

Lecture 22. Factors that discourage gene flow, Speciation

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Last time ...

Reasons for clines.

Ring species; isolation by distance.

Factors that reduce or prevent gene flow.

Premating-prezygotic

Aggressive mimicry

Postmating-prezygotic

Lock & Key; Stages at which fertilization can fail

Selection for reproductive isolation

McDonald-Kreitman test for selection in molecules

Postmating-postzygotic

Semispecies and Haldane's rule

Reasons for post-mating incompatibility

Last time....

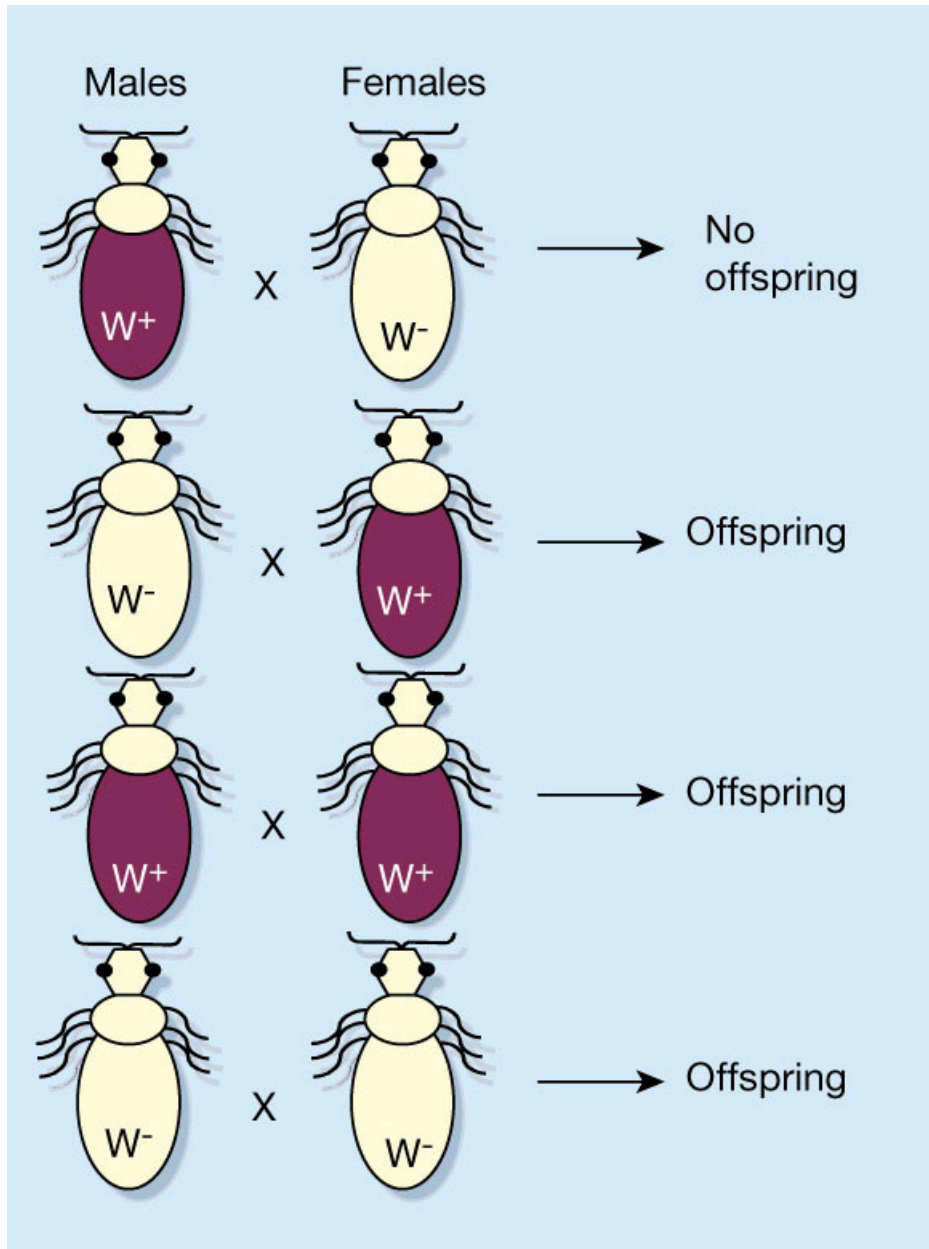
Reasons for Post-mating incompatibility with increasing genetic distance:

- a) Allele combinations are not ideal (breakdown of coadapted allele complexes)
- b) Genes or gene products don't work well together (mtDNA x nuc DNA incompatibility; or mismatch between regulatory protein and target protein)
- c) Chromosomes contain translocations, inversions, fusions or fissions (differ in number). Can't pair properly.

This time ...

- Factors that reduce or prevent gene flow continued.
- Species concepts

Factors that reduce gene flow



Special Case: Parasitic Sterility *Wolbachia*

Infect estimated 20 % to 70% of all insect species; also in spiders, isopods, nematodes

Infection leads to sterility in some crosses & reproductive isolation

Wolbachia genes can benefit hosts (provide nutrients or increase infectiveness)

Sex-biased sterility factor in human mitochondria

- A rare mtDNA mutation in humans induces male sterility.
- Mitochondria are passed through females, so selection does not oppose the transmission
- Until the extreme when all males become sterile
- Populations have been observed w/ high frequencies of this mutant.

Prezygotic isolation evolves first. Coyne and Orr, 1997. *Evolution* 51:295-303

- Reviewed 60 years of *Drosophila* studies (many different species)
- Prezygotic isolation evolves faster than postzygotic
- Prezygotic reproductive isolation stronger in sympatry (or parapatry) than in allopatry.
- Postzygotic isolation similar in sympatry, parapatry, and allopatry
- Time to speciation varied between 200,000 to 2.7 million years (fastest involving species w/ prezygotic factors in sympatry)

End: factors that influence gene flow



Note: male mantis mating with female has no head!

Species concepts: What is a species? How can species be recognized, defined?

Darwin said...

“I believe a well-marked variety may be justly called an incipient species....”

But added qualification:

“It need not be supposed that all varieties or incipient species necessarily attain the rank of species. They may whilst in this incipient state become extinct, or they may endure as varieties for long periods....”

C. Darwin: “On The Origin of Species...” Ch II. Variation Under Nature

Darwin also pointed out...

“No clear line of demarcation has as yet been drawn between species and sub-species...or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences.

These differences blend into each other in an insensible series....” A continuum

Note: Darwin knew no genetics and did not understand the complexity caused by gene flow.

C. Darwin: “On The Origin of Species...” Ch II. Variation Under Nature

Usefulness of species concepts

- 1) Enable the classification of organisms
- 2) Correspond to discrete groups of similar organisms
- 3) Help us understand how these discrete clusters arise in nature
- 4) Represent the products of evolutionary history
- 5) Applicable to a wide variety of organisms

Unlikely that one concept will work for all goals.

Coyne and Orr, 2004. Speciation. Sinauer

Practical usefulness:

- For designing species delimitation strategies; needed to understand disappearing biodiversity
- For teaching about/understanding evolution

Typological Species

- Not really a “species concept” but sometimes termed the “morphological or phenetic species concept” A proxy for a species concept.
- Species are defined by their overall morphological similarity to a type specimen. Morphological gaps separate species.

Problems w/ typological species

- 1) Many characters are polymorphic within species
- 2) Not all species are morphologically distinct (e.g., cryptic species)
- 3) Some characters may be more important than others.
- 4) To find morphological gaps, large samples are needed throughout the range of a species (to characterize within versus among species variability.)

Polymorphic; originally described as two species: *Hyla leucophyllota*, *H. favosa*

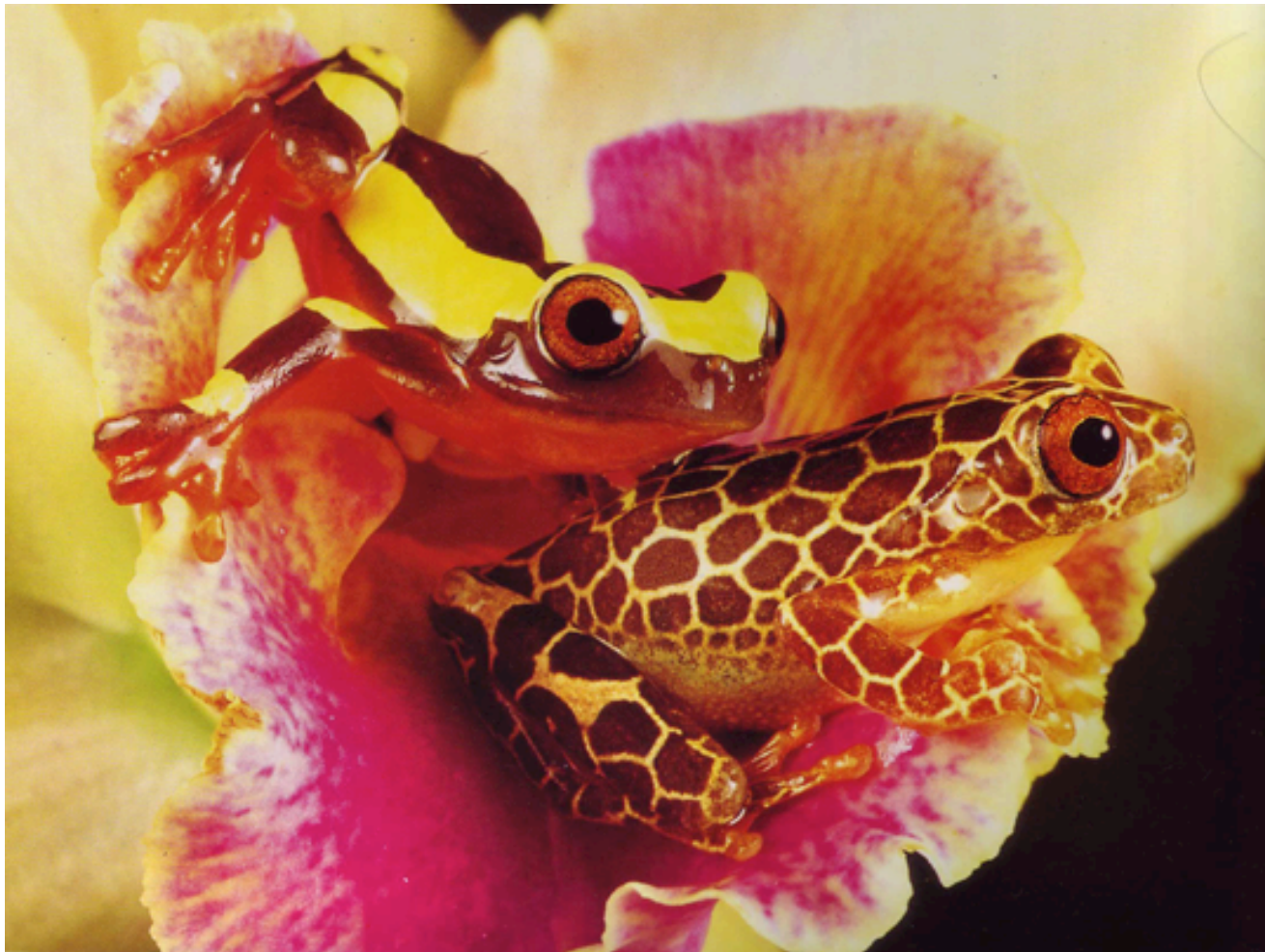
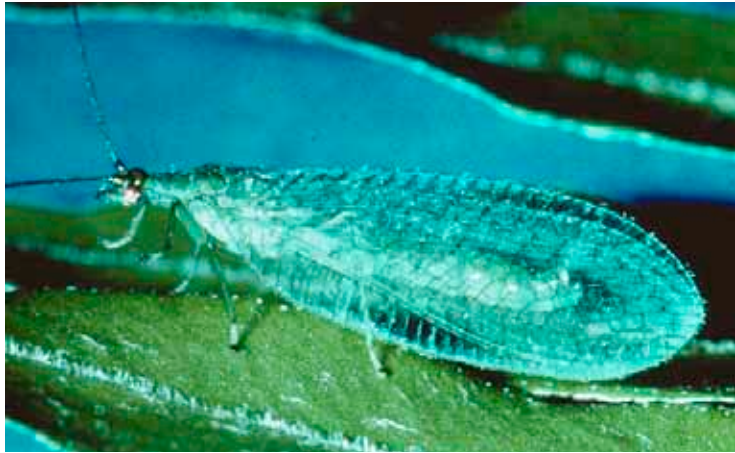


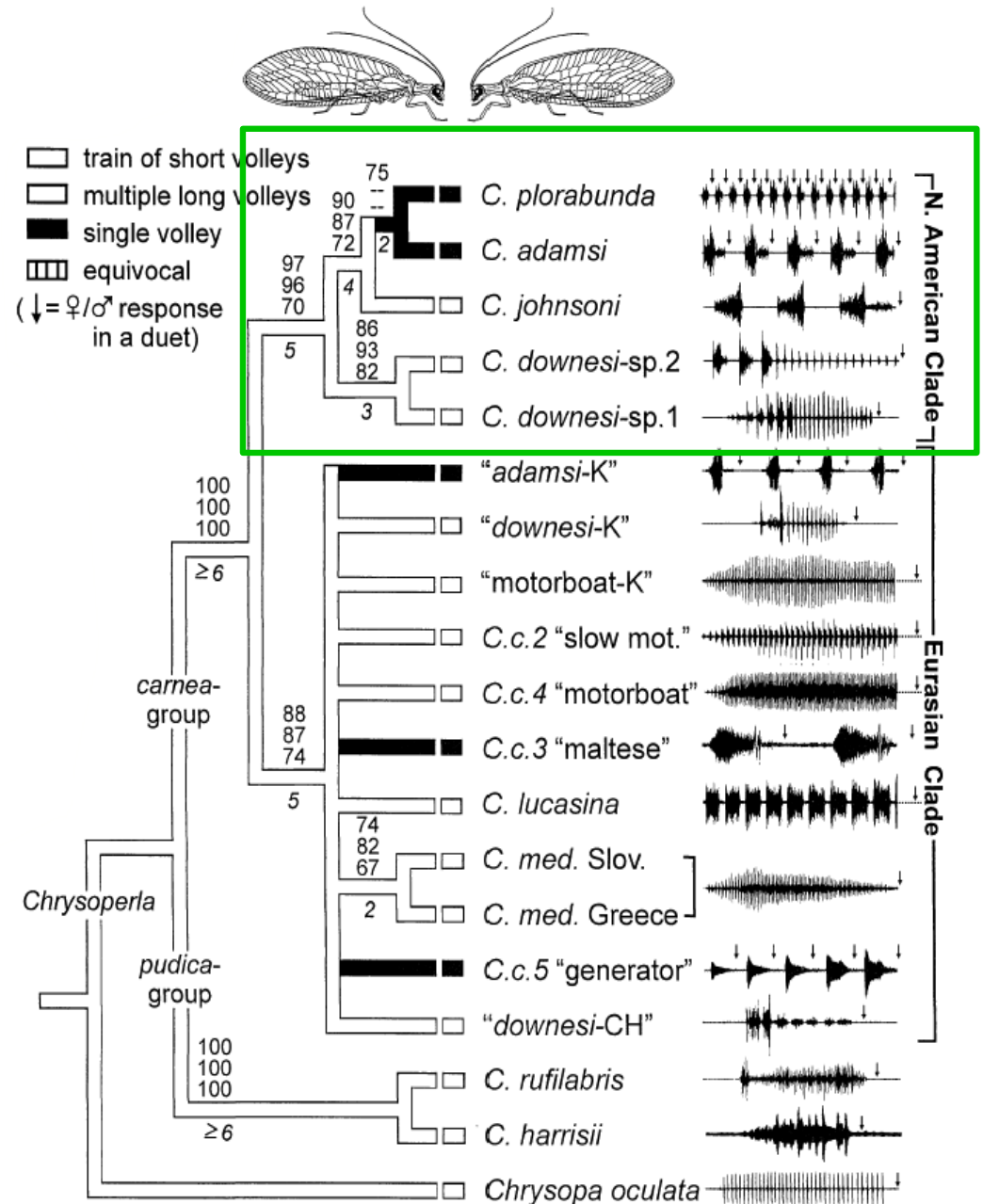
Photo: P. Carmichael, G. Shumway

Cryptic species, green lacewings



Identical morphology,
different songs.

Prof. Charles Henry, UCONN



Evolutionary Species Concept

- Species: a group of natural populations that is evolutionarily independent from other such groups. On “separate evolutionary trajectories”.
- Not operational
- Can be defined operationally using the biological, phylogenetic or the cohesion species concepts

Biological species concept (BSC)

- Most widely used. Implicit in Darwin's writings. Formal concept arose from modern synthesis. Formalized by Ernst Mayr.
- “Groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups.” A reproductive community.
- Buffon, Darwin, Wallace, and other early biologists recognized the importance of reproductive isolation.

Advantages

- All speciation mechanisms incorporate the idea of reproductive isolation
- Reproductive isolation is essential for speciation

Problems with BSC

- 1) Only applies to out-crossing sexually reproducing organisms;
- 2) Allopatric, Isolated populations can take thousands of years to become genetically different; when do they become different species?
- 3) Testing “potential to interbreed” difficult.
- 4) Hybridization is common in nature.

Testing the potential to interbreed is difficult!

Decim

M



F



Cassini

M



F



Decula

M



F



Kathryn Gannon



Testing the potential to interbreed is difficult!



Kashiwa Hereford

Recognition species concept

“the most inclusive population of individual biparental organisms that share a common fertilization system.”

Patterson, 1985

Not very different from BSC.

Phylogenetic Species Concept

“An irreducible cluster (clade) of organisms diagnosably (recognizably) distinct from other such clusters and within which there is a [phylogenetic] pattern of ancestry and descent.” (Cracraft 1989)

“The smallest monophyletic group of common ancestry” (de Queiroz & Donoghue 1990)

Advantages

- Can be applied to sexual & asexual taxa
- Provides a methodology for defining evolutionary lineages (phylogenetic tree)

Disadvantages

- Requires diagnostic characters (morphological or molecular)
- Does not consider gene flow or other population genetic parameters.
- Time consuming (but less so than BSC)

Genealogical species concept

Another phylogenetic species concept.

“Exclusive groups of organisms whose members are all more closely related to each other than they are to members outside the group.” (Baum & Shaw 1995).

‘Genotypic Cluster’ Species Concept

Drès and Mallet 2002 Phil. Trans. R. Soc. Lond. B

- Def.- Species are genotypic clusters distinguishable in sympatry by actual correlated genetic differences at multiple loci rather than by inferences about process
- Correlations between loci should be sufficient to cause a bimodal genotypic distribution such that two groups or ‘clusters’ of genotypes are identifiable, and separated by intermediates that are rarer than more extreme genotypes (Jiggins & Mallet 2000).

Genotypic Cluster Species Concept

Advantages of GCSC- Specifically allows:

- gene flow,
- non-monophyly and
- genetic differences at loci that are not necessarily fixed.

Disadvantages- Requires extensive genomic sampling throughout species ranges.

Cohesion Species Concept

(Templeton 1985)

- the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.
- Cohesion mechanisms include: stabilizing selection, gene flow, genetic drift, shared developmental program/history, ecological constraints, reproductive isolation.

Advantages of CSC

- Uses phylogenies
- Combines aspects of the phylogenetic and biological species concepts and basically everything that we've learned in population genetics in the years since the modern synthesis.

Problems with CSC

- Very time consuming! Requires studies of breeding, ecology, gene flow, phylogeny.

This is really the best way to understand a species but a study of a single species radiation of say 60 taxa could take a life time!

Unified Species Concept

- Delimitation and conceptualization different issues.
- Primary defining criterion: separately evolving metapopulation.
- Properties acquired during divergence provide evidence
 - Reproductive isolation, Diagnosability, Monophyly
 - one is enough, more better

Species Definition: What actually happens in practice for majority of species described?

- Example: Large Rainforest Canopy Study, Smithsonian Institution
- Thousands of individuals collected from a single tree, stored in alcohol
- Sorted by parataxonomists into morpho taxa, accessioned into museum.
- Sent to experts worldwide who compare them to type specimens and provide names.



<http://nature.berkeley.edu/~hwood/Chile%20008.html>



<http://www.close-up-photolibrary.com/about2.htm>, <http://www.nhm.ac.uk/research-curation/research/projects/chalcids/>