

CAMPBELL BIOLOGY IN FOCUS

URRY • CAIN • WASSERMAN • MINORSKY • REECE

21

The Evolution of Populations

Lecture Presentations by
Kathleen Fitzpatrick and
Nicole Tunbridge,
Simon Fraser University

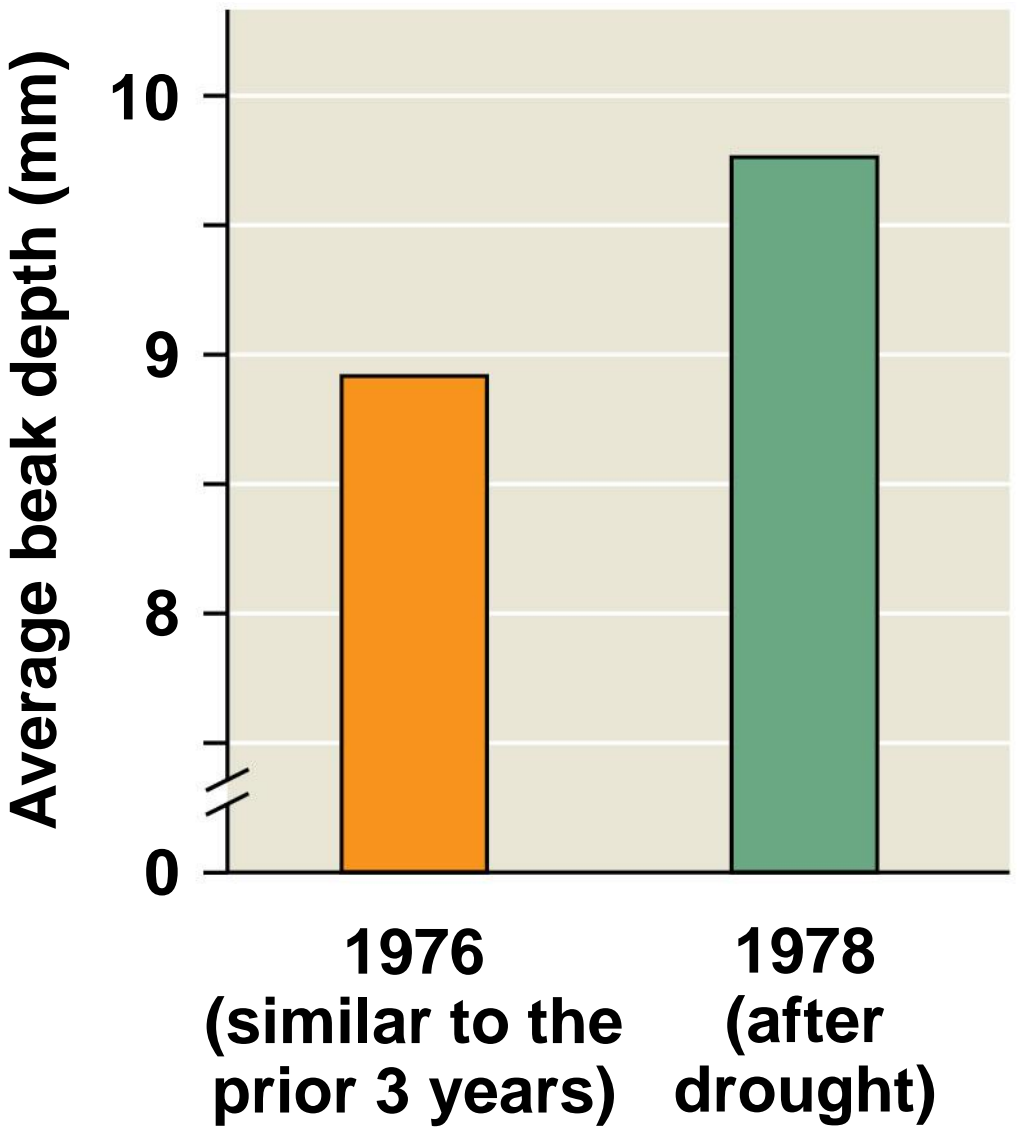
The Smallest Unit of Evolution

- One common misconception is that organisms evolve during their lifetimes
- 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 the remaining large seeds and survive

Figure 21.1



Figure 21.2



- The average beak depth increased in the finch population because birds with smaller beaks were less likely to survive the drought
- 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 21.1: Genetic variation makes evolution possible

- Variation in heritable traits is a prerequisite for evolution by natural selection
- Mendel's work on pea plants provided evidence of discrete heritable units (genes)

Genetic Variation

- Phenotypic variation often reflects **genetic variation**
- Genetic variation among individuals is caused by differences in genes or other DNA sequences
- Some phenotypic differences can be classified on an “either-or” basis
- Such traits are usually determined by a single gene
- Other phenotypic differences are due to the influence of many genes and vary in gradations along a continuum

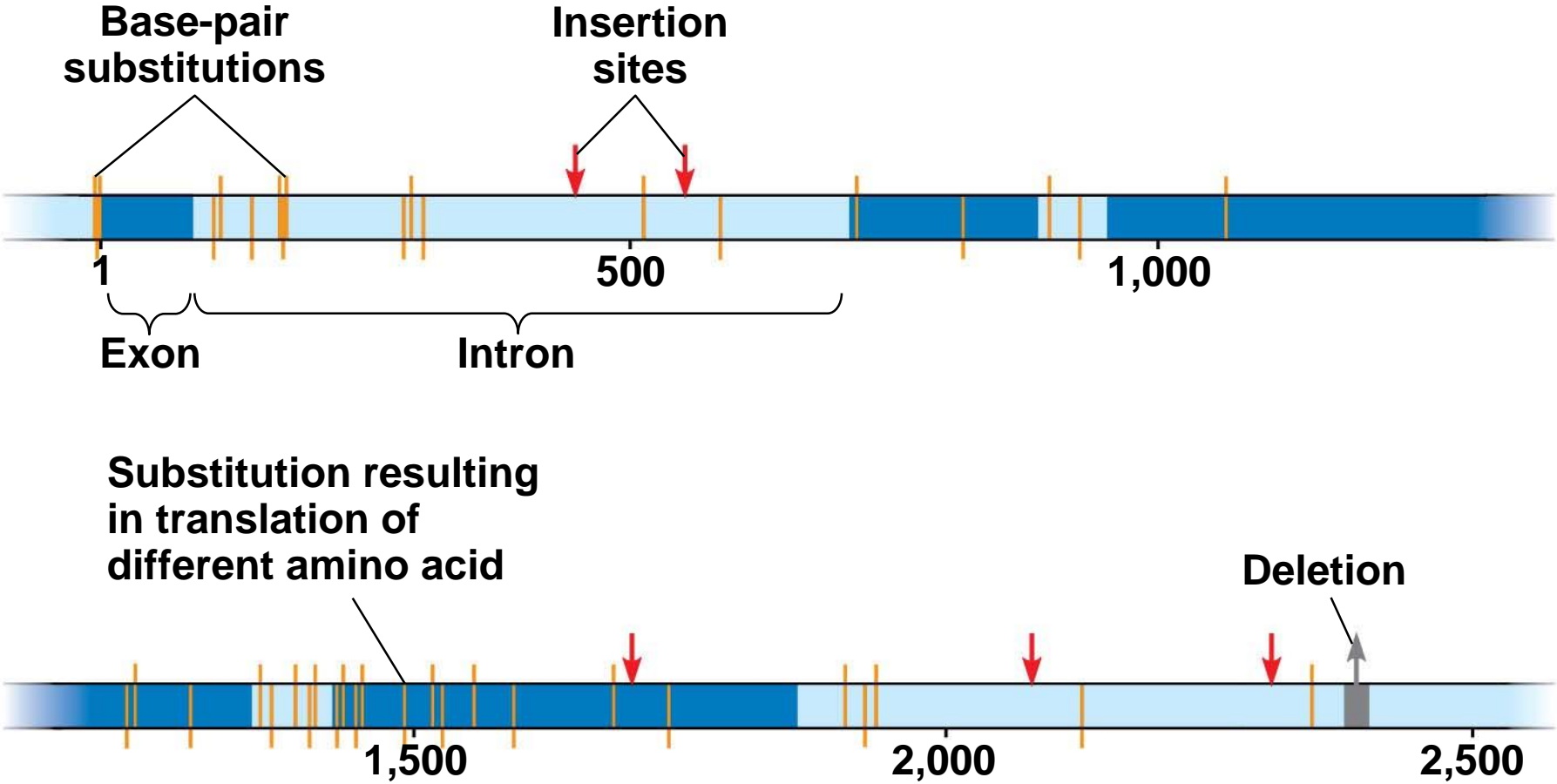
Figure 21.3



- Genetic variation at the whole gene level (gene variability) can be quantified as the average percent of loci that are heterozygous

- Genetic variation can be measured at the molecular level of DNA (nucleotide variability)
- 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 21.4



- Phenotype is the product of both inherited genotype and environmental influences
- Natural selection can only act on phenotypic variation that has a genetic component



(a) Caterpillars raised on a diet of oak flowers



(b) Caterpillars raised on a diet of oak leaves



(a) Caterpillars raised on a diet of oak flowers



(b) Caterpillars raised on a diet of oak leaves

Sources of Genetic Variation

- Genetic variation can result from the production of new genes and alleles through mutation or gene duplication
- Sexual reproduction can also result in genetic variation through the recombination of 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 of a single nucleotide in a DNA sequence

- The effects of point mutations can vary
 - Mutations in noncoding regions of DNA often result in **neutral variation**, differences that do not confer a selective advantage or disadvantage
 - Mutations in genes can also be neutral because of redundancy in the genetic code

- The effects of point mutations can vary
 - Mutations that alter the phenotype are often harmful
 - Mutations that result in a change in protein production are sometimes, though rarely, beneficial

Altering Gene Number or Position

- Chromosomal mutations that delete, disrupt, or rearrange many loci are typically harmful
- Duplication of large chromosome segments is generally harmful, but duplication of small pieces of DNA may not be
- Duplicated genes can take on new functions by further mutation

- Gene duplications likely played a major role in evolution
 - For example, an ancestral odor-detecting gene in mammals has been duplicated many times: Humans have 380 functional copies of the gene; mice have 1,200
 - The increase in the number of copies of these genes enabled mammals to detect faint odors and distinguish among many smells

Rapid Reproduction

- Mutation rates are generally 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

- Mutation rates are faster in viruses because their RNA genome cannot be repaired by host cells
- Viruses are also able to accumulate mutations rapidly due to their 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

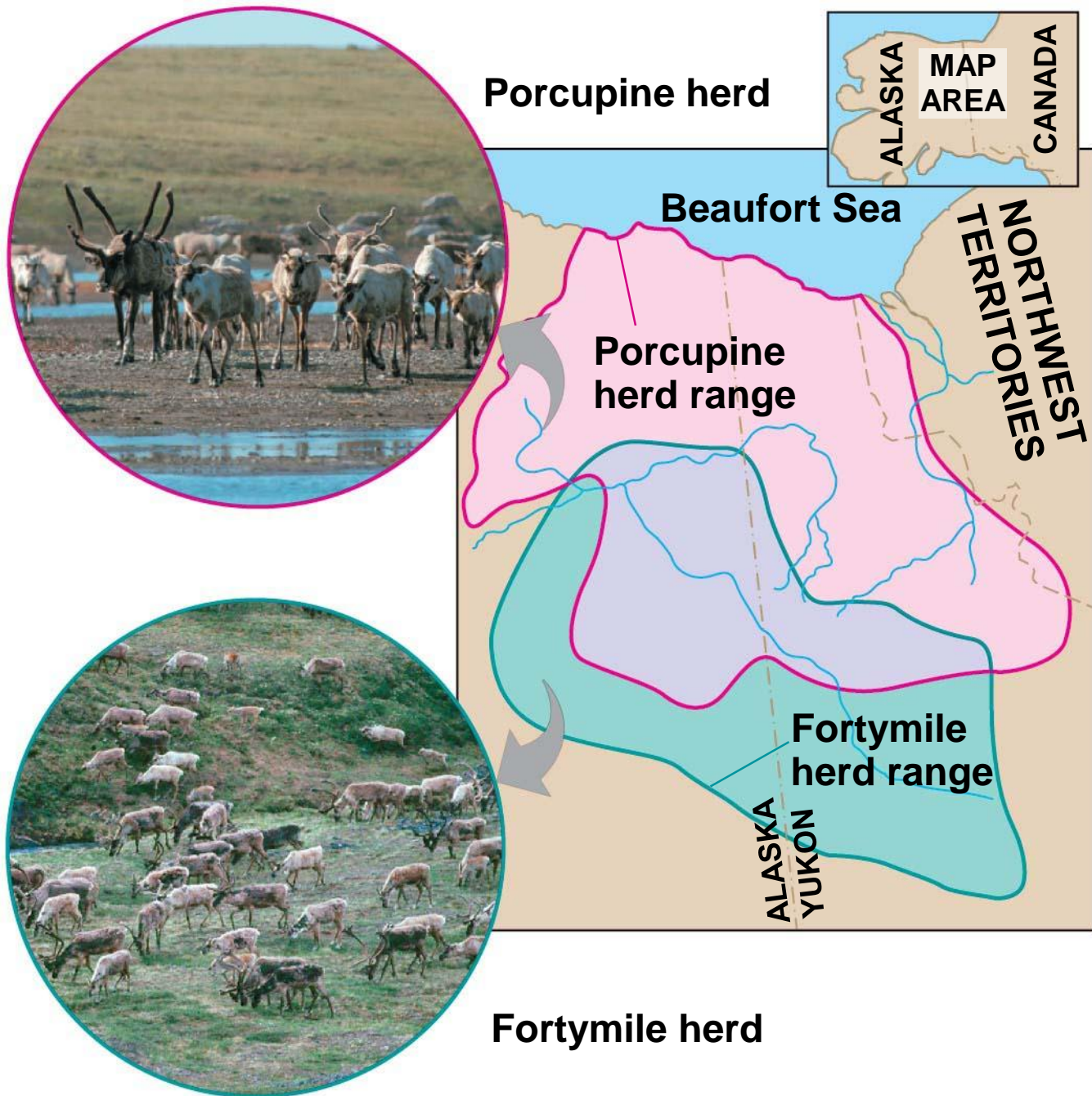
Concept 21.2: The Hardy-Weinberg equation can be used to test whether a population is evolving

- 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 isolated from one another geographically, but individuals typically breed with other members of their own population

Figure 21.6





Porcupine herd



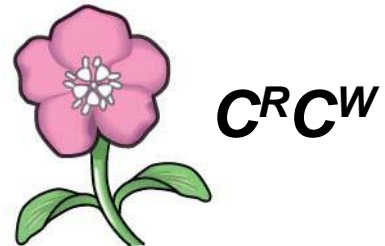
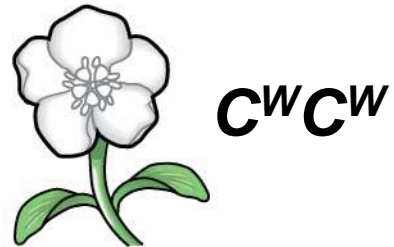
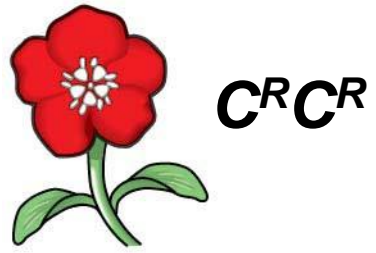
Fortymile herd

- A **gene pool** consists of all the alleles for all loci in a population
- An allele for a particular locus is fixed if all individuals in a population are homozygous for the same allele

- 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 2 alleles for each homozygous dominant individual plus 1 allele for each heterozygous individual; the same logic applies for recessive alleles

- By convention, if there are 2 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
 - For example, $p + q = 1$

- 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
 - $C^R = (320 \times 2) + 160 = 800$
 - $C^W = (20 \times 2) + 160 = 200$



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

The Hardy-Weinberg Equation

- The Hardy-Weinberg equation describes the genetic makeup expected for a population that is not evolving
- If the data observed for the population differ from the expected values, then the population may be evolving

Hardy-Weinberg Equilibrium

- A population in which mating is random and none of the mechanisms of evolution are acting is in **Hardy-Weinberg equilibrium**
- Allele and genotype frequencies remain constant from generation to generation for a population in Hardy-Weinberg equilibrium
- Mendelian inheritance preserves genetic variation in a population

- 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
 - $p = \text{freq } C^R = 0.8$
 - $q = \text{freq } C^W = 0.2$

Frequencies of alleles

p = frequency of C^R allele  = 0.8

q = frequency of C^W allele  = 0.2

Frequencies of alleles

p = frequency of C^R allele ● = 0.8

q = frequency of C^W allele ○ = 0.2



Alleles in the population

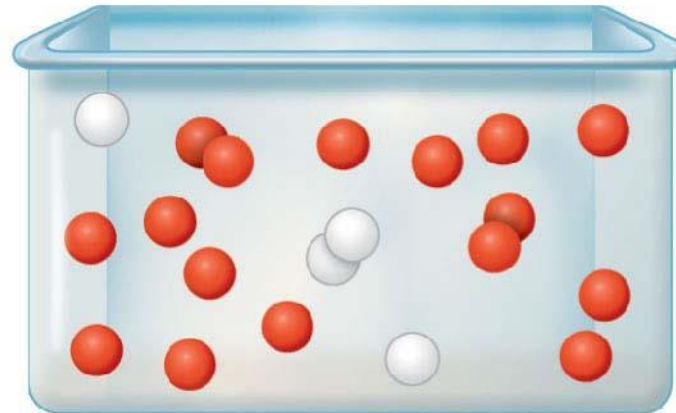


Figure 21.7-s3

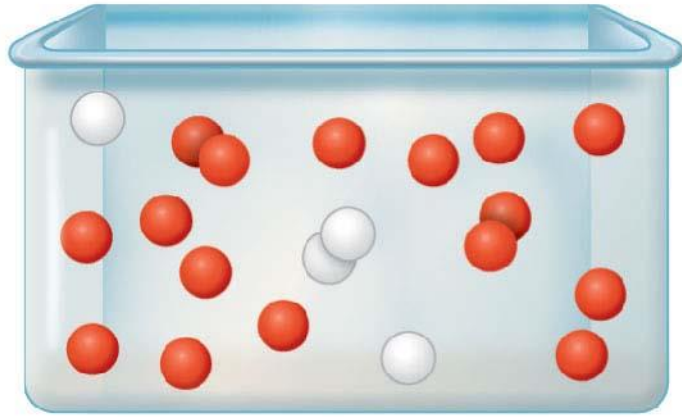
Frequencies of alleles

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%

20%

80%

20%

chance

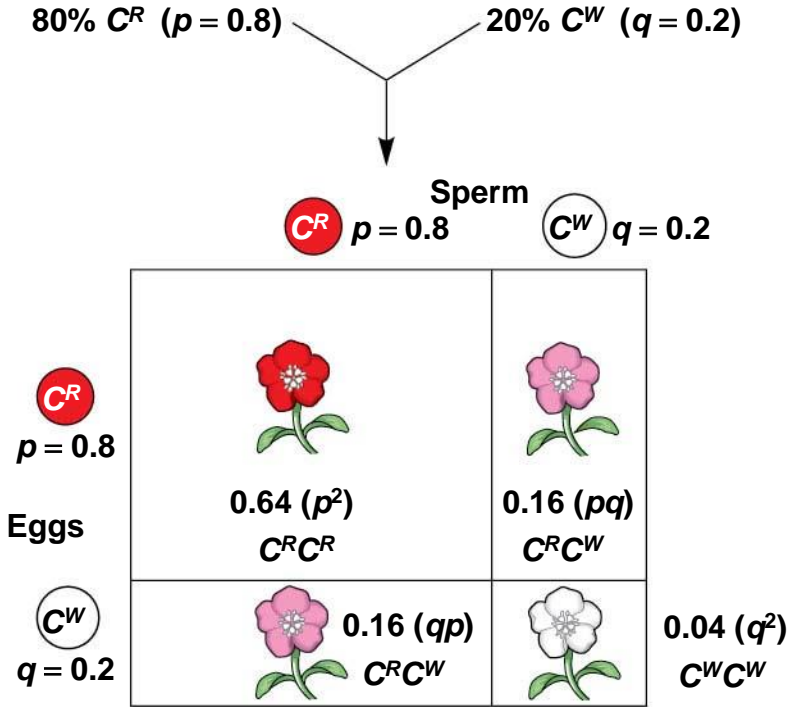
chance

chance

chance

- The frequency of genotypes can be calculated using the rule of multiplication
 - $C^R C^R = p^2 = (0.8)^2 = 0.64$
 - $C^R C^W = 2pq = 2(0.8)(0.2) = 0.32$
 - $C^W C^W = q^2 = (0.2)^2 = 0.04$
- The frequency of genotypes can be confirmed using a Punnett square

Figure 21.8



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

Gametes of this generation:

$$\begin{aligned}
 &64\% C^R \text{ (from } C^R C^R \text{ plants)} + 16\% C^R \text{ (from } C^R C^W \text{ plants)} = 80\% C^R = 0.8 = p \\
 &4\% C^W \text{ (from } C^W C^W \text{ plants)} + 16\% C^W \text{ (from } C^R C^W \text{ plants)} = 20\% C^W = 0.2 = q
 \end{aligned}$$




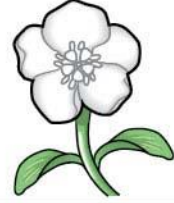
With random mating, these gametes will result in the same mix of genotypes in the next generation:

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

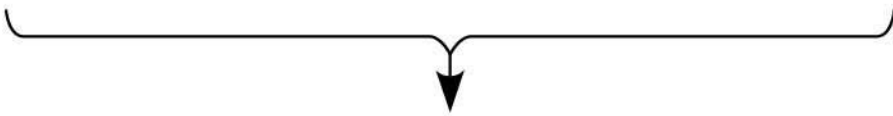
Figure 21.8-1

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

Sperm
 C^R $p = 0.8$ C^W $q = 0.2$

			
C^R $p = 0.8$	0.64 (p^2) $C^R C^R$	0.16 (pq) $C^R C^W$	
Eggs			
C^W $q = 0.2$	 0.16 (qp) $C^R C^W$	 0.04 (q^2) $C^W C^W$	

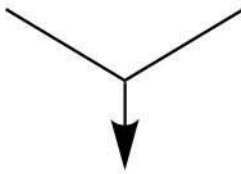
64% $C^R C^R$, 32% $C^R C^W$, and 4% $C^W C^W$



Gametes of this generation:

64% C^R (from $C^R C^R$ plants)	+	16% C^R (from $C^R C^W$ plants)	=	80% $C^R = 0.8 = p$
4% C^W (from $C^W C^W$ plants)	+	16% C^W (from $C^R C^W$ plants)	=	20% $C^W = 0.2 = q$

With random mating, these gametes 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

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

Expected frequency of genotype $C^R C^R$ + Expected frequency of genotype $C^R C^W$ + Expected frequency of genotype $C^W C^W$ = 1

Conditions for Hardy-Weinberg Equilibrium

- The Hardy-Weinberg equation describes a hypothetical population that is not evolving
- In real populations, allele and genotype frequencies do change over time

- The five conditions for a population to be in Hardy-Weinberg equilibrium are rarely met in nature
 1. No mutations
 2. Random mating
 3. No natural selection
 4. Extremely large population size
 5. No gene flow

- Natural populations can evolve at some loci while being in Hardy-Weinberg equilibrium at other loci
- Some populations evolve slowly enough that evolution cannot be detected

Applying the Hardy-Weinberg Equation

- We can assume 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 1 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 21.3: 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

Natural Selection

- Differential success in reproduction results in certain alleles being passed to the next generation in greater proportions
- For example, an allele that confers resistance to DDT increased in frequency after DDT was used widely in agriculture

Genetic Drift

- The smaller a sample, the more likely it is that chance alone will cause 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 losses of alleles, especially in small populations

Figure 21.9

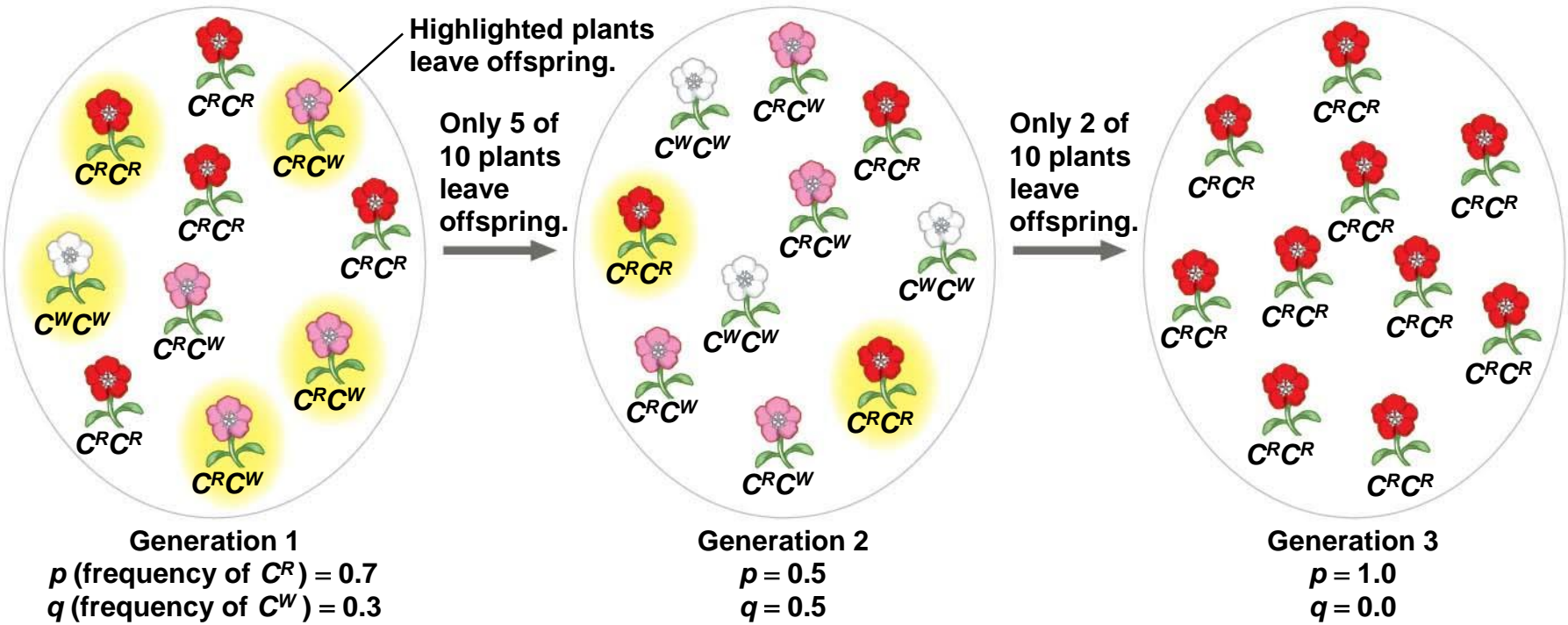
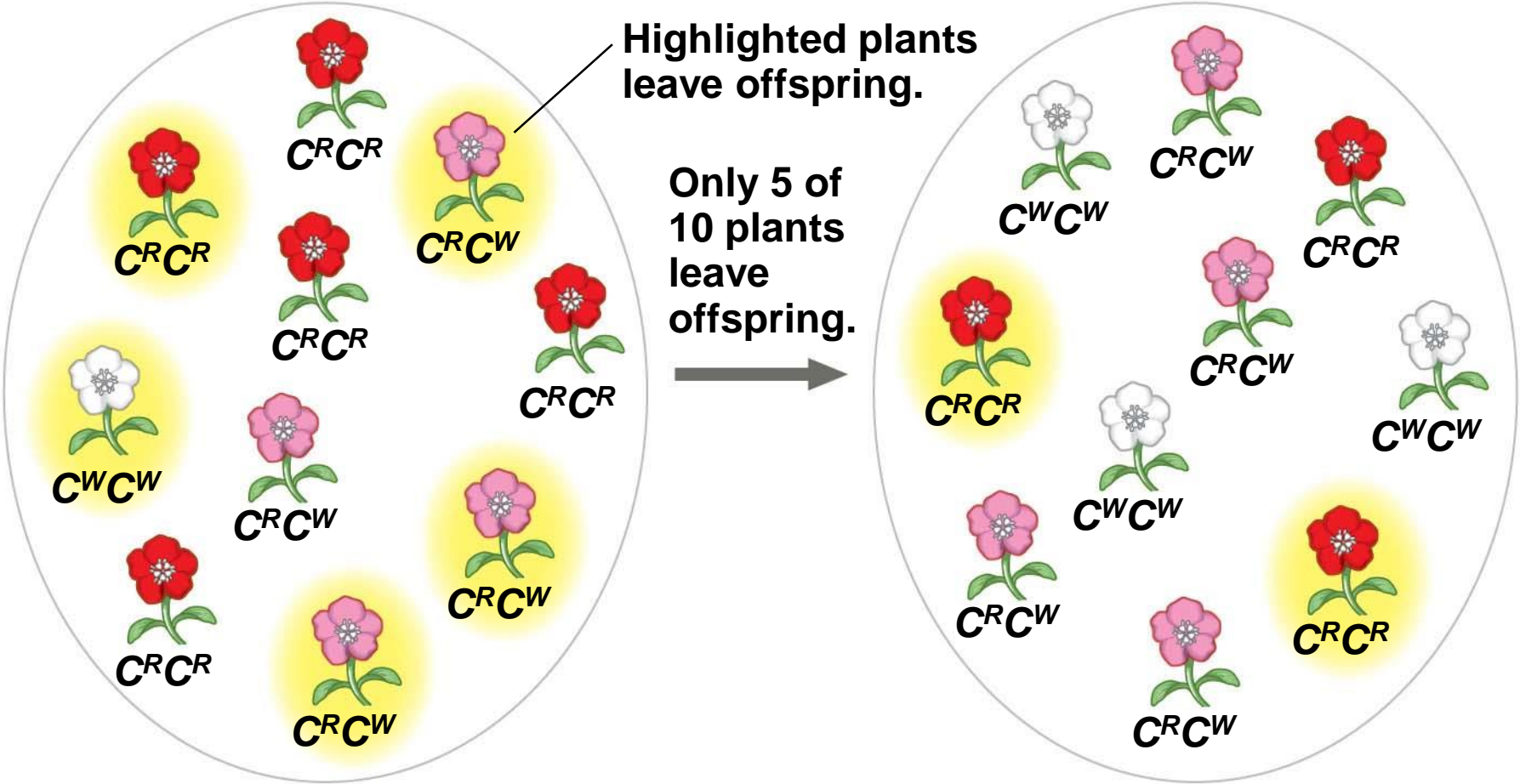


Figure 21.9-1



Highlighted plants leave offspring.

Only 5 of 10 plants leave offspring.

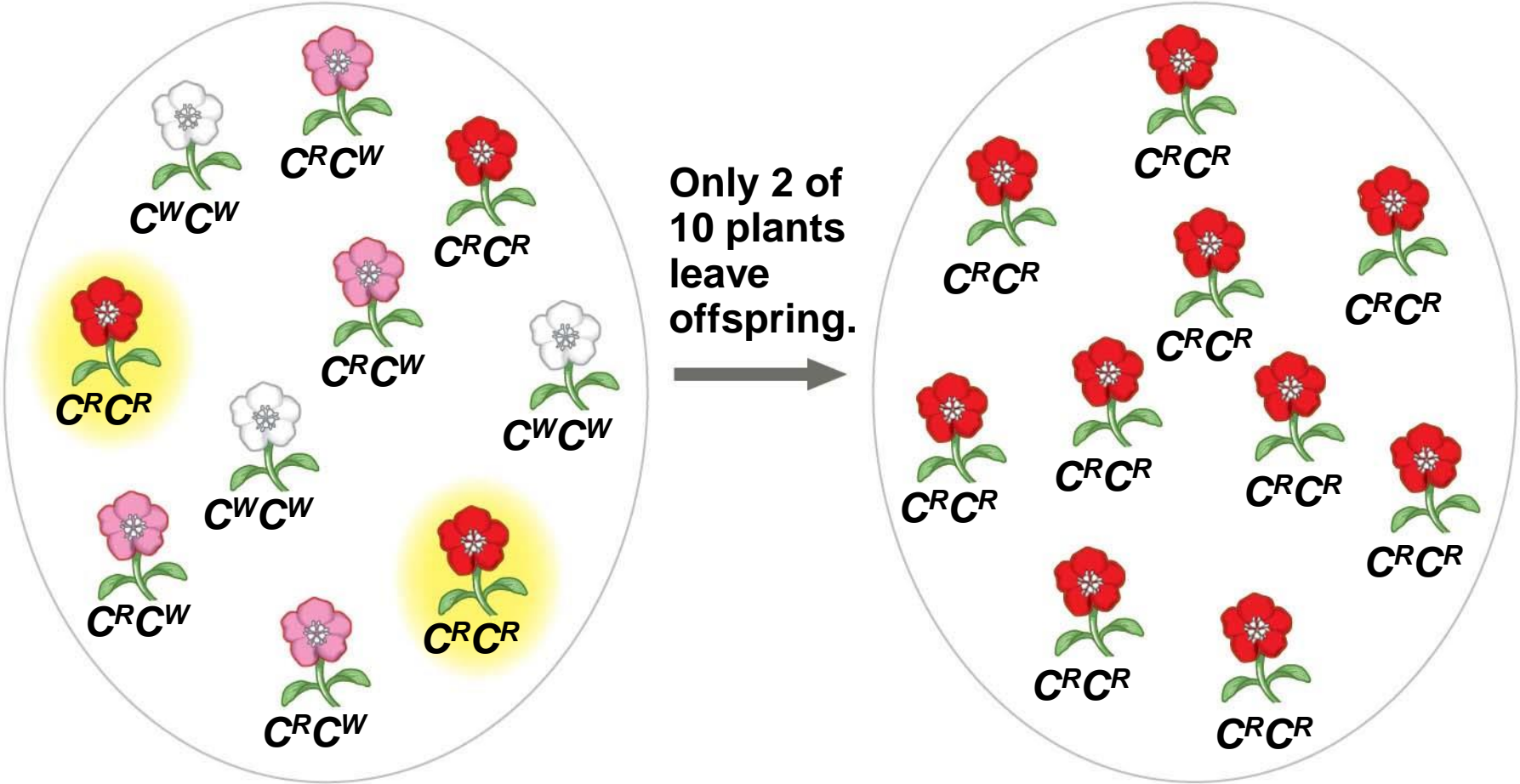
Generation 1

p (frequency of C^R) = 0.7
 q (frequency of C^W) = 0.3

Generation 2

p = 0.5
 q = 0.5

Figure 21.9-2



Generation 2
 $p = 0.5$
 $q = 0.5$

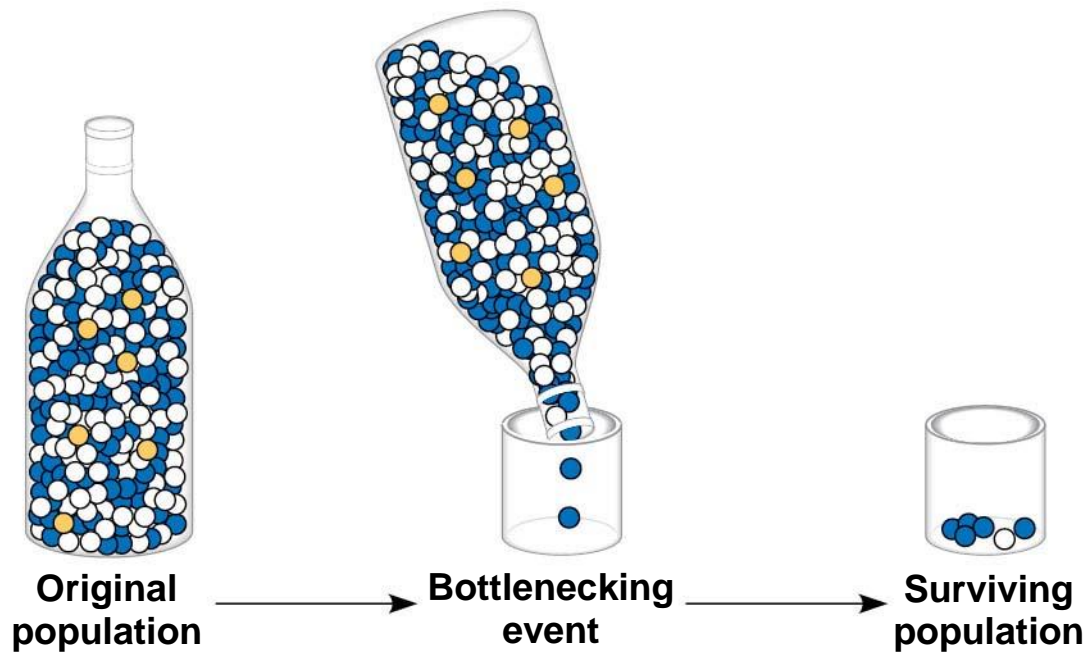
Generation 3
 $p = 1.0$
 $q = 0.0$

The Founder Effect

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

The Bottleneck Effect

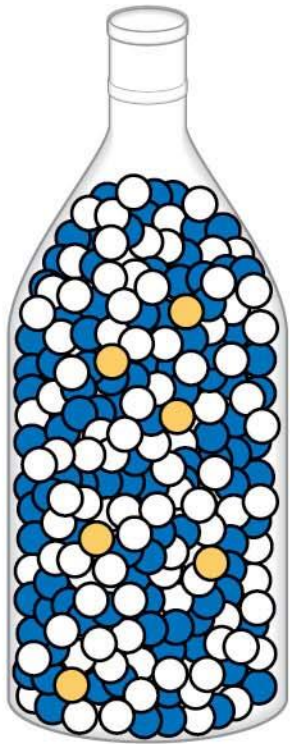
- The **bottleneck effect** can result from a drastic reduction in population size due to a sudden environmental change
- By chance, the resulting gene pool may no longer be reflective of the original population's gene pool
- If the population remains small, it may be further affected by genetic drift



(a) By chance, blue marbles are overrepresented in the surviving population, and gold marbles are absent.

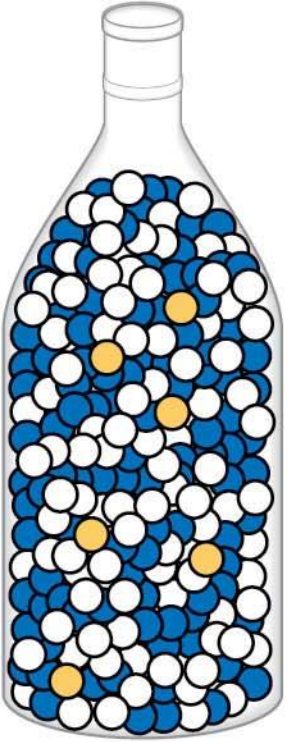


(b) Florida panther (*Puma concolor coryi*)

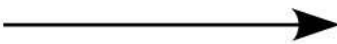


**Original
population**

Figure 21.10-1-s2

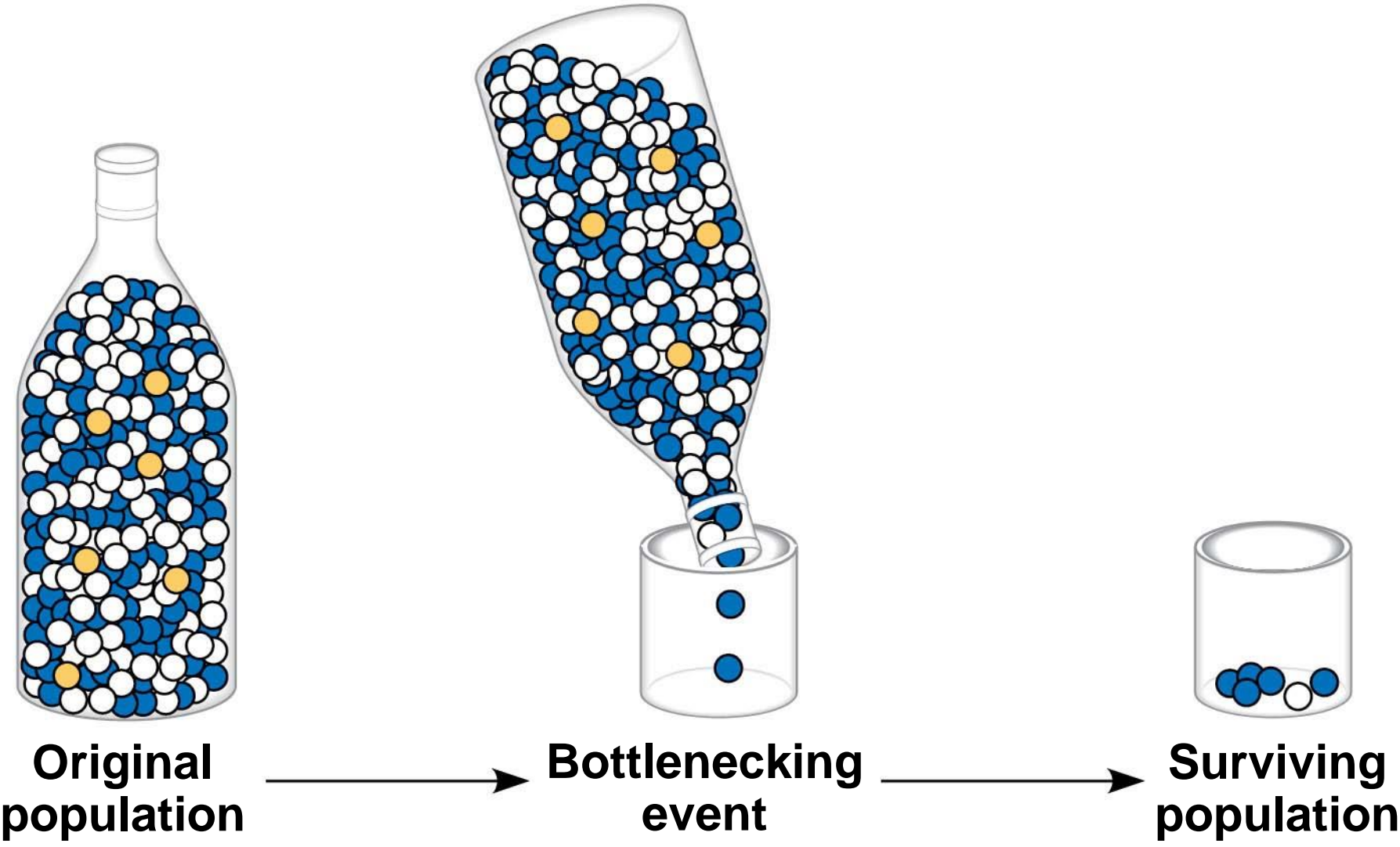


Original population



Bottlenecking event

Figure 21.10-1-s3





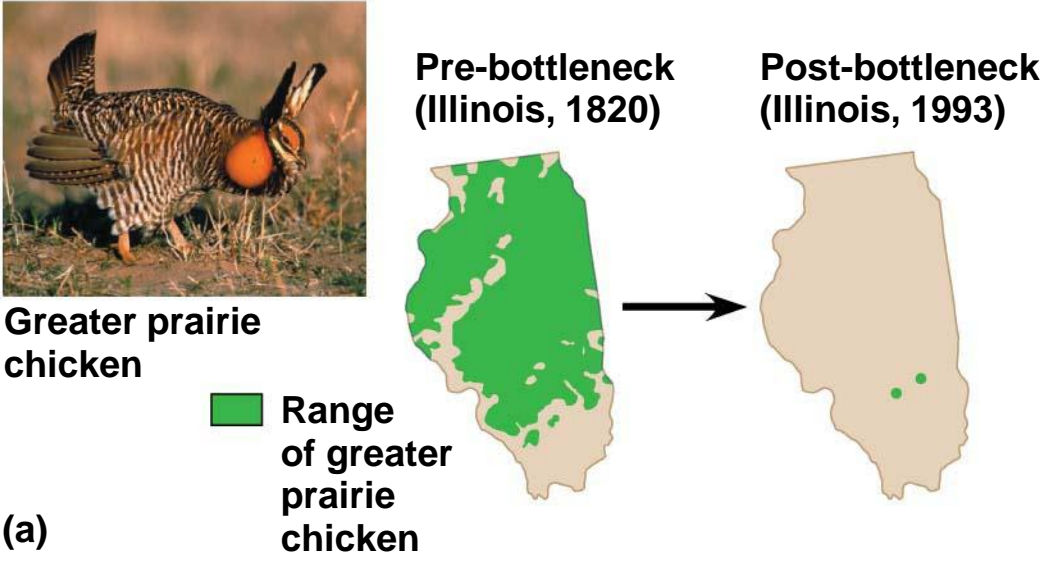
(b) Florida panther (*Puma concolor coryi*)

- 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
- Genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of harmful alleles

Figure 21.11



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

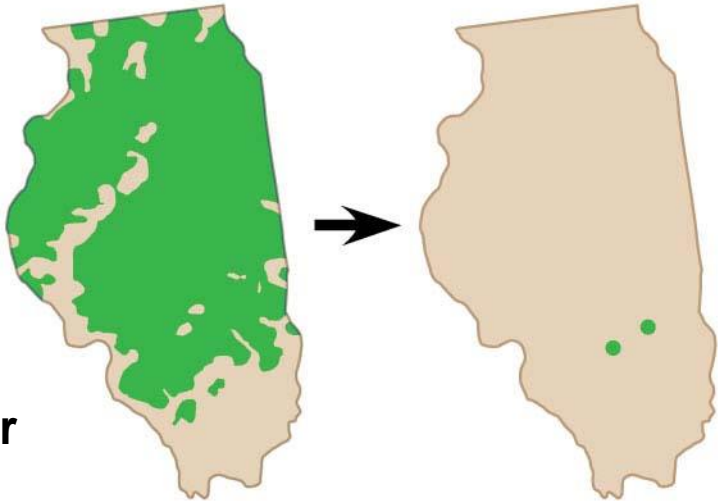
(b)



Greater prairie chicken

Pre-bottleneck
(Illinois, 1820)

Post-bottleneck
(Illinois, 1993)



 Range
of greater
prairie
chicken

(a)

Figure 21.11-2

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)



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

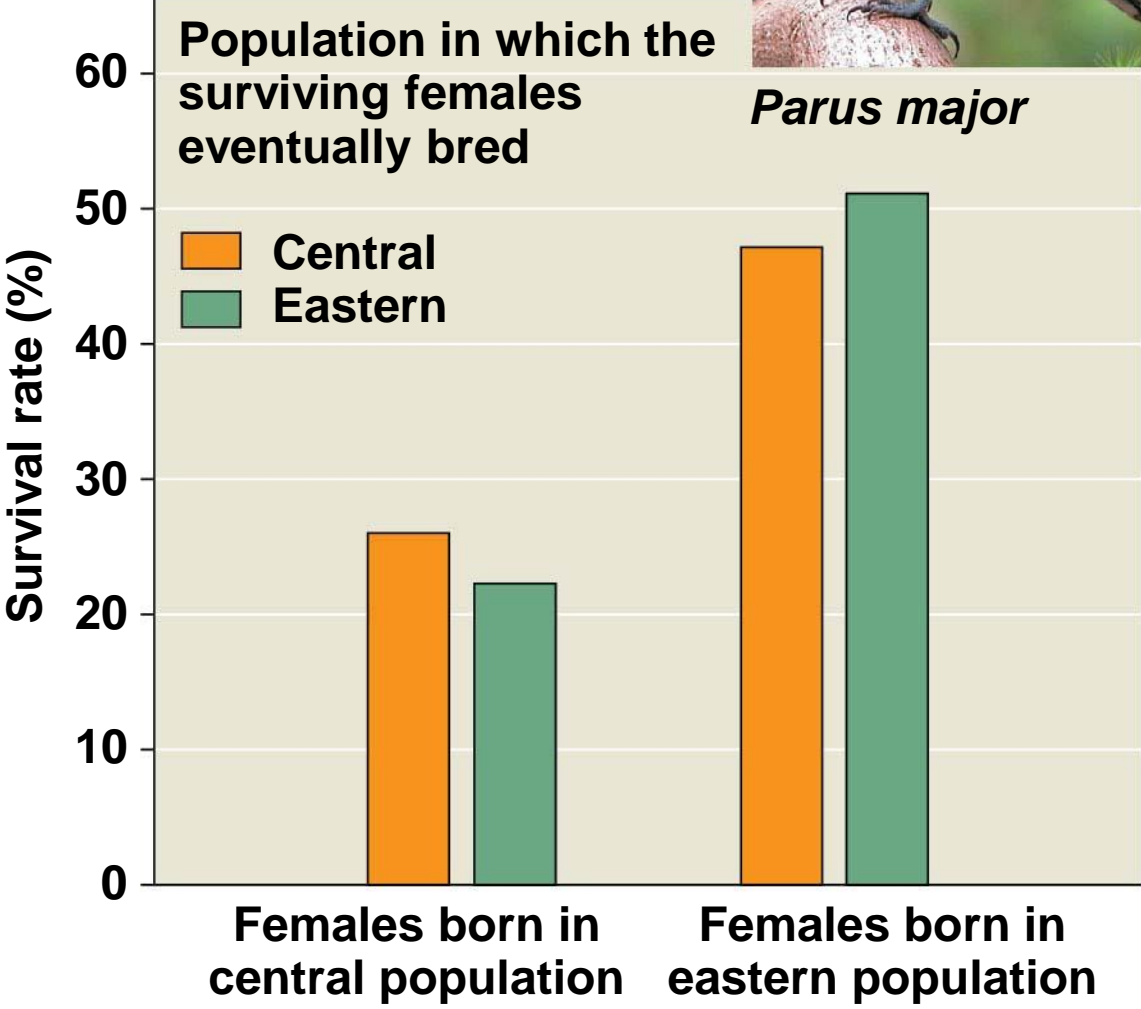
1. Genetic drift is significant in small populations
2. Genetic drift can cause allele frequencies to change at random
3. Genetic drift can lead to a loss of genetic variation within populations
4. Genetic drift can cause harmful alleles to become fixed

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 genetic variation among populations over time

- Gene flow can decrease the fitness of a population
- Consider, for example, the great tit (*Parus major*) on the Dutch island of Vlieland
 - Immigration of birds from the mainland introduces alleles that decrease fitness in island populations
 - Natural selection reduces the frequency of these alleles in the eastern population where immigration from the mainland is low
 - In the central population, high immigration from the mainland overwhelms the effects of selection

Figure 21.12





Parus major

- 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 other diseases
 - 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 21.4: 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 results in **adaptive evolution**, an increase in the frequency of alleles that improve fitness

Natural Selection: *A Closer Look*

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

Relative Fitness

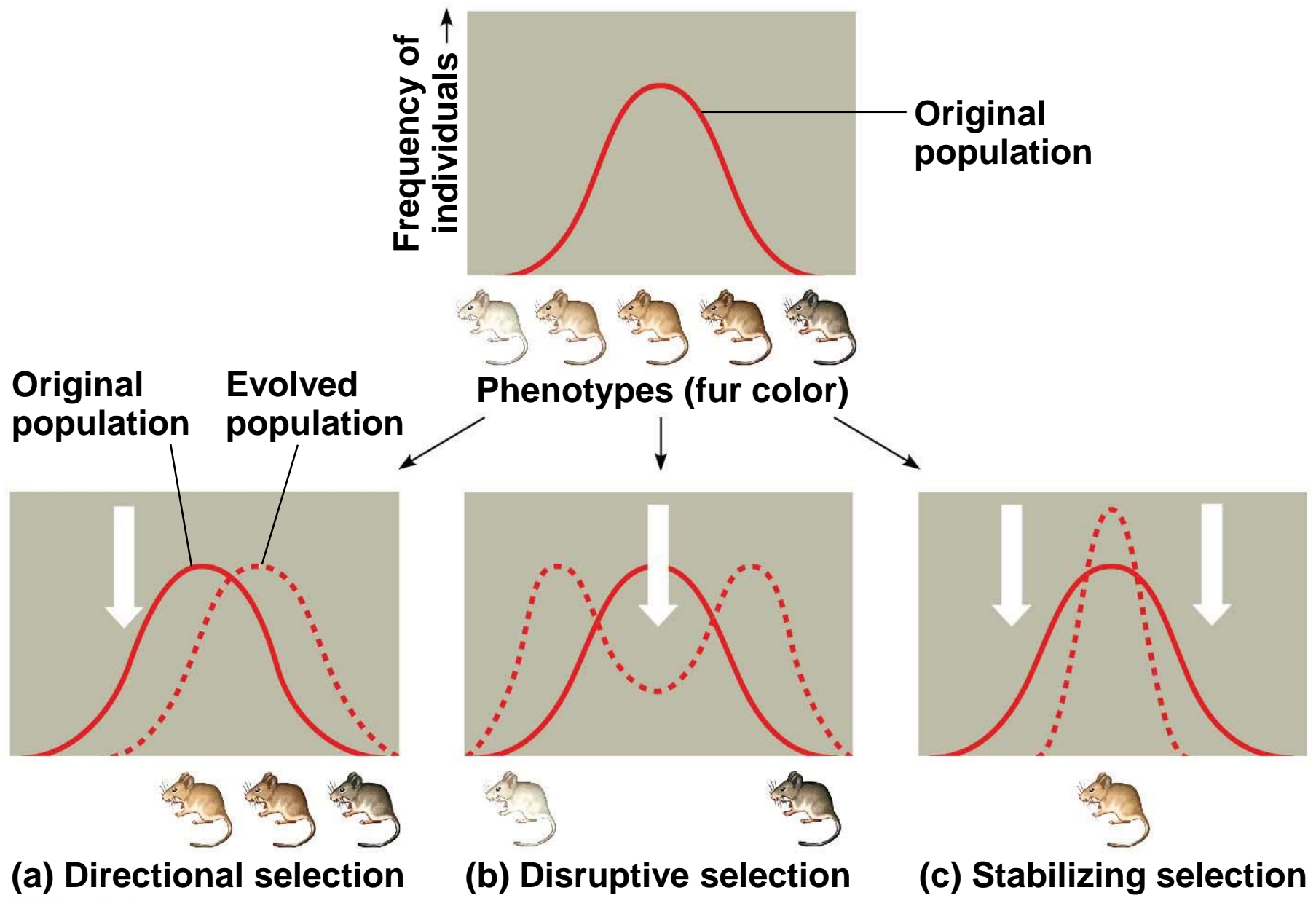
- The phrases “struggle for existence” and “survival of the fittest” are misleading, as they imply direct competition among individuals
- Reproductive success is generally more subtle and depends on many factors

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

Directional, Disruptive, and Stabilizing Selection

- There are three modes of natural selection
 - **Directional selection** occurs when conditions favor individuals at one end of the phenotypic range
 - **Disruptive selection** occurs when conditions favor individuals at both extremes of the phenotypic range
 - **Stabilizing selection** occurs when conditions favor intermediate variants and act against extreme phenotypes

Figure 21.13

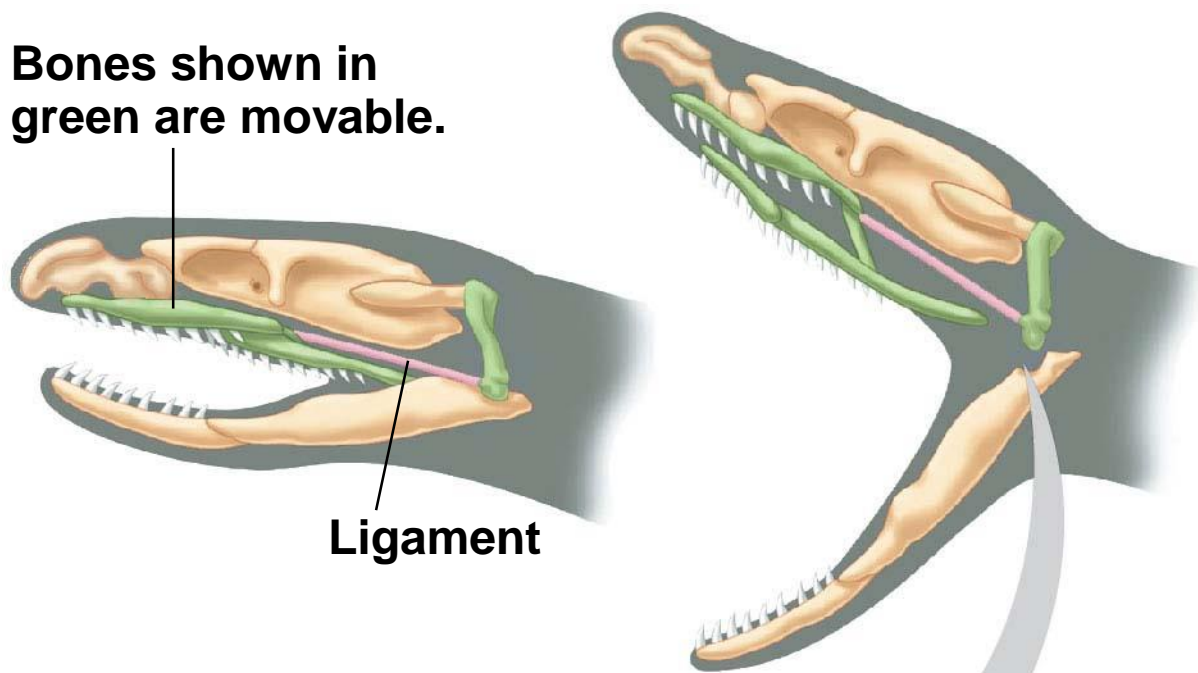


The Key Role of Natural Selection in Adaptive Evolution

- 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 21.14

Bones shown in green are movable.



Ligament



Figure 21.14-1



- Natural selection increases the frequencies of alleles that enhance survival and reproduction
- Adaptive evolution occurs as the proportion of individuals in a population that have traits favorable for the particular environment increases
- Because the environment can change, adaptive evolution is a continuous, dynamic process

- Genetic drift and gene flow do not consistently lead to adaptive evolution, as they can increase or decrease the match between an organism and its environment

Balancing Selection

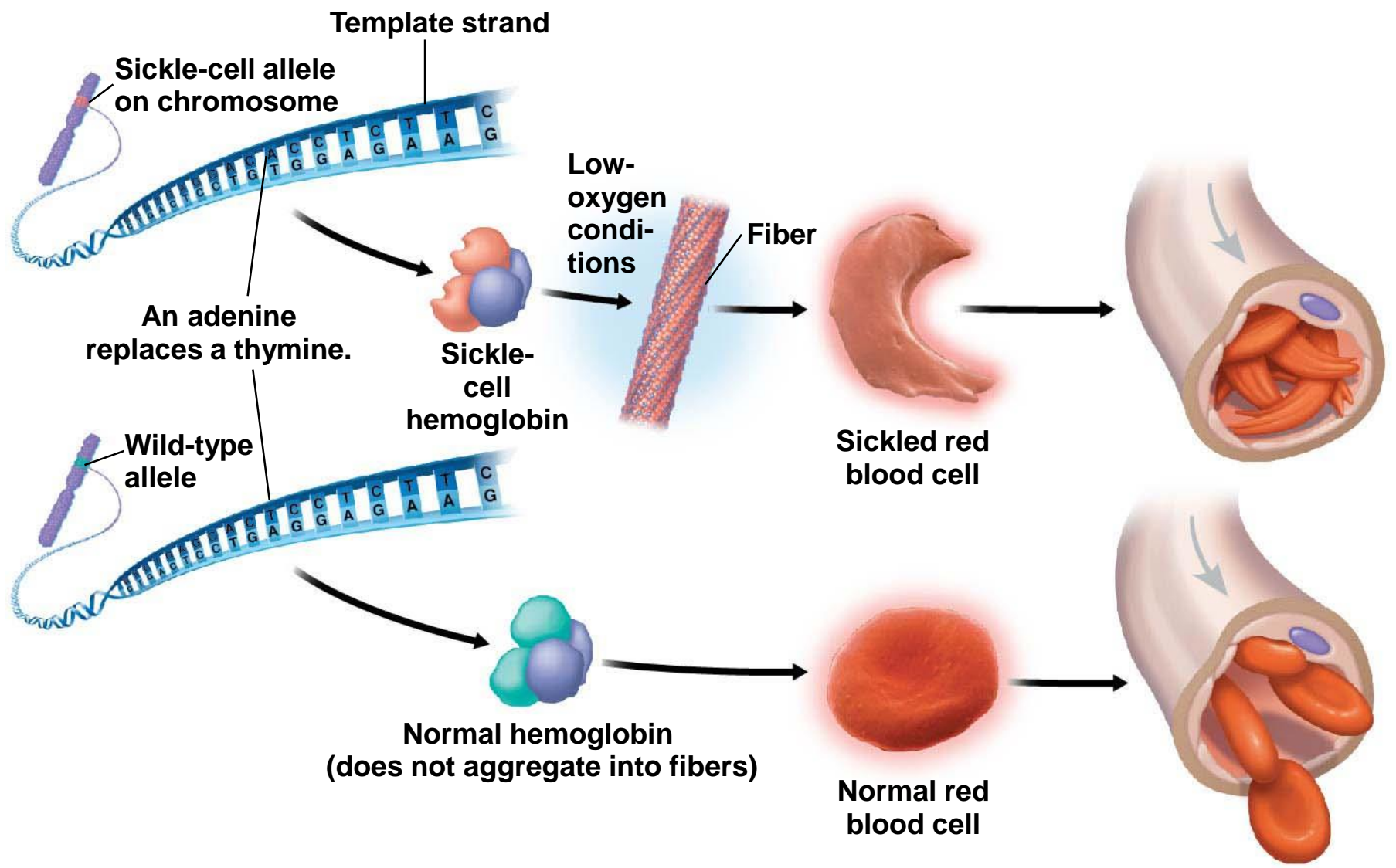
- **Balancing selection** occurs when natural selection maintains stable frequencies of two or more phenotypic forms in a population
- Balancing selection includes
 - Heterozygote advantage
 - Frequency-dependent selection

Heterozygote Advantage

- **Heterozygote advantage** occurs when heterozygotes have a higher fitness than do both homozygotes
- Natural selection will tend to maintain two or more alleles at that locus
- For example, the sickle-cell allele causes deleterious mutations in hemoglobin but also confers malaria resistance

Figure 21.15-1

Make Connections: The Sickle-Cell Allele



Events at the Molecular Level

Consequences for Cells

Effects on Individual Organisms

Figure 21.15-1a

Events at the Molecular Level

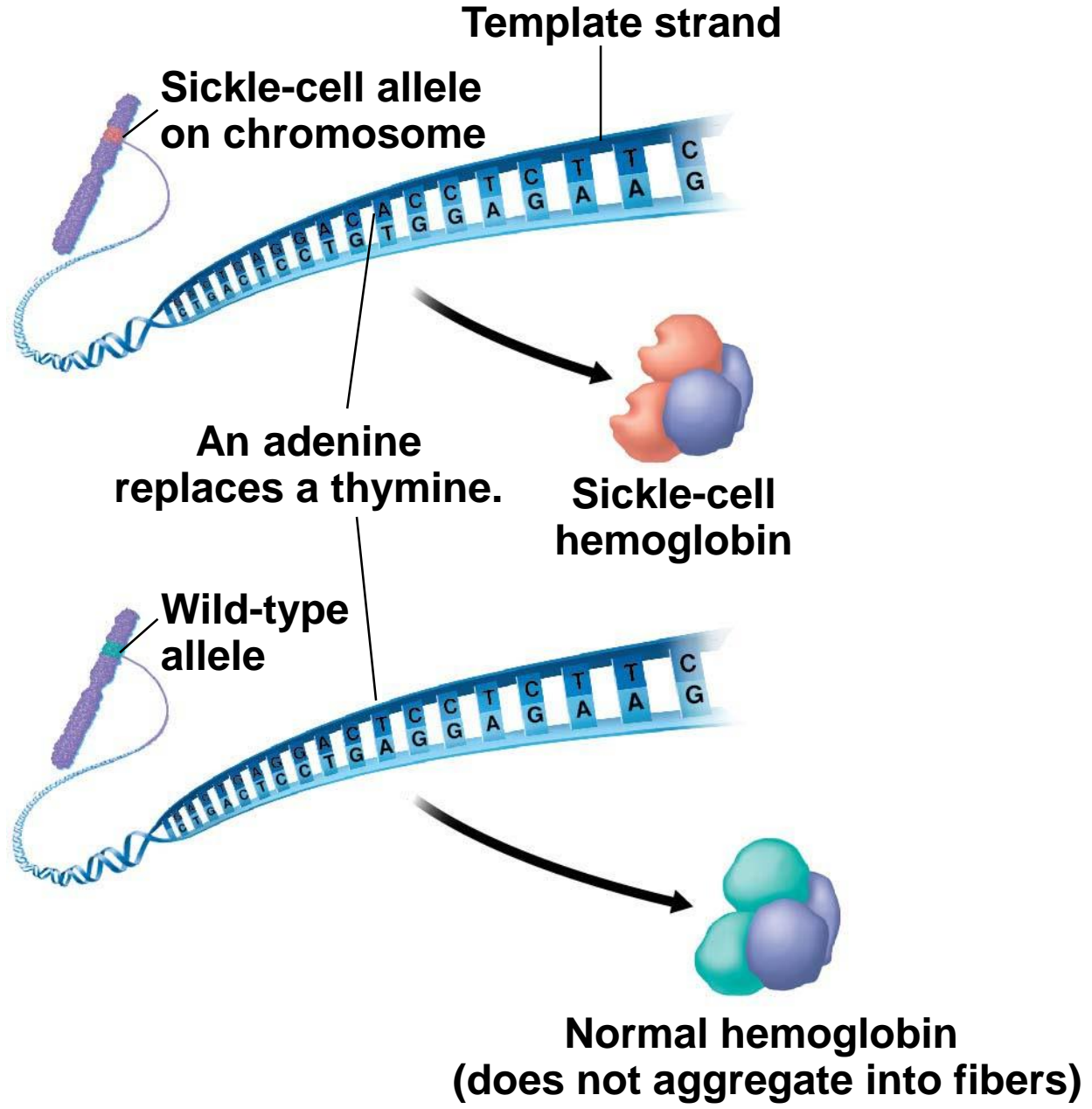
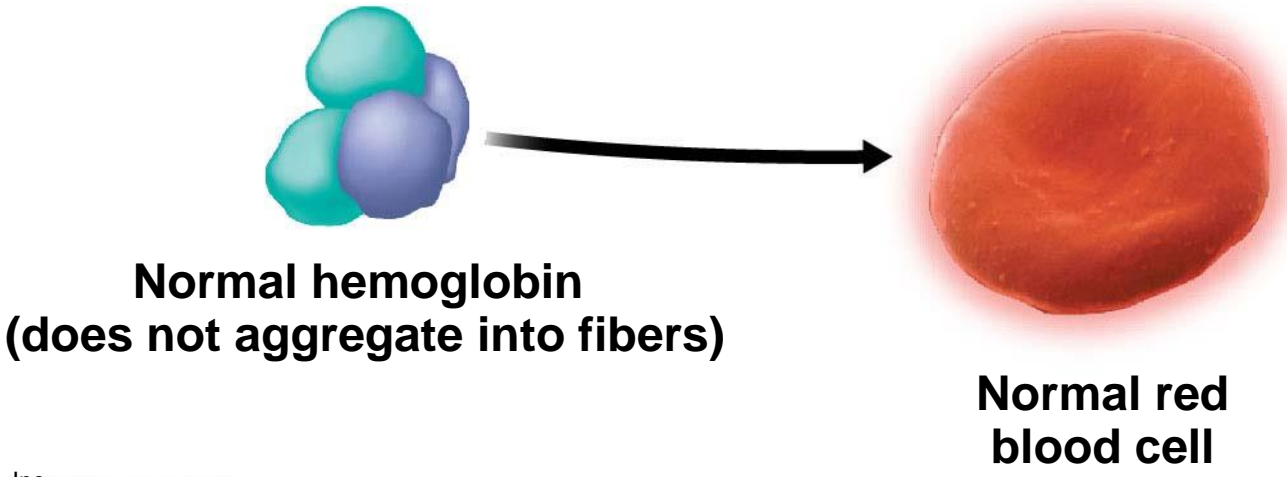
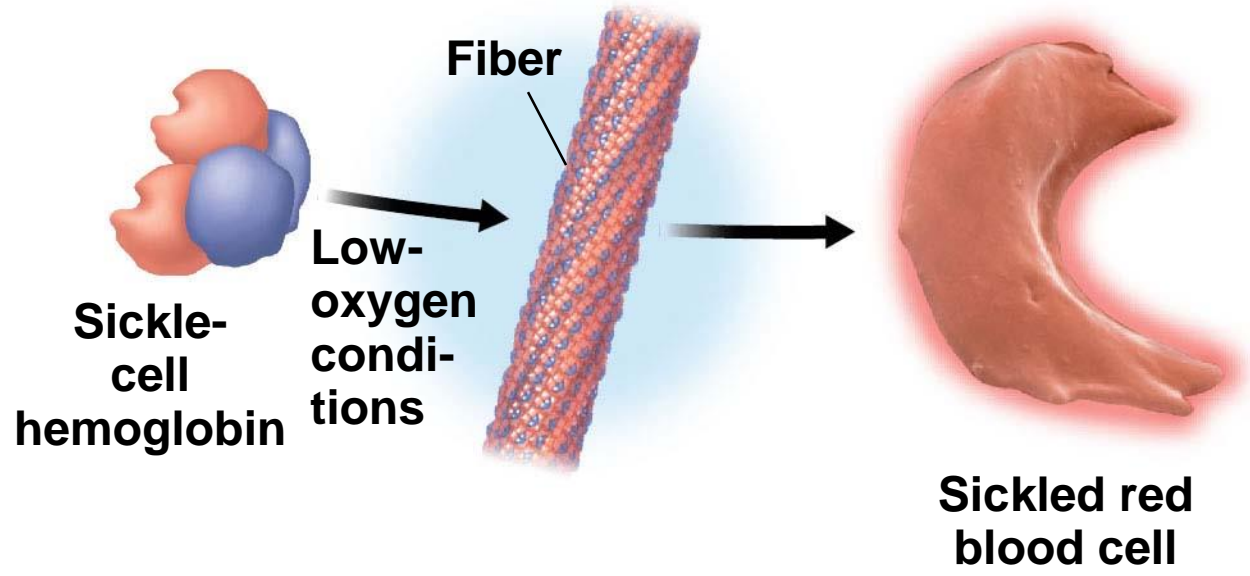
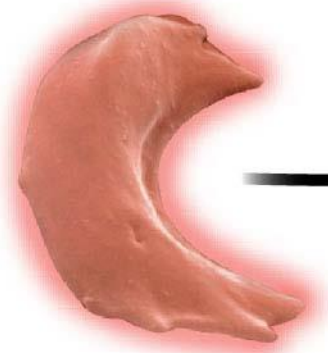


Figure 21.15-1b

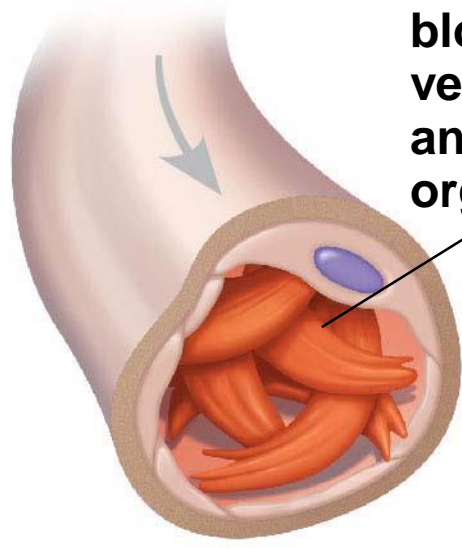
Consequences for Cells



Effects on Individual Organisms



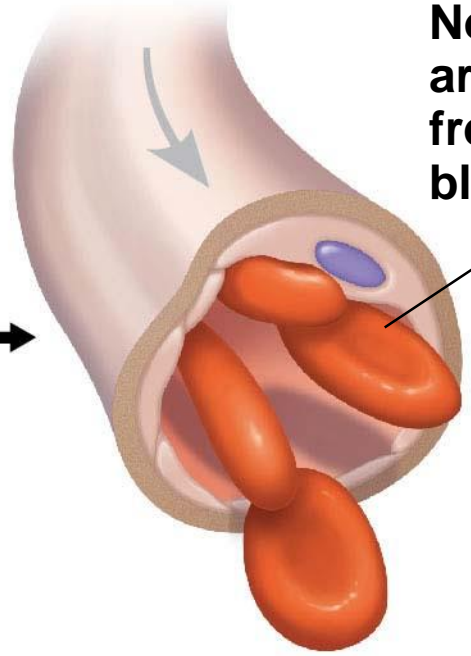
Sickled red blood cell



Sickled blood cells block small blood vessels, causing pain and damage to organs.



Normal red blood cell

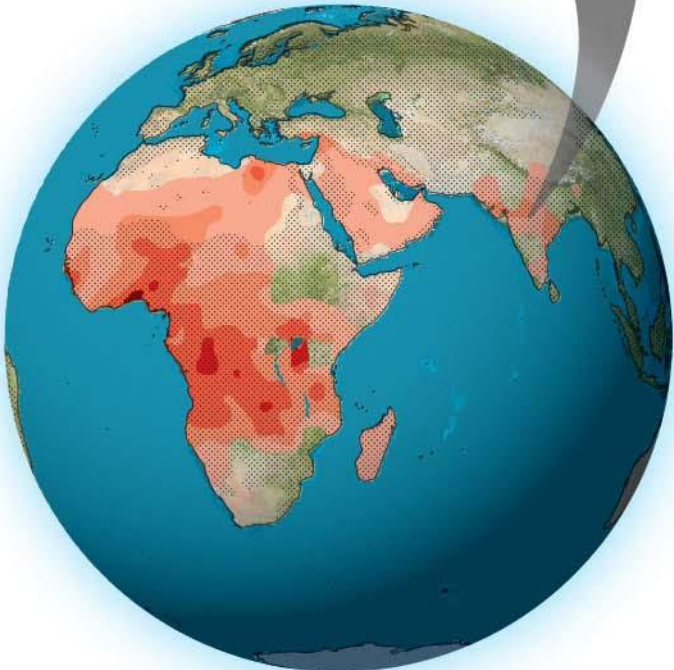


Normal blood cells are flexible and flow freely through small blood vessels.

Make Connections: The Sickle-Cell Allele



Infected mosquitoes spread malaria.



- Frequencies of the sickle-cell allele
- 3.0 – 6.0%
 - 6.0 – 9.0%
 - 9.0 – 12.0%
 - 12.0 – 15.0%
 - > 15.0%

Distribution of malaria

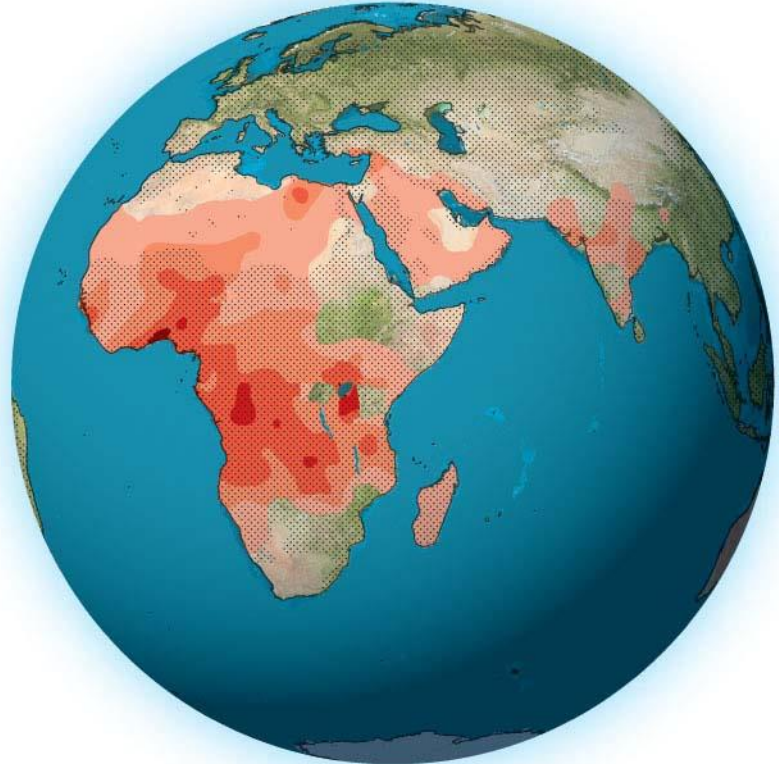
Heterozygotes are more likely to survive malaria.

Evolution in Populations



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

Evolution in Populations



Frequencies of the sickle-cell allele

- 3.0 – 6.0%
- 6.0 – 9.0%
- 9.0 – 12.0%
- 12.0 – 15.0%
- > 15.0%

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

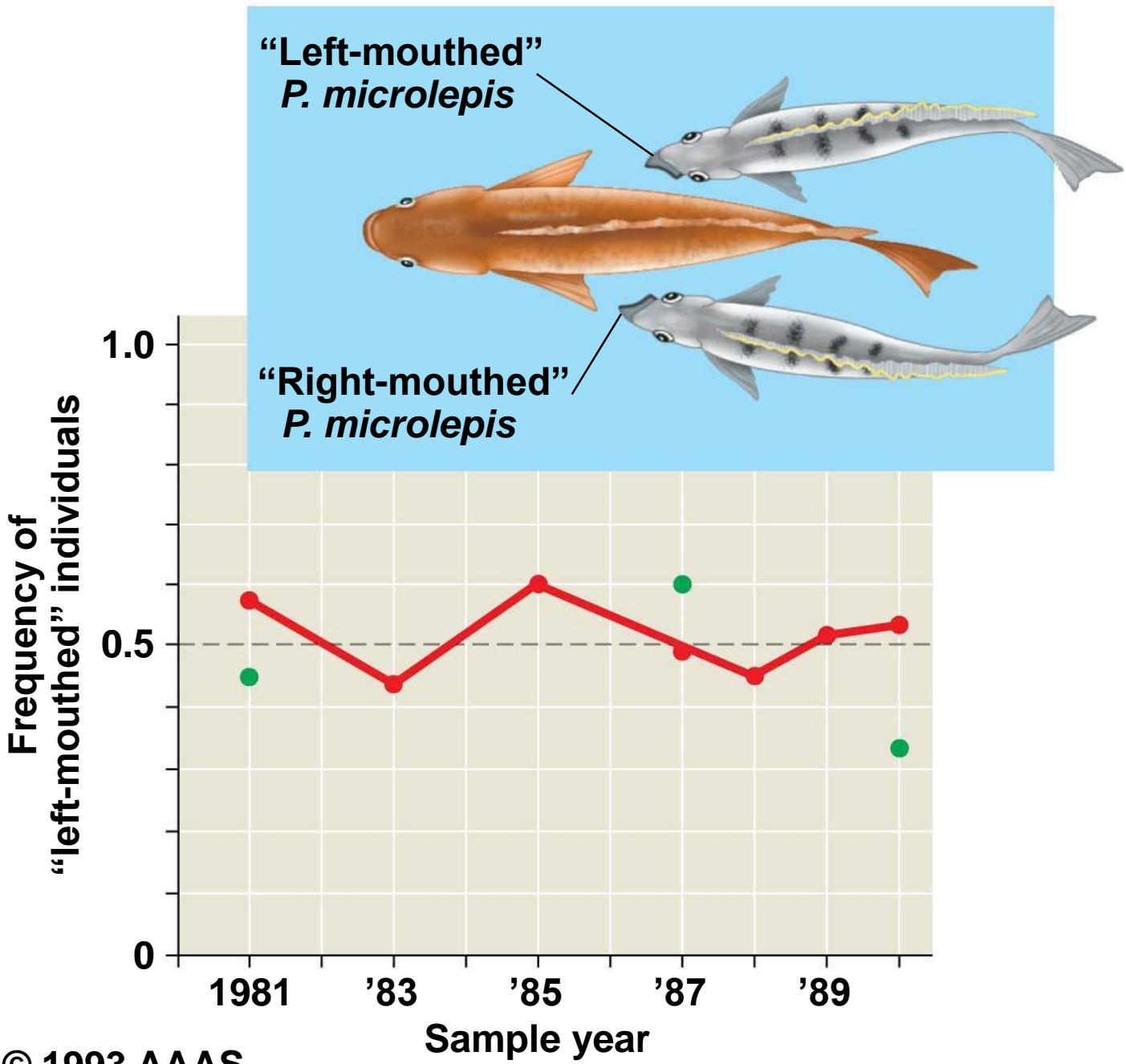


A child with the genetic disorder known as sickle-cell disease

Frequency-Dependent Selection

- **Frequency-dependent selection** occurs when the fitness of a phenotype depends on how common it is in the population
 - For example, when “right-mouthed” individuals become more common in a population of scale-eating fish, prey are more likely to guard their left side, giving an advantage to “left-mouthed” fish
 - When “left-mouthed” fish become more common, the advantage is reversed

Figure 21.16



© 1993 AAAS

- Balancing selection (due to frequency dependence) keeps the frequency of each phenotype close to 50%

Sexual Selection

- **Sexual selection** is natural selection for mating success
- It can result in **sexual dimorphism**, marked differences between the sexes in secondary sexual characteristics

Figure 21.17

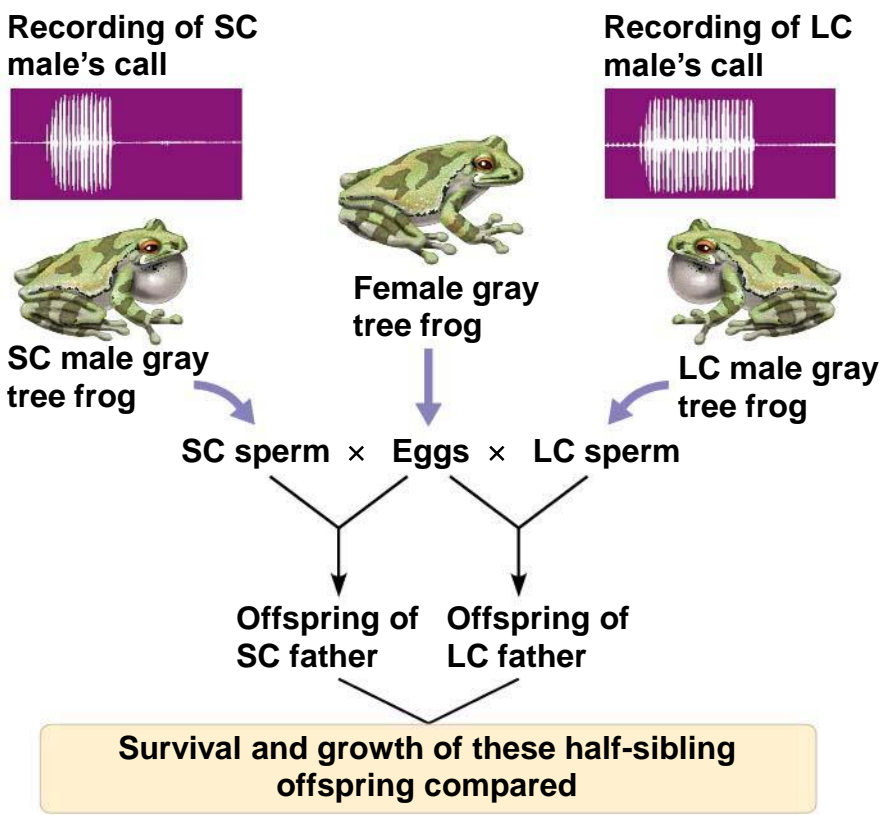


- Intrasexual selection is competition among individuals of one sex (often males) for mates of the opposite sex
- Intersexual selection, often called mate choice, occurs when individuals of one sex (usually females) are choosy in selecting their mates
- Male showiness due to mate choice can increase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

- One hypothesis for the evolution of female mate preference is the “good genes” hypothesis
- It suggests that if a trait is related to male genetic quality or health, both the male trait and female preference for that trait should increase in frequency

Figure 21.18

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)

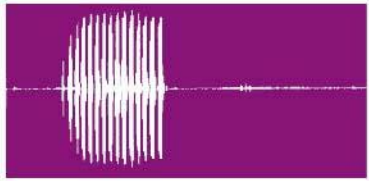
NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

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).

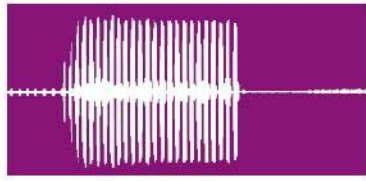
Figure 21.18-1

Experiment

Recording of SC male's call



Recording of LC male's call



SC male gray tree frog



Female gray tree frog



LC male 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.		

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).

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 21.19

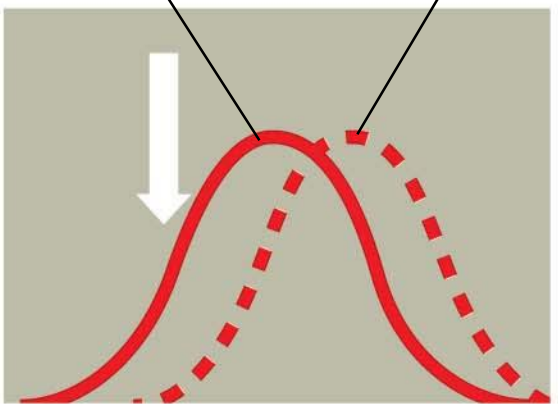


Figure 21.UN03-1

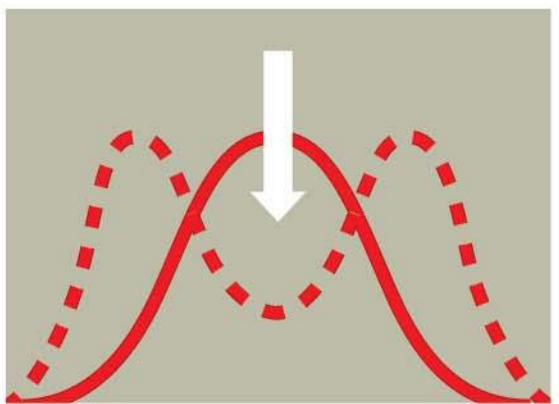
Time (days)	Number of Seedlings			Total
	Green ($C^G C^G$)	Green-yellow ($C^G C^Y$)	Yellow ($C^Y C^Y$)	
7	49	111	56	216
21	47	106	20	173



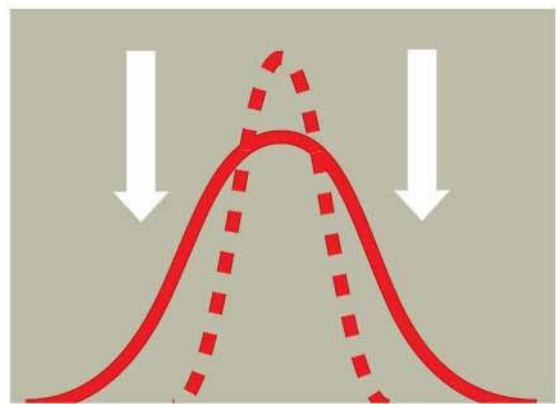
Original population **Evolved population**



Directional selection

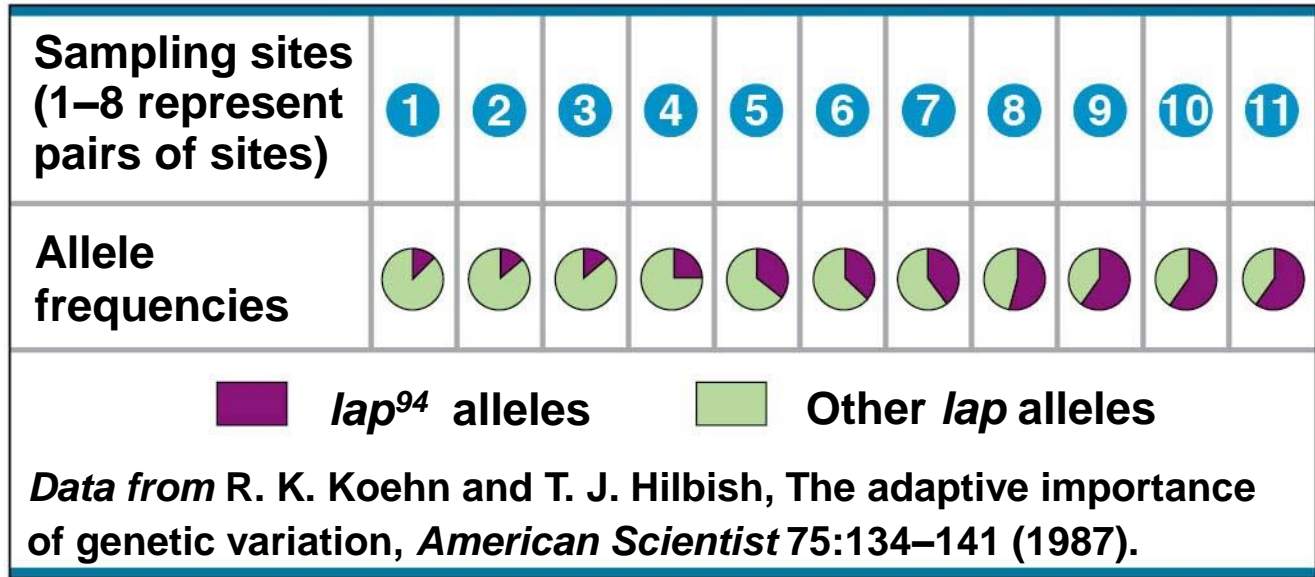


Disruptive selection



Stabilizing selection

Figure 21.UN05



Salinity increases toward the open ocean

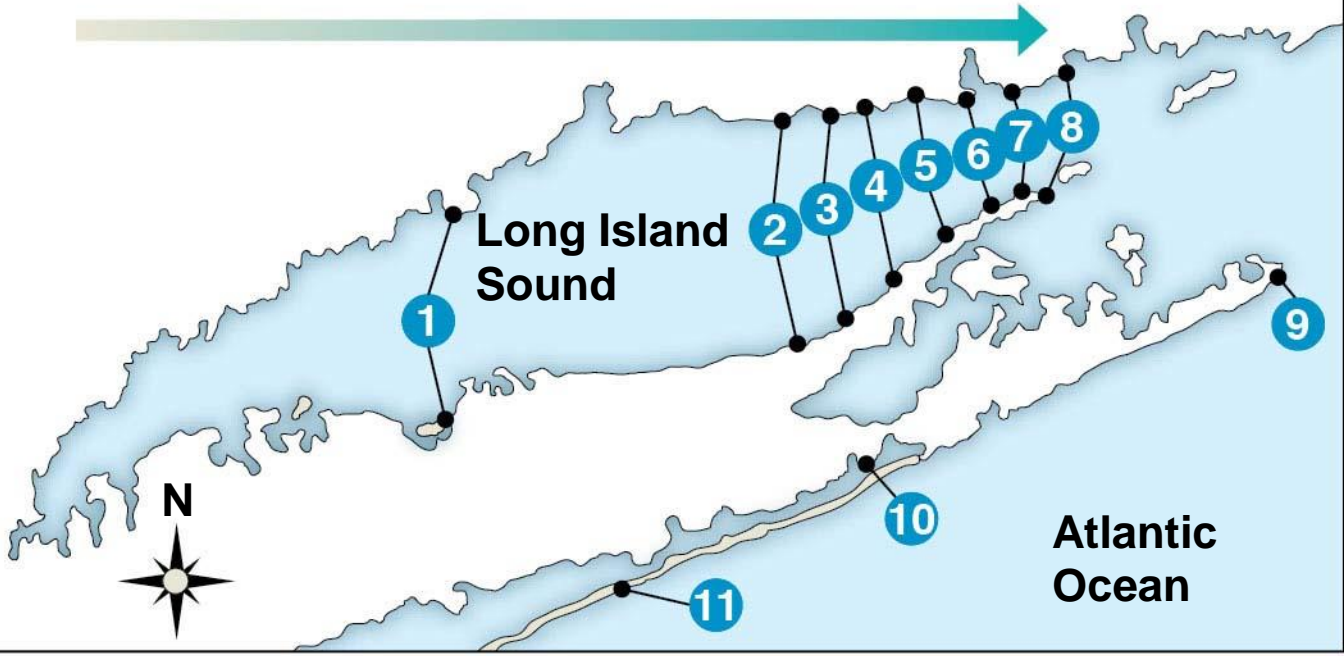


Figure 21.UN06

