# BIO4102/BIO6102/MSB315

## Evolutionary Ecology
## (Varsha 2023)

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## MODULE: PHYLOGENETIC COMPARATIVE METHODS

Acknowledgments: Some content modified from slides used by others in teaching

# Phylogenetic Comparative Methods

Testing evolutionary hypotheses using phylogenetic information

e.g., Evolution of gregariousness and unpalatability in butterfly larvae (**Sillen-Tullberg 1988 *Evolution* 42(2): 293-305**)

This involves hypothesis testing based on estimation of ***ancestral character states***

Phylogenetic Comparative Methods allow for the identification of *broad-scale patterns* across many taxa over long periods of time, whereas experimental manipulations allow for tests of *mechanistic hypotheses* implicated in driving those patterns

– Weber and Agrawal 2012 *Trends Ecol Evol* 27(7): 394-403

PCMs generally focus on hypotheses of *macroevolutionary patterns*, whereas experiments focus on hypotheses of *microevolutionary processes*

Phylogenetic comparative methods (analyses) address hypotheses related to

- Order of origin of traits – reconstruction of ancestral states of nodes
- Correlations across variables/traits
- Diversification rates

Spider webs: what evolved first - orb or cob webs?

Orb webs – complex(?), intricate, more orderly

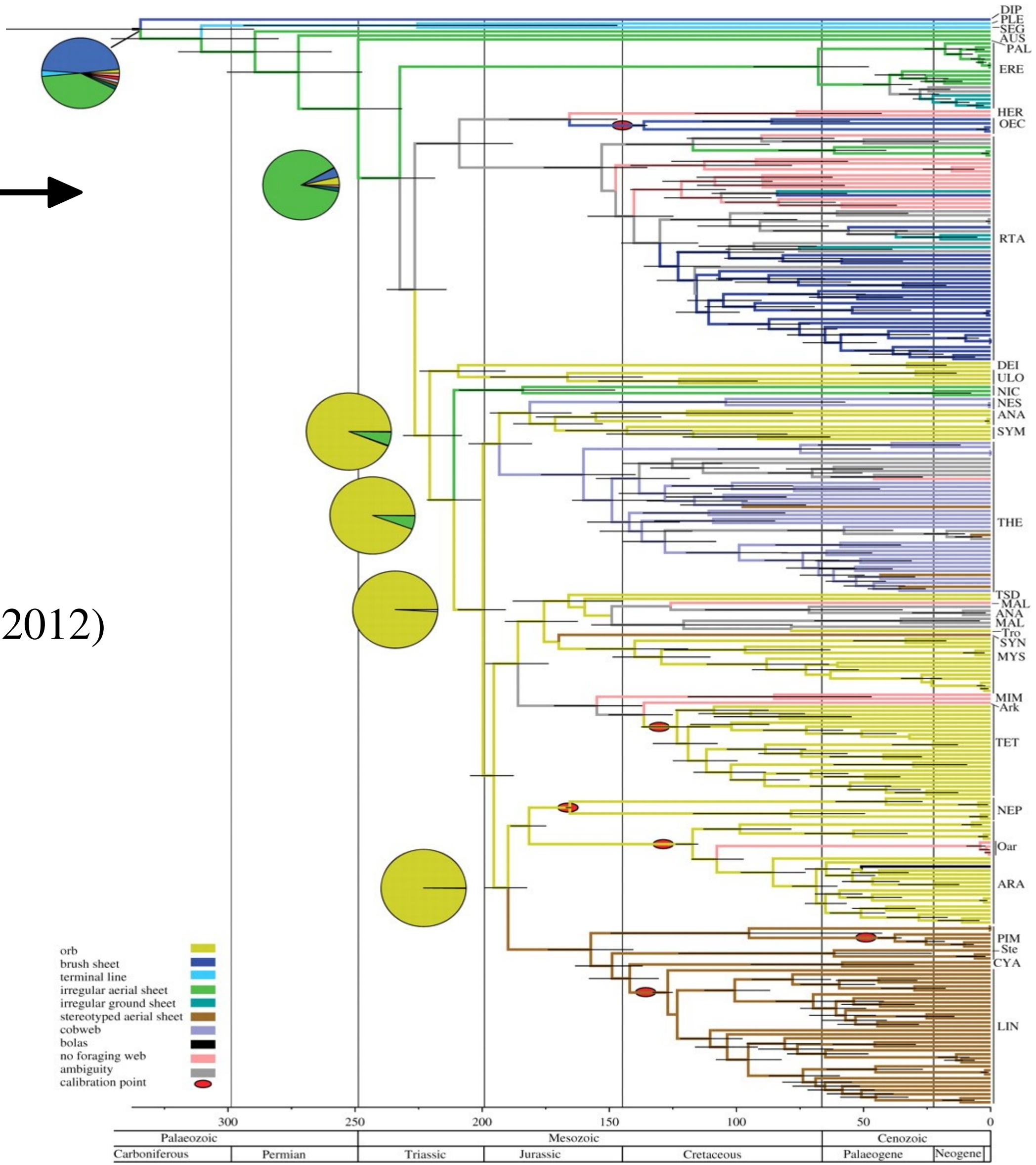
Cob webs – simpler(?), more disorderly

Photo: Fir0002; Flagstaffotos.com.au

Photo: Dinesh Rao, through inaturalist.org

This and next slide adapted from slides by Barry Sinervo

Orb web



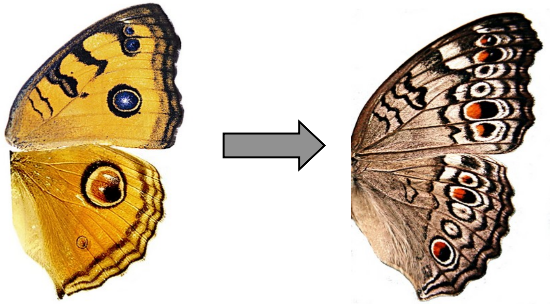

Cob web

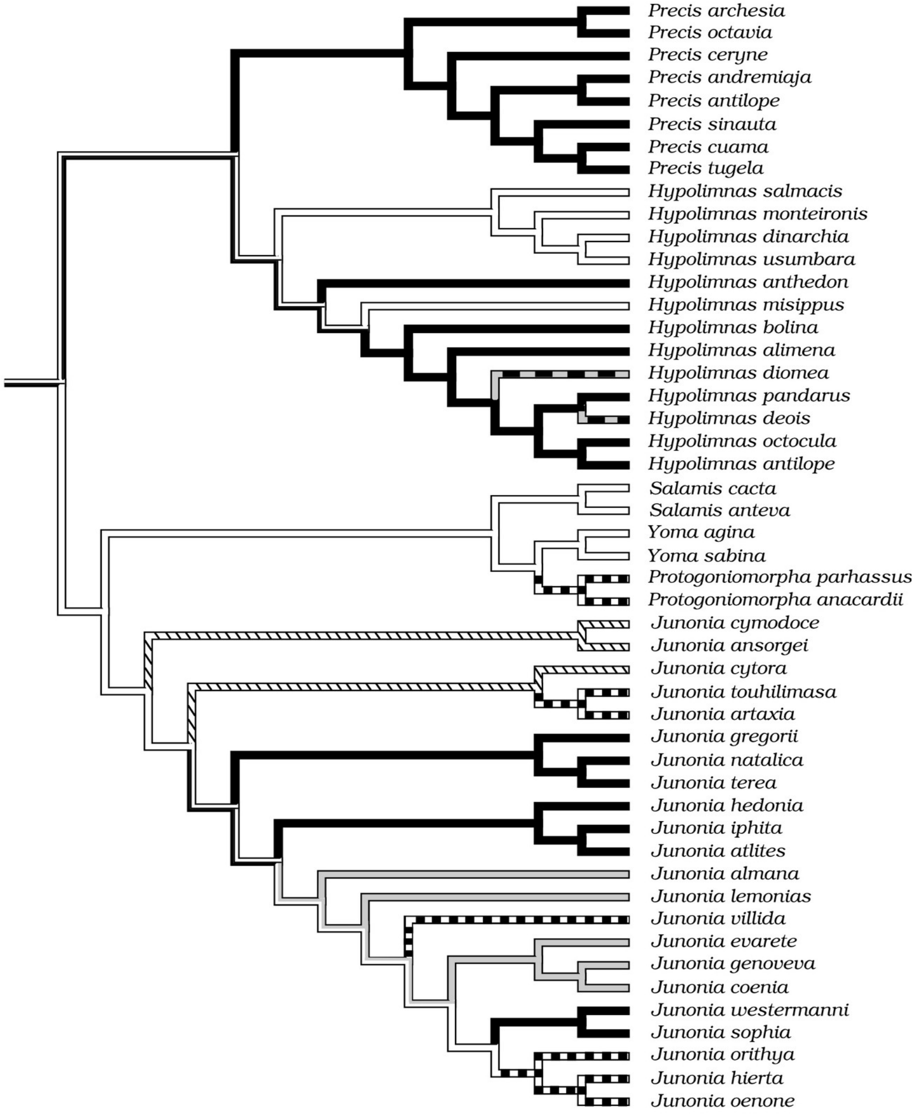
Dimitrov et al (2012)

*Proc. R. Soc. B.*

279:1341-1350

Eyespot evolution in *Junonia* & related butterflies: Did large, solitary 'intimidating' eyespots evolve from small, serial 'deflective' eyespots?






No eyespots
Serial, small

All others: Solitary, large

*Results*: Both increase and decrease of size and number

Both types have evolved convergently, and there have been reversals

*Explanation*: No consistent selection pressure for larger eyespots

# Why phylogeny cannot be ignored: Example 1

Consider an animal clade in which species are either cryptic or aposematic

*Hypothesis*: Crypsis is favoured in smaller animals, whereas aposematism is preferred in larger animals

Prediction: Cryptic species are on average smaller than aposematic ones

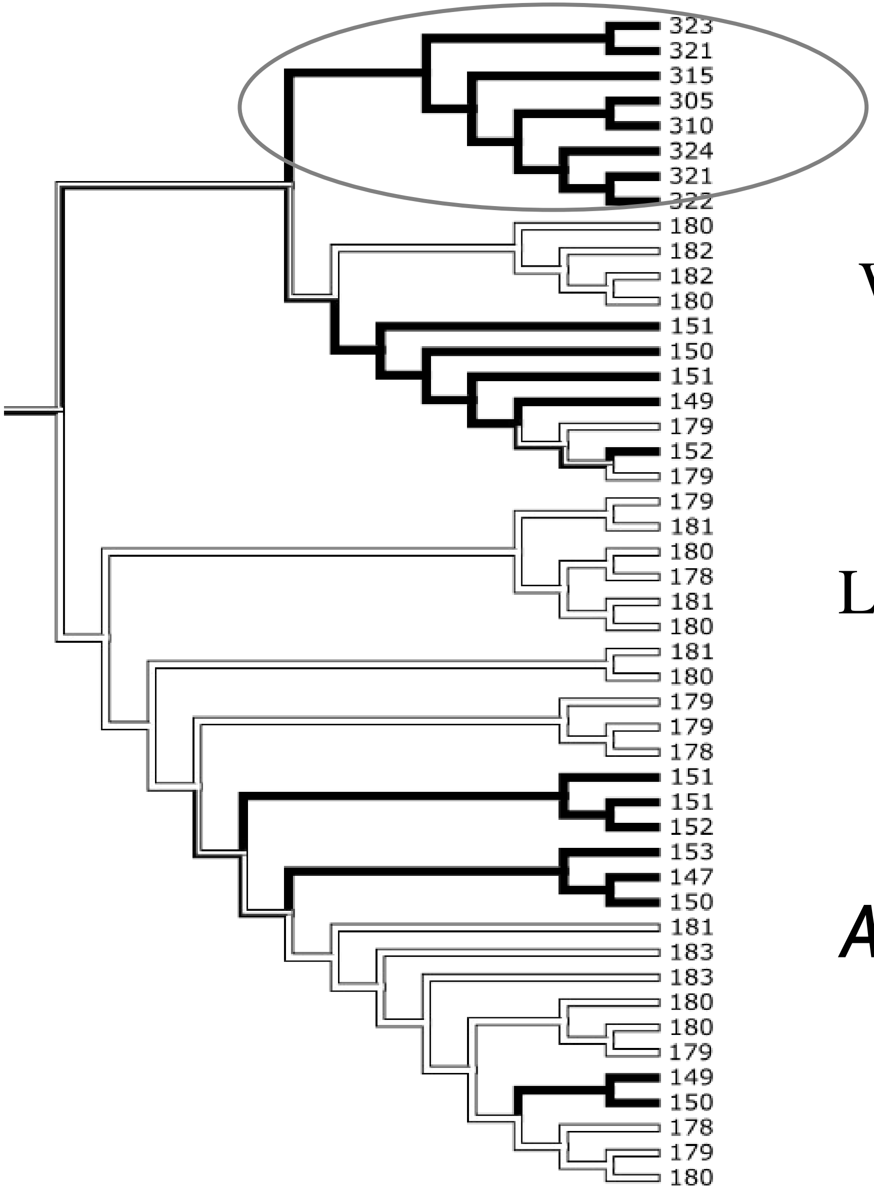
| Cryptic | Aposematic |
|---|---|
| 323 | 180 |
| 321 | 182 |
| 315 | 182 |
| 305 | 180 |
| 310 | 179 |
| 324 | 179 |
| 321 | 179 |
| 322 | 181 |
| 151 | 180 |
| 150 | 178 |
| 151 | 181 |
| 149 | 180 |
| 152 | 181 |
| 151 | 180 |
| 151 | 179 |
| 152 | 179 |
| 153 | 178 |
| 147 | 181 |
| 150 | 183 |
| 149 | 183 |
| 150 | 180 |
| | 180 |
| | 179 |
| | 178 |
| | 179 |
| | 180 |

# Hypothetical dataset (weights in mg)

*Cryptic species mean weight*: 214.14

*Aposematic species mean weight*: 180.04

$P<0.05$




# Black: cryptic; White: aposematic

What if there had been a single species (i.e. no speciation) in the marked clade? Or, if all species except one went extinct?

Lets reanalyze the data by replacing the 8 values with their average (317.625).

*Cryptic species mean weight*: 162.4

*Aposematic species mean weight*: 180.04

P<0.05

Now, we get a different answer.

Why?

Phylogenetic non-independence

# Phylogenetic Signal/Non-independence

Closely related taxa have similar trait values - ‘Phylogenetic signal’

Phylogenetic non-independence leads to a problem similar to ‘pseudoreplication’

# ‘Pseudoreplication’

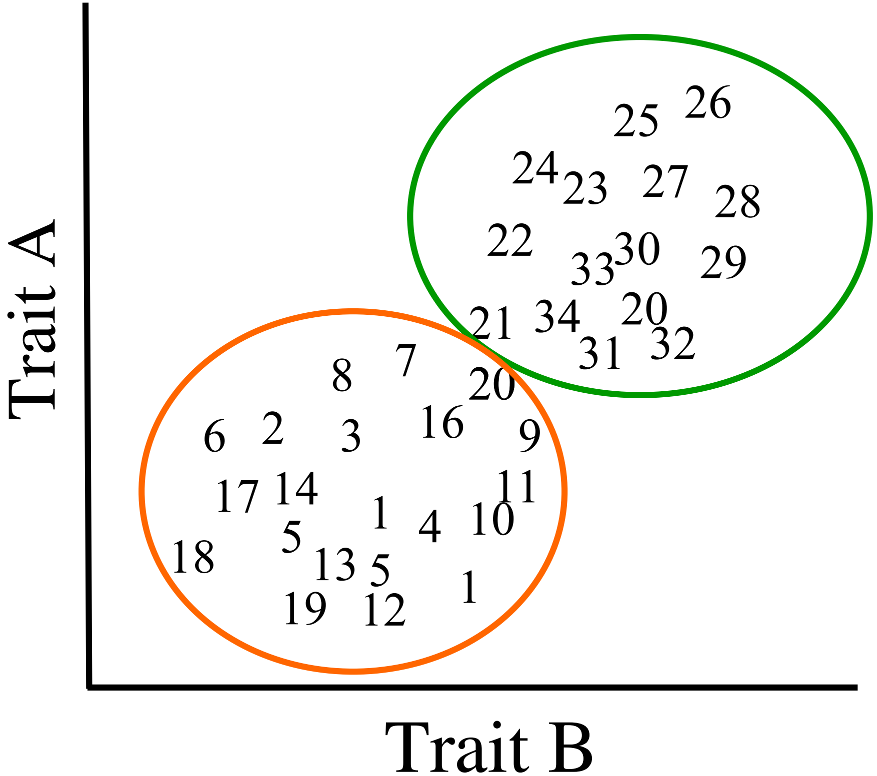
Statistical methods assume that replicates (samples) are independent of each other

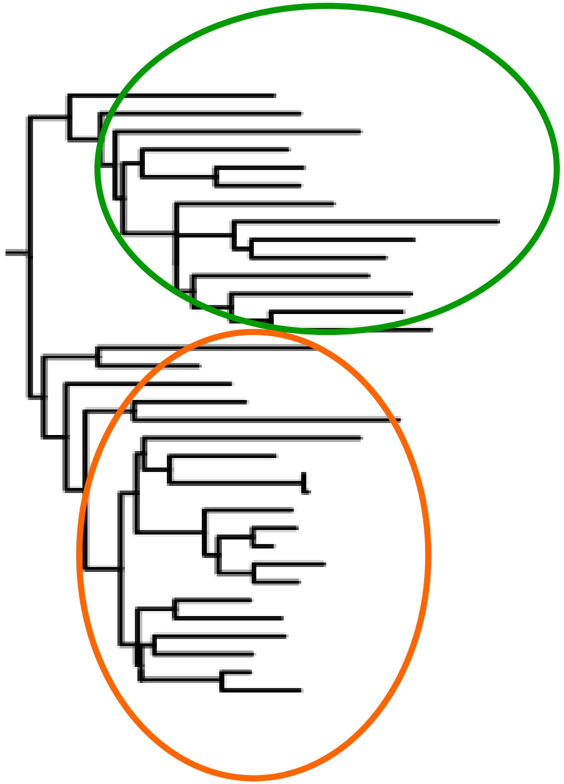
E.g. You want to test whether egg size differs between two populations of an insect species. You measure the sizes of 100 eggs each laid by a single female from population A and B. Even though you have a good sample size, the data points from each population are not independent of each other because the eggs are all from the same mother

# Why phylogeny cannot be ignored: Example 2

*Hypothesis*: Trait A is correlated with Trait B

Data from 34 species



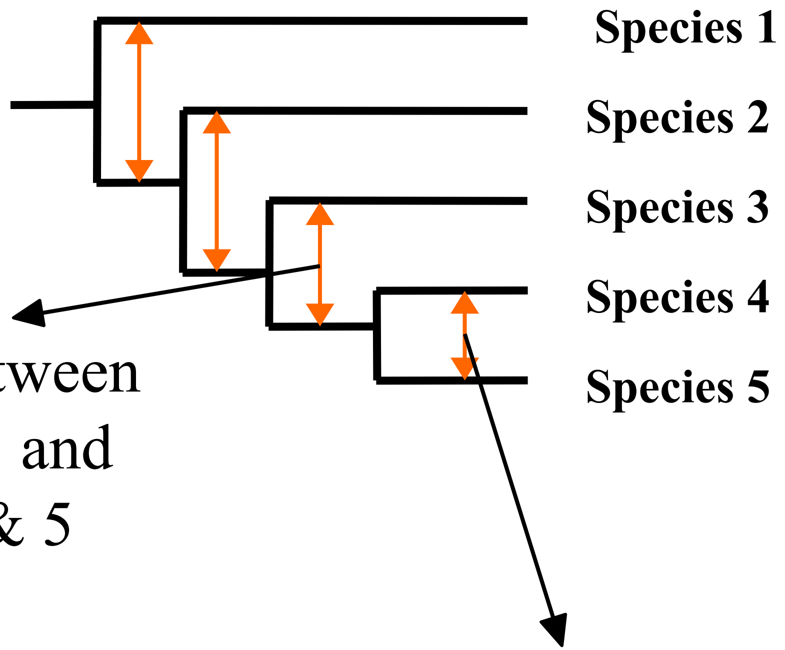
Without taking into account phylogenetic relationships, it seemed like there was a strong correlation between the two traits in this group

However, the correlation ‘disappears’ once we account for phylogeny.

# One solution: Phylogenetic Independent Contrasts Analysis

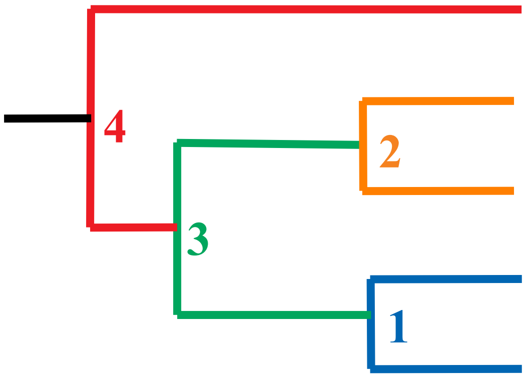
Based on the idea that **contrasts** (i.e., differences) between pairs of adjacent tips/nodes are independent of each other

Involves calculating all possible contrasts for the given trait and analyzing these contrasts, rather than the actual trait values




Contrast (difference) between trait values of species 3 and average of species 4 & 5

Contrast (difference) between trait values of species 4 and 5

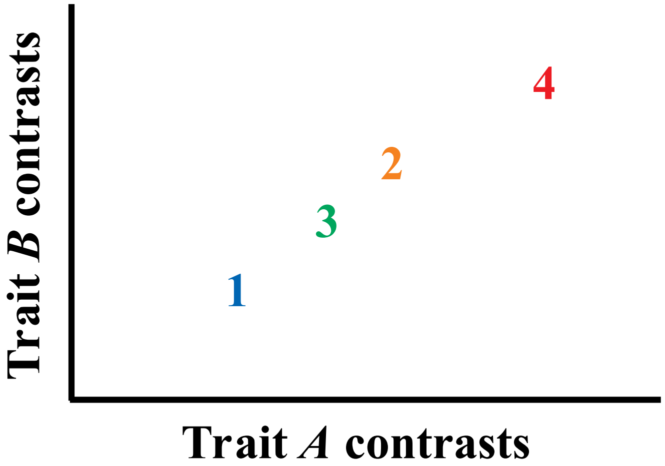



**Actual trait values**

| Trait *A* | Trait *B* |
|---|---|
| 110 | 105 |
| 60 | 50 |
| 80 | 75 |
| 80 | 75 |
| 90 | 85 |

**Contrasts**

| Trait *A* | Trait *B* |
|---|---|
| 10 | 10 |
| 20 | 25 |
| 15 | 17.5 |
| 32.5 | 33.75 |



In this example, branch lengths were assumed to be equal, but in practice branch length information is incorporated in analyses

The PIC method makes several other assumptions, which need to be verified before applying this approach

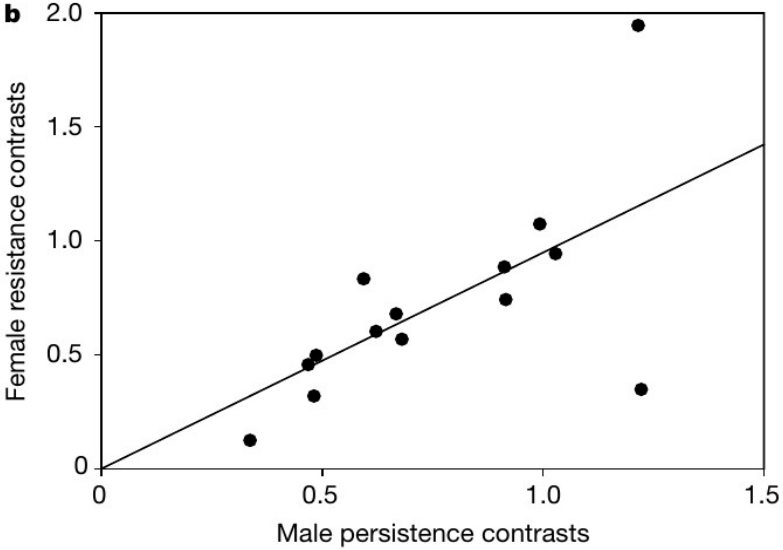
## Sexual conflict in water striders - Arnquist and Rowe 2002. *Nature* 415:787-789

Matings preceded by a pre-mating struggle where females try to dislodge harassing males to avoid superfluous and costly mating.

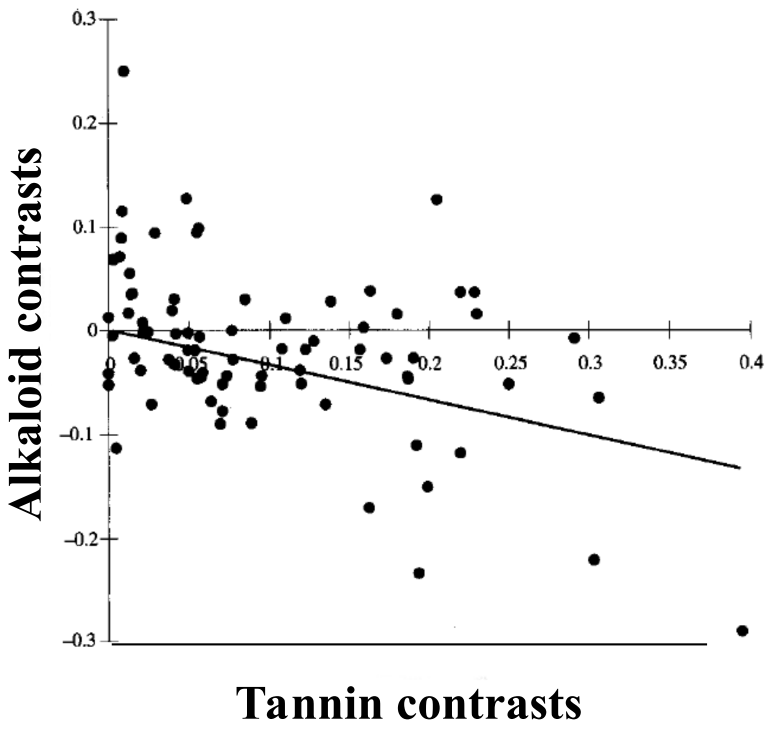
- *Male ability to withstand struggles (persistence)*: morphological grasping structures, e.g. exaggerated clasping genitalia, flattened abdomen to help grasp better
- *Female ability to resist males*: prolongation of the female abdominal spines, degree of downward tilting of the abdominal tip

Water strider. Genus *Gerris*

Photo: Markus Gayda/Wikimedia Commons



Plant secondary metabolites - Negative correlation between proportion of species in a family having alkaloids and proportion with tannins. Silvertown and Dodd 1996 *Phil. Trans. R. Soc. Lond. B* 356: 1233-1239



More PCMs have since been developed for analyzing correlations across traits

E.g. - Phylogenetic Generalized Least Squares

- Phylogenetic mixed model

Conspicuous colouration is associated with *larger* body size in poison arrow frogs (Dendrobatidae) (Hagman & Forsman 2003 *Evolution* 57: 2904-2910), but *smaller* body size in lizards (Murali and Kodandaramaiah 2017 *Animal Behaviour* 1:79–86)

Photo: Brian Gratwicke

Photo: Praveen Illa/Wikimedia Commons

Photo: Drzewołaz Niebieski

Photo: Kris Kelley/Wikimedia Commons

# Diversification patterns

Diversification rate = Speciation rate – Extinction rate

What influences diversification?

Evolution of floral nectar spurs - a key innovation that led to increased diversification in *Aquilegia* plants. Hodges & Arnold 1995 *Proc. Biol. Sci.* 1365: 343-348, Ree 2005 *Evolution* 59(2):257–65

*Aquilegia pubescens* and hawkmoth

Photo: Hodges via www.fs.fed.us

Photos: SA Hodges, MA Hodges, D Inouye via Sciencedaily.com