Lect. 12. Post-Zygotic Isolation (cont.), Species Concepts, Speciation Mechanisms

EEB 2245, C. Simon, 17 Mar 11

Lysin in abalone

Lee & Vacquier (1992) Biological Bulletin.182:97-104. Sequenced lysin gene in 7 species of abalone.

- Detected positive selection at AA level in active site
- McDonald Kreitman test:

The Genetic Code

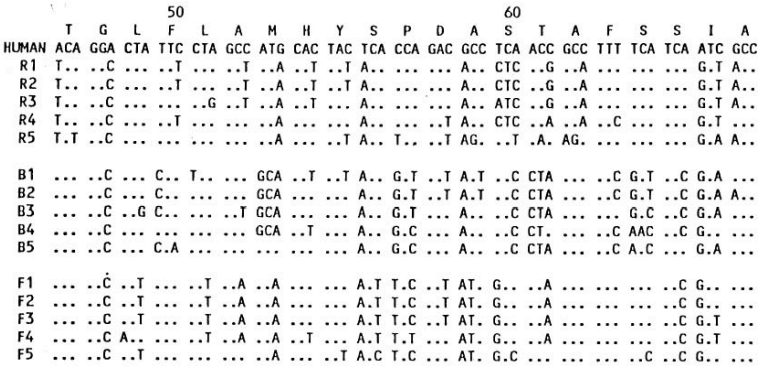
TABLE 11-2 The Genetic Code, showing the RNA codons specifying each amino acid.

GCA GCC GCG GCU	AGA AGG CGA CGC CGG CGU	GAC GAU	AAC AAU	UGC UGU	GAA GAG	CAA CAG	GGA GGC GGG GGU	CAC CAU	AUA AUC AUU	UUA UUG CUA CUC CUG CUU	AAA AAG
Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys

			AGC AGU					
		CCA CCC CCG	UCA UCC UCG	ACA ACC ACG			GUA GUC GUG	UAA
AUG	UUC UUU	CCU	UCU	ACU	UGG	UAC UAU	GUU	UAG UGA
Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val	Stop

Different probability of change in 2- vs 3- vs 4- vs 6-codon families

Protein coding genes



Primary structure substitutions influenced by triplet code

Rodent, Bird, Fish **Kocher et al. 1989. PNAS 86:6196**

III. Post-Mating, Post-Zygotic

A. Fertilization occurs, embryo dies
B. Hybrids are produced but are of low fitness
C. Adult offspring are viable but sterile or partially sterile.

Question: How does fertilization ability differ in hybrid crosses between close vs distant species?

- Breeds of dogs?
- Wolf vs. dog or coyote?
- Dog vs. cat?

Factors that reduce gene flow

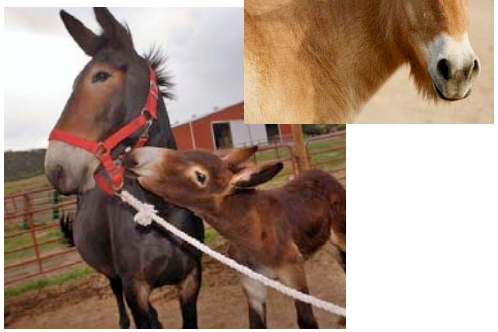
R. pipiens x R. sylvatica

Hybrid embryo stops developing at early gastrula stage

http://www.werc.usgs.gov/fieldguide/images/rapi1.jpg; http://www.cortland.edu/herp/keys/images/frogs/rsylvalg.jpg

Factors that reduce gene flow

donkey x horse = sterile mule



http://www.hedweb.com/animimag/donkey.jpg; http://animals.nationalgeographic.com/staticfiles/NGS /Shared/StaticFiles/animals/images/primary /przewalskis-horse.jpg; http://extras.mnginteractive.com/live/media/site36/2007/0725/20070725__20070726_A1_CD26MULE~p1.JPG

Reasons for Post-mating incompatibility with increasing genetic distance:

a) allele combinations are not ideal (breakdown of coadapted allele complexes)

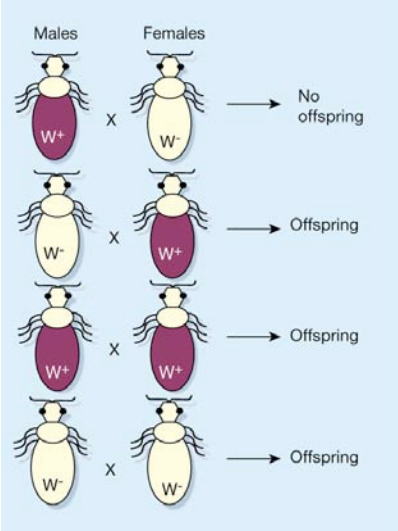
b) genes or gene products don't work well together (mtDNA x nuc DNA incompatibility)

c) chromosomes contain translocations, inversions, or differ in number. Can't pair properly.

Haldane's Rule

JBS Haldane

- Background: In Humans and *Drosophila*, males are heterogametic, but in other organisms, e.g., most amphibians, birds, butterflies and reptiles, the female is heterogametic.
- when sterility is confined to one sex, it will always be the heterogametic sex.
- Partial explanation: when recessive deleterious alleles causing hybrid problems are on sex chromosomes they are expressed in heterogametic hybrids but not in homogametic hybrids. Orr, A. 1997. Ann. Rev. Ecol. Syst.



Special Case: Parasitic Sterility

Wolbachia

Infect 15-20 % of all insect species, also found in spiders, isopods, and nematodes

Infection leads to sterility in some crosses

Species concepts, speciation mechanisms

Usefulness of species concepts

Earth's biodiversity is disappearing. How can we preserve it if we don't even know how many species are out there?

We must be able to identify the products of evolution. "Discrete clusters of similar organisms that share a unique evolutionary trajectory."

Typological Species

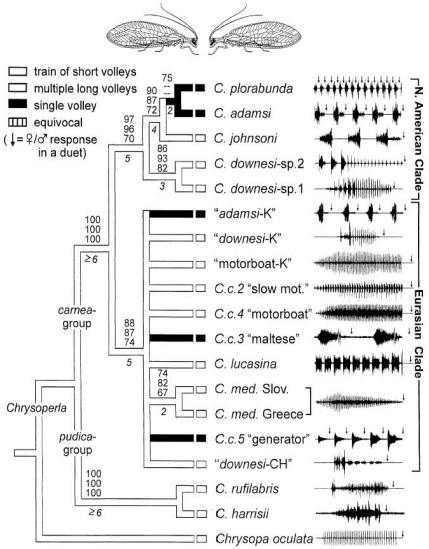
- Not really a species concept but sometimes referred to as "morphological or phenetic species concept"
- Species are defined by their overall morphological similarity to a type specimen.

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.)

Cryptic species, green lacewings

Identical morphology, different songs.



Henry, C.S., M.L.M. Wells, and C.M. Simon. 1999. Convergent evolution of courtship songs among cryptic species of the carnea-group of green lacewings (Neuroptera: Chrysopidae: Chrysoperla). Evolution 53(4): 1165-1179.

Evolutionary Species Concept

•species: a group of natural populations that is evolutionarily independent from other such groups (E.J. Lecture)

Defined operationally using the biological, phylogenetic or the cohesion species concept

Biological species concept (BSC)

- Most widely used. 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 diploid sexually reproducing organisms; not asexuals (e.g. bacteria).
2) Isolated populations can take thousands of years to become genetically different; when do they become different species?
3) Testing "potential to interbreed" difficult. Tedious field observations; Lab experiments useful but not equivalent to nature.
4) Hybridization is common in nature. Some species hybridize in some locations but do not hybridize in others. Time consuming to measure gene flow in nature.

Recognition species concept

Not very different from BSC.

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

Patterson, 1985

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

Similar to 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).

Cohesion Species Concept

- 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.
- (Templeton 1985)

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!

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%202008.html

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

Problems w/ rapid surveys and mass collecting

No information on ecology or behavior

Alcohol preserves DNA for phylogenetic studies but ruins some morphological characters.

Many proposed new taxa may exist as single specimens only (no idea of variation within species).

What actually happens in practice?

Example 2. “DNA barcoding,” “DNA taxonomy”

•A certain genetic distance or gap in phylogenetic sister taxa used to define species; based on COI gene segment

•Caution: only a preliminary step in species recognition; more characters are needed (morphology, ecology, mating behavior, more genes)

Speciation Mechanisms

Categories of Speciation Mechanisms

I) Involving spatial isolation
   - A) Allopatric (vicariance vs founder)
   - B) Parapatric
   - C) Sympatric

II) Involving Chromosomes

III) Temporal Isolation

IV) Caused by Parasites

Allopatric, Parapatric, Sympatric Genetic Mechanisms

- Genetic drift
- Natural selection
  - Ecological selection (due to environment)
  - Sexual selection

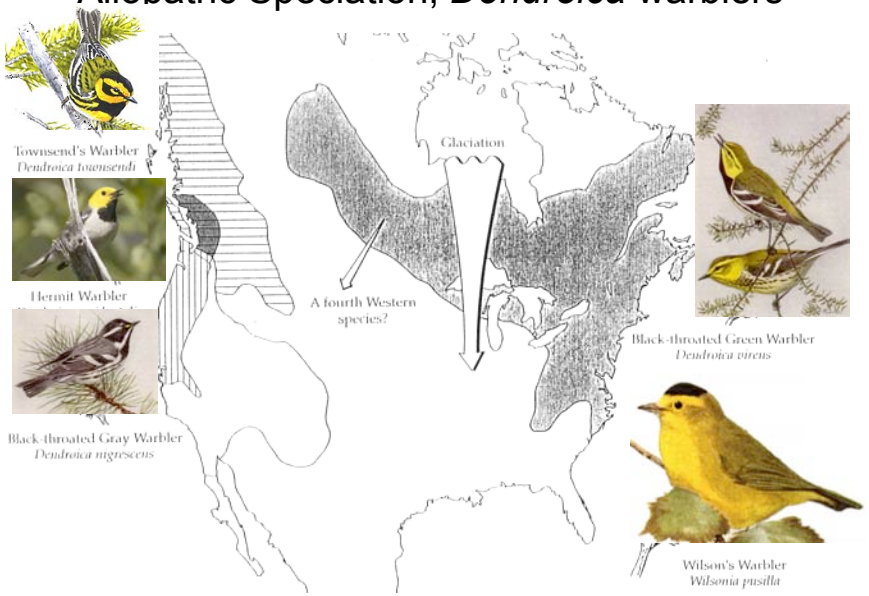
Allopatric Speciation

- Speciation by Vicariance: a large population is split into two parts by a barrier
- Founder effect speciation- colonization of a new territory by a small number of individuals.

Allopatric Speciation

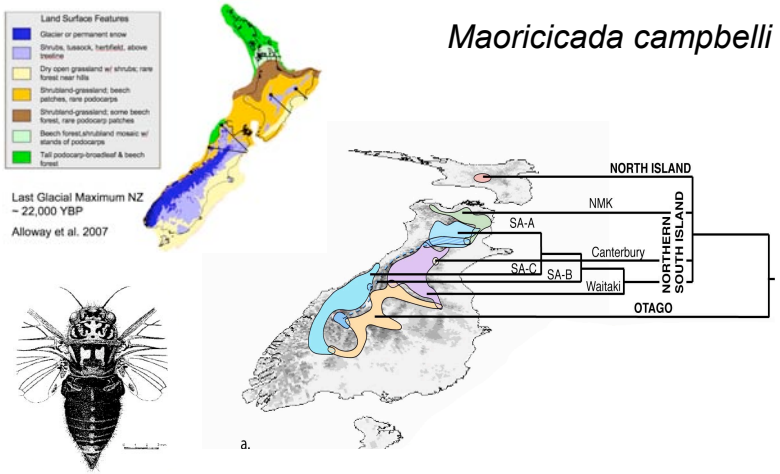
- Speciation by Vicariance: a large population is split into two parts by a barrier
  - Speed of genetic drift will depend on population size & amount of gene flow
  - Selection may be strong (fast) or weak (slow); do environments differ on either side of barrier

Allopatric Speciation, *Dendroica* warblers



Allopatric speciation

Maoricicada campbelli



Hill, K.B.R., C. Simon, D.C. Marshall, and G.K. Chambers. 2009. Surviving Glacial Ages within the Biotic Gap: Phylogeography of the New Zealand cicada *Maoricicada campbelli*. Journal of Biogeography 36: 675-692.

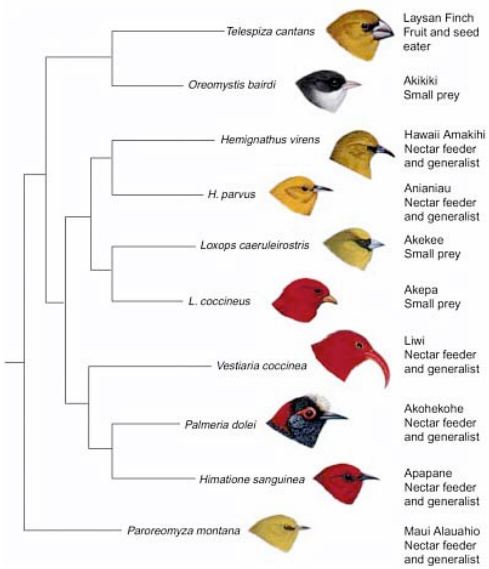
Buckley, T.R., C. Simon, and G.K. Chambers. 2001. Phylogeography of the New Zealand cicada *Maoricicada campbelli* based on mitochondrial DNA sequences: Ancient clades associated with Cenozoic environmental change. Evolution 55:1395-1407.

Allopatric Speciation

- Founder effect speciation- colonization of a new territory by a small number of individuals. Genetic revolution due to…
  - reduction in number of alleles
  - Genetic drift & inbreeding if extended bottleneck
  - Selection in a new island environment

Hawaiian honeycreepers founder speciation

Single colonizing ancestor > 50 species adapted to different feeding niches (more than half extinct!)



http://ncse.com/image/honeycreeper-phylogeny

Parapatric Speciation

- Model: Two adjacent populations on either side of a strong step cline maintained by natural selection--e.g., ecotone (boundary between two habitat types that generate different selection pressures).
- To create reproductive isolation, other traits must be linked to the clinal traits and some of these must affect reproductive isolation (e.g., male or female choice genes).

Parapatric Speciation

- Similar to models of reproductive character displacement; if the trait is different enough in the adjacent populations and has a fitness effect, selection act to increase the difference. Termed: reinforcement. Increases assortative mating.
- Example: grasses growing on toxic mine tailings have developed partial reproductive isolation in flowering time & degree of self compatibility compared to nearby non-tolerant grass of same species.

Sympatric Speciation

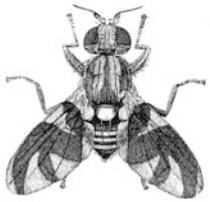
- Difficult to envision since sympatric populations overlap!
- Need extreme assortative mating & disruptive selection to eliminate any heterozygotes for mating genes (as in parapatric speciation)

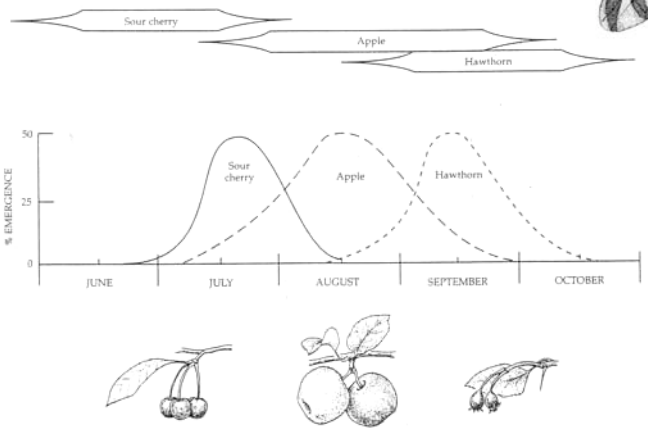
Sympatric Speciation

Best examples involve "host race speciation"

1) True fruit flies (family Tephritidae) of the genus *Rhagoletis*. On native hawthorn vs. introduced cherry vs. introduced apple.
- *Enchenopa* Treehoppers. Distributed from Panama to S. Canada. Host races on seven genera of NE forest plants: walnut, black locust, bittersweet vine, viburnum, redbud, tulip tree and Hoptree.

Host races of *Rhagoletis pomenela*





http://www.cals.ncsu.edu/course/ent425/text18/applemaggot.jpg

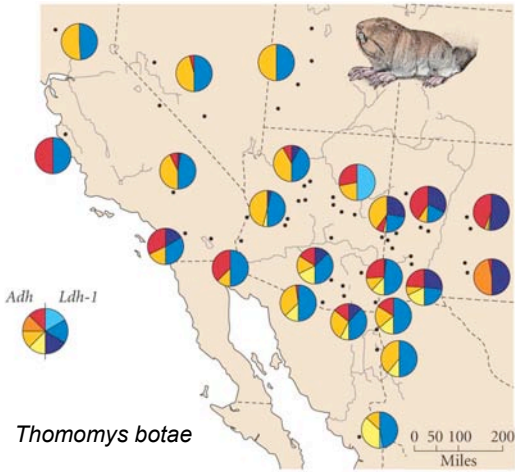
Enchenopa tree hoppers

http://farm3.static.flickr.com/2156/2535390394_4b8d20ede2.jpg?v=0

Chromosomal Speciation

- Involving Chromosomal rearrangements
- Involving Polyploidy (with and w/o hybridization)

Pocket Gopher. Two electrophoretic loci show high among popln. differentiation.



Nearby localities differ strongly in allele frequency.

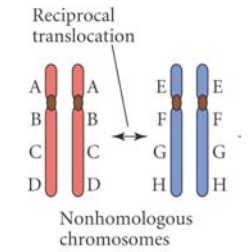
Gene flow low.

Populations small.

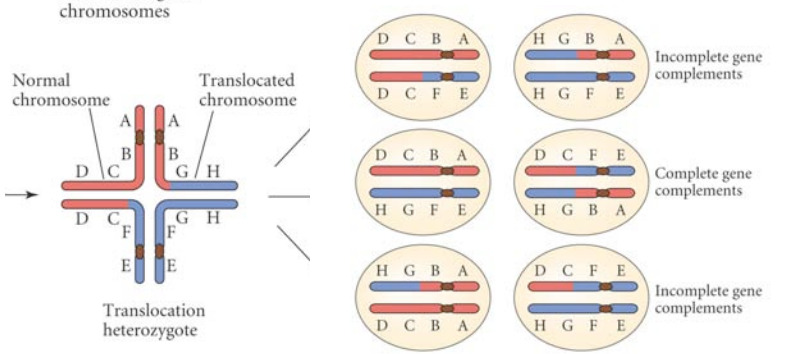
Chromosome number/ configuration differ among populations more than other mammals.

> 150 named subspecies.

Futuyma 2e



Translocations reduce fitness of heterozygotes. So must occur by drift in small populations!



Chromosomal Speciation

- Involving Polyploidy (but no hybridization)

Example: tree frogs; Ptacek, Gerhardt, and Sage. 1994. Evolution 48(3):898-908.

Hyla chrysoscelis is diploid. Found in east & central west.

Hyla versicolor is a tetraploid. Tetraploids cannot mate with diploids. It is larger, has larger cell size and its mating song has a slower pulse rate. Cyt. B. phylogeny shows three separate, independent origins of *H. versicolor*!

Species are not supposed to be polyphyletic (multiple origins not allowed in most species definitions)!

Chromosomal speciation

Hyla chrysoscelis 2N

Hyla versicolor 4N

polyploid

Polyphyletic species?

Hyla chrysocelis

http://www.marietta.edu/~biol/biomes/images/deciduous/hylavers.jpg http://www.biology.duke.edu/dnhs/pics/Hylachry2.jpg

Chromosomal Speciation

Involving Polyploidy & hybridization

Example: Sunflowers

Many sunflower species are polyploid and hybridize with other polyploid sunflower species.

Polyploid allows species with different chromosome numbers to reproduce successfully because chromosomes can pair with their polyploid duplicate in the zygote rather than with the chromosomes from the other hybrid parent species.

Organisms can get around the chromosome pairing problem if they are polyploid… (common in plants)

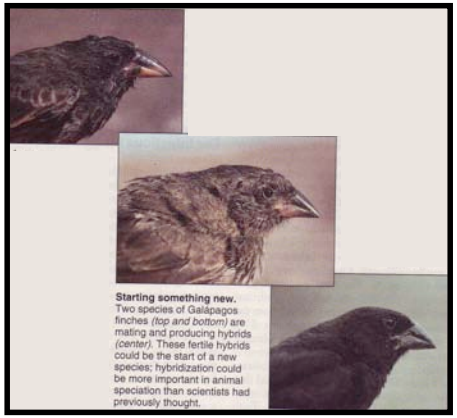
non-polyploid species can't hybridize	polyploidy species can hybridize
Parent sp. 1- 2N = 6, N = 3	2N = 12 (6+6), N = 6 (3+3)
Parent sp. 2- 2N = 8, N = 4	2N = 16 (8+8), N = 8 (4+4)

In the polyploids, the duplicated chromosomes can pair with each other so that normal segregation and cell division can occur.

Hybrid speciation w/o polyploidy

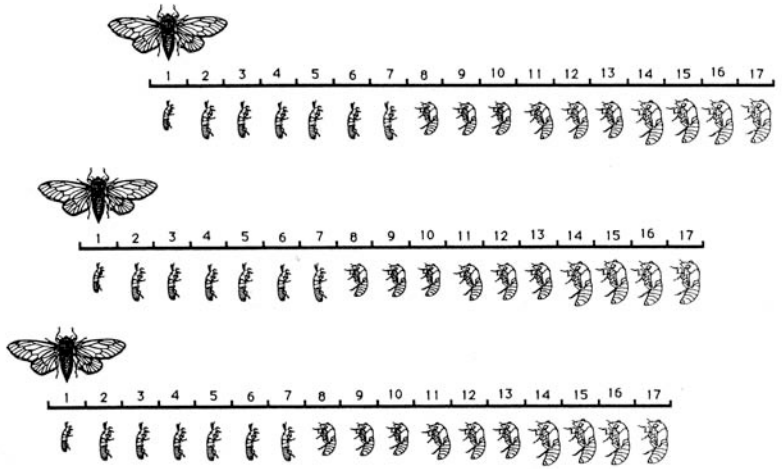
G. scandens hybridizes with *G. fortis* on Daphne Major

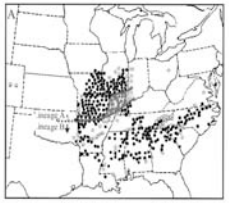
Over 20 years of observations hybrid became much more fit



Starting something new. Two species of Galápagos finches *(top and bottom)* are mating and producing hybrids *(center)*. These fertile hybrids could be the start of a new species; hybridization could be more important in animal speciation than scientists had previously thought.

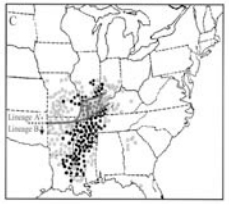
Allochronic speciation in periodical cicadas





13-year
Brood XIX

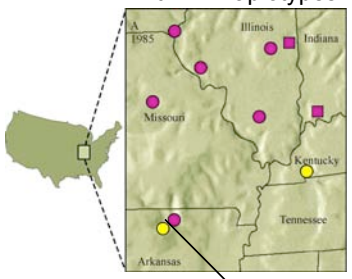
All 17-year
Cicadas



13-year
Brood XXIII

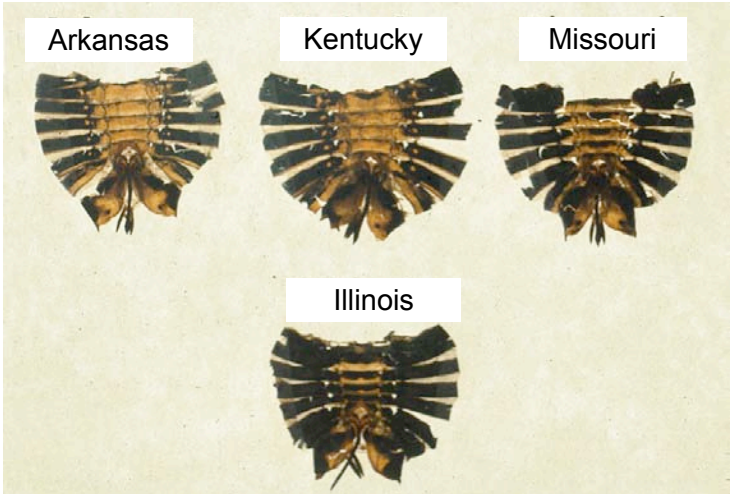
Both large 13-year cicada broods have populations that fill a hole in the distribution of 17-year cicadas

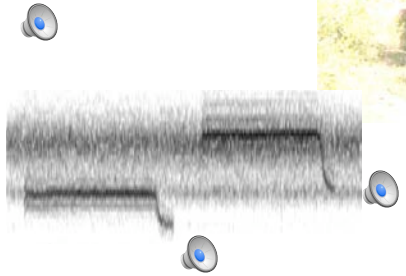
mtDNA haplotypes

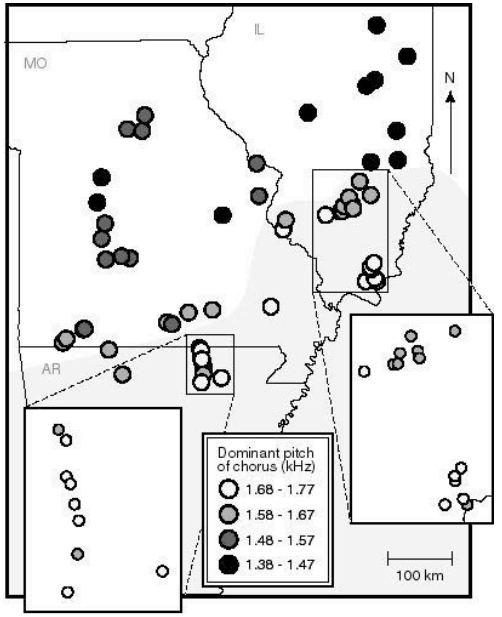


Hardy Co., Arkansas

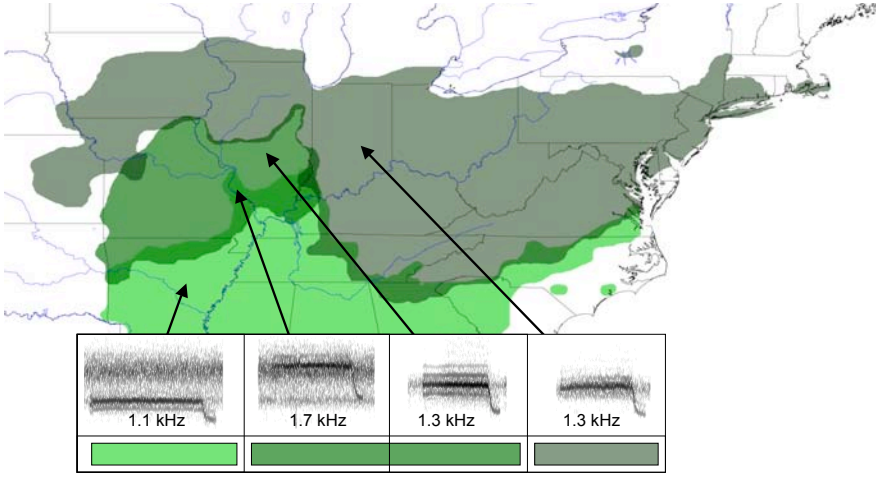
Abdomen color in 13-year cicadas







Reproductive character displacement in *Magicicada*

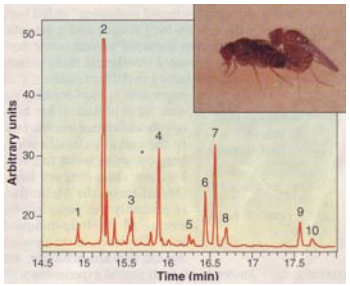


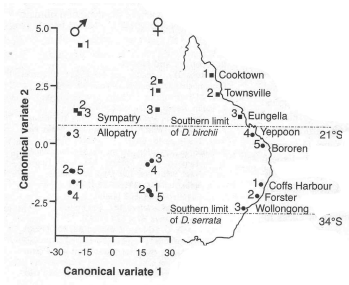
Reproductive Character Displacement

- Selection favors individuals that leave the most offspring
- Hybridization lowers fitness
- Strong evidence for character displacement in mate recognition characters
- Reinforcement (A.R. Wallace)

Higgie et al. 2000. 20 Oct. Science.

- *D. birchii* in north
- *D. serrata* in south
- Differences in cuticular hydrocarbons accentuated at contact zone
- This result was repeated in lab experiments that combined undisplaced flies from N & S extremes of range.
- Undisplaced flies produce viable/fertile hybrid offspring
- Reproductive character displacement in hydrocarbons developed in just 9 generations!





Possible consequences of secondary contact:

1)

2)

3)

4)