

ELEVENTH EDITION

# CAMPBELL BIOLOGY

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## Chapter 23

# The Evolution of Populations

Lecture Presentations by  
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# The Smallest Unit of Evolution

- A common misconception is that individual organisms evolve
- Natural selection acts on individuals, but only populations evolve
- Consider, for example, a population of medium ground finches on Daphne Major Island
  - During a drought, large-beaked birds were more likely to crack large seeds and survive

Figure 23.1

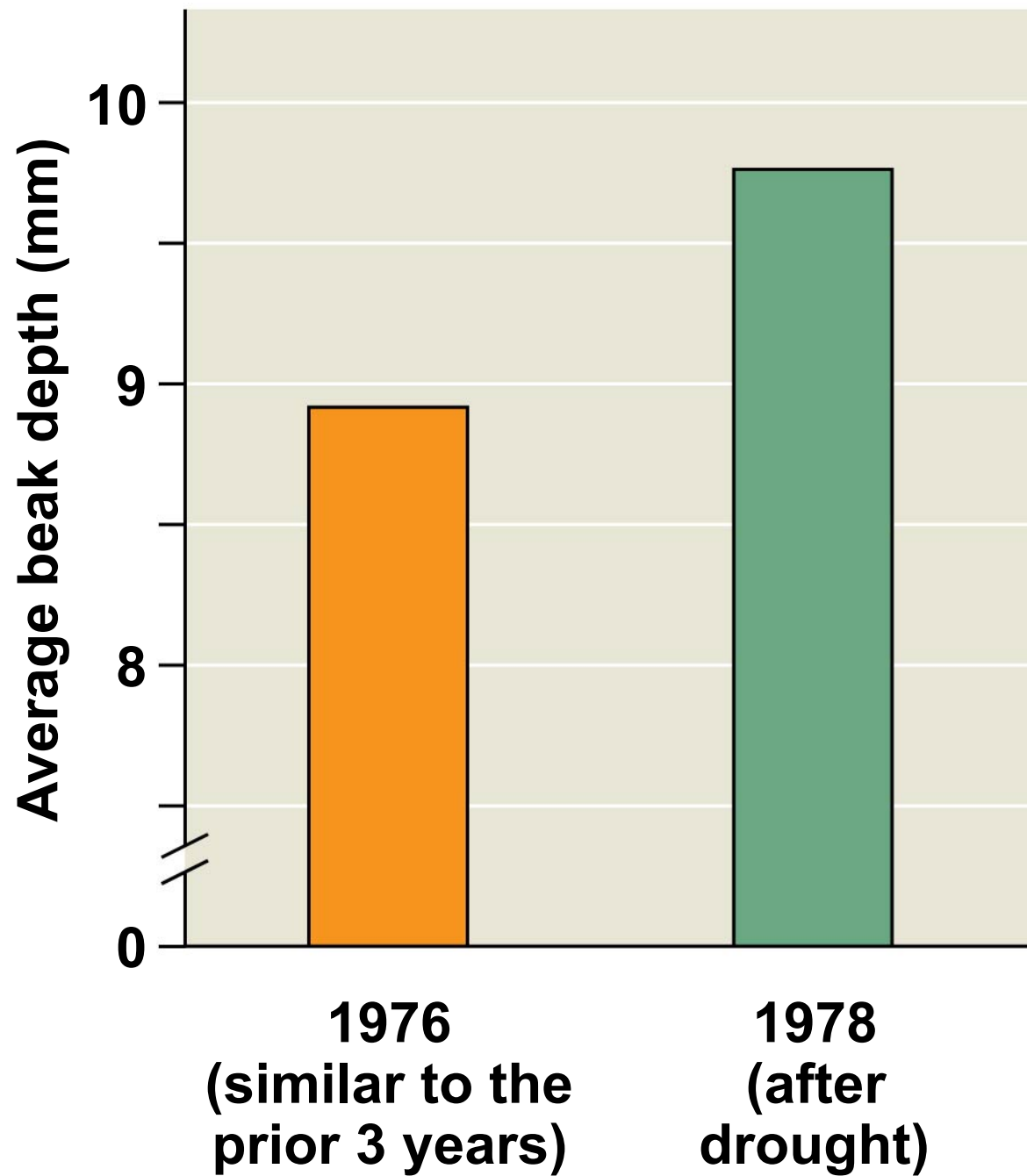




Figure 23.1a



Figure 23.2



- The finch population evolved, not its individual members

- **Microevolution** is a change in allele frequencies in a population over generations
- Three main mechanisms cause allele frequency change:
  - Natural selection
  - Genetic drift
  - Gene flow
- Only natural selection consistently causes adaptive evolution

# Concept 23.1: Genetic variation makes evolution possible

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

- Some phenotypic differences are determined by a single gene and can be classified on an “either-or” basis
- Other phenotypic differences are determined by the influence of two or more genes and vary along a continuum within a population

Figure 23.3

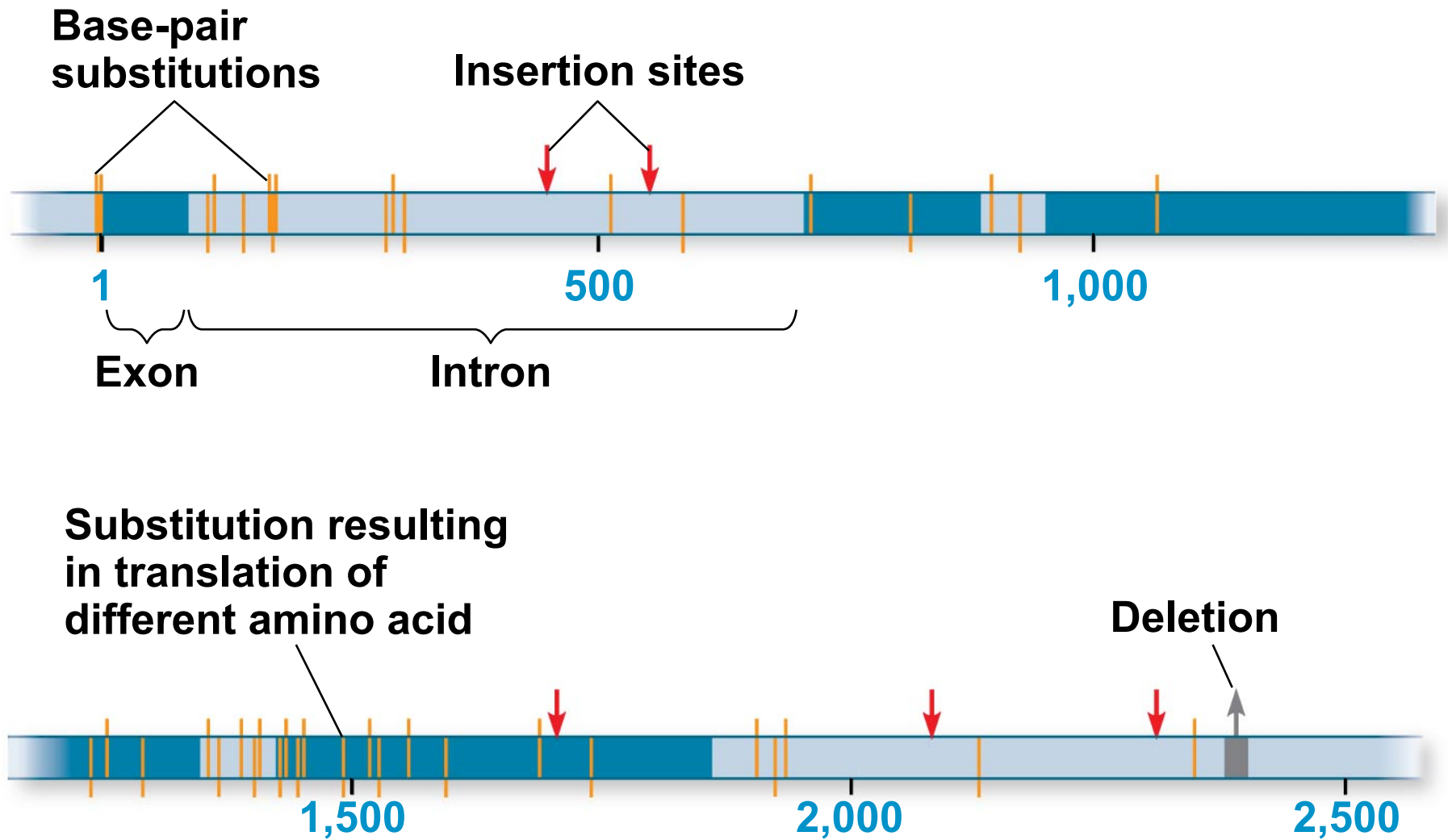


- Genetic variation can be measured as gene variability or nucleotide variability
- For gene variability, average heterozygosity measures the average percent of loci that are heterozygous in a population

- Nucleotide variability is measured by comparing the DNA sequences of two or more individuals
- Nucleotide variation rarely results in phenotypic variation
- Most differences occur in noncoding regions (introns)
- Variations that occur in coding regions (exons) rarely change the amino acid sequence of the encoded protein



Figure 23.4



- Some phenotypic variation does not result from genetic differences among individuals, but rather from environmental influences
- Only genetically determined variation can have evolutionary consequences

Figure 23.5



Figure 23.5a



Figure 23.5b





# Sources of Genetic Variation

- New genes and alleles can arise by mutation or gene duplication
- Sexual reproduction can result in genetic variation by recombining existing alleles

# ***Formation of New Alleles***

- New alleles arise by mutation, a change in the nucleotide sequence of DNA
- Only mutations in cells that produce gametes can be passed to offspring
- A point mutation is a change in a single nucleotide in a DNA sequence

- The effects of point mutations can vary
  - Mutations that alter the phenotype are often harmful
  - Harmful mutations can be hidden from selection in recessive alleles
  - Mutations that result in a change in phenotype are sometimes, though rarely, beneficial

- The effects of point mutations can vary
  - Point mutations in noncoding regions generally result in **neutral variation**, conferring no selective advantage or disadvantage
  - Mutations to genes can be neutral because of redundancy in the genetic code

# ***Altering Gene Number or Position***

- Chromosomal mutations that delete, disrupt, or rearrange many loci are typically harmful
- Duplication of small pieces of DNA increases genome size and is usually less harmful
- Duplicated genes can take on new functions by further mutation
- An ancestral odor-detecting gene has been duplicated many times: Humans have 380 copies of the gene, and mice have 1,200



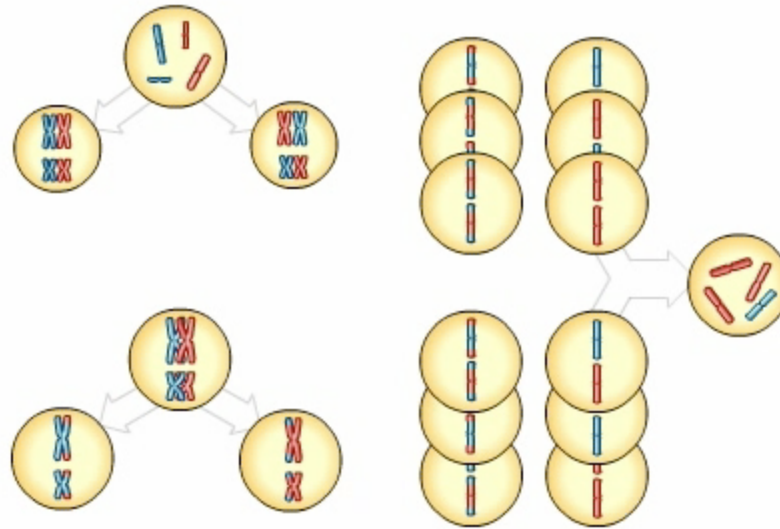
# ***Rapid Reproduction***

- Mutation rates are low in animals and plants
- The average is about one mutation in every 100,000 genes per generation
- Mutation rates are often lower in prokaryotes, but short generation times allow mutations to accumulate rapidly
- Viruses have both high mutation rates and short generation times

# ***Sexual Reproduction***

- In organisms that reproduce sexually, most genetic variation results from recombination of alleles
- Sexual reproduction can shuffle existing alleles into new combinations through three mechanisms: crossing over, independent assortment, and fertilization

# Animation: Genetic Variation from Sexual Recombination



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

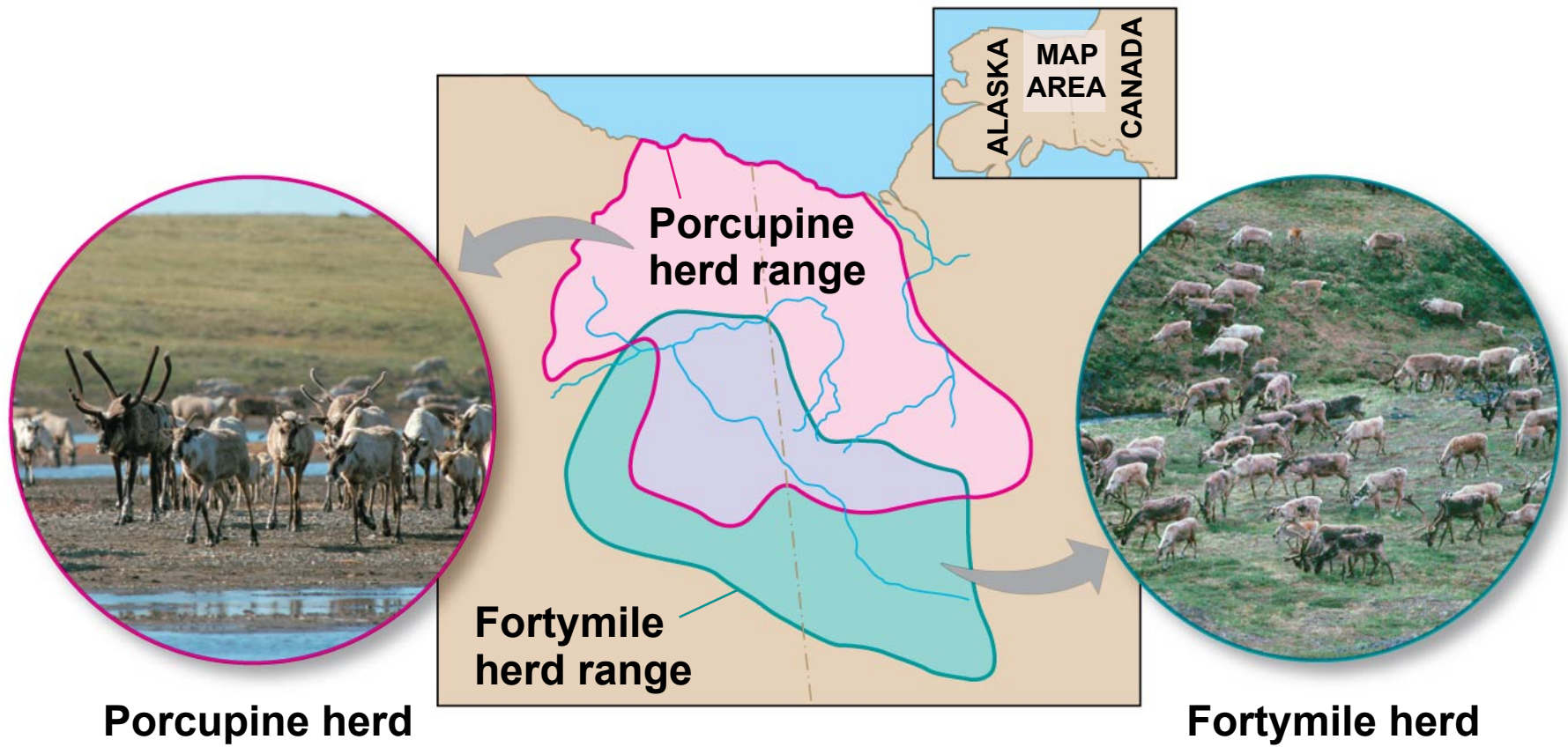
- Genetic variation is required for a population to evolve, but does not guarantee that it will
- One or more factors that cause evolution must be at work for a population to evolve

# Gene Pools and Allele Frequencies

- A **population** is a localized group of individuals capable of interbreeding and producing fertile offspring
- Populations are not always geographically isolated, but individuals typically only breed with members of their own population



Figure 23.6





**Porcupine herd**

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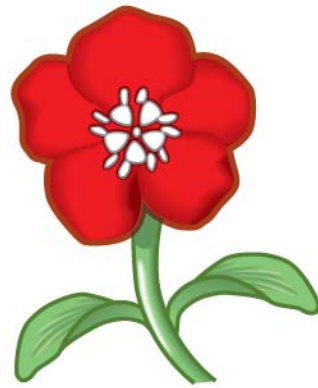
Figure 23.6b



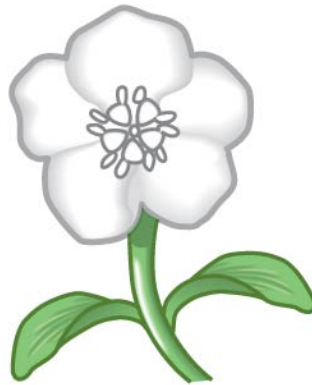
**Fortymile herd**

- A **gene pool** consists of all the alleles for all loci in a 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, diploid individuals may be either homozygous or heterozygous

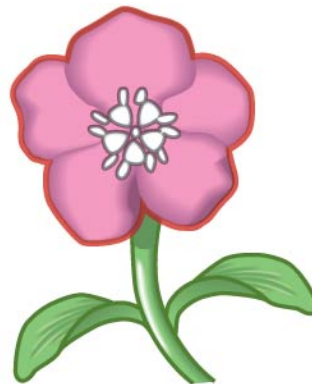
Figure 23.8c



$C^R C^R$



$C^W C^W$



$C^R C^W$

- The frequency of an allele in a population can be calculated
  - For diploid organisms, the total number of alleles at a locus is the total number of individuals times 2
  - The total number of dominant alleles at a locus is two alleles for each homozygous dominant individual plus one allele for each heterozygous individual; the same logic applies for recessive alleles

- 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,  $p + q = 1$

- For example, consider a population of wildflowers that is incompletely dominant for color
  - 320 red flowers ( $C^R C^R$ )
  - 160 pink flowers ( $C^R C^W$ )
  - 20 white flowers ( $C^W C^W$ )
- Calculate the number of copies of each allele
  - $C^R = (320 \times 2) + 160 = 800$
  - $C^W = (20 \times 2) + 160 = 200$



- Calculate the frequency of each allele
  - $p = \text{frequency of } C^R = 800/(800 + 200) = 0.8 \text{ (80\%)}$
  - $q = 1 - p = 0.2 \text{ (20\%)}$
- The sum of alleles is always 1 (100%)
  - $0.8 + 0.2 = 1$

# The Hardy-Weinberg Equation

- The Hardy-Weinberg equation describes the genetic makeup we expect 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, it suggests that the population may be evolving

# ***Hardy-Weinberg Equilibrium***

- In a population where gametes contribute to the next generation randomly and Mendelian inheritance occurs, allele and genotype frequencies remain constant from generation to generation
- Such a population is in **Hardy-Weinberg equilibrium**

- Hardy-Weinberg equilibrium describes the constant frequency of alleles in such a gene pool
- Consider, for example, the same population of 500 wildflowers and 1,000 alleles where
  - $p$  = frequency of  $C^R = 0.8$
  - $q$  = frequency of  $C^W = 0.2$

Figure 23.7

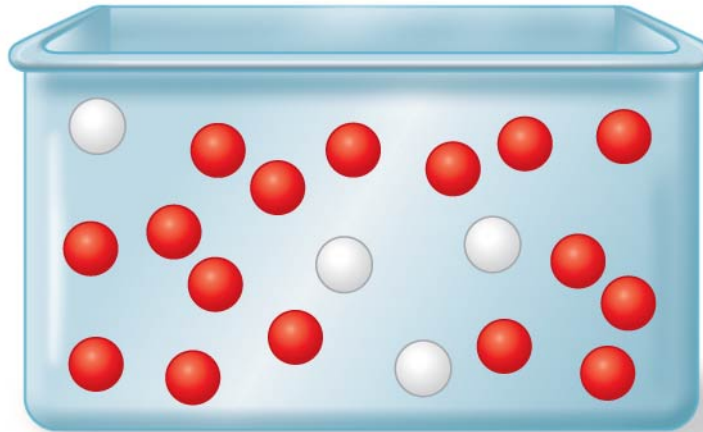
## Frequencies of alleles

$p$  = frequency of  $C^R$  allele  = 0.8

$q$  = frequency of  $C^W$  allele  = 0.2



## Alleles in the population



## Gametes produced

Each egg:



80%

chance



20%

chance

Each sperm:



80%

chance



20%

chance

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

Figure 23.8

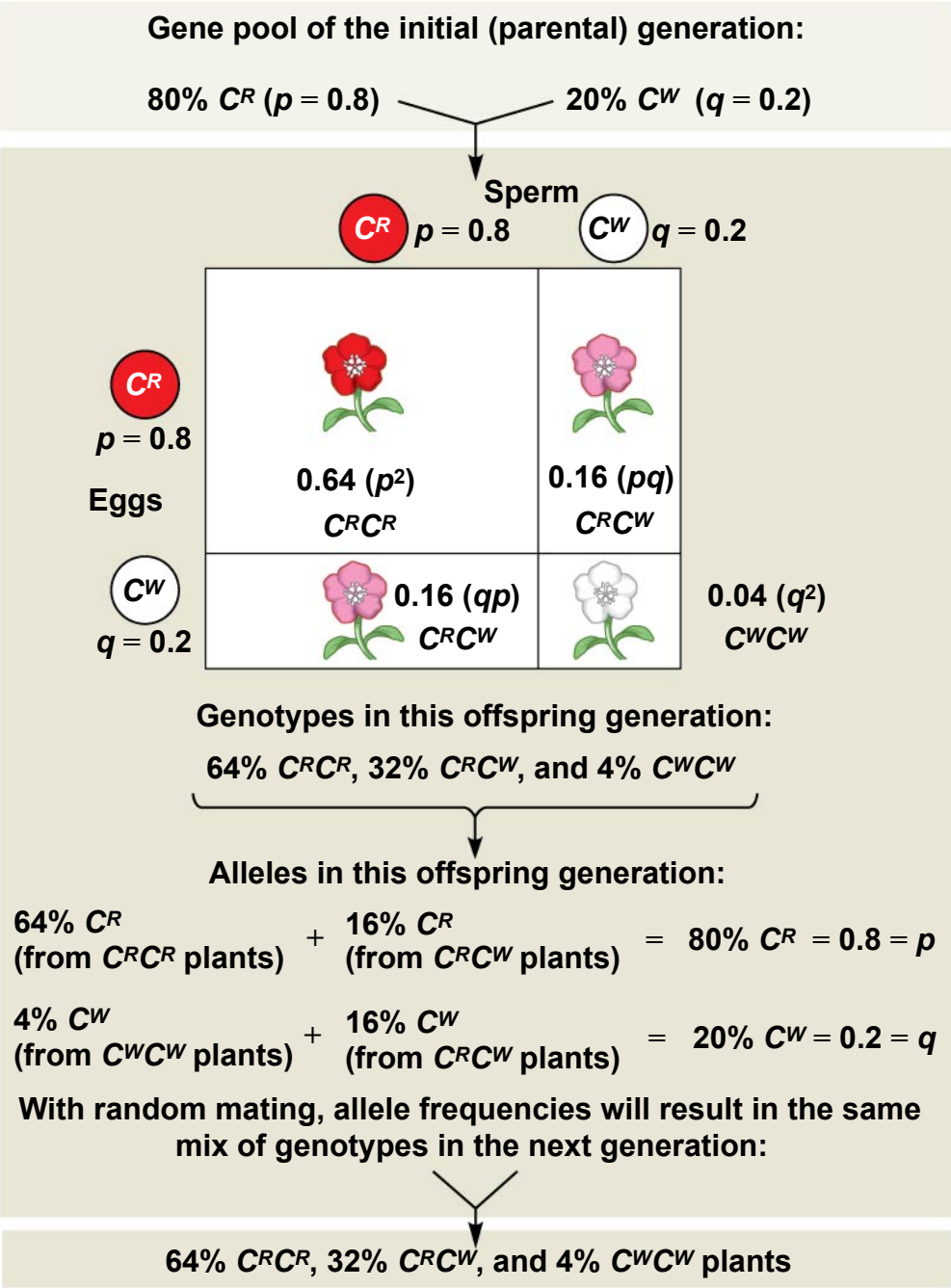




Figure 23.8a

# Gene pool of the initial (parental) generation:

80%  $C^R$  ( $p = 0.8$ )      20%  $C^W$  ( $q = 0.2$ )

Sperm



$p = 0.8$



$q = 0.2$



$p = 0.8$

Eggs



$q = 0.2$



0.64 ( $p^2$ )

$C^R C^R$



0.16 ( $pq$ )

$C^R C^W$



0.16 ( $qp$ )

$C^R C^W$

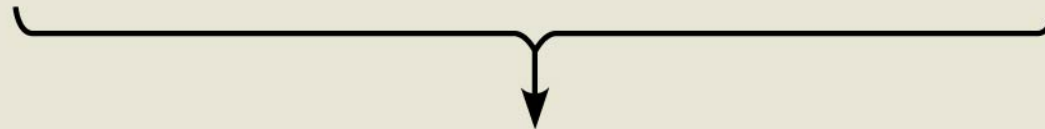


0.04 ( $q^2$ )

$C^W C^W$

**Genotypes in this offspring generation:**

**64%  $C^R C^R$ , 32%  $C^R C^W$ , and 4%  $C^W C^W$**



**Alleles in this offspring generation:**

$$\begin{array}{l} 64\% C^R \\ \text{(from } C^R C^R \text{ plants)} \end{array} + \begin{array}{l} 16\% C^R \\ \text{(from } C^R C^W \text{ plants)} \end{array} = 80\% C^R = 0.8 = p$$

$$\begin{array}{l} 4\% C^W \\ \text{(from } C^W C^W \text{ plants)} \end{array} + \begin{array}{l} 16\% C^W \\ \text{(from } C^R C^W \text{ plants)} \end{array} = 20\% C^W = 0.2 = q$$

**With random mating, allele frequencies will result in the same mix of genotypes in the next generation:**



**64%  $C^R C^R$ , 32%  $C^R C^W$ , and 4%  $C^W C^W$  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

$$\begin{array}{ccccccc} p^2 & + & 2pq & + & q^2 & = & 1 \\ \text{Expected} & & \text{Expected} & & \text{Expected} & & \\ \text{frequency} & & \text{frequency} & & \text{frequency} & & \\ \text{of genotype} & & \text{of genotype} & & \text{of genotype} & & \\ C^R C^R & & C^R C^W & & C^W C^W & & \end{array}$$

# ***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
<b>1. No mutations</b>	The gene pool is modified if mutations occur or if entire genes are deleted or duplicated.
<b>2. Random mating</b>	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.
<b>3. No natural selection</b>	Allele frequencies change when individuals with different genotypes show consistent differences in their survival or reproductive success.
<b>4. Extremely large population size</b>	In small populations, allele frequencies fluctuate by chance over time (a process called genetic drift).
<b>5. No gene flow</b>	By moving alleles into or out of populations, gene flow can alter allele frequencies.

- Natural populations can evolve at some loci while being in Hardy-Weinberg equilibrium at other loci



# ***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

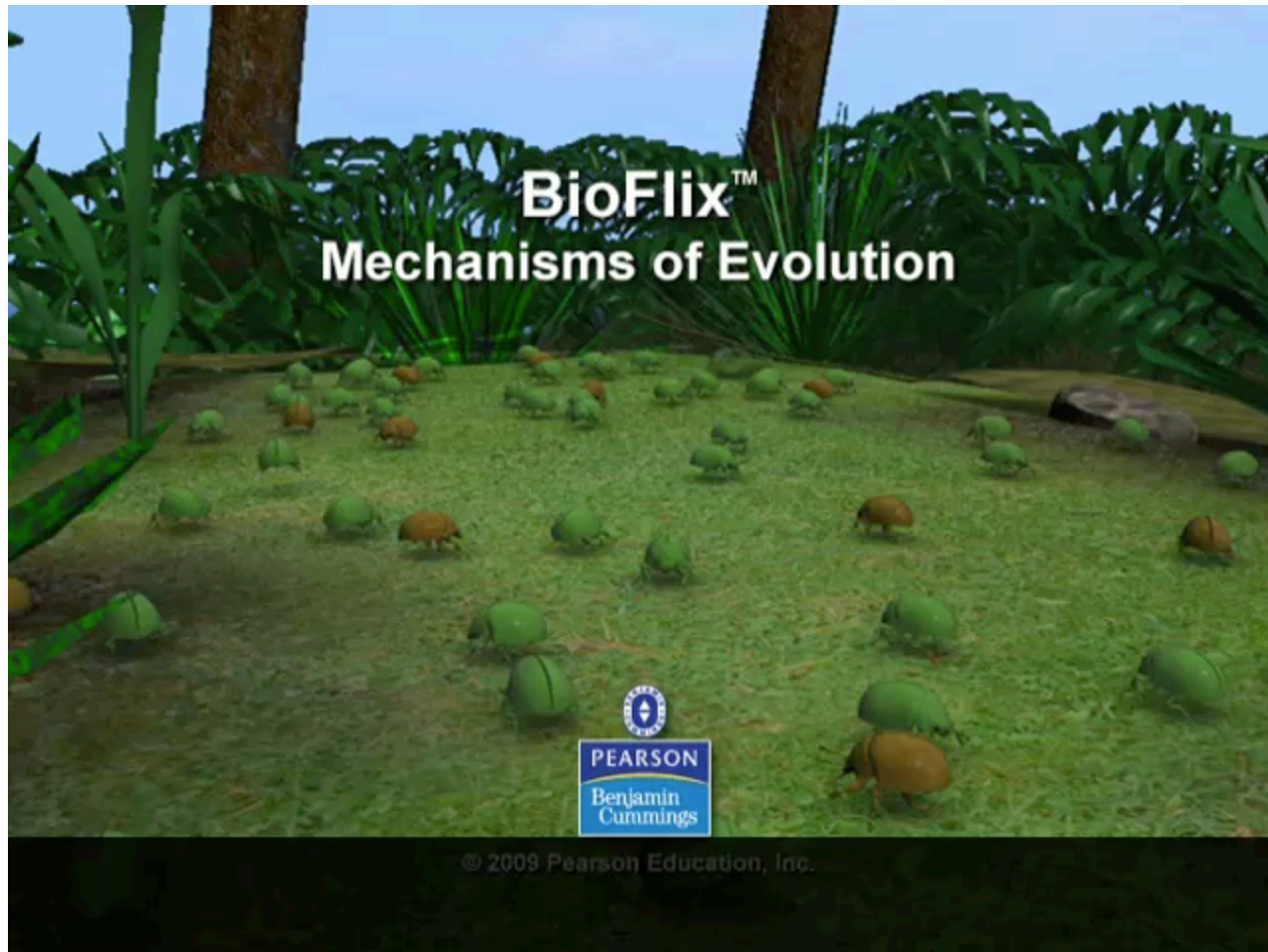
3. Natural selection can only act on rare homozygous individuals who do not follow dietary restrictions
4. The population is large
5. Migration has no effect, as many other populations have similar allele frequencies

- The occurrence of PKU is one per 10,000 births
  - $q^2 = 0.0001$
  - $q = 0.01$
- The frequency of normal alleles 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**

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

# Bioflix: Mechanisms of Evolution



# Animation: Causes of Evolutionary Change



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# Natural Selection

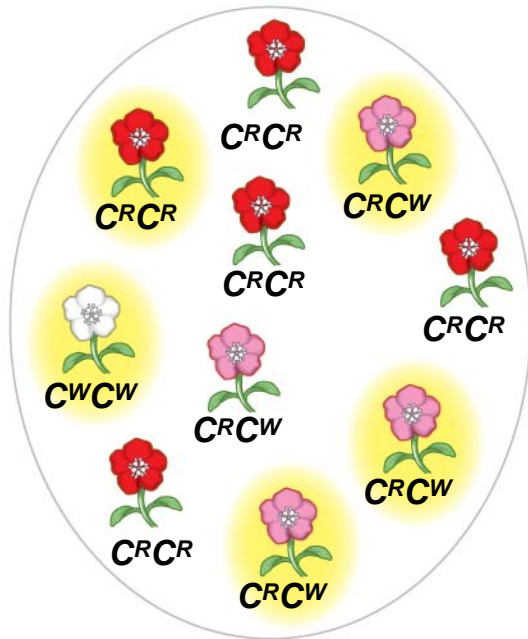
- Selection results in alleles being passed to the next generation in proportions that differ from those in the present generation
- For example, an allele that confers resistance to DDT in fruit flies increased in frequency after DDT was used widely in agriculture

- 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 a sample, the greater the chance of random deviation from a predicted result
- **Genetic drift** describes how allele frequencies fluctuate unpredictably from one generation to the next
- Genetic drift tends to reduce genetic variation through the random loss of alleles

Figure 23.9\_1



**Generation 1**

**$p$  (frequency of  $C^R$ ) = 0.7**

**$q$  (frequency of  $C^W$ ) = 0.3**

Figure 23.9\_2

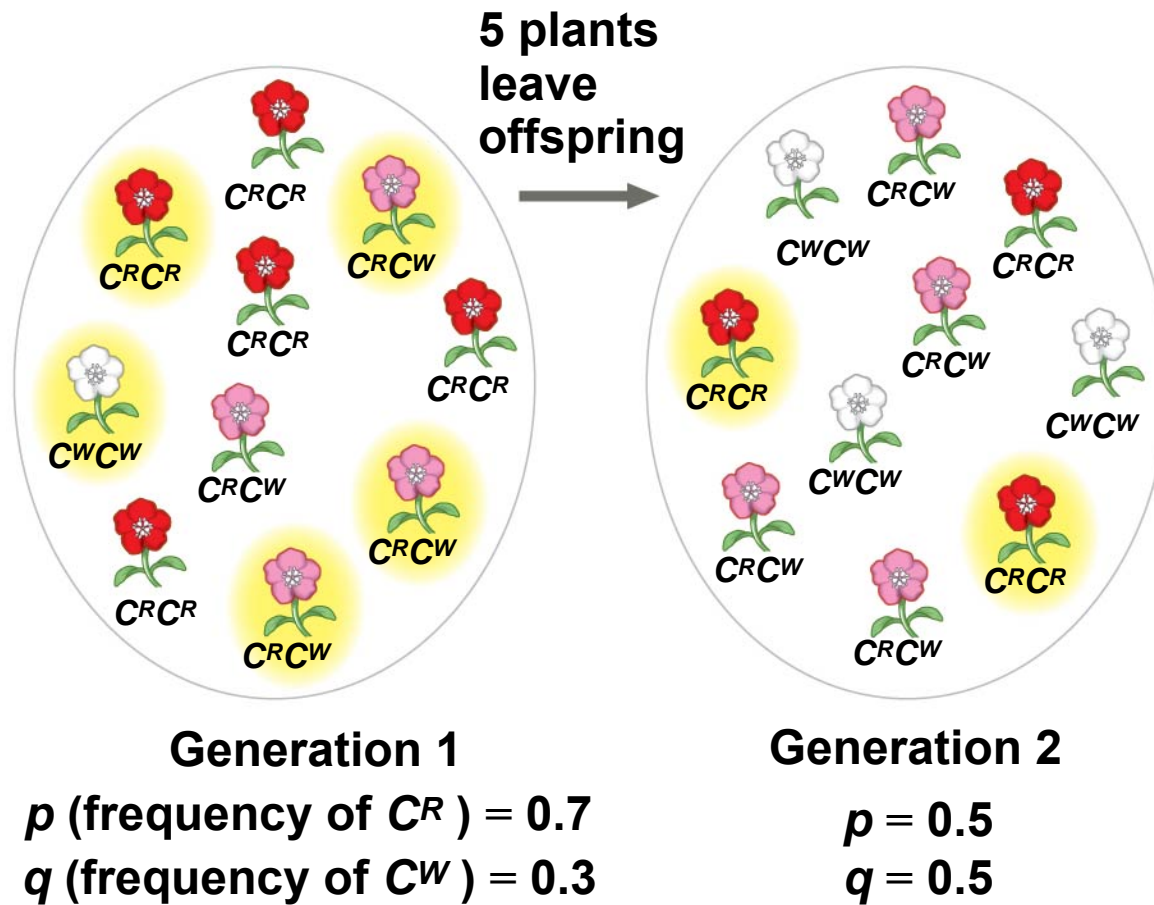
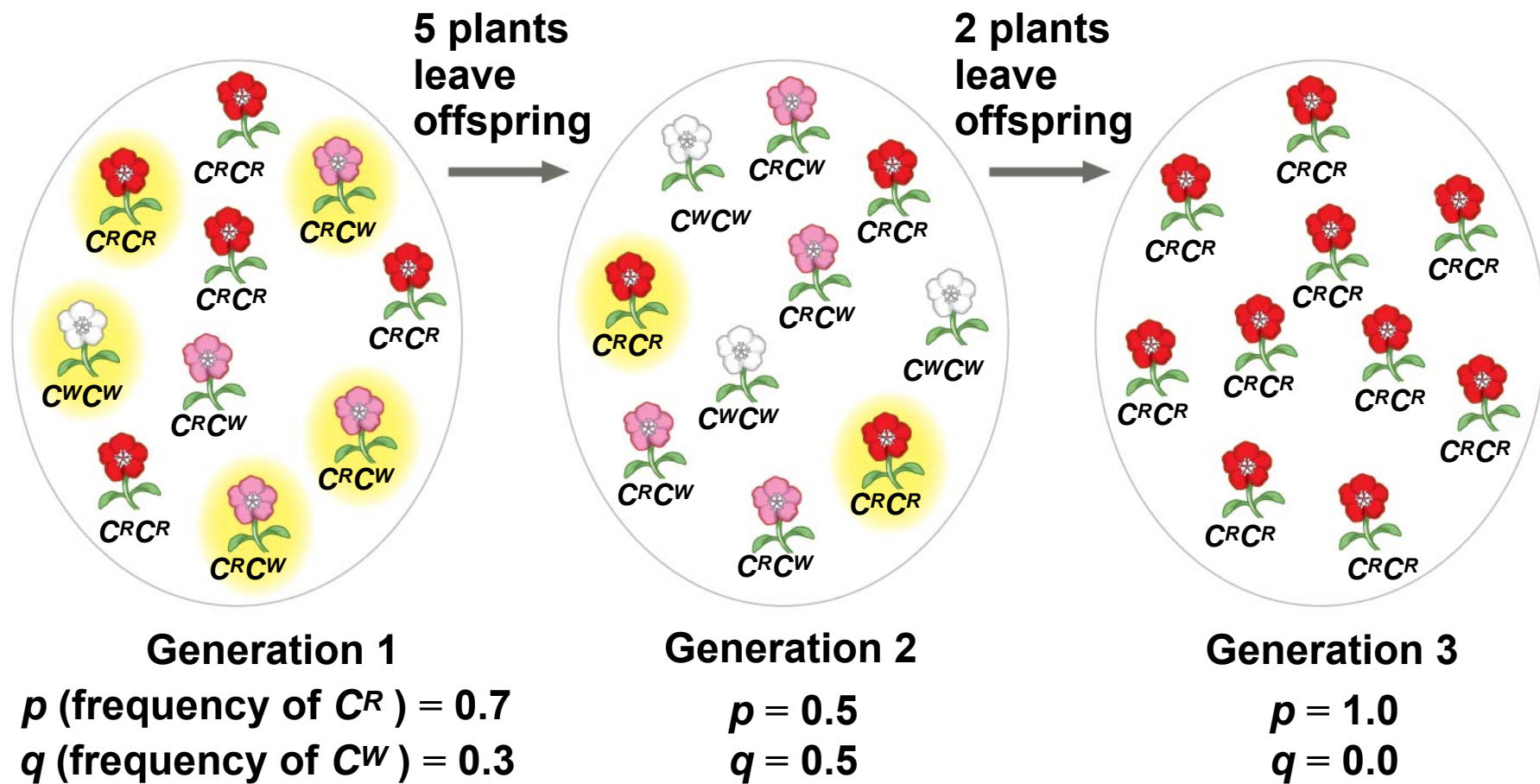


Figure 23.9\_3



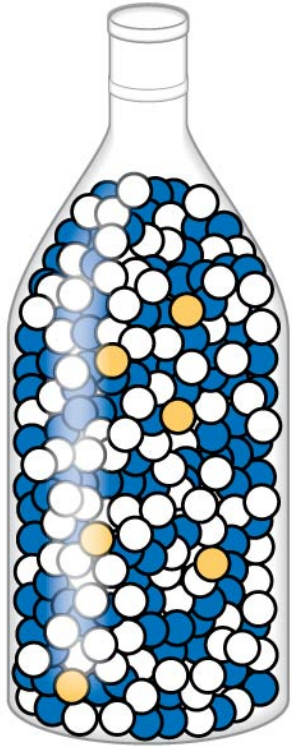
# ***The Founder Effect***

- The **founder effect** occurs when a few individuals become isolated from a larger population
- Allele frequencies in the small founder population can be different from those in the larger parent population

# ***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





**Original  
population**

Figure 23.10\_2

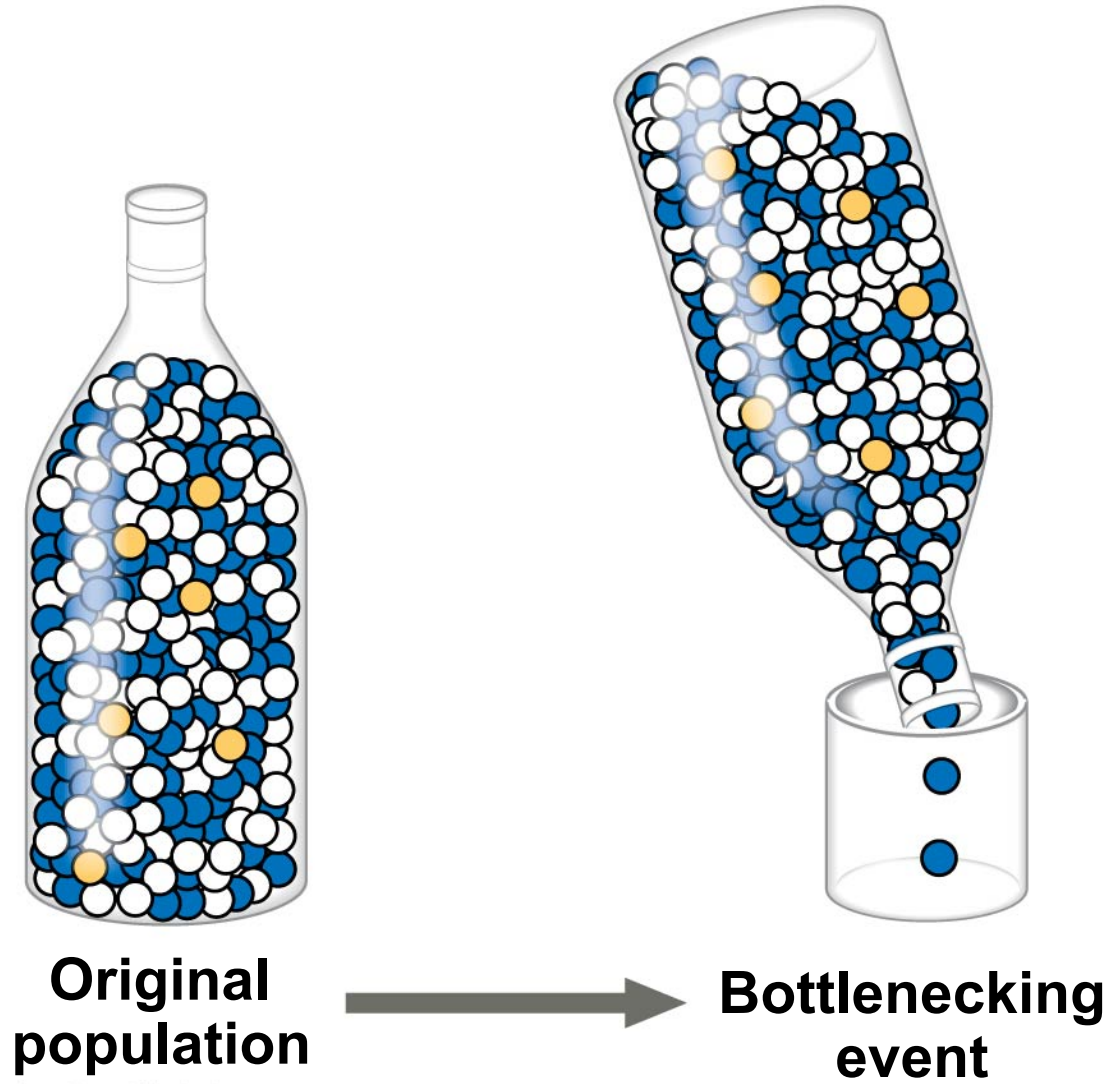
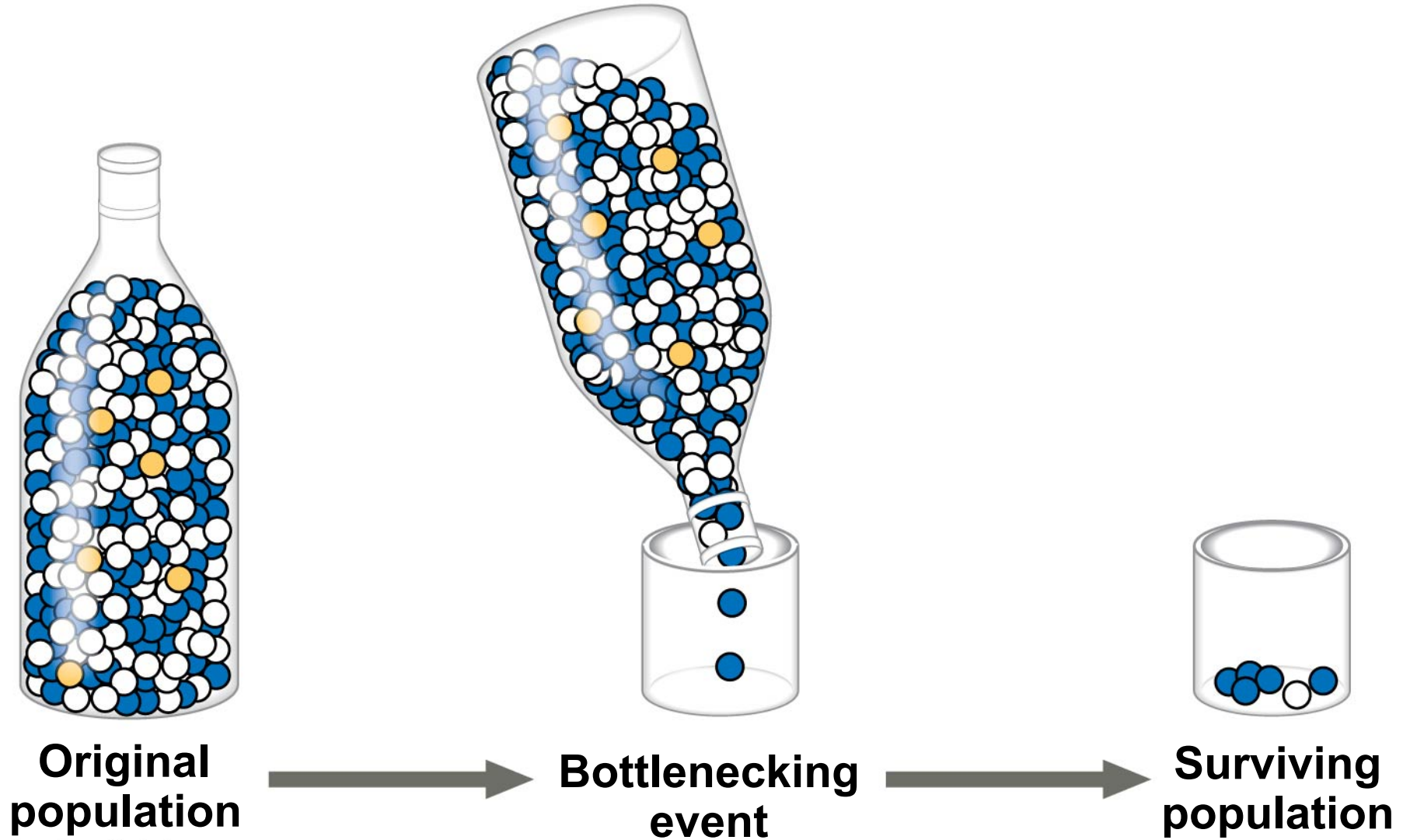


Figure 23.10\_3



- Understanding the bottleneck effect can increase understanding of how human activity affects other species

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

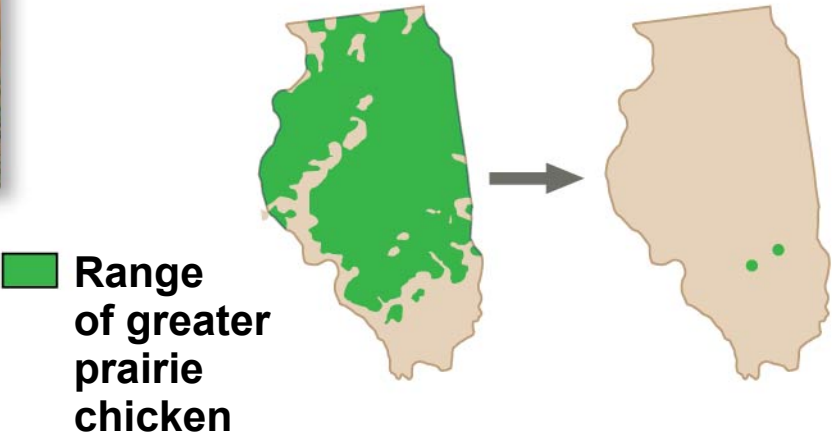
- Loss of prairie habitat caused a severe reduction in the population of greater prairie chickens in Illinois
- The surviving birds had low levels of genetic variation, and only 50% of their eggs hatched

Figure 23.11



**Greater prairie chicken**

**Pre-bottleneck (Illinois, 1820)**      **Post-bottleneck (Illinois, 1993)**



**(a)**

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

**(b)**



**Greater prairie  
chicken**

**(a)**

 **Range  
of greater  
prairie  
chicken**

**Pre-bottleneck  
(Illinois, 1820)**



**Post-bottleneck  
(Illinois, 1993)**

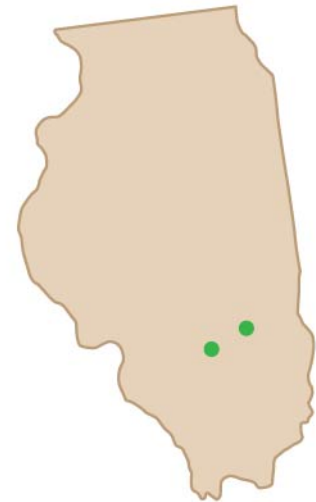


Figure 23.11b

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

(b)





**Greater prairie  
chicken**

- Researchers used DNA from museum specimens to compare genetic variation in the population before and after the bottleneck
- The results showed a loss of alleles at several loci
- Researchers introduced greater prairie chickens from populations in other states and were successful in introducing new alleles and increasing the egg hatch rate to 90%

# 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 can affect adaptation to local environments
- For example, variation in banding pattern in Lake Erie water snakes represents adaptation to mainland and island habitats
  - Most snakes on the mainland are strongly banded; most island snakes are unbanded or intermediate
  - Unbanded snakes are better camouflaged in island habitats, but migration of banded snakes from mainland to island populations maintains alleles for the banded pattern in island populations

Figure 23.12

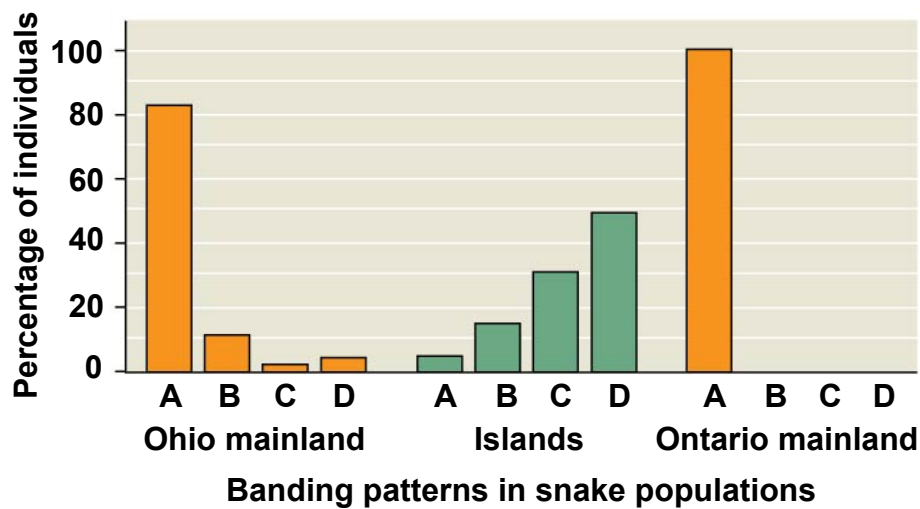


Figure 23.12a





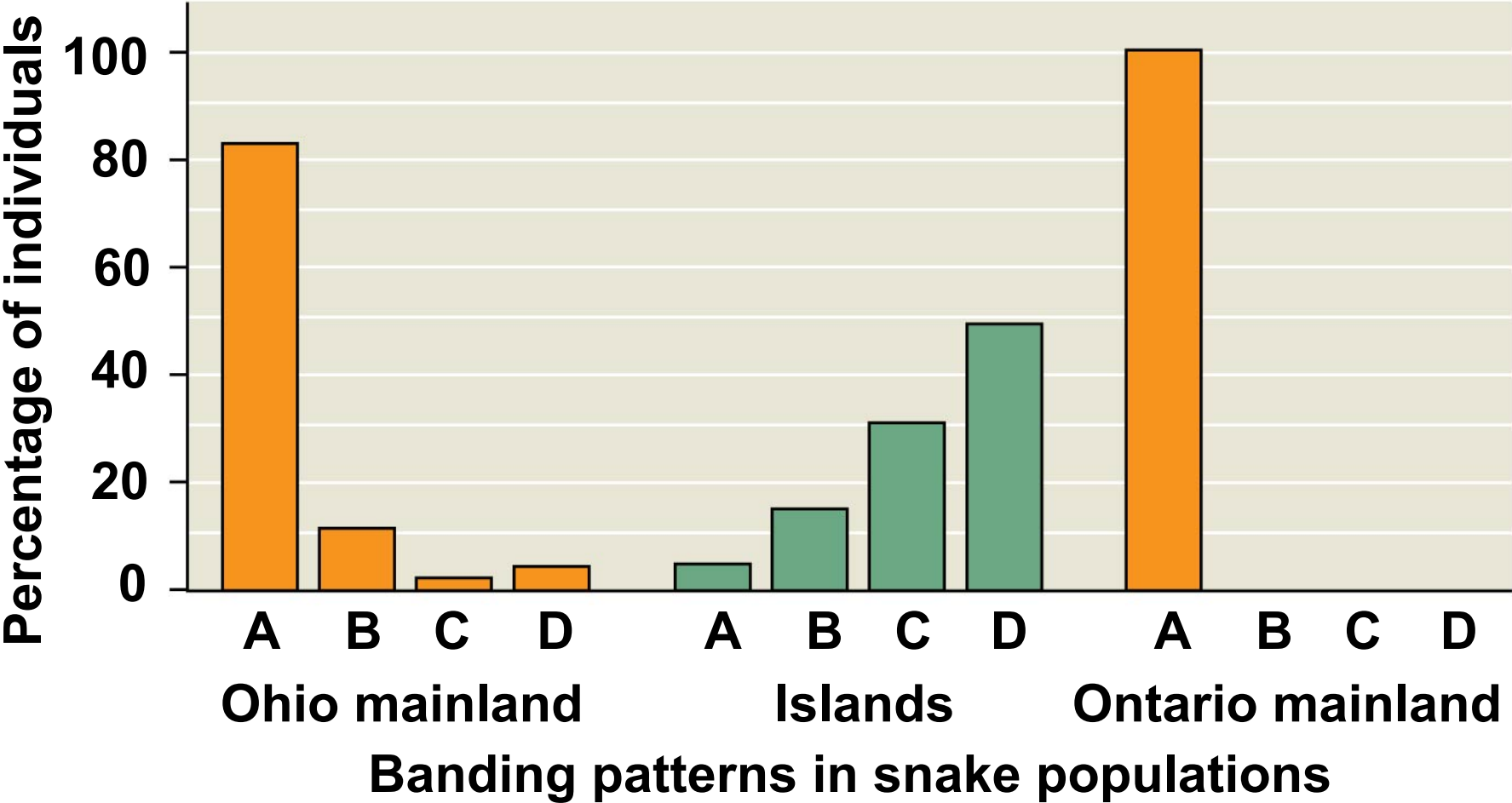
**Banded *N. sipedon*  
(Pattern C)**





**Unbanded *N. sipedon*  
(Pattern D)**

Figure 23.12b



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

- Gene flow is an important agent of evolutionary change in modern human populations

# **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 and depends on many factors

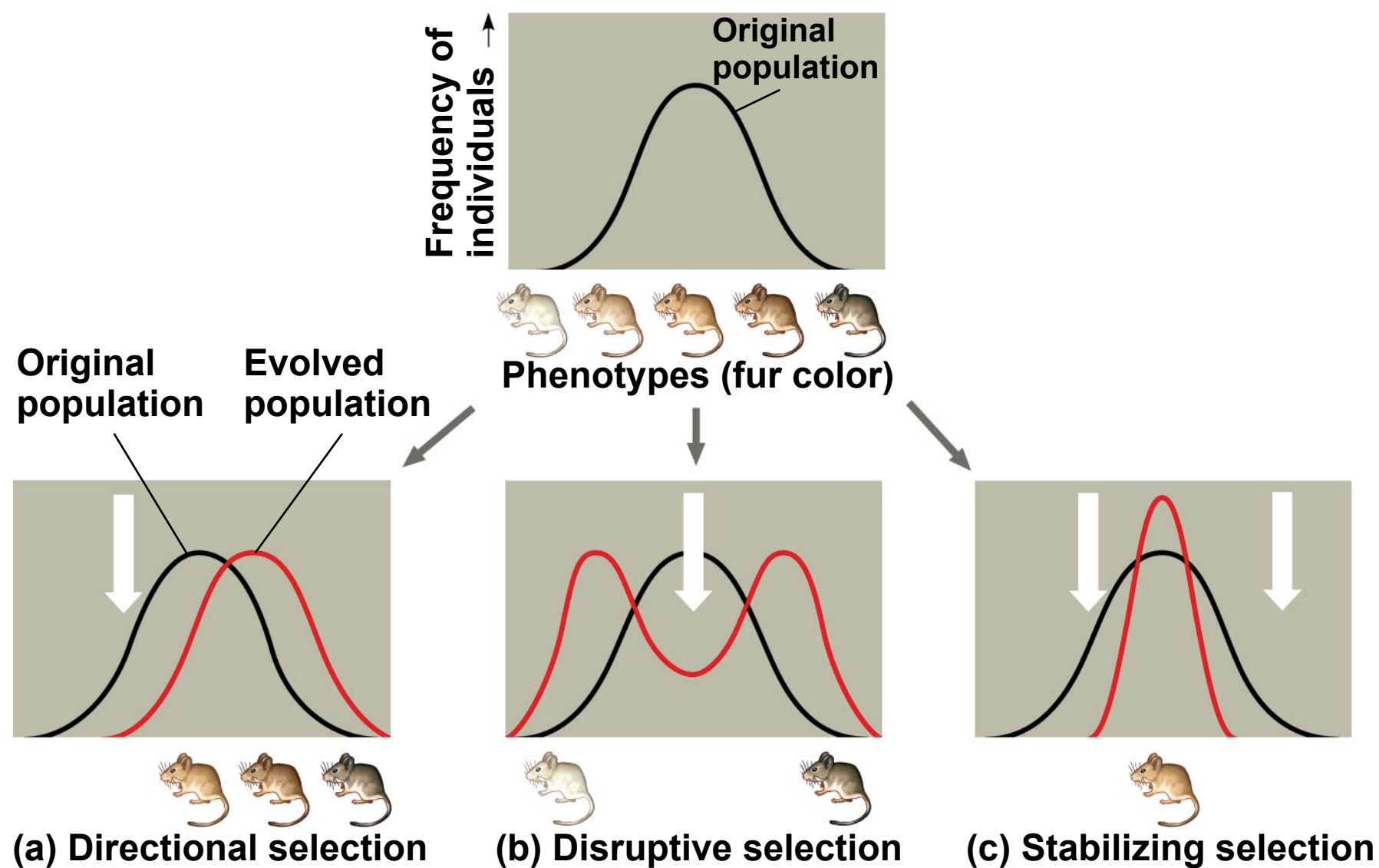
- **Relative fitness** is the contribution an individual makes to the gene pool of the next generation relative to the contributions of other individuals
- Selection favors certain genotypes by acting on the phenotypes of individuals



# ***Directional, Disruptive, and Stabilizing Selection***

- There are three modes of selection:
  - **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

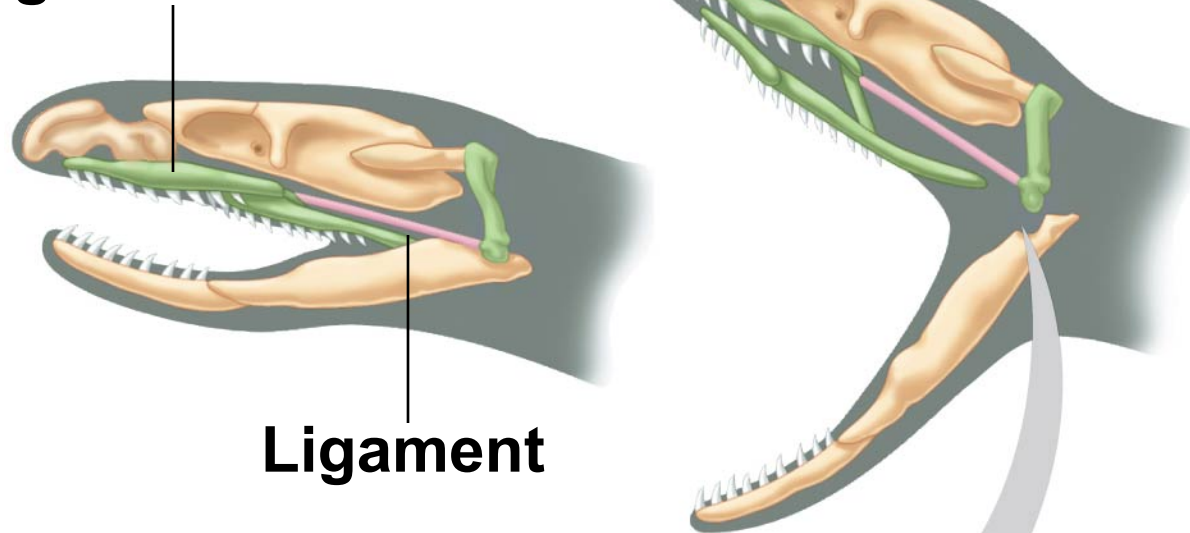


# The Key Role of Natural Selection in Adaptive Evolution

- 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

**Bones shown in  
green are movable.**



**Ligament**



Figure 23.14a



- Natural selection increases the frequencies of alleles that enhance survival and reproduction
- Adaptive evolution occurs as the degree to which a species is well suited for life in its environment improves
- Because the environment can change, adaptive evolution is a continuous process

- 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

# Sexual Selection

- **Sexual selection** is a process in which individuals with certain inherited characteristics are more likely to acquire mates than other individuals of the same sex
- It can result in **sexual dimorphism**, marked differences between the sexes in secondary sexual characteristics



Figure 23.15

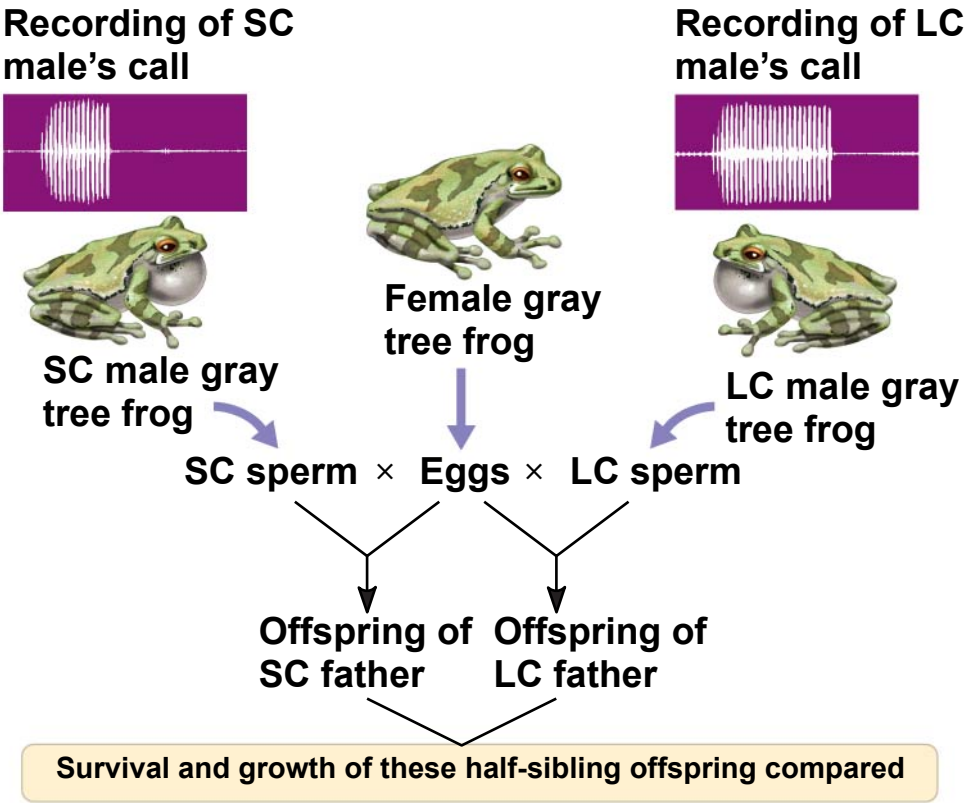


- **Intrasexual selection** is direct competition among individuals of one sex (often males) for mates of the opposite sex
- **Intersexual selection**, often called mate choice, occurs when individuals of one sex (usually females) are choosy in selecting their mates
- Showiness of male appearance can increase a male's chances of attracting a female while decreasing his chances of survival

- How do female preferences evolve?
- The “good genes” hypothesis suggests that if a trait is related to male genetic quality, both the male trait and female preference for that trait should increase in frequency

Figure 23.16

Experiment



Results

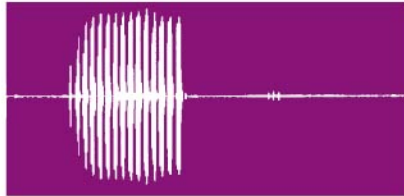
Offspring Performance	1995	1996
Larval survival	LC better	NSD
Larval growth	NSD	LC better
Time to metamorphosis	LC better (shorter)	LC better (shorter)

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).

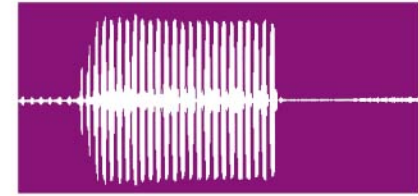
## Experiment

**Recording of SC  
male's call**



**SC male gray  
tree frog**

**Recording of LC  
male's call**



**LC male gray  
tree frog**



**Female gray  
tree frog**

**SC sperm × Eggs × LC sperm**

**Offspring of  
SC father**

**Offspring of  
LC father**

**Survival and growth of these half-sibling offspring compared**

## 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.

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# Balancing Selection

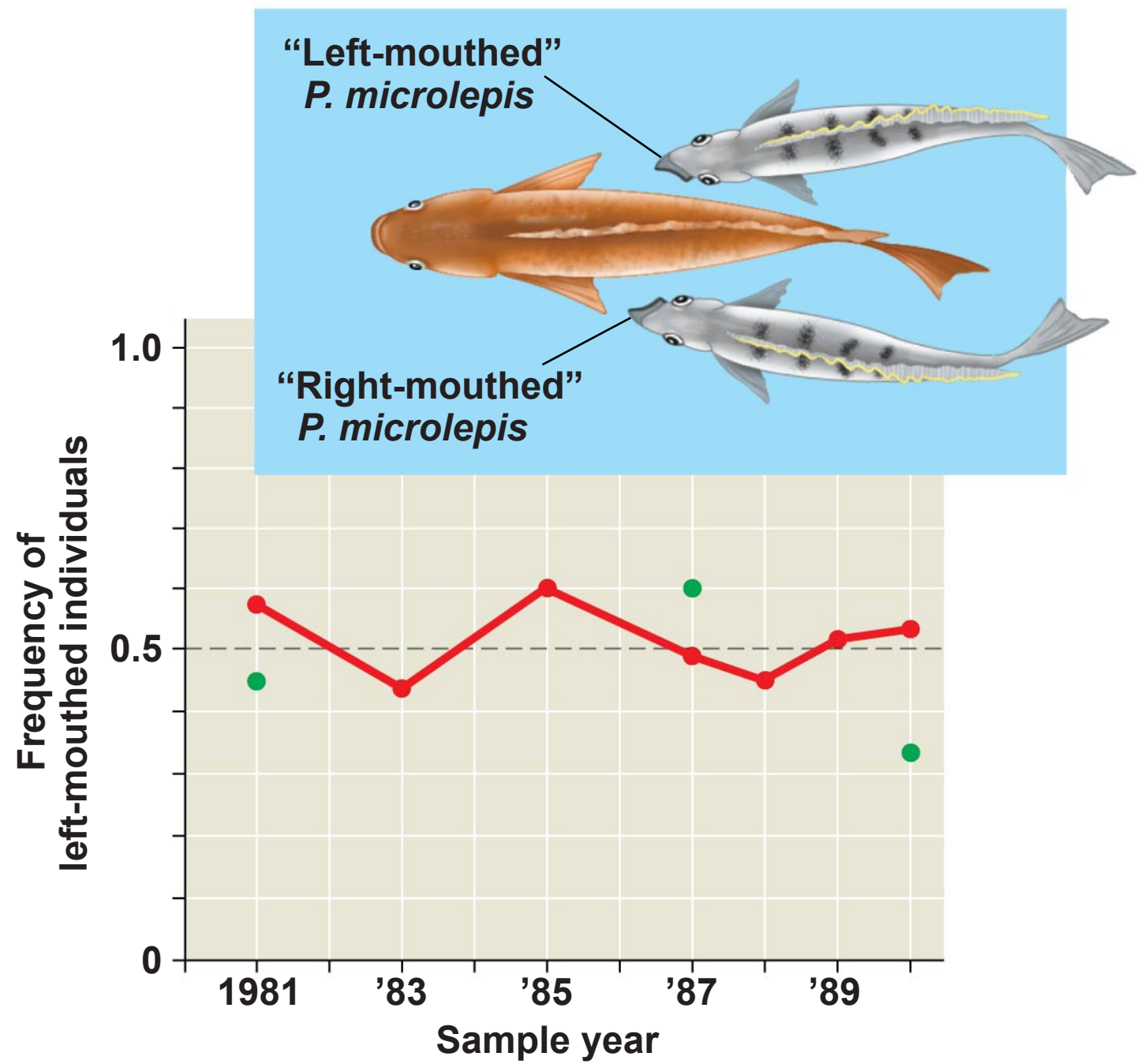
- Diploidy maintains genetic variation in the form of recessive alleles hidden from selection in heterozygotes
- **Balancing selection** occurs when natural selection maintains stable frequencies of two or more phenotypic forms in a population
- Balancing selection includes
  - Frequency-dependent selection
  - Heterozygote advantage

# ***Frequency-Dependent Selection***

- In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population
- For example, frequency-dependent selection results in approximately equal numbers of “right-mouthed” and “left-mouthed” scale-eating fish



Figure 23.17



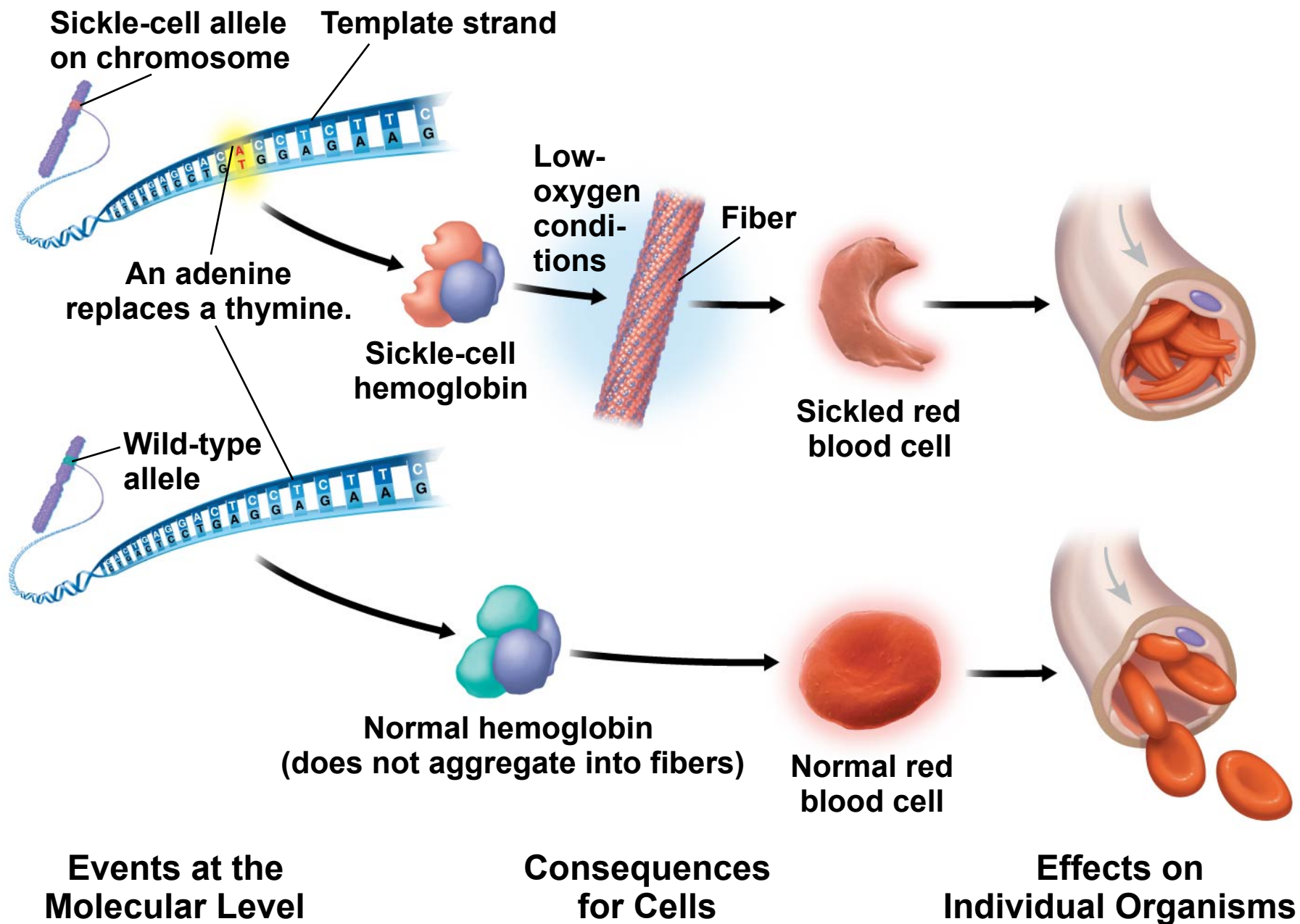
# ***Heterozygote Advantage***

- **Heterozygote advantage** occurs when heterozygotes have a higher fitness than both homozygotes
- Natural selection will tend to maintain two or more alleles at that locus
- Heterozygote advantage can result from stabilizing or directional selection

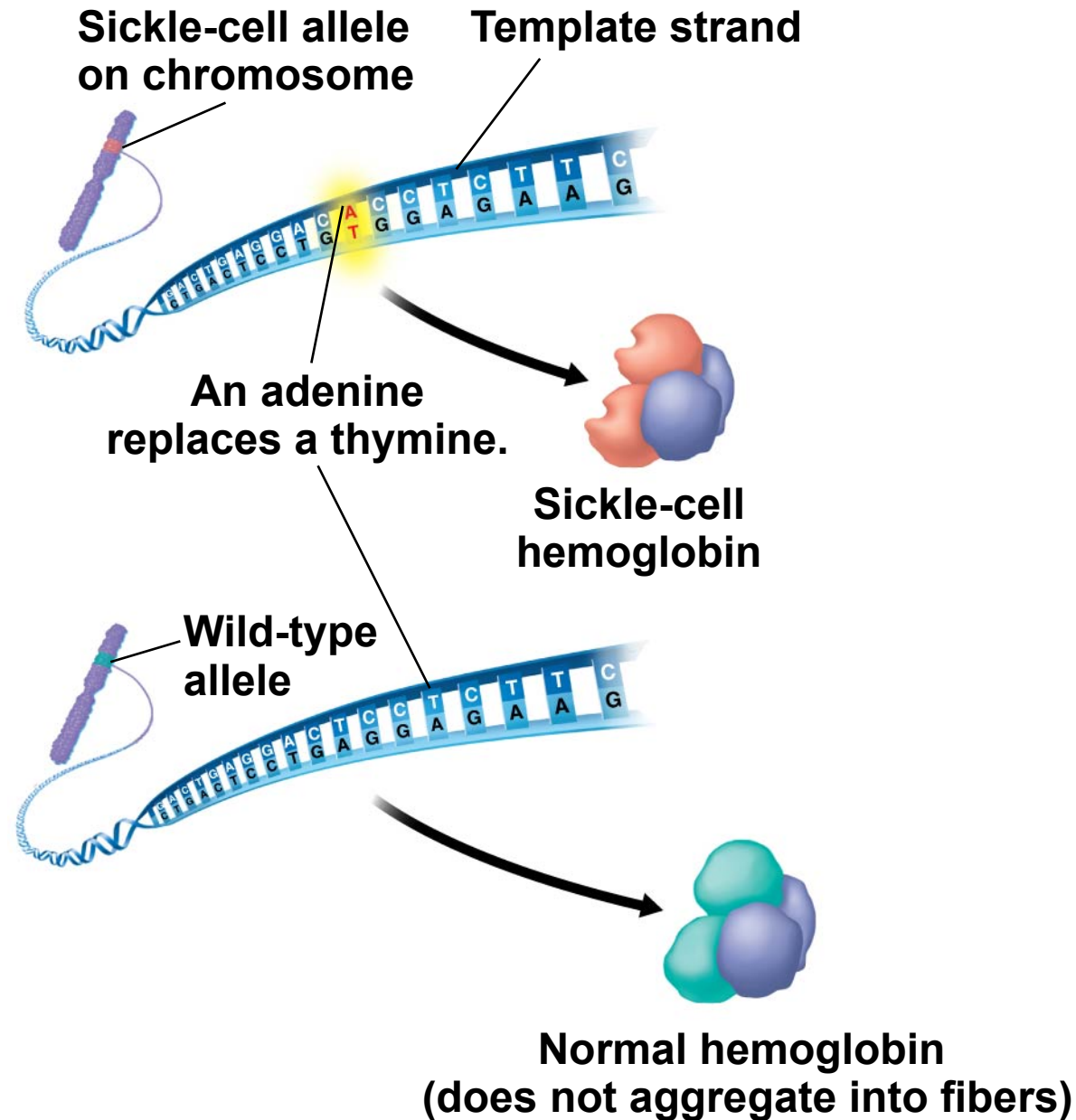
- A mutation in an allele that codes for part of the hemoglobin protein causes sickle-cell disease, but also confers malaria resistance
- In regions where the malaria parasite is common, selection favors individuals heterozygous for the sickle-cell allele

Figure 23.18a

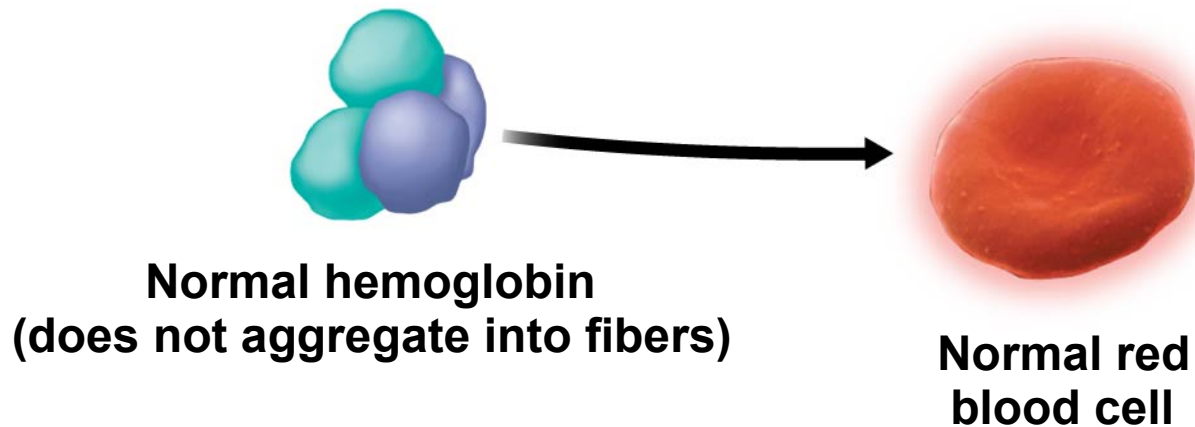
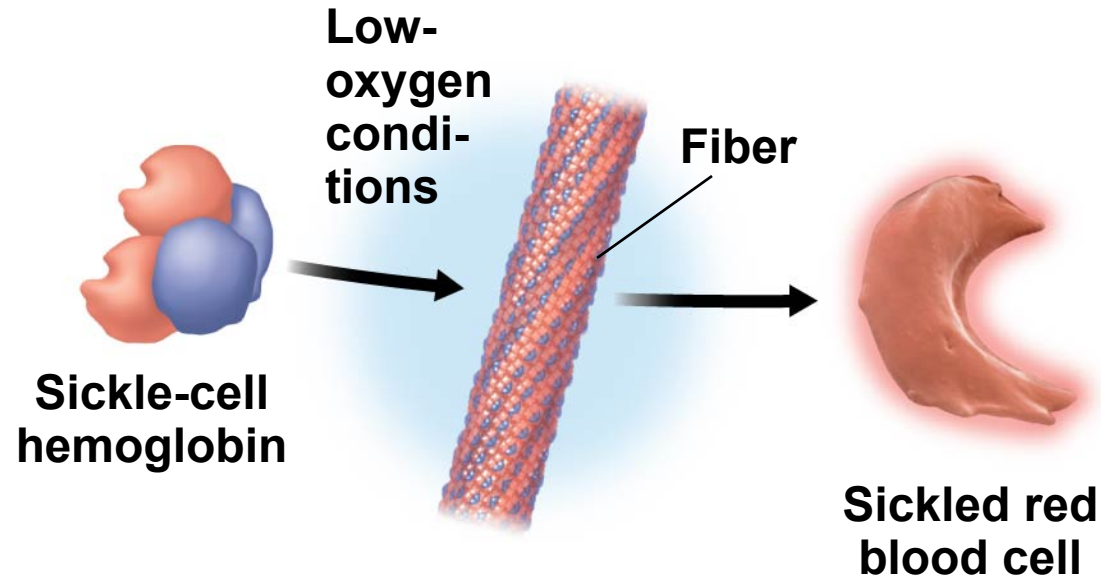
## Make Connections: The Sickle-Cell Allele



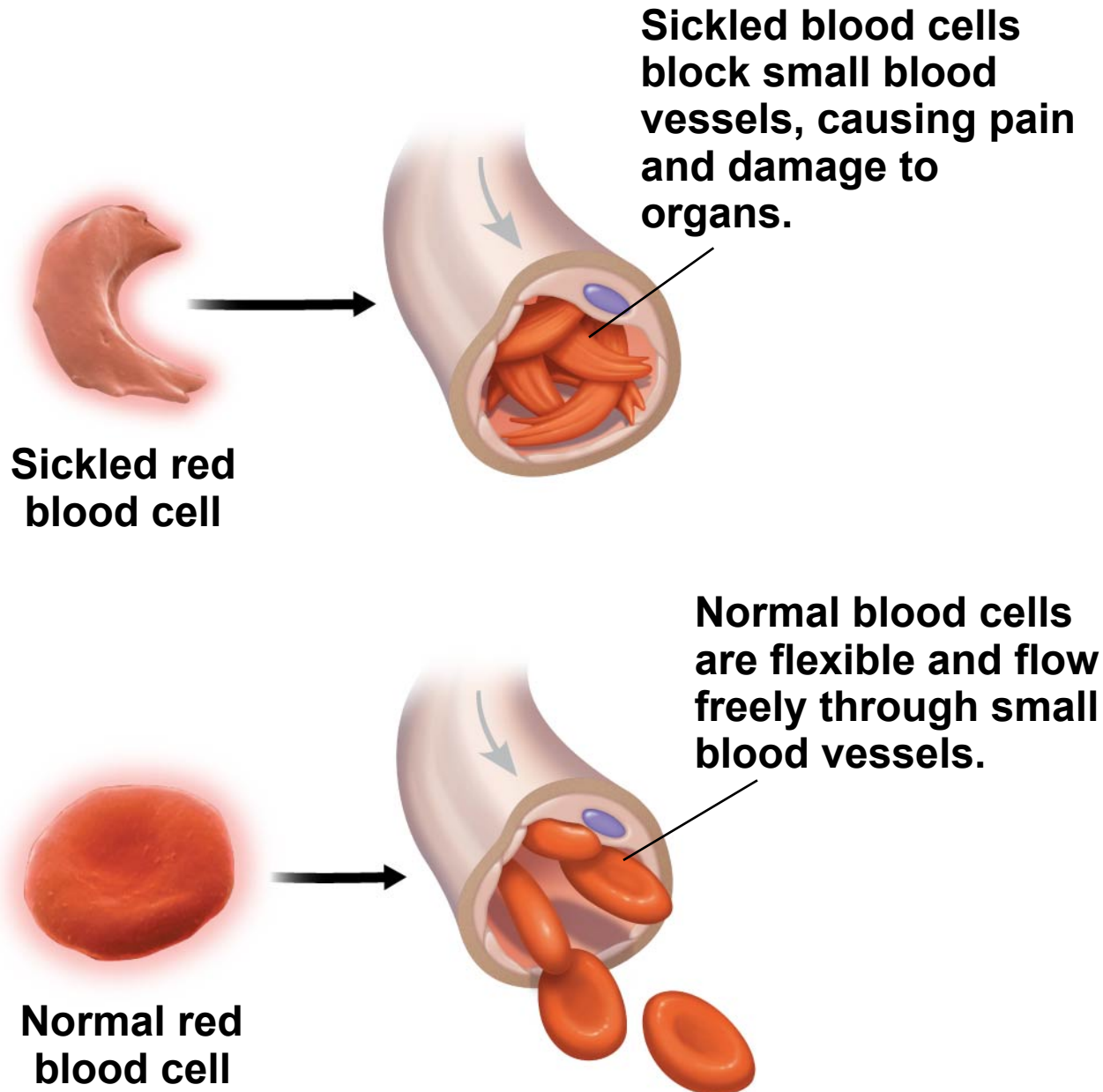
## Events at the Molecular Level



## Consequences for Cells

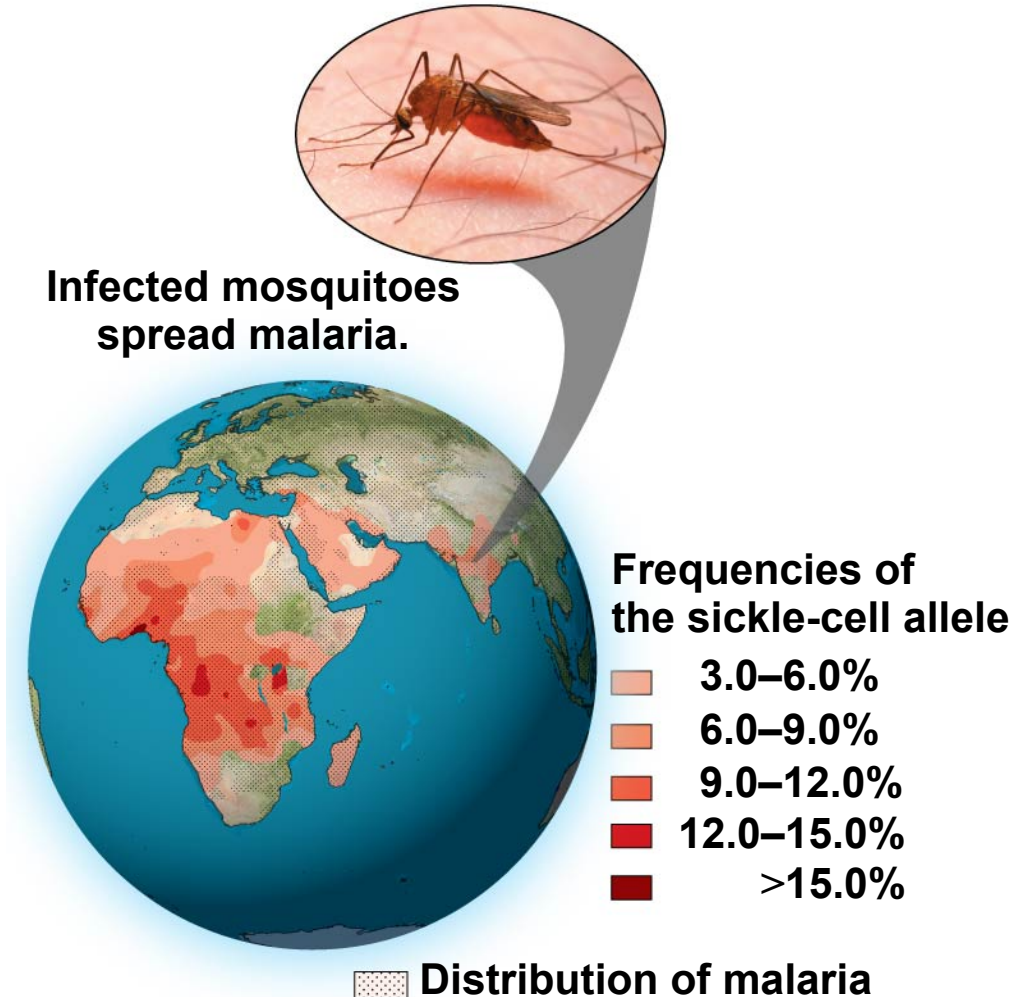


## Effects on Individual Organisms





## Make Connections: The Sickle-Cell Allele



**Heterozygotes are more likely to survive malaria.**

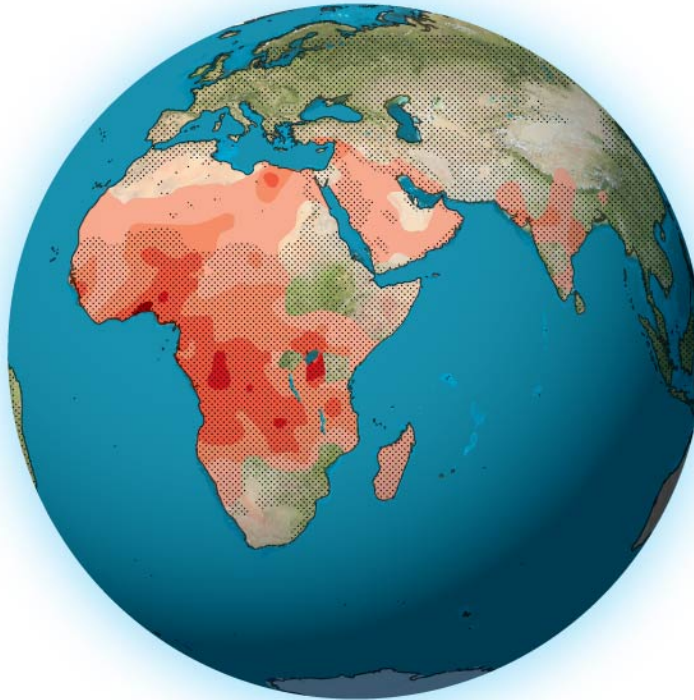
**Evolution in Populations**



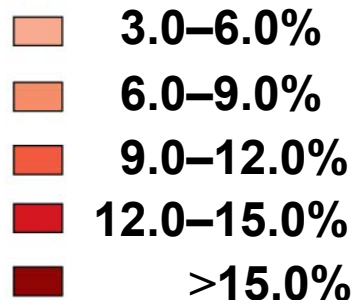
**This child has sickle-cell disease, a genetic disorder.**



## Evolution in Populations



### Frequencies of the sickle-cell allele



 Distribution of malaria caused by *Plasmodium falciparum* (a parasitic unicellular eukaryote)

**Heterozygote advantage in regions where malaria is common**

## Evolution in Populations



**A vector of malaria, the mosquito**

## Evolution in Populations



**A child with the genetic disorder known as sickle-cell disease**

# 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

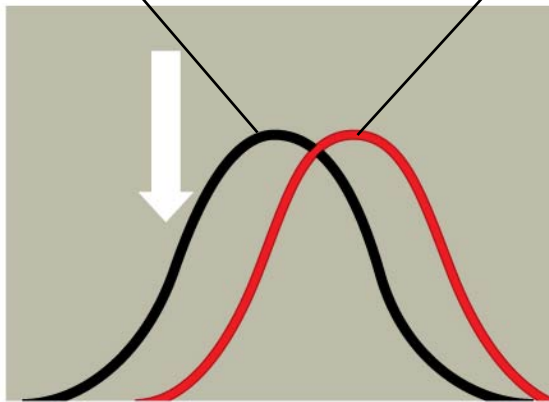
## Data from the Experiment

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

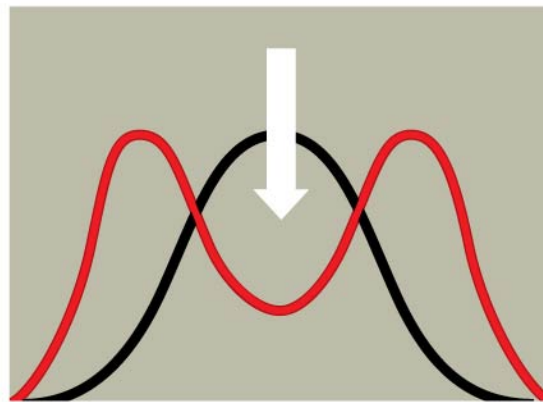
Figure 23.UN01b



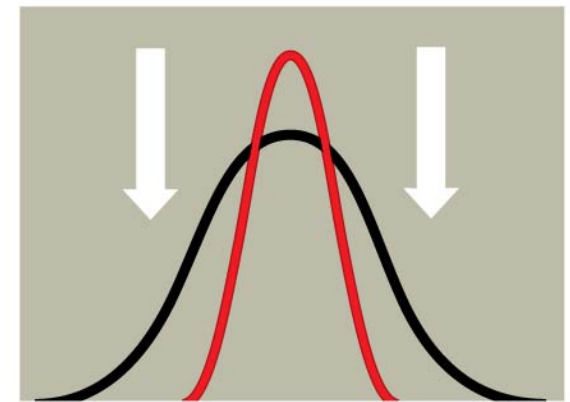
**Original population**  
**Evolved population**



**Directional selection**



**Disruptive selection**



**Stabilizing selection**

Figure 23.UN03

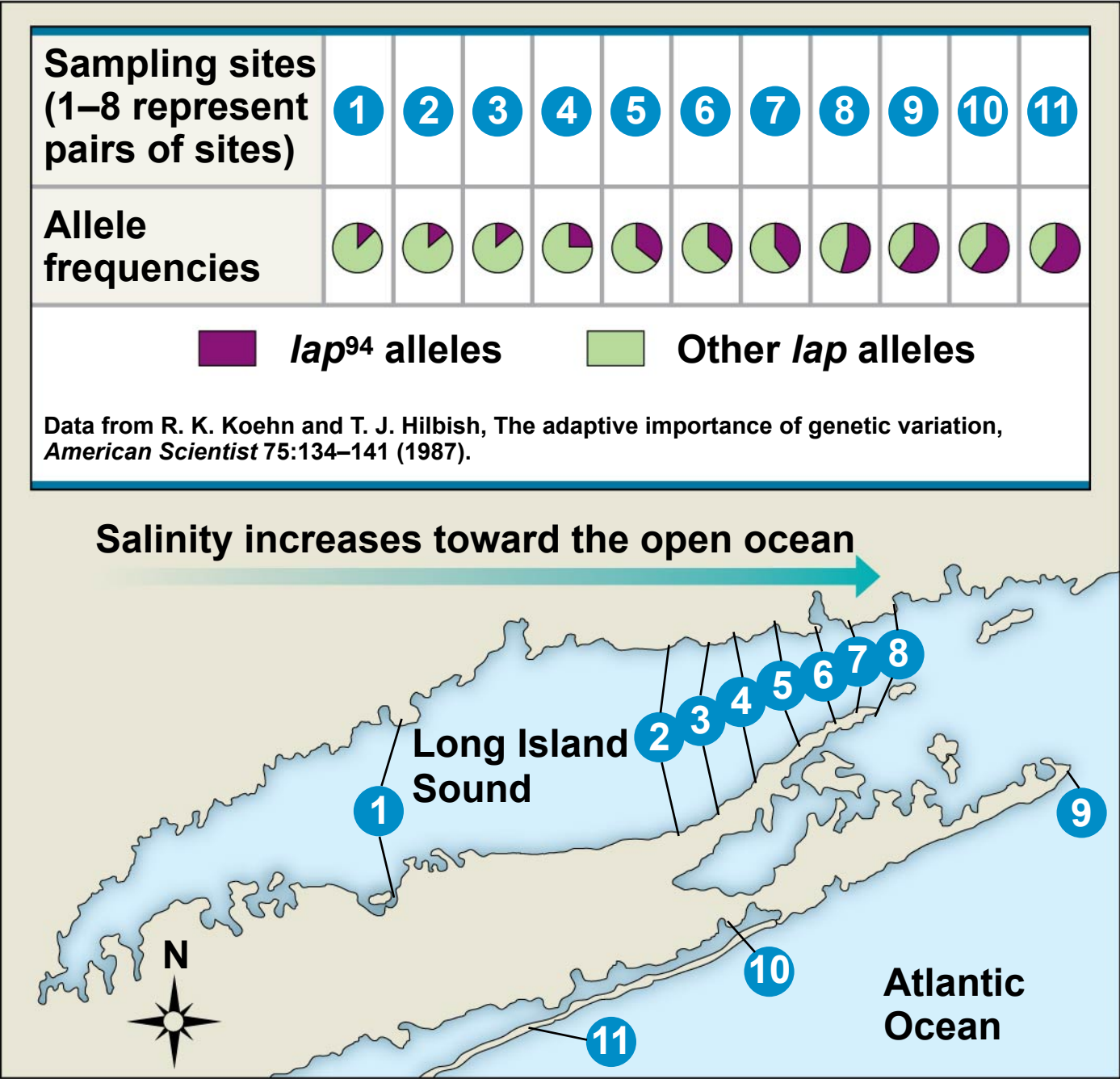




Figure 23.UN04

