Lecture 24. Speciation Mechanisms

EEB 2245, C. Simon

25 April 17

Last time …

- DNA barcoding (finish species concepts)
- Speciation mechanisms
  - Spatial/Temporal vs Mechanistic Categories
  - Allopatric vicariance vs peripheral isolate
  - Founder event speciation
  - Butlin et al. 2008 temporal framework for speciation
  - Consequences of secondary contact
  - Reproductive character displacement
  - Concept of Reinforcement

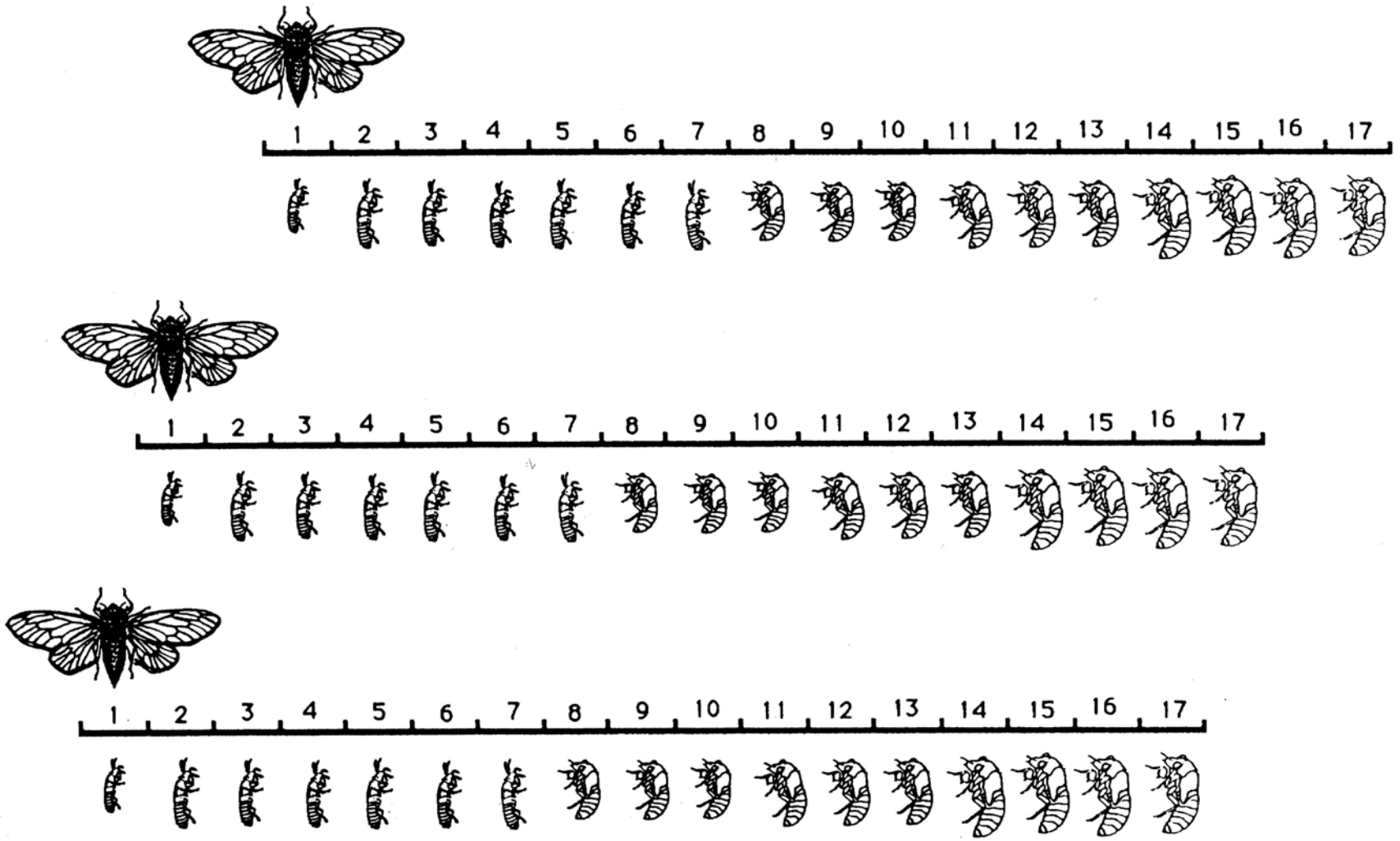
This time …

- *Magicicada* case study
- Parapatric speciation
- Divergence with gene flow
- Sympatric speciation
- Host race speciation
- Chromosomal speciation (with and without polyploidy)
- Polyploid speciation (with and without hybridization)

Case Study:

Allochronic speciation, reproductive character displacement and reinforcement in 13- and 17-year periodical cicadas (Decim group)

Reproductively isolated year classes called broods.



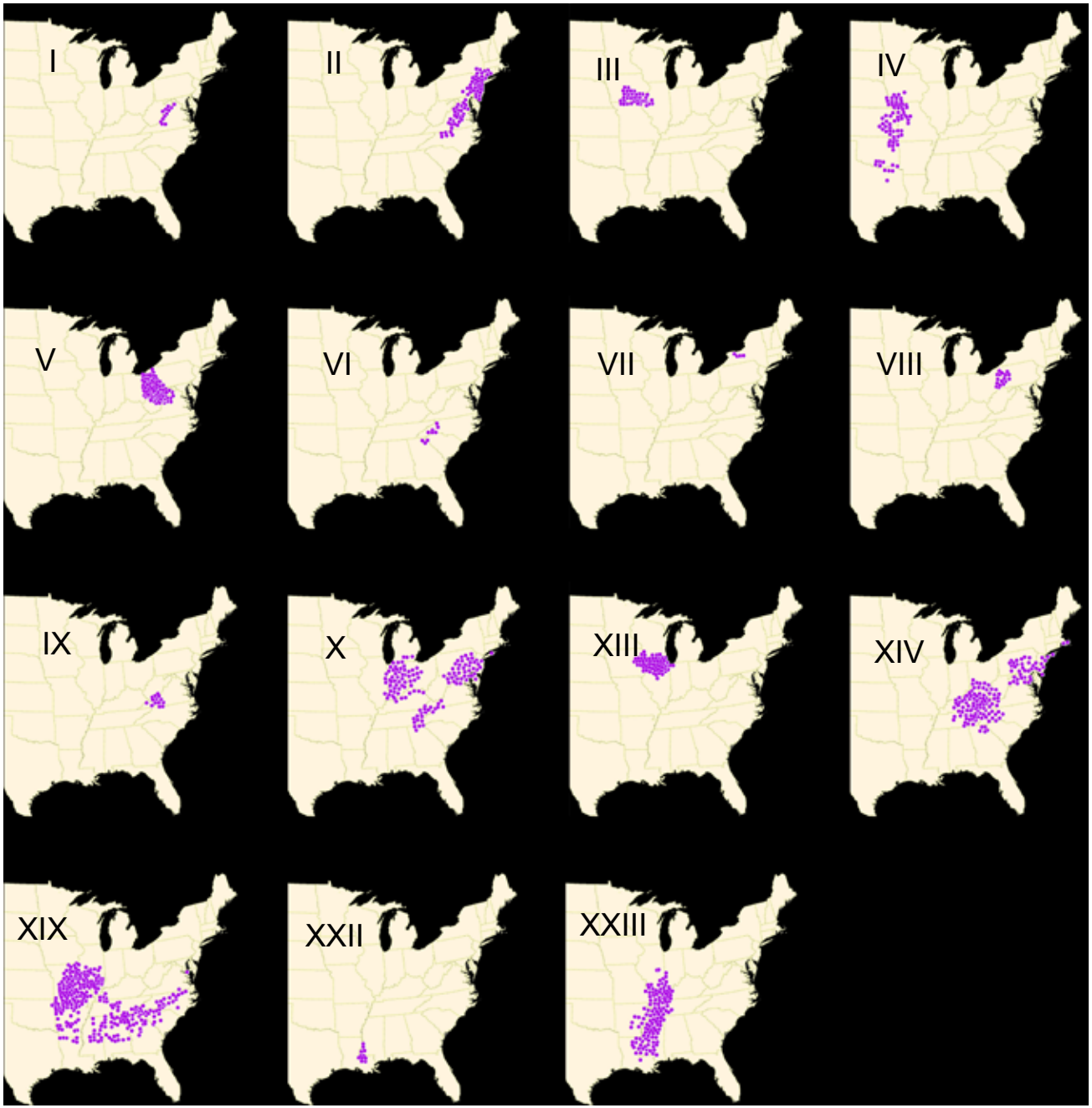
Broods

17-year

I-XVII

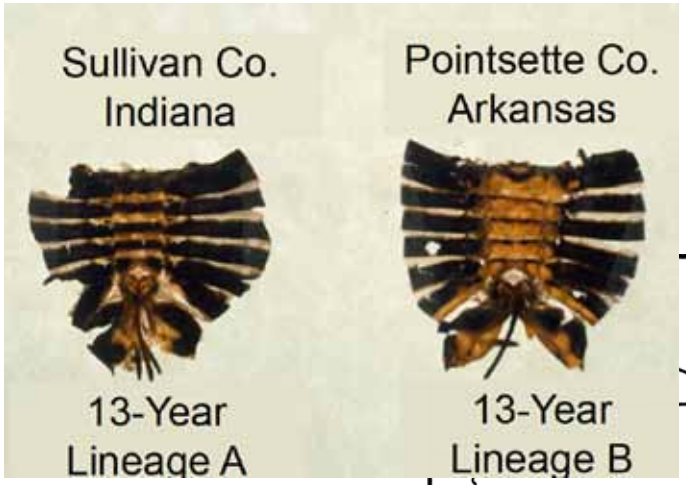
13-year

XVIII- XXX

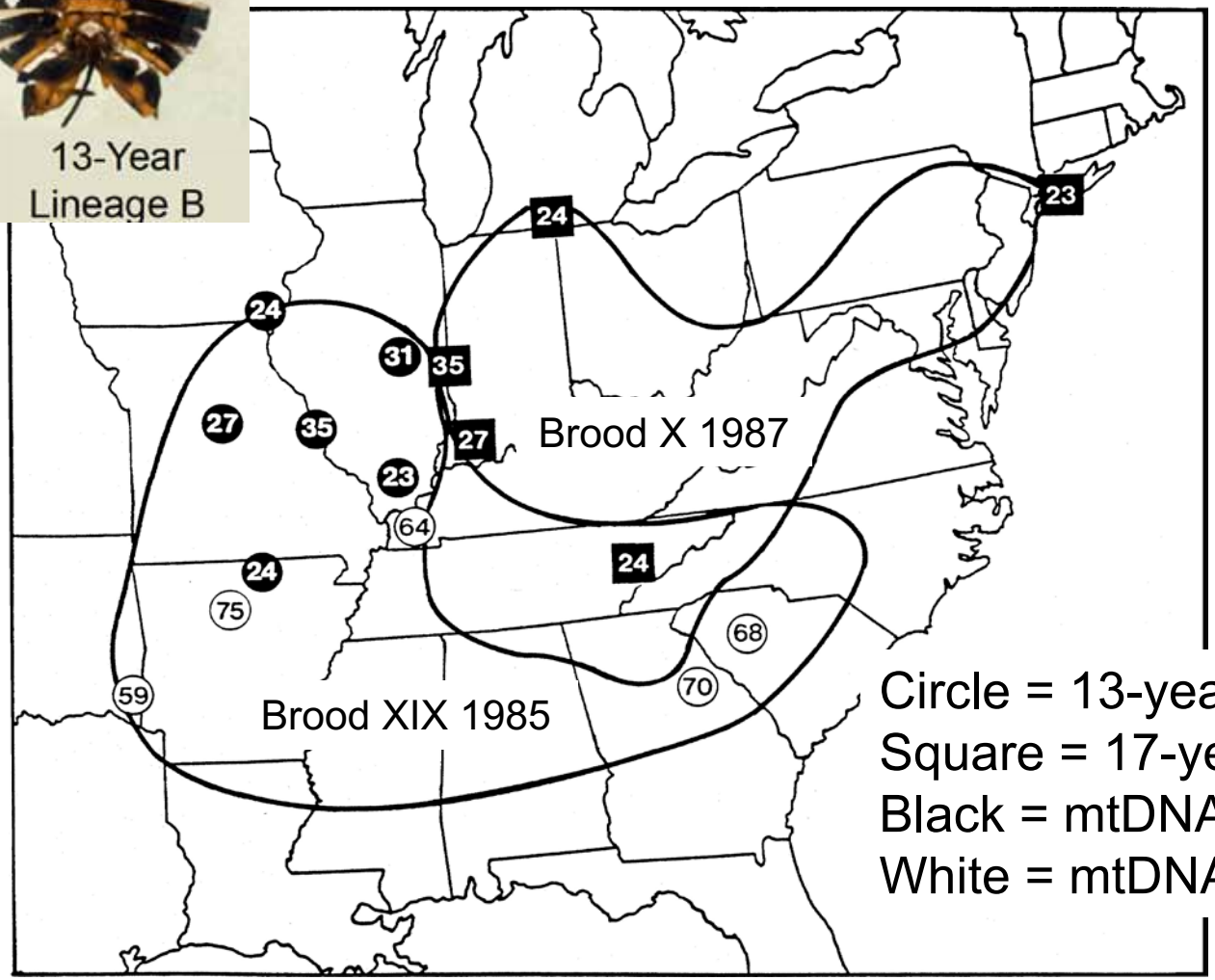


Marlatt 1907, Simon 1988

Martin & Simon. 1988. 1990.
Surveyed largest 17-yr brood (X)
& Largest 13-yr brood (XXIII)



Low numbers
= blacker
High numbers
= oranger

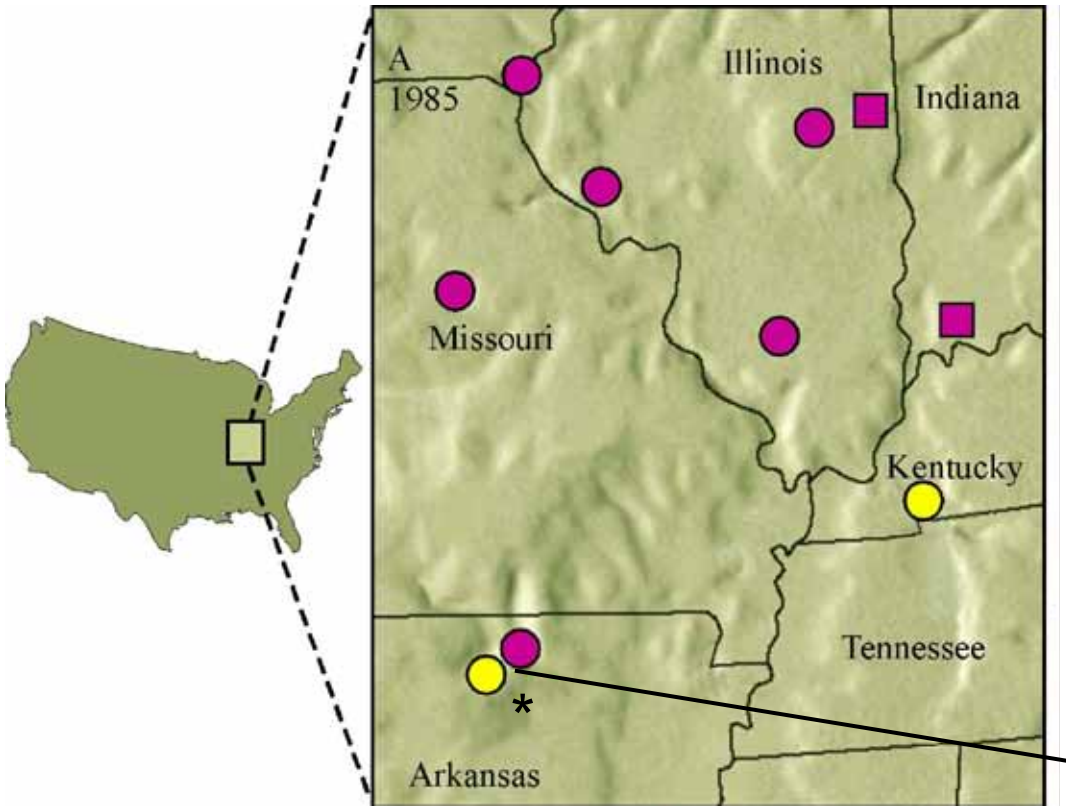


Circle = 13-year
Square = 17-year
Black = mtDNA A
White = mtDNA B

Two mtDNA lineages …..

Purple = lineage A; Yellow = lineage B

Brood XIX

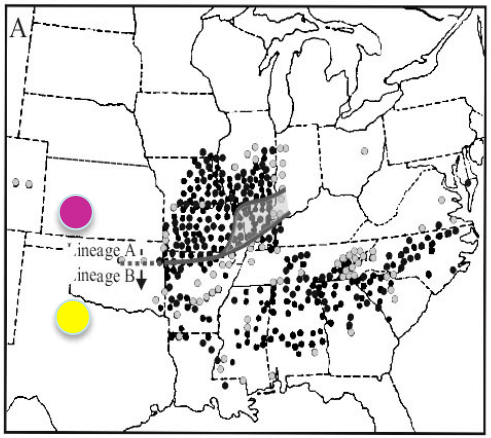


Square = 17-yr life cycle
Circle = 13-yr life cycle

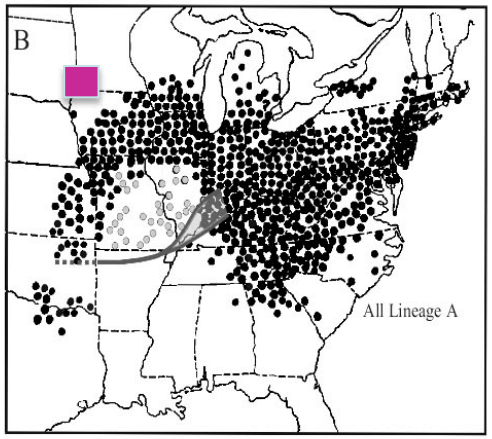
We did not search for a contact zone in Brood XIX because we were not expecting to find one.

Hardy Co., Arkansas

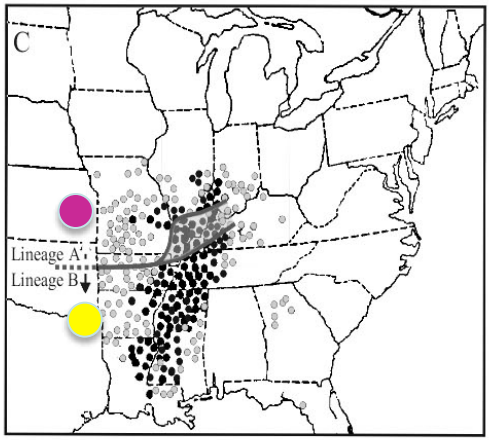
Martin & Simon1988, Nature;
Martin & Simon 1990, Evolution



13-year
Brood XIX



All 17-year
Cicadas



13-year
Brood XXIII

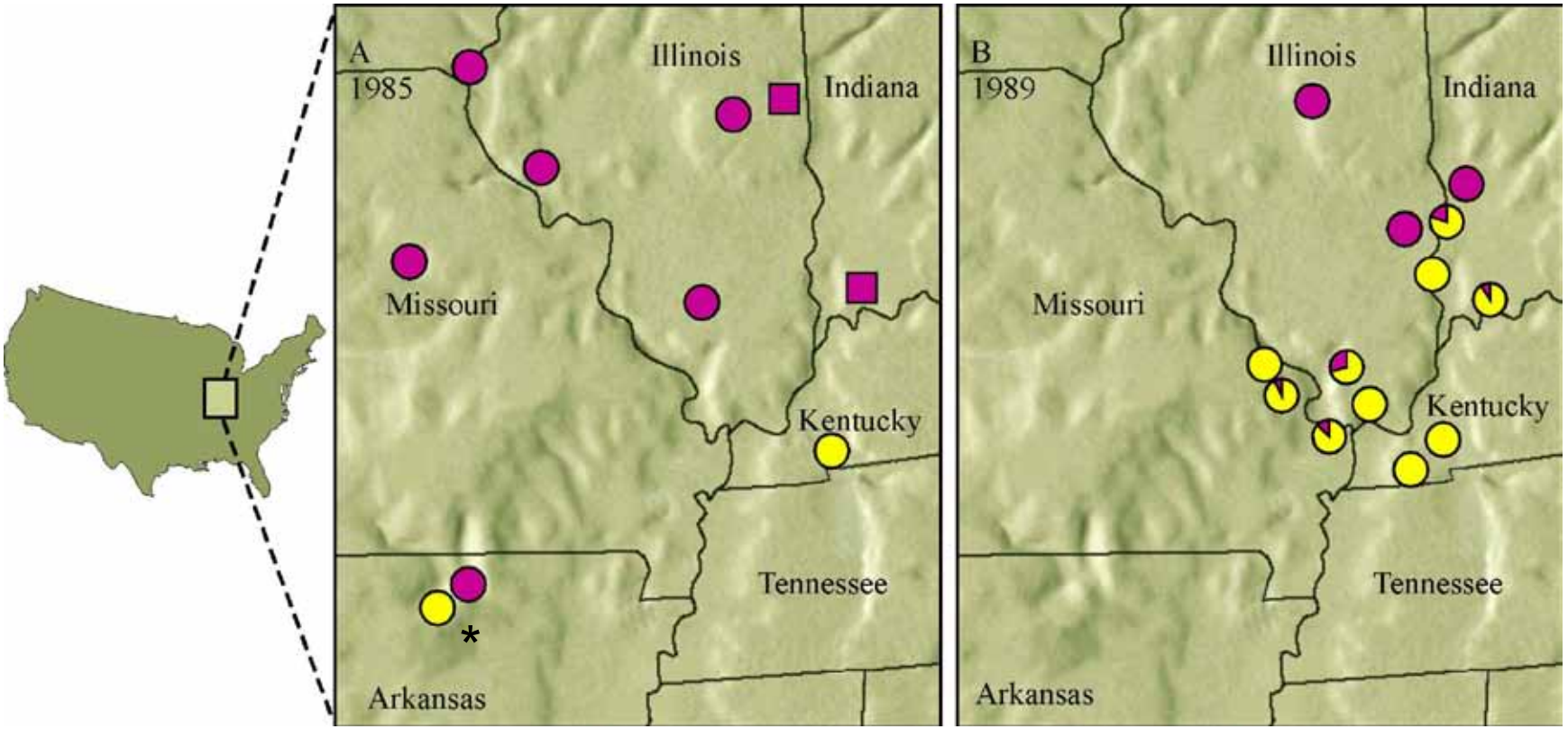
Both of the large 13-year cicada broods have populations that fill a hole in the distribution of 17-year cicadas.

We wondered if Brood XXIII had the same northern mtDNA lineage with black striped abdomen color.

Brood XIX

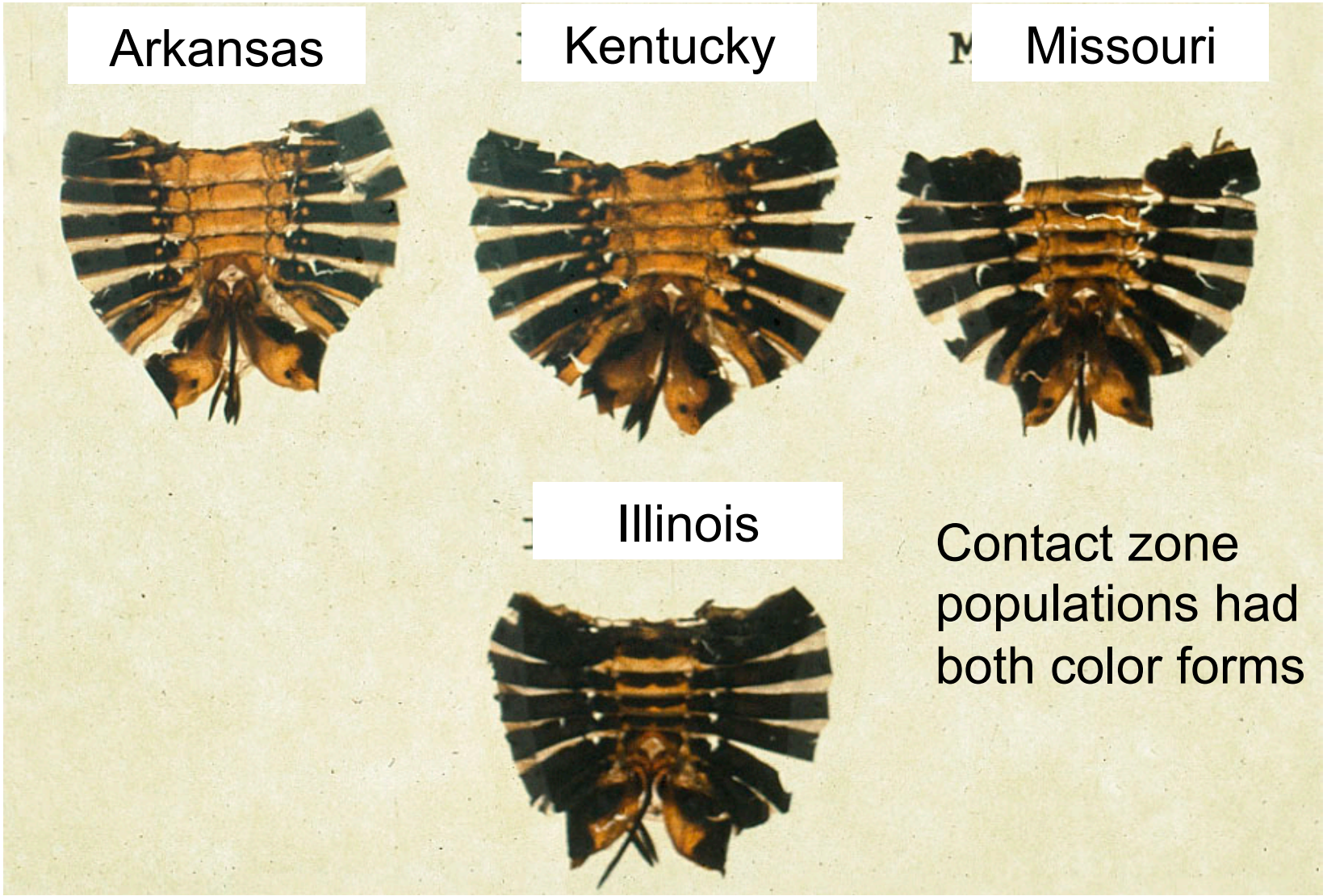
Brood XXIII

Purple = lineage A ; Yellow = lineage B



Four years after we found the two mtDNA types in Brood XIX, We surveyed Brood XXIII and found northern lineage A, southern lineage B, and a contact zone with both mtDNA types.

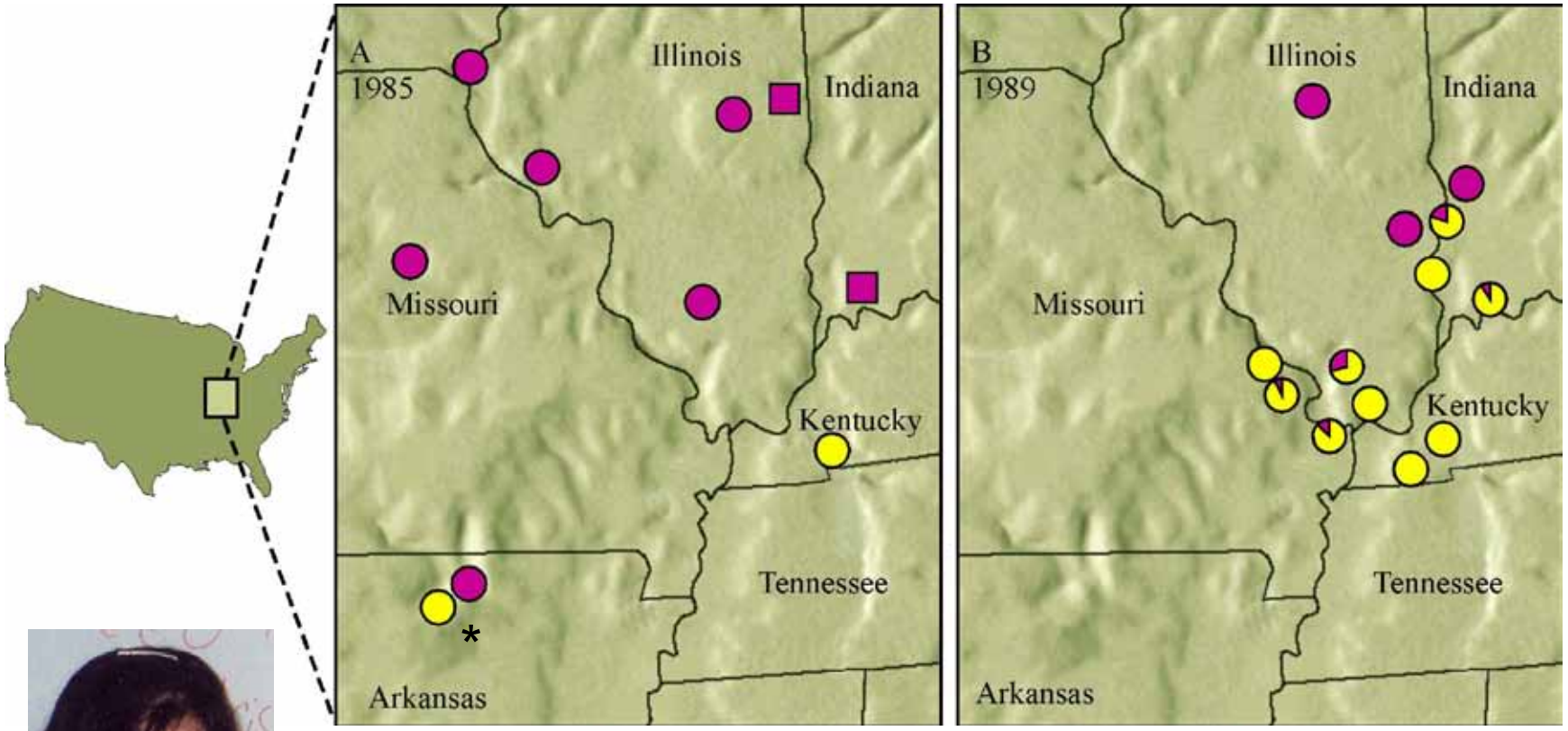
13-yr cicada orange (south) black abdomen color (north).



Brood XIX

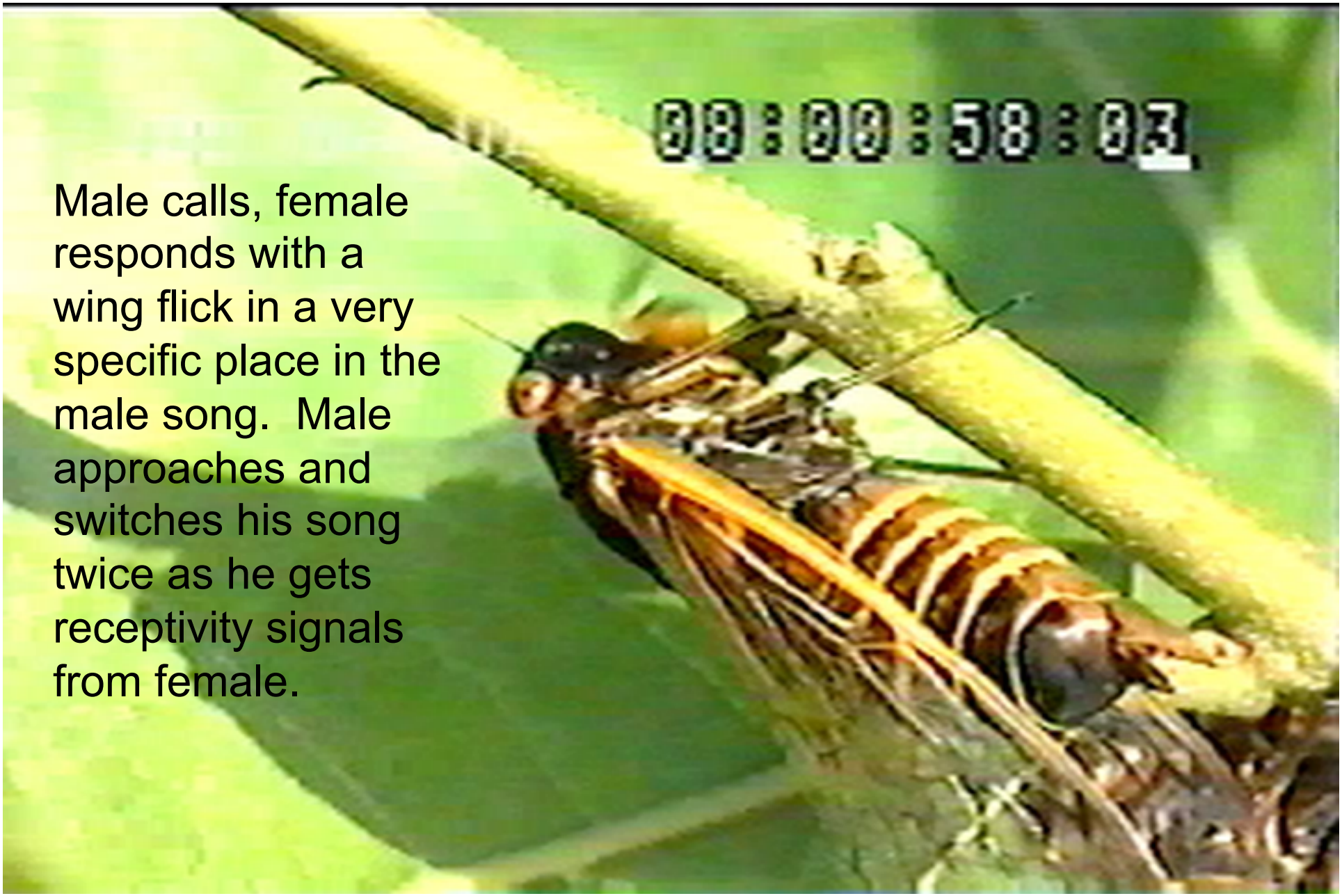
Brood XXIII

Purple = lineage A ; Yellow = lineage B



Sejal Dalwadi

We predicted random mating in mixed lineage populations… but mating was assortative! Simon et al. 2000.

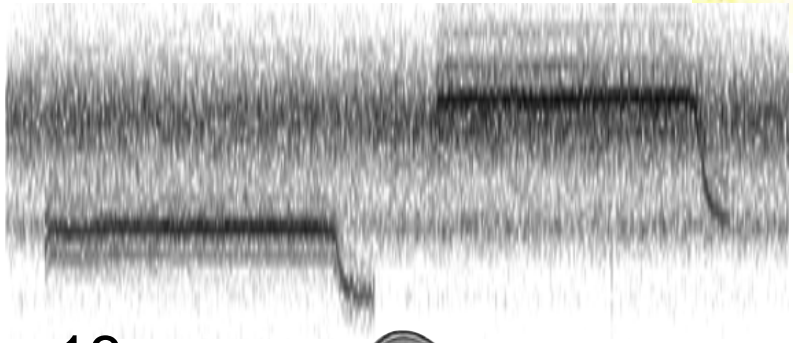


Japan TV Network

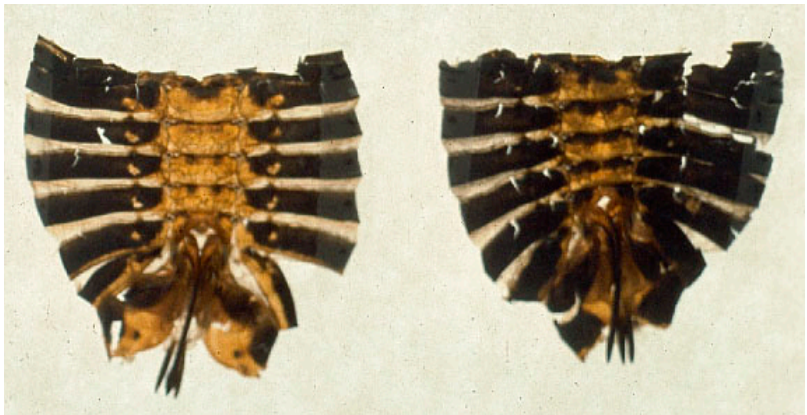
John Cooley &
David Marshall

Normal 17-year

Displaced higher
than 17-year



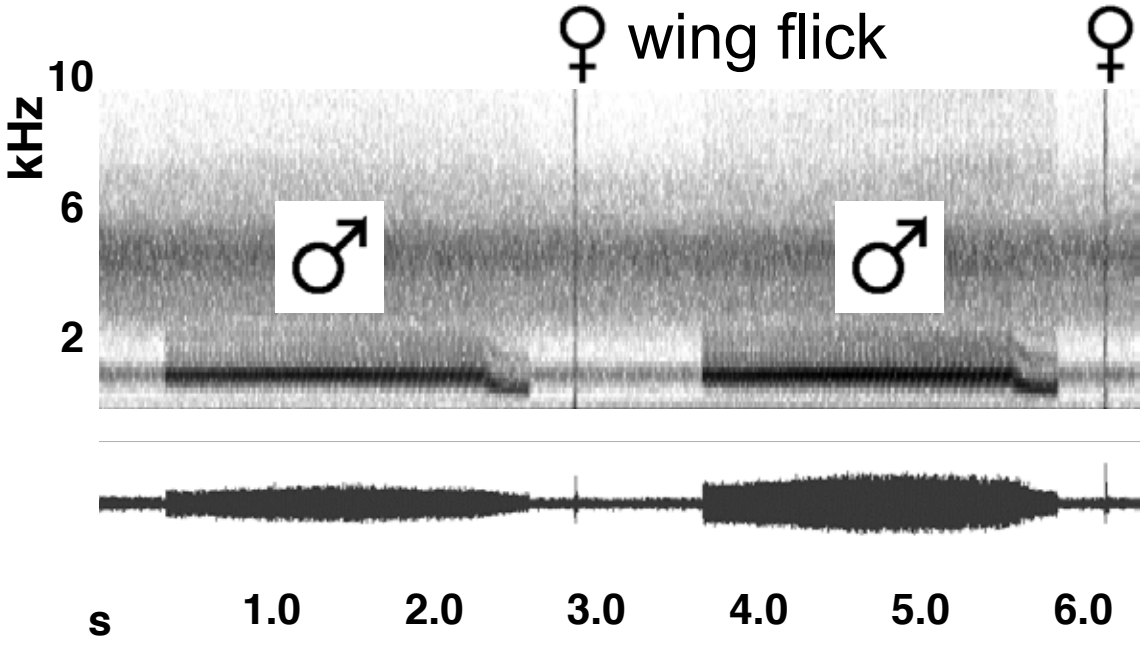
13-year



Marshall & Cooley. 2000. Evolution.

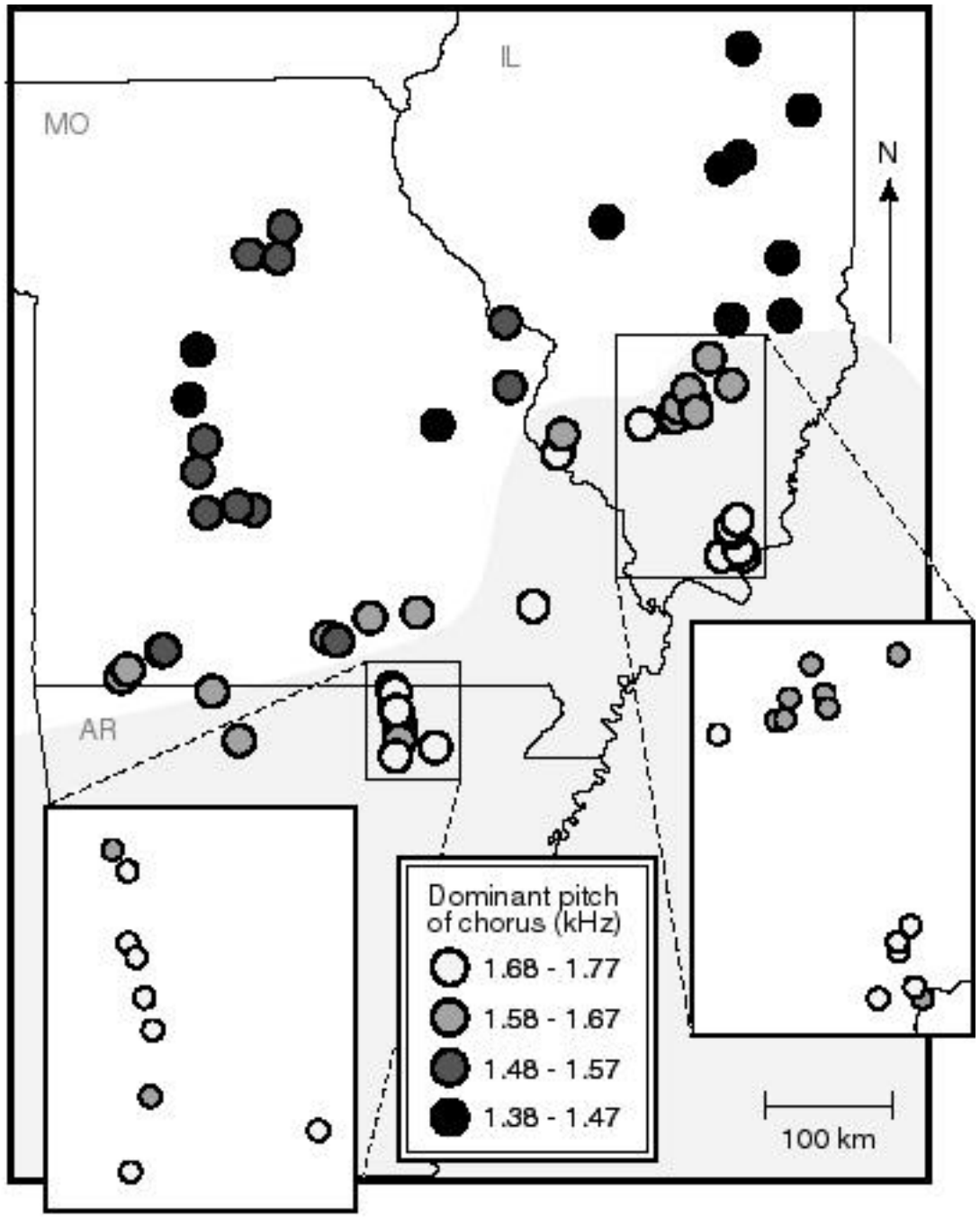
Females respond in a specific place in male song:

Magicicada neotredecim

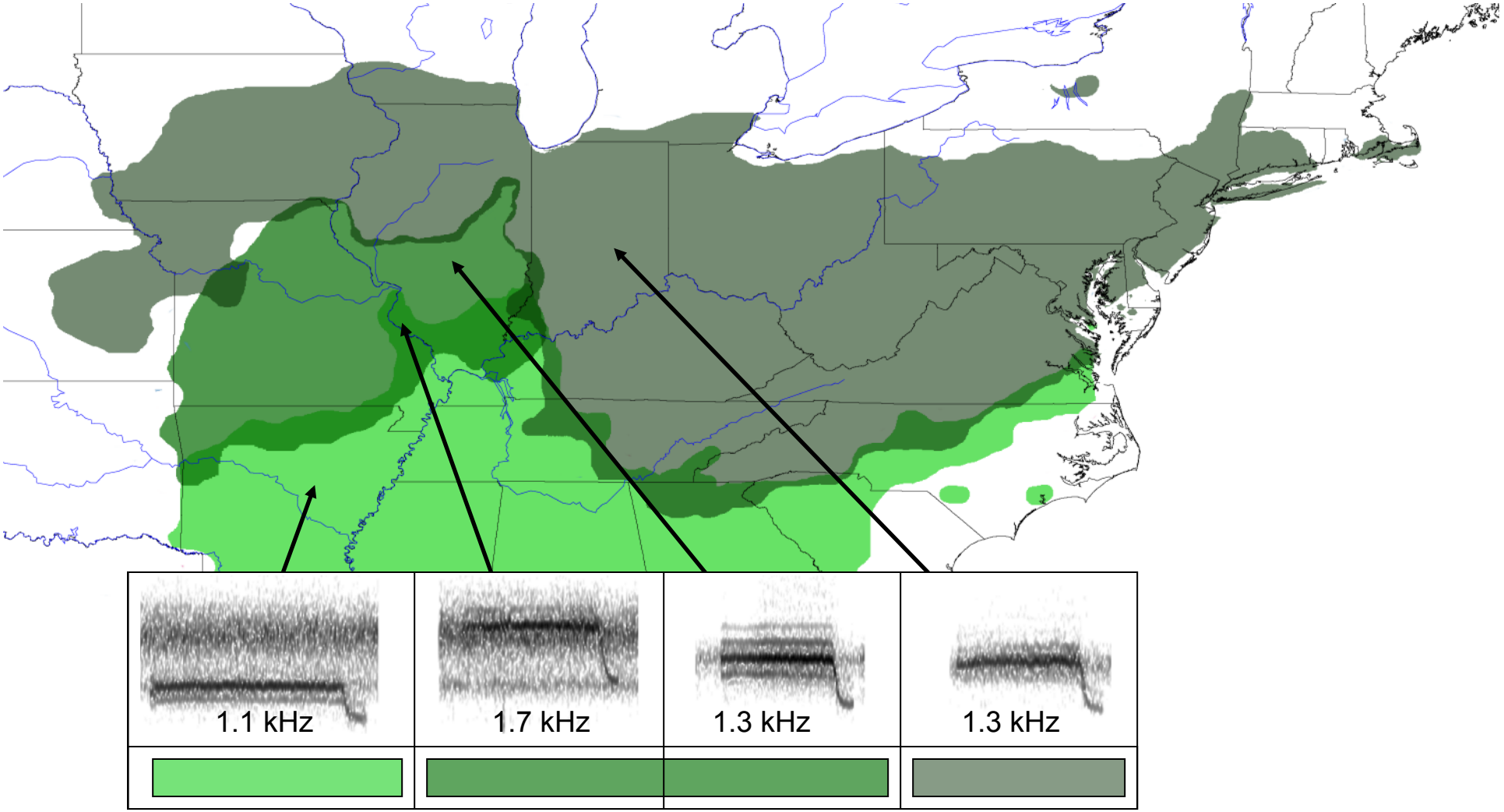


Magicicada decim species are unusual in having 3 courtship songs

Evidence for character displacement



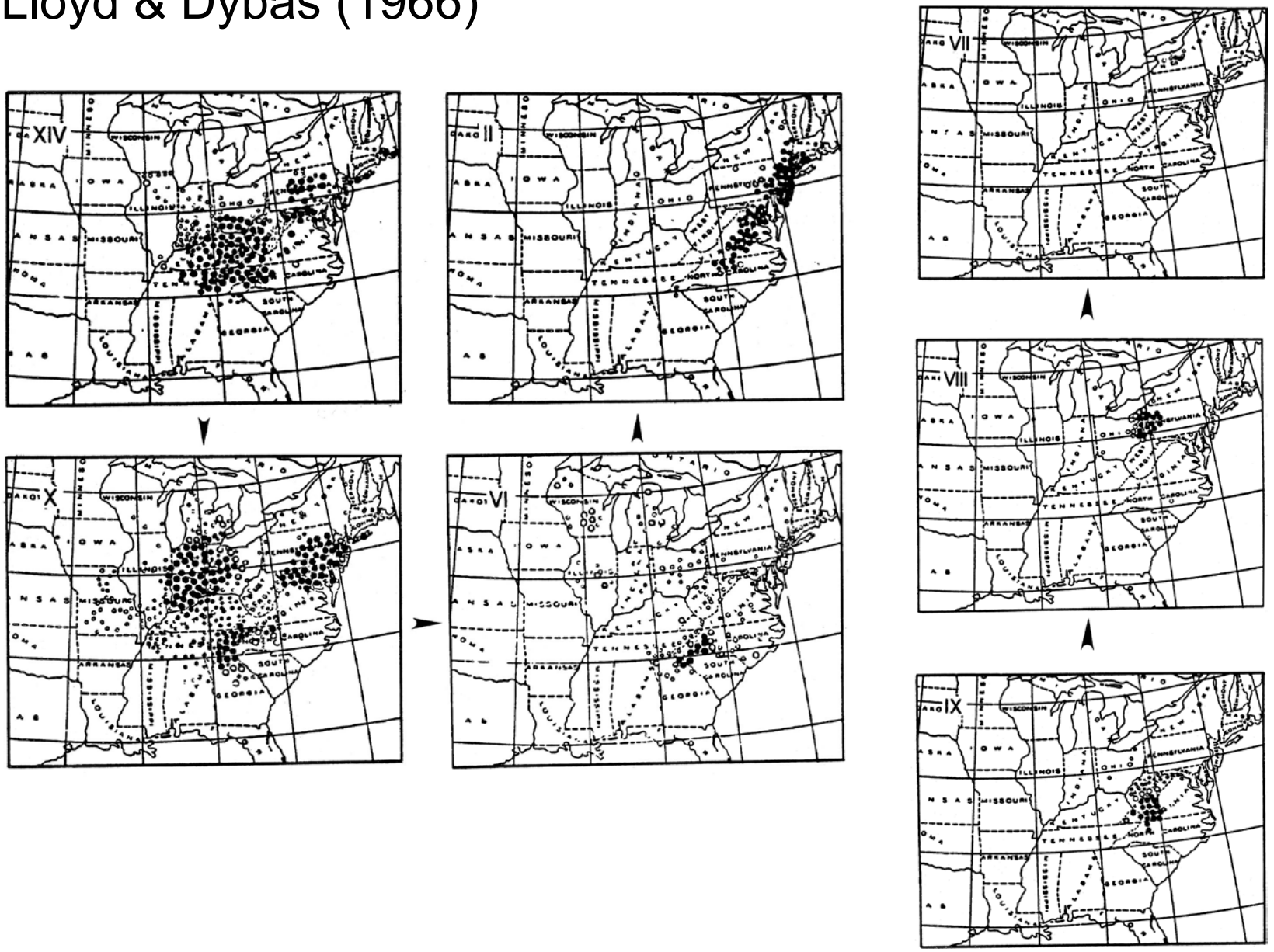
Reproductive character displacement in *Magicicada*



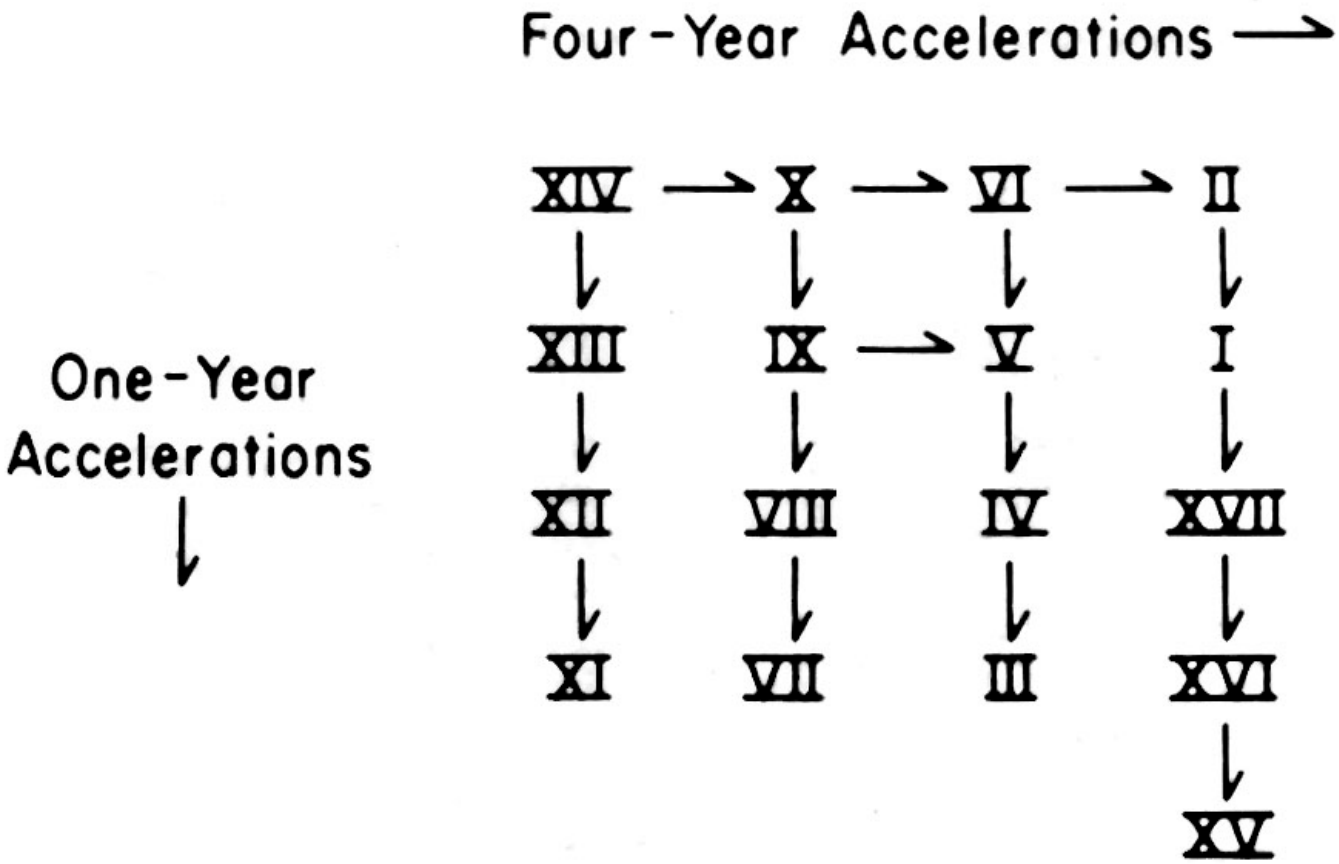
M. tredecim *M. neotredecim** *M. septendecim*

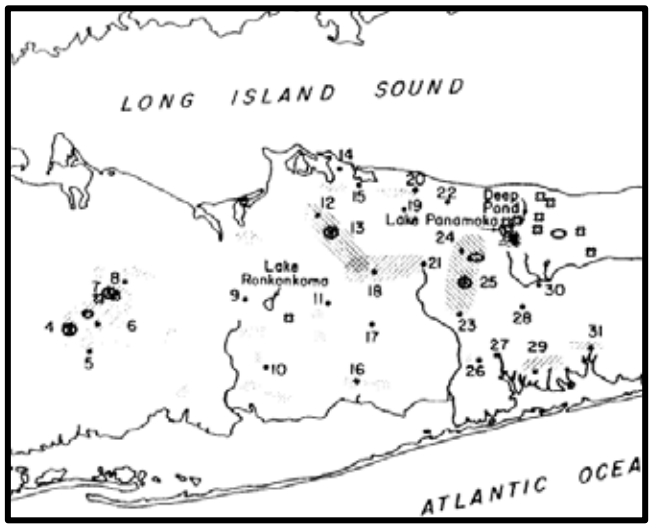
* A new species: life cycle switching resulted in parapatry.

Lloyd & Dybas (1966)



Lloyd and Dybas (1966) scheme for the evolution of the 17-year broods





Long Island Scenario

Four Years Early →

One Year Early ↓

XIV	→	X	→	VI	→	II
↓		↓		↓		↓
XIII		IX	→	V	→	I
↓		↓		↓		↓
XII		VIII		IV		XVII
↓		↓		↓		↓
XI		VII		III		XVI

Lloyd & Dybas (1966) modified
Simon & Lloyd (1982), Simon et al. 1981.

Magicicada.org Crowd-Sourced Records, GIS mapping

magicicada.org

www.magicicada.org/magicicada_2014.php

Periodical cicadas
@www.magicicada.org

May 8, 2014

- Maps and Information (media kit)
- Species
- Broods
- Behavior
- F.A.Q.
- About the project
- Geospatial Data
- Citizen Science Projects using cicadas
- Links
- Contact...

2014 will be an exciting year for periodical cicadas. 13-year Brood XXII, the Lower Mississipian Brood, will emerge in April and May. Then, 17-year Brood III, the Iowan Brood, will emerge in Iowa and north western Illinois.

The 2014 emergence of periodical cicadas will be extraordinary. First, 13-year Brood XXII will emerge in the Lower Mississippi River Valley. This brood contains *Magicicada tredecim*, *M. tredecassini*, and *M. tredecula*. Adults of Brood XXII are expected to start emerging in the Baton Rouge area in late April.

In Mid- to late May, 17-year Brood III will emerge in Iowa and north western Illinois. *Magicicada septendecim*, *M. cassini*, and *M. septendecula* are all found in this brood. Brood III occurs in close proximity to 13-year Brood XIX, and the stability of the boundary of these broods has been a topic of considerable research interest.

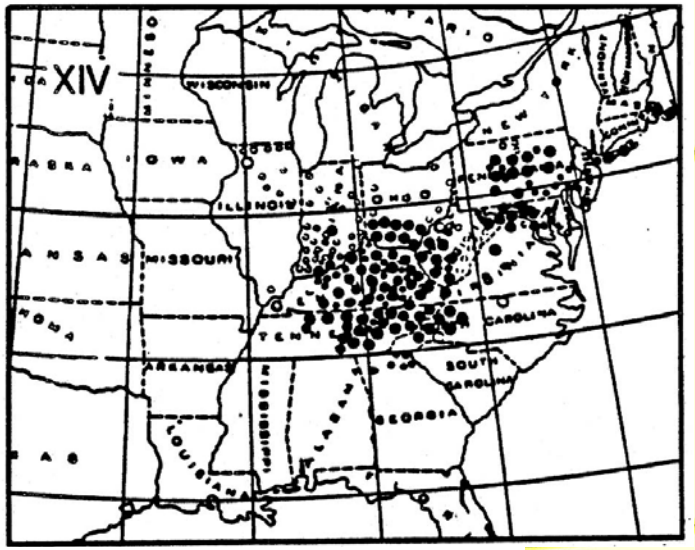
Brood III was mapped in detail in 1997, and 2014 will allow

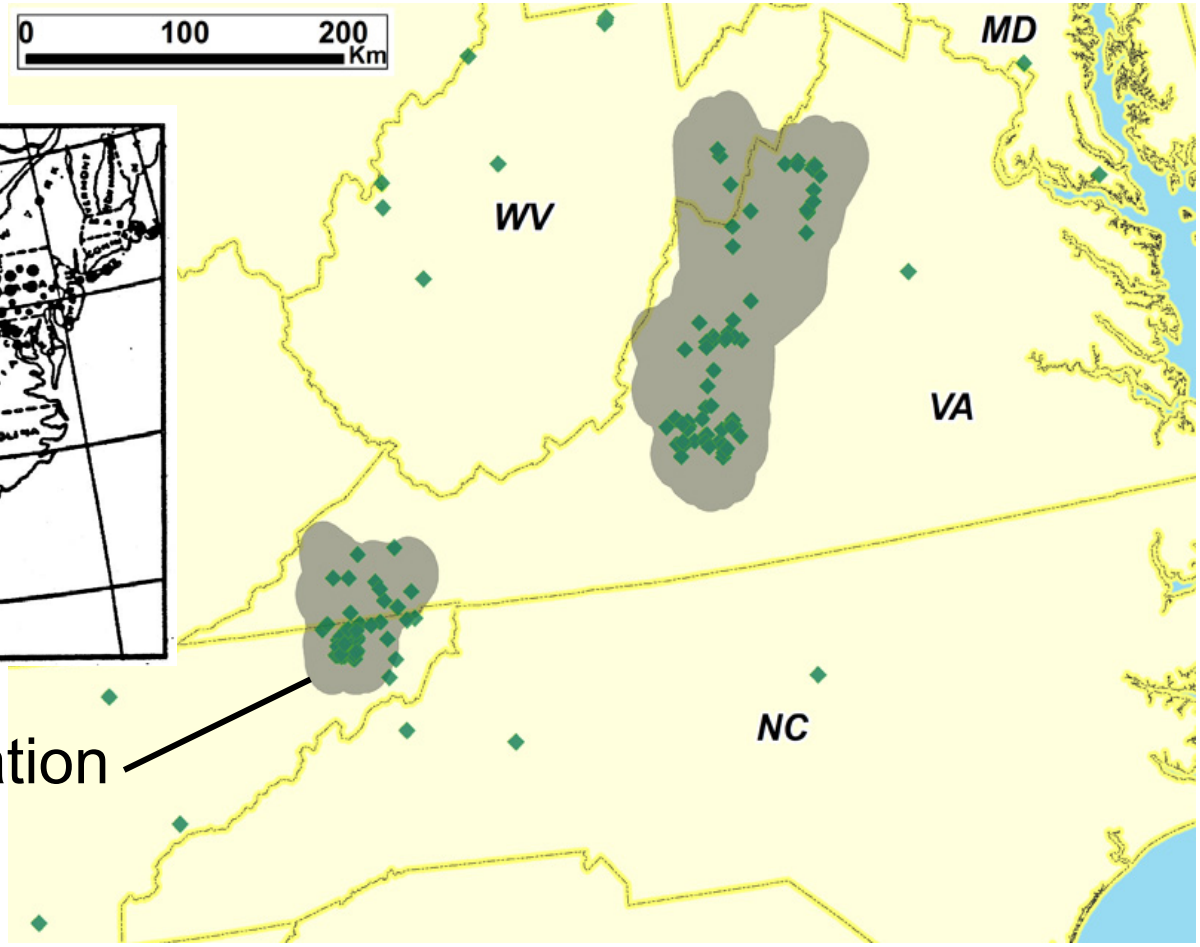
Periodical Cicada Maps

Report 2014 emergences here

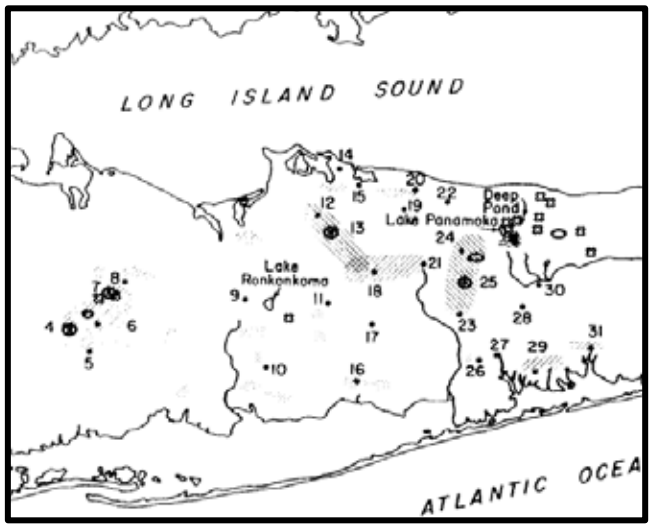
2014 sightings

Brood I, 2013, 1996, 1979, 1962 ….
Cooley, 2015. Amer. Entmol.

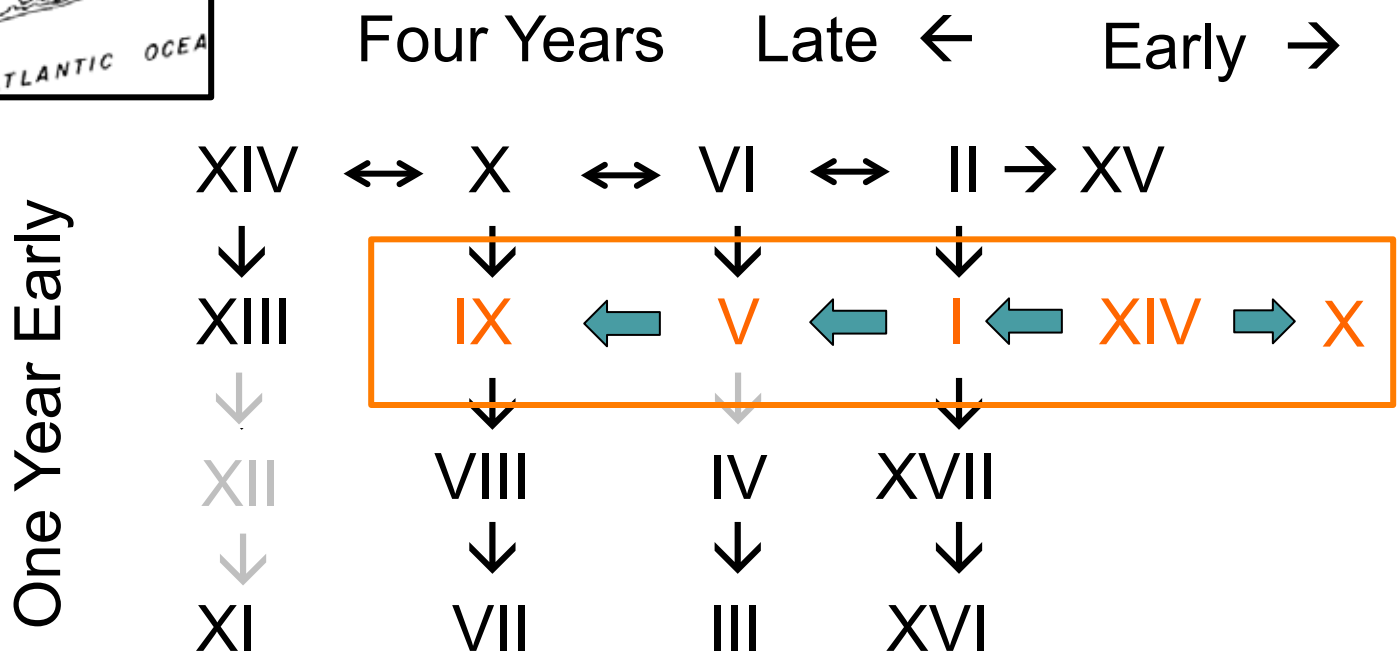




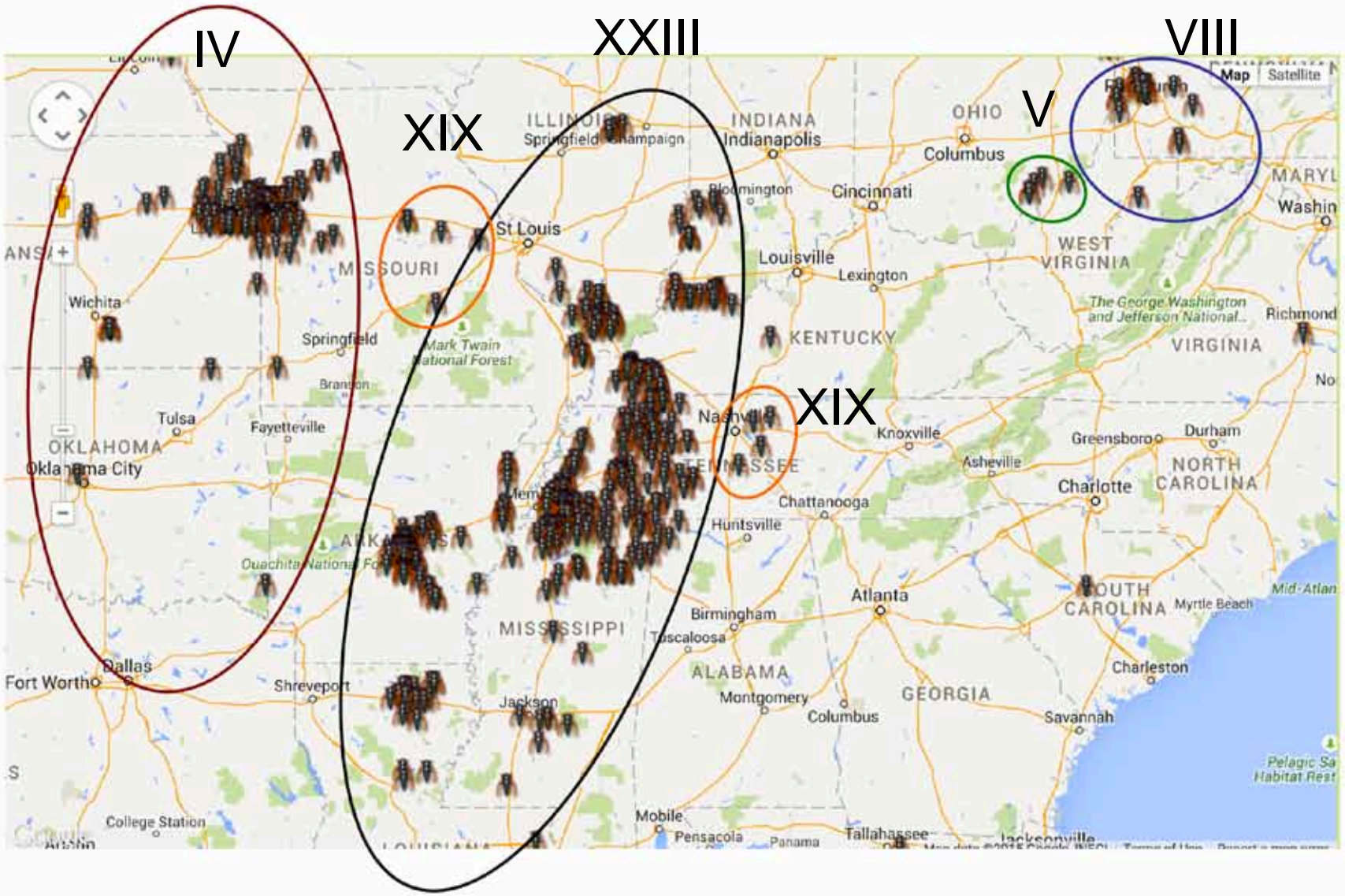
Disjunct population surrounded by Brood XIV … four years late?



Revised Long Island Scenario
Emphasizing late emergences.



Lloyd & Dybas (1966) modified
Simon & Lloyd (1982), Simon et al. 1981.



www.magicicada.org, 26 May 2015, Brood XXIII, and Brood IV plus 4-yr early Brood VIII in PA and 1-yr early Brood V in Ohio. And 4-yr late Brood XIX in TN.

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.

Parapatric Speciation (cont.)

- Alternatively, genetic isolation can be due to interactions between two gene loci where certain allele combinations are incompatible (e.g., male fitness and female choice genes).

- $A_1A_1B_1B_1$ ancestor→ $A_1A_1B_2B_2$ and $A_2A_2B_1B_1$ individuals where $A_2A_2B_2B_2$ sterile (Dobzhansky-Mueller Interactions). (Futuyma, pg 476).

Parapatric Speciation

Remember….In some cases—when subpopulations do not differ enough in mating system--character displacement does not evolve, rather subpopulations merge back together and speciation does not occur.

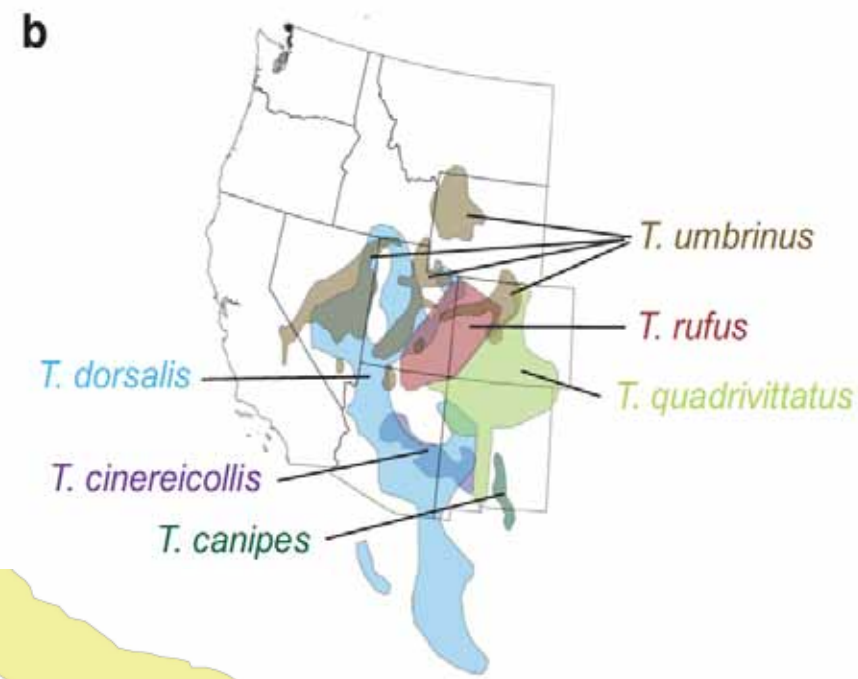
In other cases, divergence occurs even with gene flow; this divergence will be slower than that in complete isolation.

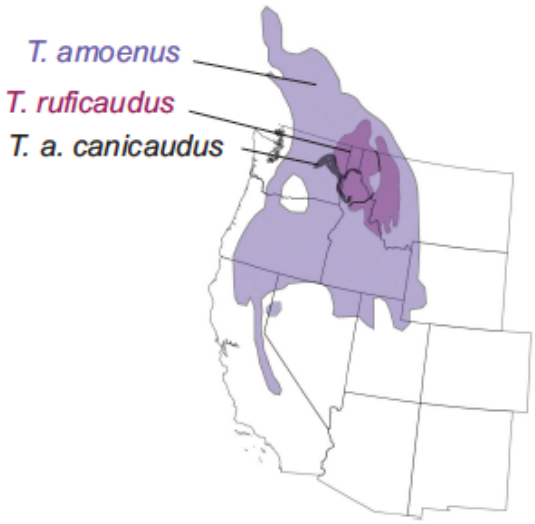
More and more cases have been discovered.

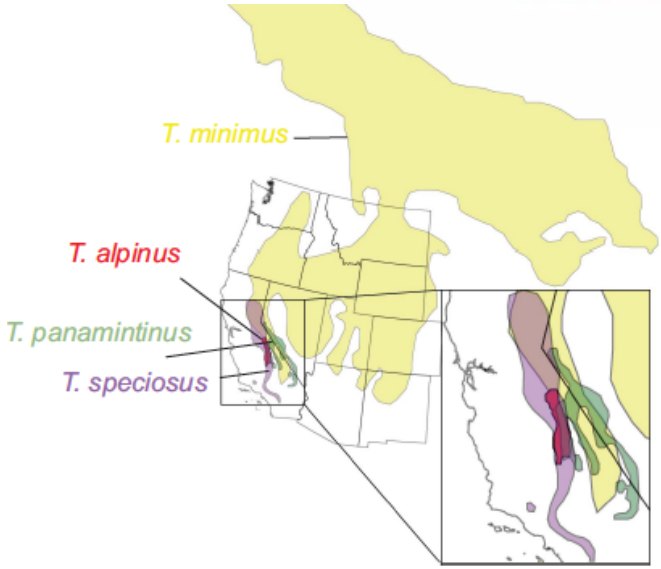
Divergence with gene flow in *Tamias* chipmunks

Sullivan, Demboski, Bell, Hird, Sarver, Reid and Good. 2014. Heredity.

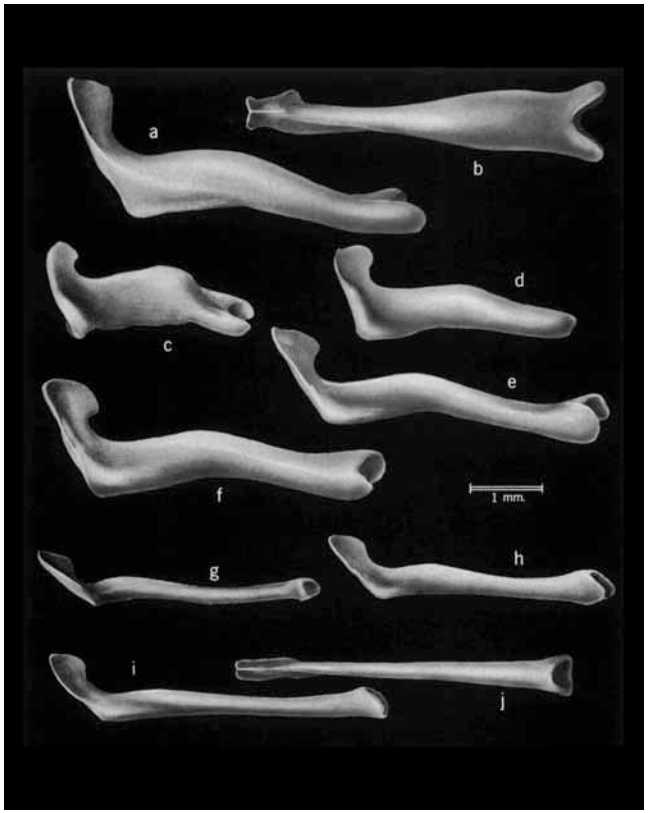
13 Species in western US



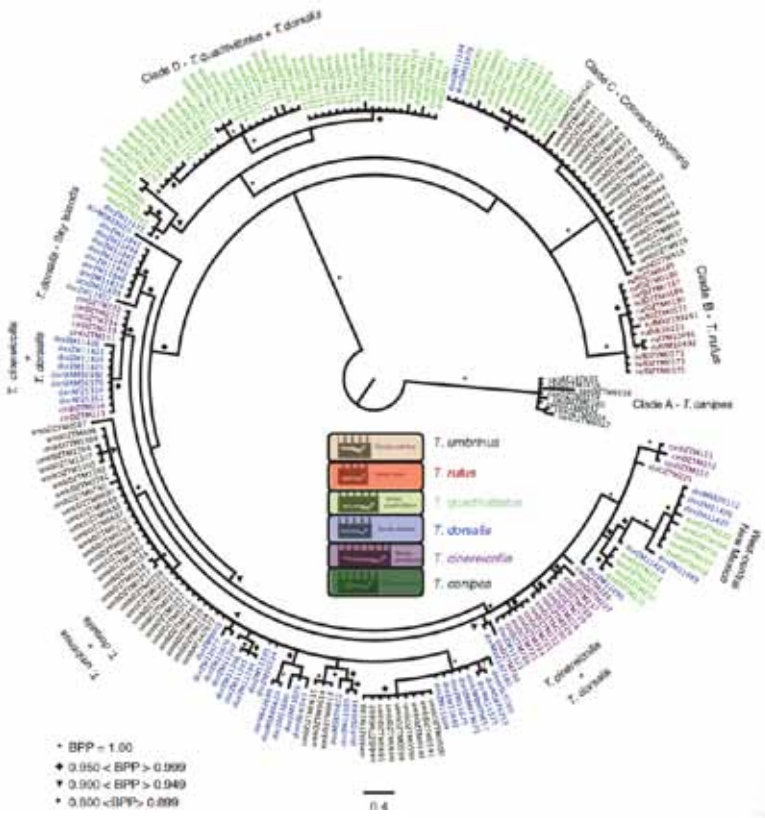




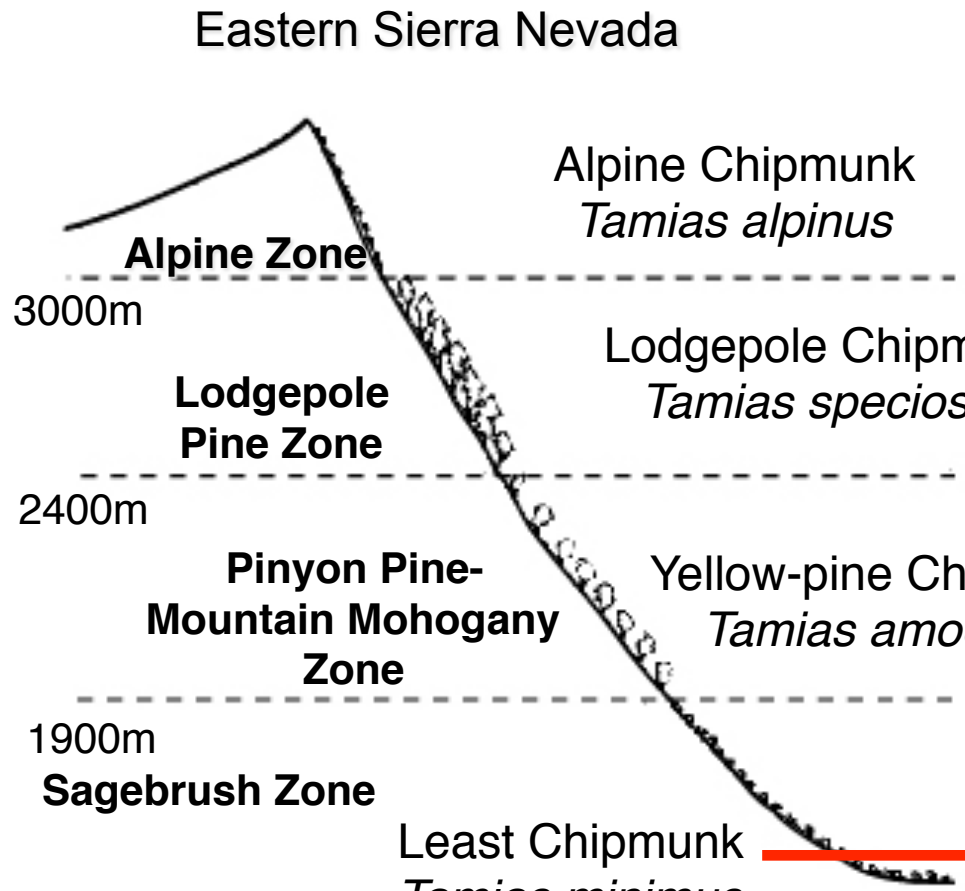
Identification based on trait important in reproduction; extensive geographic sampling including contact zones
Nuclear DNA and mtDNA



Chipmunk Bacula
(male genital bones)



Conspicuous Examples of Niche Partitioning w altitude



Alpine Chipmunk
Tamias alpinus

Lodgepole Chipmunk
Tamias speciosus

Yellow-pine Chipmunk
Tamias amoenus

Least Chipmunk
Tamias minimus

(Modified from Chappel, 1978)

Findings: Divergence-with-Gene-Flow in *Tamias*

Early divergence (~0.325 MY)
Lots of introgression – mtDNA & Nuclear

T. r. ruficaudus X *T. r. simulans*


Intermediate divergence (~0.62 - 1.7 MY)
Lots of mtDNA introgression, hints of Nuclear?

T. quadrivittatus group




Strong divergence (~2.7 MY)
Current mtDNA introgression, almost no Nuclear

T. r. ruficaudus X *T. a. luteiventris*


Complete isolation (>2.7 MY)
Ancient mtDNA introgression.
Completion of reproductive isolation.

T. a. canicaudus X *T. r. simulans*


Conclusions of Sullivan Lab Chipmunk Studies:

1) There numerous independent introgressions in the *Tamias* radiation, and these occur across a range of divergence times.

2) In at least one of these events, hybridization may have given rise to a new species.

3) There appears to be an attenuation of gene flow with increasing divergence.

4) Nuclear gene flow attenuates much more quickly than mtDNA gene flow.

Divergence with Gene Flow

1) Hybridization is expected.

   It may be substantial early in divergence and decrease with time since divergence.

   It may generate new species

2) Evidence of gene flow will differ across genome.

   Genes involved in species recognition may not show evidence of gene flow, even if other genes do.

Slide modified from Sullivan et al. 2014. Heredity

Sympatric Speciation

- Difficult to envision since sympatric populations overlap!
- Need extreme assortative mating and disruptive selection to eliminate any heterozygotes for mating genes (as in parapatric speciation)
- Current day overlap is not evidence for sympatric speciation. Most likely secondary contact.

Sympatric Speciation

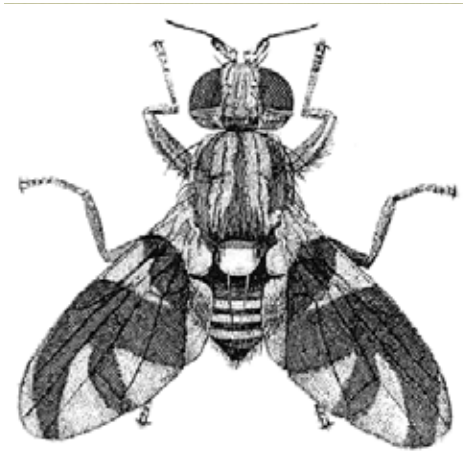
Best examples involve “host race speciation”

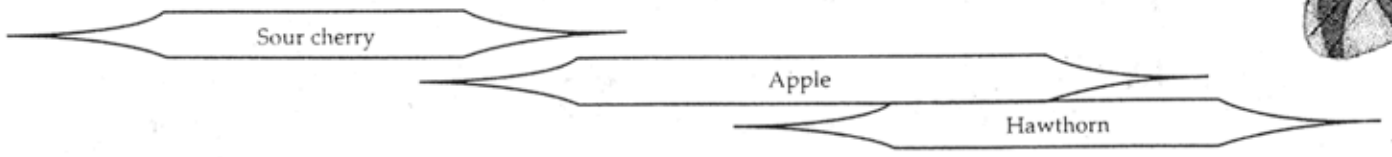
- True fruit flies (family Tephritidae) of the genus *Rhagoletis*. On native hawthorn vs. introduced cherry vs. introduced apple.
- *Enchenopa* Treehoppers. Distributed from Panama to S. Canada. Host races on seven genera of NE forest plants: walnut, black locust, bittersweet vine, viburnum, redbud,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

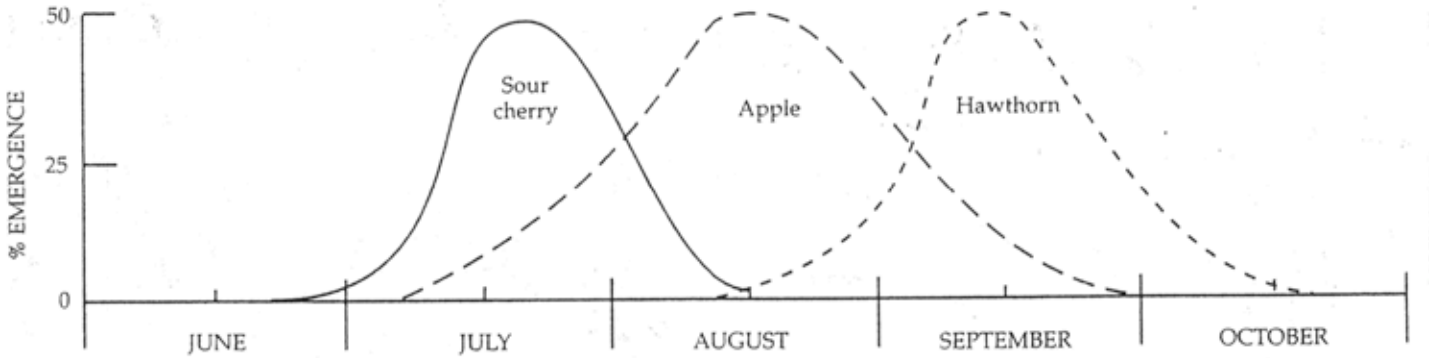
Micro-allopatric speciation? Allochrony involved.

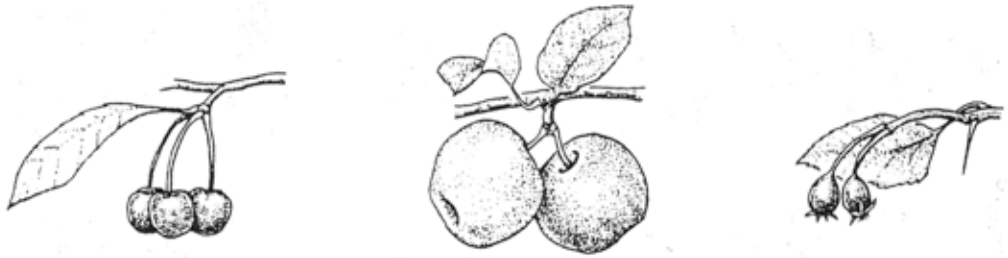
End of Lecture 24
25 Apr 17

Host races of *Rhagoletis pomenela*









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

Enchenopa tree hoppers: Tom Wood, U. Delaware

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

Criteria for defining host races

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

1a. Use different host taxa in the wild.

1b. Individuals exhibit fidelity to particular hosts.

2. Coexist in sympatry w/ other races (at least in part)

3a. Are genetically differentiated at more than one locus.

3b. More genetically similar to distant populations on the same host than to sympatric populations on different hosts.

4a. Display a correlation between host choice and mate choice.

4b. Undergo actual gene flow (hybridization/backcrossing) at an appreciable rate (≥1% per generation).

5a. Have higher fitness on natal than alternative hosts; and

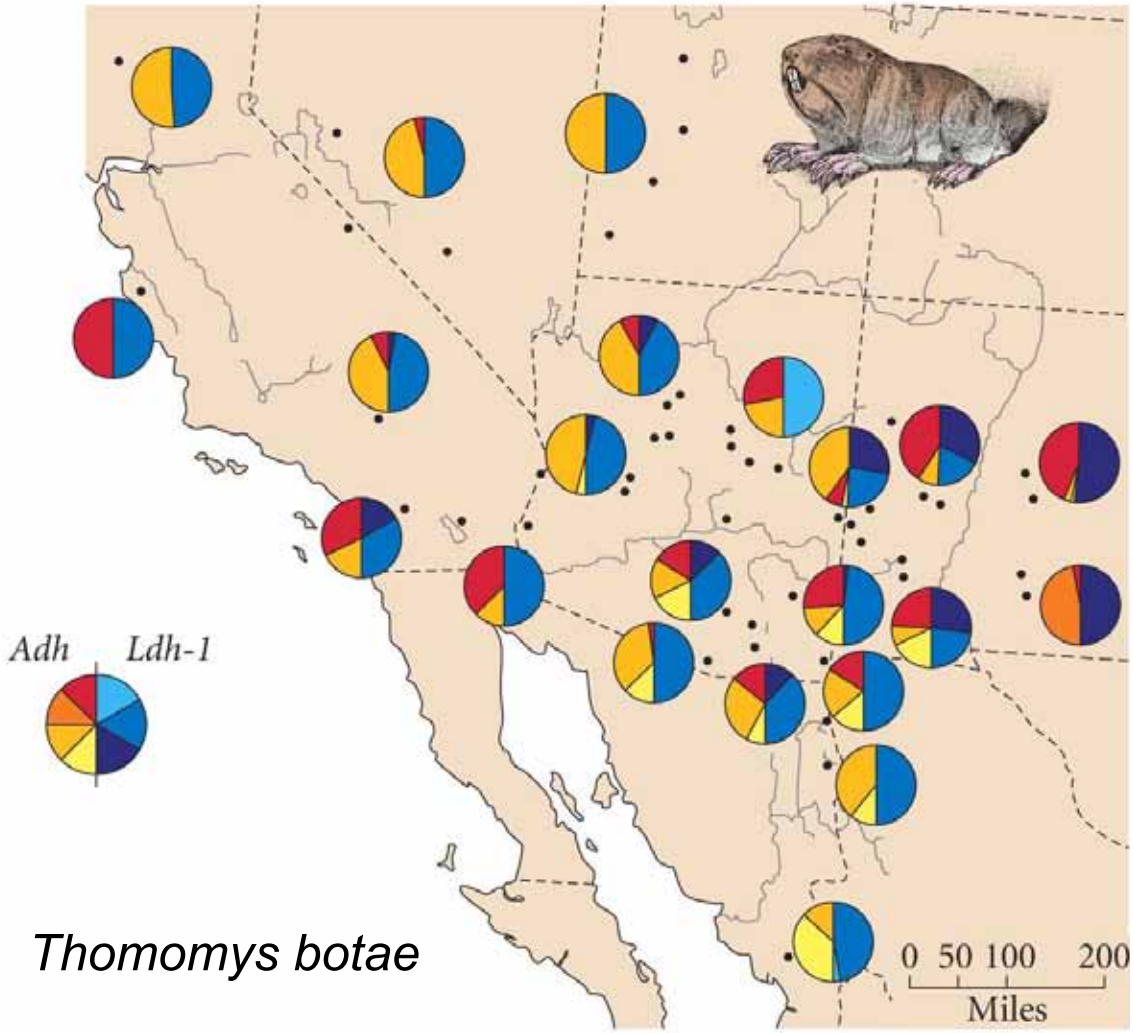
5b. Produce hybrids that are less fit than parental forms.

Spatial speciation is not instantaneous

Chromosomal Speciation

- Can be instantaneous
- Involving chromosomal rearrangements
- Involving polyploidy (with and w/o hybridization)

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



Thomomys botae

Nearby localities differ strongly in allele frequency.

Gene flow low.

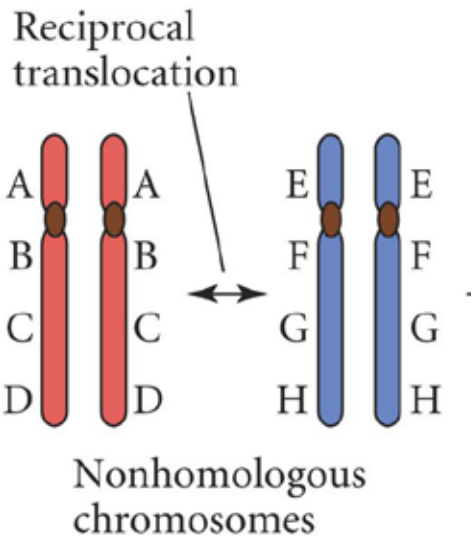
Populations small.

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

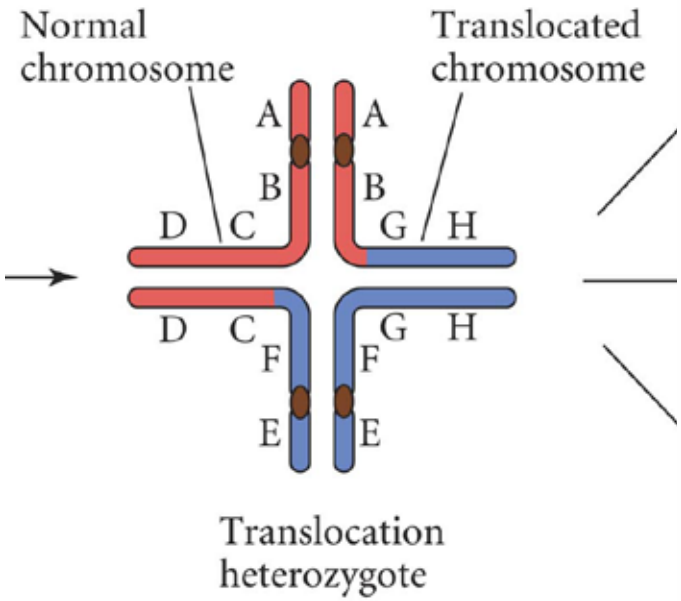
> 150 named subspecies.

Futuyma text

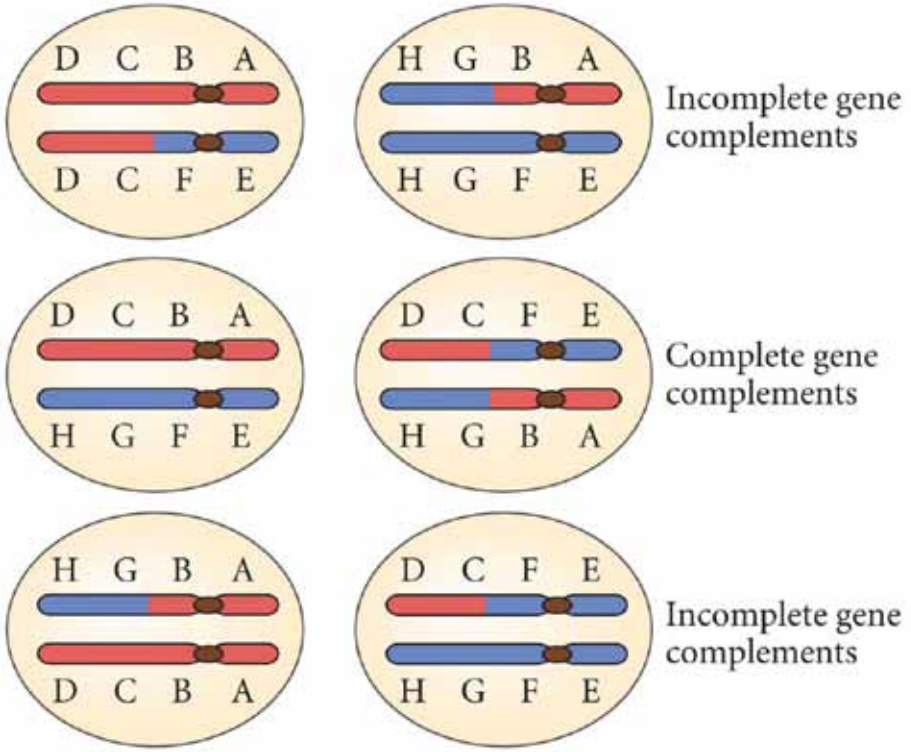
From Futuyma Text



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



Possible Gametes



Chromosomal Speciation

- Involving Polyploidy (but no hybridization)

Example: eastern North American tree frogs
Ptacek, Gerhardt, and Sage. 1994. Evolution 48(3):898-908; Holloway, Cannatella, Gerhardt, & Hillis. 2010. Amer. Natur. 167 (4): E 88- E 101

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

•*Hyla versicolor* is a tetraploid. Larger body, larger cell size, mating song slower pulse rate. Three disjunct popnls.

•Tetraploids cannot mate with diploids.

•Cyt. B. phylogeny shows multiple, independent origins of *H. versicolor*!

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

The end