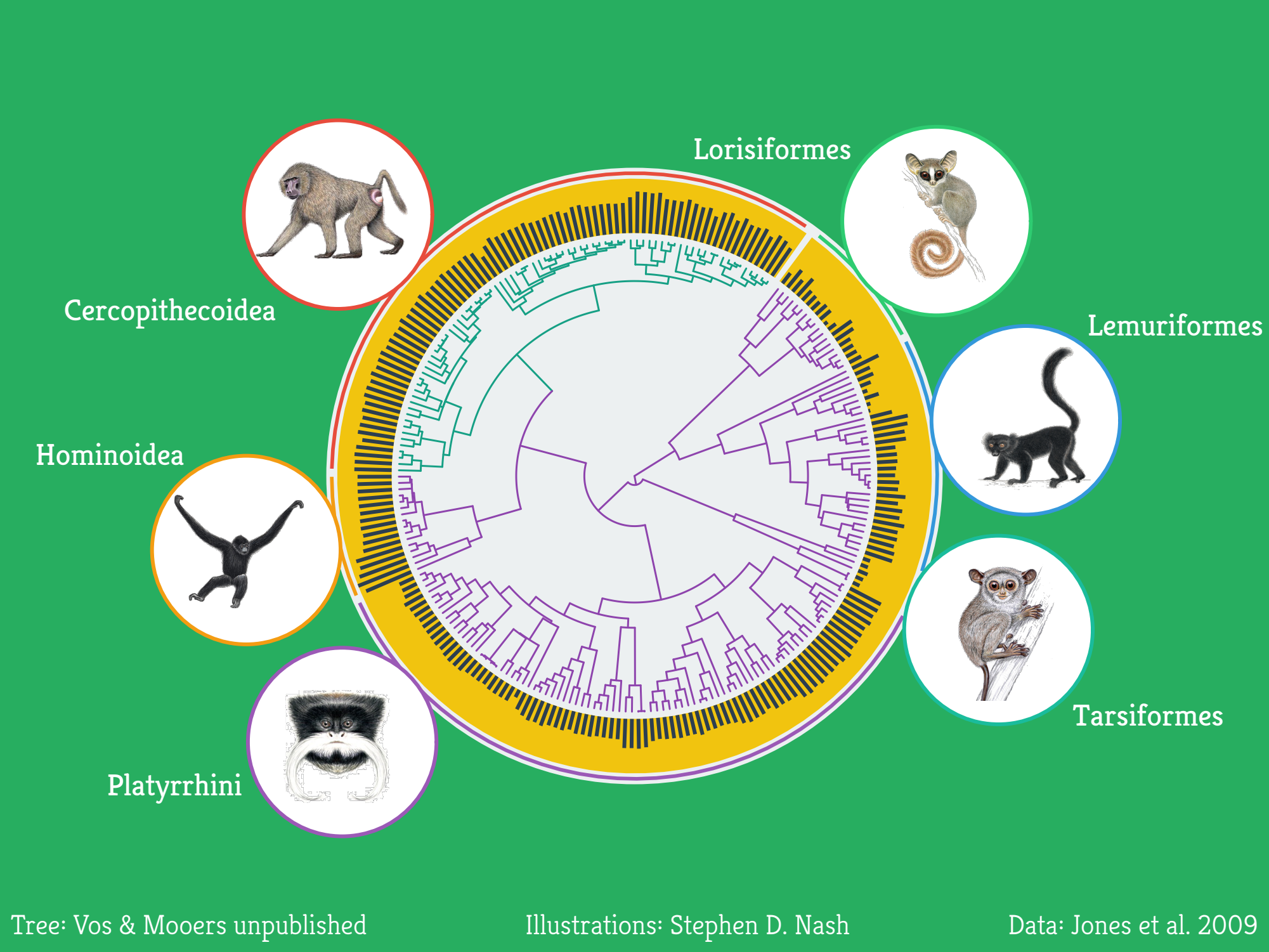

0.3
0.0
Speciation rate
Delphinidae
Remaining Cetacea
1 kg
1 tonne
100 tonnes
Body mass (g; log scale)



Tree: Vos & Mooers unpublished

Illustrations: Stephen D. Nash

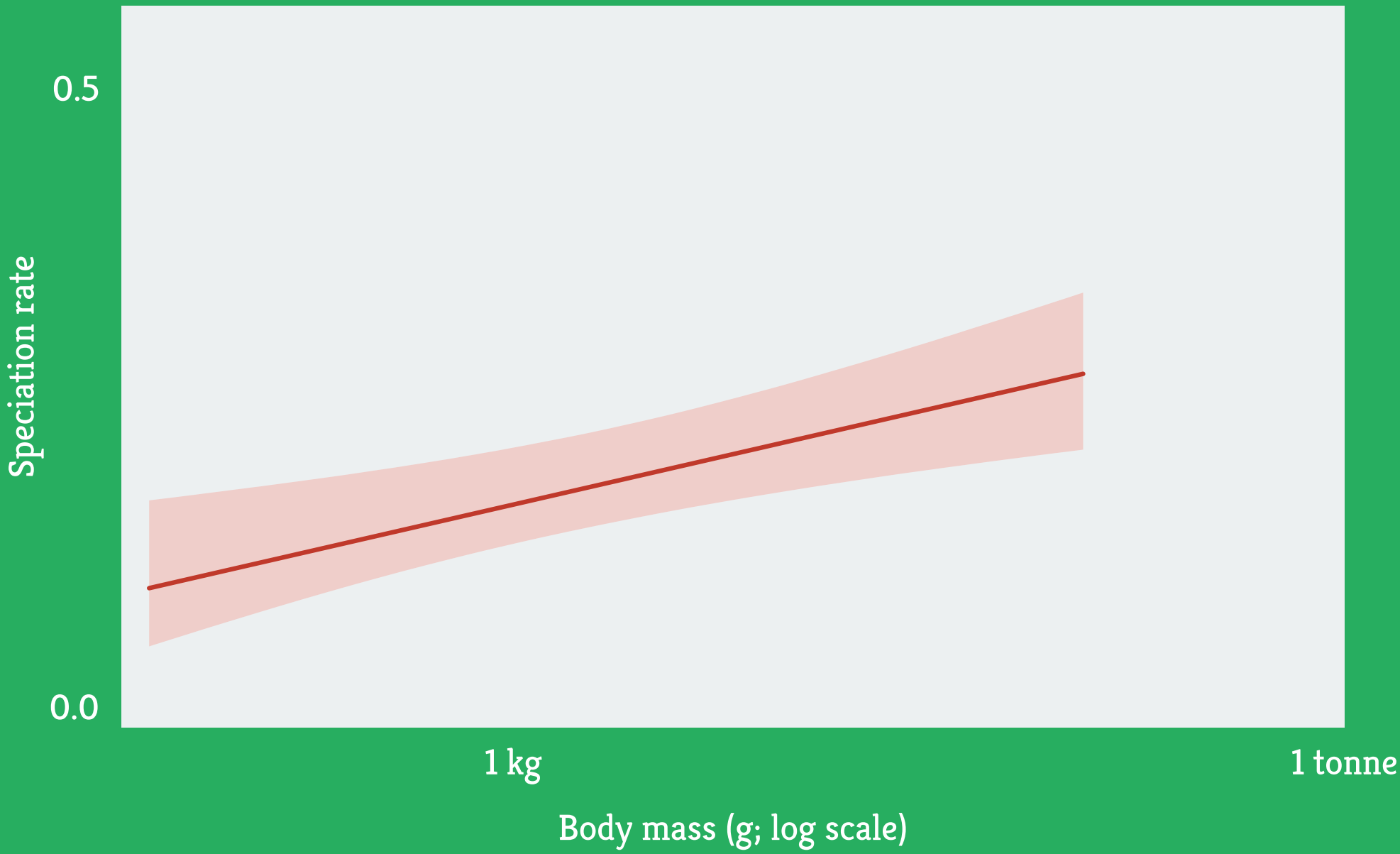
Data: Jones et al. 2009

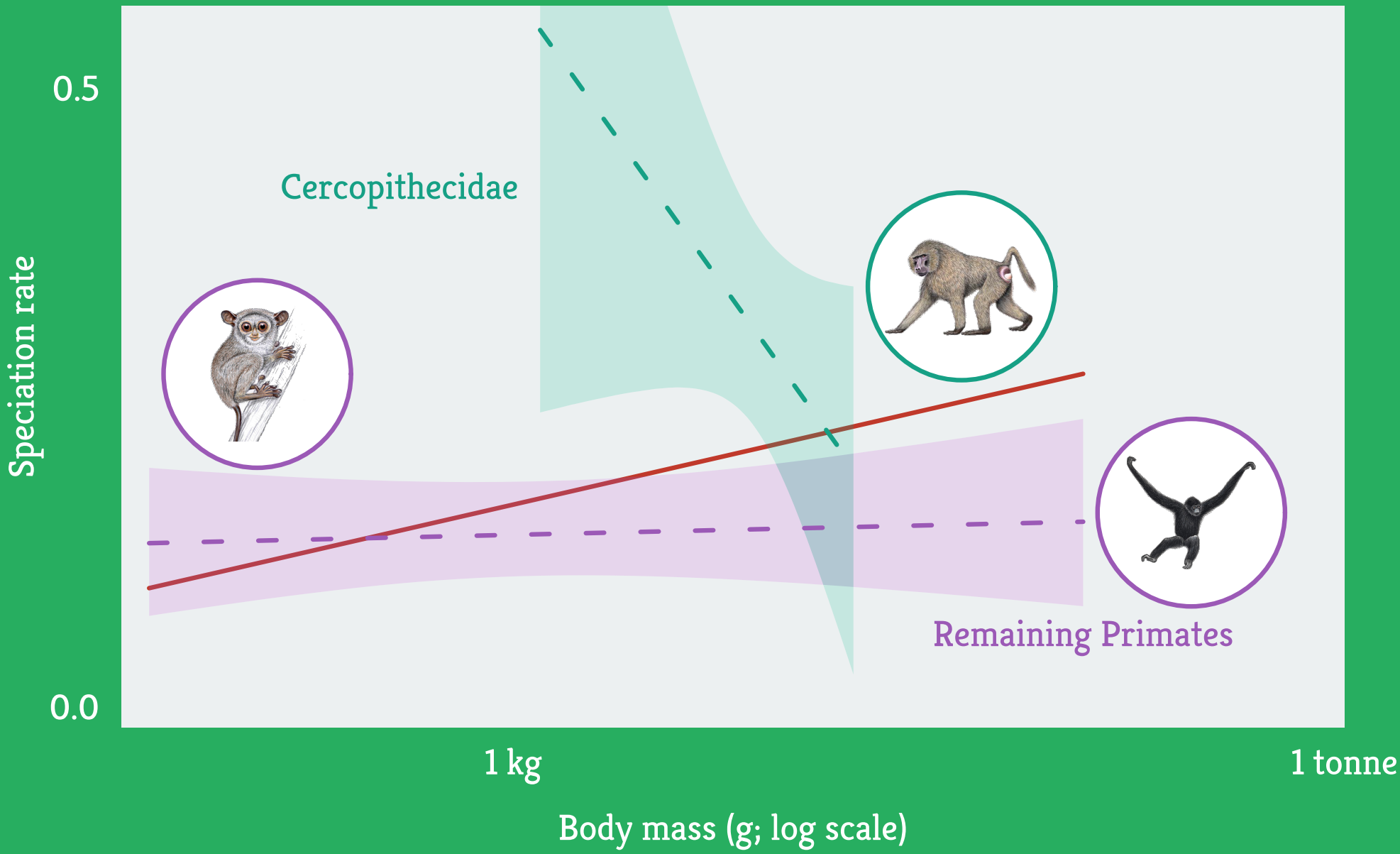


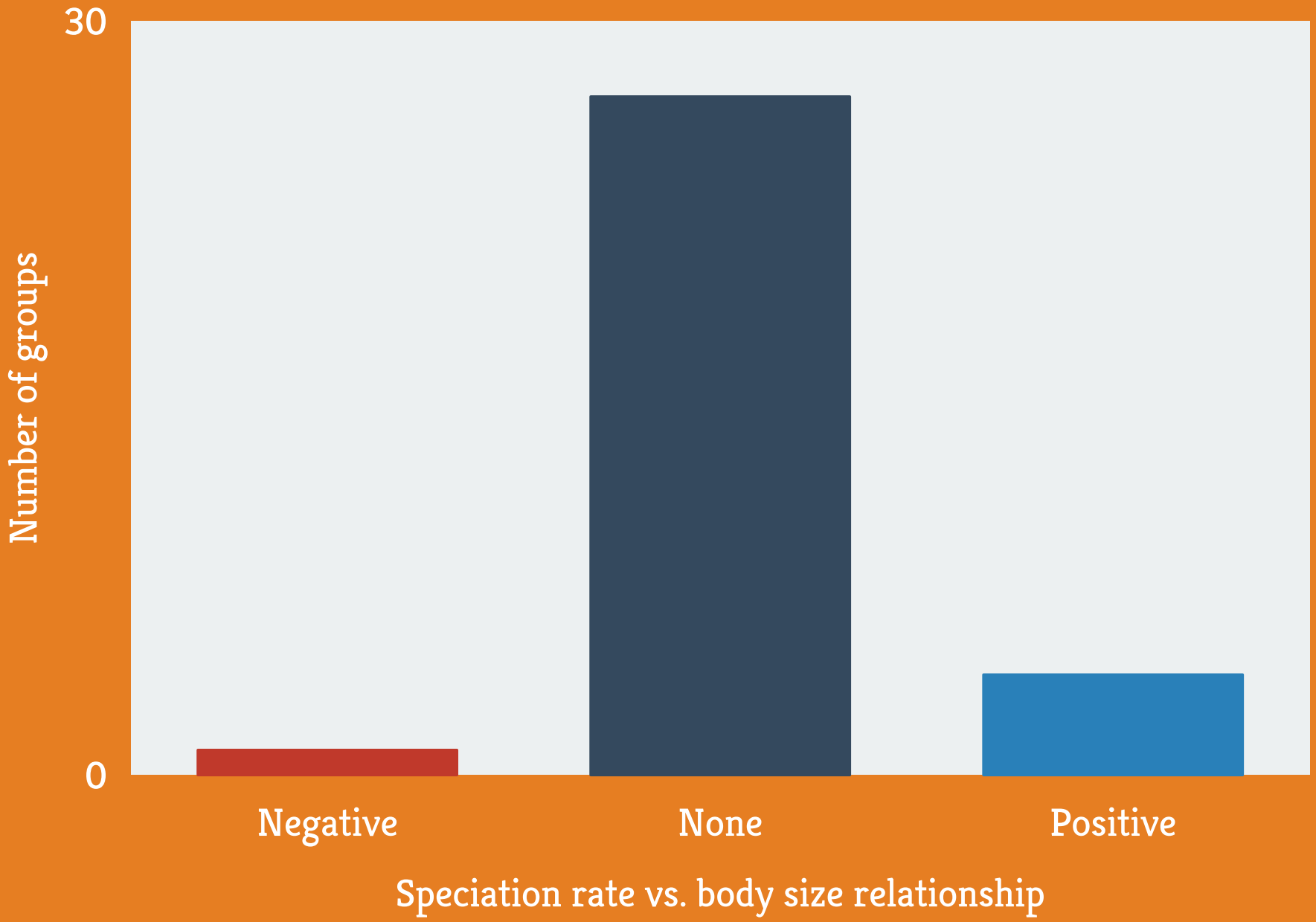
Tree: Vos & Mooers unpublished

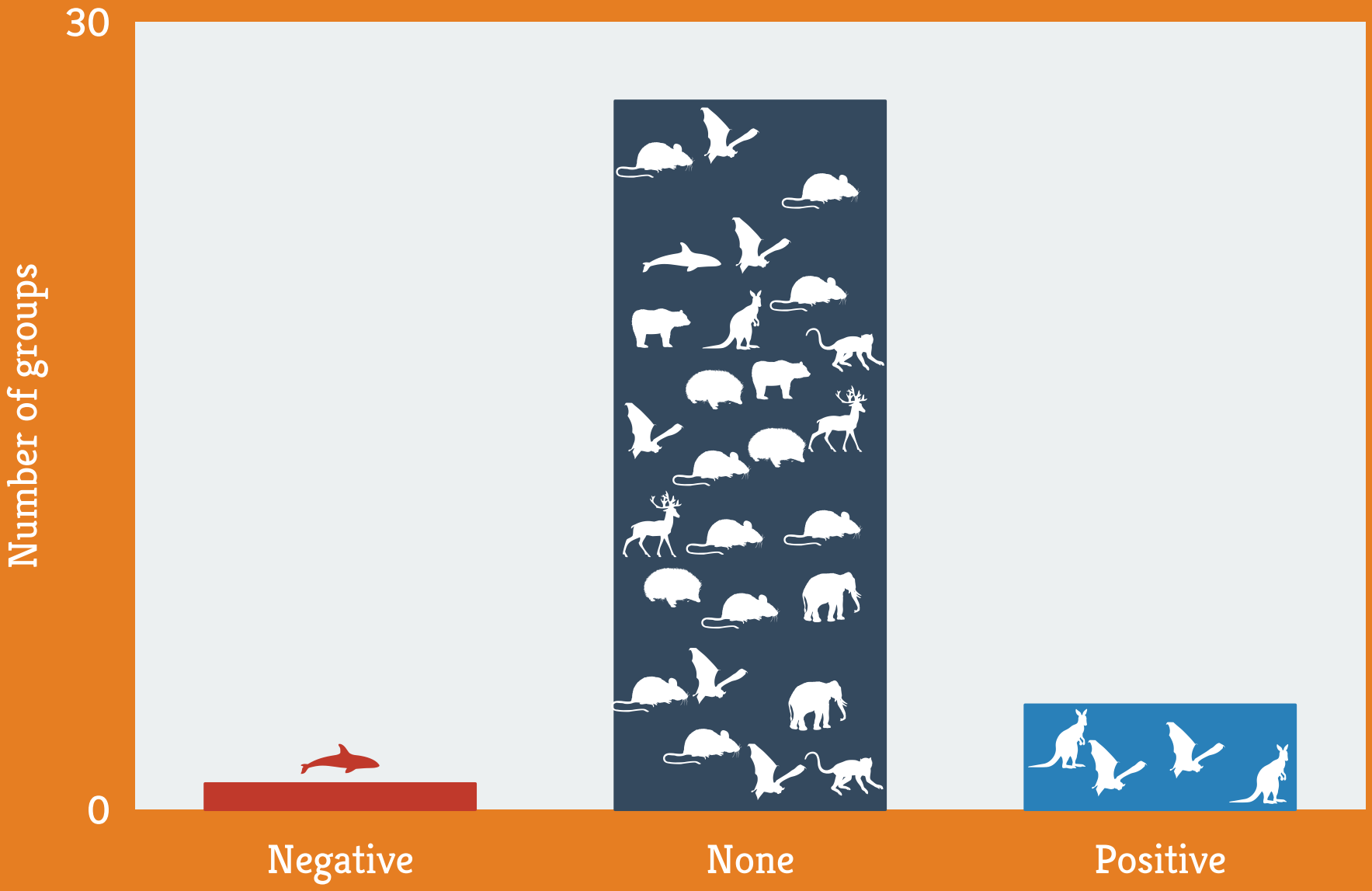
Illustrations: Stephen D. Nash

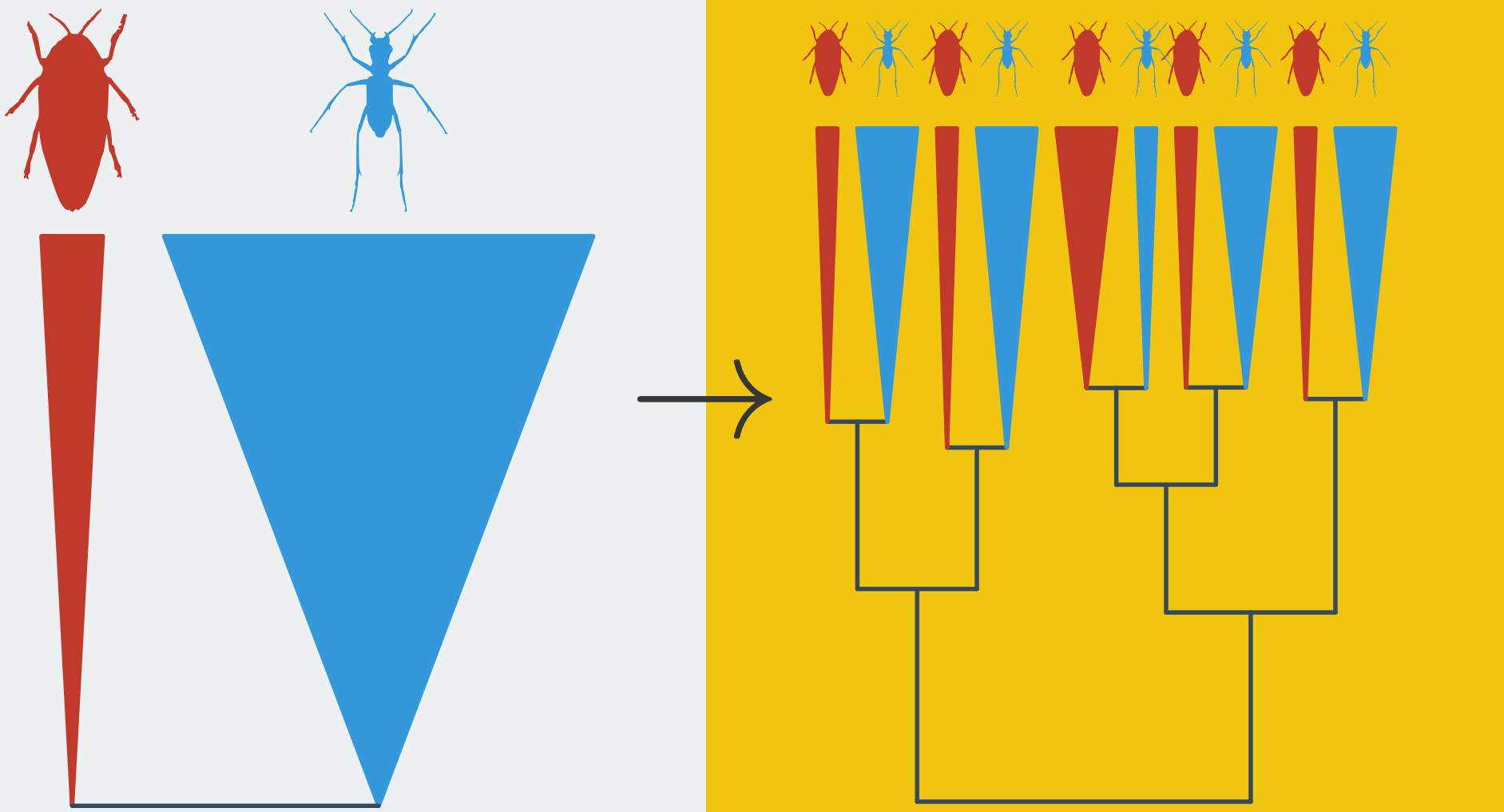
Data: Jones et al. 2009

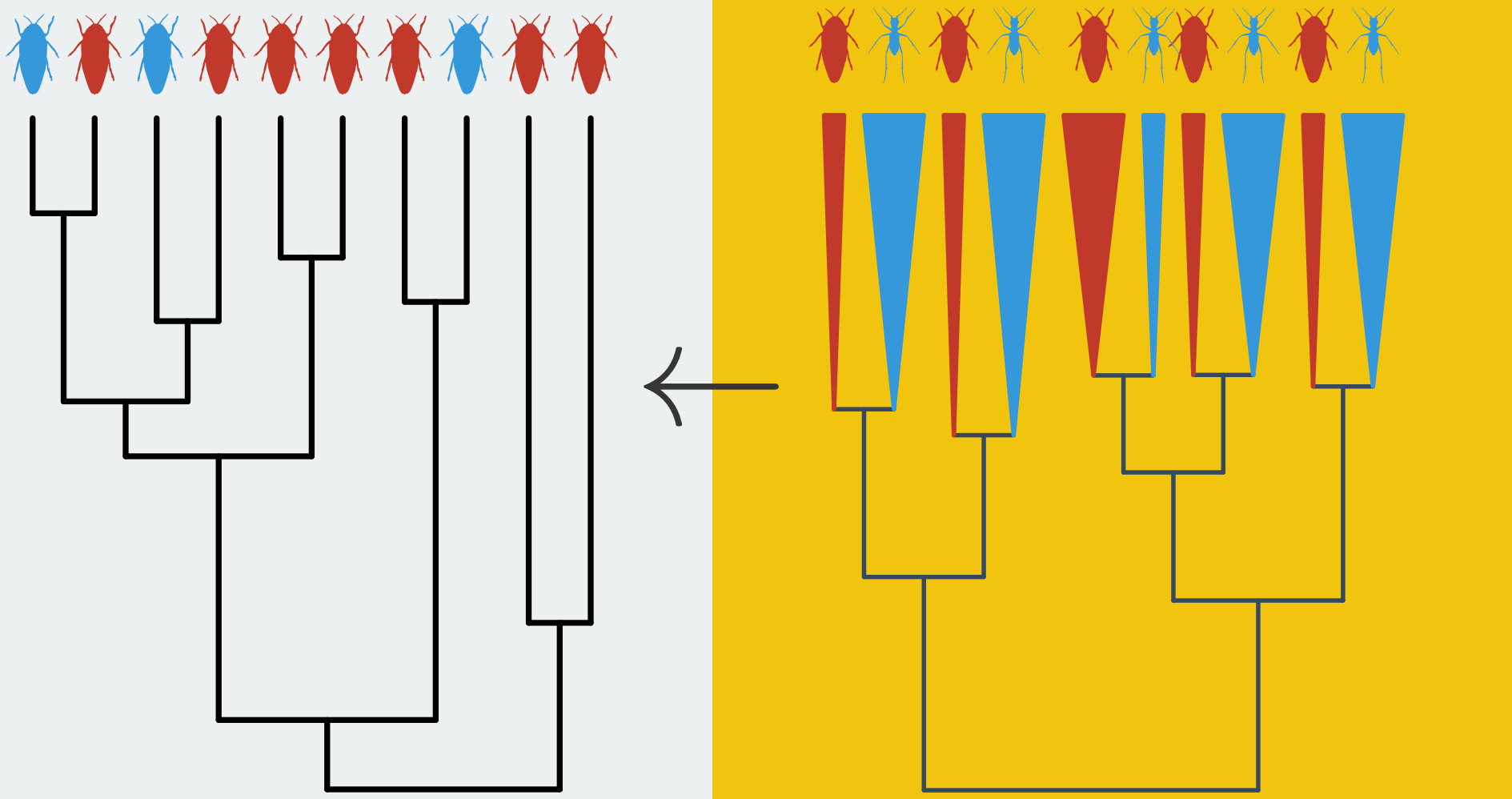

0.5
0.0
Speciation rate
1 kg
1 tonne
Body mass (g; log scale)

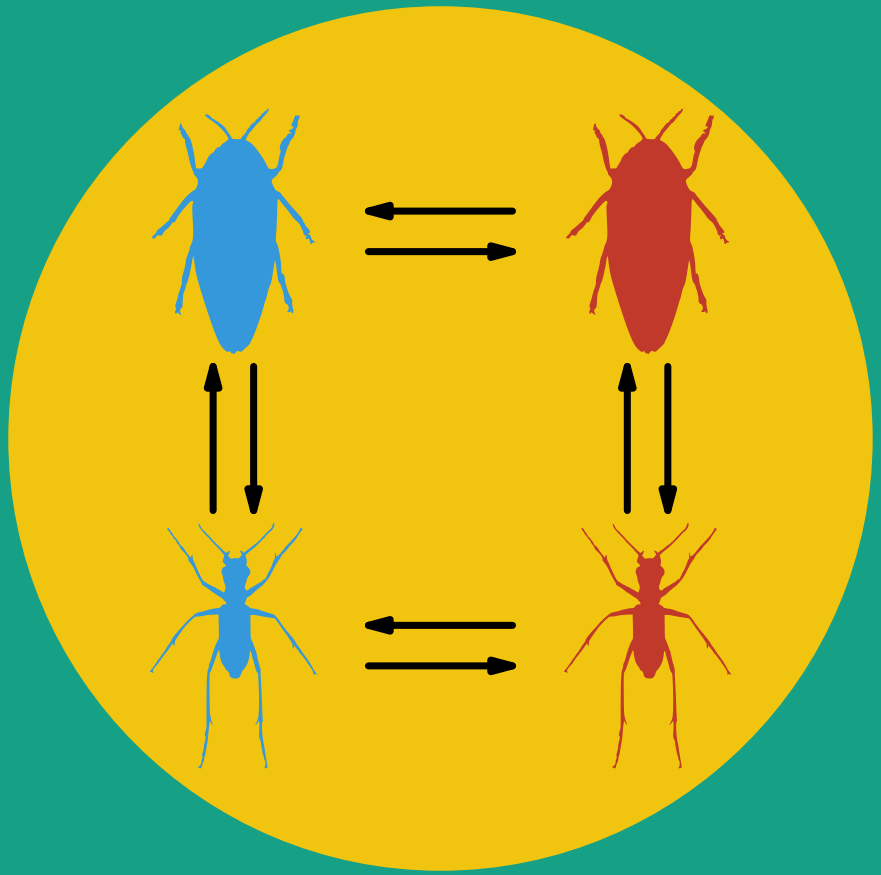

0.5
0.0
Speciation rate
Cercopithecidae
Remaining Primates
1 kg
1 tonne
Body mass (g; log scale)


30
0
Number of groups
Negative
None
Positive
Speciation rate vs. body size relationship

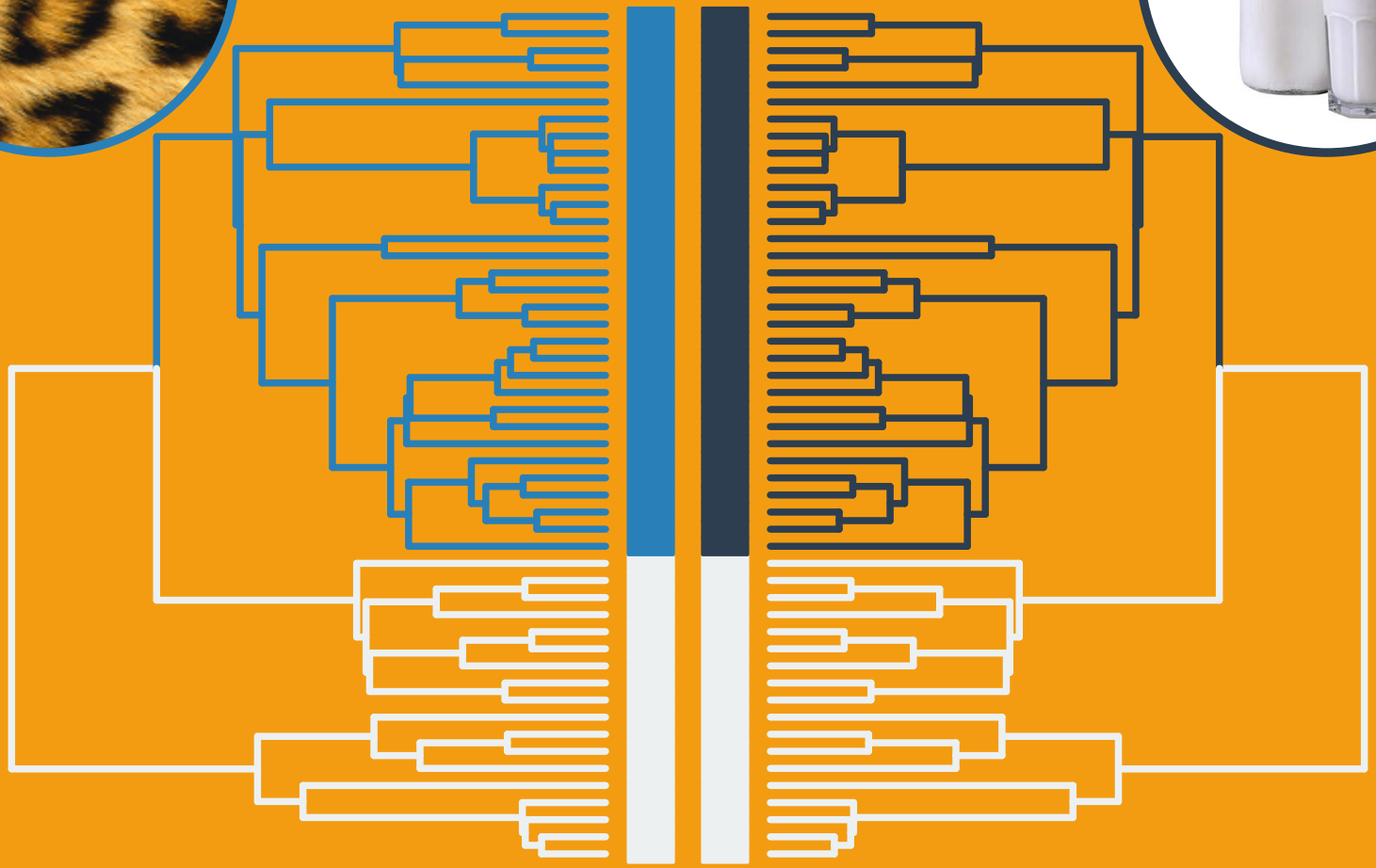

30
0
Number of groups
Negative
None
Positive
Speciation rate vs. body size relationship

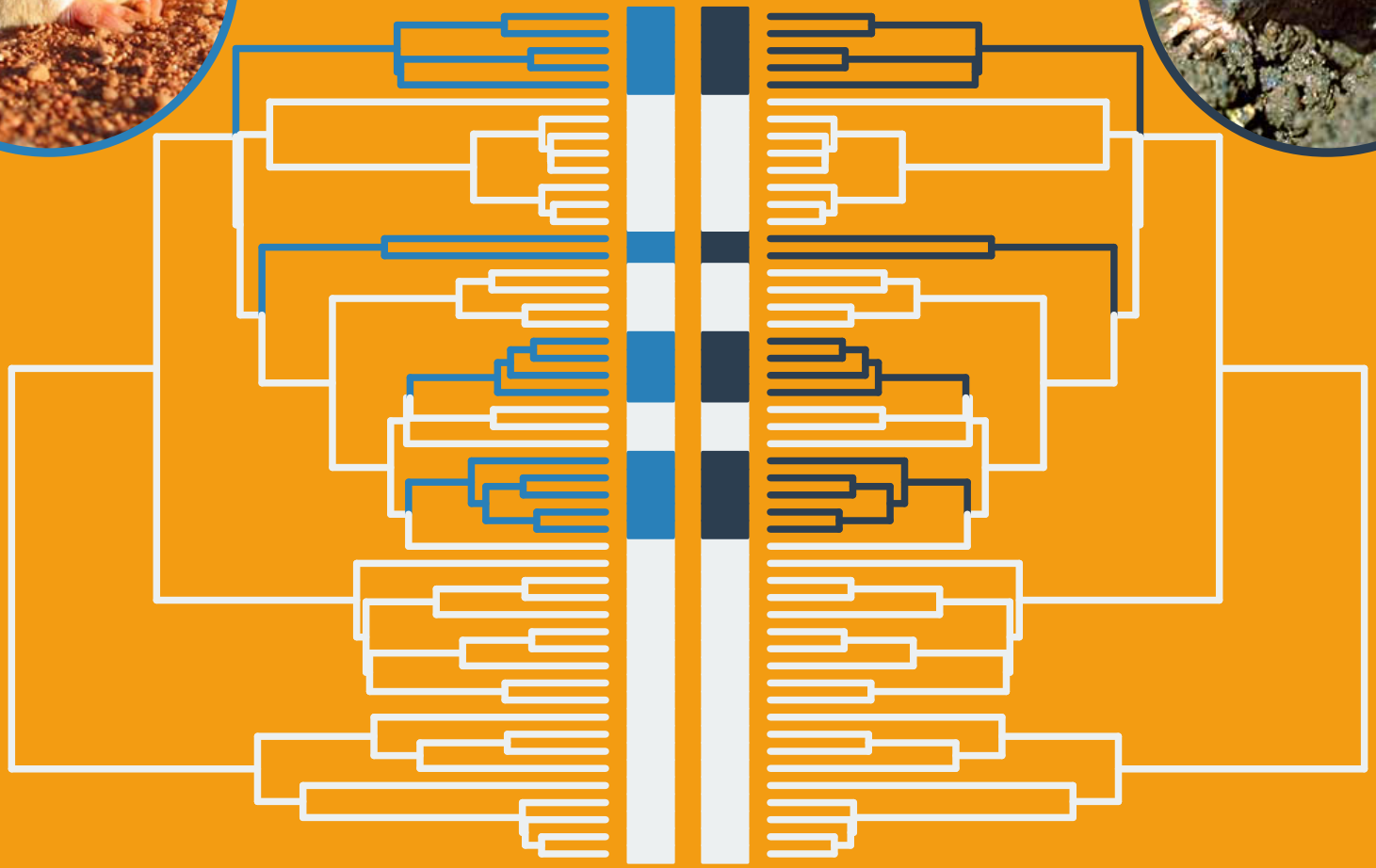


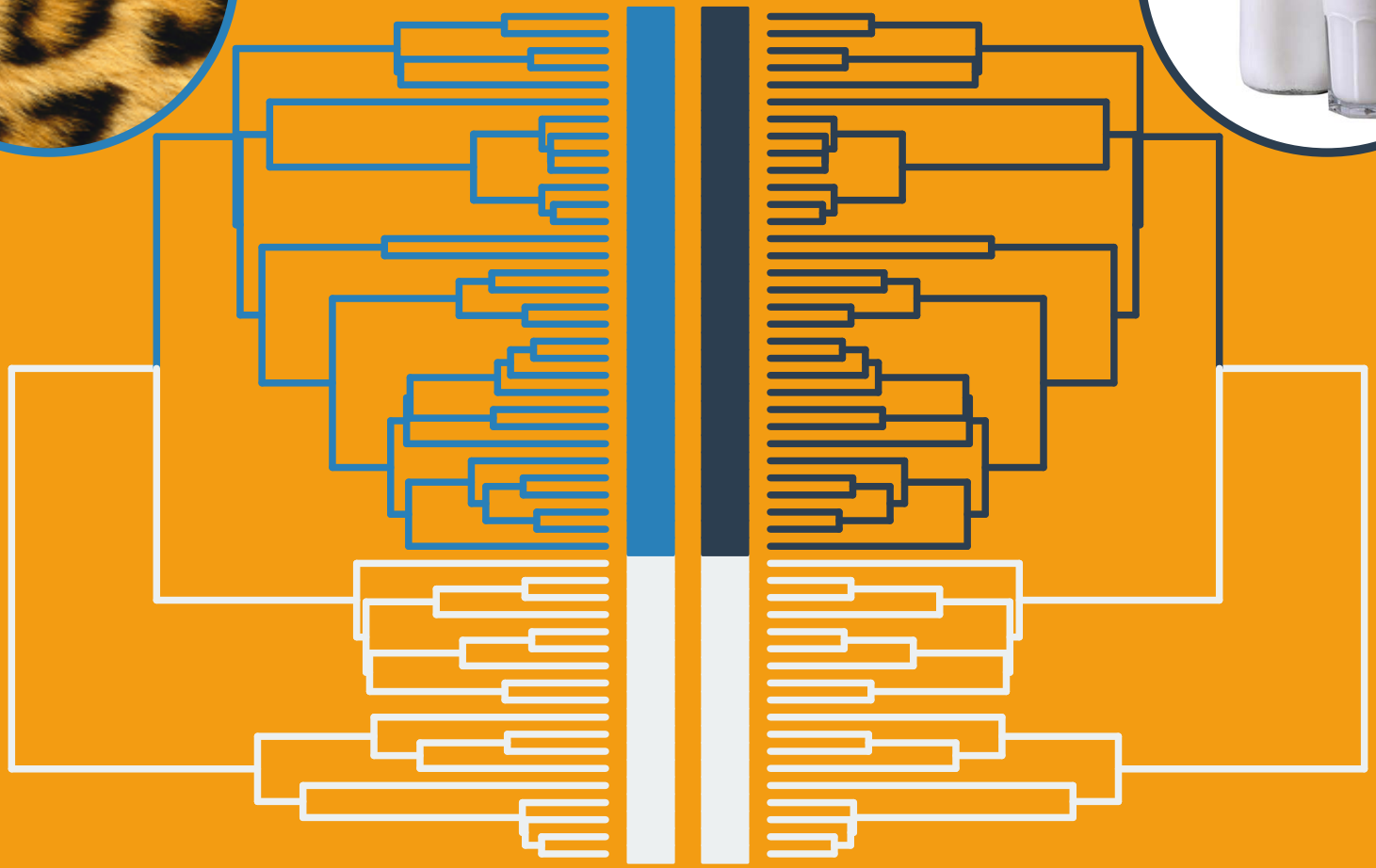


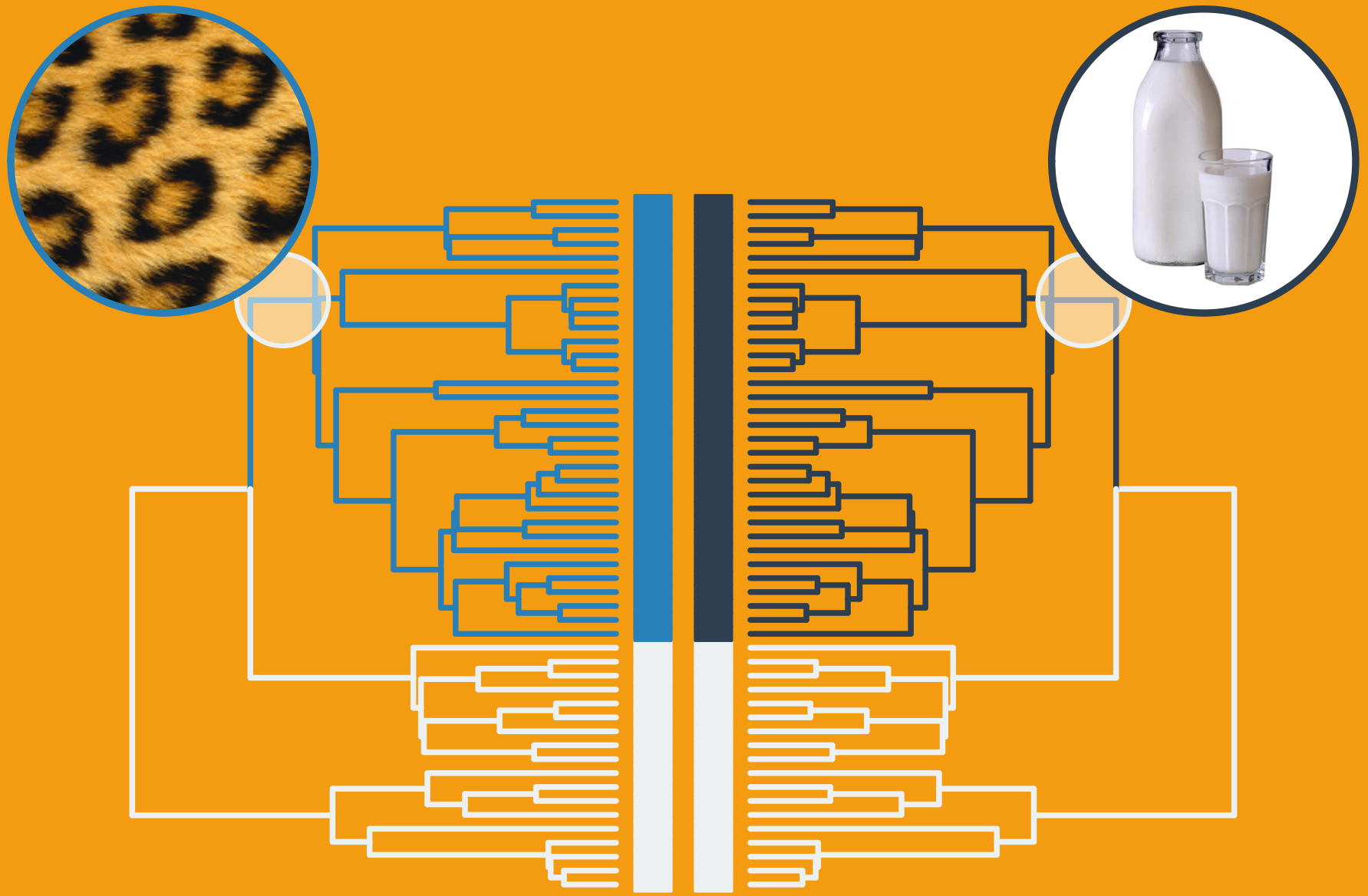


with Wayne Maddison









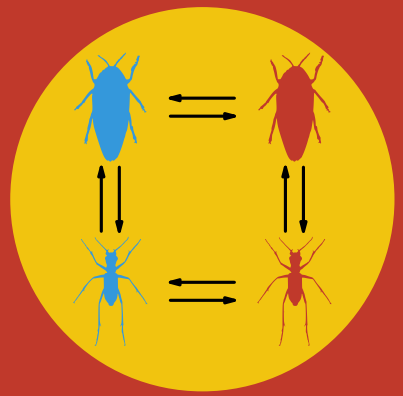
WE HAVE

VERY SIMPLE MODELS

Morphological traits

do not evolve like

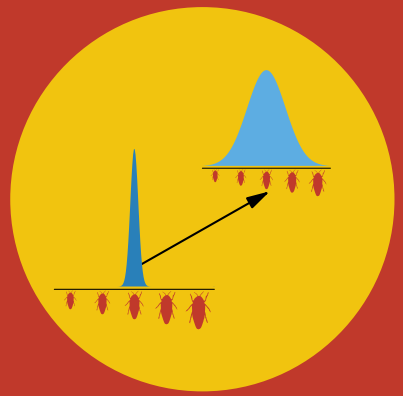
DNA



Quantitative traits

do not follow

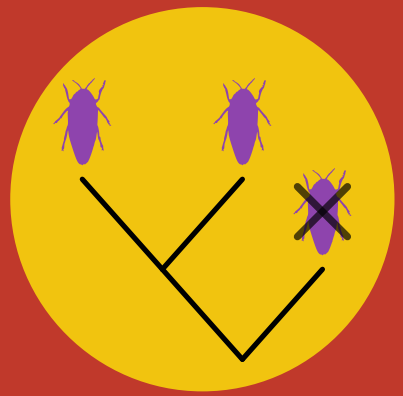
Brownian motion



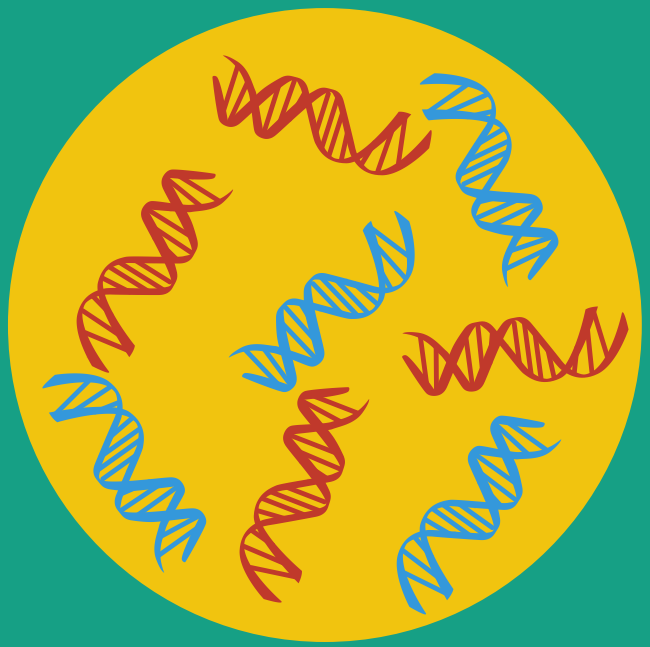
Diversification

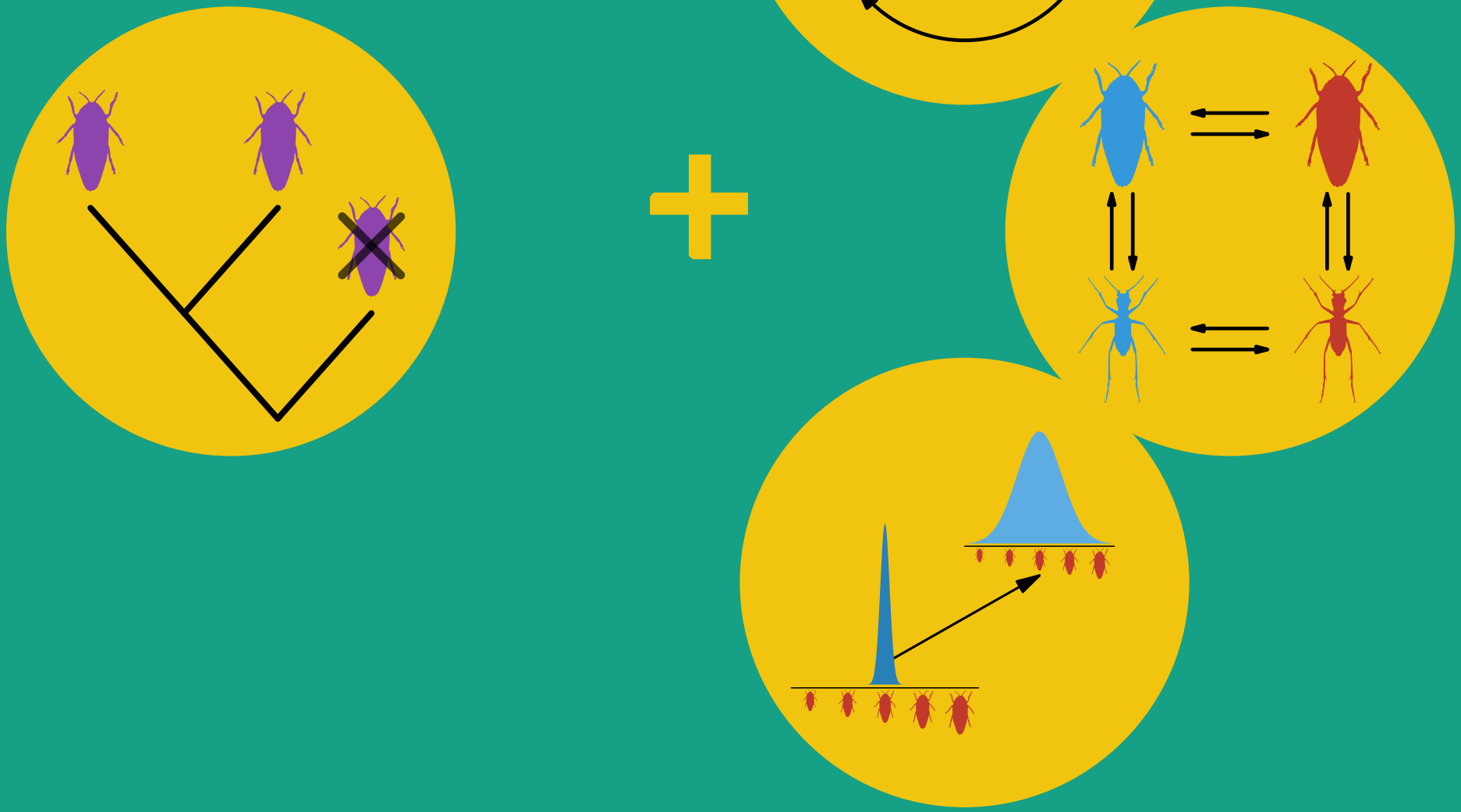
does not follow

a birth death process



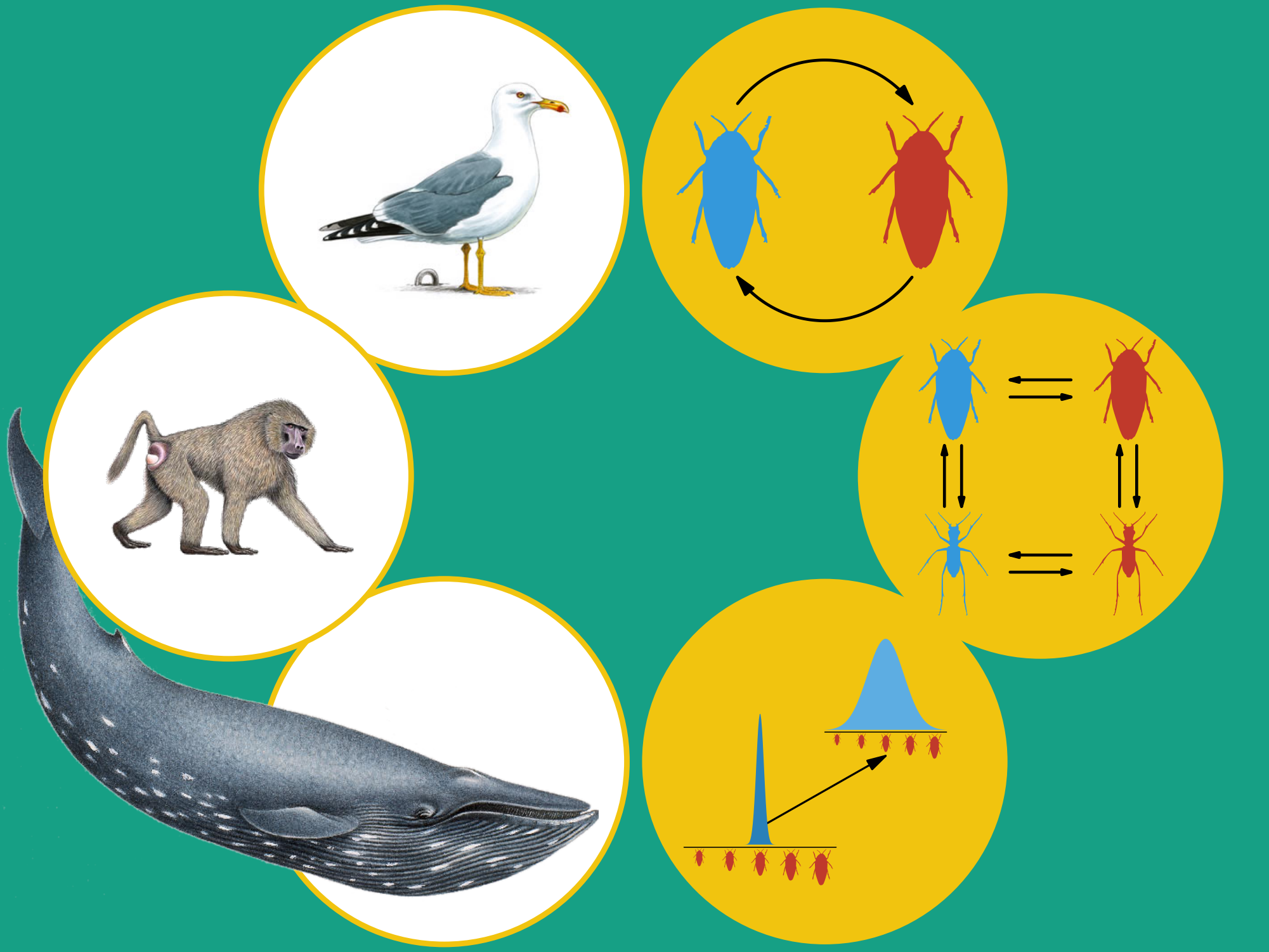
SUMMARY





www.zoology.ubc.ca/prog/diversitree

github.com/richfitz/diversitree



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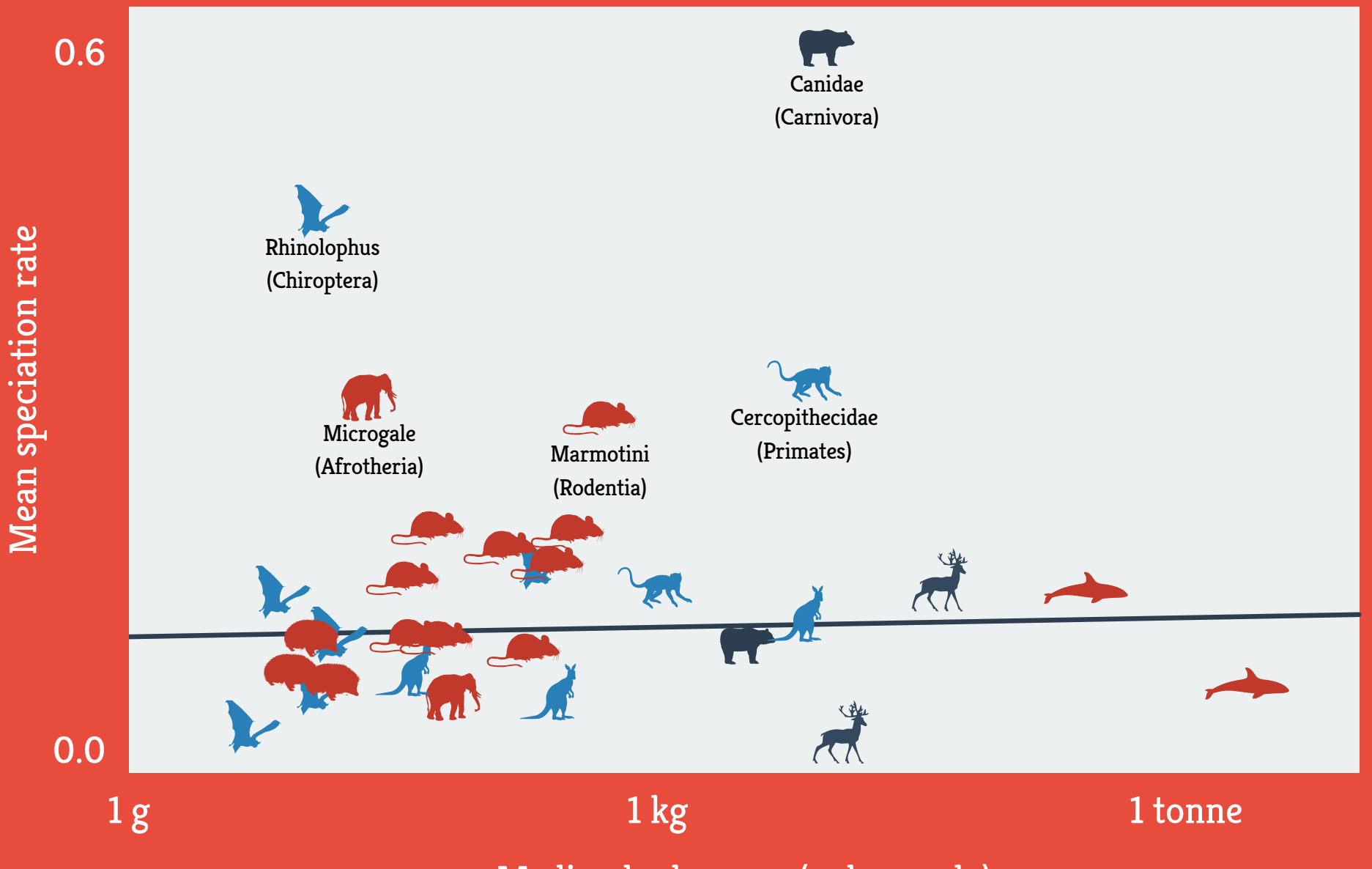
Rutger Vos, David Redding, Arne Mooers (primates)
Olaf Bininda-Emonds, Kate Jones, Nick Isaac (all mammals)
Mette Steeman, Nick Pyenson (Cetacea)

Images: Biodiversity Heritage Library: `flickr.com/photos/biodivlibrary`


0.6
0.0
Mean speciation rate
Canidae
(Carnivora)
Rhinolophus
(Chiroptera)
Microgale
(Afrotheria)
Marmotini
(Rodentia)
Cercopithecidae
(Primates)
1 g
1 kg
1 tonne
Median body mass (g; log scale)