Ecology and speciation

1) What are species

2) Reproductive isolation evolves with time

3) Spatial separation increases likelihood of speciation.

4) Speciation frequency increases with area

5) Speciation is driven by selection

6) Rapid speciation in postglacial fishes

7) Tests of ecological speciation

8) Speciation and sexual selection

9) Example exam questions

On the Origin of Species
by Means of Natural Selection,
or the Preservation of Favoured Races
in the Struggle for Life

Charles Darwin, M.A.,
Fellow of the Royal, Geological, Linnæan, etc. societies; Author of Journal of researches during H.M.S. Beagle's Voyage round the world.

London: John Murray,
Albemarle Street, 1859

Introduction

WHEN on board H.M.S. Beagle, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species; that mystery of mysteries, as it has been called by one of our greatest philosophers. On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it. After five years' work I allowed myself to speculate on the subject, and drew up some short notes; these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me probable: from that period to the present day I have steadily pursued the same object. I hope that I may be excused for entering on these personal details, as I give them to show that I have not been hasty in coming to a decision.

1) What are species

Darwin’s definition of species

“I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other...”

“...the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties.”

– Darwin (1859)

1) What are species

Biological species concept

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

- Mayr (1942)

Speciation question: How does reproductive isolation evolve?

1) What are species

Biological species concept

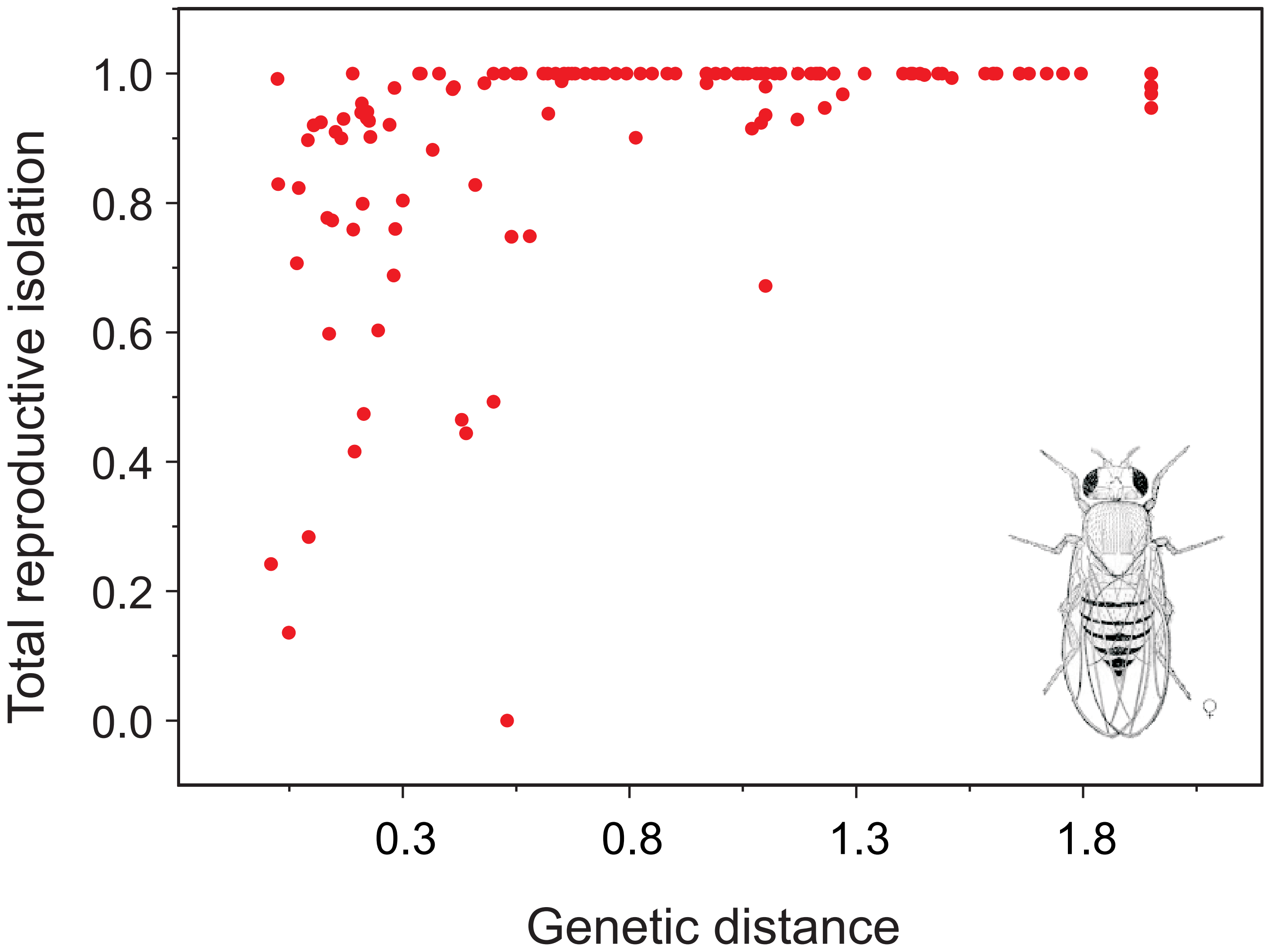
Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

- Mayr (1942)

Reproductive isolation refers to *evolved* characteristics of populations that prevent gene flow, rather than geographic barriers.

Reproductive isolation need not be 100 percent (absolutely no gene flow) between species. Many, perhaps most, species hybridize to some degree with closely related species. Good species are “mostly” reproductively isolated.

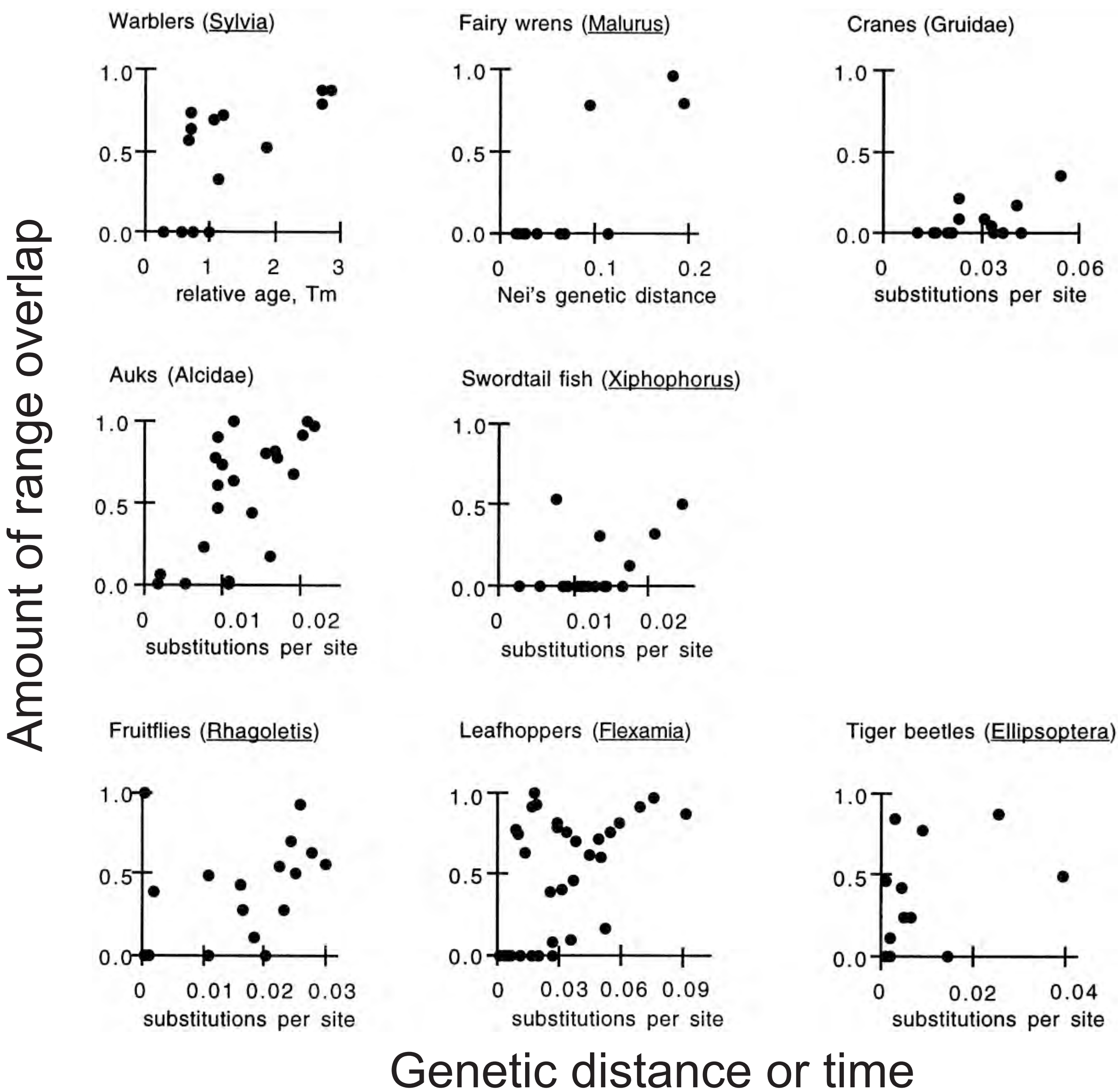
2) Reproductive isolation evolves with time



Each dot in this figure indicates a pair of fly (*Drosophila*) species or subspecies. The *y*-axis indicates the total amount of reproductive isolation between them. The *x*-axis indicates their genetic difference, reflecting their age.

Coyne & Orr (2004) Speciation

3) Spatial separation increases likelihood of speciation



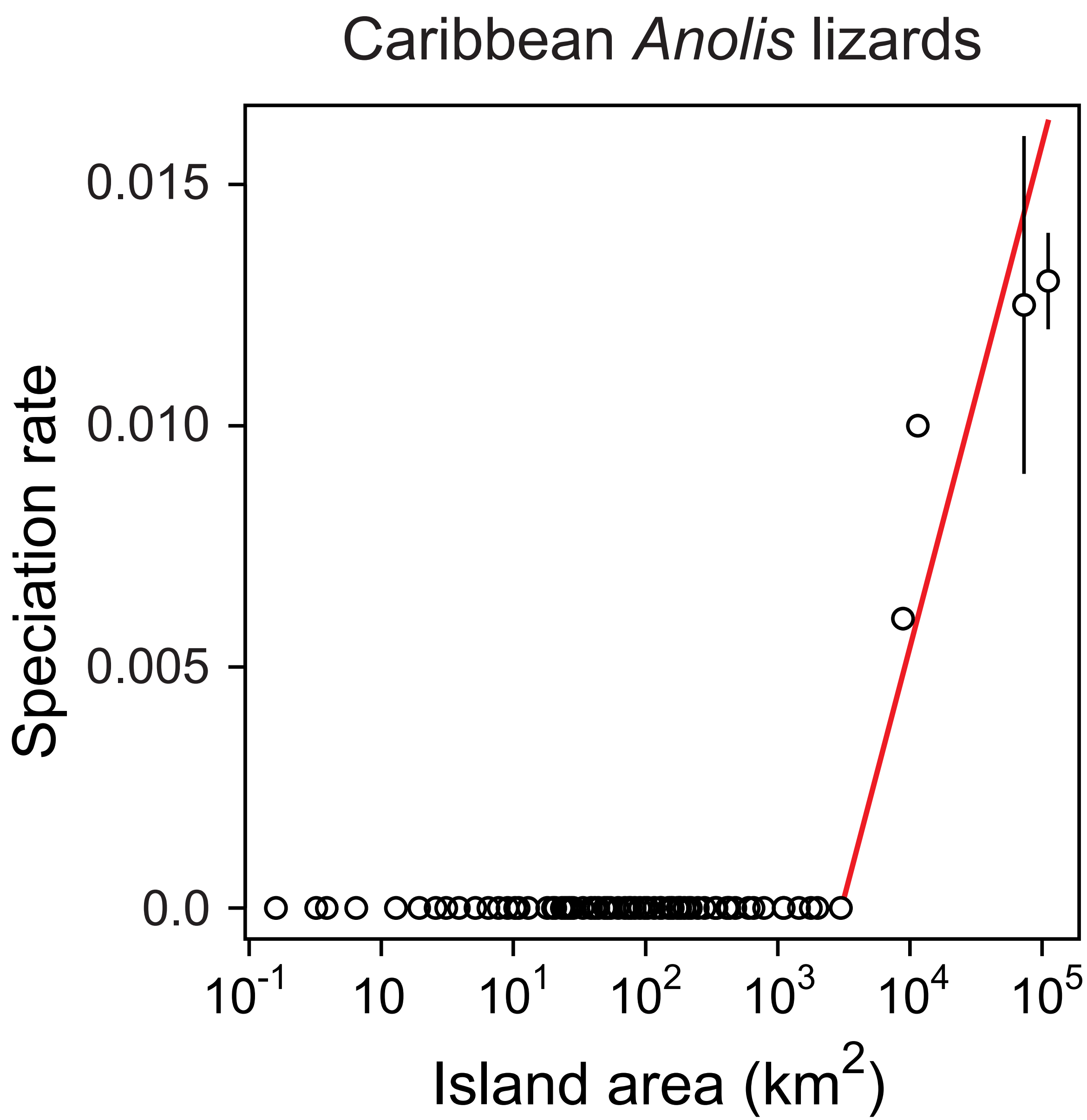
Young species tend to be spatially separated.

Older species tend to have greater overlap of geographic ranges.

Barraclough & Vogler (2000) *Am Nat*

4) Speciation rate increases with area

Each dot in this figure is a Caribbean island. Speciation in *Anolis* lizards has taken place within islands only on the largest islands.

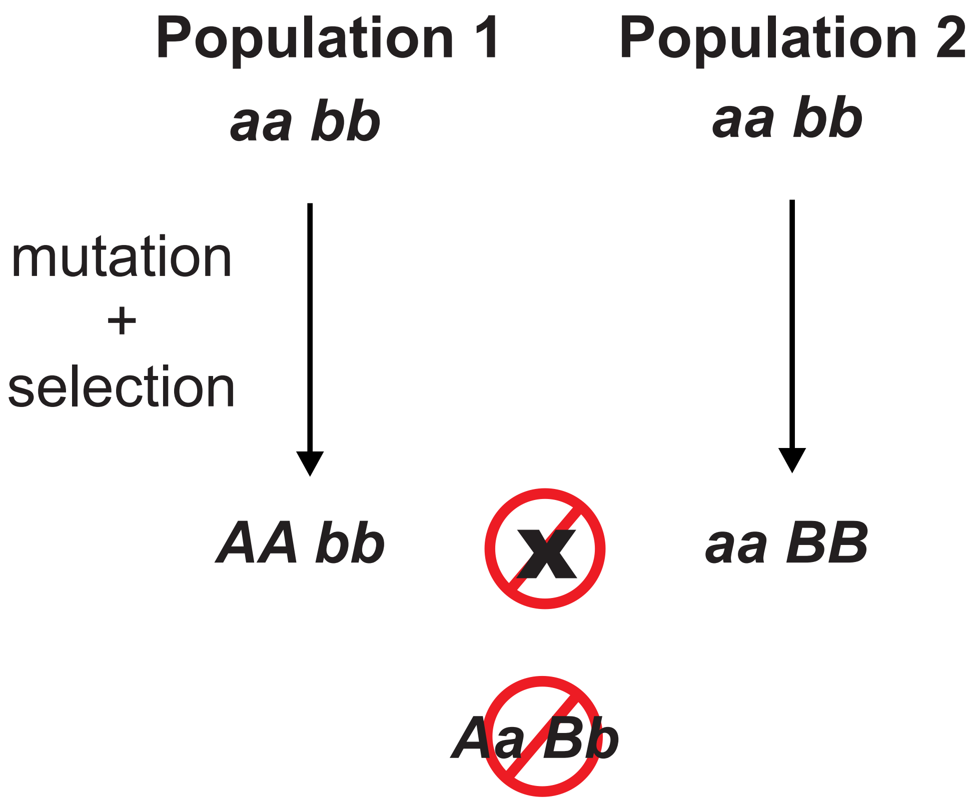


Losos & Schluter (2000) *Nature*

5) Speciation is usually driven by selection

"...the formation of isolating mechanisms entails building up of systems of complementary genes" – Dobzhansky (1937, 256)

Two populations initially genetically identical



The two populations accumulate genetic differences through time because of mutation and selection.

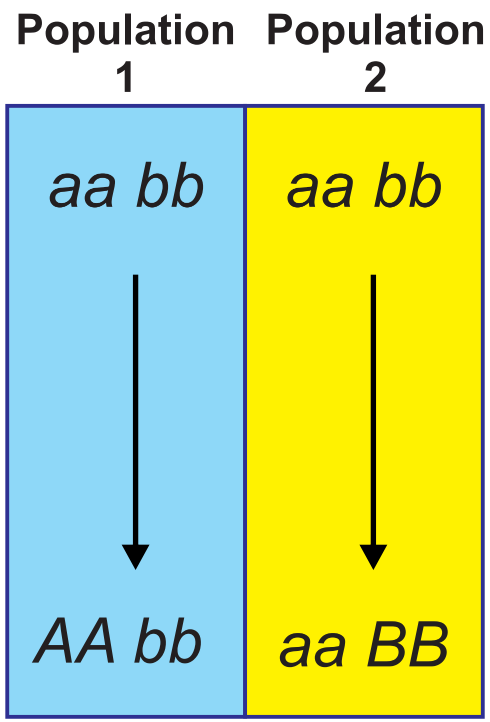
Eventually, these genetic differences cause individuals to avoid encountering/mating with one another,

or they cause problems in the hybrid offspring of individuals

5) Speciation is usually driven by selection

Hypothesis of *ecological speciation*:
Reproductive isolation evolves as a by-product of divergent natural selection between environments.

Two populations in *different* environments



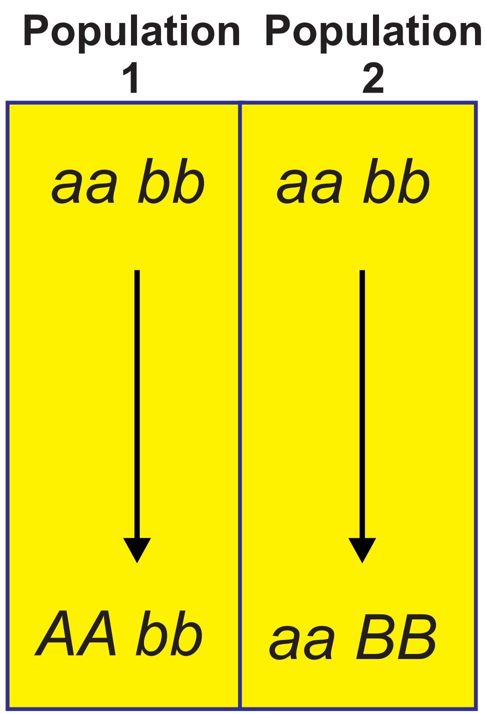
Under divergent natural selection, *different* alleles are favored in different environments, causing populations to diverge genetically.

This is potentially how adaptation to ecological environments can lead to the origin of new species.

5) Speciation is usually driven by selection

Hypothesis of “mutation-order” speciation:
Reproductive isolation evolves via the spread of different, incompatible mutations despite similar selection pressures.

Two populations in *similar* environment

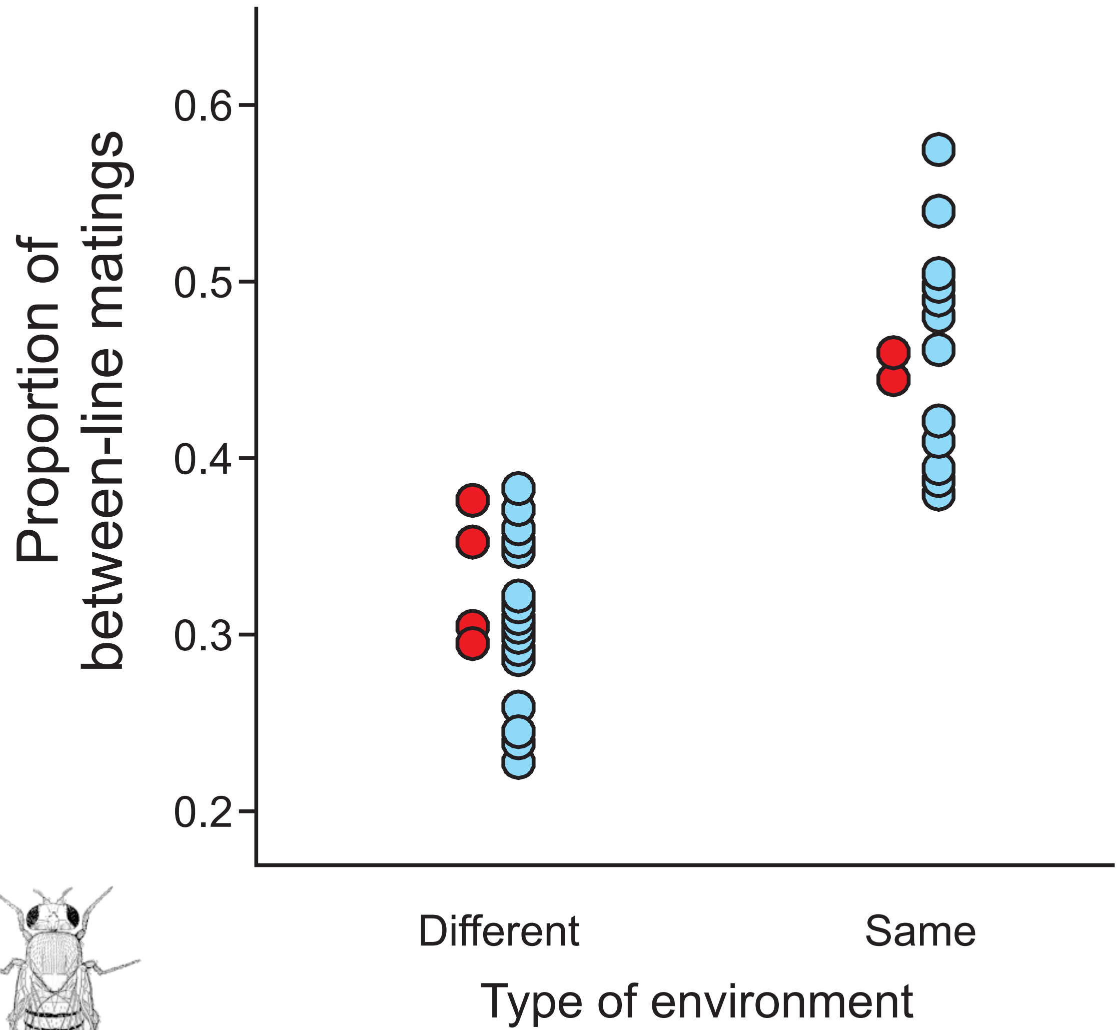


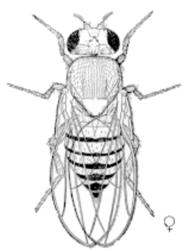
Selection pressures are similar on the two populations.

But by chance, populations experience different mutations. The different mutations would be favored in both populations, but each arises and spreads in just one, causing populations to diverge genetically.

5) Speciation is usually driven by selection

The “parallel evolution test” of ecological speciation in the lab





Each dot in this figure estimates the probability of mating between two experimental fly populations evolving for many generations either in the same environment or in different environments.

Repeatedly, greater reproductive isolation has evolved between the populations evolving in different environments than between populations evolving in similar environments.

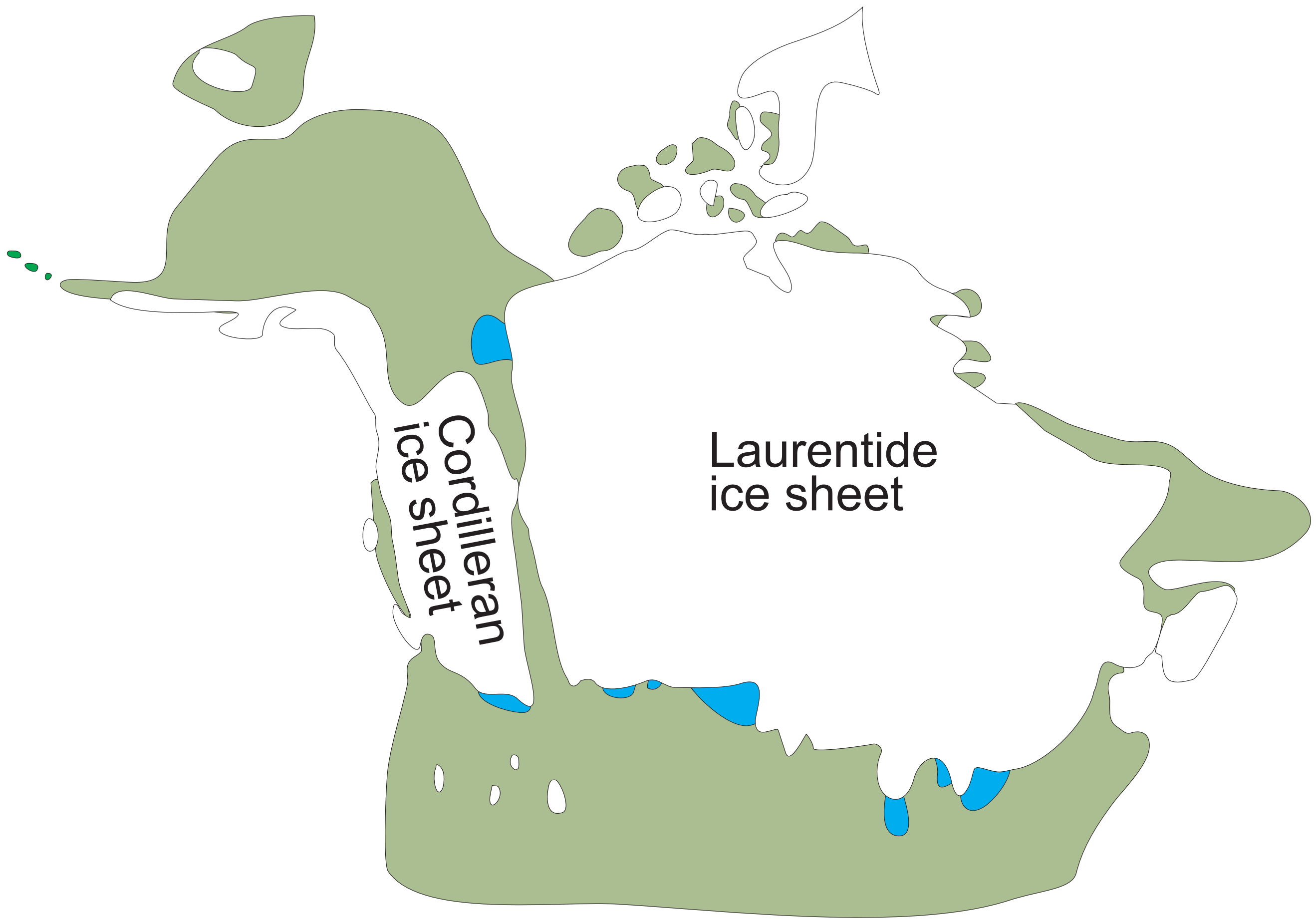
The red and blue dots are from two separate studies and experiments – both show the same pattern.

This pattern is consistent with the ecological model and inconsistent with the mutation-order model for the evolution of reproductive isolation.

6) Rapid speciation in postglacial fishes

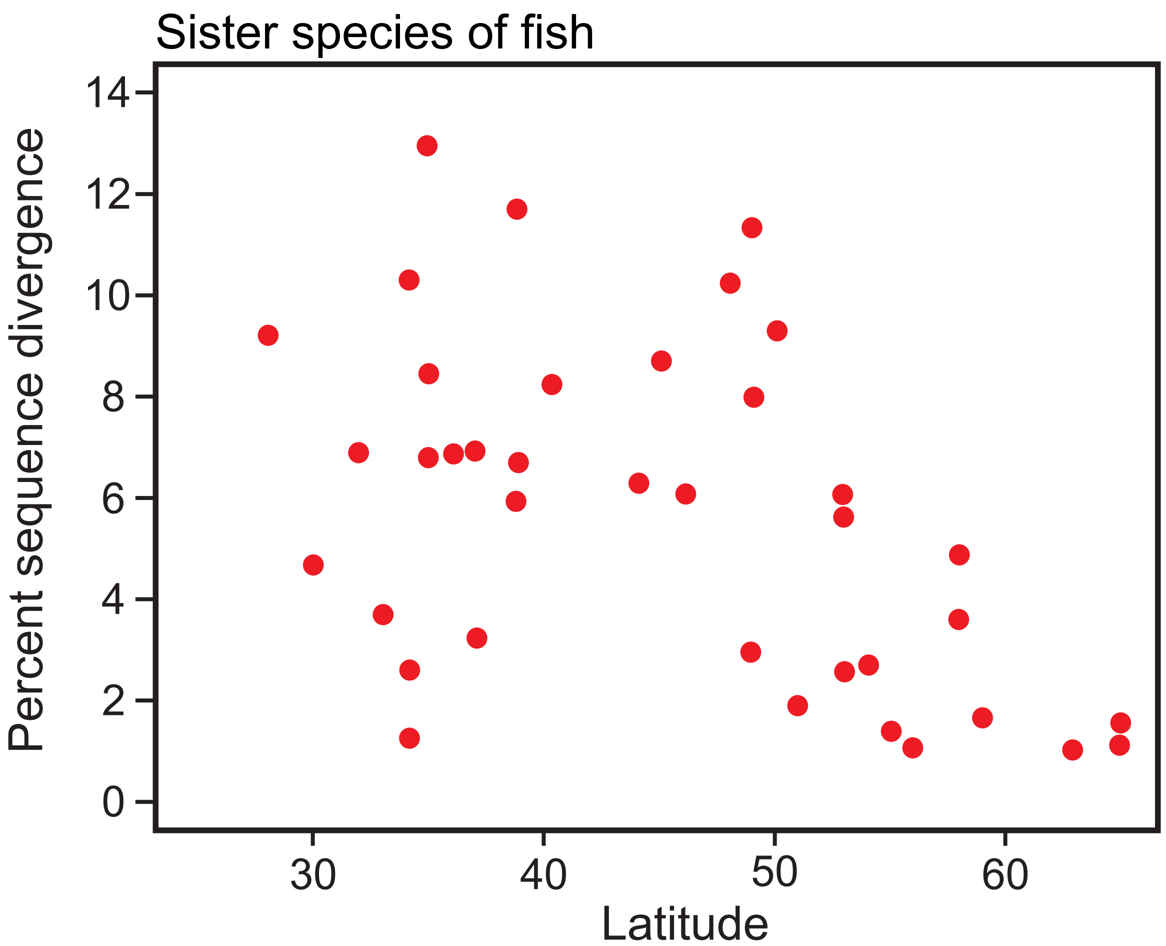
Are similar processes responsible for the origin of species in nature?

Northern N. America 13,000 years ago



6) Rapid speciation in postglacial fishes

Fish species at high latitudes tend to be younger, on average



Each dot in this figure is a pair of closely related fish species. The *y*-axis is genetic difference (reflecting age) and the *x*-axis is the midpoint of their latitudinal ranges.

6) Rapid speciation in postglacial fishes

Even younger species are found in some postglacial bodies of water

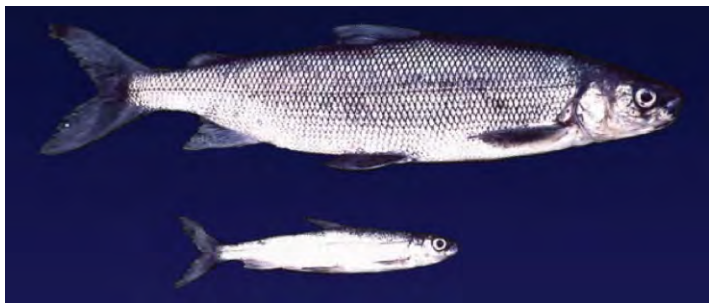
smelt

sockeye

benthic - limnetic stickleback

marine - stream stickleback

whitefish



7) Tests of ecological speciation

Employ the parallel evolution test

We can use the same test as in the laboratory experiments on flies. Compare the amount of reproductive isolation between populations that have evolved in similar versus different ecological environments.

Paxton Lake | Priest Lake | Little Quarry Lake

Benthic species

Limnetic species

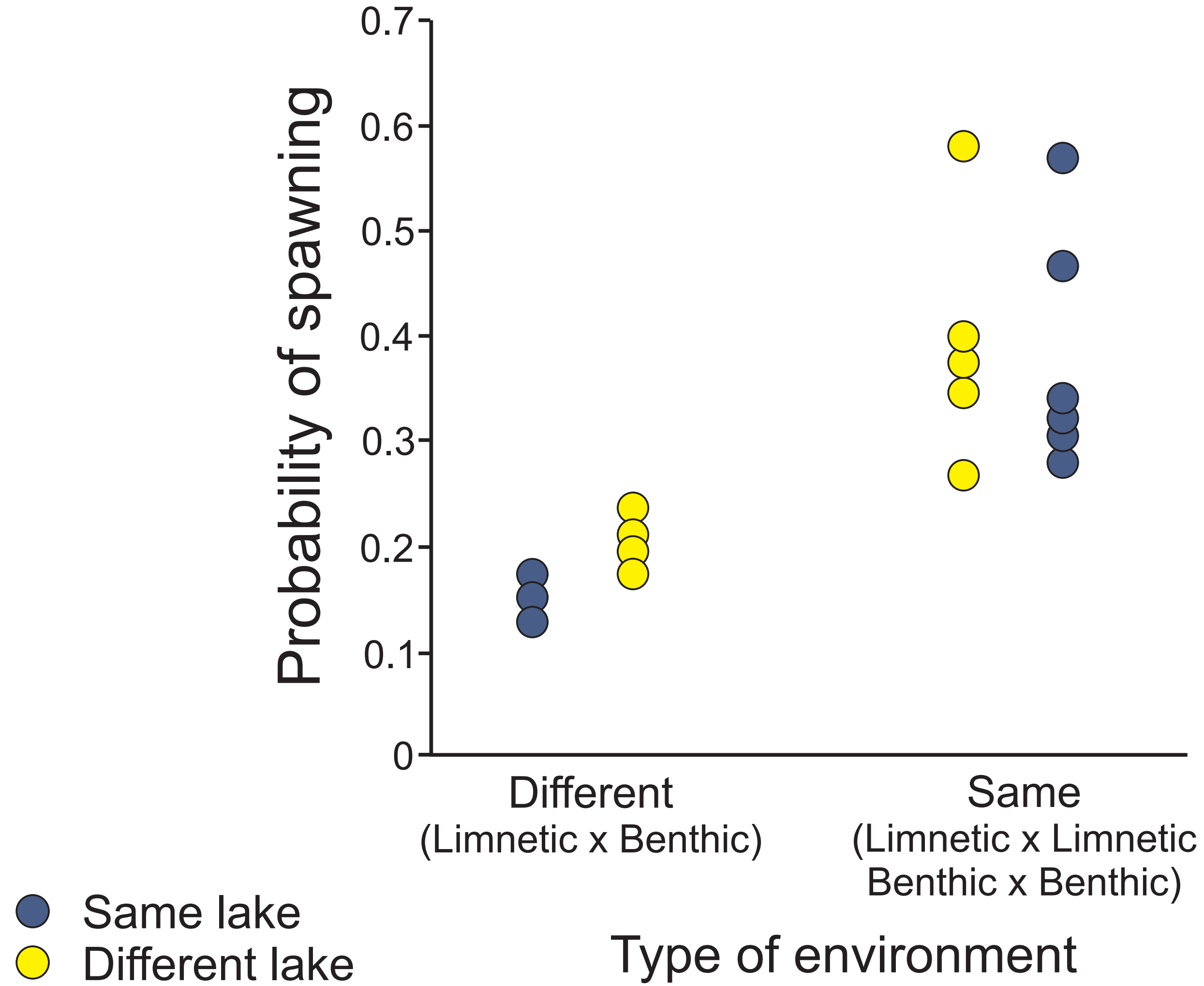
Photos: Ken Thompson

7) Tests of ecological speciation

Lab mating trials using wild-caught fish

7) Tests of ecological speciation

The parallel speciation test with stickleback



Each dot in this figure estimates the probability of mating between two stickleback populations evolving either the same environment or in different environments.

Repeatedly, more reproductive isolation has evolved between populations evolving in different environments than between populations evolving in similar environments.

7) Tests of ecological speciation

The reason is that mating preferences have evolved in concert with parallel adaptations to their two environments, especially body size.

Paxton Lake | Priest Lake | Little Quarry Lake

Benthic species

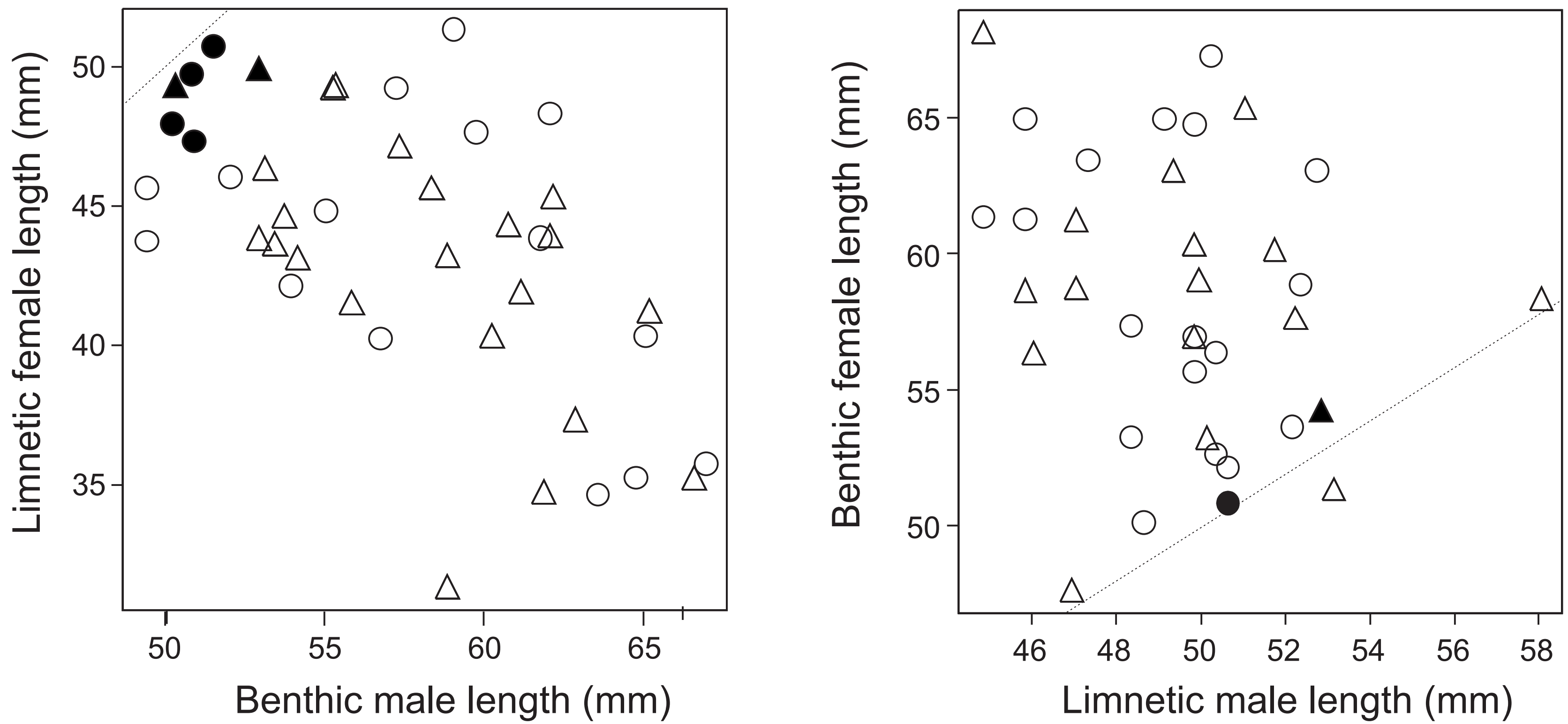
Limnetic species

Photos: Ken Thompson

7) Tests of ecological speciation

Probability of hybridizing depends on similarity of body size

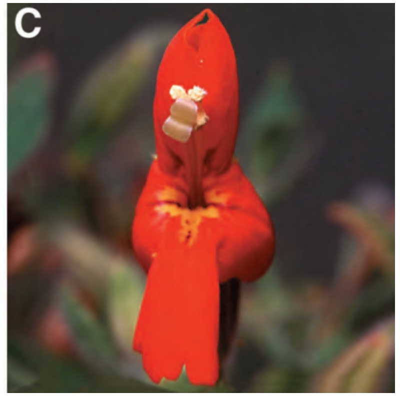
Each dot in the plot indicates the body sizes (length) of male and female fish that were paired during mating trials. The filled dots indicate trials that resulted in spawning; open dots indicate no spawning. The dotted lines indicate size equality, *Y=X*



Within-lake trials: Paxton Lake ○, Priest Lake △

7) Tests of ecological speciation

A second case study in which ecological adaptations are also associated with mating patterns and reproductive isolation



Mimulus lewisii
- bee-pollinated
- pink flowers low in anthocyanin and carotenoid pigments
- wide corolla
- small volume of nectar
- inserted anthers and stigma
- petals thrust forward, a wide landing platform
- ridges of brushy hairs (nectar guides)
- wet habitats between1600m and 3000 m

M. cardinalis
- hummingbird-pollinated
- red flowers high in anthocyanin and carotenoid pigments
- narrow tubular corolla
- a large nectar reward
- exerted anthers and stigma
- reflexed petals

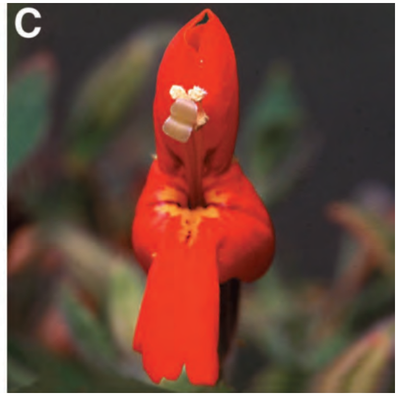
- no nectar guides
- wet habitats from sea level to 2000 m

Schemske & Bradshaw (1999) *PNAS*

7) Tests of ecological speciation

Trait differences represent adaptations to contrasting pollinators, whose preferences then cause reproductive isolation between the plant species.

Mimulus lewisii



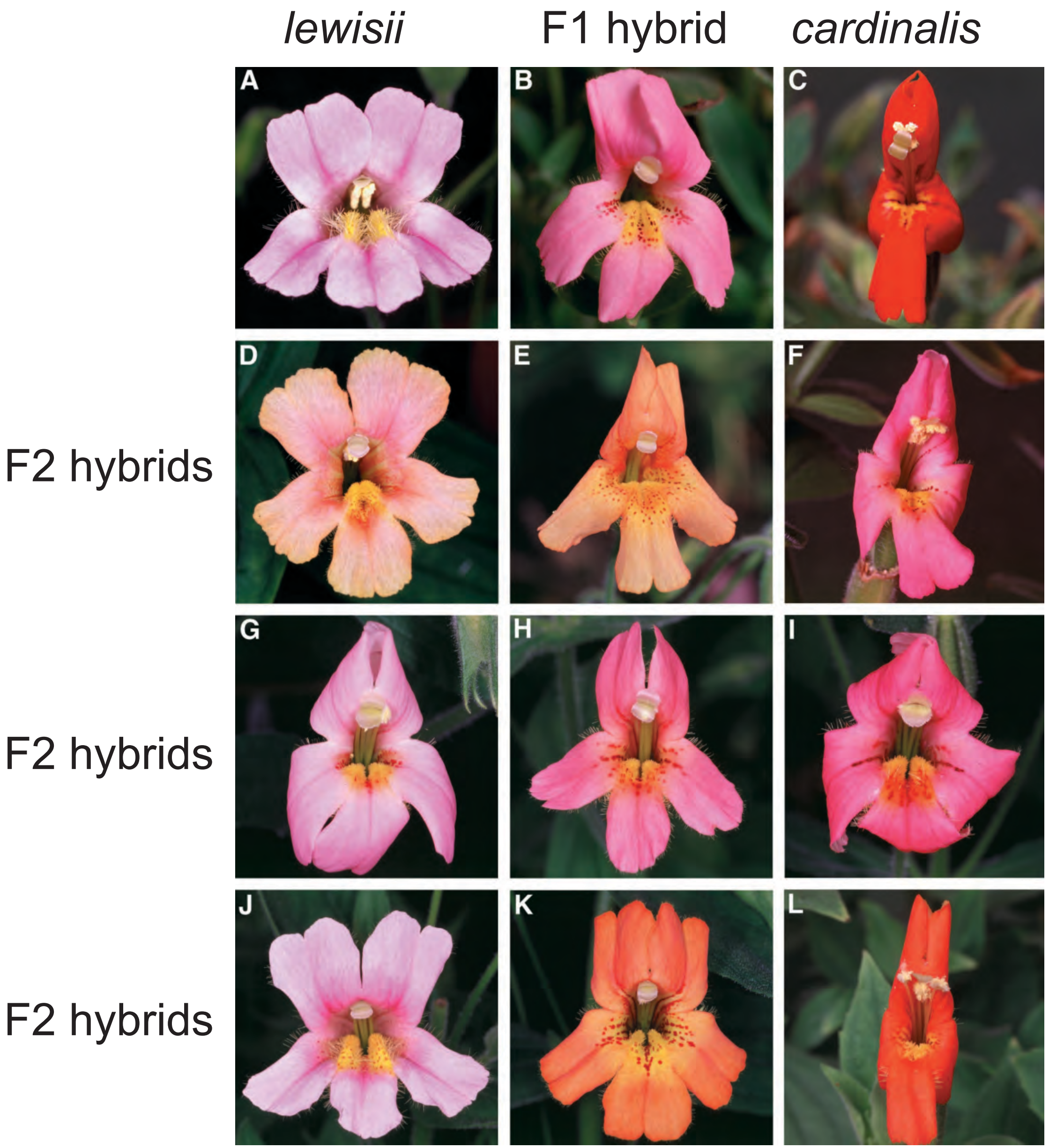
M. cardinalis

Despite striking morphological differences, the two monkeyflower species are very closely related.

The floral traits that confer pollinator specificity (bee vs hummingbird) also contribute to premating reproductive isolation.

Schemske & Bradshaw (1999) carried out a field experiment to investigate what floral traits caused pollinator discrimination and the genetic basis of the traits. They used genetic markers to determine the genetic basis of pollinator visitation.

7) Tests of ecological speciation



The researchers generated F2 hybrids in the lab in Seattle, creating an experimental population in which different traits varied more or less independently.

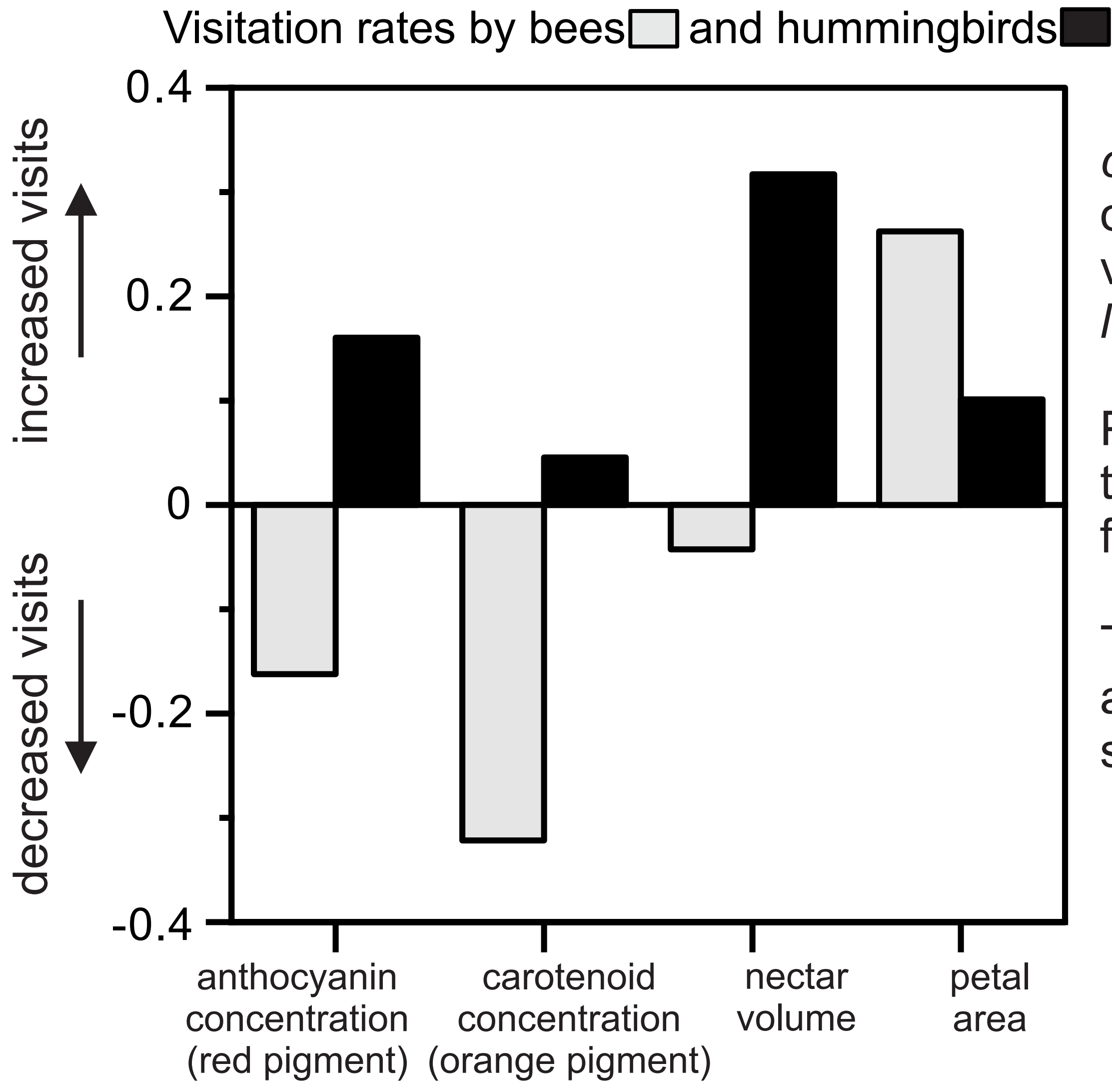
They transported the plants in pots to plots in Yosemite National Park where the field experiment was carried out.

They then correlated the visitation rates by bees and by hummingbirds to characteristics of the F2 plants.

Schemske & Bradshaw (1999) *PNAS*

7) Tests of ecological speciation

Specific traits linked to pollinator preference



cardinalis has high concentrations of the two pigments, high nectar volume, and small area, whereas *lewisii* has the opposite.

Pollinators choose based on the traits that most differentiate the flowers of the two species.

These traits thus contribute to assortative mating between the species.

Schemske & Bradshaw (1999) *PNAS*

7) Tests of ecological speciation

Specific traits linked to pollinator preference

lewisii

cardinalis

Near-isogenic lines of *M. lewisii* and *M. cardinalis* with alternate alleles at the YUP locus. The wild-type allele at the YUP locus (left) has been substituted with the allele from the other species (right).

YUP controls carotenoid concentrations in petals (high in *cardinalis,* low in *lewisii*). The *cardinalis* allele produces red flowers when present with a high concentration of anthocyanins.

This single gene had substantial effects on pollinator preference and thus could affect reproductive isolation.

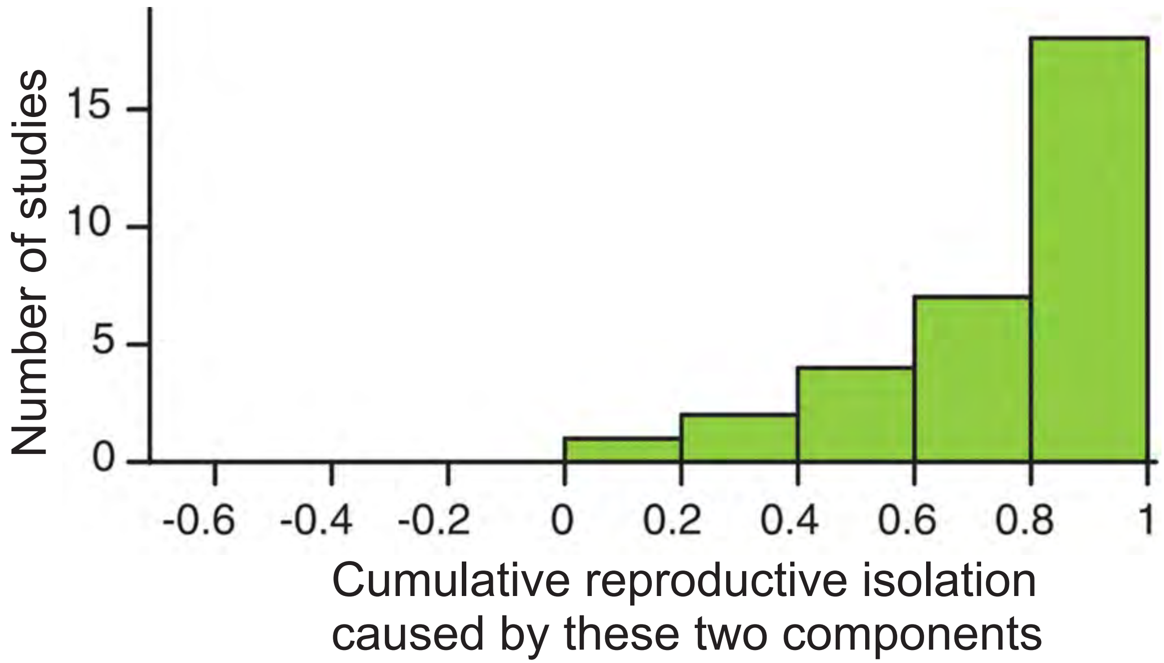
	Bees (visits per 1000 flowers per hour	Hummingbirds (visits per 1000 flowers per hour
lewisii lines		
Wild type (pink)	15.4	0.02
Mutant (yellow-orange)	2.63	1.44
cardinalis		
Wild type (red)	0.15	189
Mutant (dark pink)	10.9	168

Bradshaw & Schemske (2003) *Nature*

7) Tests of ecological speciation

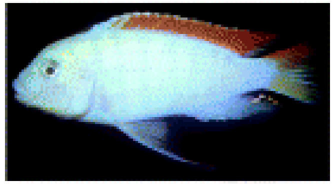
Cumulative reproductive isolation linked to traits that adapt populations to contrasting ecological environments

The cumulative contribution of contrasting ecological adaptations to total reproductive isolation between different populations is substantial, according to published studies.

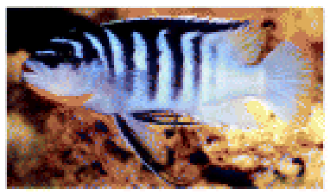


Schluter (2009) *Science*

8) Speciation by sexual selection





Many differences between the closely related species are in traits seemingly unrelated to ecology, such as color, song, gamete recognition.

Evidently, the speciation process often involves the evolution of traits involves in mate choice/recognition, which implicates sexual selection.

But how?

8) Speciation by sexual selection

The key to understanding the role of sexual selection in speciation seems to be understanding the forces driving the rapid evolution of the preferences, since the preferences drive the evolution of sexually-selected traits.

Preferences might evolve rapidly for at least two reasons:

1. The preferences evolve by natural selection on the sensory system.

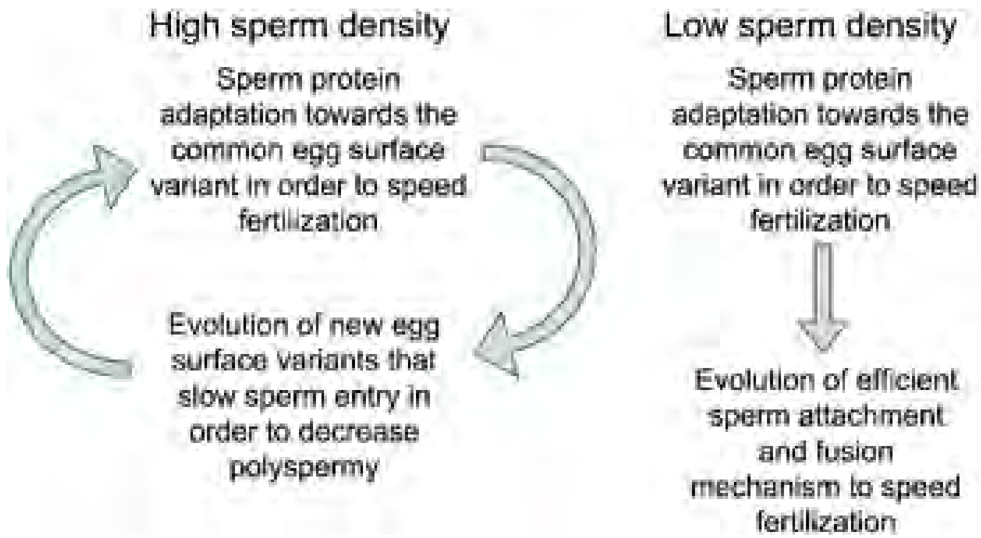
2. Conflict between the sexes, which drives continual adaptation in one sex and counter-adaptation in the other.

We don’t know very much about either of these processes.

8) Speciation by sexual selection

Sexual conflict has been suggested as the process driving the extremely rapid evolution of gamete recognition proteins observed in some groups of broadcast-spawning marine invertebrates, such as shallow water sea urchins, abalone, mussels and snails.

When sperm concentrations are high, multiple sperm entry into eggs — polyspermy — can kill developing embryos. The conflict hypothesis is that when the risk of polyspermy is high, an allele at an egg surface protein gene is favored that slows sperm entry. Fixation of such an allele would create evolutionary pressure on sperm proteins to evolve more efficient egg entry. The cycle could ultimately lead to lack of recognition of sperm and eggs from different populations, i.e., reproductive isolation.



8) Speciation by sexual selection

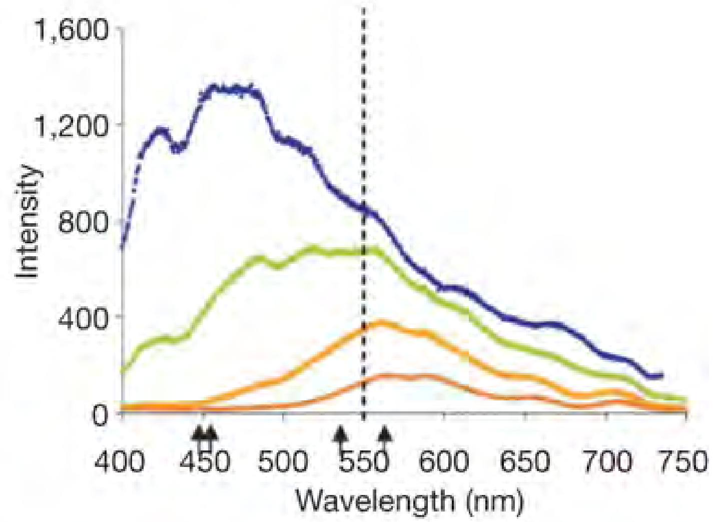
In contrast, work on this pair of Lake Victoria cichlid fishes provides evidence that natural selection on the sensory system is driving divergence and reproductive isolation. This is ecological speciation but involving sexual selection.

‘blue’, typical *P. pundamilia*

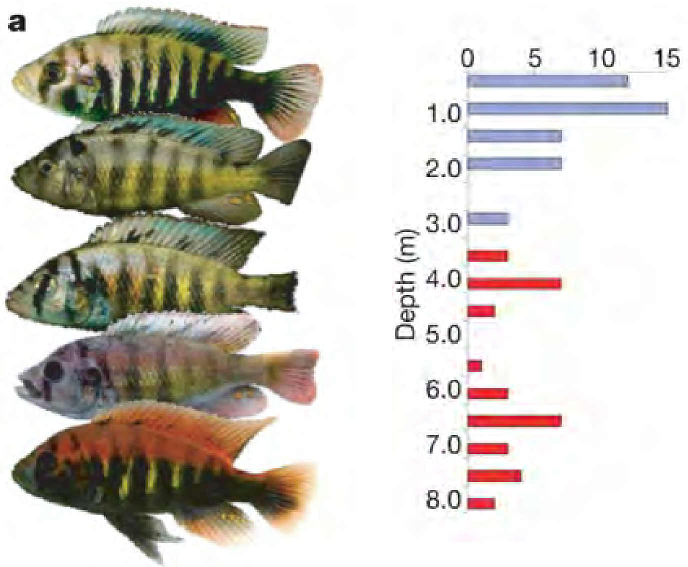
‘red’, typical *P. nyererei*

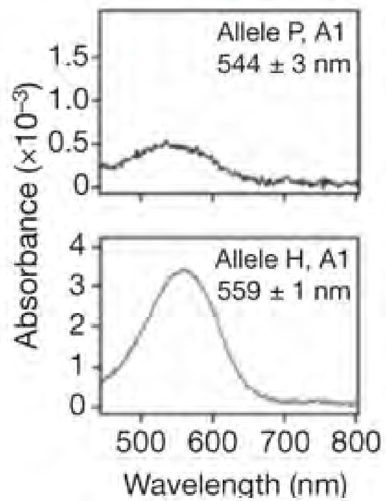
Seehausen et al (2008) *Nature*

8) Speciation by sexual selection



Low wavelength (blue) light doesn’t penetrate very deep in Lake Victoria, so light at greater depths is red-shifted. Blue objects look brown at even moderate water depths. In areas of clear water and moderate depth gradients, both species are found. The blue species lives in the shallower water, the red species at depth.





The two species have different long-wave sensitive pigments in the eye (opsins) that affect color vision. The pigment of the red species is more red-shifted.

Ecology and speciation

The evidence suggests that natural selection drives the origin of new species, as Darwin claimed.

Evidence support the ecological hypothesis of speciation in many systems. Reproductive isolation often evolves as a consequence of adaptation to contrasting ecological environments.

Natural selection might also lead to divergence by the “mutation-order” mechanism, in which each population adapts by a unique series of mutations. We didn’t talk much about this, but there are examples involving intragenomic conflict (e.g., nuclear - mitochondrial).

Sexual selection may be an important component of speciation by ecological (e.g., adaptation of sensory system to environment) and mutation-order (e.g., sexual conflict) mechanisms.

Other mechanisms are also known to be involved in speciation, such as hybridization and polyploidy, which we haven’t discussed. There is continuing interest in the possibility of speciation by genetic drift, but evidence is wanting.

9) Example exam questions

What is a species, according to the biological species concept?

Distinguish briefly: ecological speciation and mutation-order speciation.

Provide an explanation for why speciation occurs more frequently in larger geographic areas than in smaller areas.

A new pair of herbivorous insect species is discovered on a group of islands. On each island, one species utilizes *Abutilon* as its host plant, whereas the other uses *Scalesia*. Phylogenetic evidence suggests that each island pair evolved independently. Design one experiment to test whether the pairs evolved via ecological speciation.

Suggest a mechanism by which sexual conflict might lead to the evolution of reproductive isolation between populations.