

2. You have collected and genotyped 200 individuals from a population of the fruit fly, *Drosophila pseudoobscura*. Your sequencing study revealed 20 individuals with genotype AA, 70 individuals with genotype Aa, and 110 individuals with genotype aa.

Additional information:

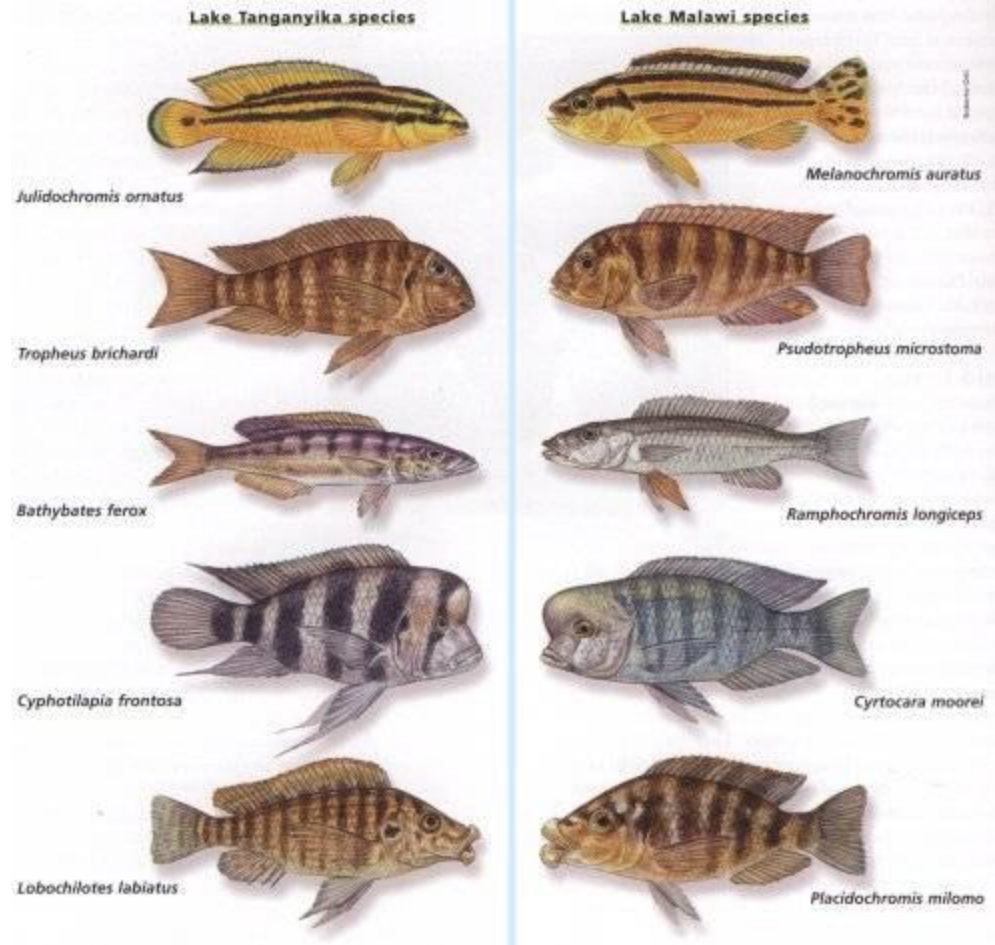
$$G = 2 \sum_{i=1}^m x_i \ln \left[ \frac{x_i}{\hat{x}_i} \right]$$

A table of  $\chi^2$  values can be found on the last page of your exam.

A (20pts). What are your *a priori* expectations for the number of individuals with each genotype if the population is in Hardy-Weinberg equilibrium?

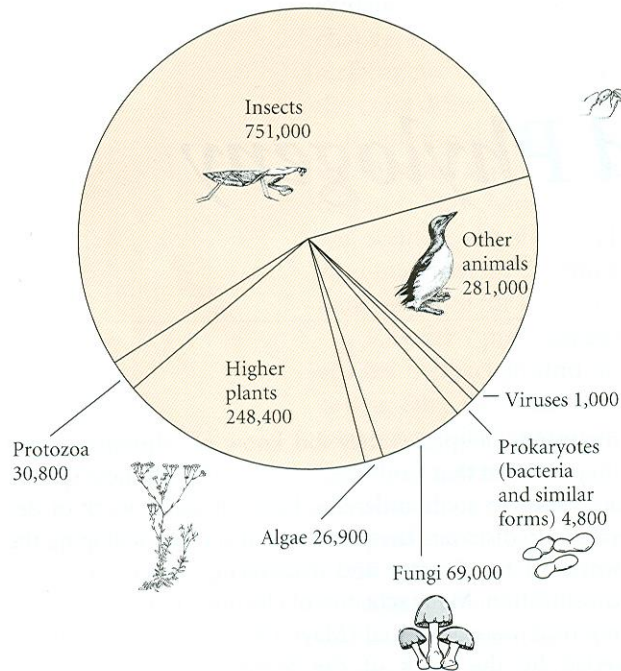
B (20pts). Based on the genotype counts you observe, is there evidence that this population of fruit flies deviates from your *a priori* expectations under Hardy-Weinberg equilibrium?

# Speciation

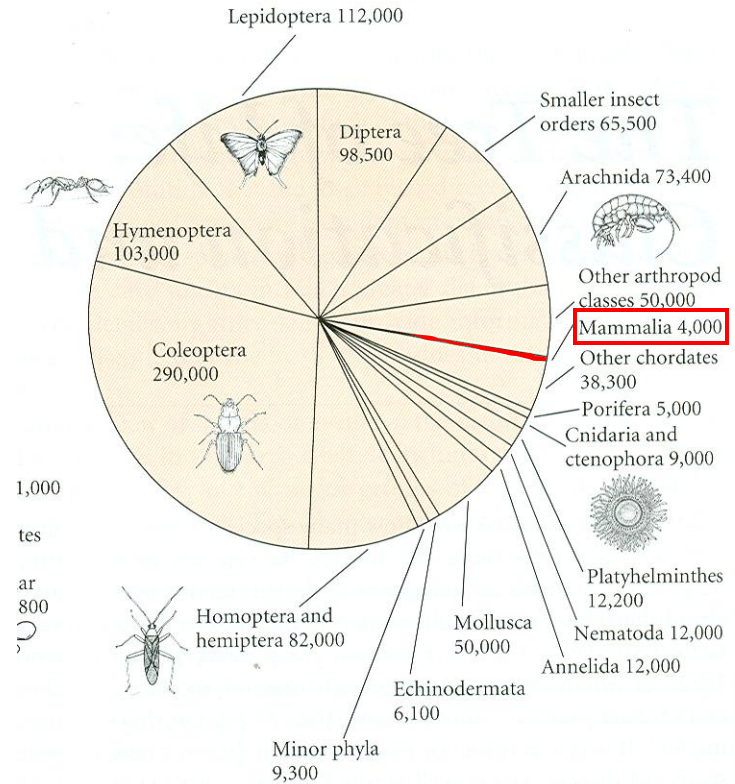


# How many species are there?

## All organisms



## Just animals



**In short, an awful lot!**

# What is a species?

**Species** – The members of a group of populations that interbreed or potentially interbreed with each other under natural conditions.

# Speciation: some definitions

**Speciation** – Evolution of **reproductive isolation** within an ancestral species, resulting in two or more descendant species.

## Reproductive isolating mechanisms:

**1. Prezygotic isolating mechanisms** – Prevent or reduce the likelihood of the formation of hybrid zygotes, often through positive assortative mating.

**2. Postzygotic isolating mechanisms** – Factors that reduce the fitness of hybrid zygotes by reducing their survival or reproductive rates.

# Prezygotic isolating mechanisms

## **1. Potential mates do not meet**

- A. Temporal isolation – Mating occurs at different times
- B. Habitat isolation – Mating occurs in different areas

## **2. Potential mates meet, but do not mate (Behavioral isolation)**

## **3. Copulation occurs but no transfer of male gametes takes place (Mechanical isolation)**

## **4. Gamete transfer occurs, but egg is not fertilized (Gametic incompatibility)**

# Prezygotic isolating mechanisms: an example



**Green Lacewing**

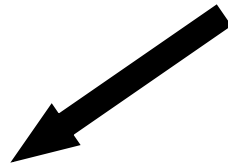
- Three morphologically indistinguishable species
- Males attempt to initiate a duet of low frequency songs produced by abdominal vibrations
- Mating does not occur unless the female responds
- Females respond much more frequently to songs of their own species

# Postzygotic isolating mechanisms

- 1. Zygote dies (zygotic mortality soon after fertilization)**
- 2. Hybrid has reduced viability (hybrid inviability)**
- 3. Hybrid has reduced fertility (hybrid sterility)**



# Postzygotic isolating mechanisms: an example



# Practice Question

A species of endangered frog is found only in 150 small ponds scattered over a high mountain plateau. Detailed studies of this frog have shown that the level of heterozygosity/genetic polymorphism within a population is a very accurate predictor of the population's long term viability. Specifically, a detailed study of survival probabilities demonstrated that if the heterozygosity of a population falls below a critical value of 1/4, it is virtually certain to go extinct. If, however, the heterozygosity of a population remains above the critical value of 1/4 it has a reasonable probability of surviving.

A (5pts). If there is no gene flow between these populations, and the effective population size in each pond is approximately 40 individuals, what do you predict will happen to the level of heterozygosity within ponds over the next 100 years? Why?

B (15pts). In lecture you saw that the level of heterozygosity that will be maintained in a finite population experiencing genetic drift and gene flow can be predicted using the following equation:

$$\hat{H} = \frac{4Nm}{1 + 4Nm}$$

Use this equation to predict the rate of gene flow that would need to occur between frog populations for the level of heterozygosity within populations to be maintained above the critical level of 1/4.

C (20pts). Using a mark and recapture study, a group of scientists determined that the actual rate of gene flow between frog populations was .00004. Based upon the data presented and your calculations in B, do you think this species of frog is likely to persist? Why?

# Modes of speciation

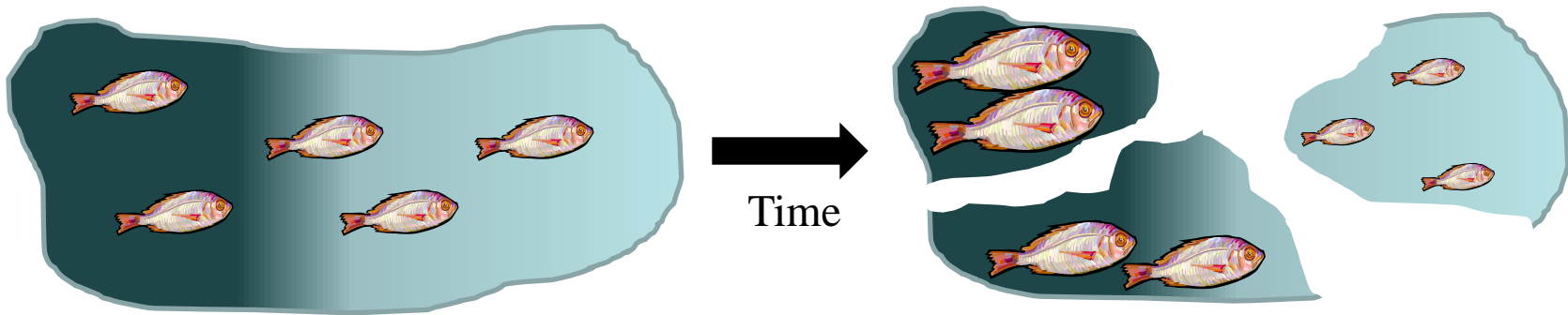
- 1. Allopatric speciation – The evolution of reproductive isolation between populations that are geographically separated.**
- 2. Parapatric speciation – The evolution of reproductive isolation between populations that are continuously distributed in space.**
- 3. Sympatric speciation – The evolution of reproductive isolation within a single randomly mating population.**

# Allopatric speciation

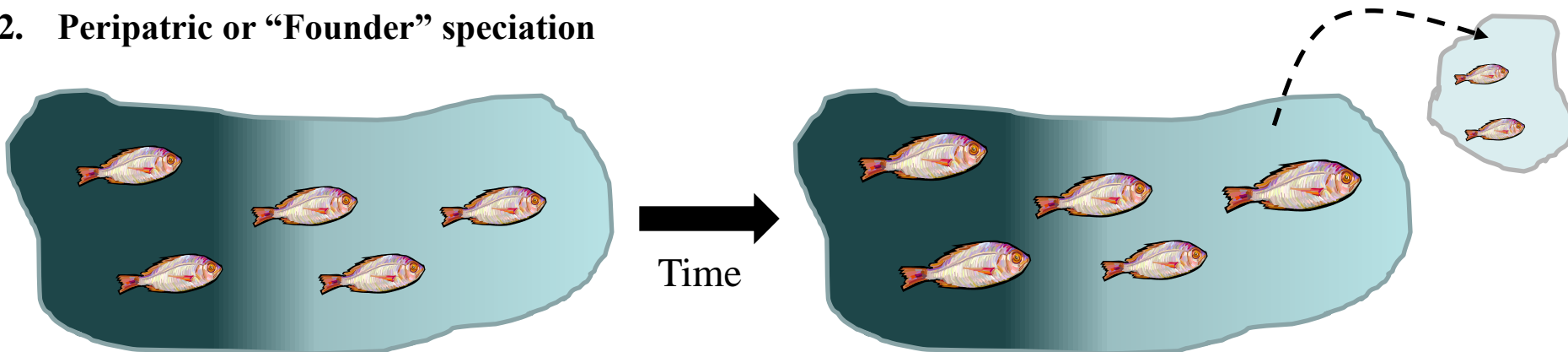
*The evolution of genetic reproductive barriers between populations that are geographically separated*

**Allopatric speciation can occur in two ways:**

## 1. Vicariant speciation

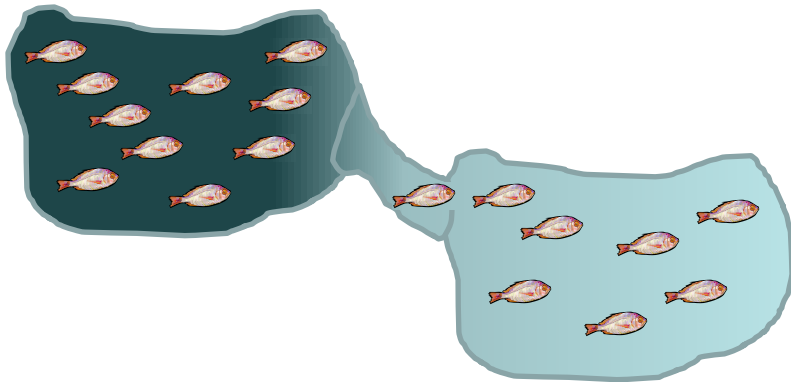


## 2. Peripatric or "Founder" speciation



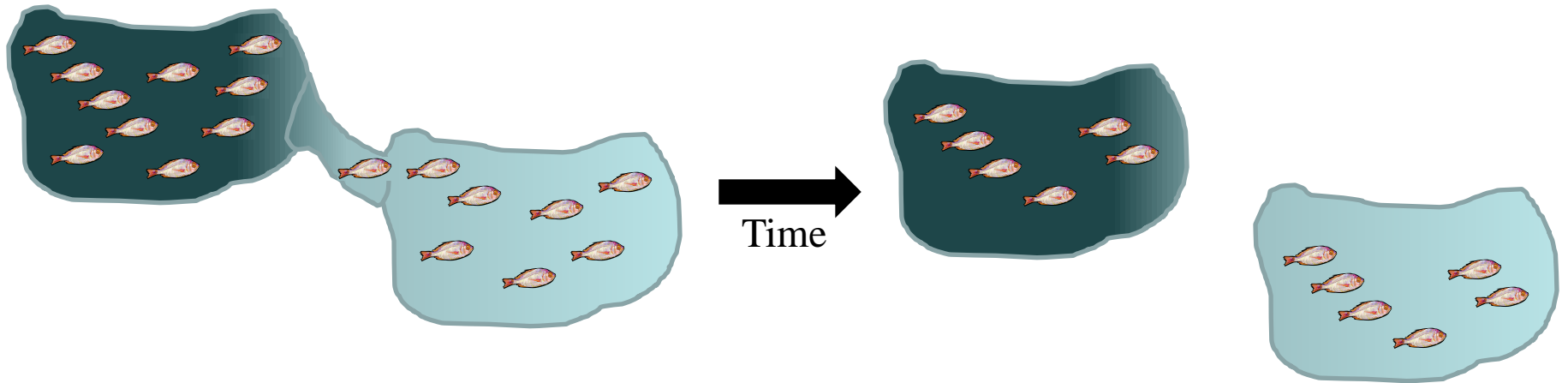
# The process of allopatric speciation: Step 1

**Begin with a single species whose populations are physically connected.  
Gene flow substantial.**



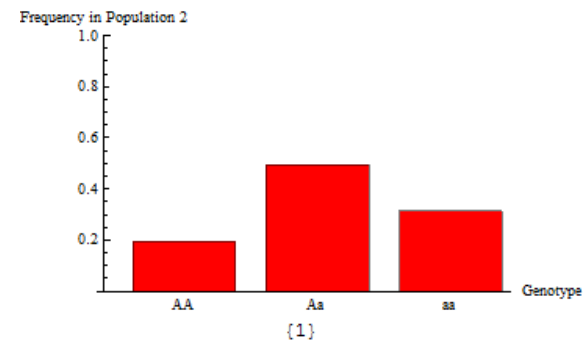
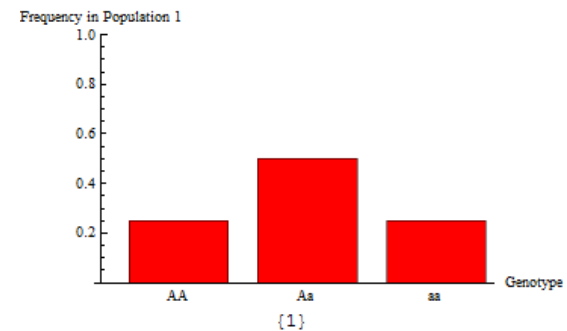
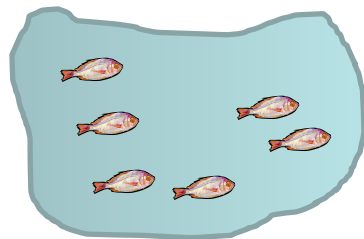
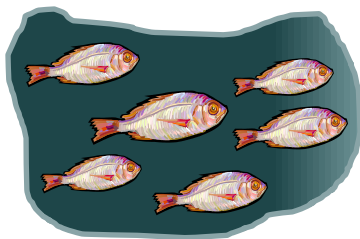
# The process of allopatric speciation: Step 2

**Next, one or more populations becomes isolated from the main population either through vicariance or through a colonization event. Gene flow stops**



# The process of allopatric speciation: Step 3

**Finally, genetic differences accumulate through drift or selection, resulting in divergent populations which can no longer interbreed**

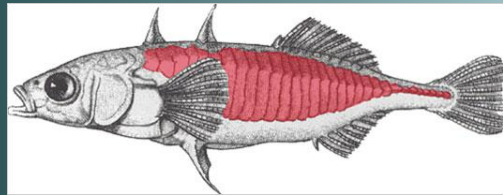


# The process of allopatric speciation: an example from sticklebacks

> 13,000 years ago



Three-spined stickleback  
*Gasterosteus aculeatus*



Drawing of marine sticklebacks. Credit: David Kingsley, Stanford University (based on Cuvier & Valenciennes, 1829).

Pacific Ocean

Ice



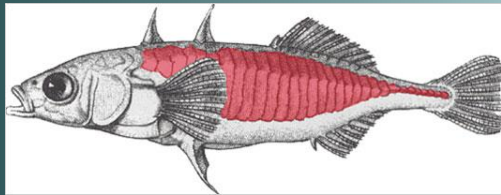


# The process of allopatric speciation: an example from sticklebacks

≈ 13,000 years ago

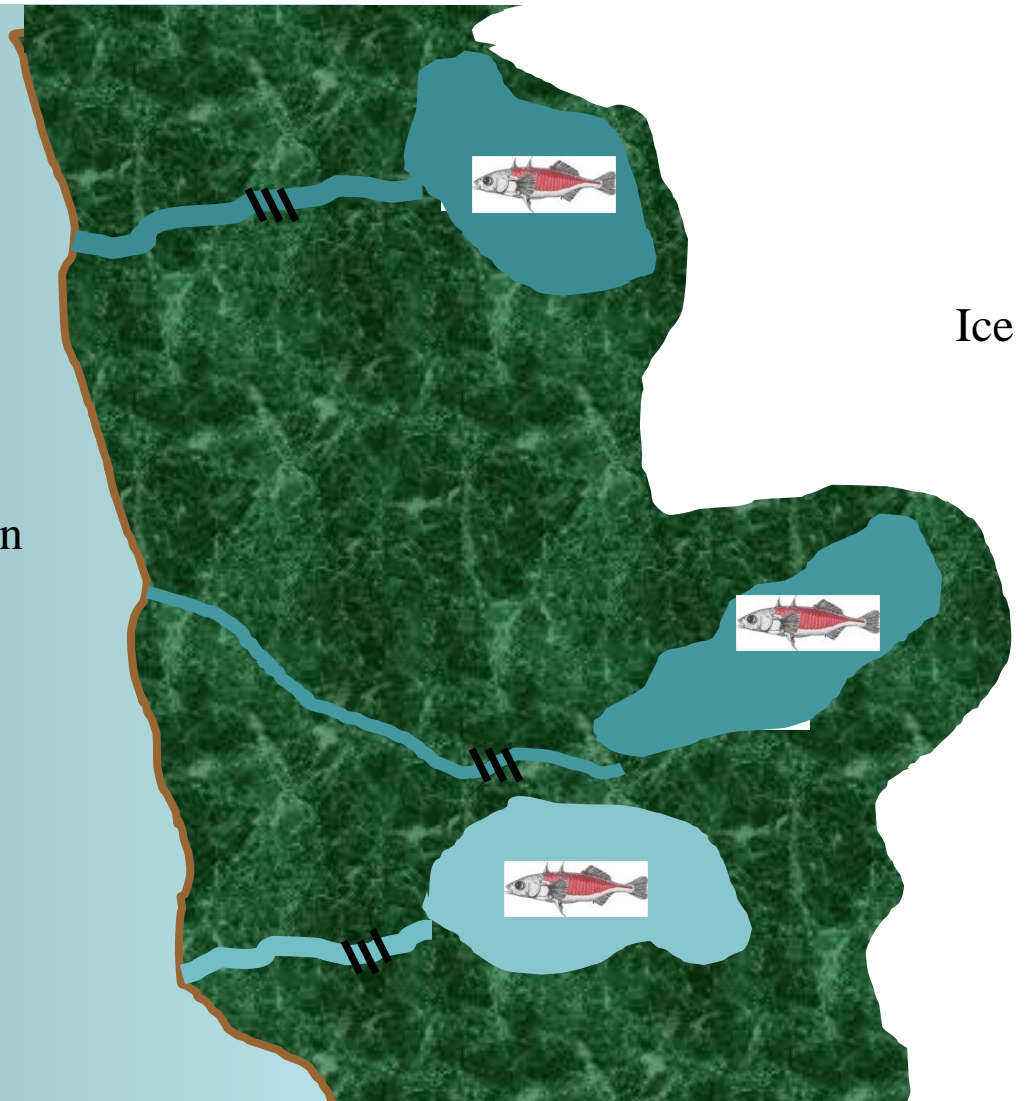


Three-spined stickleback  
*Gasterosteus aculeatus*



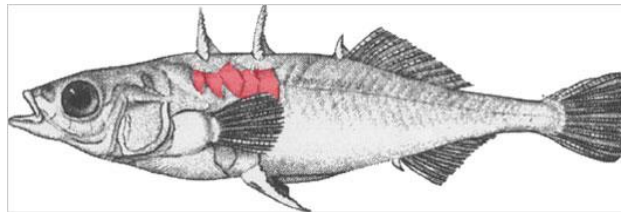
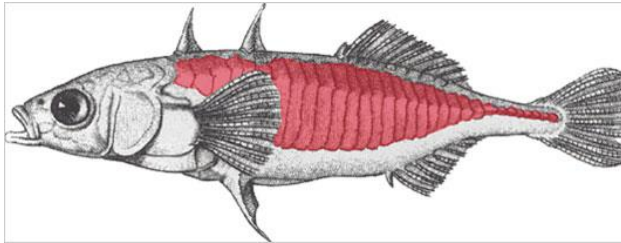
Drawing of marine sticklebacks. Credit: David Kingsley, Stanford University (based on Cuvier & Valenciennes, 1829).

Pacific Ocean



# The process of allopatric speciation: an example from sticklebacks

- Since the glaciers retreated and the rivers became impassible ( $\approx 13,000$  years ago), substantial morphological evolution has occurred
- This evolution is hypothesized to be the result of natural selection for life in freshwater



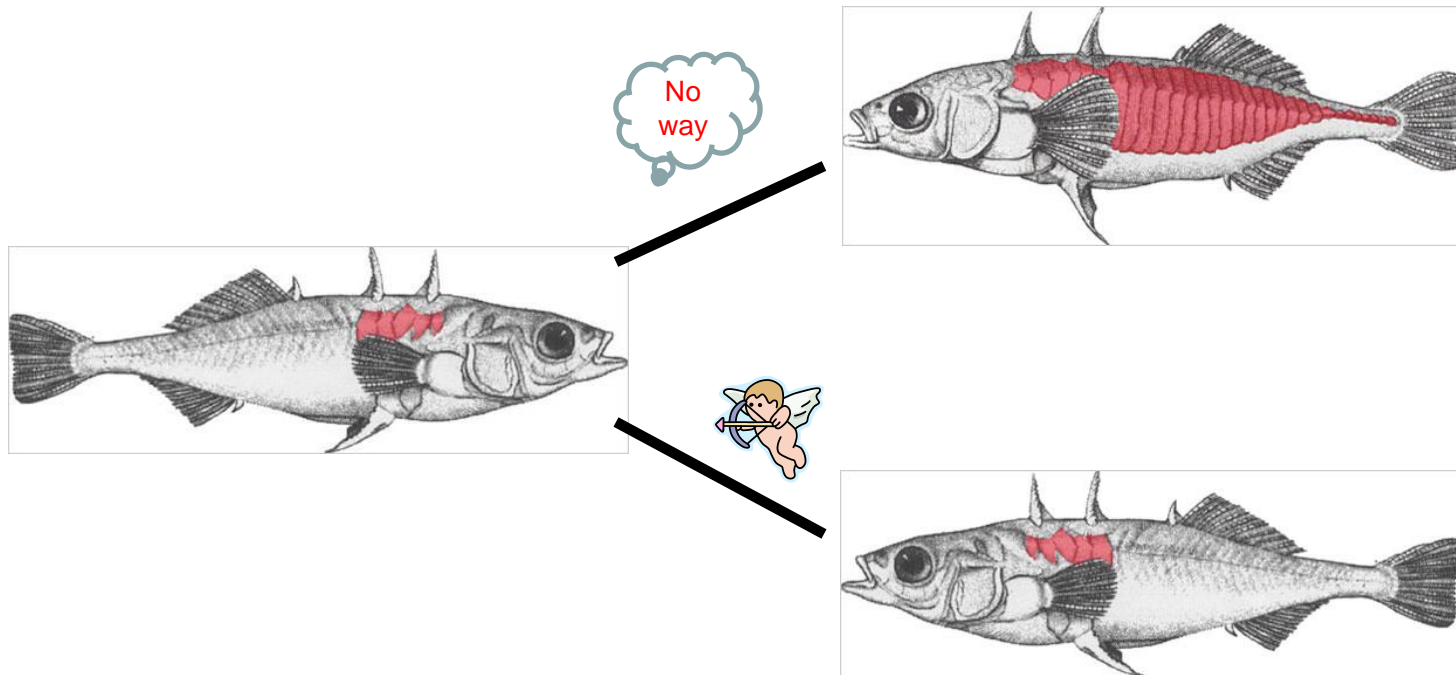
Drawings of sticklebacks showing armor in red



Sticklebacks with armor stained

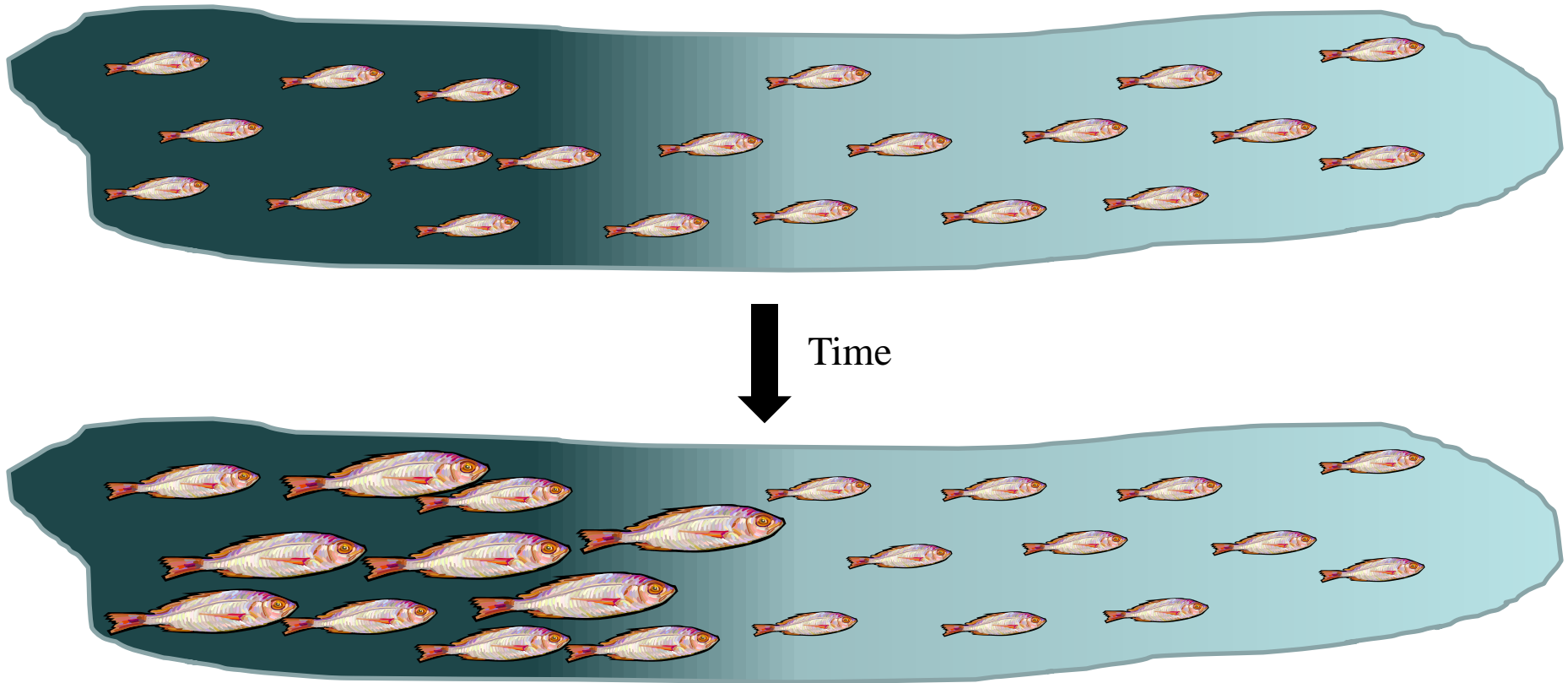
# The process of allopatric speciation: an example from sticklebacks

- If females of one type are now given a choice between the two types of males, they prefer their sympatric type
- This suggests that we are observing the initial stages of allopatric speciation



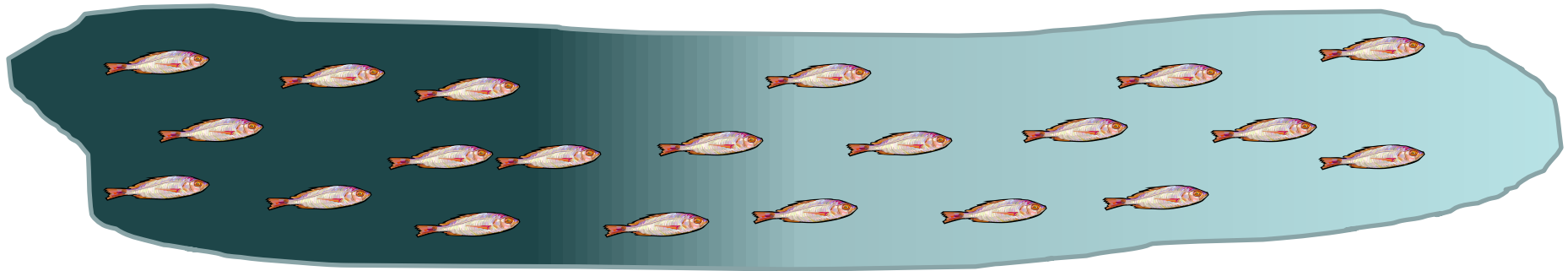
# Parapatric speciation

*The evolution of reproductive isolation between populations that are continuously distributed in space*



# The process of parapatric speciation: Step 1

**Begin with a single species whose populations are physically connected. Gene flow is substantial, although it decreases with distance**

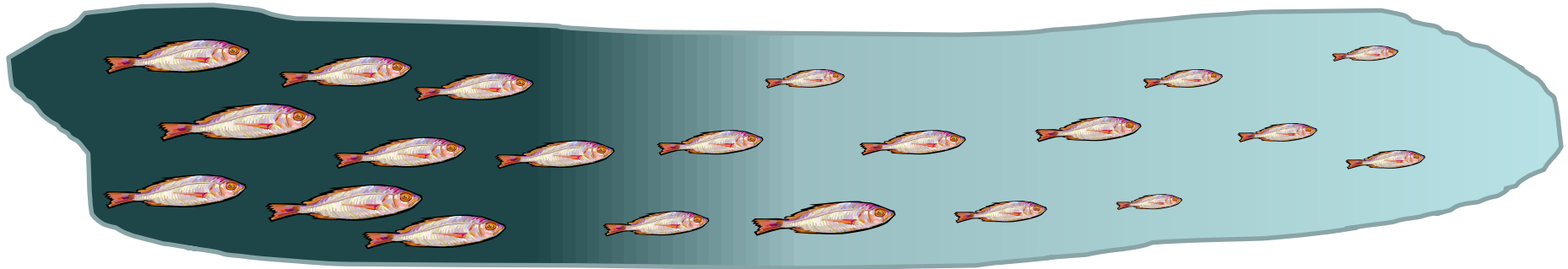


# The process of parapatric speciation: Step 2

**Spatially variable selection drives local adaptation**

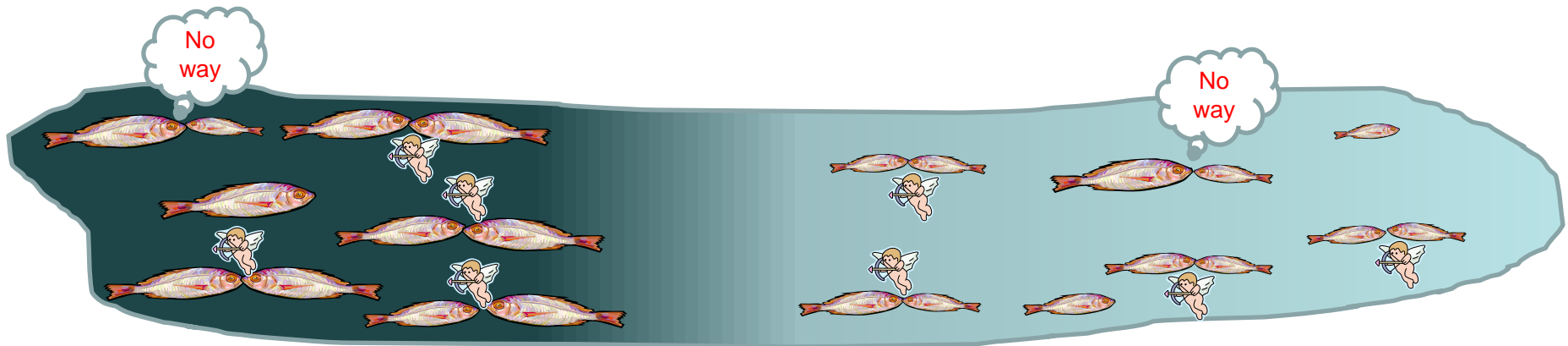
**Deep water selects  
for large fish**

**Shallow water  
selects for small fish**



# The process of parapatric speciation: Step 3

**Selection favors the evolution of pre-zygotic isolating mechanisms because such mechanisms reduce the production of less fit offspring with intermediate phenotype → gene flow reduced or eliminated**



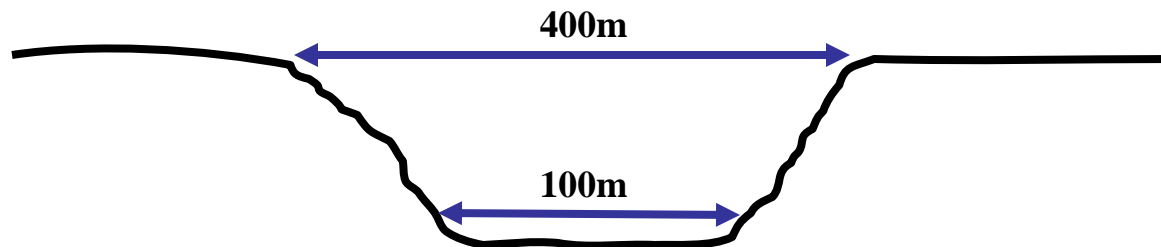
# The process of parapatric speciation: an example from 'Evolution canyon' Israel



**North facing slope  
(Cool and wet)**



**South facing slope  
(Hot and dry)**



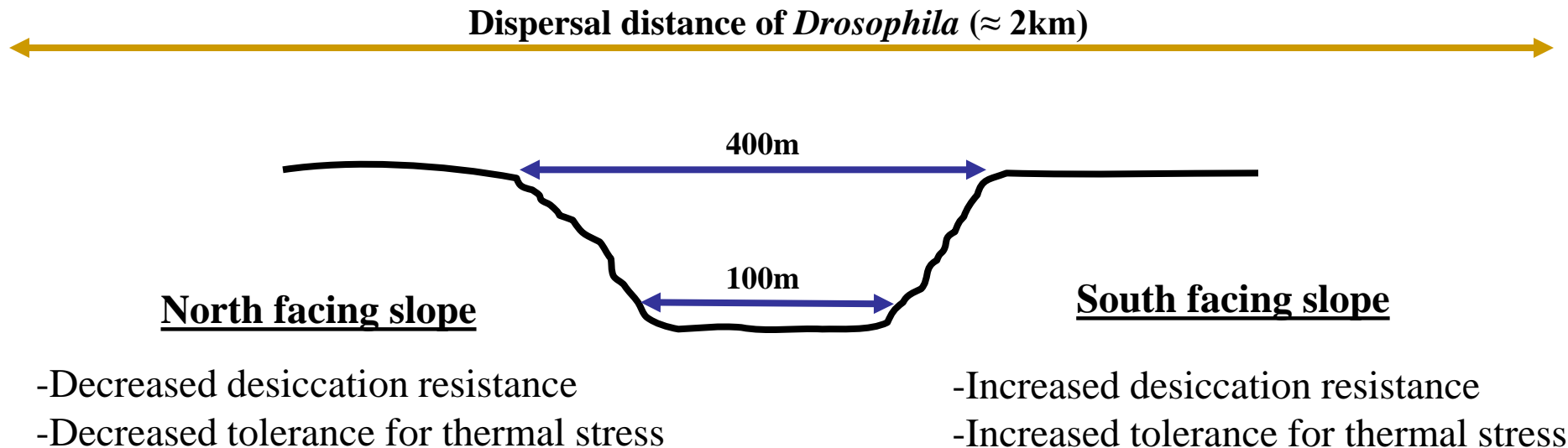


# Parapatric speciation: an example from 'Evolution canyon' Israel



*Drosophila  
melanogaster*

**Genetic differences for adaptive traits persist on the different sides of the canyon despite the potential for substantial gene flow**



# Parapatric speciation: an example from 'Evolution canyon' Israel

## How are these adaptive differences maintained?

- **Strong assortative mating exists**
- **South side males prefer south side females and vice versa**
- **North side males prefer North side females and vice versa**

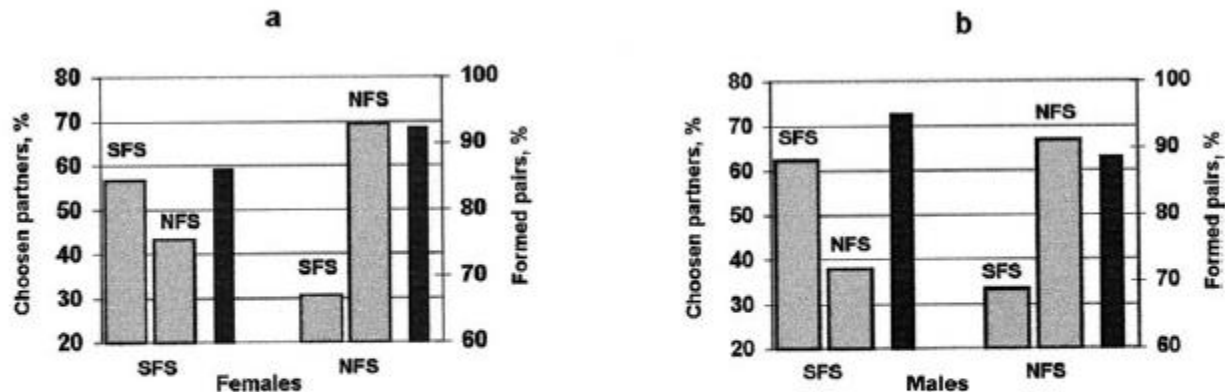


Fig. 1. Single mate-choice tests. (a) Female choice; (b) male choice. Proportions of pairs resulting from same- and other-slope choice are presented. The black column on the right-hand side for each test represents the percent of formed pairs (of a possible 78 pairs total for each test). For a detailed analysis of the results, see Table 3.

# Parapatric speciation: an example from 'Evolution canyon' Israel

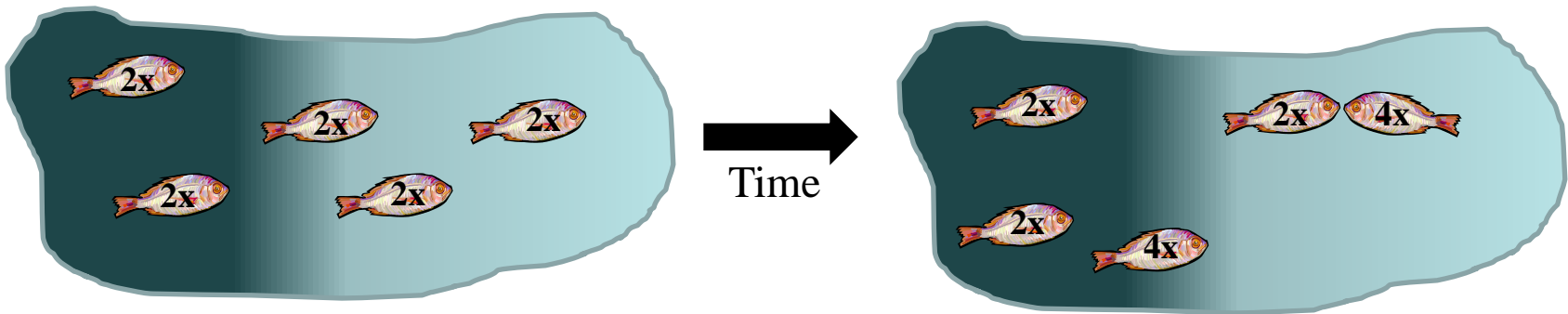
- **Studies of neutral loci suggest that substantial genetic differentiation exists between south side and north side populations**
- **These studies estimate that the number of migrants per generation,  $Nm$ , is somewhere between .405-.562.**
- **This result demonstrates that genetic differentiation is occurring despite the potential for significant gene flow between north and south side populations.**
- **Taken together, these results suggest that these flies may be in the process of speciation.**

# Sympatric speciation

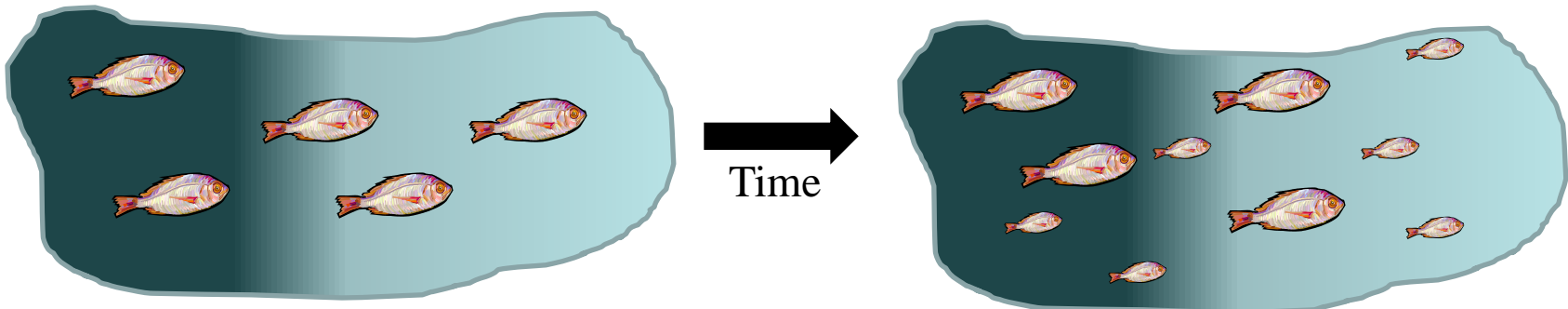
*The evolution of reproductive isolation within a single randomly mating population*

Sympatric speciation can occur in two ways:

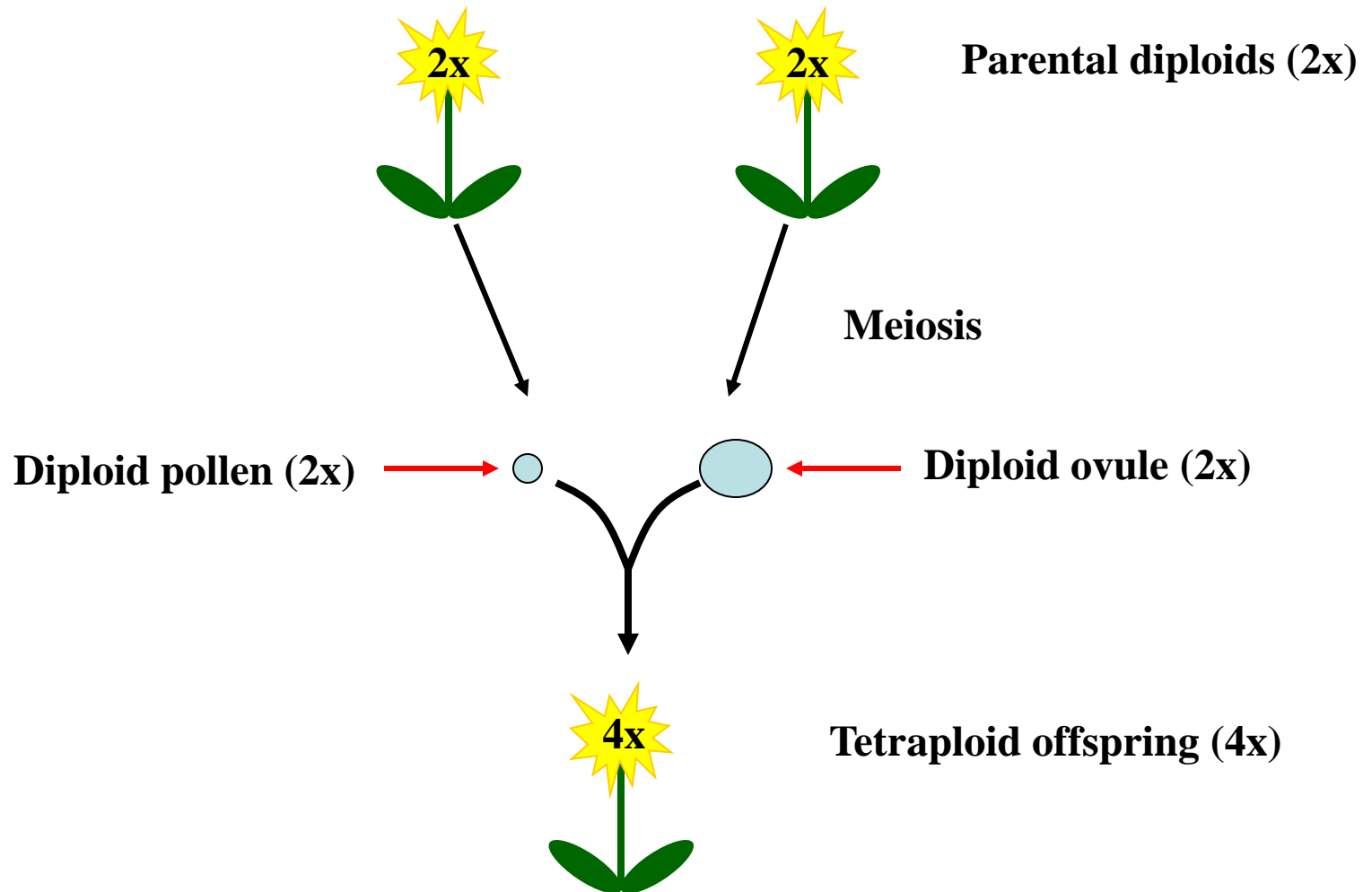
## 1. Instantaneous post-zygotic isolation



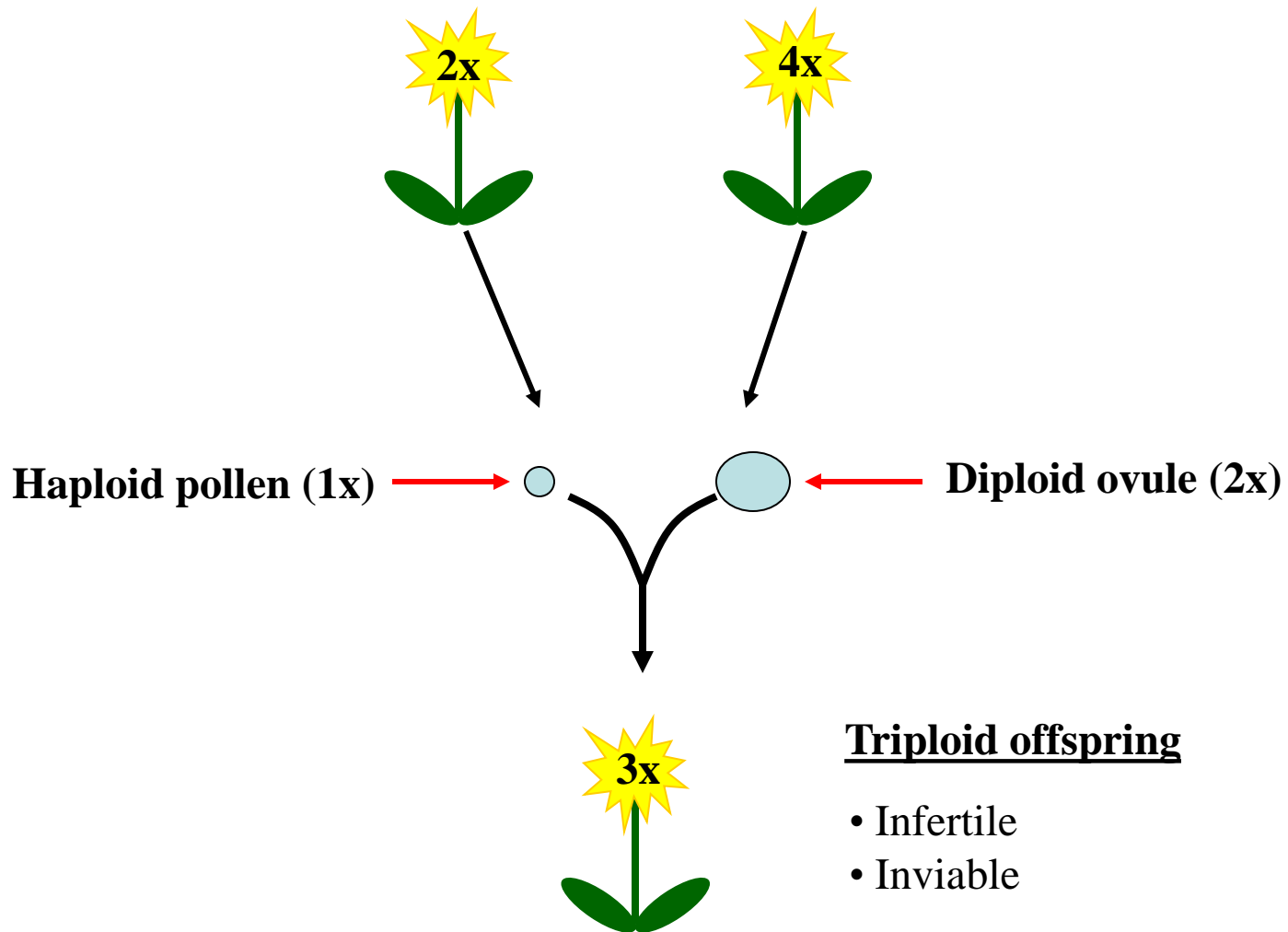
## 2. Adaptive or ecological speciation



# The process of instantaneous sympatric speciation: polyploidy



# The process of instantaneous sympatric speciation: polyploidy



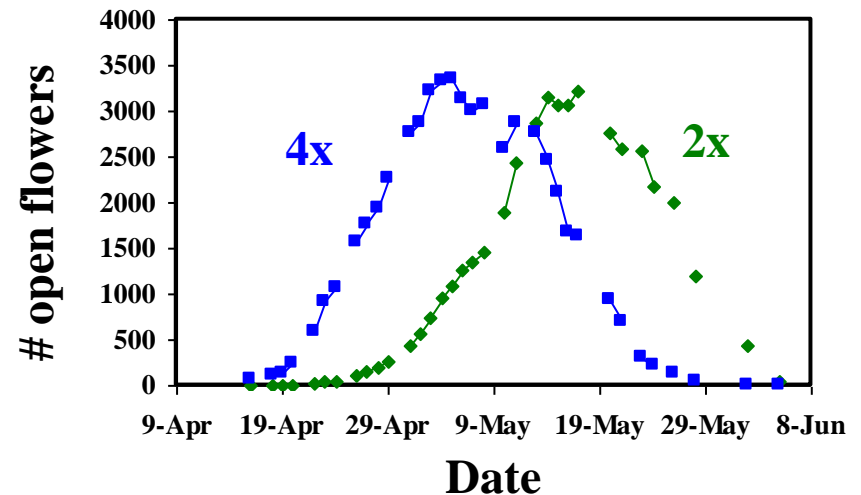
**As a result, polyploidy generates immediate reproductive isolation and sympatric speciation**

# The process of instantaneous sympatric speciation: an example from *Heuchera grossulariifolia*



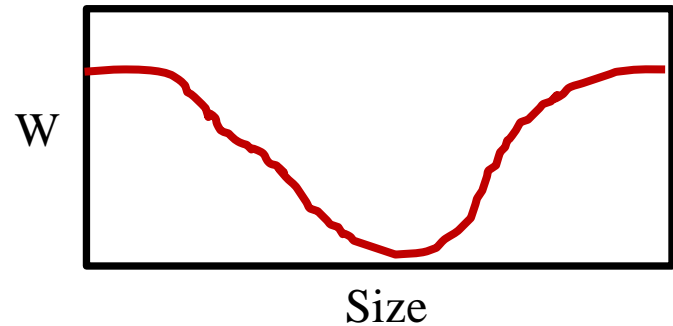
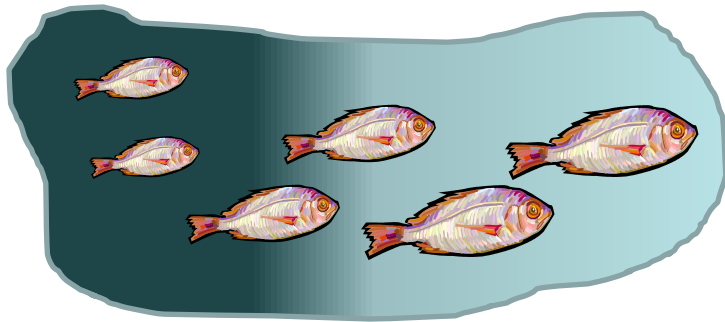
*Heuchera grossulariifolia* on the Salmon River

- Autotetraploid plants have formed multiple times
- Triploid hybrids have low fitness and low fertility
- The two ploidies have diverged greatly in morphology and phenology



# The process of adaptive sympatric speciation: Step 1

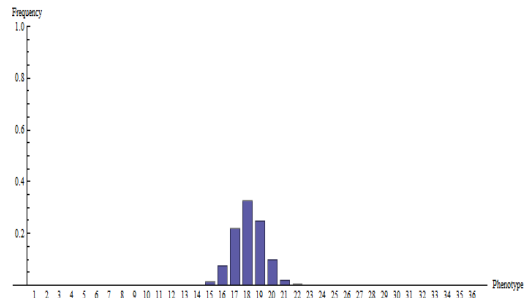
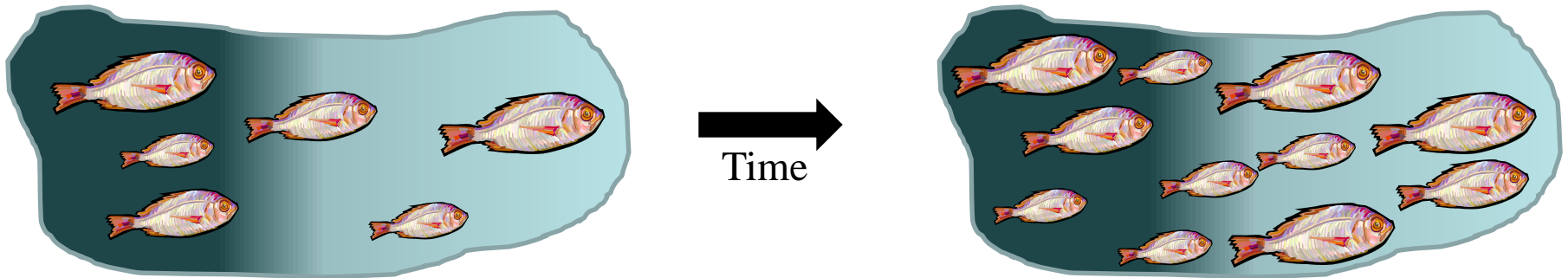
**Begin with a species composed of a single panmictic population. Individuals with similar phenotypes compete more intensely than individuals with disparate phenotypes**





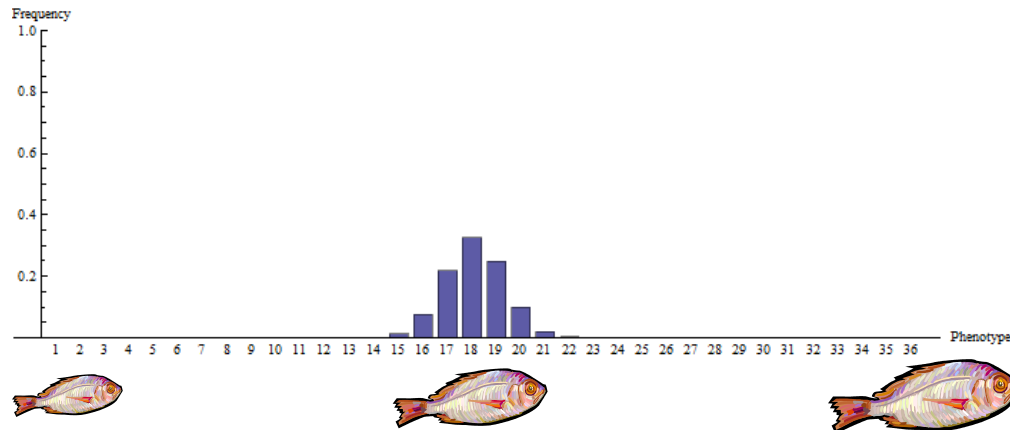
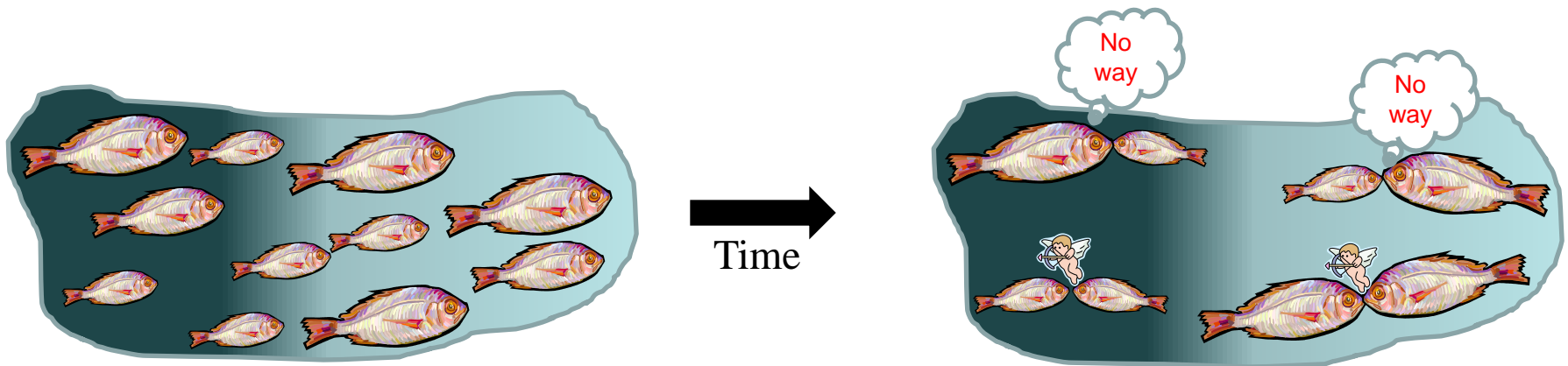
# The process of adaptive sympatric speciation: Step 2

Because individuals with extreme phenotypes compete less, extreme phenotypes are favored by natural selection and begin to increase in frequency within the population



# The process of adaptive sympatric speciation: Step 3

Because extreme individuals which mate with extreme individuals of the other type produce intermediate and unfit offspring, assortative mating is favored by natural selection, leading to the elimination of intermediate phenotypes



# The process of adaptive sympatric speciation: an example from apple maggot fly



Mmmmm... Yummy!

*Rhagoletis pomonella*  
(apple maggot fly)

# An example of host race formation



**Native Hawthorne**

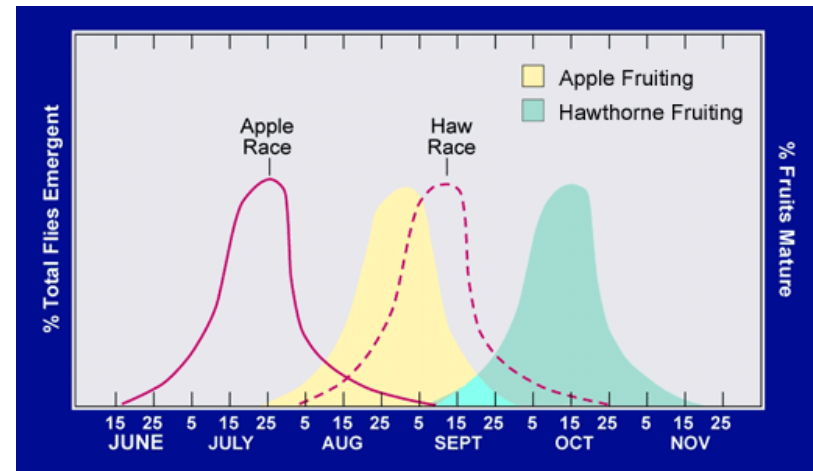


**Apple**  
**Introduced  $\approx$  1647**

- **Flies originally used native Hawthorne species as hosts**
- **Populations (species?) of flies now use introduced apple**
- **These plants grow sympatrically**

# Testing for host race formation

- Flies on apples emerge earlier
- Apple flies prefer to mate with apple flies rather than Hawthorne flies and vice versa
- Apple flies have higher fitness on apples than on Hawthorne and vice versa
- Substantial genetic divergence exists between apple and Hawthorne fly populations
- Appears to be a case of sympatric speciation ‘in action’



# Practice Question

A group of scientists is studying the evolution of insecticide resistance in a recently identified insect parasite of garbanzo bean crops, *Trichoplusia Garbanzi*. Research to date has demonstrated that the strength of selection favoring a novel (dominant) insecticide resistance gene is  $s \approx .054$  within populations living in Garbanzo fields and thus exposed to seasonal insecticide application. Additional research has demonstrated that as long as the frequency of this novel insecticide resistance gene remains below 0.23 within populations living in Garbanzo fields, the population density of *T. Garbanzi* remains sufficiently low for the Garbanzo crop to be financially viable. In an effort to understand whether gene flow from wild populations of *T. Garbanzi* not exposed to insecticide (where the insecticide resistance gene is absent) will swamp the evolution of insecticide resistance within cultivated fields and thus avert financial catastrophe, the scientists have estimated the rate of gene flow from wild populations into cultivated fields as  $m \approx .026$ .

Use this data, along with the equation shown below which predicts the equilibrium frequency of a selectively favored allele in the face of maladaptive gene flow,

$$\hat{p}_{Island} = 1 - \frac{\sqrt{m}}{\sqrt{s}}$$

to answer the following questions:

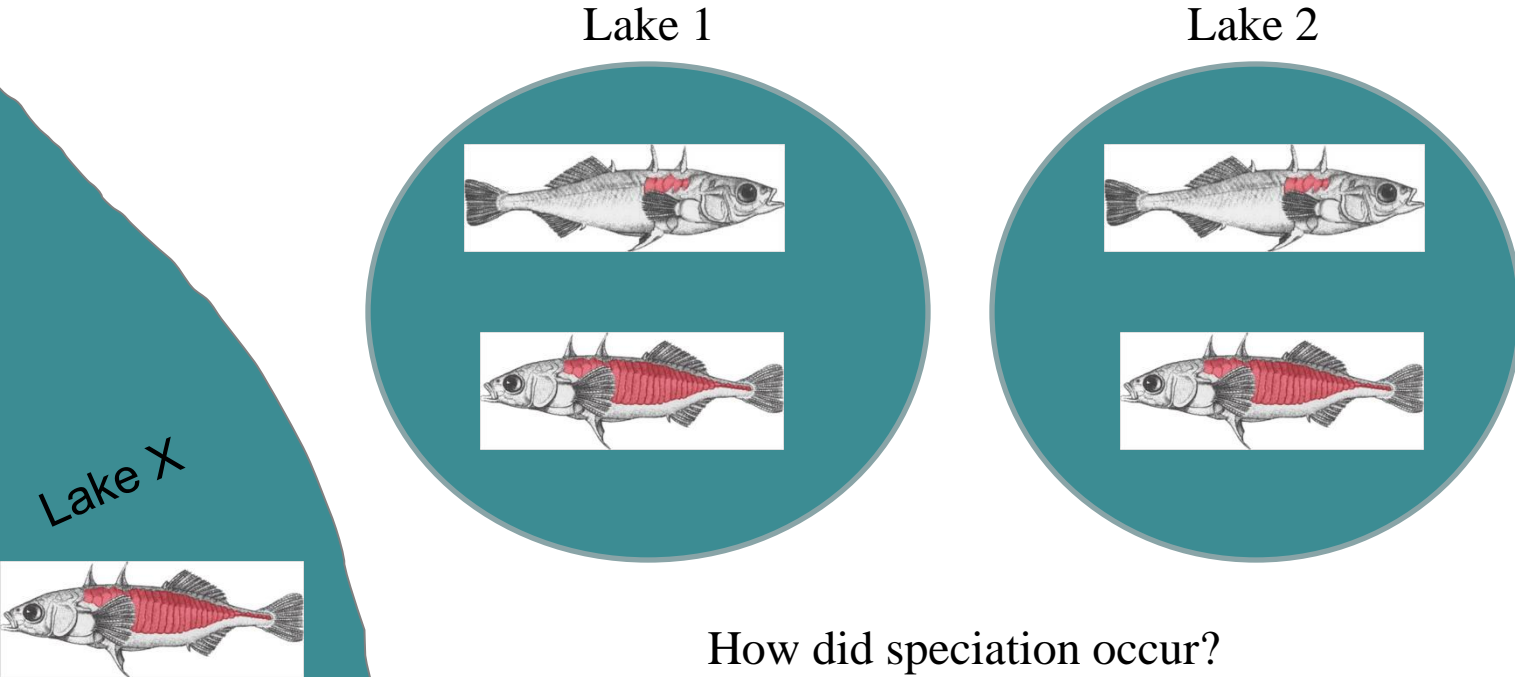
A. Do you predict that the Garbanzo crop will remain financially viable, or that insecticide resistance will evolve beyond the critical threshold and the crop decimated?

B. If your answer to (A) predicts evolution beyond the critical threshold, how much would the strength of selection need to be reduced (by decreasing the use of insecticide) in order to prevent the decimation of the Garbanzo crop?

C. If your answer to (A) predicts evolution will fail to drive insecticide resistance beyond the critical threshold, how much could the strength of selection be increased (by increasing the use of insecticide) without jeopardizing the Garbanzo crop?

# How can we infer the process by which speciation occurred?

- We have covered examples that illustrate the *process* of speciation
- Demonstrating that current species pairs formed through a particular mechanism, however, is extremely difficult and very contentious

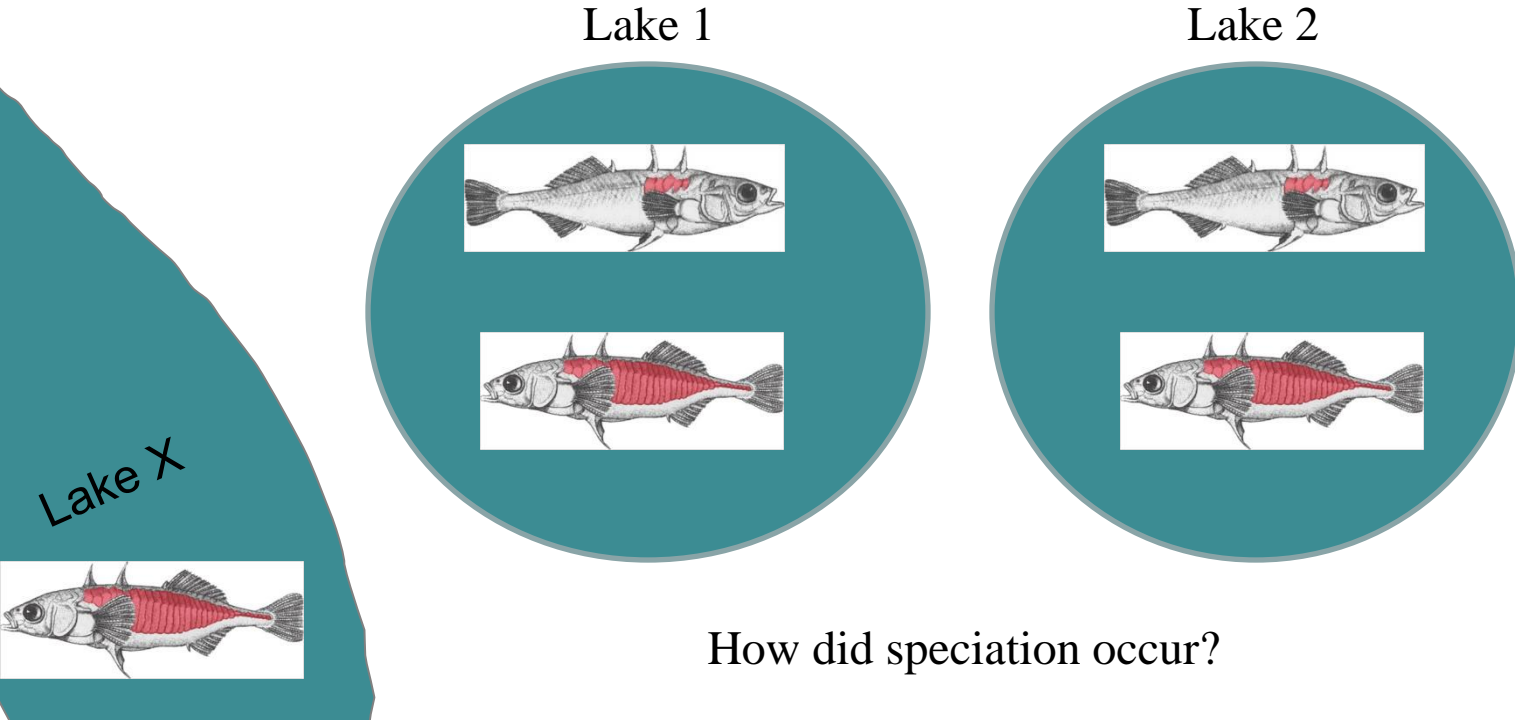


# Some hypotheses...

H1: Two sympatric speciation events

H2: Speciation in allopatry followed by recolonization

H3: Speciation in allopatry followed by dispersal and extinction

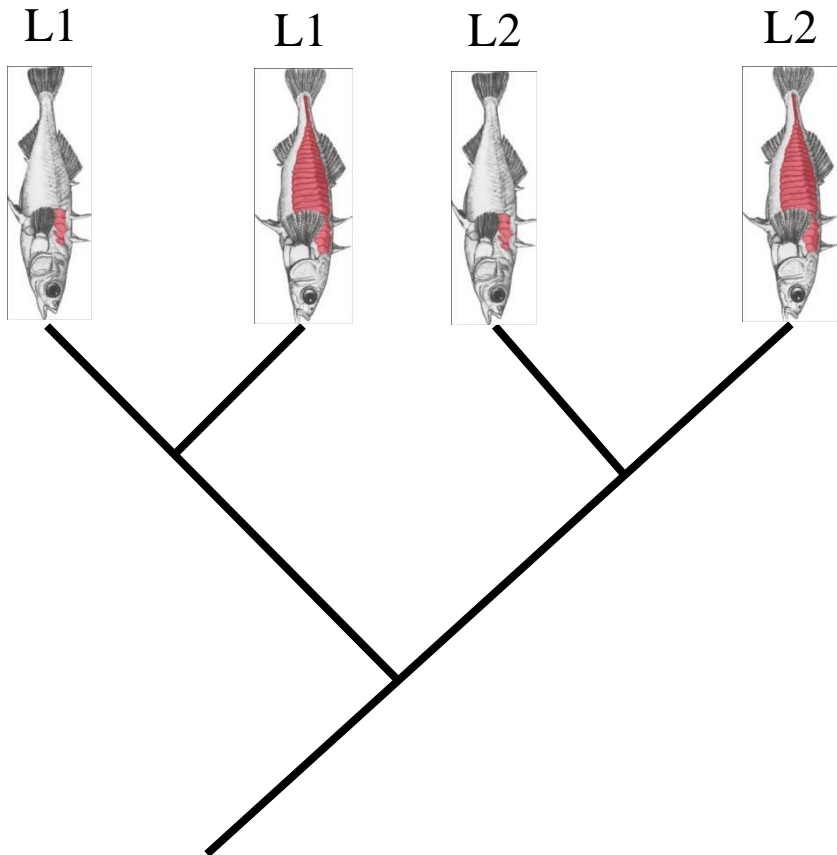




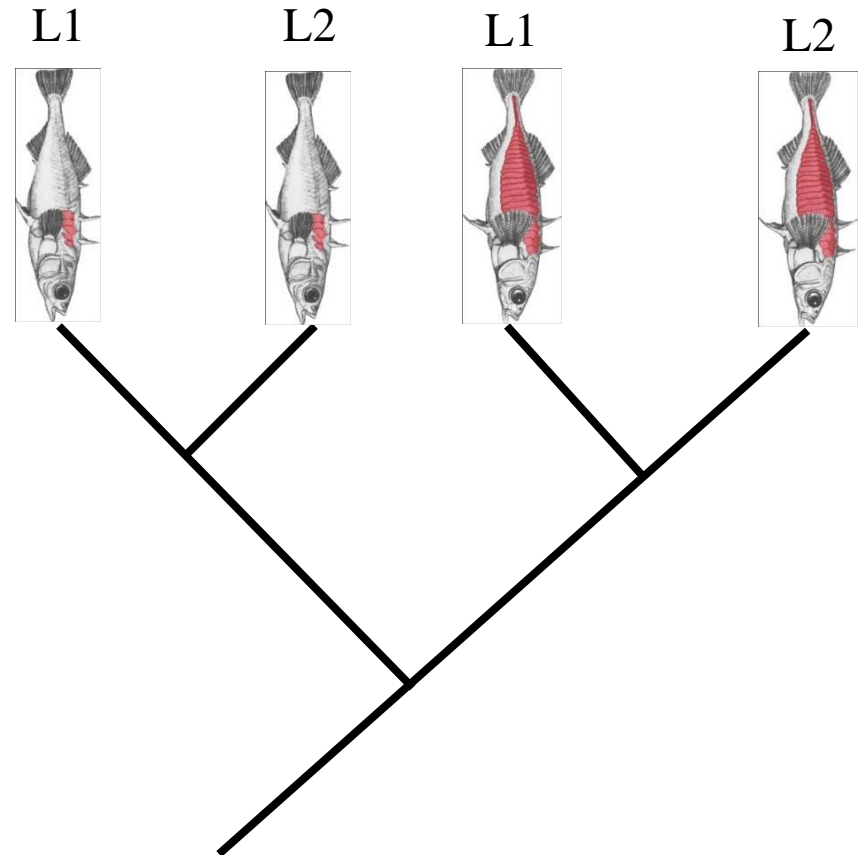
# How can we infer the process by which speciation occurred?

Using phylogenies to infer the mechanism of speciation

Possible phylogeny 1

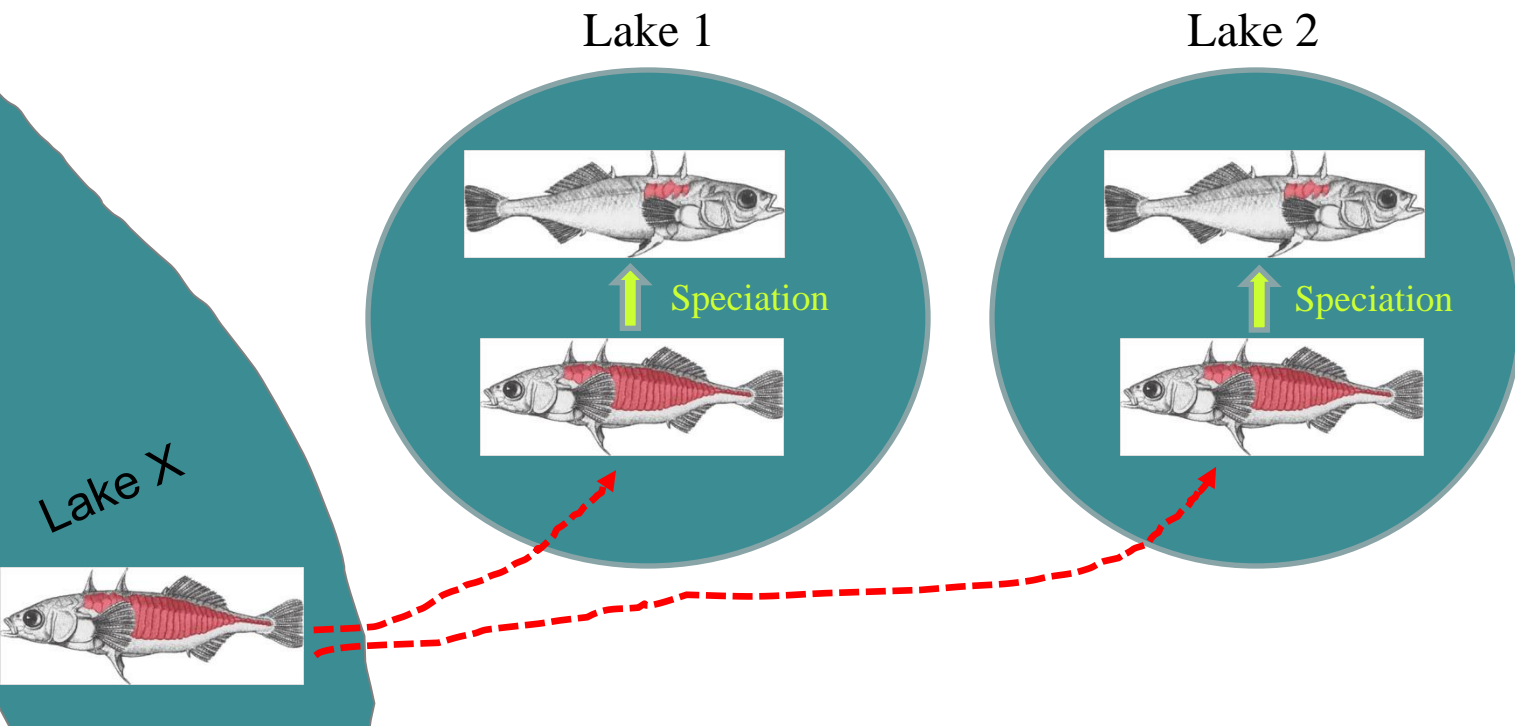


Possible phylogeny 2



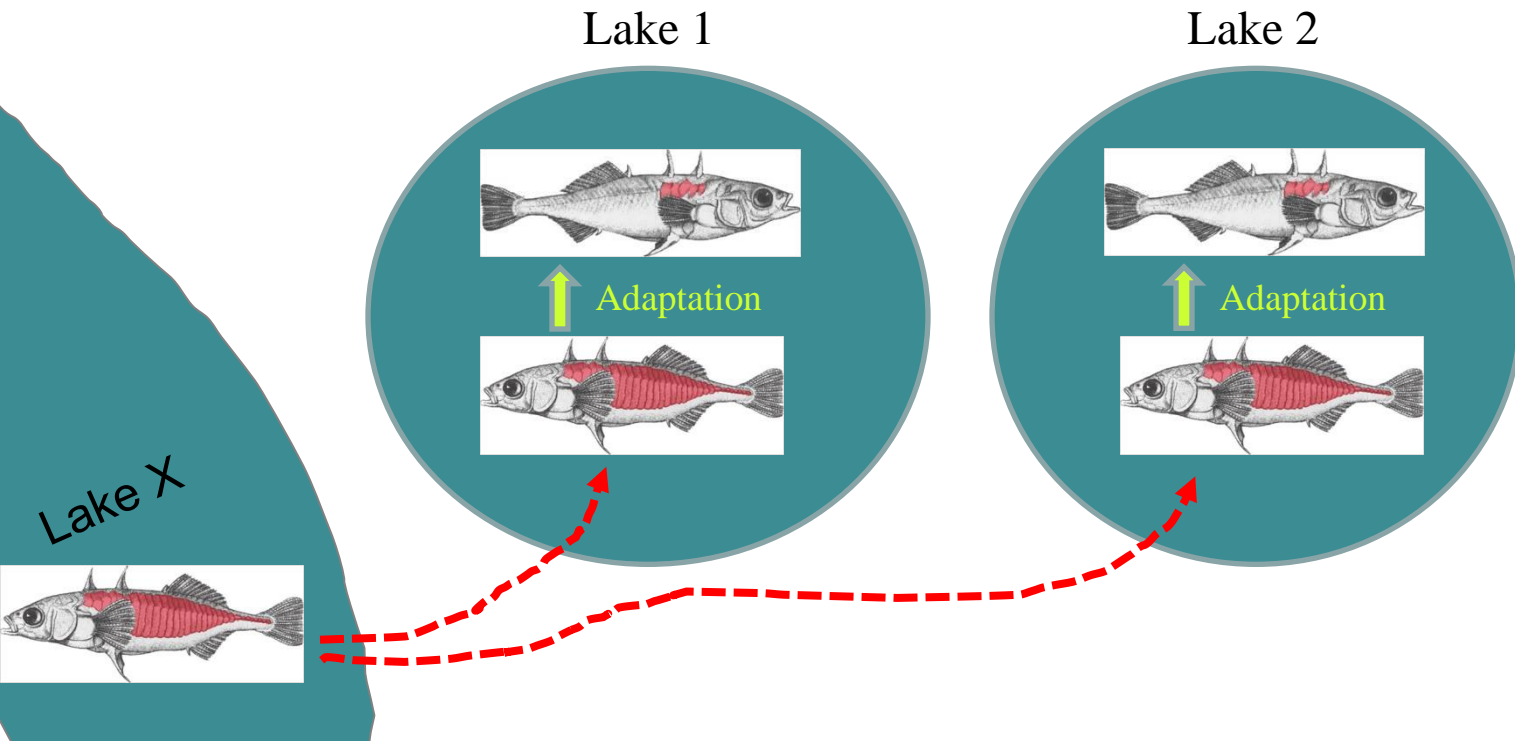
How did speciation occur?

# Phylogeny 1 suggests sympatrically



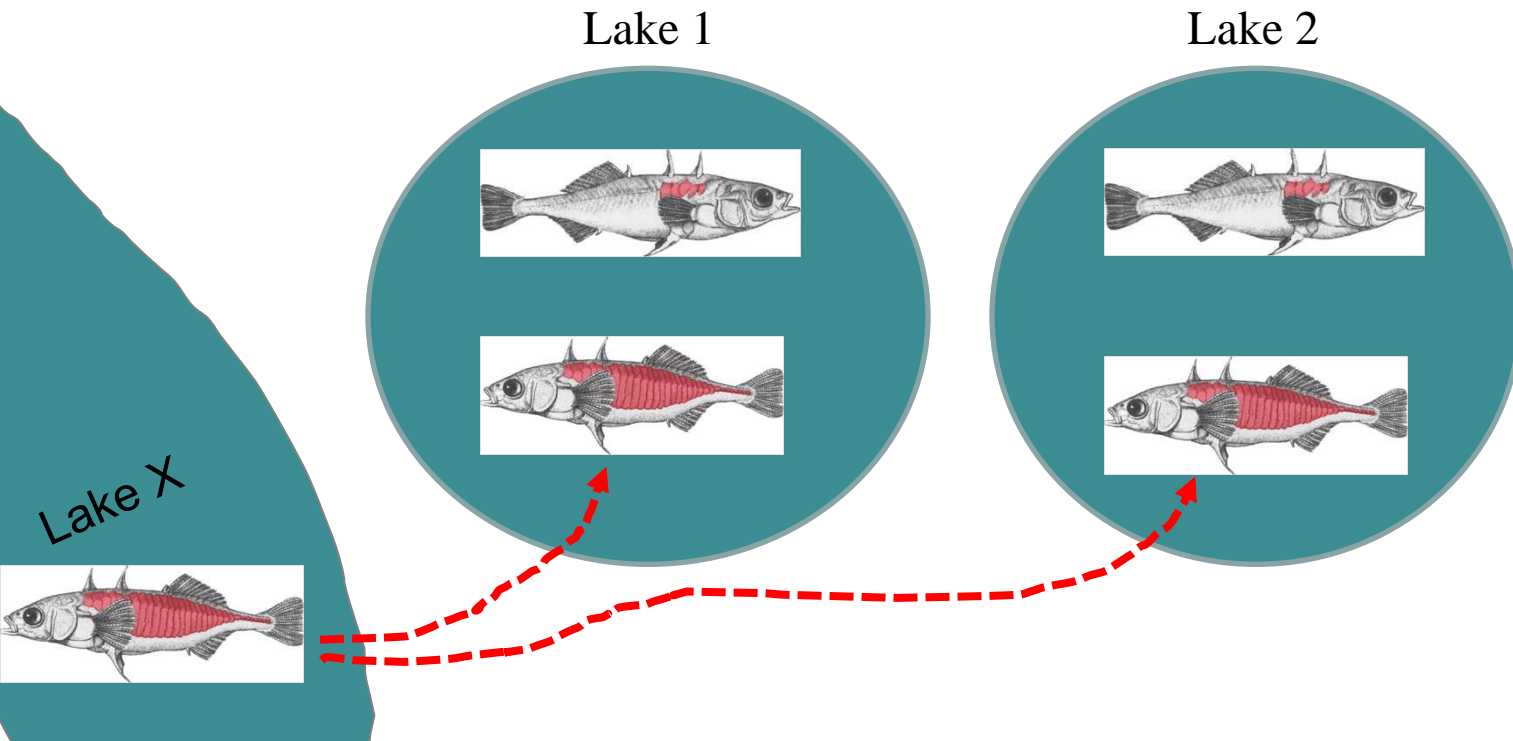
# Phylogeny 2 suggests allopatrically

Step 1: Both lakes colonized, adaptation to lakes causes formation of new species in allopatry



# Phylogeny 2 suggests allopatrically

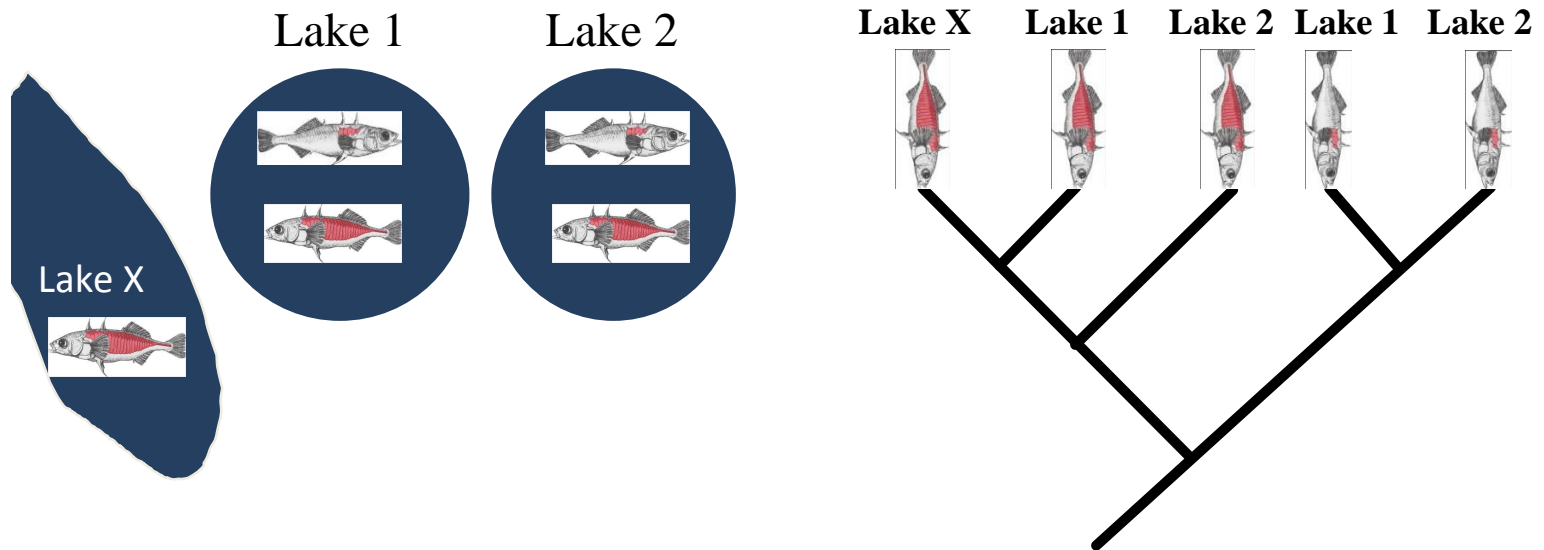
Step 2: After a significant amount of time, lakes are re-colonized



# Summary of Speciation

- Species are maintained through pre-zygotic and post-zygotic isolating mechanism
- Speciation can occur in sympatry, parapatry, or allopatry
- Studying the process of speciation is relatively easy, and we have good evidence for each process
- In contrast, inferring how existing species actually formed is very difficult and contentious

A group of researchers studying the morphology of stickleback species living in three freshwater lakes in British Columbia has found that Lake X has a single species with an armored phenotype, Lake 1 has two species, one armored and one unarmored, and Lake 2 has two species, one armored and one unarmored as shown in the figure below (left side). Based on this work, these researchers published a paper claiming that their work demonstrates two independent sympatric speciation events, one within Lake 1 and one within Lake 2. As part of your graduate research, you constructed a phylogeny of these species based on molecular markers. Your phylogeny is shown on the right.



Does your phylogeny support or refute the researchers' claim of two independent sympatric speciation events (10pts)? **Justify your response in four sentences or less (30pts).**