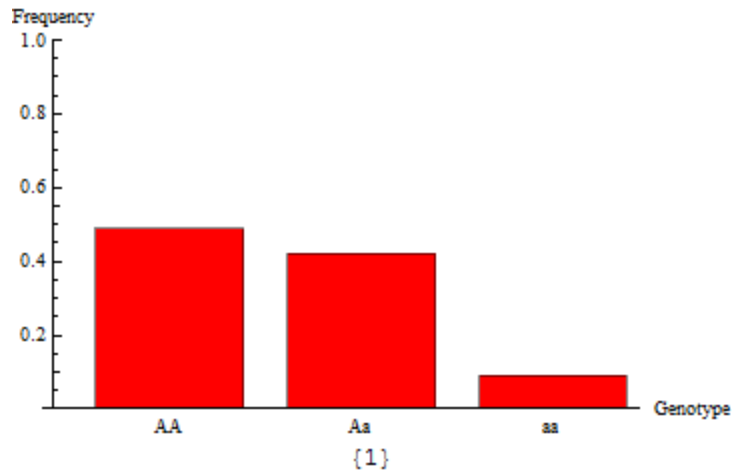
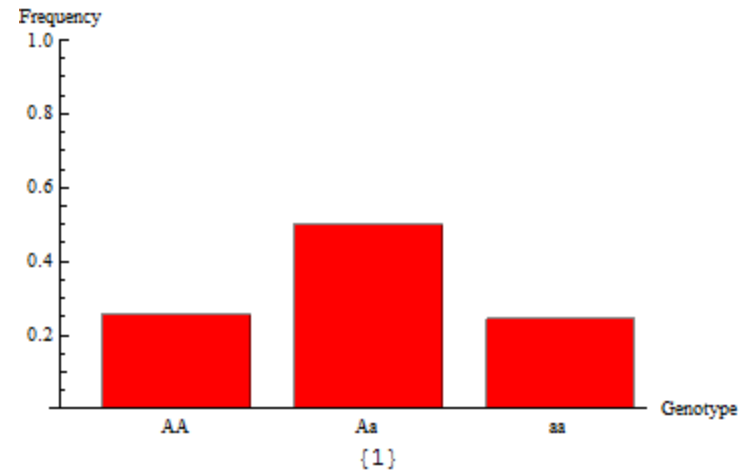


Gene flow and genetic differentiation

This population is composed of only 20 individuals



In this population, selection favors the AA genotype by 10%



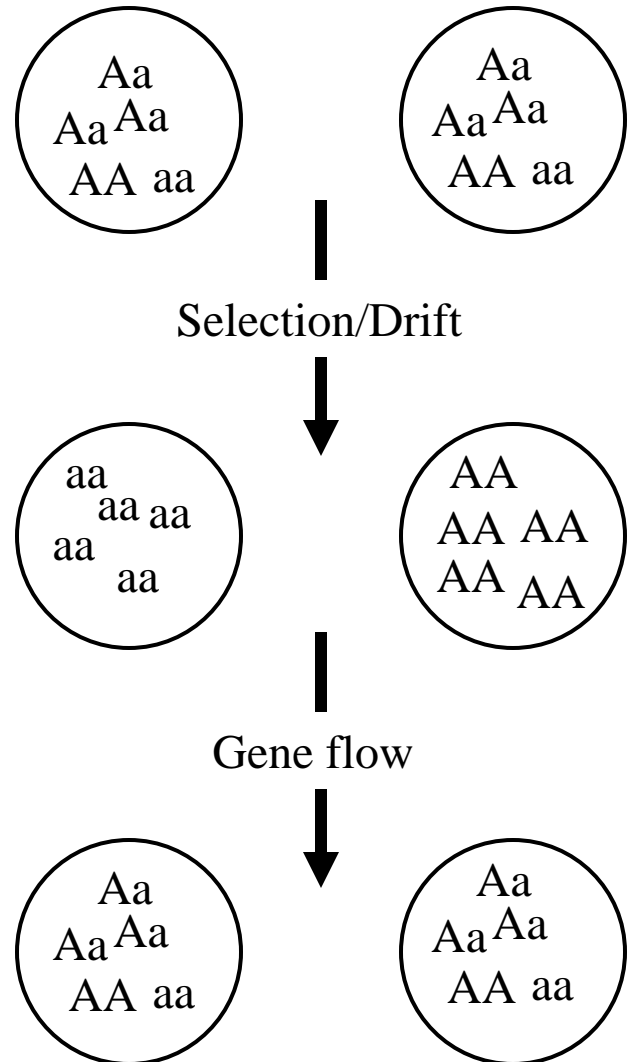
Gene flow, differentiation and speciation

Outline

1. Gene flow in isolation

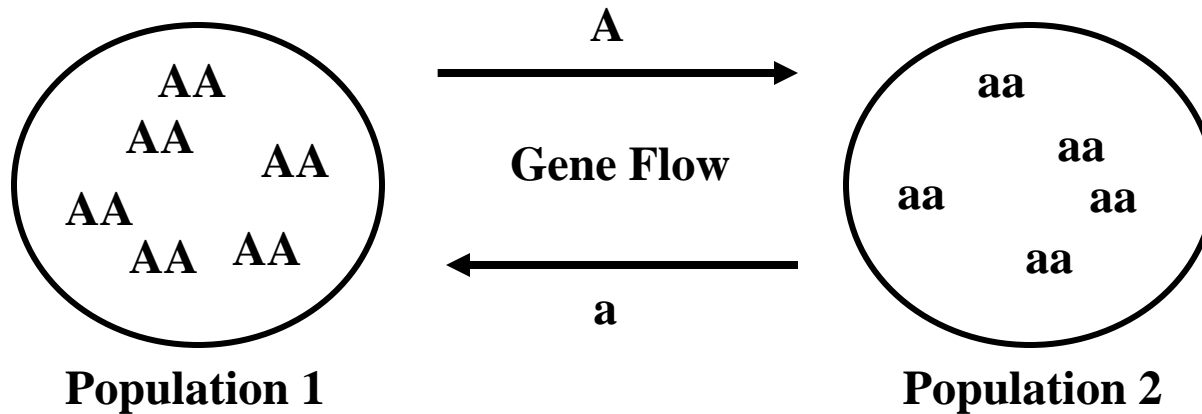
2. Interaction between gene flow and drift

3. Interaction between gene flow and selection



Gene flow

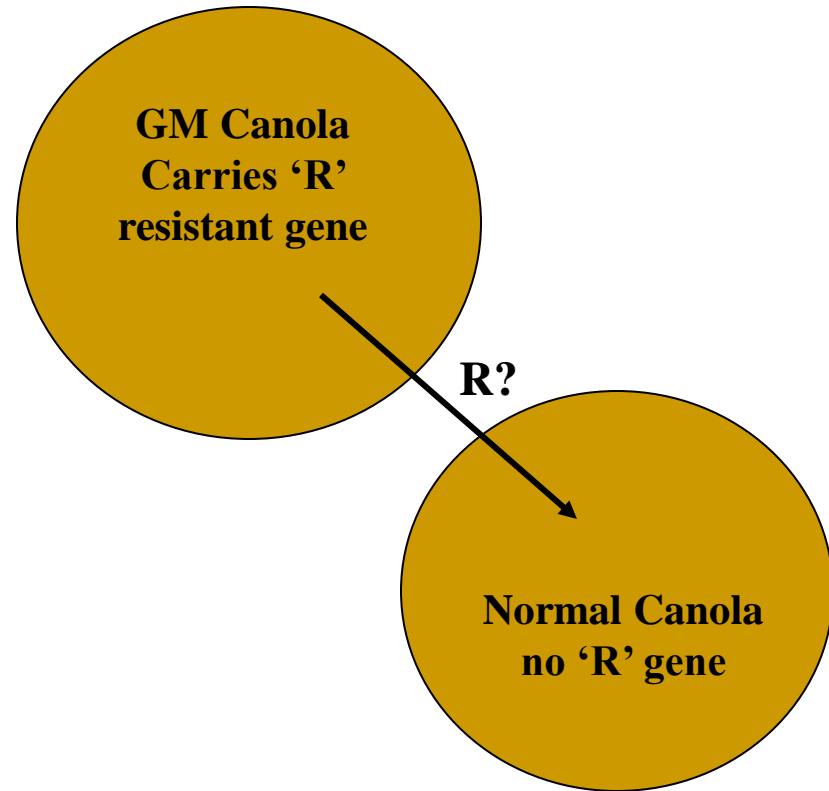
Gene flow – The incorporation of genes into the gene pool of one population from one or more other populations



An example of gene flow: genetically modified Canola



Canola field
(Brassica rapus)



- Genetically modified to be herbicide resistant
- Gene flow could introduce herbicide resistance genes into unmodified populations
- Gene flow could also introduce herbicide resistance into weedy non-crop species

Pollen-Mediated Movement of Herbicide Resistance Between Commercial Canola Fields

Mary A. Rieger,^{1,2*} Michael Lamond,³ Christopher Preston,^{1,2}
Stephen B. Powles,³ Richard T. Roush¹

There is considerable public and scientific debate for and against genetically modified (GM) crops. One of the first GM crops, *Brassica napus* (oilseed rape or canola) is now widely grown in North America, with proposed commercial release into Australia and Europe. Among concerns of opponents to these crops are claims that pollen movement will cause unacceptable levels of gene flow from GM to non-GM crops or to related weedy species, resulting in genetic pollution of the environment. Therefore, quantifying pollen-mediated gene flow is vital for assessing the environmental impact of GM crops. This study quantifies at a landscape level the gene flow that occurs from herbicide-resistant canola crops to nearby crops not containing herbicide resistance genes.

Found evidence for substantial gene flow

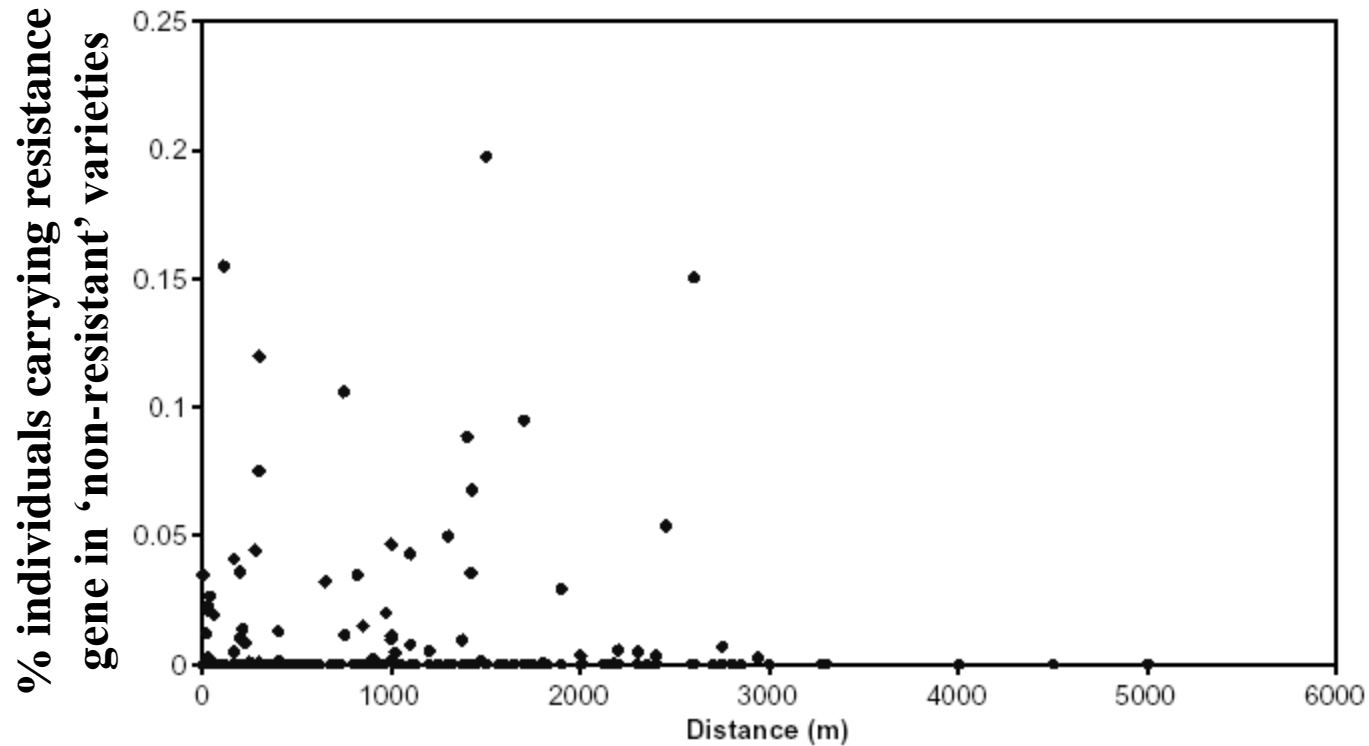
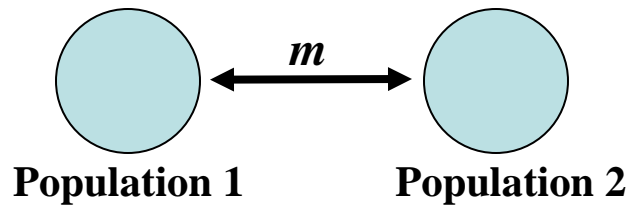


Fig. 1. Percentage of ALS herbicide-resistant individuals in seed from nonresistant varieties in relation to distance from the source field. Three individual samples were collected per field, with 190 individual collection locations.

Quantifying gene flow

- Assume that a proportion, m , of each population moves in every generation.



- The allele frequency in Population 1 after one generation is:

$$p'_1 = p_1(1 - m) + m(p_2)$$

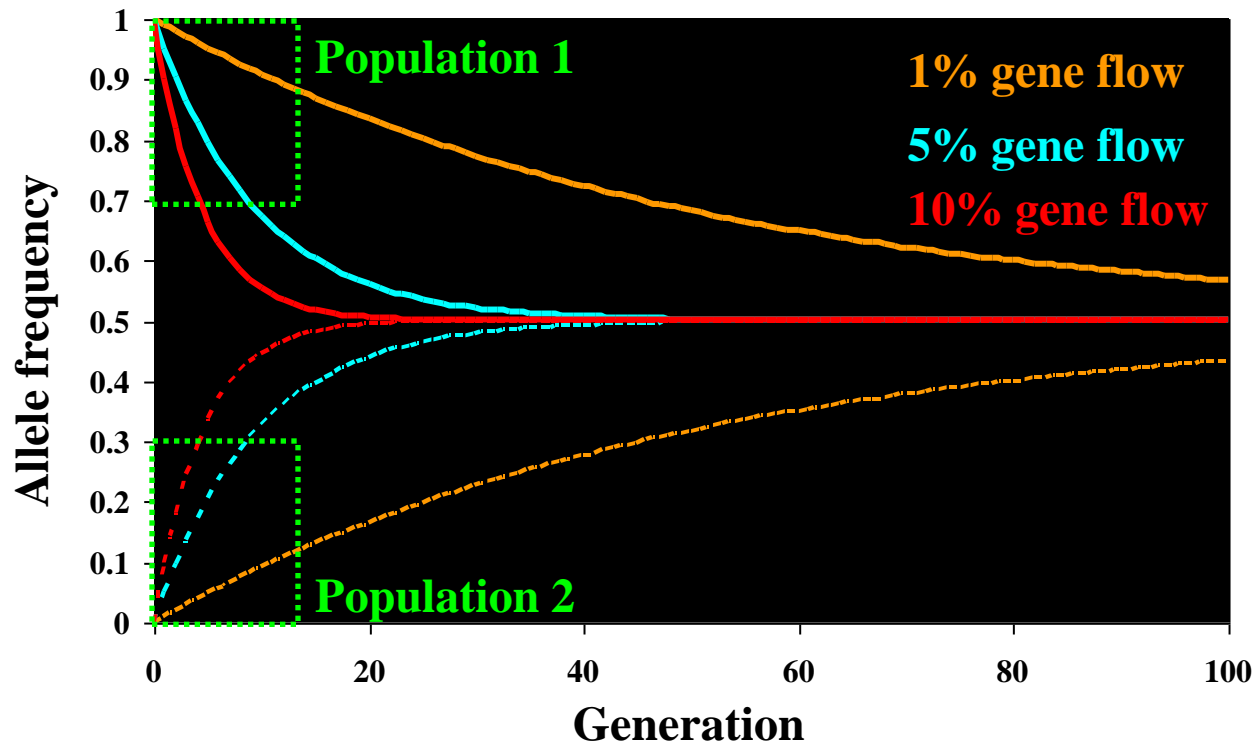
- So the change in the allele frequency of Population 1 in one generation is:

$$\Delta p_1 = p'_1 - p_1 = p_1(1 - m) + m(p_2) - p_1 = m(p_2 - p_1)$$

So what are the equilibria? What do they mean biologically?

Quantifying gene flow

$$\Delta p_1 = m(p_2 - p_1)$$



Confirms that the only equilibrium occurs when allele frequencies are equal!

Summary of gene flow

- **Gene flow homogenizes populations genetically**
- **Gene flow decreases genetic variance across populations**
- **Gene flow increases genetic variance within populations**

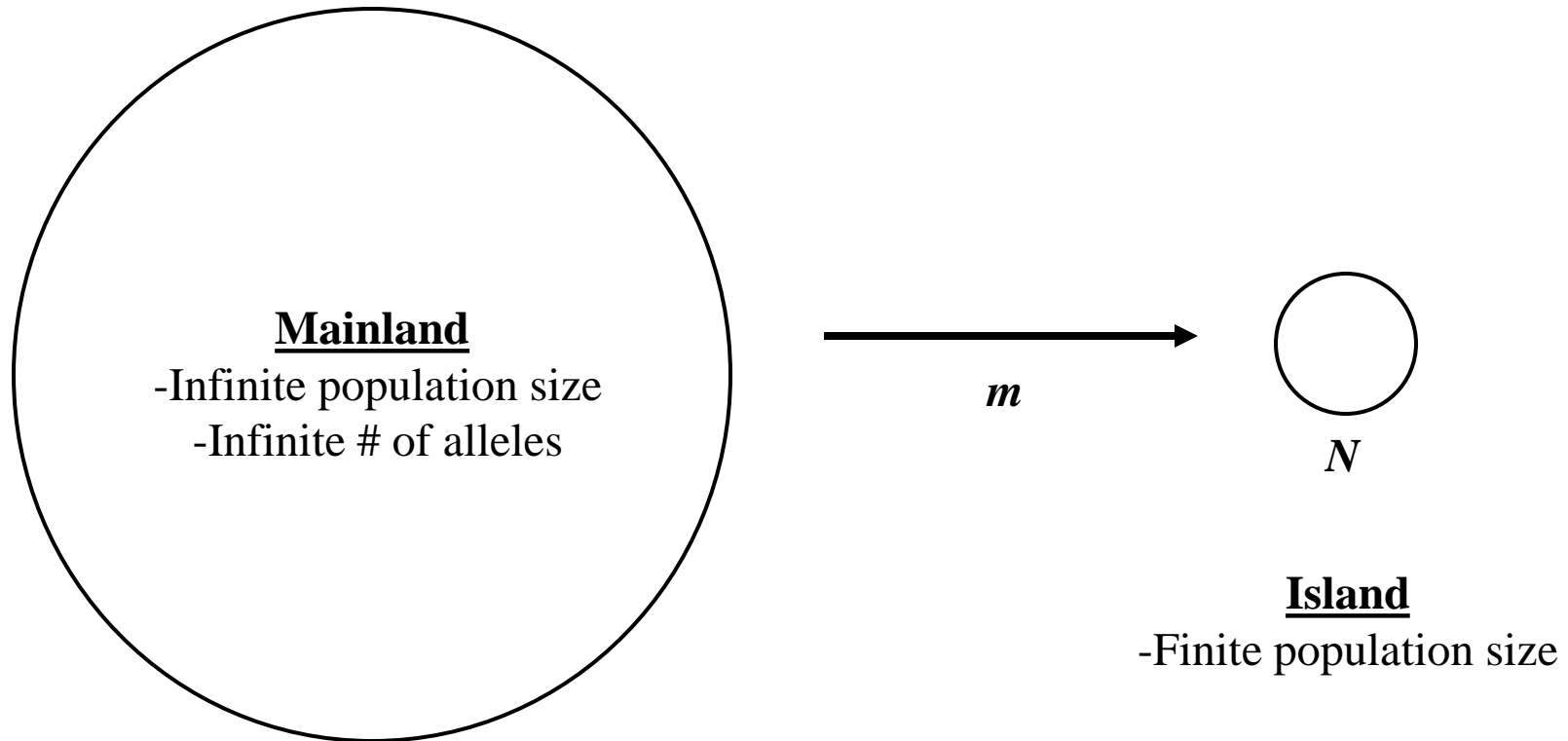
The effects of gene flow are precisely opposite those of drift!

Gene flow and drift

Lets start by ignoring selection and consider 'neutral' genetic loci

- **In finite populations, drift should cause populations to differentiate genetically**
- **Gene flow will cause these same populations to become homogenized**
- **How will these opposing forces balance out?**

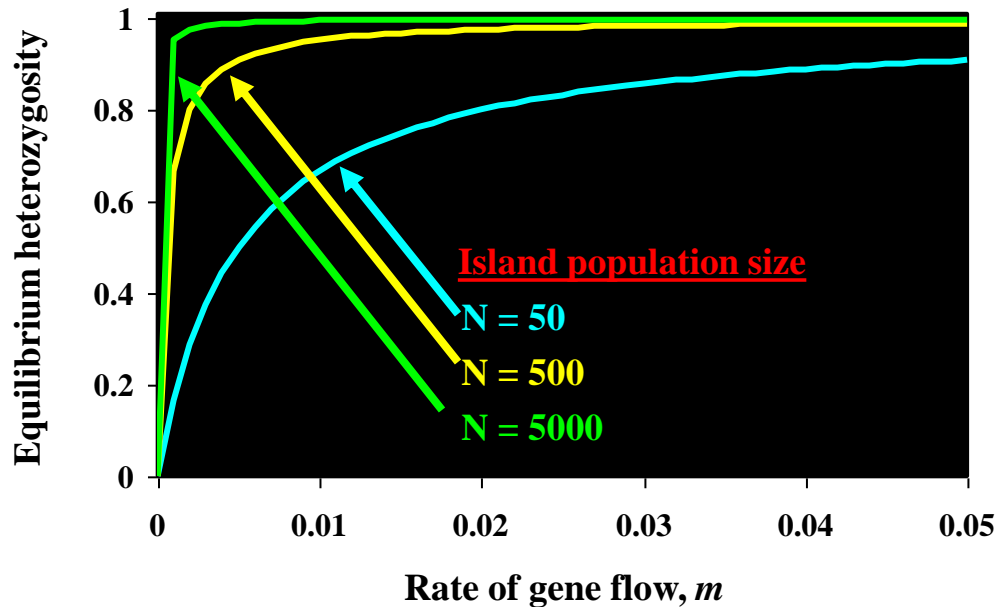
A 'mainland-island' model



How much polymorphism will be maintained by gene flow in the island population?

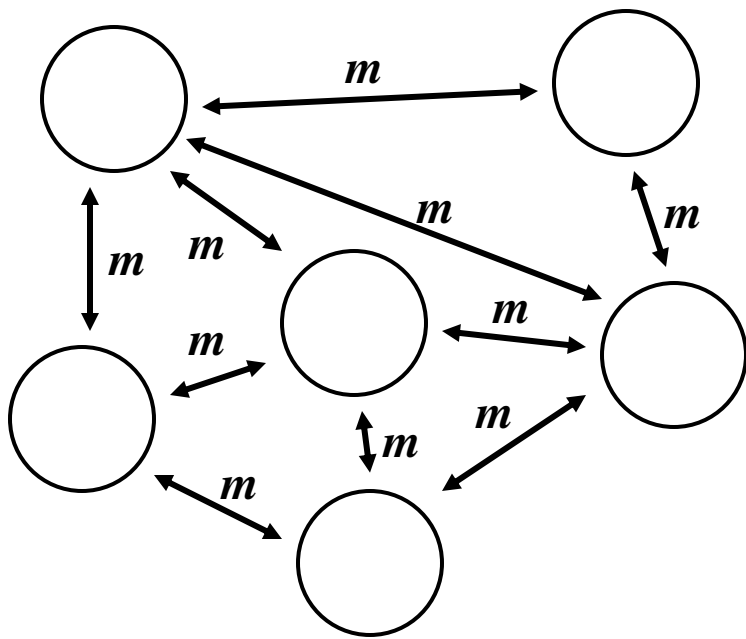
The balance between gene flow and drift

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



It takes very little gene flow to overwhelm the effects of drift!

A 'demic' model of gene flow and drift



-A set of finite populations

-Connected by gene flow

-As the number of populations increases to infinity, this model becomes the mainland-island model and we expect:

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

in every population.

A general rule of thumb

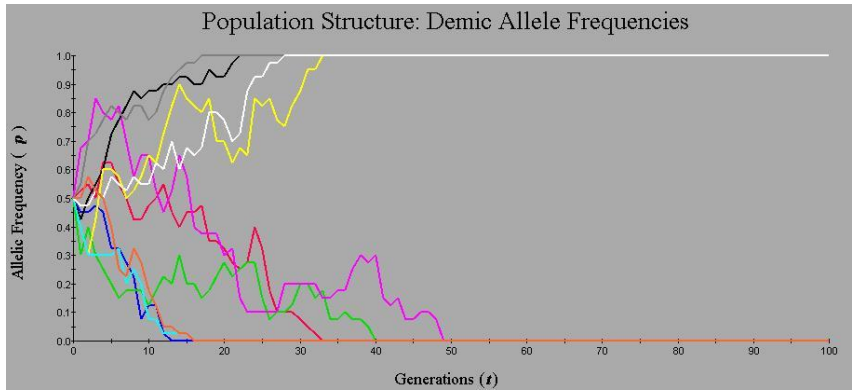
If $Nm \gg 1$ drift does not lead to the genetic differentiation of populations

If $Nm < 1$ drift leads to the genetic differentiation of populations

Simulations from the ‘demic’ model

$$m = 0.00$$

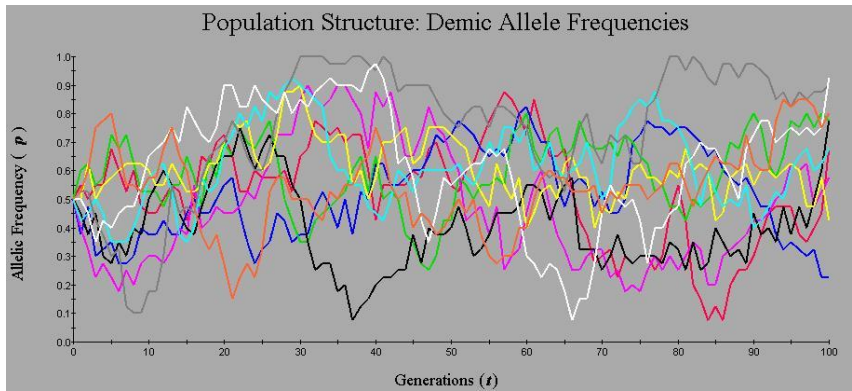
$$Nm = 0$$



**10 populations, each
containing 20 individuals.**

$$m = 0.05$$

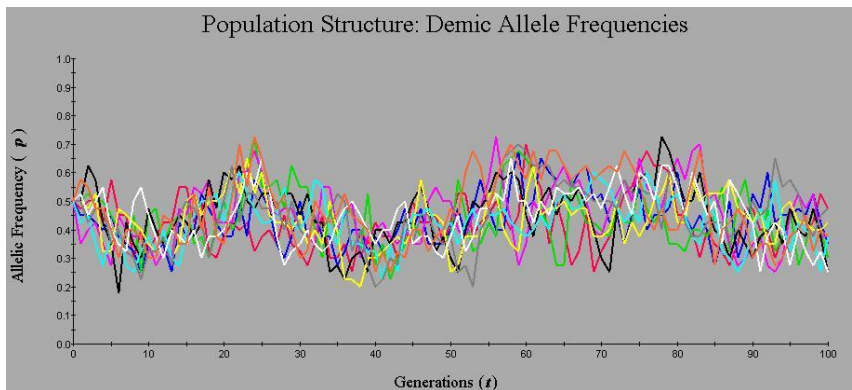
$$Nm = 1$$



- Increased gene flow
 - A) Maintains polymorphism
 - B) Prevents differentiation

$$m = 0.50$$

$$Nm = 10$$



Estimates of Nm from a real population



Black-tailed prairie dog

Level of comparison	Locus	Nm
Among 12 populations in one region	<i>Ada</i>	14.63
	<i>Gdh</i>	4.00
	<i>Got-2</i>	2.84
	<i>Np</i>	3.38
	<i>6-Pgd</i>	3.71
	<i>Pgm-2</i>	4.40
Average across loci		4.86

Chesser (1983)

Data from a study of molecular variation estimates that:
 $Nm = 4.86$

Gene flow is sufficiently low that populations are somewhat genetically differentiated

Gene flow and Drift: Summary

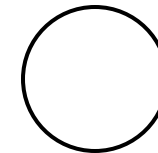
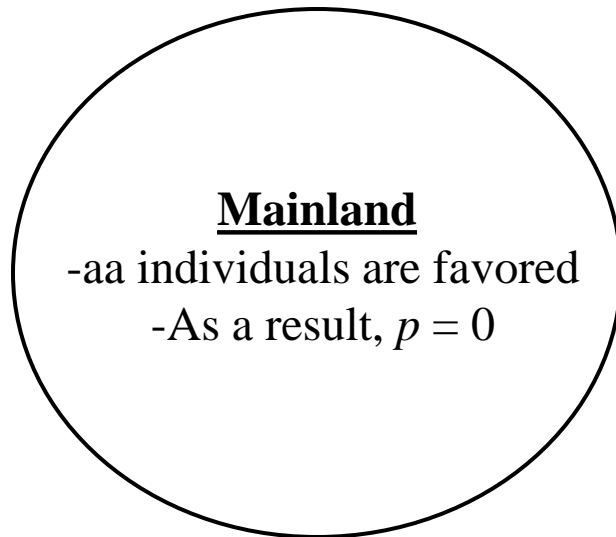
- **Drift acts to differentiate populations genetically**
- **Gene flow acts to homogenize populations genetically**
- **Mathematical results suggest that it should take very little gene flow to overpower genetic drift**
- **Studies of real organisms suggest, however, that levels of gene flow often fall below these critical levels, allowing drift to generate substantial ‘population genetic structure’.**

Gene flow and selection

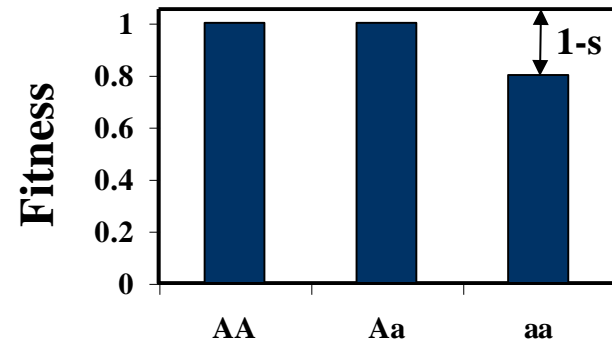
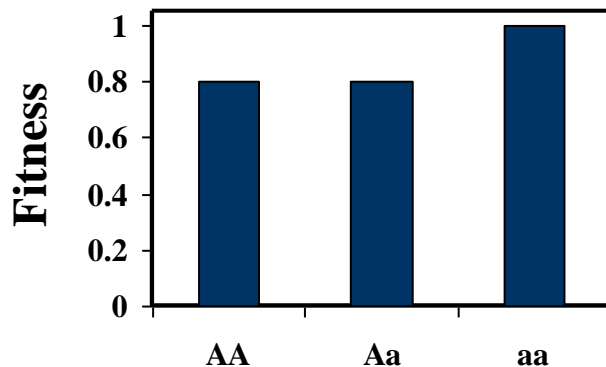
Lets now consider loci that are exposed to natural selection

- **Natural selection causes populations to diverge genetically as individual populations adapt to local ecological conditions**
- **Gene flow will cause these same populations to become homogenized, impeding local adaptation through natural selection**
- **How will these opposing forces balance out?**

A simple 'mainland-island' model



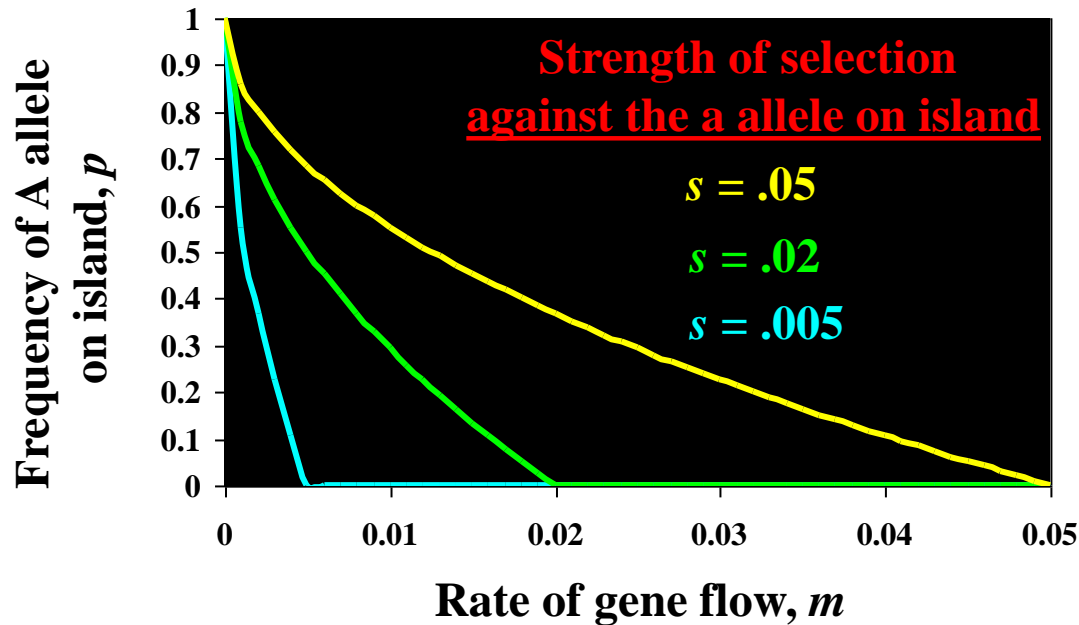
Island
-AA individuals are favored



How much polymorphism will gene flow maintain on the island?

How much polymorphism can gene flow maintain?

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

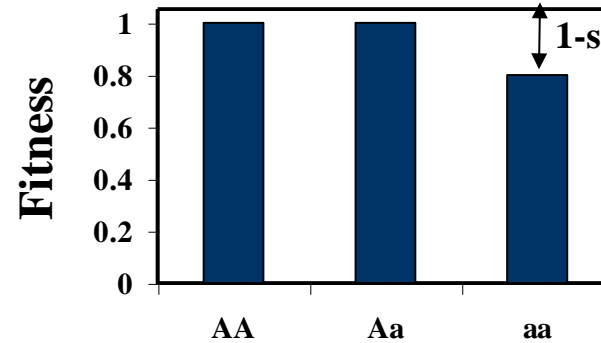
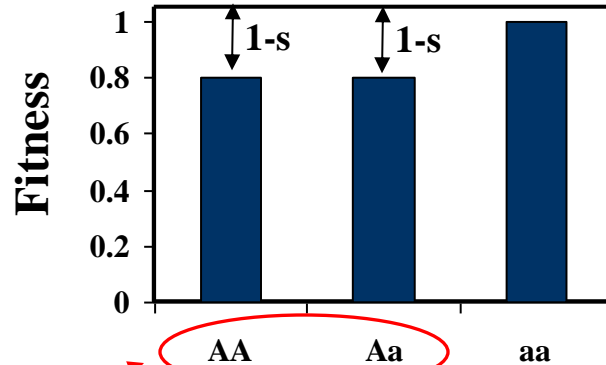


The greater the strength of local selection,
the less likely gene flow is to prevent local adaptation

A hypothetical example

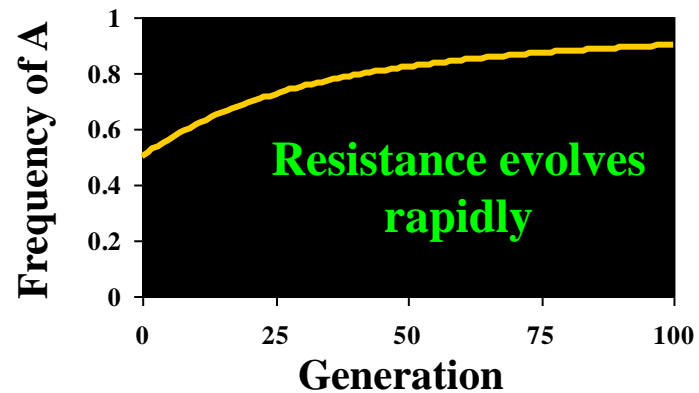
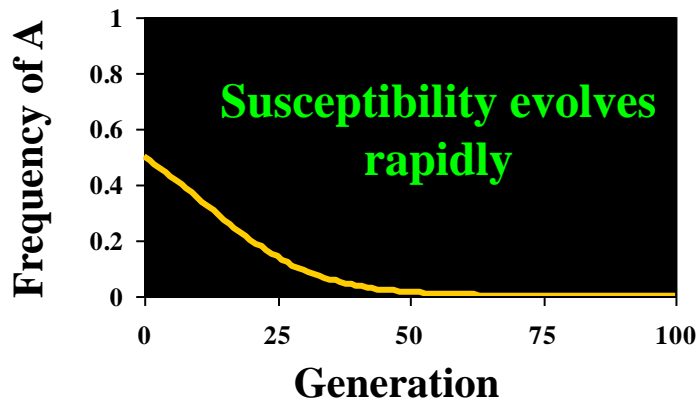
Insecticide
not used

Insecticide
used

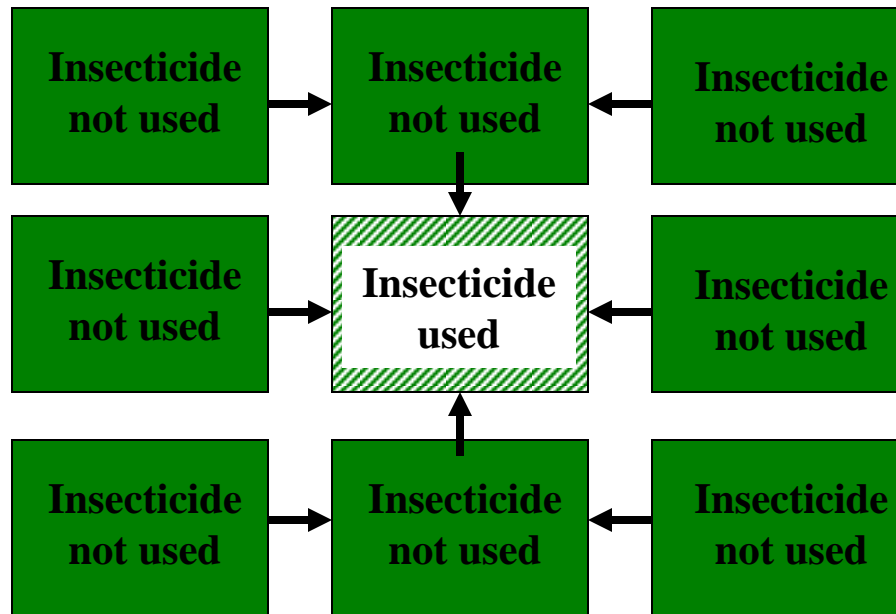


Resistant
genotypes

If there is no gene flow between populations



Now consider the effect of gene flow



If the selection coefficient for insecticide resistance is .1, and 5% of individuals move between populations in every generation, we can predict the ultimate fate of the resistance allele in a population exposed to insecticide:

$$\hat{p}_{Insecticide} = 1 - \frac{\sqrt{m}}{\sqrt{s}} = 1 - \frac{\sqrt{.05}}{\sqrt{.1}} = .293$$

Gene flow prevents the evolution of high levels of insecticide resistance!

A real example of gene flow and selection: Lake Erie water snakes



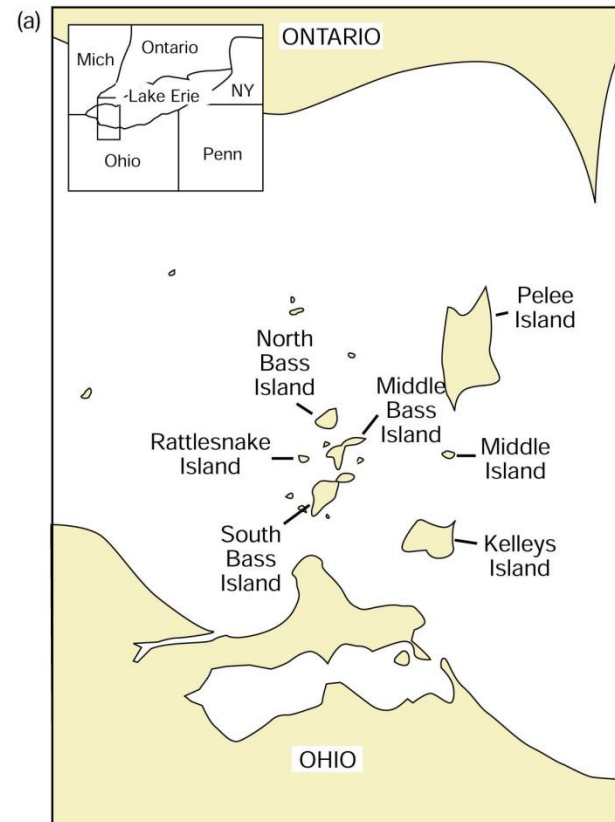
Nerodia sipedon

**Banding is controlled (approximately)
by a single locus**

-AA and Aa individuals are banded

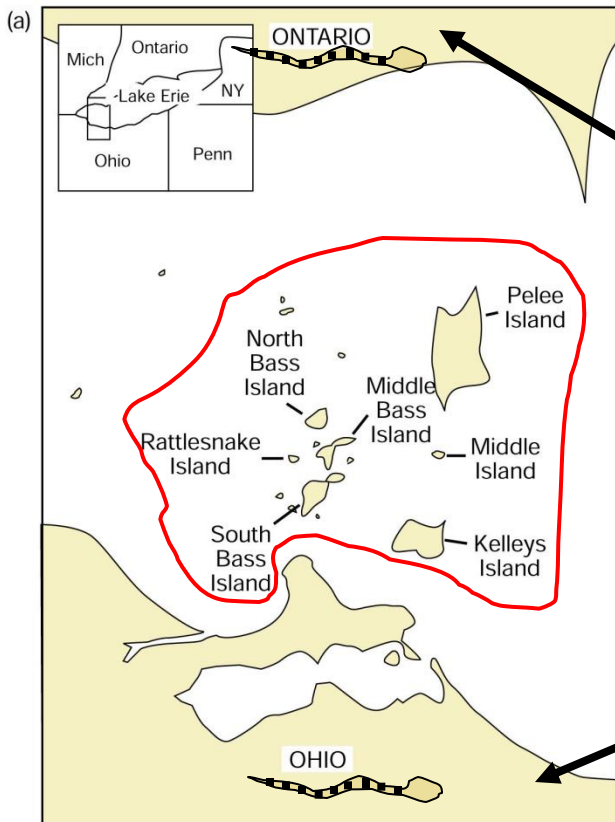


-aa individuals are unbanded

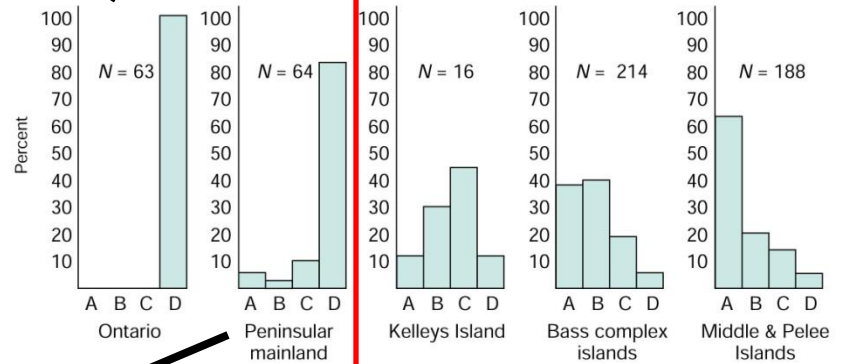


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A real example of gene flow and selection: Lake Erie water snakes



**Island populations
are polymorphic**



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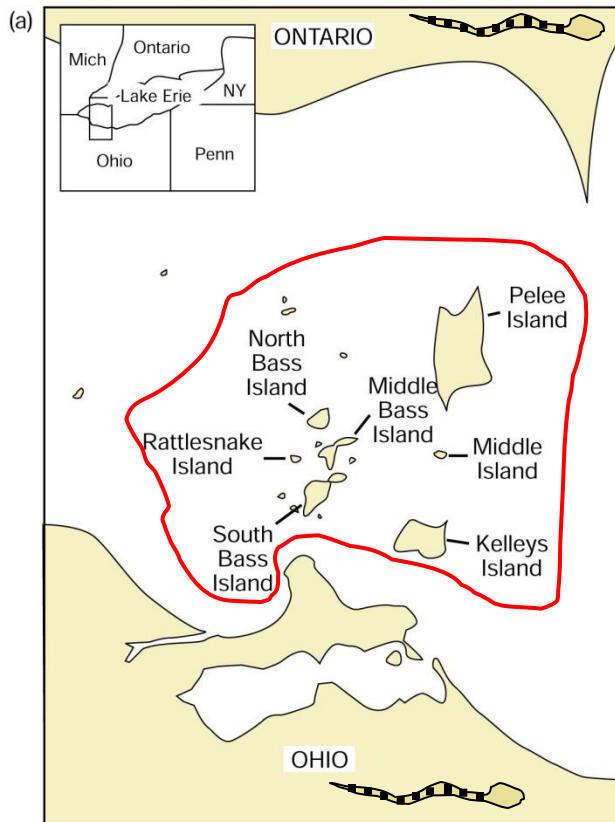
A = Unbanded 
D = Banded 

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Data from Camin and Ehrlich, 1958

A real example of gene flow and selection

Lake Erie water snakes

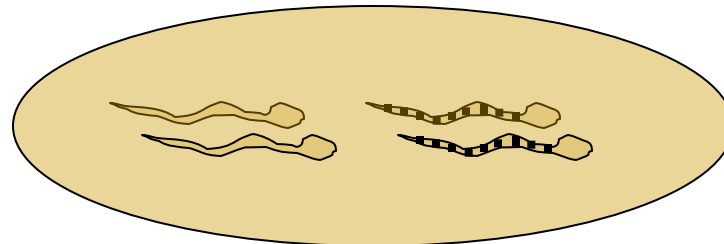


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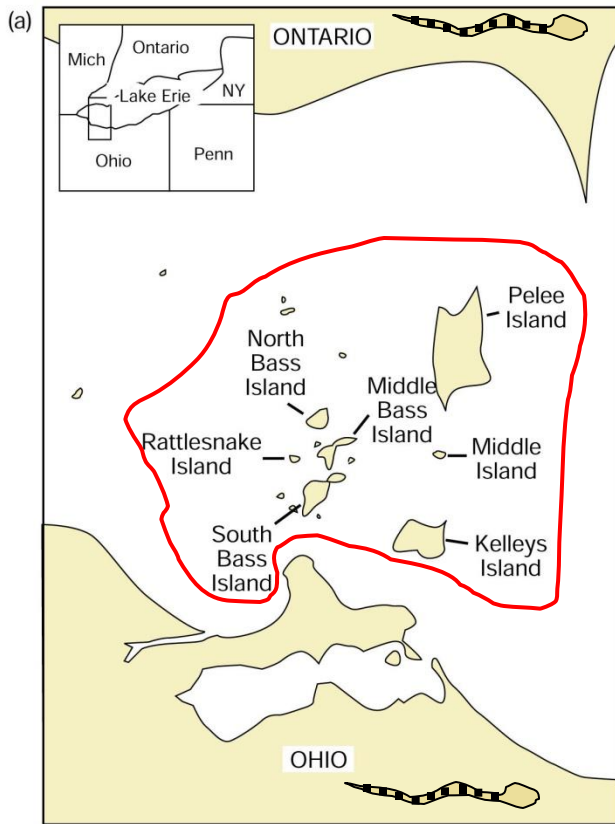
What explains the difference in ‘bandiness’?

- Snakes living on islands bask in the sun on limestone rocks adjacent to the water
- Unbanded snakes are more cryptic on limestone rocks. As a result, predators are more likely to eat banded snakes.

Suggests that selection might favor unbanded snakes on islands!



A real example of gene flow and selection: Lake Erie water snakes



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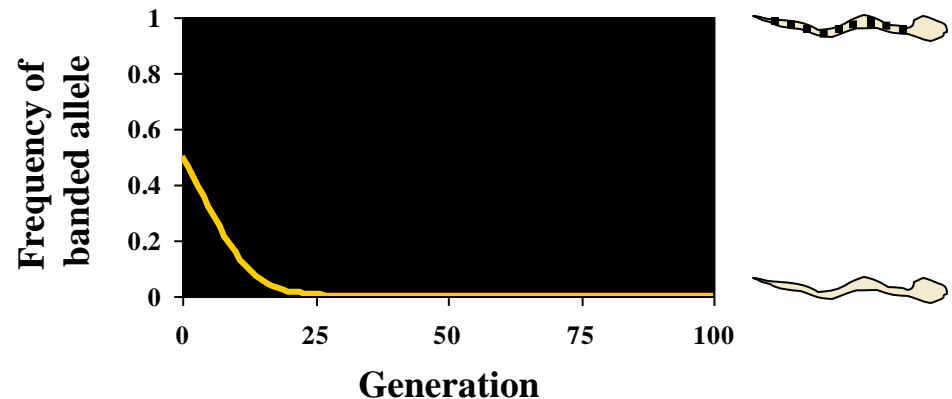
Using a mark recapture experiment, King (1993) showed that, on islands, unbanded (aa) snakes have higher survival than banded (AA, Aa) snakes:

$$W_{AA} \approx .78 - .90$$

$$W_{Aa} \approx .78 - .90$$

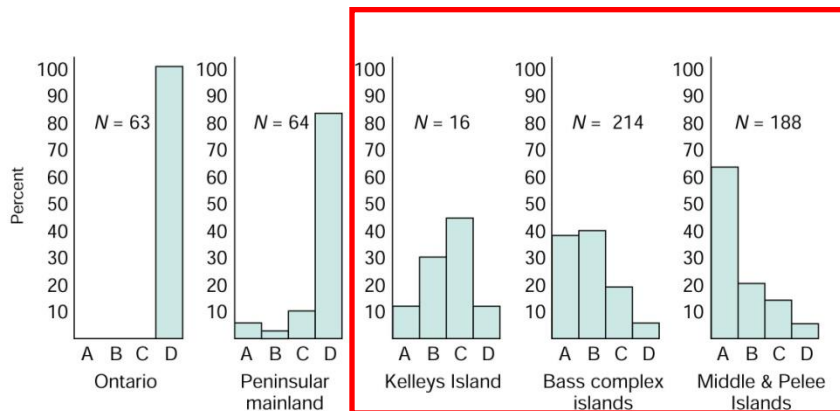
$$W_{aa} = 1$$

Given this result we would expect the A (Banded) allele to be lost from the island populations:



A real example of gene flow and selection: Lake Erie water snakes

But that's not what we see on islands!



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Gene flow from the mainland appears to be the answer:

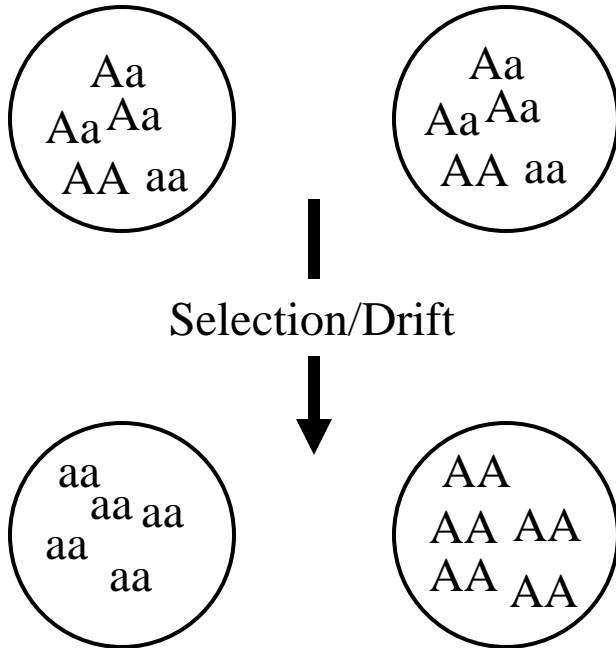
- King and Lawson (1995)** estimated the rate of gene flow from mainland to island to be $m = .01$
- This level of gene flow is sufficient to maintain the maladaptive banding allele, A, in the island populations despite selection by predators for the loss of this allele!**

Summary: Gene flow and selection

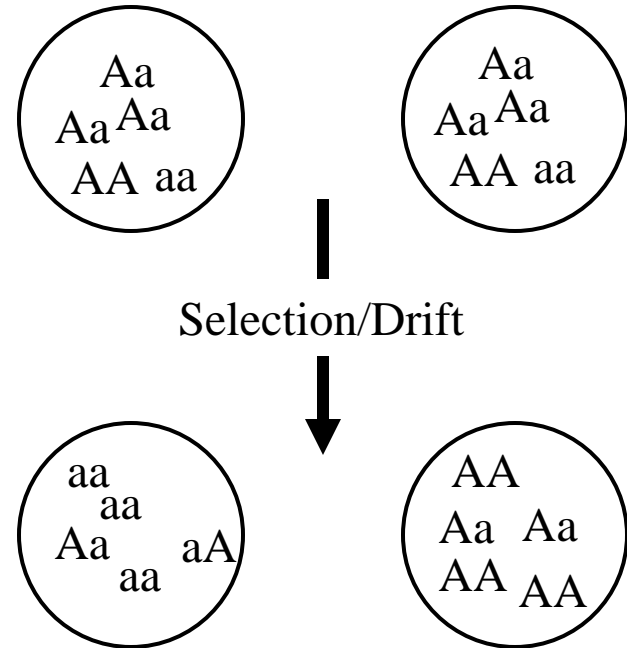
- **In the absence of gene flow natural selection generally leads to local adaptation**
- **Gene flow can hinder natural selection by introducing new and selectively disfavored alleles**
- **The balance between gene flow and selection depends upon their relative strengths**

Gene flow acts as genetic glue

In the absence of gene flow



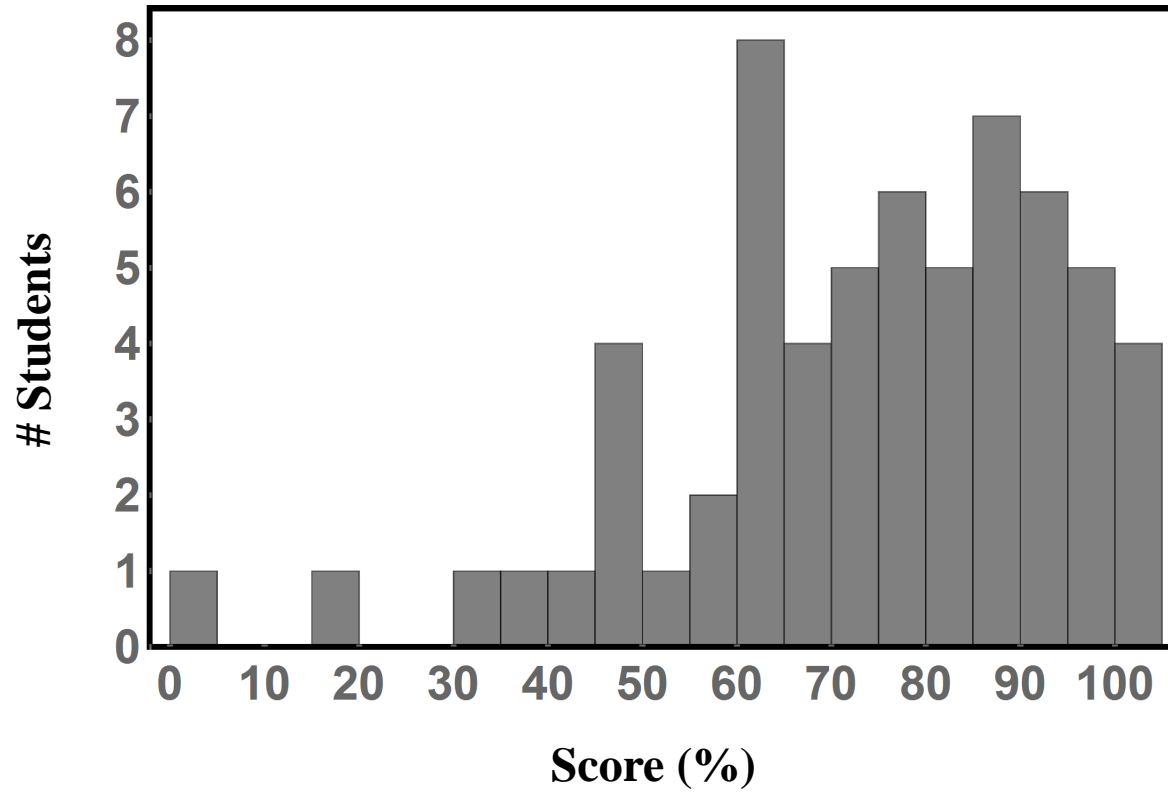
In the presence of gene flow



When the homogenizing effects of gene flow are insufficient, speciation occurs

Exam 1 Results

Average: 117 points or $\approx 73\%$



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?

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?