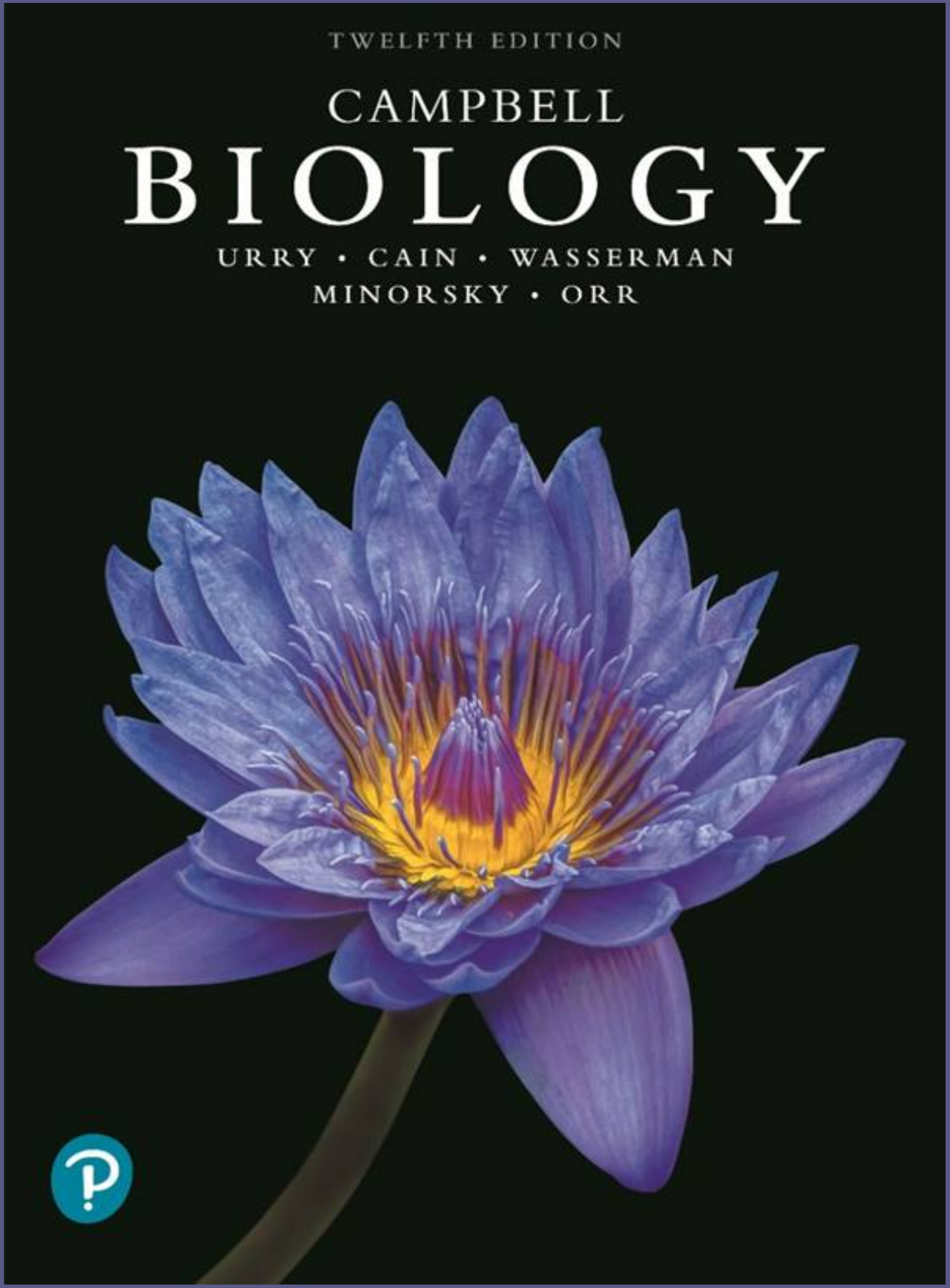


Chapter 23

The Evolution of Populations

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

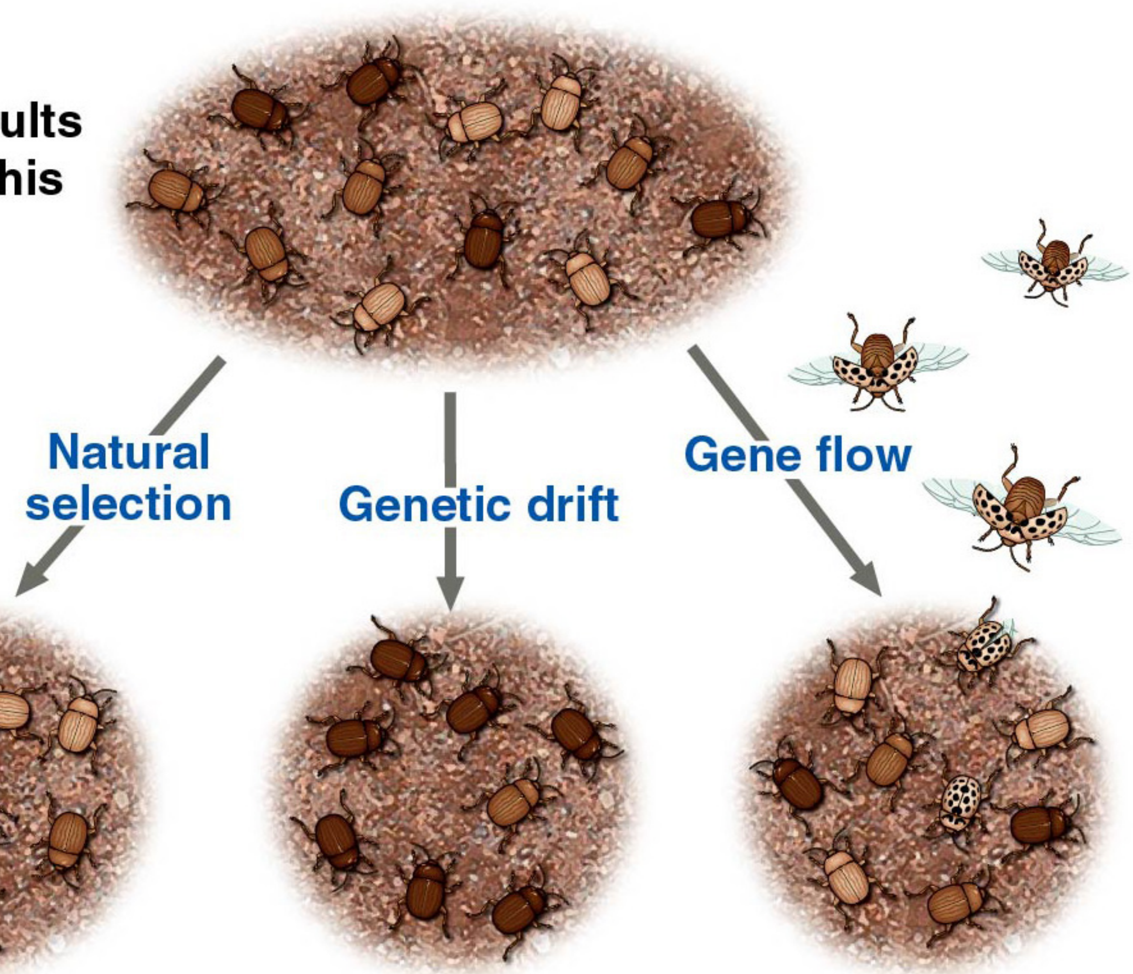
Figure 23.1a

Figure 23.1b

What mechanisms can cause the evolution of populations?

Evolution occurs when the allele frequencies of a population change over time.

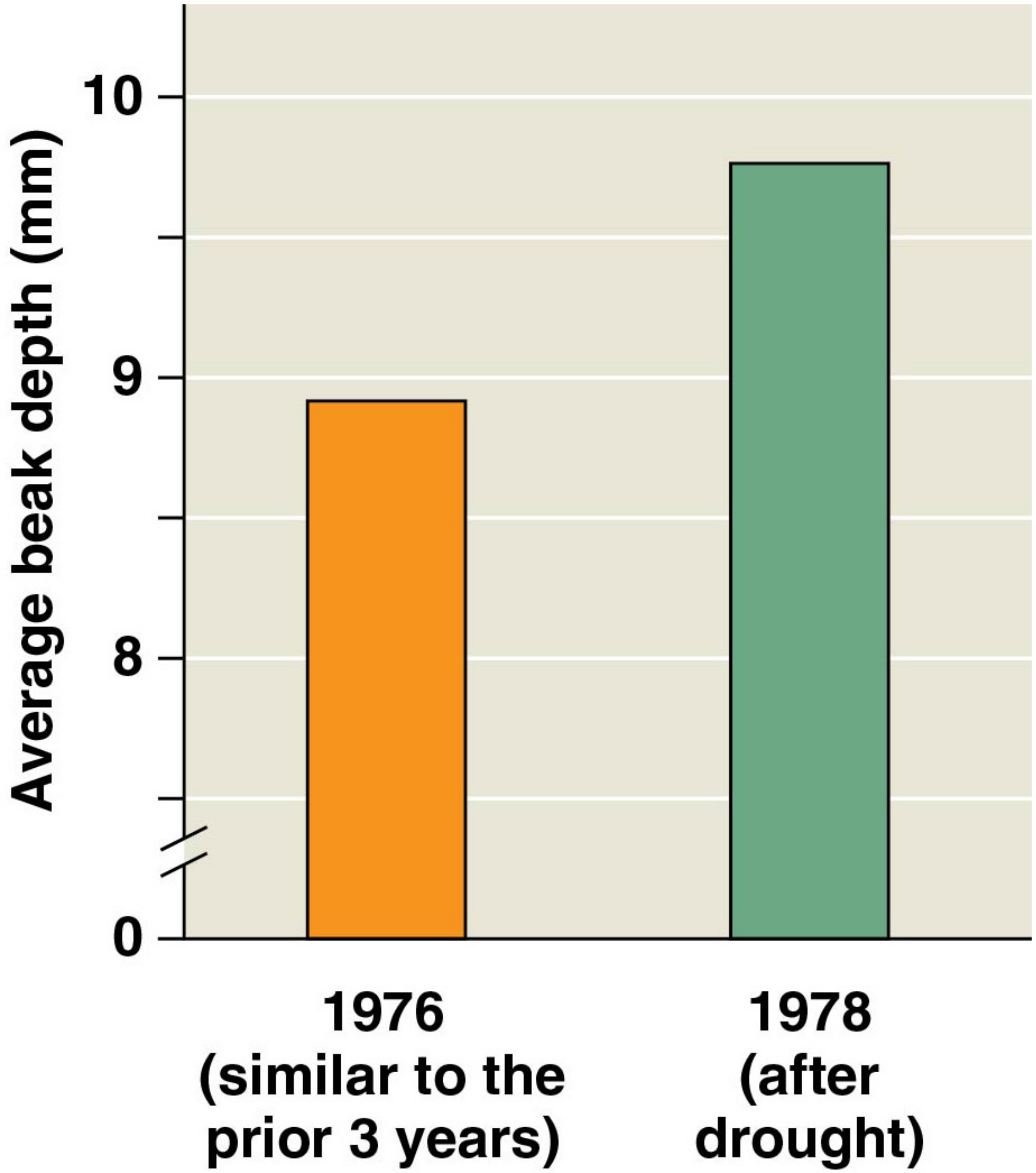
Genetic variation results in color variation in this hypothetical beetle population.



What mechanisms can cause the evolution of populations?

- Natural selection acts on individuals, but only populations, not individuals, evolve
  - For example, medium ground finches evolved in response to seed shortage on Daphne Major
  - Larger-beaked birds that could eat the more plentiful large seeds survived at a higher rate
  - Offspring of the survivors tended to have large beaks; average beak depth increased in the next generation
  - The population, not its individual members, evolved

Figure 23.2



Average beak depth (mm)
10
9
8
0
1976
(similar to the prior 3 years)
1978
(after drought)

- **Microevolution**, the change in allele frequencies in a population over generations, is evolution at its smallest scale
- Three mechanisms cause allele frequency change:
  - Natural selection (adaptation to the environment)
  - Genetic drift (chance events alter allele frequencies)
  - Gene flow (transfer of alleles between populations)

CONCEPT 23.1: Genetic variation makes evolution possible

- Genetic variation, variation in heritable traits, is a prerequisite for evolution by natural selection
- Gregor Mendel’s work on pea plants provided evidence of discrete heritable units (genes)

Genetic Variation

- **Genetic variation** refers to the differences in genes or other DNA sequences among individuals
- Phenotype is the product of inherited genotype and environmental influences
- Natural selection can only act on variation with a genetic component

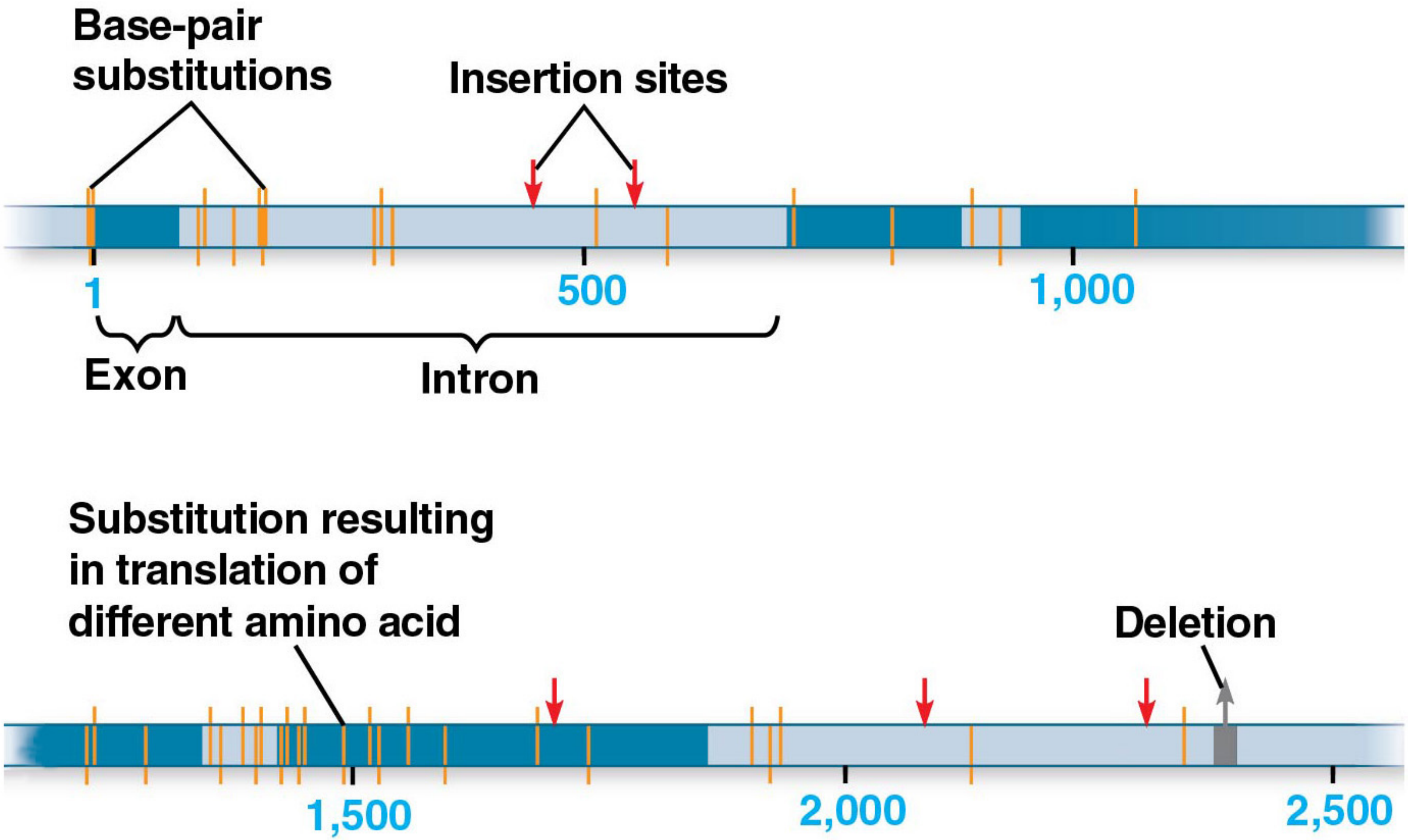
- Phenotypic differences determined by a single gene can usually be classified on an “either-or” basis
  - For example, pea flowers are either purple or white
- Phenotypic differences determined by two or more genes usually vary in gradations along a continuum
  - For example, coat color in horses or height in humans

Figure 23.3

- At the gene level, genetic variation is quantified by the percentage of heterozygous loci in a population
- At the molecular level, genetic variation is quantified by comparing the nucleotide sequences of two or more individuals

- Nucleotide variability rarely results in phenotypic variation
  - Most nucleotide differences occur within noncoding DNA segments (introns)
  - Variations in coding regions (exons) rarely change the amino acid sequence of the encoded protein

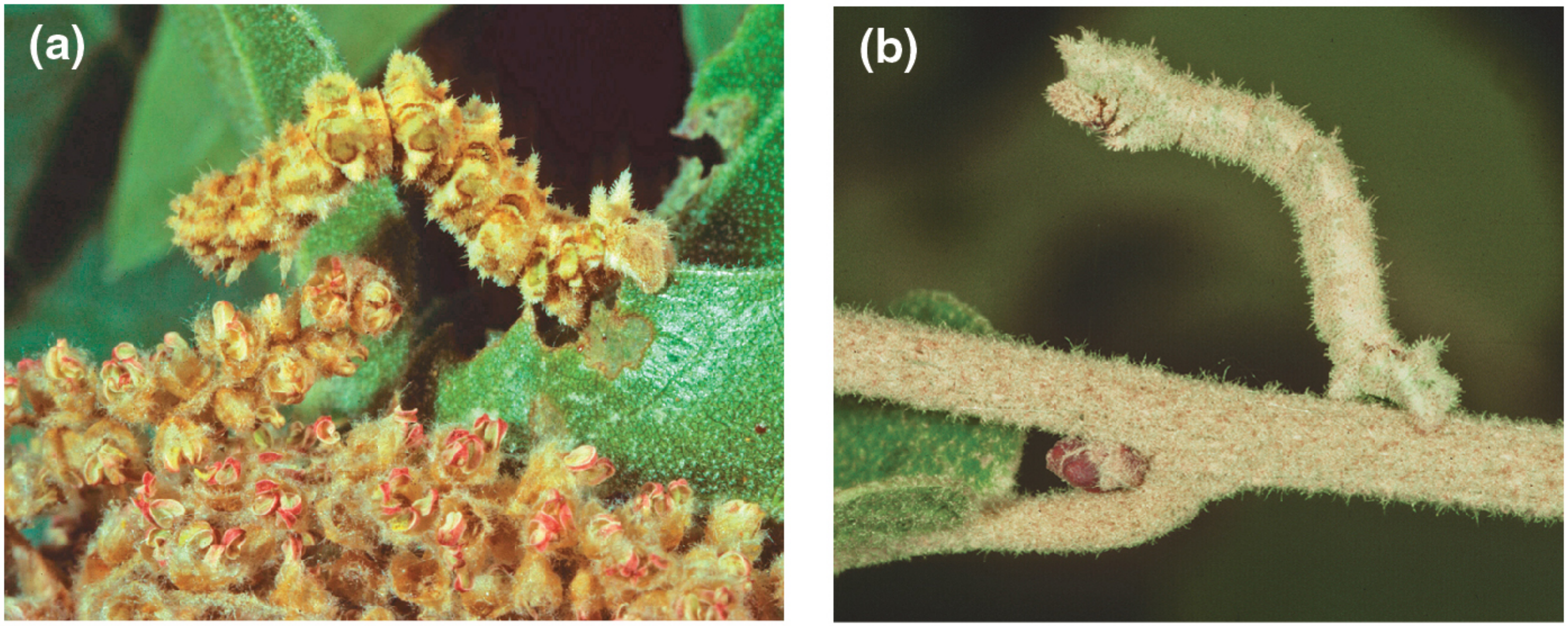
Figure 23.4



Base-pair substitutions
Insertion sites
1
500
1,000
Exon
Intron
Substitution resulting in translation of different amino acid
Deletion
1,500
2,000
2,500

- Phenotypic variation can result from environmental influences, as well as genetic differences
- Only the genetically determined part of phenotypic variation can have evolutionary consequences

Figure 23.5



Sources of Genetic Variation

- Genetic variation originates when new genes and alleles arise by mutation, gene duplication, or other processes
- Genetic variations are produced rapidly in organisms with short generation times
- Sexual reproduction can produce genetic variation by recombining existing alleles

Formation of New Alleles

- New alleles arise by mutation, change in the nucleotide sequence of DNA
- Mutations can be caused by replication errors or exposure to certain types of radiation or chemicals
- Even a point mutation, change in a single nucleotide, can have significant impact on phenotype

- Most mutations that alter phenotype are at least slightly harmful
- Harmful mutations that are recessive can be hidden from selection in heterozygous individuals
- “Heterozygote protection” maintains a pool of alleles that could be beneficial if the environment changes

- Not all mutations are harmful
  - Point mutations in noncoding regions usually cause **neutral variation**, variation with no selective advantage or disadvantage
  - Neutral variation occurs within genes due to the redundancy in the genetic code
- Mutations that result in a change in phenotype are sometimes, though rarely, beneficial
- In multicellular organisms, only mutations in cell lines that produce gametes are passed to offspring

Altering Gene Number or Position

- Large chromosomal mutations that delete, disrupt, or rearrange many loci are usually harmful
- Duplication of small segments of DNA, including genes, is a key potential source of genetic variation
- If duplicated genes persist over generations, then mutations can accumulate, and new functions may arise

- Increases in gene number likely played a major role in evolution
  - For example, an ancestral mammalian gene for detecting odors has been duplicated many times
  - Humans have about 380 functional olfactory receptor genes, and mice have about 1,200

Rapid Reproduction

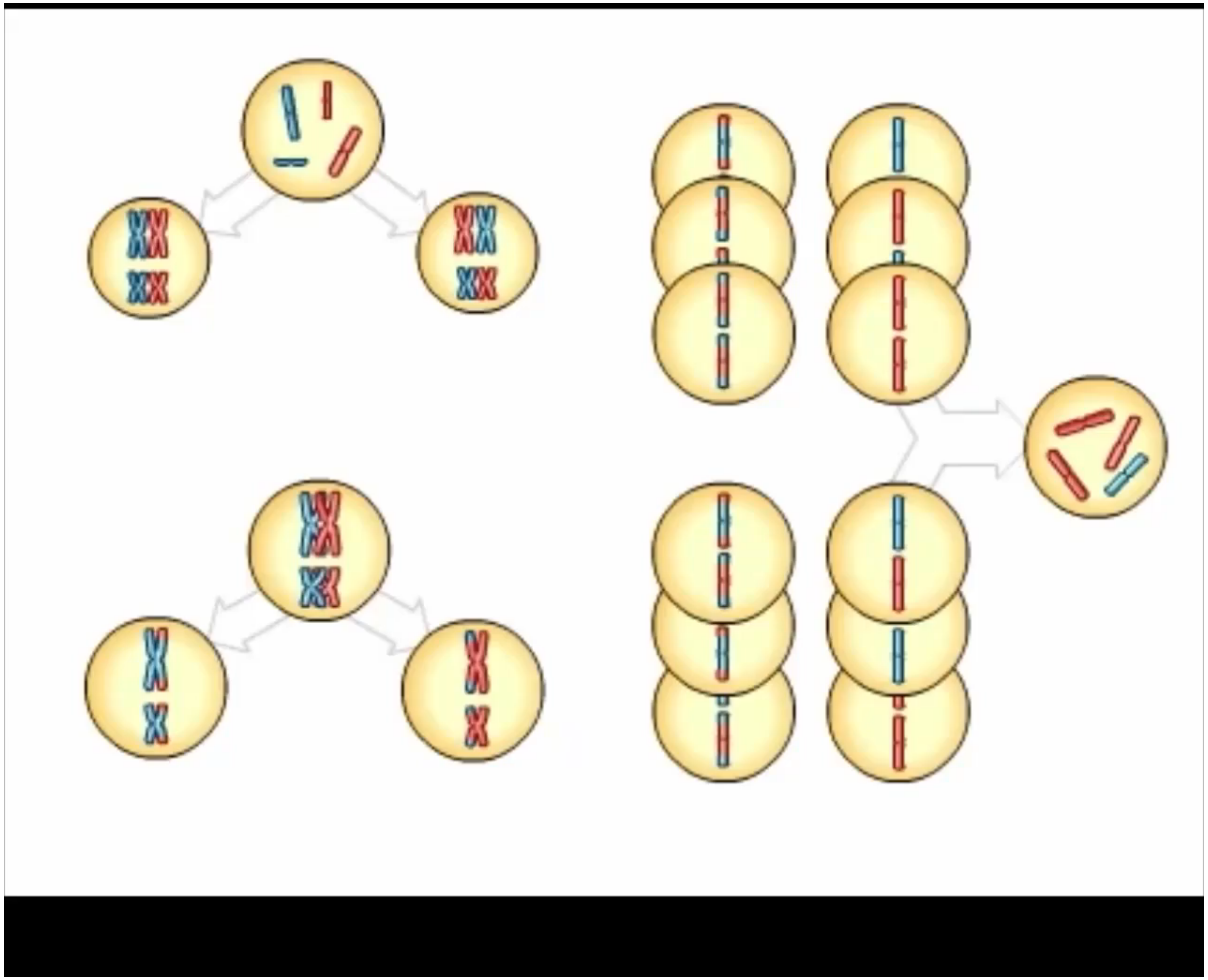
- Mutation rates are low in animals and plants, averaging about one in every 100,000 genes per generation
- Prokaryotes have lower rates, but shorter generation times allow mutations to accumulate rapidly

- Mutations can accumulate rapidly in viruses due to short generation times and rapid mutation rates
  - For example, drug resistance proliferates rapidly in HIV, which has a generation time of about two days
  - HIV also has a high mutation rate because its RNA genome lacks repair mechanisms

Sexual Reproduction

- Most genetic variation in sexually reproducing organisms results from recombination of alleles
- New combinations of existing alleles occur through three mechanisms:
  - Crossing over (exchange of genetic material between homologous chromosomes during meiosis)
  - Independent assortment (random distribution of chromosomes into gametes during meiosis)
  - Fertilization (random combination of gametes)

Animation: Origins of Genetic Variation



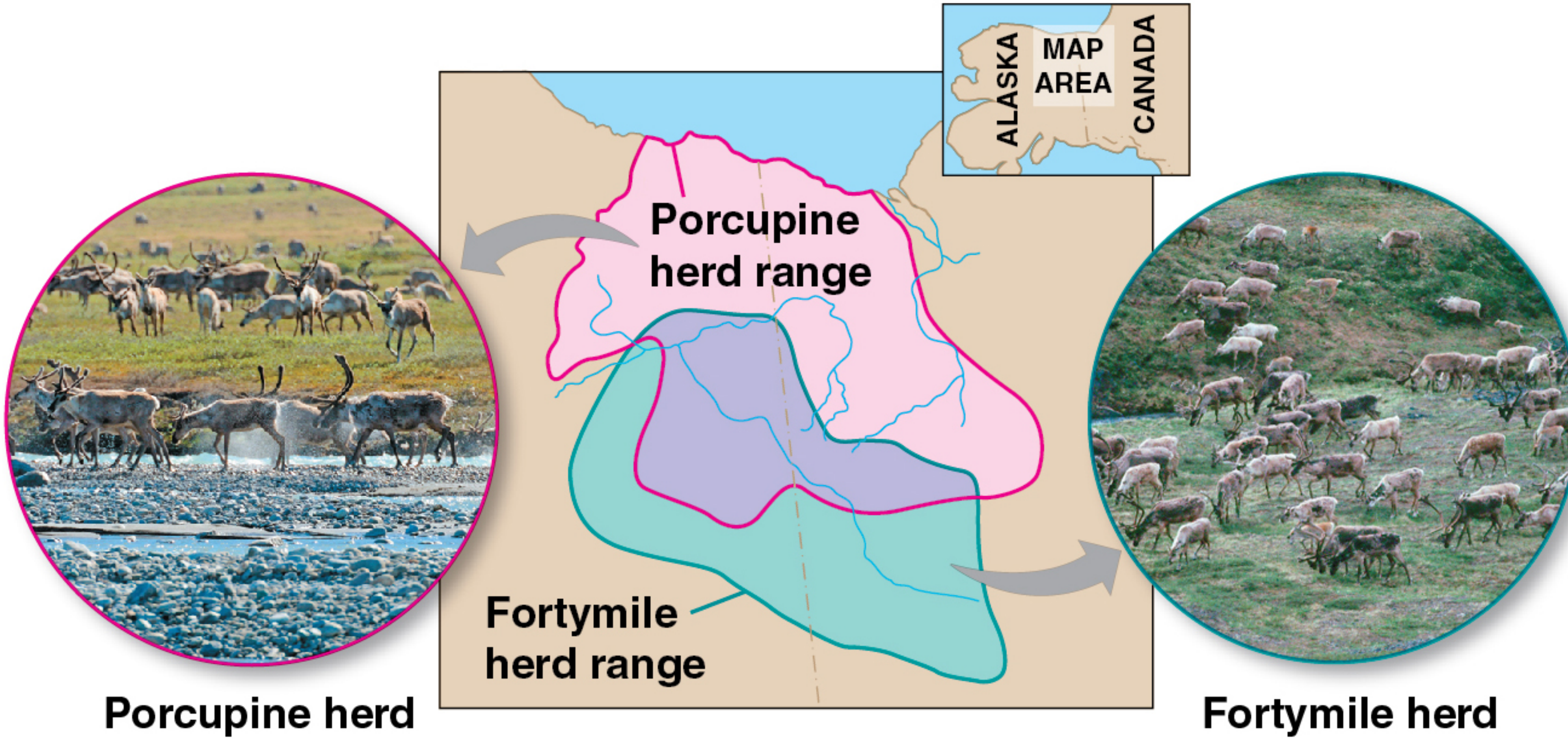
CONCEPT 23.2: The Hardy-Weinberg equation can be used to test whether a population is evolving

- Genetic variation is required for a population to evolve, but does not guarantee that it will
- One or more factors that cause evolution must be at work for a population to evolve

Gene Pools and Allele Frequencies

- A **population** is a group of individuals of the same species that live in the same area and interbreed
- Geographically isolated populations rarely exchange genetic material
- If populations are not isolated, individuals still usually only breed with members of their own population

Figure 23.6



MAP AREA
ALASKA
CANADA
Porcupine herd range
Fortymile herd range
Porcupine herd
Fortymile herd

- The **gene pool** consists of all copies of every allele at every locus in all members of the population
- A locus is fixed if all individuals in a population are homozygous for the same allele
- If there are two or more alleles for a locus, individuals may be homozygous or heterozygous
- Each genotype and each allele has a frequency in the population that can be calculated

Figure 23.UN01

$C^R C^R$

$C^W C^W$

$C^R C^W$

- Consider a population of 500 wildflowers with 320 red flowers (C^RC^R), 160 pink flowers (C^RC^W) and 20 white flowers (C^WC^W)
- To calculate genotype frequencies, divide the number of individuals of each genotype by the total number of individuals in the population
  - C^RC^R is 0.64 (320/500)
  - C^RC^W is 0.32 (160/500)
  - C^WC^W is 0.04 (20/500)

- Allele frequencies can also be calculated for a population
  - For diploid organisms, the total number of alleles at a locus is the total number of individuals times two
  - Count two dominant alleles for each homozygous dominant individual and one for each heterozygote
  - The same logic applies for recessive alleles

- Consider the population of 500 wildflowers with 320 red flowers (C^RC^R), 160 pink flowers (C^RC^W) and 20 white flowers (C^WC^W)
- Calculate the number of copies of each allele
  - $C^R = (320 \times 2) + 160 = 800$
  - $C^W = (20 \times 2) + 160 = 200$

- By convention, if there are two alleles at a locus, p and q are used to represent their frequencies
- The frequency of all alleles in a population will add up to 1
  - That is, $p + q = 1$

- To calculate the frequency of each allele, divide the number of copies of each allele by the total number of alleles in the population
  - p = frequency of C^R = 800/(800 + 200) = 0.8 (80%)
  - $q = 1 - p$ = 0.2 (20%)
- The sum of alleles is always 1 (100%)
  - 0.8 + 0.2 = 1

The Hardy-Weinberg Equation

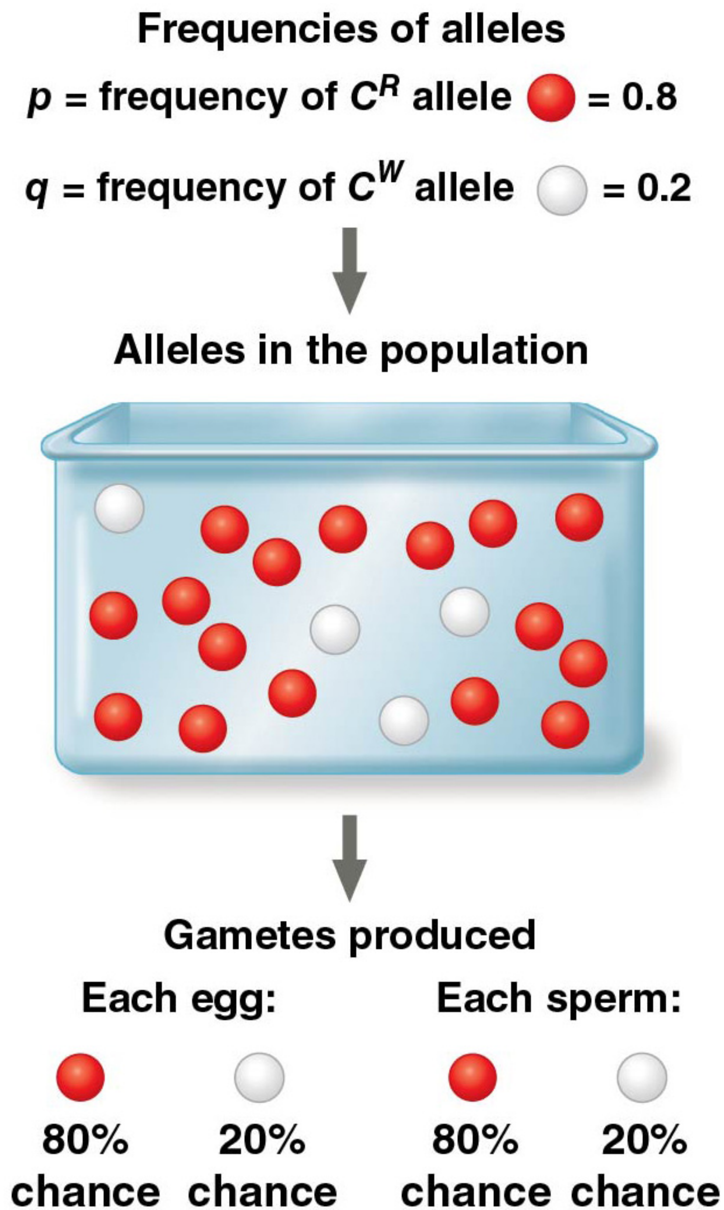
- The Hardy-Weinberg equation describes the expected genetic makeup for a population that is *not* evolving at a particular locus
- If the observed genetic makeup of the population differs from expectations under Hardy-Weinberg, then the population may be evolving

Hardy-Weinberg Equilibrium

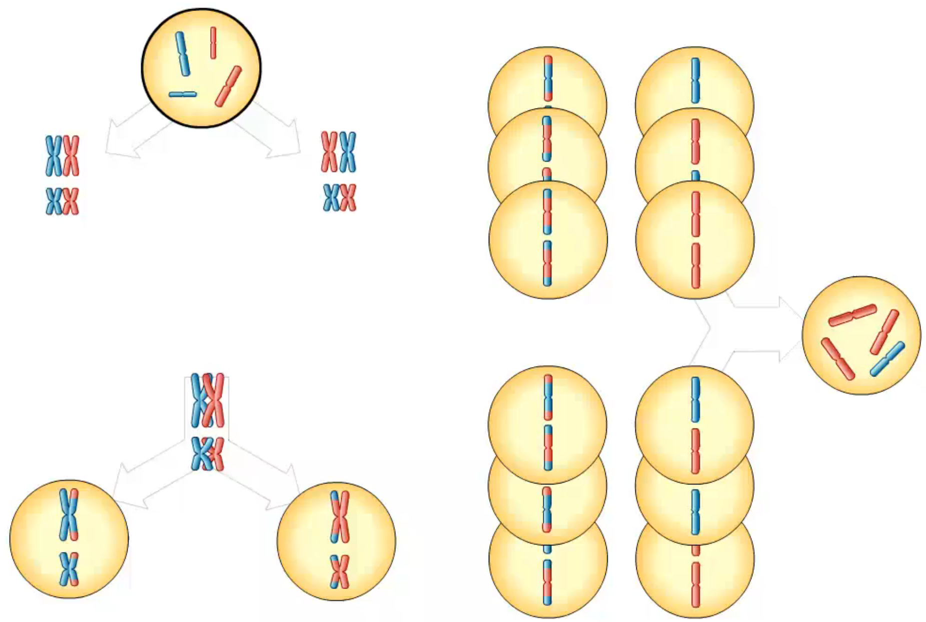
- If a population is not evolving, genotype and allele frequencies will be constant from generation to generation
- Mendelian segregation and recombination of alleles must also occur for frequencies to remain constant
- Such a population is in **Hardy-Weinberg equilibrium**

- Imagine all alleles for a given locus for all individuals in a population are placed in a bin
- “Reproduction” occurs by randomly selecting and combining alleles from the bin
- Apply this analogy to the population of 500 wildflowers with 1,000 alleles where
  - p = frequency of C^R = 0.8
  - q = frequency of C^W = 0.2

Figure 23.7

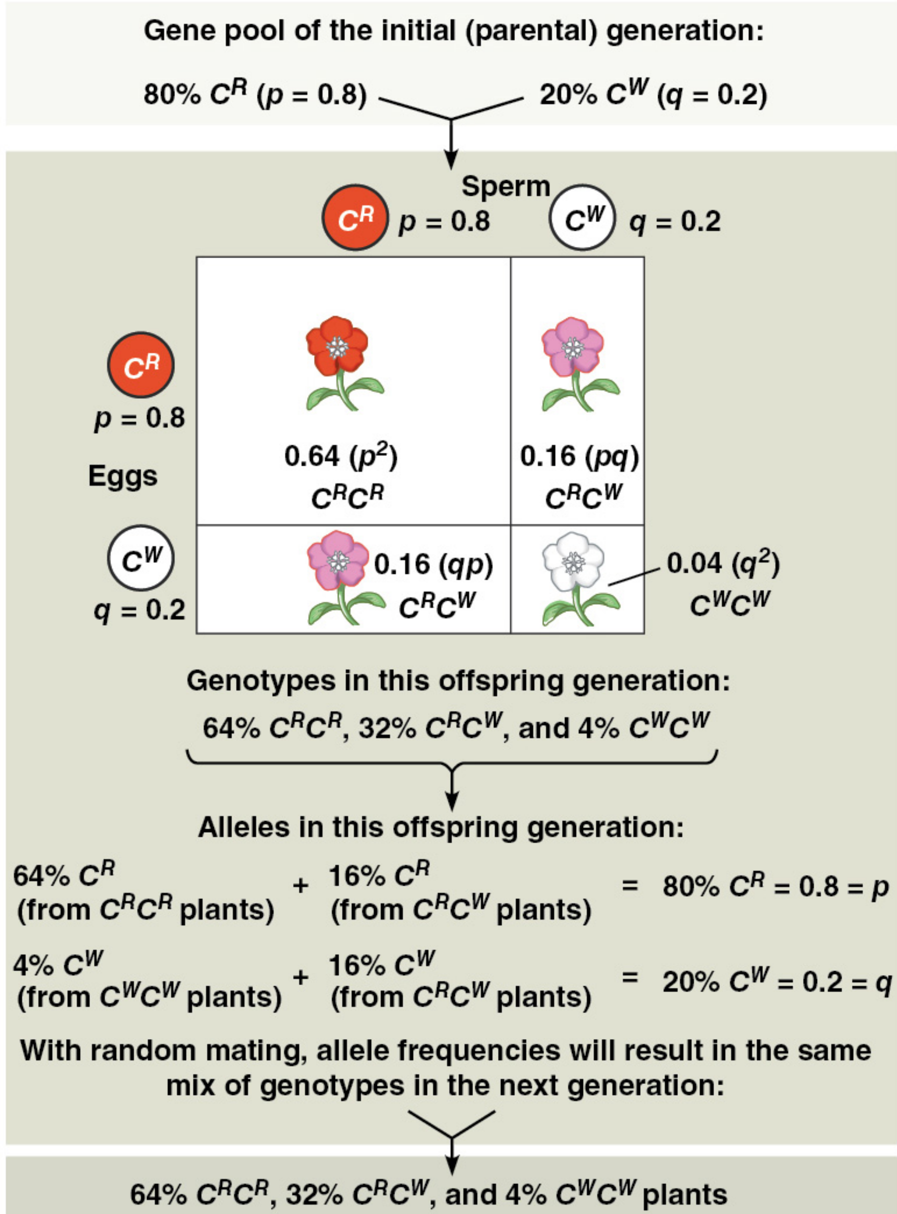

Frequencies of alleles
p = frequency of C^R allele = 0.8
q = frequency of C^W allele = 0.2
Alleles in the population
Gametes produced
Each egg:
Each sperm:
80% chance
20% chance
80% chance
20% chance

BioFlix® Animation: Allele Frequencies



- The frequency of genotypes can be calculated
  - $C^RC^R = p \times p = p^2 = 0.8 \times 0.8 = 0.64$
  - $C^RC^W = pq + qp = 2pq = 2 \times 0.8 \times 0.2 = 0.32$
  - $C^WC^W = q \times q = q^2 = 0.2 \times 0.2 = 0.04$
- The frequency of genotypes can be confirmed using a Punnett square

Figure 23.8


Gene pool of the initial (parental) generation:
80% C^R (p = 0.8)
20% C^W (q = 0.2)
Sperm
C^R p = 0.8
C^W q = 0.2
Eggs
C^R p = 0.8
C^W q = 0.2
0.64 (p^2) C^RC^R
0.16 (pq) C^RC^W
0.16 (qp) C^RC^W
0.04 (q^2) C^WC^W
Genotypes in this offspring generation:
64% C^RC^R, 32% C^RC^W, and 4% C^WC^W
Alleles in this offspring generation:
64% C^R (from C^RC^R plants) + 16% C^R (from C^RC^W plants) = 80% C^R = 0.8 = p
4% C^W (from C^WC^W plants) + 16% C^W (from C^RC^W plants) = 20% C^W = 0.2 = q
With random mating, allele frequencies will result in the same mix of genotypes in the next generation:
64% C^RC^R, 32% C^RC^W, and 4% C^WC^W plants

- If p and q represent the relative frequencies of the only two possible alleles in a population at a particular locus, then
  - $p^2 + 2pq + q^2 = 1$
  - where p^2 and q^2 represent the frequencies of the homozygous genotypes, and $2pq$ represents the frequency of the heterozygous genotype

Figure 23.UN02

$$p^2 + 2pq + q^2 = 1$$

p^2	+	$2pq$	+	q^2	= 1
Expected frequency of genotype C^RC^R		**Expected frequency of genotype** C^RC^W		**Expected frequency of genotype** C^WC^W	

Conditions for Hardy-Weinberg Equilibrium

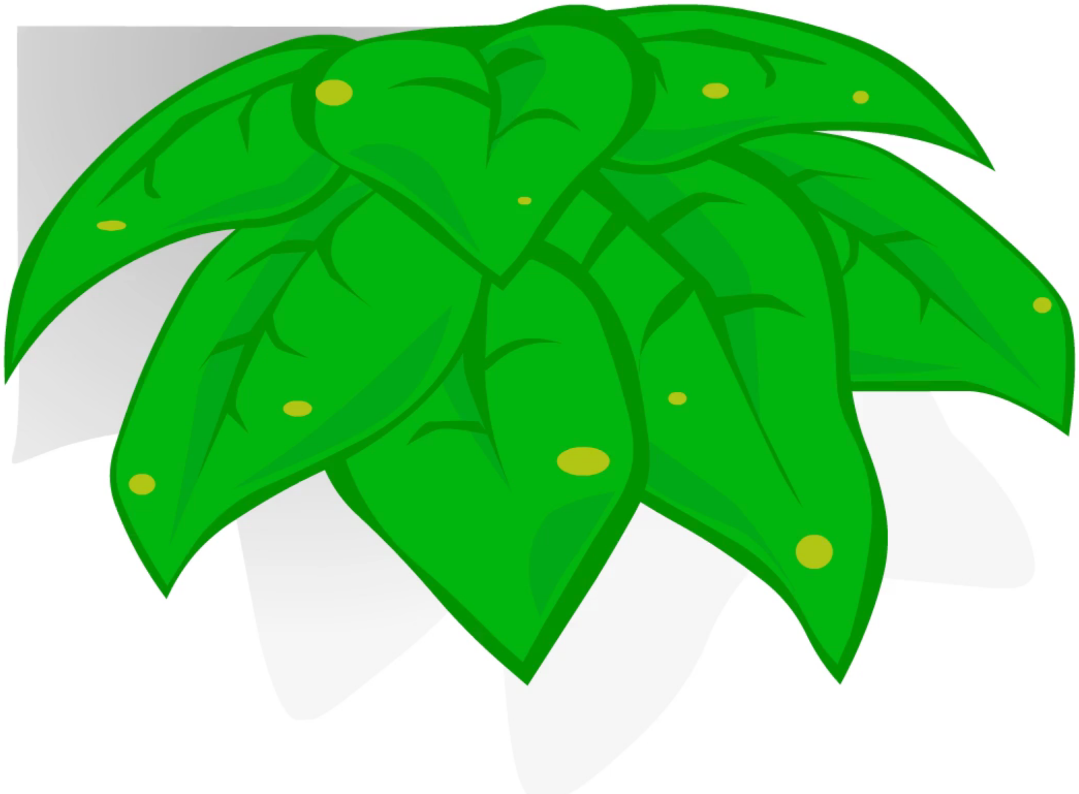
- The Hardy-Weinberg approach describes a population that is not evolving
- In real populations, allele and genotype frequencies often do change over time
- Such changes occur when one or more of the conditions for Hardy-Weinberg equilibrium are not met

Table 23.1 Conditions for Hardy-Weinberg Equilibrium

Condition	Consequence if Condition Does Not Hold
1. No mutations	The gene pool is modified if mutations occur or if entire genes are deleted or duplicated.
2. Random mating	If individuals mate within a subset of the population, such as near neighbors or close relatives (inbreeding), random mixing of gametes does not occur and genotype frequencies change.
3. No natural selection	Allele frequencies change when individuals with different genotypes show consistent differences in their survival or reproductive success.
4. Extremely large population size	In small populations, allele frequencies fluctuate by chance over time (genetic drift).
5. No gene flow	By moving alleles into or out of populations, gene flow can alter allele frequencies.

Animation: Causes of Evolutionary Change

Causes of Evolutionary Change



- If selection alters frequencies only at specific loci, a population could be in Hardy-Weinberg equilibrium for some genes, but not others
- Some populations evolve so slowly that change in allele and genotype frequencies is indistinguishable from that expected for a non-evolving population

Applying the Hardy-Weinberg Equation

- The Hardy-Weinberg equation can be used to test whether evolution is occurring in a population
- It is also used to determine the percentage of a population carrying a specific allele

- For example, we can assume that the locus that causes phenylketonuria (PKU) is in Hardy-Weinberg equilibrium given that
  1. The PKU gene mutation rate is low
  2. Mate selection is random with respect to whether or not an individual is a carrier for the PKU allele

3. Natural selection can only act on rare homozygous individuals who do not follow dietary restrictions
4. The population is large; genetic drift is not a factor
5. Migration has no effect, as many other populations have similar allele frequencies

- The occurrence of PKU is one per 10,000 births
  - $q^2 = 0.0001$
  - $q = \sqrt{0.0001} = 0.01$
- The frequency of the dominant allele is
  - $p = 1 - q = 1 - 0.01 = 0.99$
- The frequency of carriers is
  - $2pq = 2 \times 0.99 \times 0.01 = 0.0198$
  - or approximately 2% of the U.S. population

CONCEPT 23.3: Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

- Deviation from any of the required conditions can take a population out of Hardy-Weinberg equilibrium
- New mutations can alter allele frequencies, but effects are minimal because mutations are rare
- Nonrandom mating can affect genotype frequencies, but not allele frequencies

- Three major factors alter allele frequencies directly and bring about most evolutionary change:
  - Natural selection
  - Genetic drift
  - Gene flow

Natural Selection

- Natural selection is based on differential success in survival and reproduction
  - Individuals have variations in their heritable traits
  - Those with traits better suited to the environment produce more offspring than others

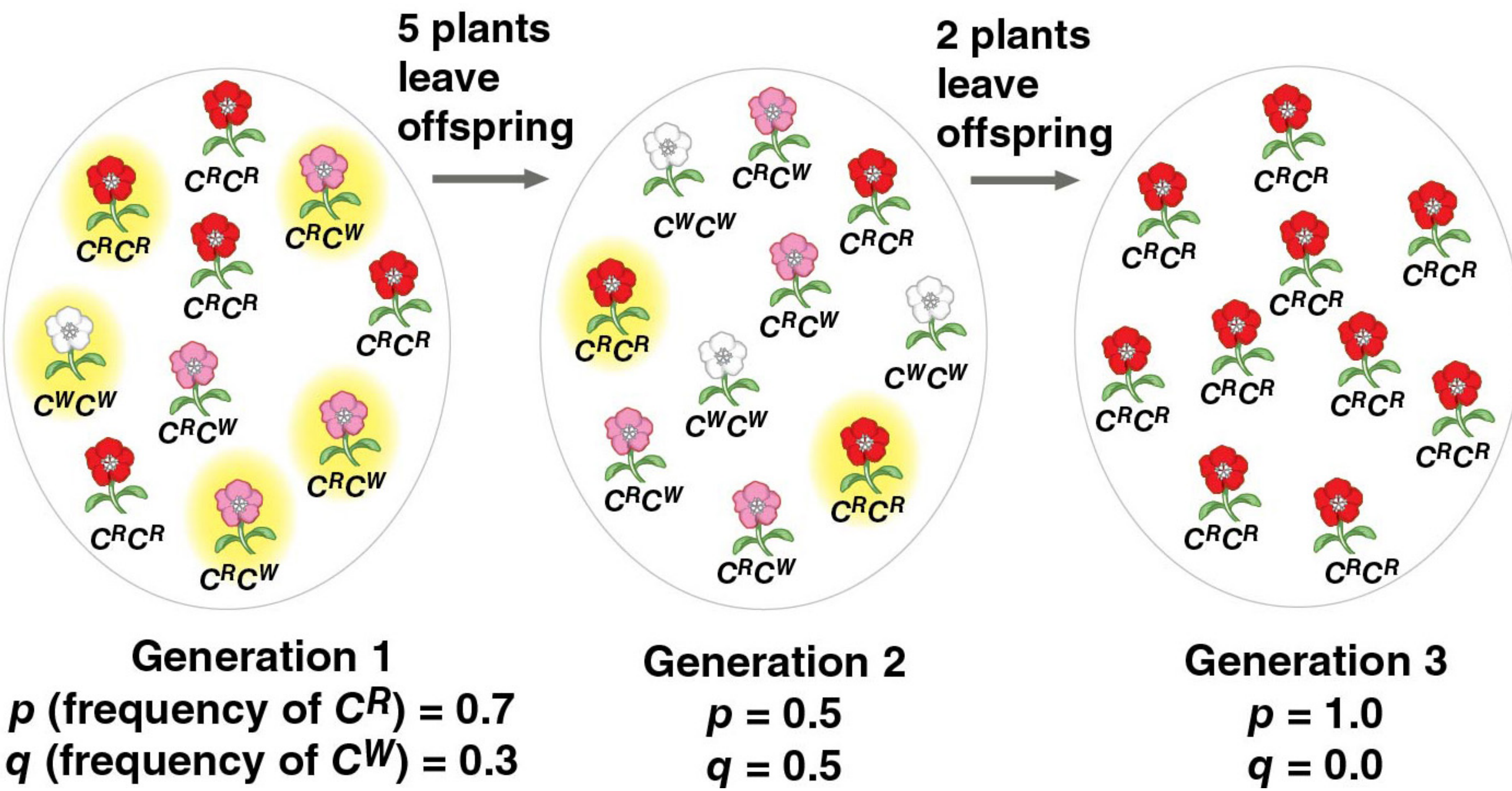
- Selection results in alleles being passed to the next generation in proportions that differ from those in the present generation
  - For example, an allele for DDT resistance increased in frequency in wild fruit flies after 20 or more years of DDT use

- Natural selection can cause **adaptive evolution**, a process in which traits that enhance survival or reproduction increase in frequency over time

Genetic Drift

- The smaller the sample, the greater the chance of random deviation from a predicted result
- **Genetic drift** is a process in which chance events cause allele frequencies to fluctuate unpredictably from one generation to the next
- Genetic drift tends to reduce genetic variation through the random loss of alleles

Figure 23.9


5 plants leave offspring
2 plants leave offspring
C^RC^R
C^RC^W
C^WC^W
Generation 1
p (frequency of C^R) = 0.7
q (frequency of C^W) = 0.3
Generation 2
p = 0.5
q = 0.5
Generation 3
p = 1.0
q = 0.0

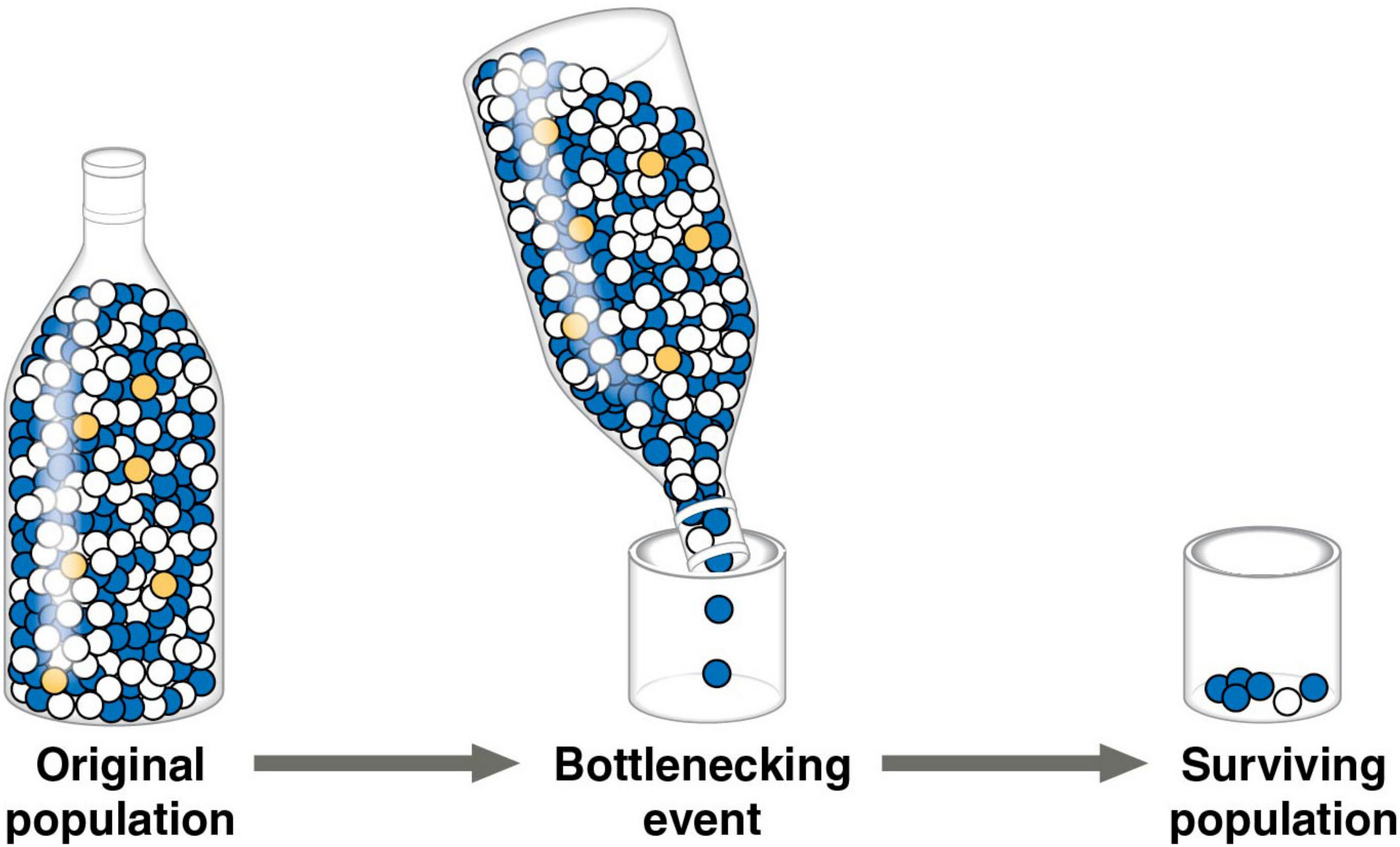
The Founder Effect

- The **founder effect** occurs when a few individuals become isolated from a larger population
- Allele frequencies in the smaller founder population are different from those in the parent population
  - For example, genetic drift could occur if a few individuals are indiscriminately blown to a new island by a storm

The Bottleneck Effect

- The **bottleneck effect** occurs when there is a drastic reduction in population size due to a sudden change in the environment
- The resulting gene pool may no longer be reflective of the original population’s gene pool
- If the population remains small, it may be further affected by genetic drift

Figure 23.10


Original population
Bottlenecking event
Surviving population

Case Study: Impact of Genetic Drift on the Greater Prairie Chicken

- Loss of prairie habitat caused a severe reduction in the population of greater prairie chickens in Illinois
- The surviving birds had low levels of genetic variation, and only 50% of their eggs hatched
- Genetic drift during the bottleneck likely reduced genetic variation and increased the frequency of harmful alleles

- Researchers compared variation in DNA between museum specimens and the current population
- Genetic variation declined and harmful alleles likely increased in frequency in the current population
- Researchers added 271 birds from populations in neighboring states to the Illinois population
- New alleles entered the population, and the egg-hatching rate improved to over 90%

Figure 23.11

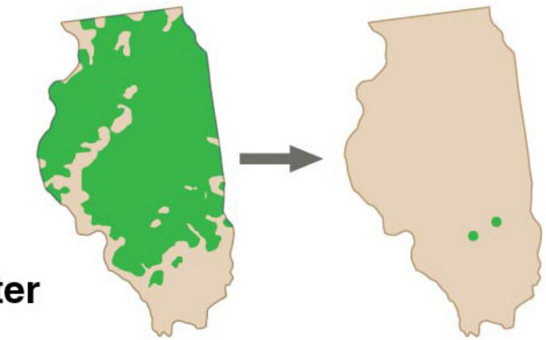
Greater prairie chicken

(a)

Range of greater prairie chicken

Pre-bottleneck (Illinois, 1820)

Post-bottleneck (Illinois, 1993)



Location	Population size	Number of alleles per locus	Percentage of eggs hatched
Illinois			
1930–1960s	1,000–25,000	5.2	93
1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96

(b)

Effects of Genetic Drift: *A Summary*

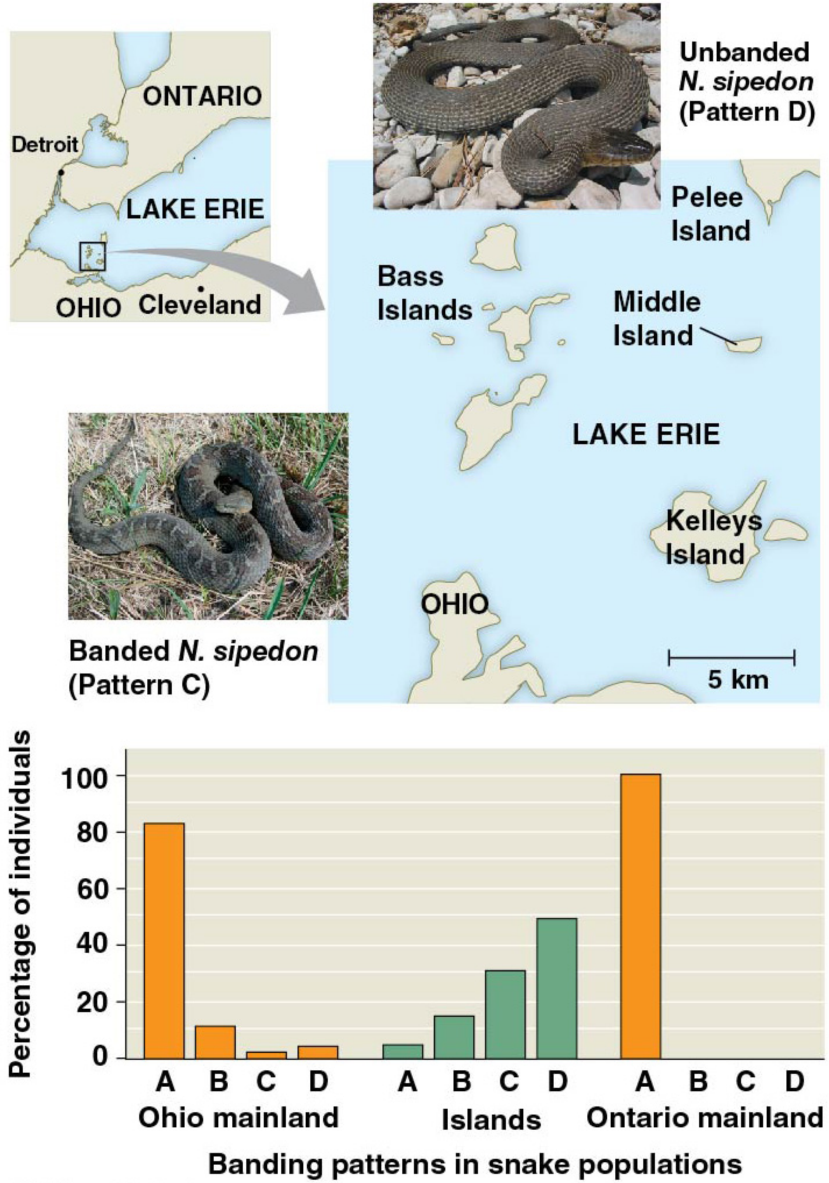
1. Genetic drift is significant in small populations
2. Genetic drift can cause allele frequencies to change at random
3. Genetic drift can lead to a loss of genetic variation within populations
4. Genetic drift can cause harmful alleles to become fixed

Gene Flow

- **Gene flow** consists of the movement of alleles among populations
- Alleles can be transferred through the movement of fertile individuals or gametes (for example, pollen)
- Gene flow tends to reduce variation among populations over time

- Gene flow affects adaptation to local environments
  - For example, mainland and island populations of Lake Erie water snakes have different color patterns
  - A strong banding pattern is favored on the mainland; unbanded snakes are better camouflaged on islands
  - Ongoing migration of banded snakes from the mainland population maintains disadvantageous alleles for banding pattern on the islands

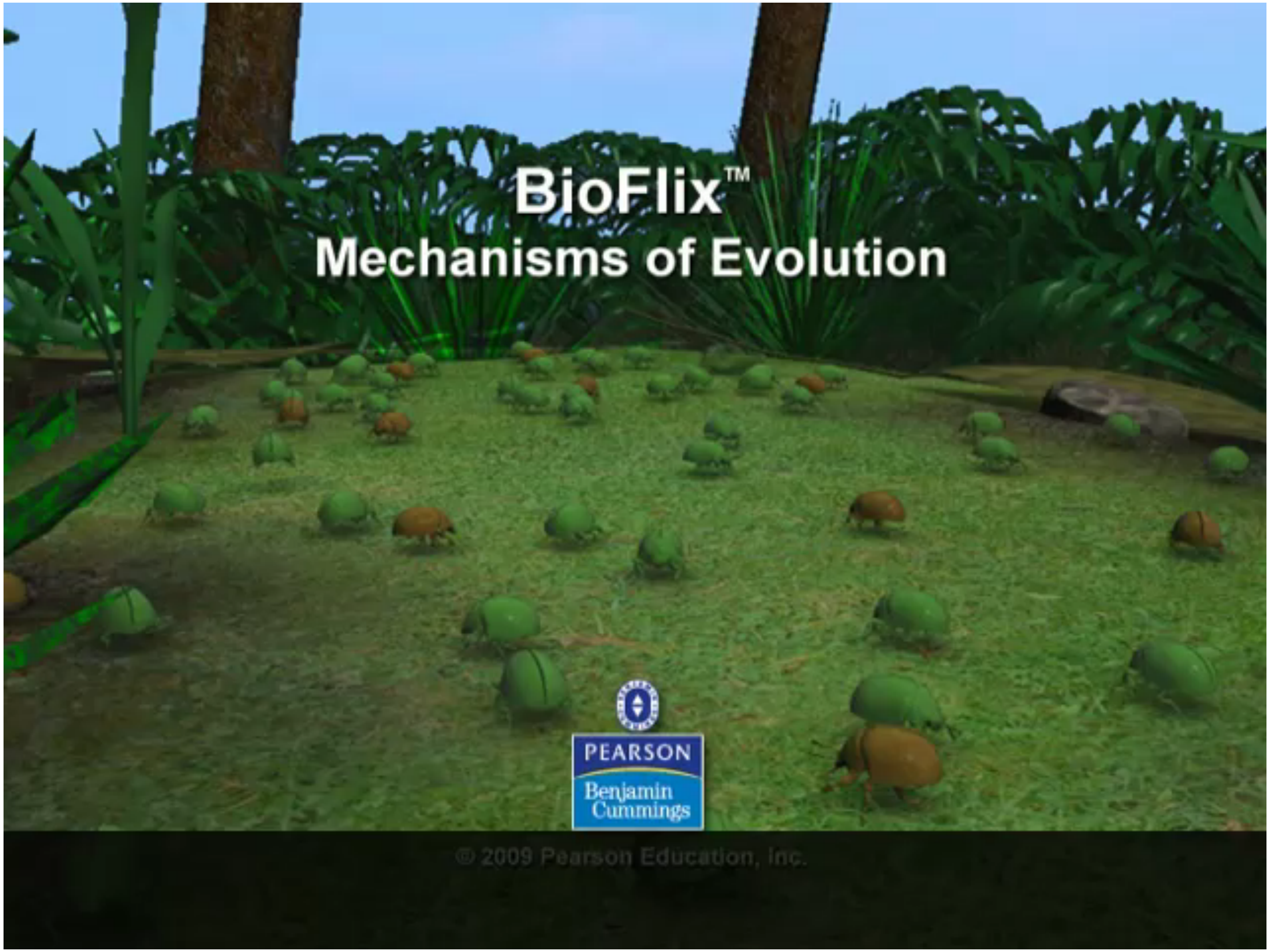
Figure 23.12



ONTARIO
Detroit
LAKE ERIE
OHIO
Cleveland
Unbanded
N. sipedon
(Pattern D)
Pelee
Island
Bass
Islands
Middle
Island
LAKE ERIE
Kelleys
Island
OHIO
5 km
Banded N. sipedon
(Pattern C)
Percentage of individuals
100
80
60
40
20
0
A B C D
Ohio mainland
A B C D
Islands
A B C D
Ontario mainland
Banding patterns in snake populations

- Gene flow can also increase a population's fitness
- Consider, for example, the spread of alleles for resistance to insecticides
  - Insecticides have been used to target mosquitoes that carry West Nile virus and other diseases
  - Alleles have evolved in some populations that confer insecticide resistance to these mosquitoes
  - The flow of resistance alleles into a new population can increase its fitness

Bioflix: Mechanisms of Evolution



CONCEPT 23.4: Natural selection is the only mechanism that consistently causes adaptive evolution

- Evolution by natural selection involves both chance and “sorting”
  - New genetic variations arise by chance
  - Beneficial alleles are “sorted” and favored by natural selection
- Only natural selection consistently increases the frequencies of alleles that provide reproductive advantage

Natural Selection: *A Closer Look*

- Natural selection brings about adaptive evolution by acting on an organism's phenotype

Relative Fitness

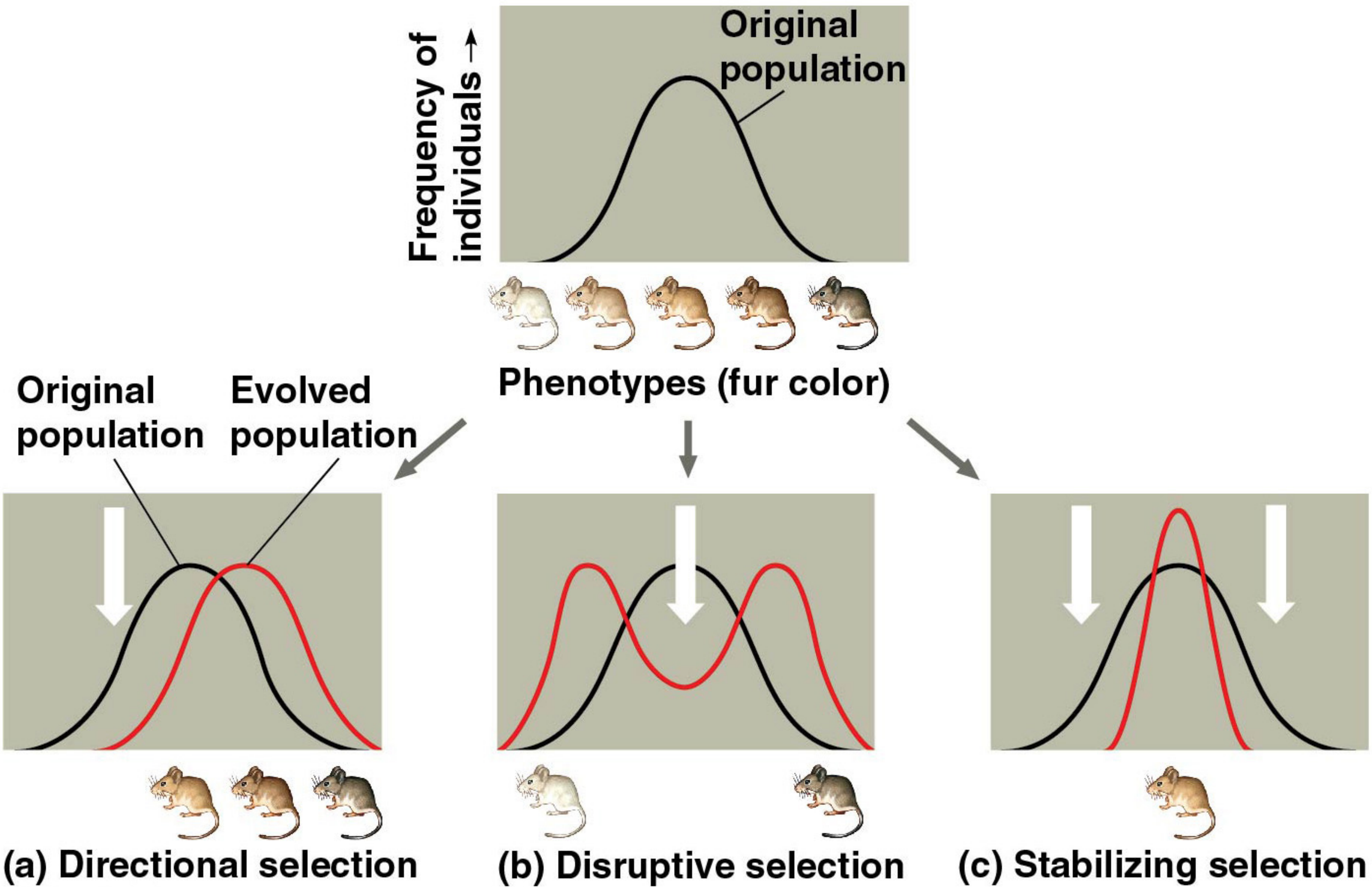
- The phrases “struggle for existence” and “survival of the fittest” are misleading, as they imply direct competition among individuals
- Reproductive success is generally more subtle
  - For example, a barnacle that is more efficient at food collection than others will have more energy to invest in egg production

- **Relative fitness** is the contribution an individual makes to the gene pool of the next generation relative to the contributions of other individuals
- Selection favors certain genotypes by acting on the phenotypes of individuals

Directional, Disruptive, and Stabilizing Selection

- There are three ways in which natural selection can alter the frequency distribution of heritable traits:
  - **Directional selection** favors individuals at one extreme end of the phenotypic range
  - **Disruptive selection** favors individuals at both extremes of the phenotypic range
  - **Stabilizing selection** favors intermediate variants and acts against extreme phenotypes

Figure 23.13

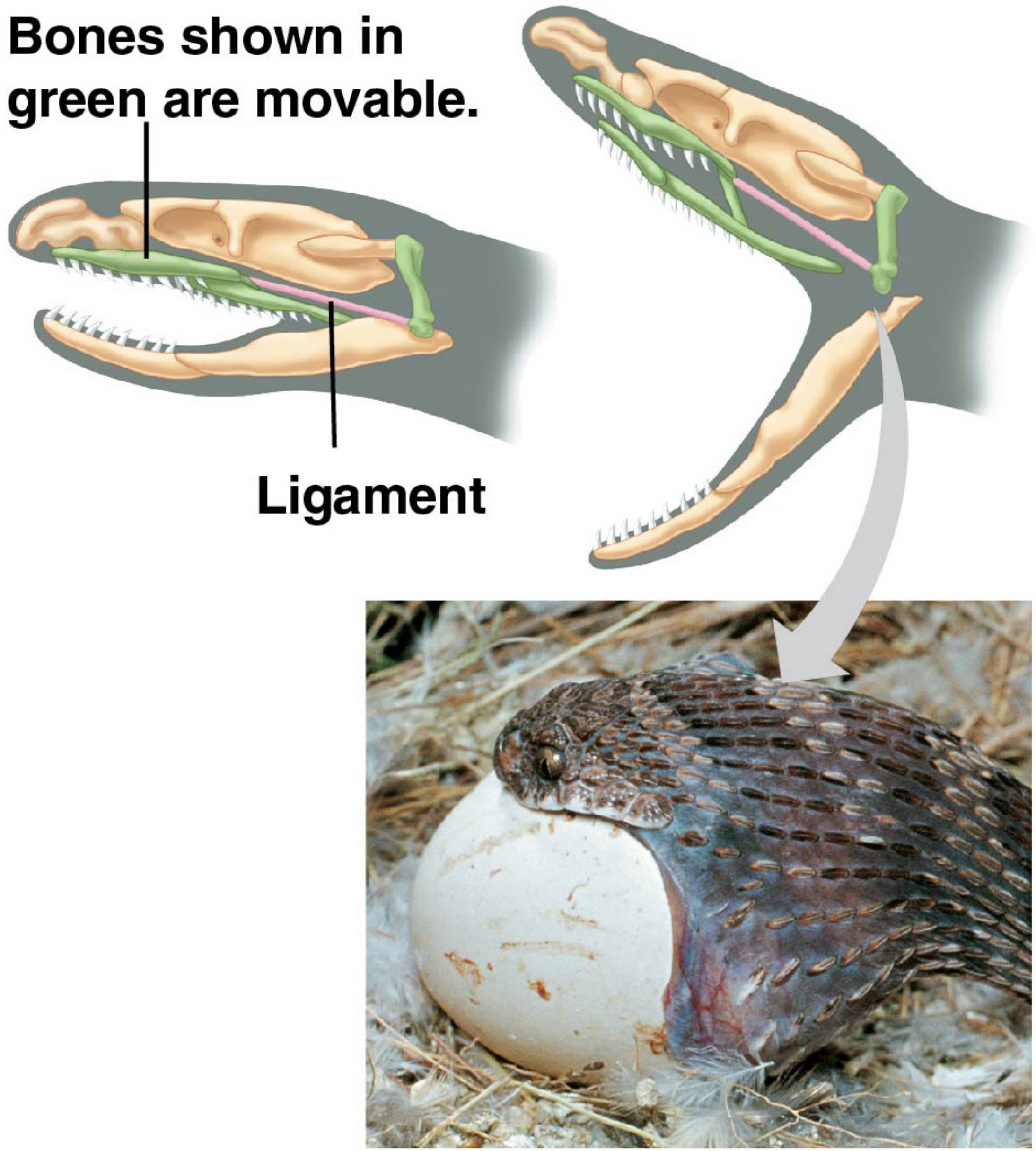


Frequency of individuals →
Original population
Phenotypes (fur color)
Original population
Evolved population
(a) Directional selection
(b) Disruptive selection
(c) Stabilizing selection

The Key Role of Natural Selection in Adaptive Evolution

- Striking adaptations have arisen by natural selection
  - For example, certain octopuses can change color rapidly for camouflage
  - For example, the jaws of snakes allow them to swallow prey larger than their heads

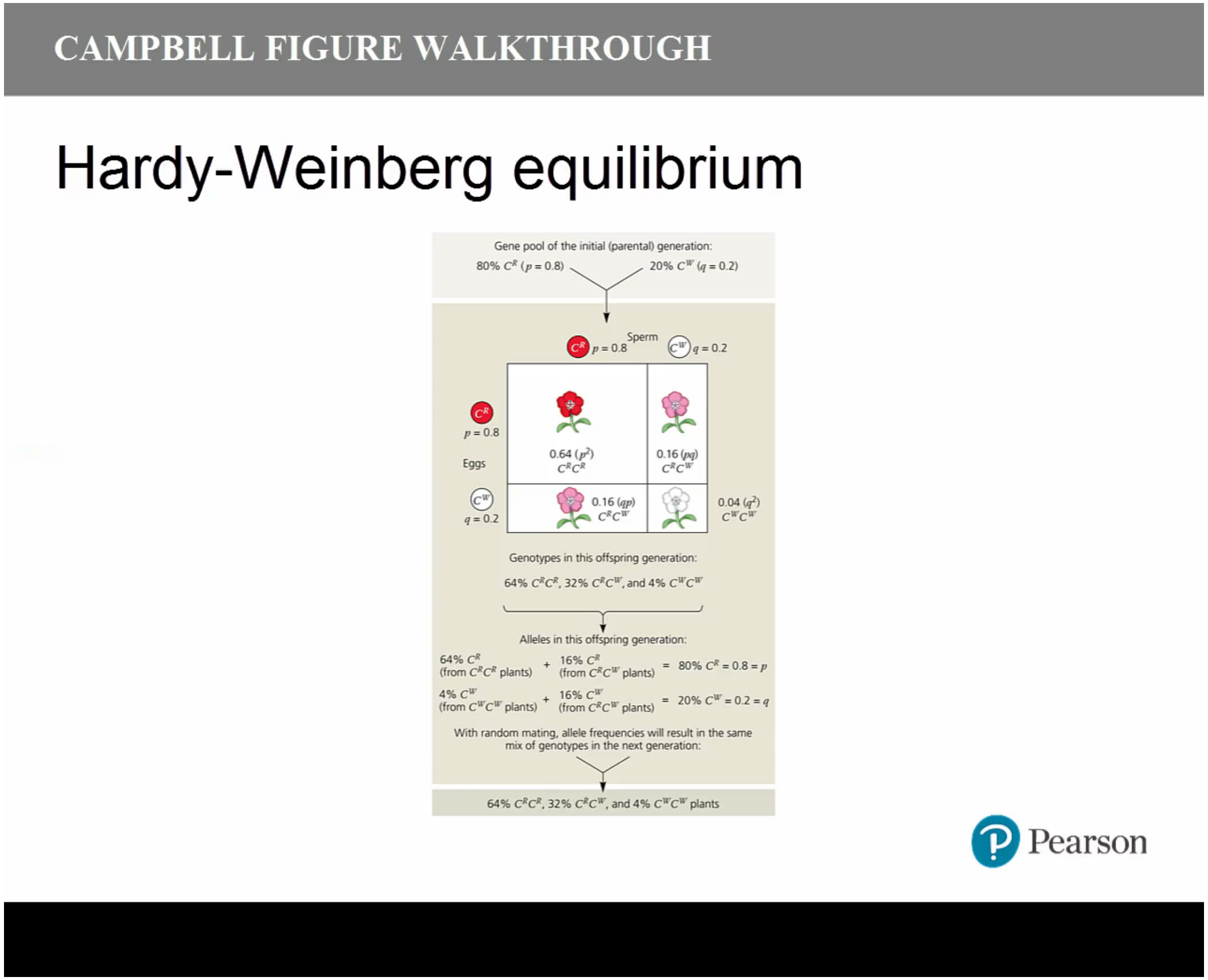
Figure 23.14



- Natural selection increases the frequencies of alleles that enhance survival and reproduction
- Adaptive evolution results from an increase in the degree to which a species is well suited for life in its environment
- Because the environment can change, adaptive evolution is a continuous process that varies from place to place

- Genetic drift and gene flow do not consistently increase the frequency of alleles that enhance survival and reproduction
- Both processes may increase or decrease the frequency of beneficial alleles in a population

Video: Got Lactase? The Co-evolution of Genes and Culture



Sexual Selection

- **Sexual selection** is a process in which individuals with certain heritable traits are more likely to obtain mates than other individuals of the same sex
- It can result in **sexual dimorphism**, a difference in secondary sexual characteristics between the sexes
  - For example, males and females may differ in size, color, ornamentation, and behavior

Figure 23.15

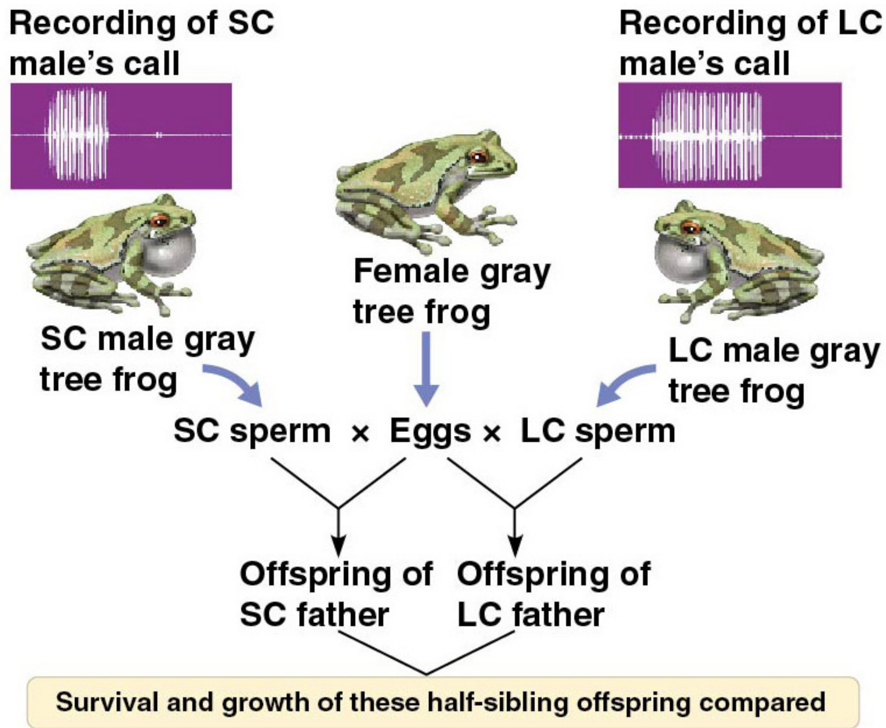
- **Intrasexual selection** is direct competition among individuals of one sex (often males) for mates of the opposite sex
  - For example, males may patrol a group of females and prevent weaker males from mating by defeating them in combat

- **Intersexual selection** (mate choice) occurs when individuals of one sex (usually females) are choosy in selecting their mates
- Female choice is often dependent on the showiness of the male’s appearance or behavior
- Though showiness can increase the likelihood of mating, it can also decrease the chances of survival

- The “good genes” hypothesis proposes that females select males with traits that are related to their genetic quality or overall health
- If true, then both the male trait and female preference for it should increase in frequency

Figure 23.16

Experiment



Results

Offspring Performance	1995	1996
Larval survival	LC better	NSD
Larval growth	NSD	LC better
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

Data from A. M. Welch et al., Call duration as an indicator of genetic quality in male gray tree frogs, *Science* 280:1928–1930 (1998).

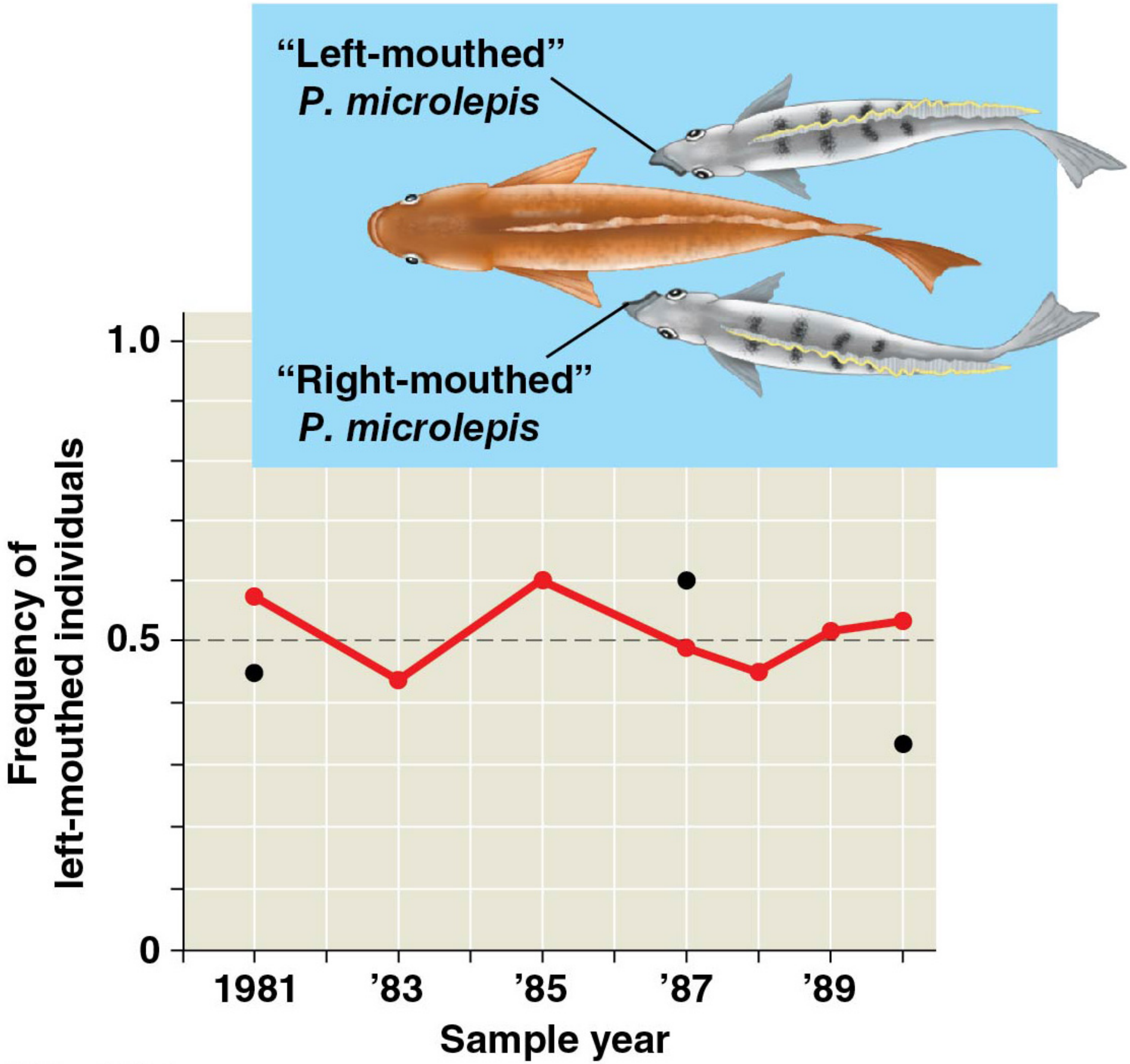
Balancing Selection

- Balancing selection preserves variation at some loci by maintaining stable frequencies of two or more phenotypes
- Balancing selection includes
  - Frequency-dependent selection
  - Heterozygote advantage

Frequency-Dependent Selection

- In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is
  - For example, frequency-dependent selection results in approximately equal numbers of “right-mouthed” and “left-mouthed” scale-eating fish
  - Prey maintain both phenotypes by altering their behavior to defend against whichever is most common

Figure 23.17



"Left-mouthed"
P. microlepis
"Right-mouthed"
P. microlepis
1.0
0.5
0
Frequency of
left-mouthed individuals
1981
'83
'85
'87
'89
Sample year

Heterozygote Advantage

- **Heterozygote advantage** occurs when heterozygotes have a higher fitness than both kinds of homozygotes
- Natural selection will tend to maintain two or more alleles at that locus
  - For example, the deleterious sickle-cell allele is maintained at relatively high frequencies in some regions due to heterozygote advantage

The Sickle Cell Allele

- Sickle-cell disease is a genetic disorder that strikes individuals with two copies of the sickle-cell allele
- This allele affects the structure and function of hemoglobin, reducing the oxygen carrying capacity of red blood cells
- Though sickle-cell disease is lethal, frequency of the allele is as high as 15–20% in some regions

Events at the Molecular Level

- A point mutation in the sickle-cell allele changes one amino acid, causing improper protein folding, and binding of the proteins into chains forming a fiber

Consequences for Cells

- Abnormal hemoglobin fibers distort the red blood cell into a sickle shape in low-oxygen conditions

Effects on Individual Organisms

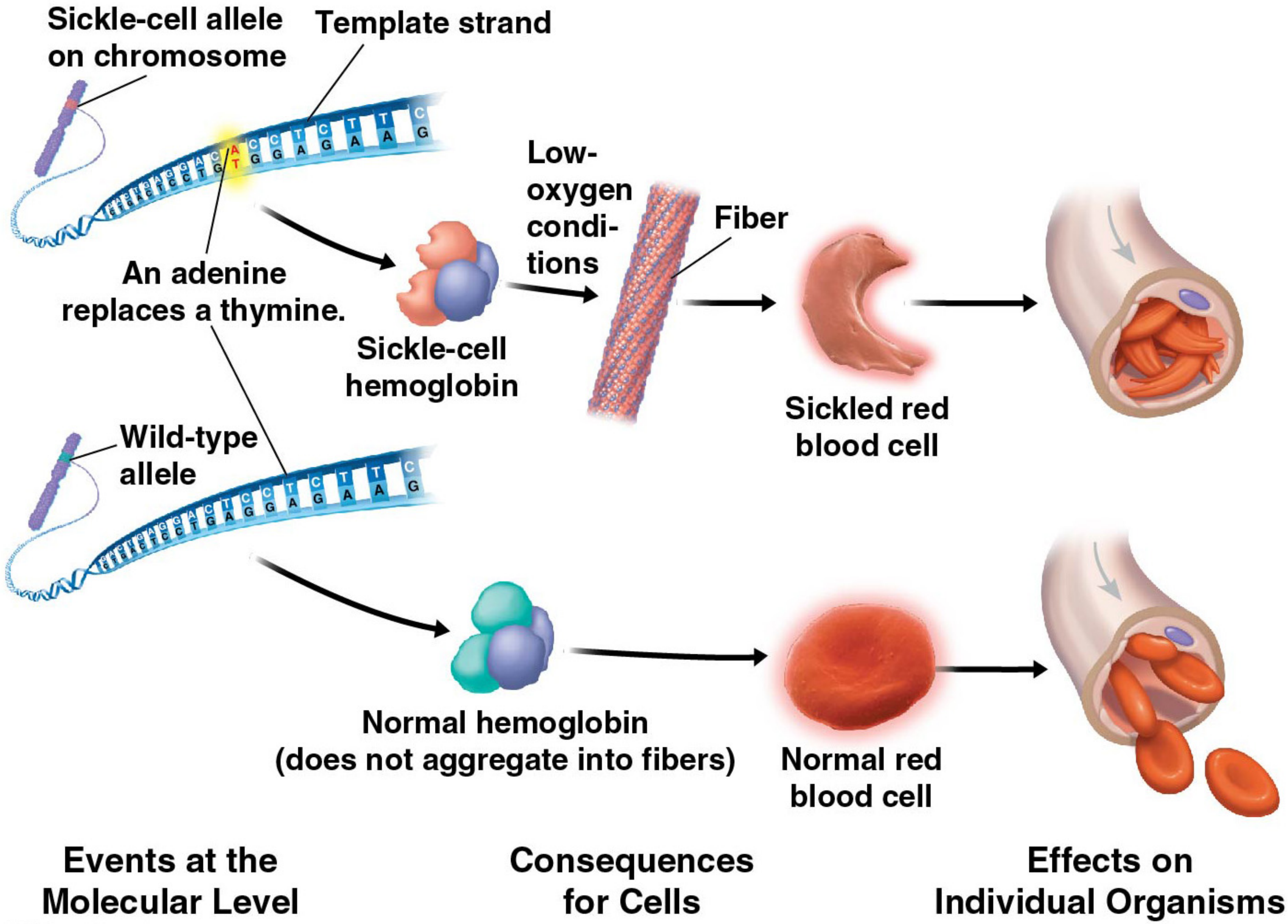
- Individuals homozygous for the sickle-cell allele have sickle-cell disease
- In heterozygotes, some sickling occurs, but not enough to cause the disease

Evolution in Populations

- Individuals that are homozygous for the sickle-cell allele are strongly selected against
- Heterozygotes experience few harmful effects, but are more likely to survive malaria than homozygotes
- Where malaria is common, heterozygote advantage increases the frequency of sickle-cell alleles

Figure 23.18

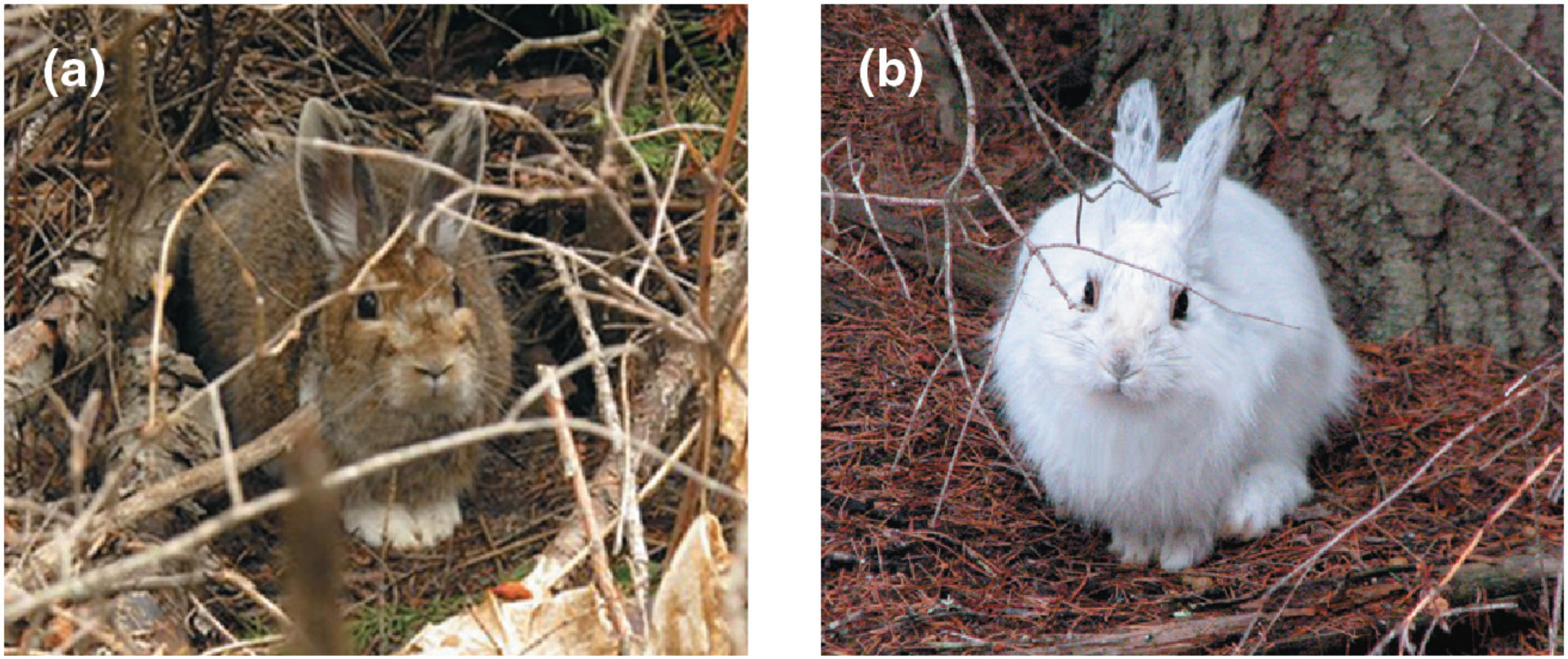
Make Connections: The Sickle-Cell Allele



Why Natural Selection Cannot Fashion Perfect Organisms

1. Selection can act only on existing variations
2. Evolution is limited by historical constraints
3. Adaptations are often compromises
4. Chance, natural selection, and the environment interact

Figure 23.19



Data from the Experiment

Time (days)	Number of Seedlings			
	Green (C^GC^G)	Green-yellow (C^GC^Y)	Yellow (C^YC^Y)	Total
7	49	111	56	216
21	47	106	20	173

Figure 23.UN03b

Figure 23.UN04

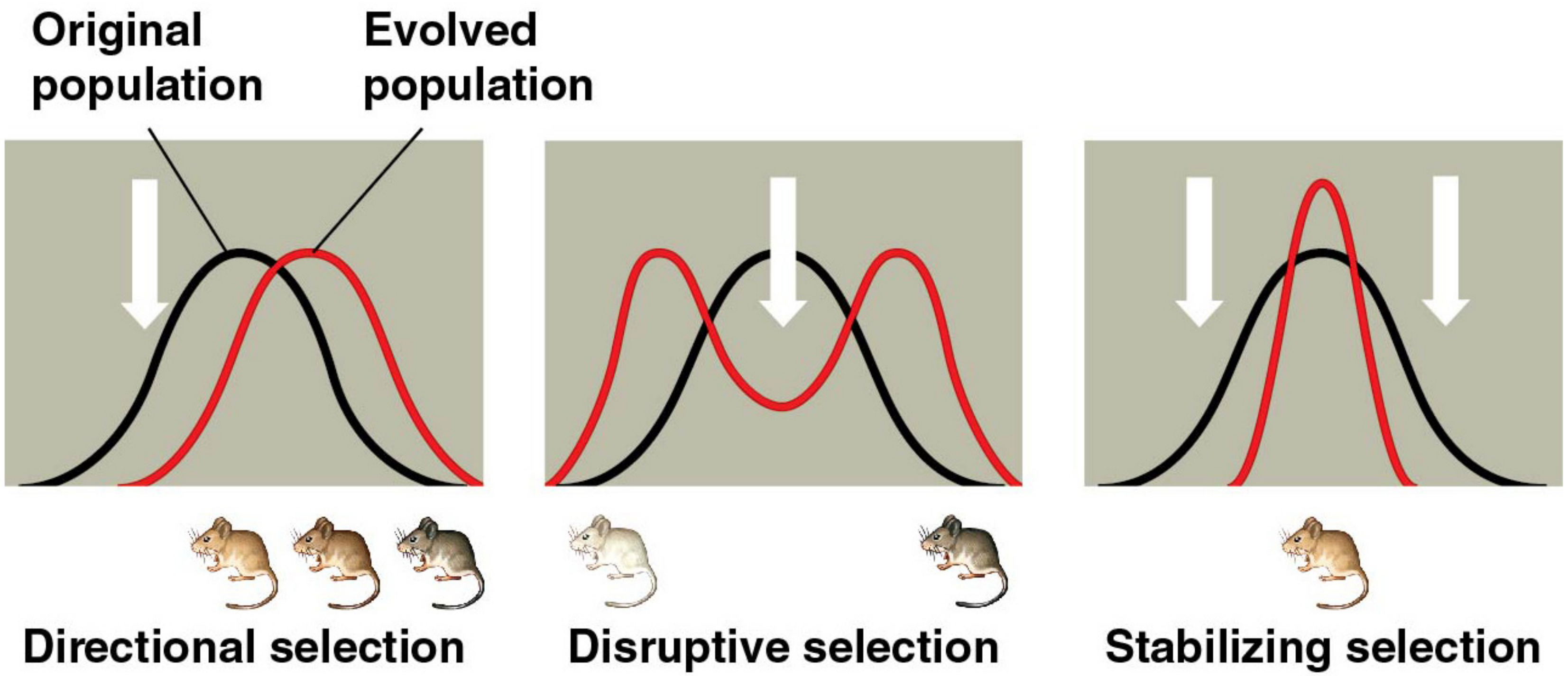


Figure 23.UN05

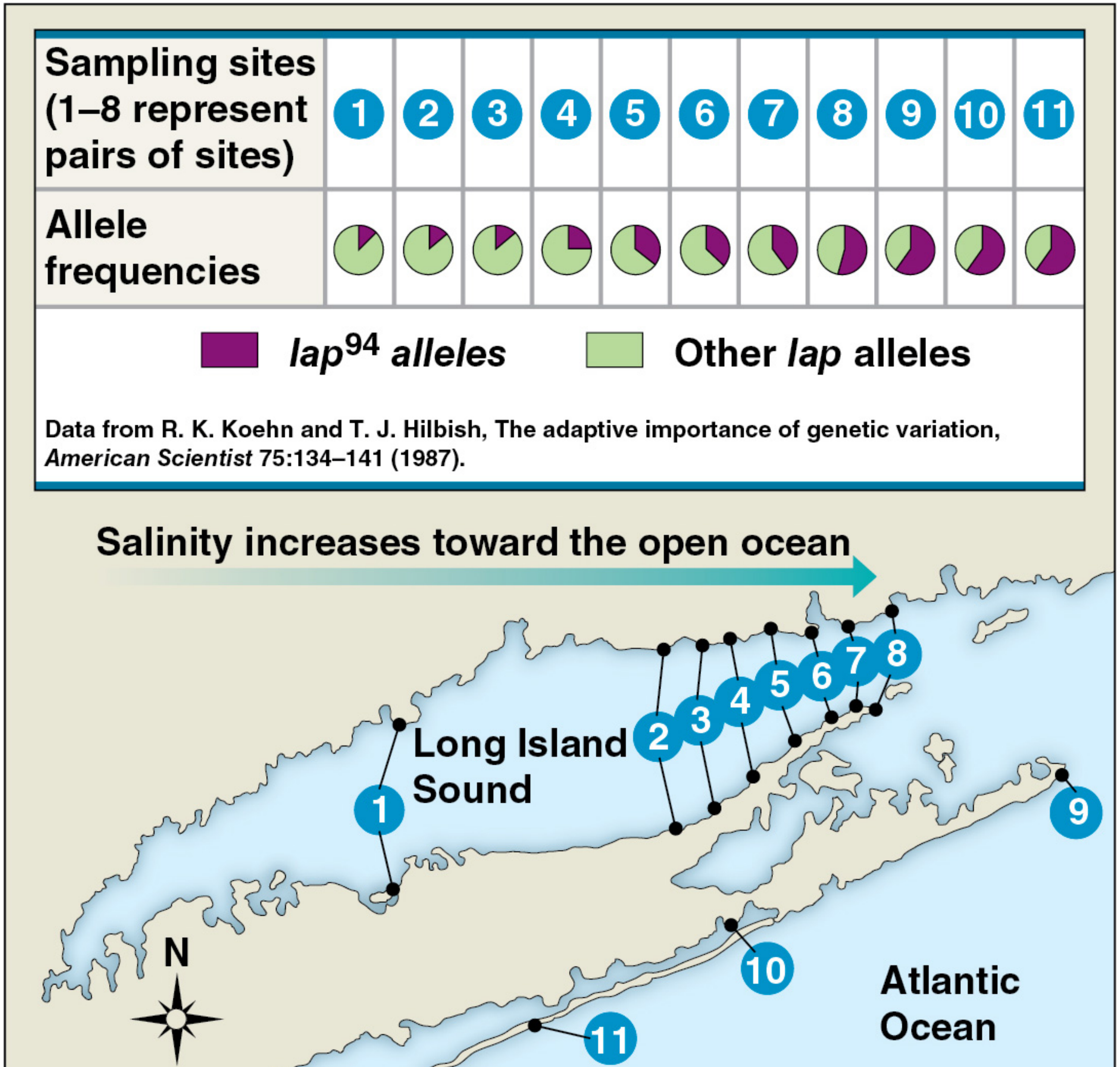


Figure 23.UN06