Lect. 21. Geographic Variation (cont.)

13 April 2017

Four test questions most often missed.

8) Which of the following diseases is likely to evolve the strongest virulence?

   a) Hepatitis C (transmitted by contact with contaminated bodily fluids)

   b) Tuberculosis (airborne contamination)

   c) Cholera (waterborne transmission)

Most missed test questions

20) You are a population biologist and you sample two populations, thinking that you have sampled just one. Which of the HW assumptions will appear to have been violated in your composite population as a result of your mistaken sampling?

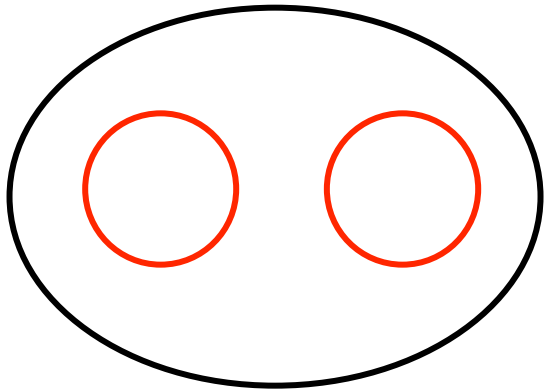
a) No new mutations,

b) Random mating (panmixia),

c) Infinite population size,

d) No migration,

e) No selection.



Most missed test questions

41) How will a short bottle neck affect number of alleles in a population?

a) Little effect,

b) Strong effect,

c) No effect

Most missed test questions

47) Pocket gophers have strong among-population differences in allozyme frequency. Chromosomal translocations differ among populations and contribute to a lack of gene exchange and suggest speciation in progress. Why is it suspected that something other than natural selection has led to differences among populations in chromosomal translocation type?

a) Because 4 out of six gametes have incomplete gene complements and natural selection does not act to lower fitness

b) Because no gene flow is occurring

c) Because the populations are small

d) All of the above.

Last time …

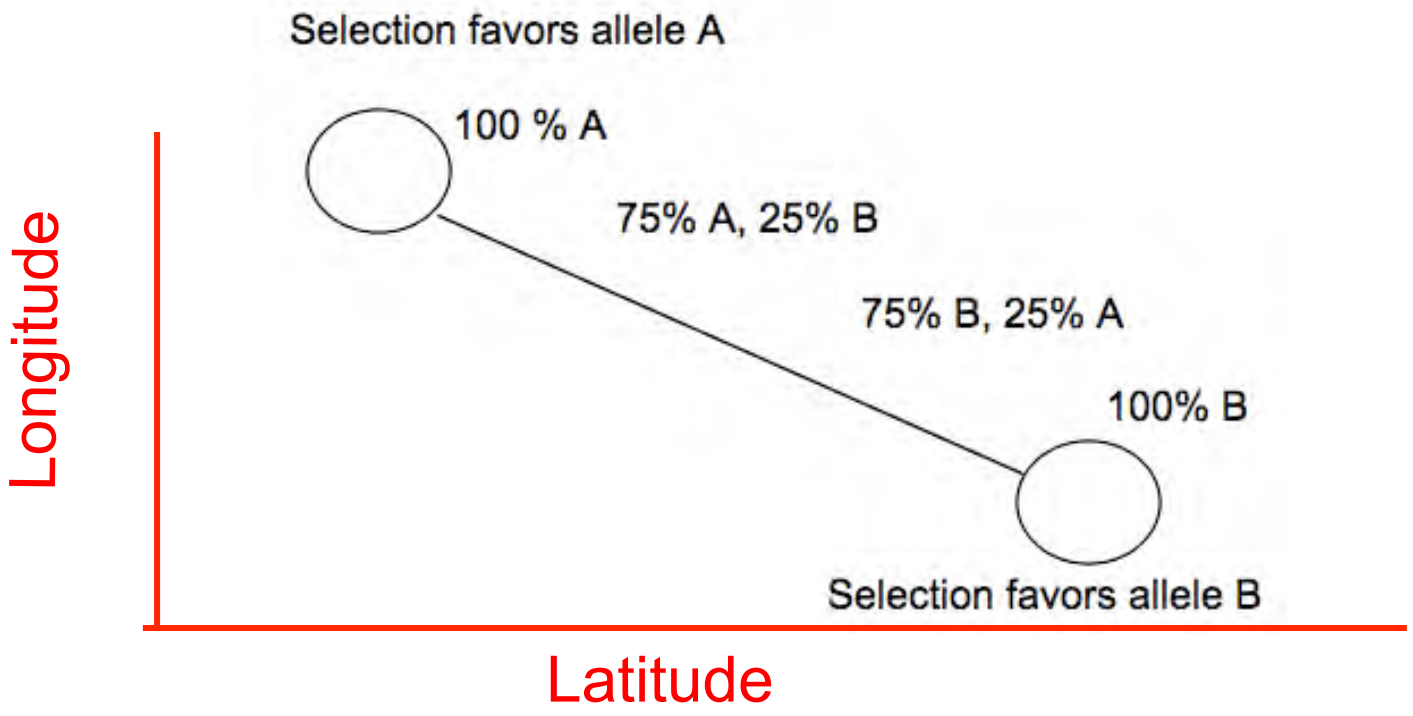
- Competitive character displacement
- Sexual Selection
- Conflicting selection pressures (sexual selection and predation)
- Frequency dependent selection
- Multiple niche polymorphisms
- Balancing selection
- Begin Geographic Variation – clines, geographic races, selection & clines.

This time …

- Reasons for clines.
- Factors that reduce or prevent gene flow

Reasons for clines

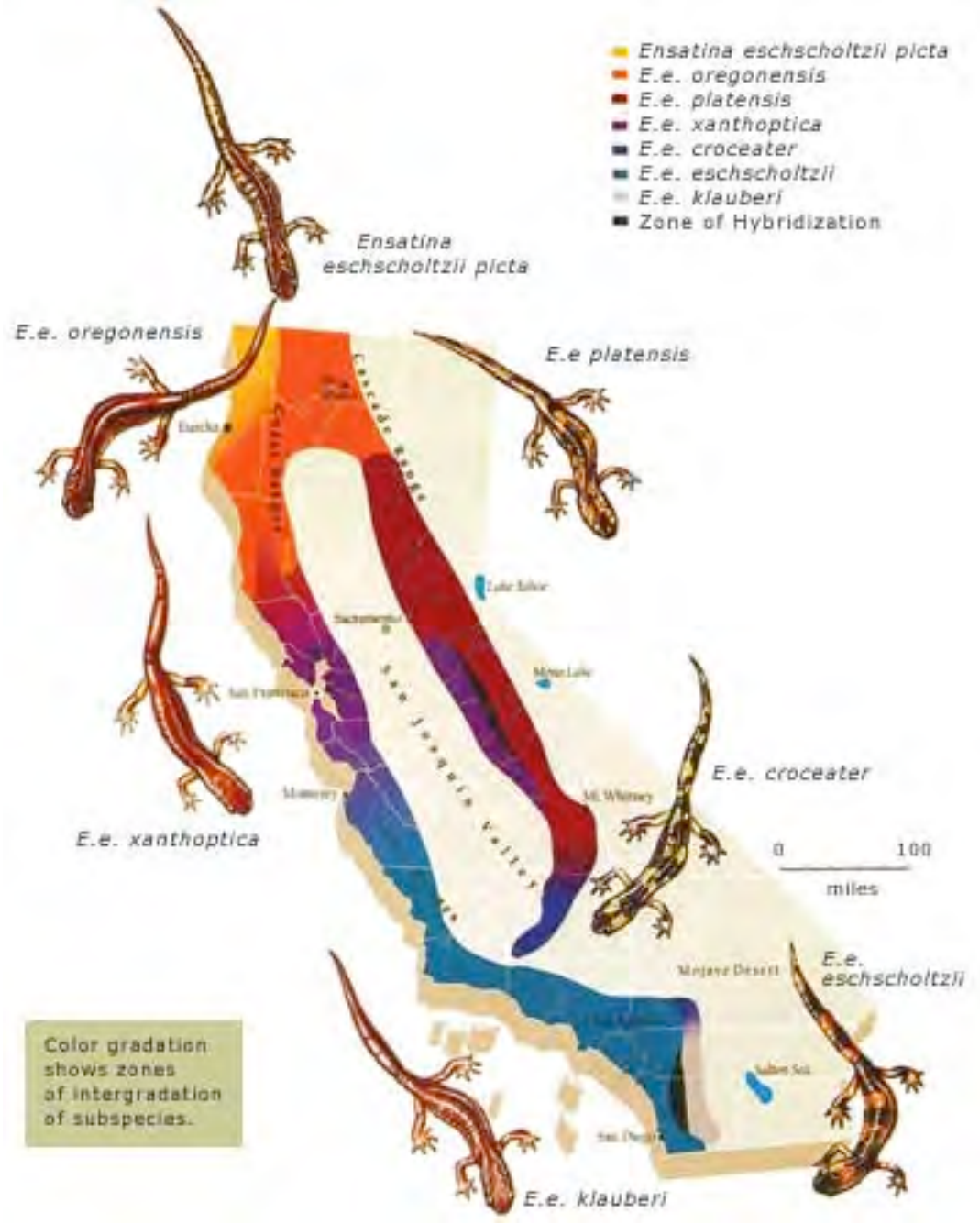
1) Correlation w environmental variables (abiotic or biotic)
2) Genetic Hitching w selected trait
3) Secondary contact btw two formerly isolated populations- maintained by balance btw gene flow & selection; can be permanent or temporary.



Ensatina salamanders “Ring Species”

What are the consequences of isolation by distance?

What are the consequences of secondary contact?



http://www-tc.pbs.org/wgbh/evolution/library/05/2/images/l_052_05_l.jpg

Ring species

A natural experiment.

Ensatina salamanders

Northern populations migrated south in mountains

Interbreeding (intergradation) around the ring

E. e. eschscholtzii & E. e. klauberi do not interbreed!

Factors that Reduce or Prevent Gene Flow Between Species

- Pre-Mating, Pre-zygotic
- Post Mating, Pre-zygotic
- Post Mating, Post-zygotic

What determines the success of mating?

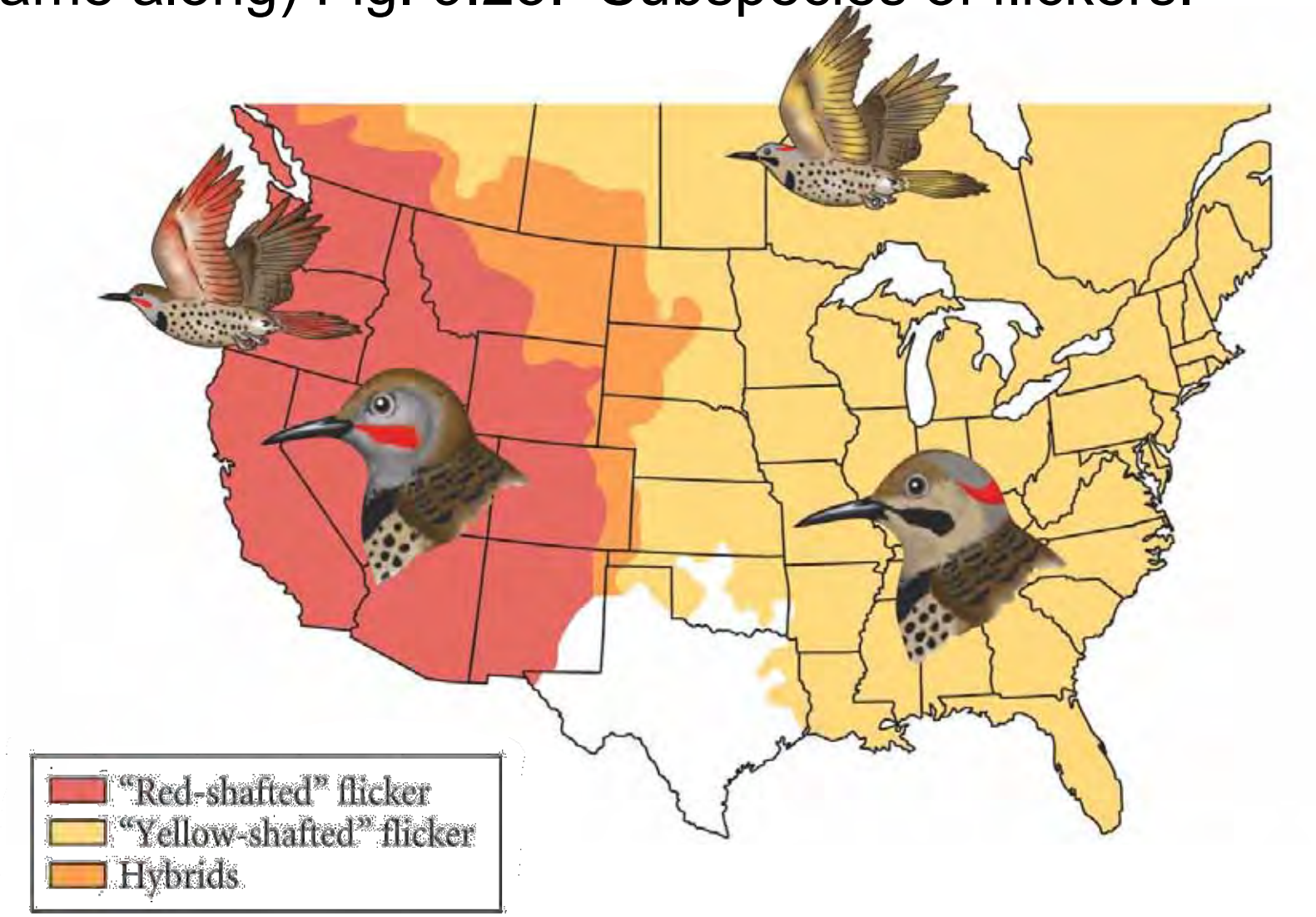
- Ability to attract mates
- Physical ability to mate
- Ability of offspring to develop
- Ability of offspring to survive and reproduce

I. Pre-Mating, Pre-Zygotic

- Adults do not meet: Spatial Isolation
  - – Red- & yellow-shafted flickers (next slide)
  - -- Hawaiian *Banza* katydid species on different islands or volcanoes

Factors that reduce gene flow

Adults do not meet (well, they didn't until people came along) Fig. 9.25. Subspecies of flickers.

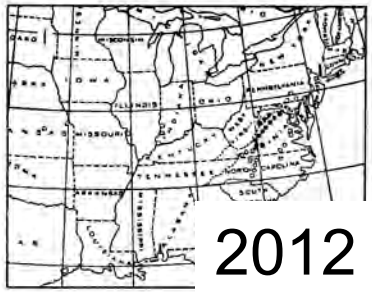


I. Pre-Mating, Pre-Zygotic (cont.)

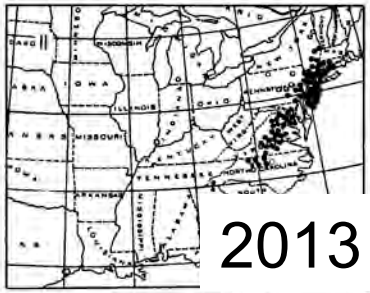
- Adults do not meet: Temporal Isolation
  - All 17-year cicada broods
  - Plants with anthers maturing at times different from stigmas.
  - *Gryllus veletis* & *Gryllus pennsylvanicus* crickets w/ spring vs. fall adults

Gryllus pensylvanicus, fall field cricket: Sept. Oct.

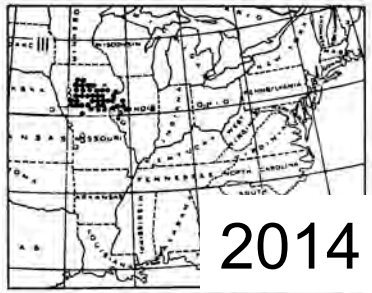
Allochronic 17-year cicada broods



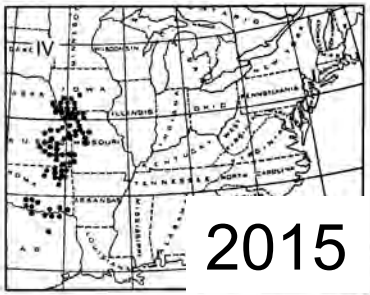
2012



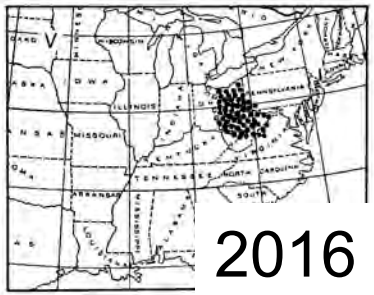
2013



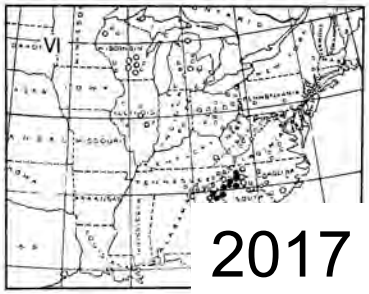
2014



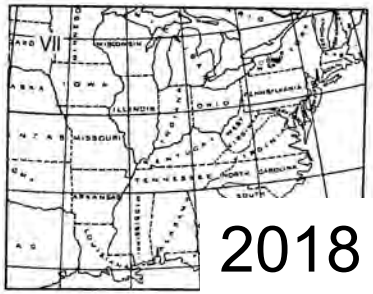
2015



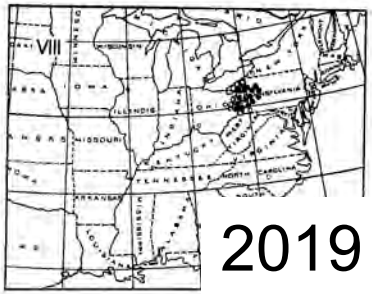
2016



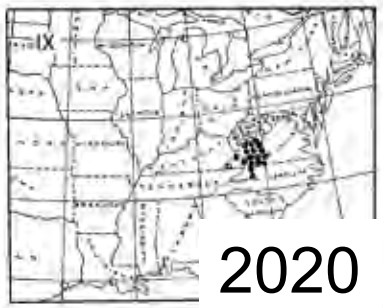
2017



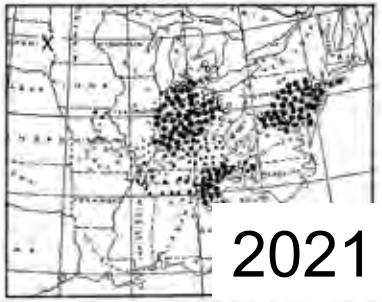
2018



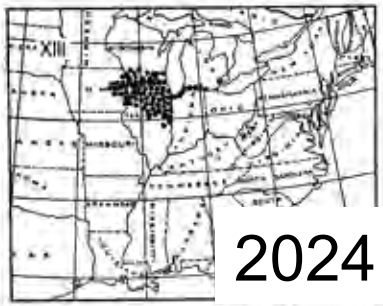
2019



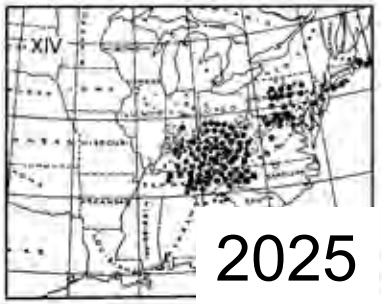
2020



2021



2024



2025

If in different populations, anthers mature at different times than stigmas, crossing is inhibited.

I. Pre-Mating, Pre-Zygotic (cont.)

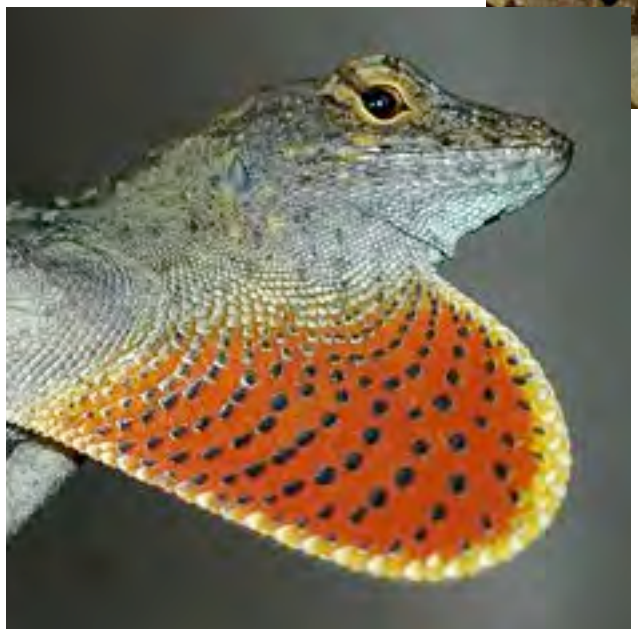
- Adults meet but don't mate
  - Visual- color, dances, light flashes
  - Auditory- substrate borne vibrations, air-borne vibrations
  - Chemical- pheromones

Factors that reduce gene flow

I. Pre-Mating, Pre-Zygotic (cont.)

Color pattern, dances (push-ups)

Anolis dulaps



http://images.dpchallenge.com/images_challenge/89/Copyrighted_Image_Reuse_Prohibited_18556.jpg; http://www.avila.edu/bobpowell/images/anole-2.jpg; http://upload.wikimedia.org/wikipedia/commons/thumb/7/7e/Anolis_sagrei_t%C3%AAte.JPG/300px-Anolis_sagrei_t%C3%AAte.JPG

Factors that reduce gene flow

Australian Peacock Spider

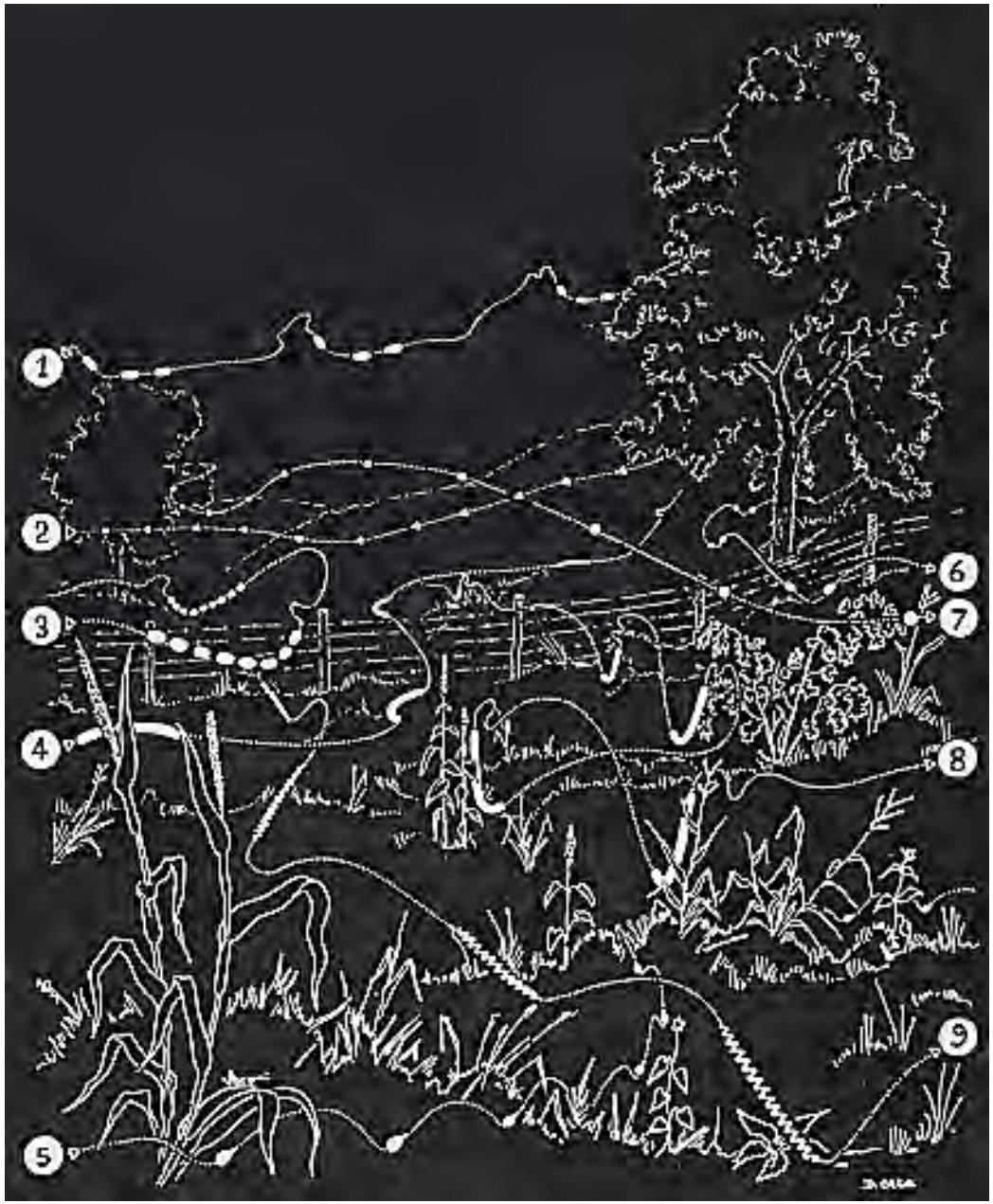
http://www.youtube.com/watch?feature=player_embedded&v=9GgAbyYDFeg

Birds of Paradise

Color pattern, songs, & dances

http://gallery.photo.net/photo/2271187-lg.jpg; http://www.hpfineprints.com/images/LearGould-birds/Birds_of_Paradise1.jpg

Factors that reduce gene flow



Fireflies

Light flashes

Species specific timing & flight paths

Aggressive mimicry

http://ase.tufts.edu/biology/Firefly/flying.jpg; http://www.sciencenewsforkids.org/articles/20060614/a1156_art962.jpg

Massimo Gugliucciello http://yourshot.nationalgeographic.com/photos/3618920/?source=gallery

Factors that reduce gene flow

Hawaiian picture-wing *Drosophila mating dance, + song and pheromones*

Photo by William Mull

Factors that reduce gene flow

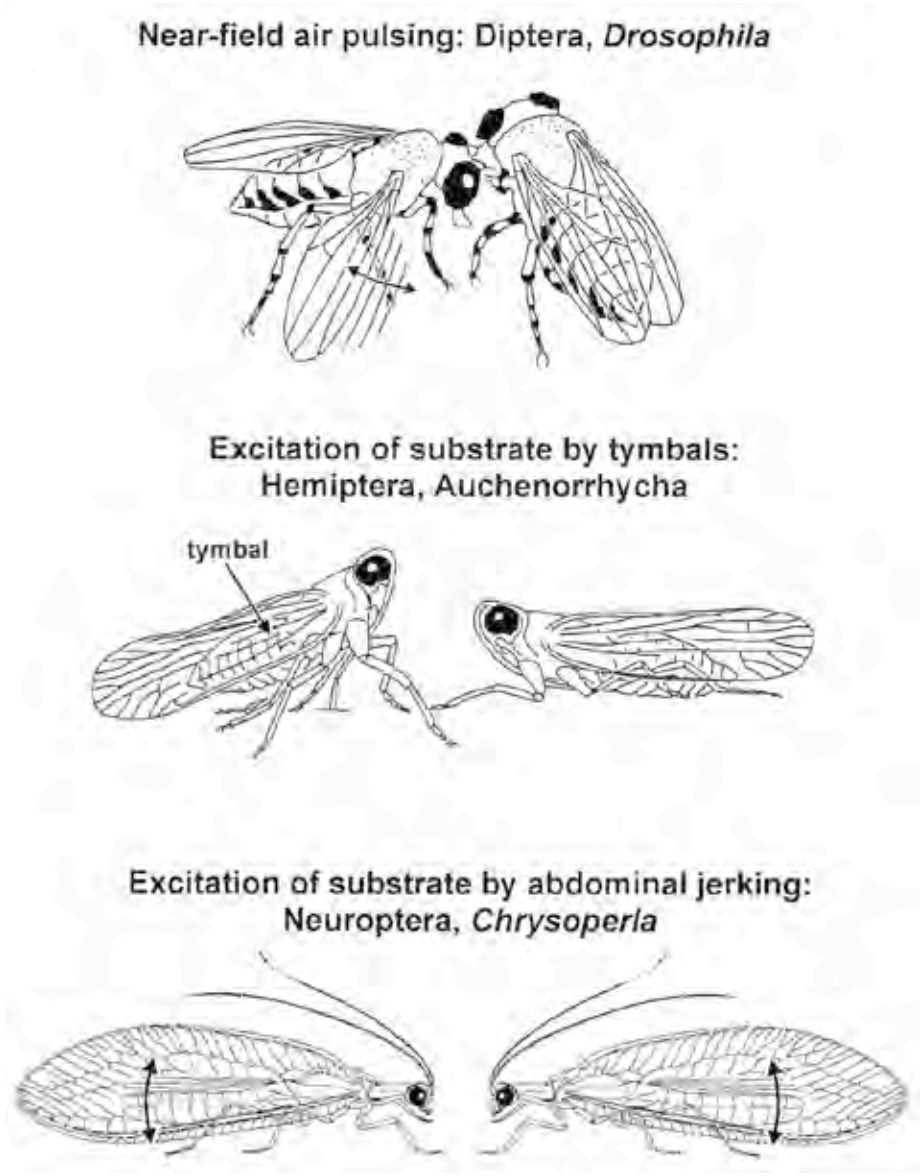
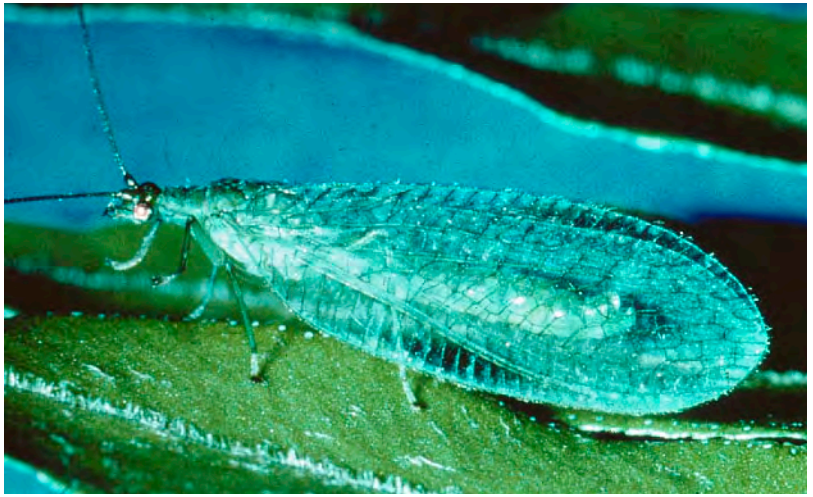


Illustration by Charles Henry

Substrate borne vibrations

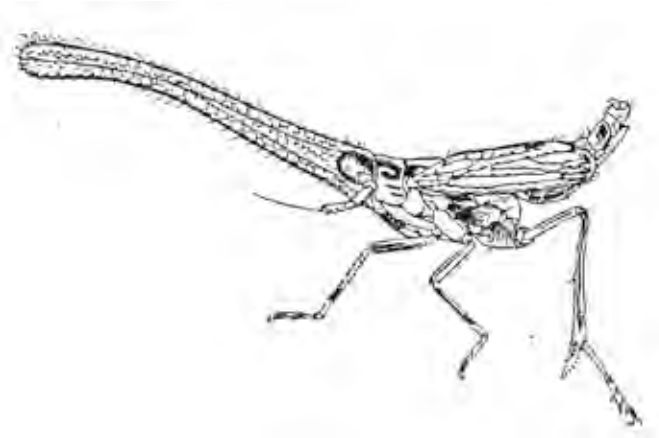


Photos by William Mull

Factors that reduce gene flow

Hawaiian planthoppers

Male-female duets



Dictyophorodelphax miriabilis

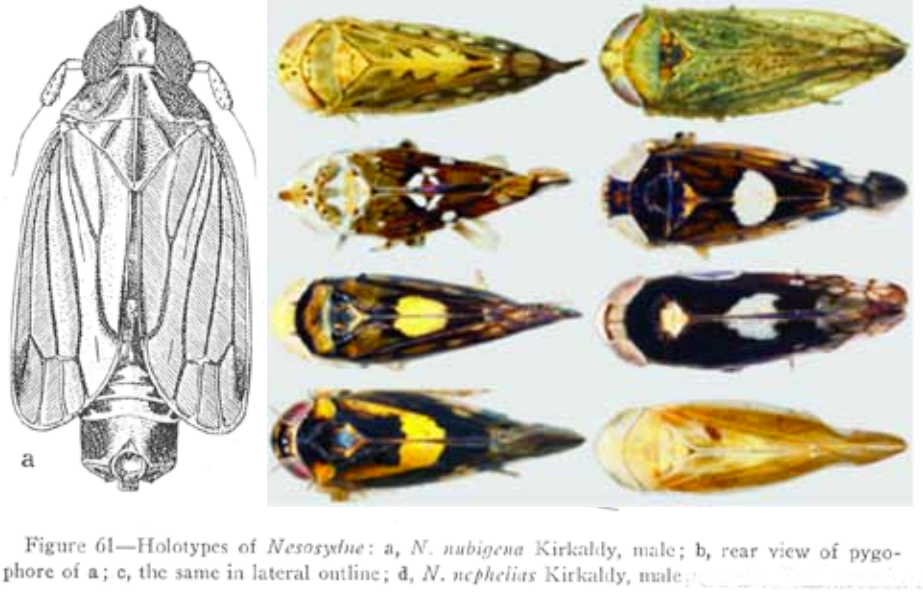


Figure 61—Holotypes of *Nesosydne*: a, *N. nubigena* Kirkaldy, male; b, rear view of pygophore of a; c, the same in lateral outline; d, *N. nephelias* Kirkaldy, male.

Planthopper genus: *Nesosydne*

Sounds from Hannelore Hoch & Manfred Asche

Illustrations from Zimmerman “Insects of Hawaii”

Factors that reduce gene flow

Audible songs

Cicadas

The NZ clicking cicada:

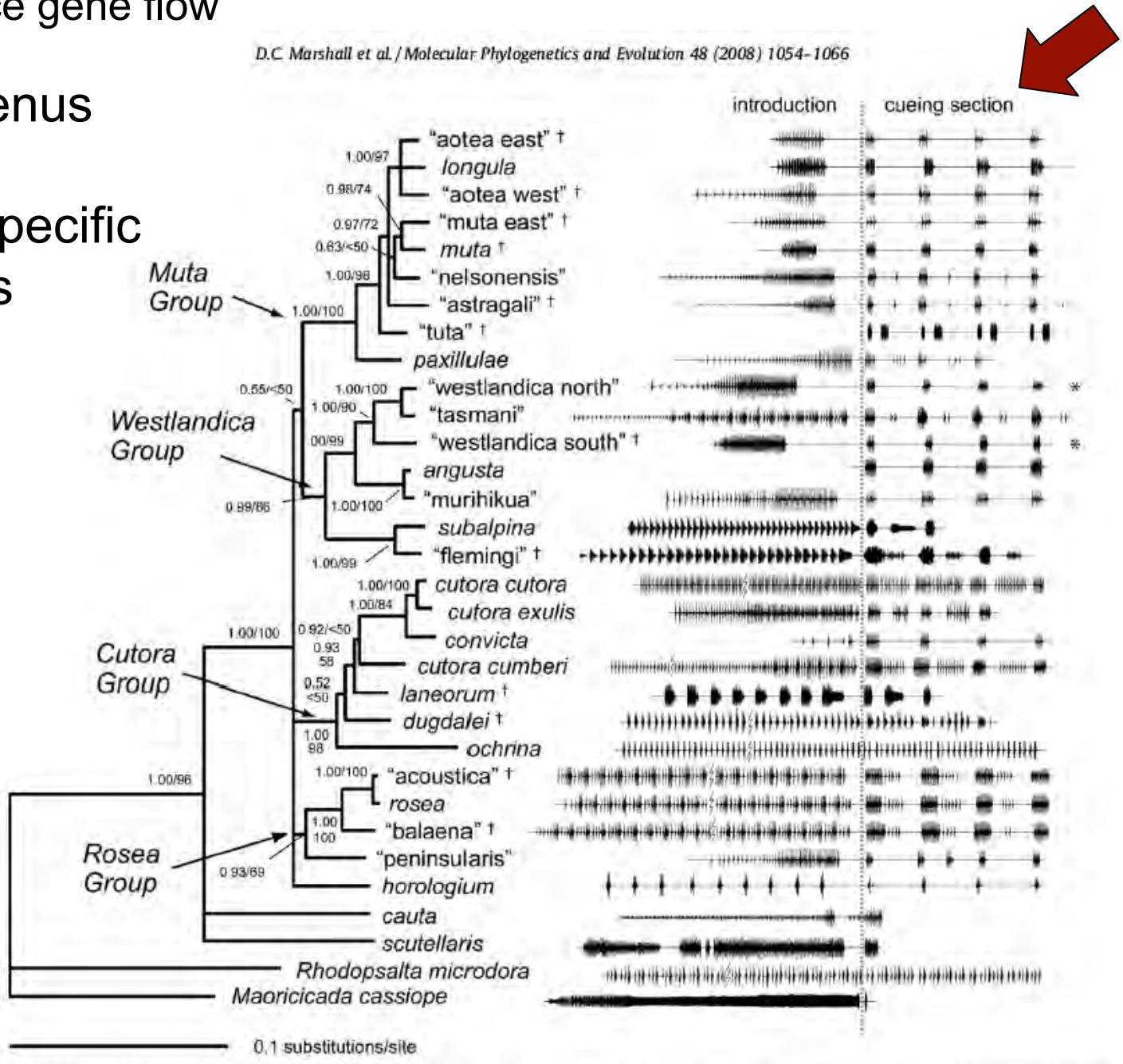
Amphipsalta zelandica

Wing clicks

Timbal vibrations

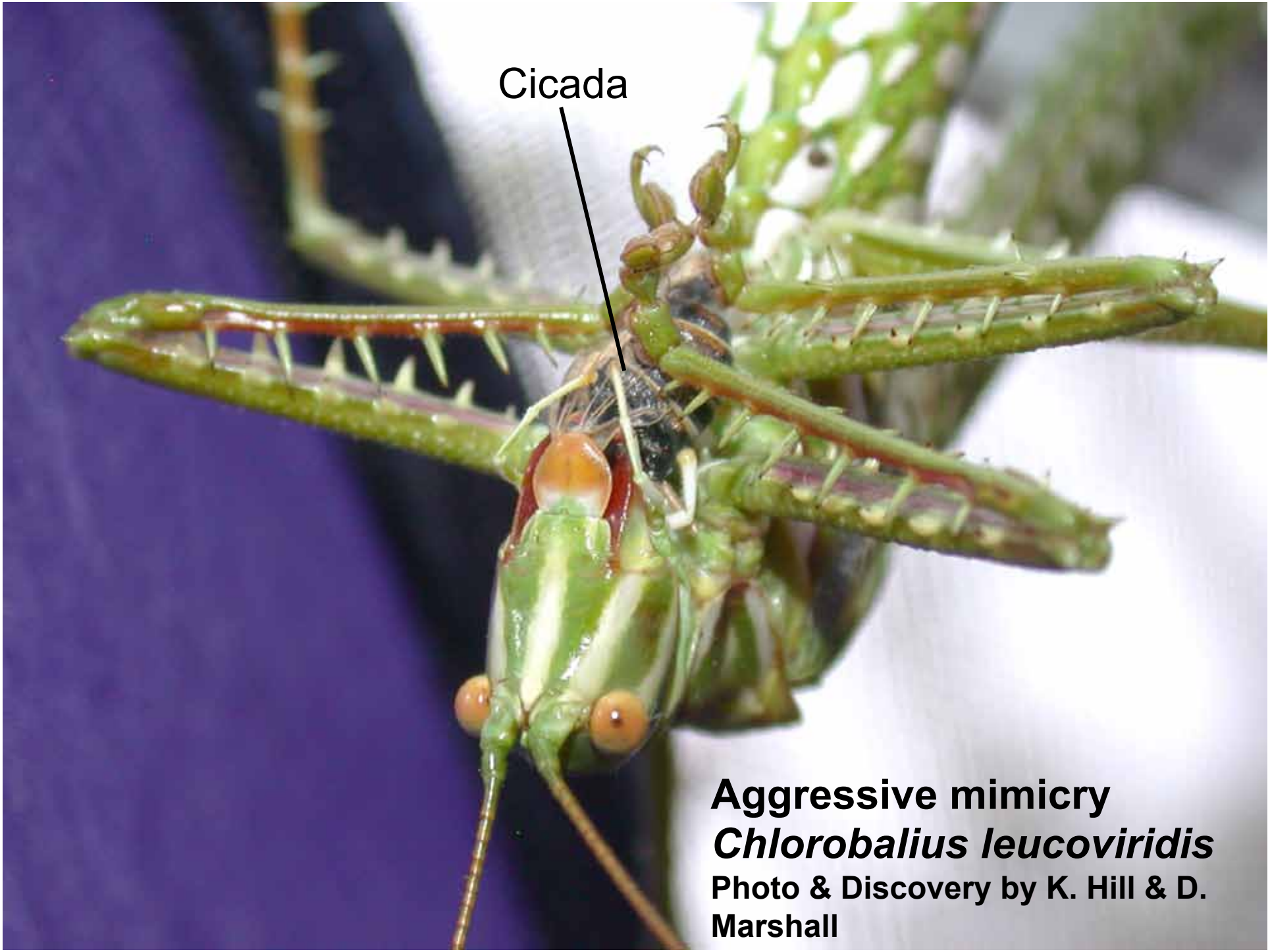
Factors that reduce gene flow

NZ cicada genus
Kikihia
30 species-specific
mating songs



In NZ cicadas, females respond to male song by wing flicking to denote receptivity:

Dan Vanderpool demonstrates w/ *Maoricicada campbelli*



Aggressive mimicry
Chlorobalius leucoviridis
Photo & Discovery by K. Hill & D. Marshall

II. Post-Mating, Pre-Zygotic

- Lock and Key Hypothesis
- Sexual selection by female choice
  - Evidence for selective elimination of sperm from multiple fathers
  - F evaluate M quality during, & after copulation
- Zygote mechanically fails to form

Phyllophaga May beetles > 200 spp.

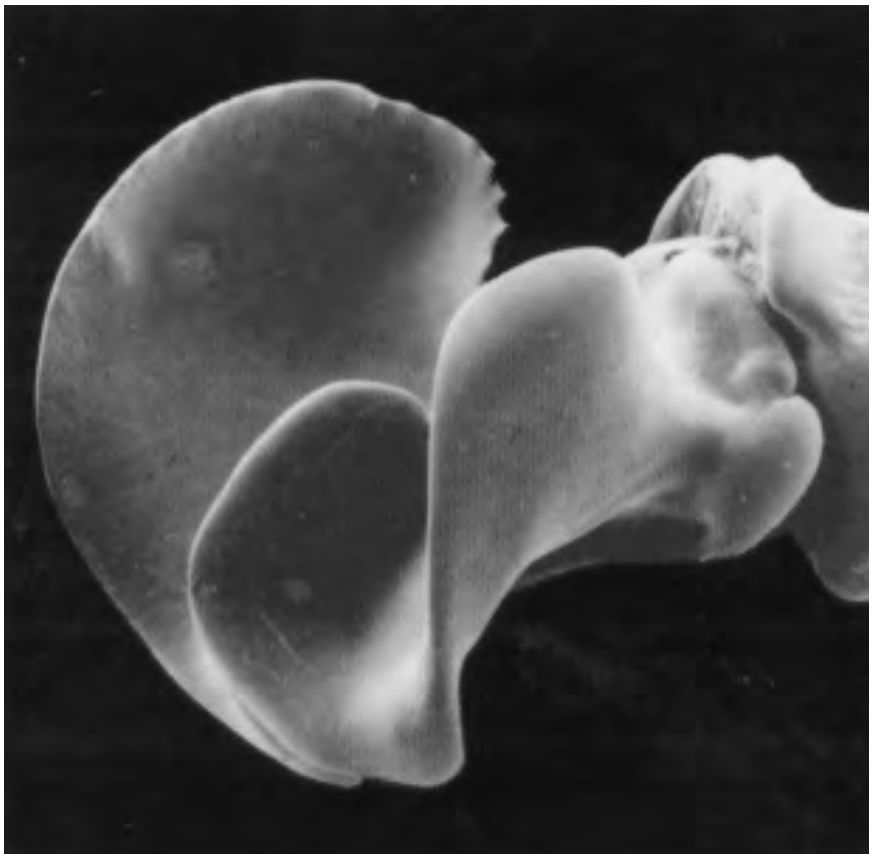
Photos by Maxi Polihronakis

Factors that reduce gene flow

Male genitalia of *Phyllophaga* sp.

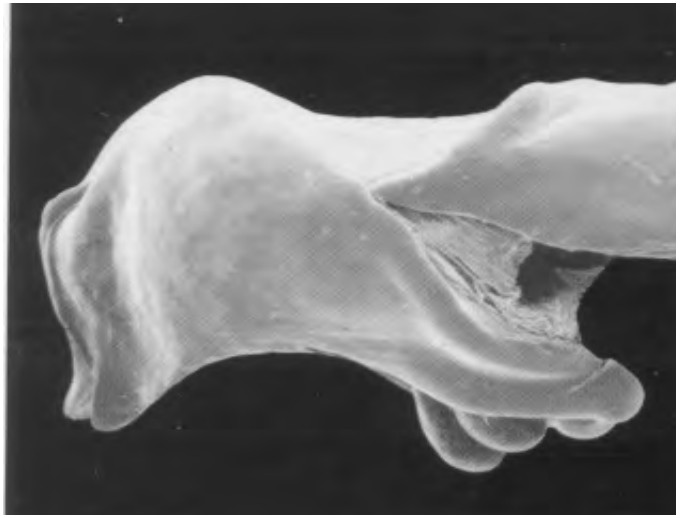
P. infidelis- Lateral view

P. knochii- Lateral view

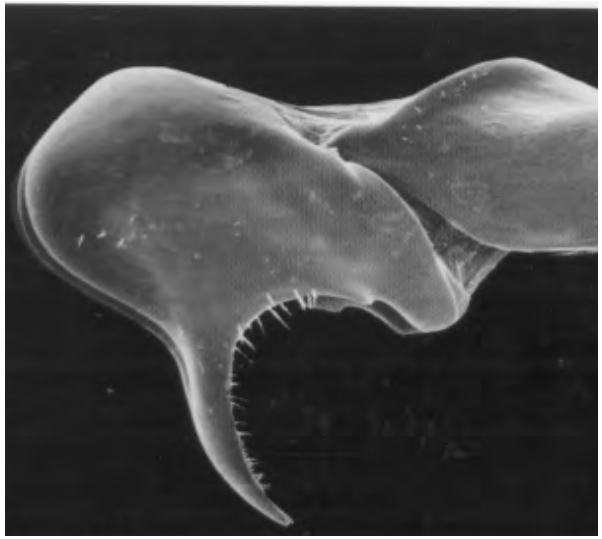


Photos by Maxi Polihronakis

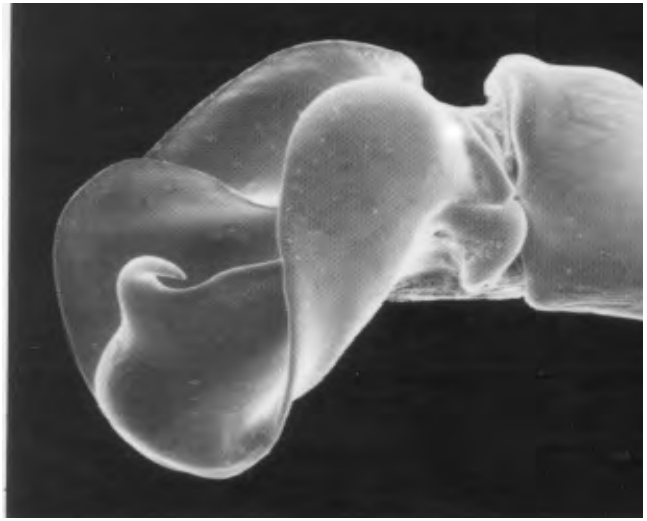
P. glaberrima- lateral view



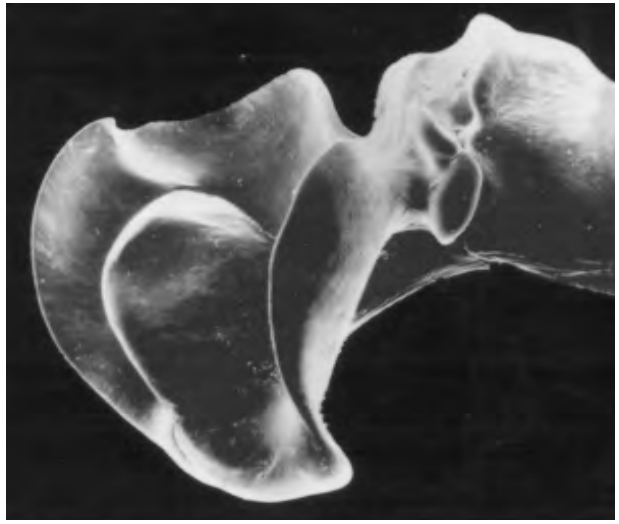
P. gracilis- lateral View



P. hornii- lateral view



P. ilicis- lateral view

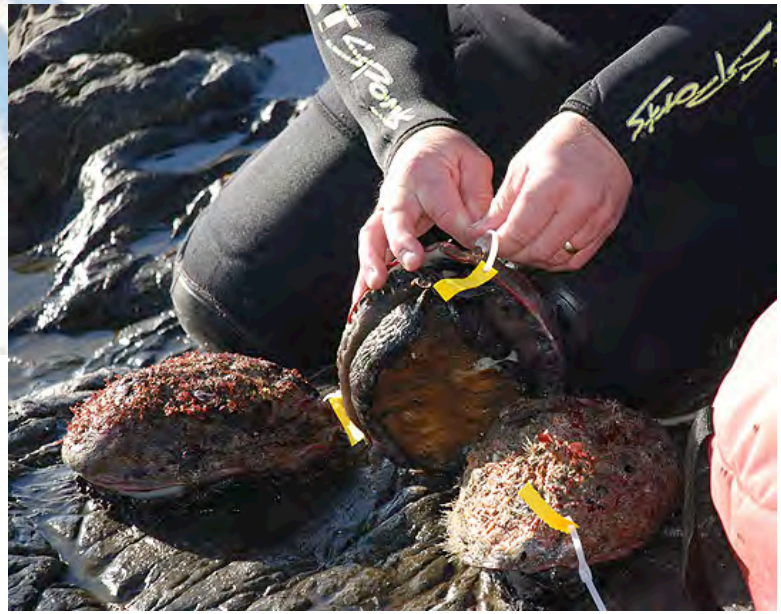


Photos by Maxi Polihronakis

Stages at which zygote formation can fail

1. Attraction of sperm to egg
2. Induction of sperm acrosome by egg surface proteins.
3. Adhesion of sperm to egg envelope
4. Penetration of egg envelope by sperm
5. Fusion of sperm and egg cell membranes
6. Fusion of sperm and egg nuclei

Lee & Vacquier sequenced Lysin gene in seven species of Abalone



Abalone

Lysin in abalone

Lee & Vacquier (1992) Biological Bulletin.182:97-104.

- Sequenced 7 species of abalone.
- Detected positive selection at AA level in active site of Lysin protein in 20/21 pairwise comparisons.
- McDonald Kreitman test: d_N/d_S where

  N= non-synonymous (AA replacement) and

  S = synonymous (Silent)
- $d_N/d_S > 1$ = positive selection

Swanson and Vacquier. 2002. Ann. Rev. Ecol. Evol. Syst. 33: 161-179.

Table 1. Evidence that reproductive genes evolve quickly

Gene (locus)	Organism	Evidence for + selection	Reference
Pollen coat proteins	Arabidopsis	None	(Mayfield et al. 2001)
Lysin	*Tegula* & *Haliotis* (turban snails and abalone)	Overall $d_N/d_S > 1$	(Hellberg & Vacquier 1999, Lee et al. 1995)
sp18	*Haliotis* (abalone)	Overall $d_N/d_S > 1$	(Swanson & Vacquier 1995a)
TMAP	Tegula (*turban snails*)	Overall $d_N/d_S > 1$	(Hellberg et al. 2000)
Bindin	Sea urchins	Region with $d_N/d_S > 1$	(Metz & Palumbi 1996)
Acp26Aa	Drosophila	Lineage with $d_N/d_S > 1$	(Tsaur & Wu 1997)
Acp36DE	Drosophila	Polymorphism survey	(Begun et al. 2000)
ZP3	Mammals	Class of sites with $d_N/d_S > 1$	(Swanson et al. 2001c)
ZP2	Mammals	Class of sites with $d_N/d_S > 1$	(Swanson et al. 2001c)
OGP	Mammals	Class of sites with $d_N/d_S > 1$	(Swanson et al. 2001c)
Zonadhesin	Mammals	None	(Gao & Garbers 1998)
TCTE1	Mammals	None	(Juneja et al. 1998)
Protamines	Mammals	$d_N/d_S > 1$	(Wyckoff et al. 2000)

Swanson & Vacquier. 2002. AREES.

III. Post-Mating, Post-Zygotic

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

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

Drosophila paulistorum semispecies

- Guatemala to southern Brazil
- Six genetically homogeneous “strains” or semispecies: 1) Centroamerican, 2) Andean-Brazilian, 3) Orinocan, 4) Interior, 5) Amazonian, 6) Transitional.
- Outcomes of crosses:

a) Hybrids F1 males sterile; F1 females fertile.

b) No hybrids form

c) In one case: vigorous fertile F1 hybrids (“Transitional” group x Centroamerican or Andean-Brazilian).

Factors that reduce gene flow

JBS Haldane

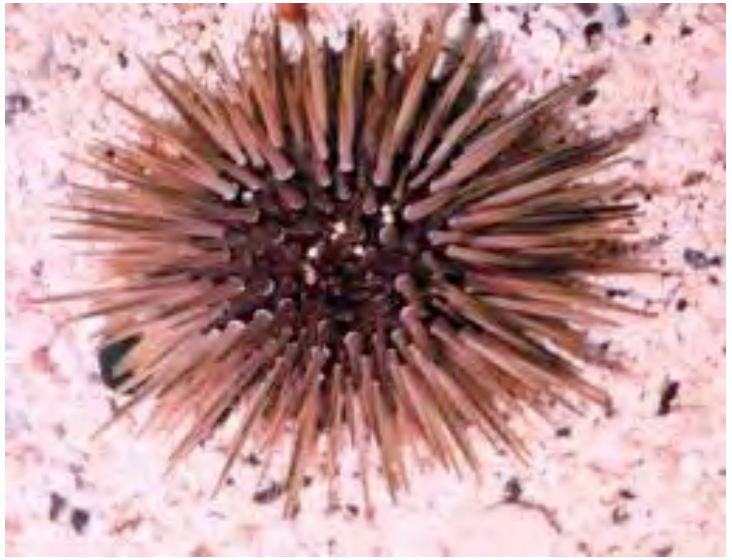
Haldane's Rule

- Background: In Humans and *Drosophila*, males are heterogametic, but in other organisms, e.g., most amphibians, birds, butterflies and reptiles, the female is heterogametic.
- Rule: when sterility is confined to one sex, it will always be the heterogametic sex. Why?
- 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.

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?

Hawaiian *Echinometra* sea urchins



Exception to the rule:

- In most sea urchins, the more distantly related are two species, the lower the percentage of hybrid zygotes.
- In Hawaii, two very closely related species live in same environment and show complete reproductive isolation. What is the cause of this isolation?

Selection at the bindin locus varies across genera of Sea Urchins

- Positive selection is indicated at the active site of bindin in *Echinometra* and *Stronglyocentrotus*
- No evidence of selection in four species of *Arbacia*. Bindin sequences conserved across species. Why?
  - One hypothesis, these four spp. are all allopatric.
  - Alternatively, bindin in *Arbacia* species may be under increased functional constraint.

Arbacia lixula

Stronglyocentrotus purpuratus

Echinometra mathaei

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, or differ in number. Can't pair properly.

End Lecture 21

- To be continued next time…