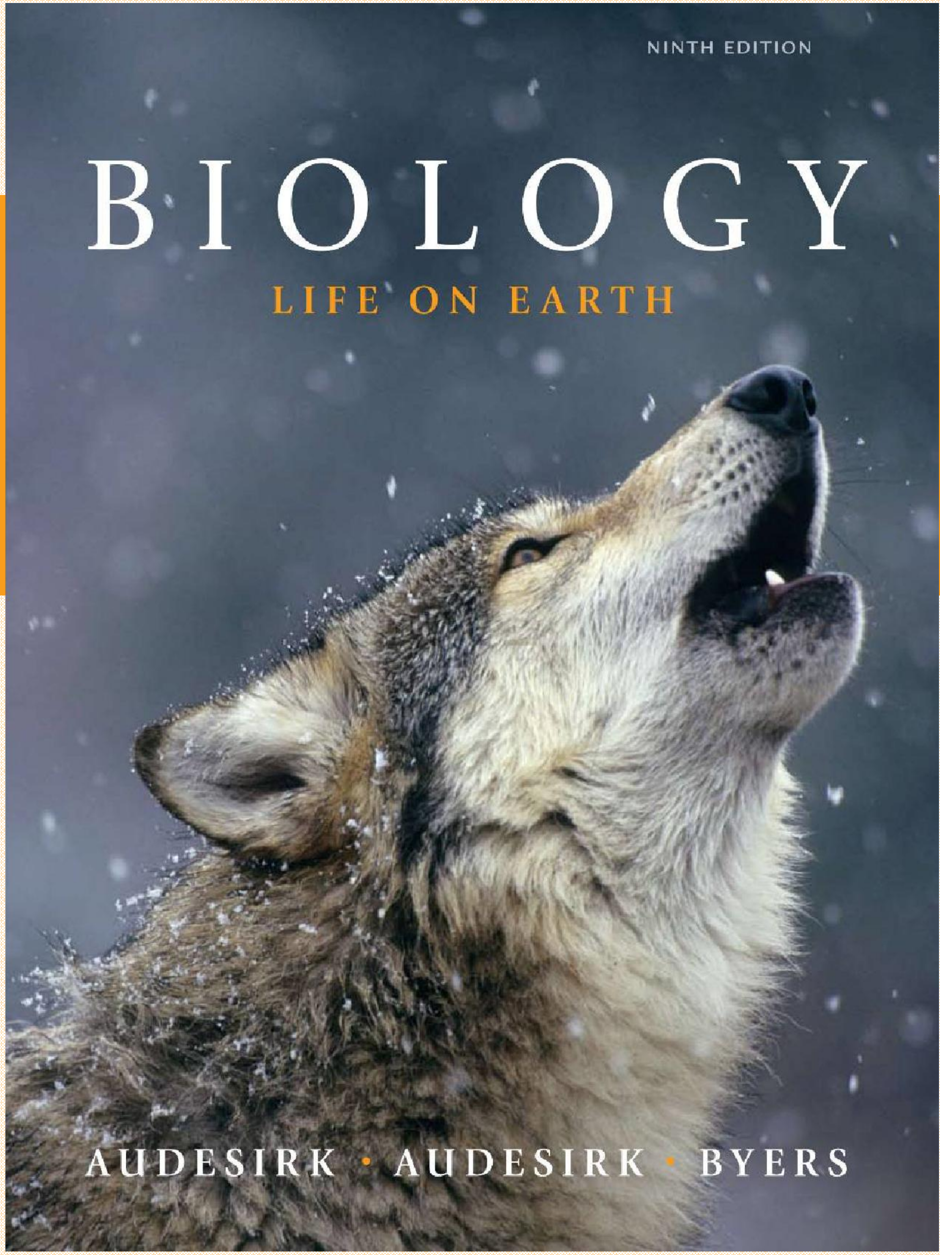

Chapter 15

How Populations Evolve

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Chapter 15 At a Glance

- 15.1 How Are Populations, Genes, and Evolution Related?
- 15.2 What Causes Evolution?
- 15.3 How Does Natural Selection Work?

15.1 How Are Populations, Genes, and Evolution Related?

- Evolutionary changes occur from generation to generation, causing descendants to differ from their ancestors
- Evolution is a property not of individuals, but of populations
  - A **population** is a group that includes all members of a species living in a given area

15.1 How Are Populations, Genes, and Evolution Related?

- **Genes and the environment interact to determine traits**
  - All cells contain DNA
  - A **gene** is a segment of DNA found at a specific place on a chromosome

15.1 How Are Populations, Genes, and Evolution Related?

- **Genes and the environment interact to determine traits (continued)**
  - In diploid(二倍体的) individuals, each gene consists of two *alleles* (等位基因) (the organism's genotype (基因型))
    - Individuals whose alleles are the same are *homozygous*(纯合子) for that gene
    - Individuals whose alleles are different are *heterozygous*(杂合子) for that gene
  - The specific alleles borne on an organism's chromosomes (its genotype) interact with the environment to influence the development of its physical and behavioral traits (its phenotype(表现型))

15.1 How Are Populations, Genes, and Evolution Related?

- **Genes and the environment interact to determine traits (continued)**
  - Coat color in hamsters illustrates the interaction between genotype and phenotype
  - Coat color is determined by two alleles in hamsters
    - The *dominant* (显性的)allele encodes for an enzyme that catalyzes black pigment formation
    - The *recessive* (隐性的)allele encodes for an enzyme that catalyzes brown pigment

15.1 How Are Populations, Genes, and Evolution Related?

- **Genes and the environment interact to determine traits (continued)**
  – Hamsters with at least one dominant allele (homozygous(纯合子的) dominant or heterozygous(杂合子的)) produce black pigment
  – Hamsters with two recessive alleles (homozygous recessive) produce brown pigment

Alleles, Genotype, and Phenotype in Individuals

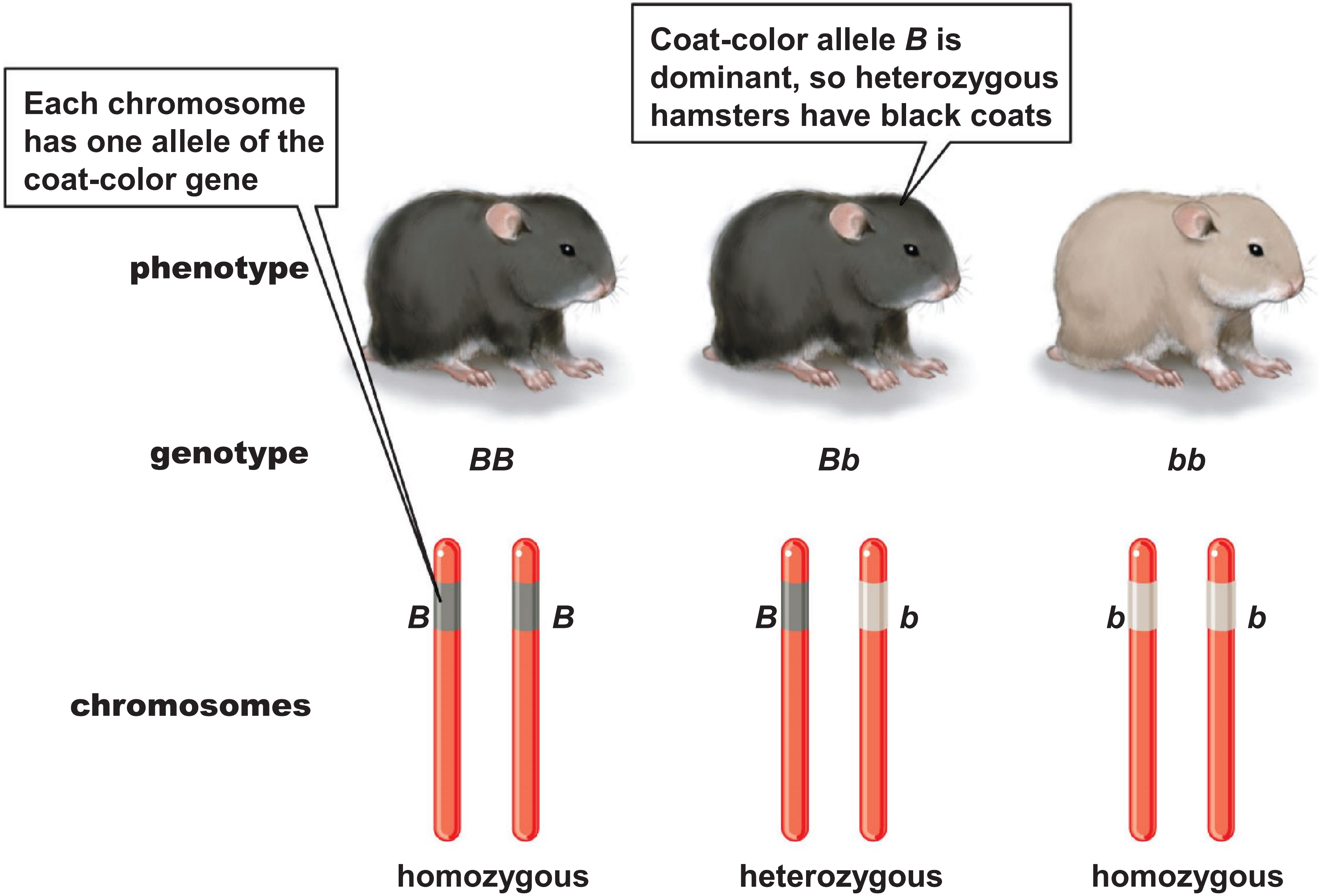


Fig. 15-1

15.1 How Are Populations, Genes, and Evolution Related?

- **The gene pool is the sum of the genes in a population**
  - Population genetics deals with the frequency, distribution, and inheritance of alleles in populations
  - A **gene pool** (基因库)consists of all the alleles of all the genes in all individuals of a population
  - For a given gene, the proportion of times a certain allele occurs in a population relative to the occurrence of all the alleles for that gene is called its **allele frequency(等位基因频率)**

15.1 How Are Populations, Genes, and Evolution Related?

- **The gene pool is the sum of the genes in a population (continued)**
  - Again, coat color in hamsters can be used to illustrate the idea of allele frequency
    - A population of 25 hamsters contains 50 alleles of the coat color gene (hamsters are diploid)
    - If 20 of those 50 alleles code for black coats, then the frequency of the black allele is 0.40, or 40% (20/50 = 0.40)

A Gene Pool

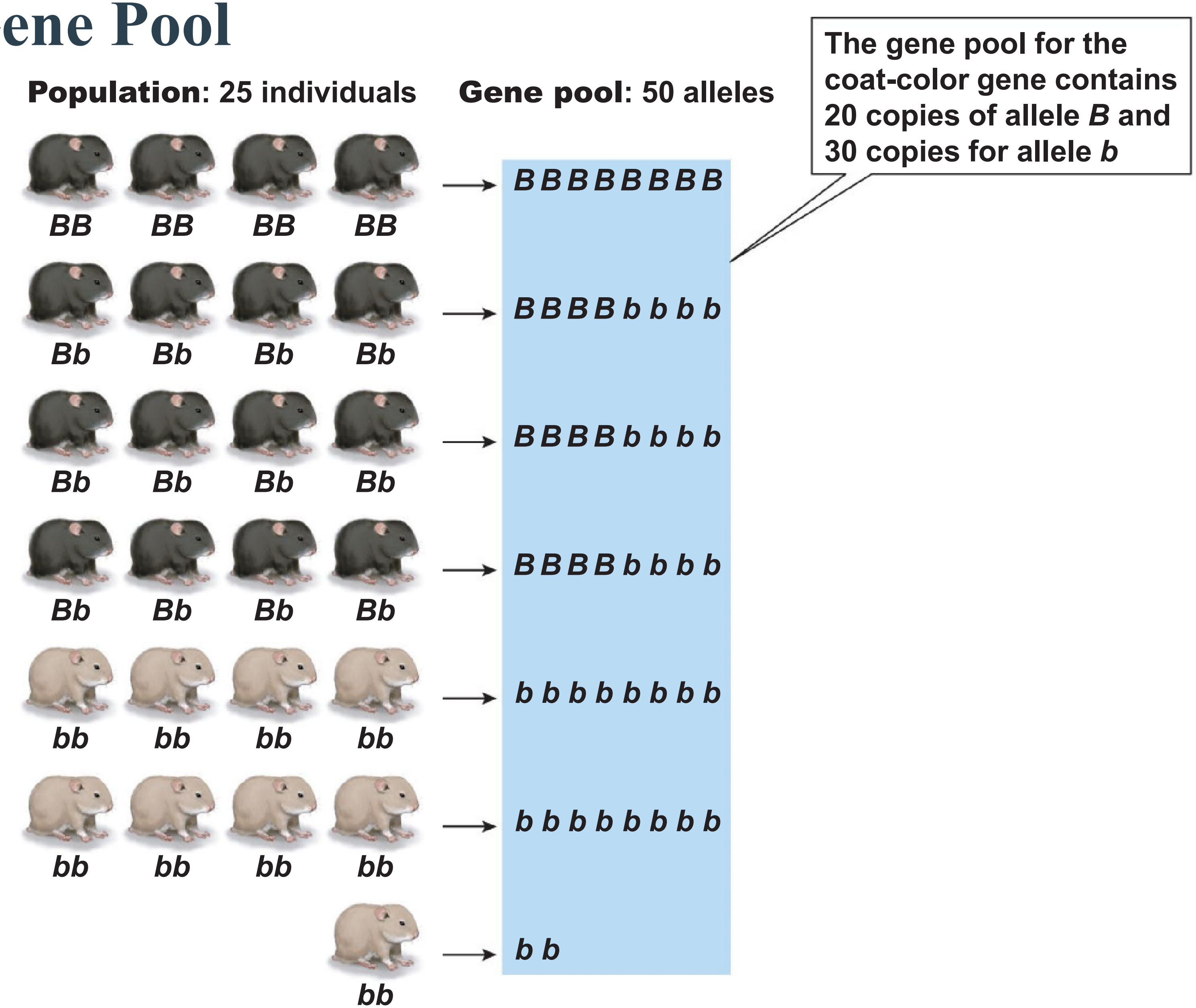


Fig. 15-2

15.1 How Are Populations, Genes, and Evolution Related?

- **Evolution is the change of allele frequencies within a population**
  - A casual observer might define evolution on the basis of changes in the outward appearance or behaviors of the members of a population
  - A population geneticist, however, defines evolution as the changes in allele frequencies that occur in a gene pool over time

15.1 How Are Populations, Genes, and Evolution Related?

- **The equilibrium population is a hypothetical population in which evolution does not occur**
  - The **Hardy-Weinberg principle** is a mathematical model proposed independently in 1908 by an English mathematician, Godfrey H. Hardy, and a German physician, Wilhelm Weinberg

15.1 How Are Populations, Genes, and Evolution Related?

- **The equilibrium population is a hypothetical population in which evolution does not occur (continued)**
  - The Hardy-Weinberg principle demonstrates that, under certain conditions, the frequencies of alleles and genotypes in a sexually reproducing population remain constant from one generation to the next
  - An **equilibrium population** is an idealized population in which allele frequencies do not change from generation to generation

15.1 How Are Populations, Genes, and Evolution Related?

- **The equilibrium population is a hypothetical population in which evolution does not occur (continued)**
  - An equilibrium can be maintained so long as five conditions are satisfied
    1. No mutations(突变) must occur in the population
    2. There must be no gene flow(基因流) between populations
    3. The population must be very large
    4. Mating must be completely random
    5. There can be no natural selection

15.1 How Are Populations, Genes, and Evolution Related?

- **The equilibrium population is a hypothetical population in which evolution does not occur (continued)**
  – Violation of one or more of these five conditions may allow changes in allele frequencies, and the population will evolve

15.2 What Causes Evolution?

- **From the conditions that disturb a Hardy-Weinberg equilibrium, we might predict five major causes of evolutionary change**
  – Mutation
  – Gene flow
  – Small population size
  – Non-random mating
  – Natural selection

15.2 What Causes Evolution?

- **Mutations are the original source of genetic variability**
  - Mutations are rare changes in the base sequence of DNA in a gene
    - They usually have little or no immediate effect and can be passed to offspring only if they occur in cells that give rise to gametes
    - They are the source of new alleles and can be beneficial, harmful, or neutral
    - Mutations arise spontaneously, not as a result of or in anticipation of, environmental necessity

Mutations Occur Spontaneously

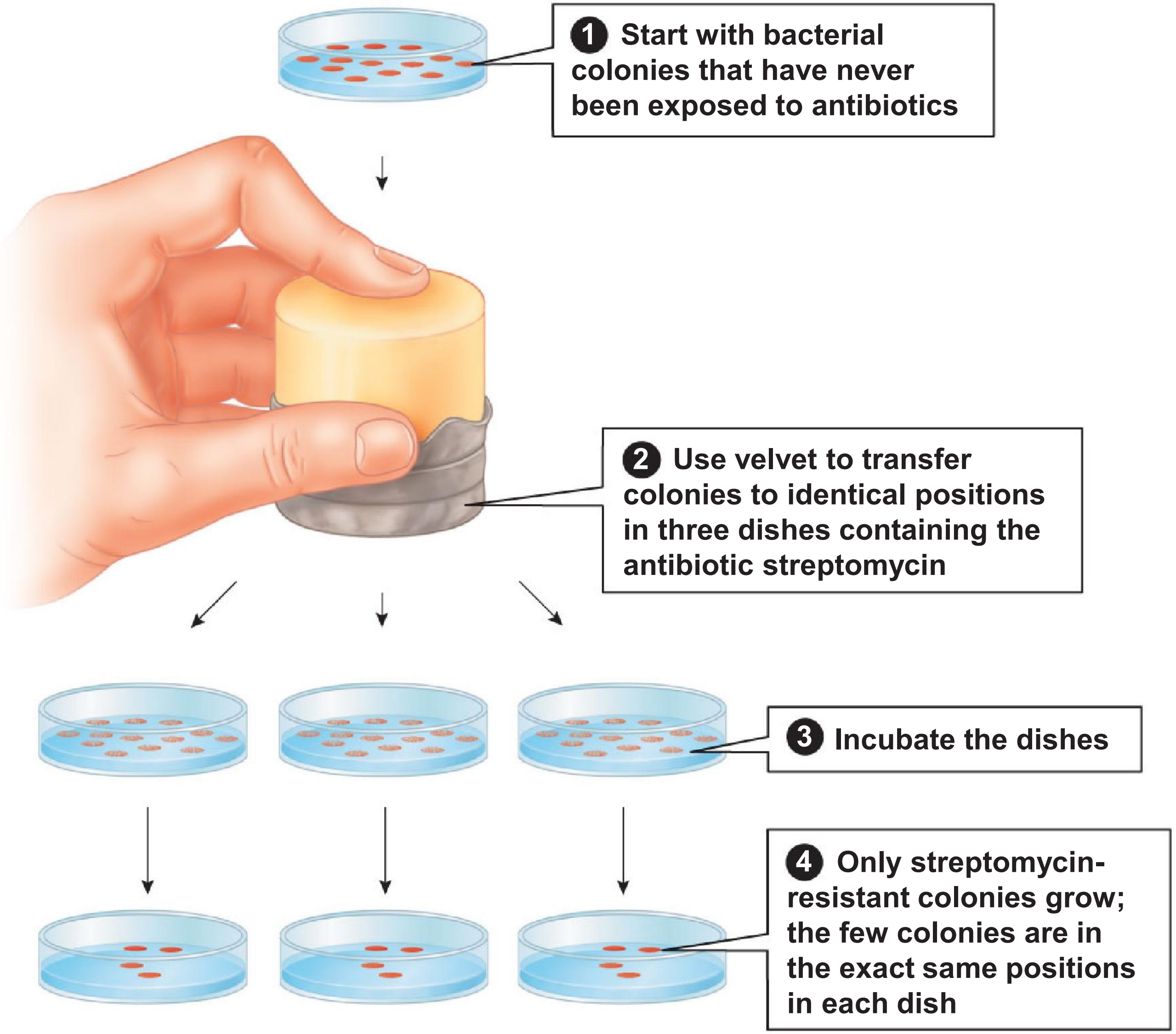


Fig. 15-3

15.2 What Causes Evolution?

- **Gene flow between populations changes allele frequencies**
  - Gene flow is the movement of alleles from one population to another
    - Movement of individuals between populations is a common cause of gene flow
    - However, alleles can move between populations even if organisms do not
    - Pollen (sperm) and seeds from flowering plants can move and distribute alleles

Pollen Can Be an Agent of Gene Flow

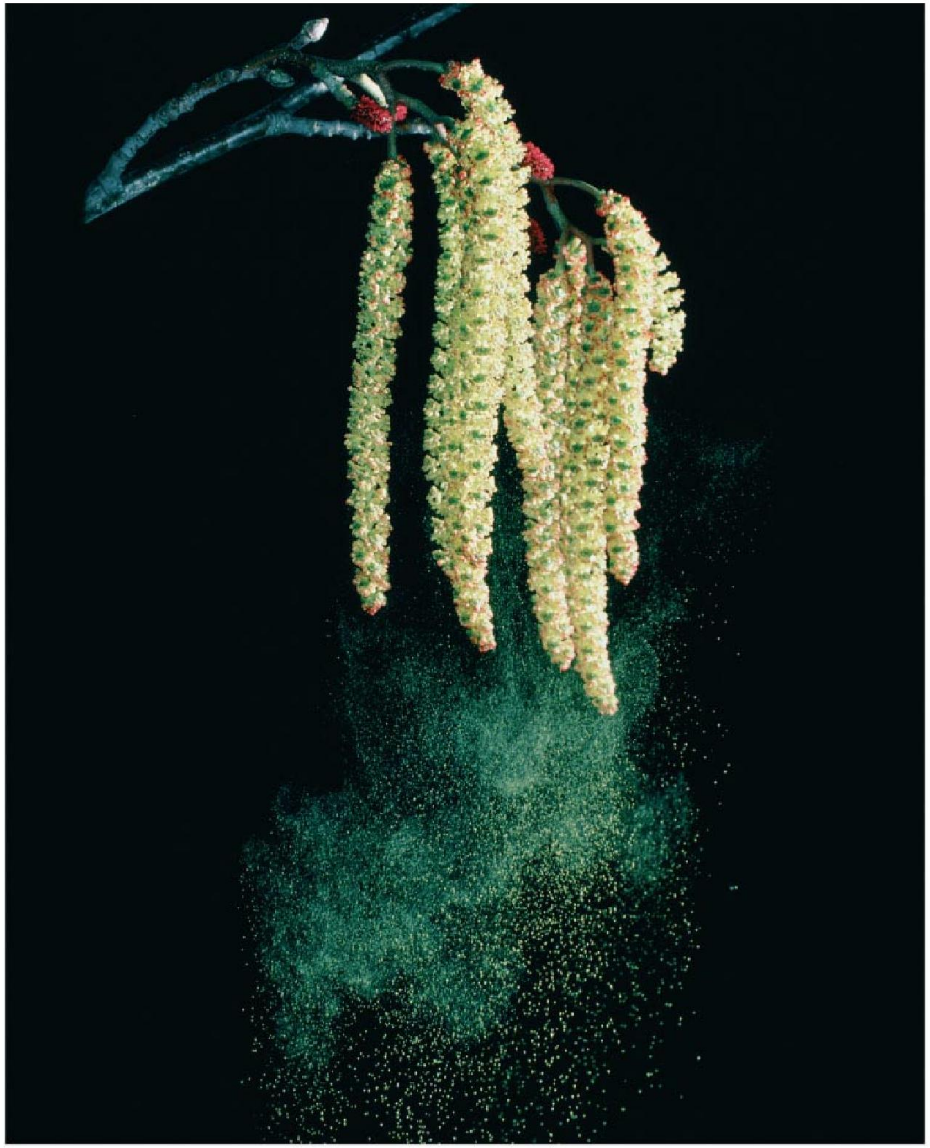


Fig. 15-4

15.2 What Causes Evolution?

- **Gene flow between populations changes allele frequencies (continued)**
  - The evolutionary effect of gene flow is to increase the genetic similarity of different populations of a species
  - Mixing alleles prevents the development of large differences in genetic compositions of populations
  - If gene flow between populations of a species is blocked, the resulting genetic differences may grow so large that one of the populations becomes a new species

15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations**
  - **Genetic drift** (遗传漂变)is the random change in allele frequencies over time brought about by chance alone
    - Genetic drift has little effect in very large populations, where chance is less likely to reduce significantly the proportion of individuals passing alleles on to the next generation
    - Genetic drift occurs more rapidly and has a bigger effect on small populations, where chance may dictate that the alleles of only a few individuals are passed on

Genetic Drift

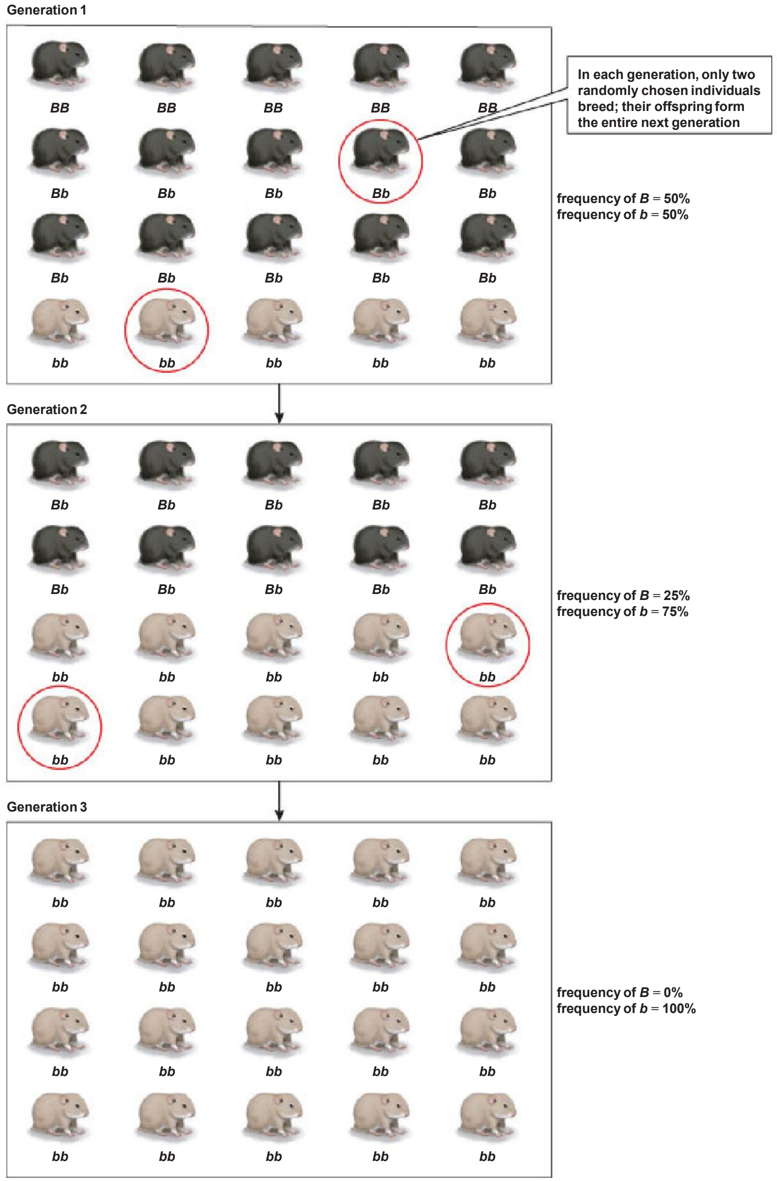


Fig. 15-5

15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations (continued)**
  - In very small populations, drift can result in the complete loss of an allele in only a few generations, even if it is the more frequent one

The Effect of Population Size on Genetic Drift

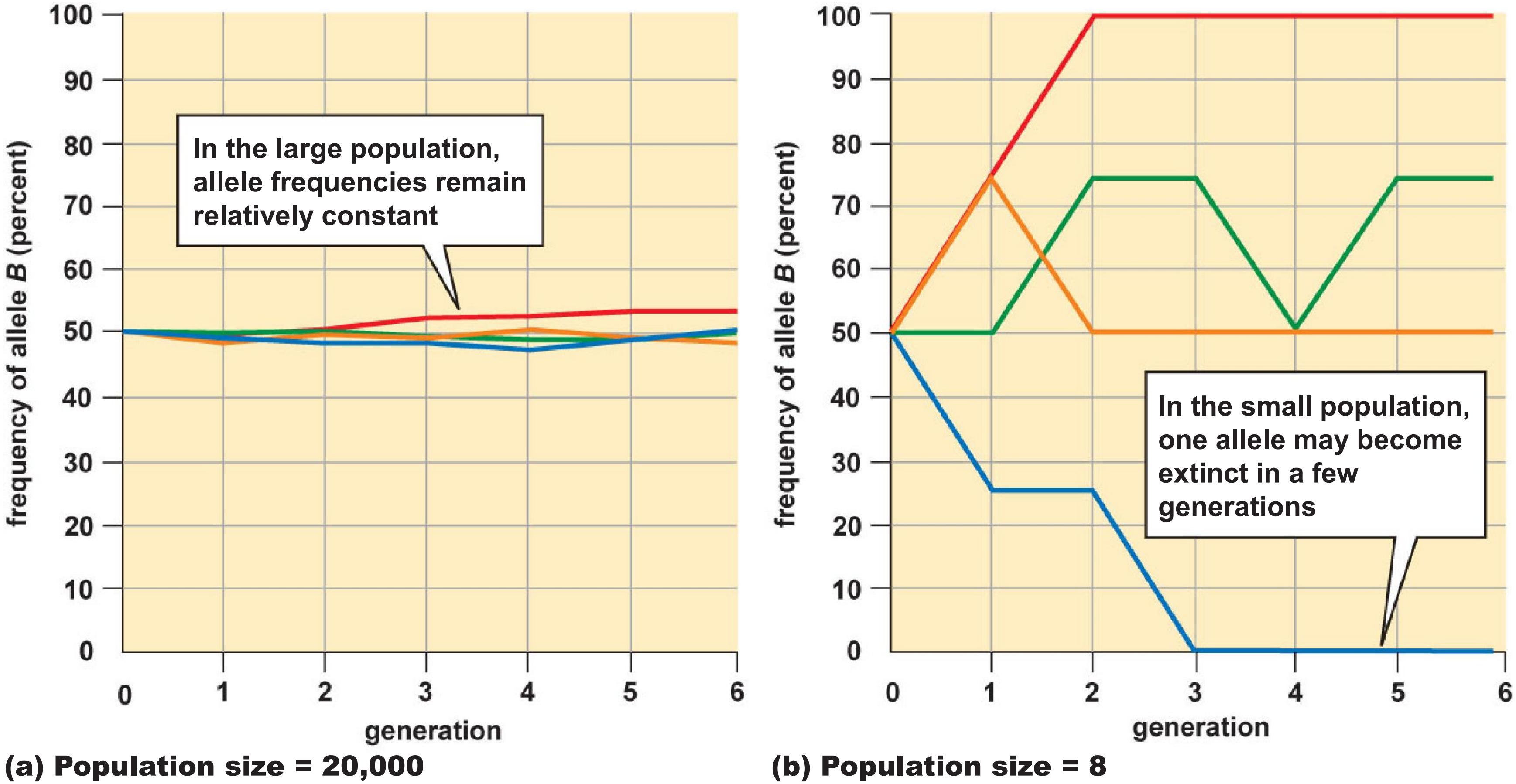


Fig. 15-6

15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations (continued)**
  - There are two causes of genetic drift
    - Population bottleneck (瓶颈)
    - Founder effect (奠基者效应)

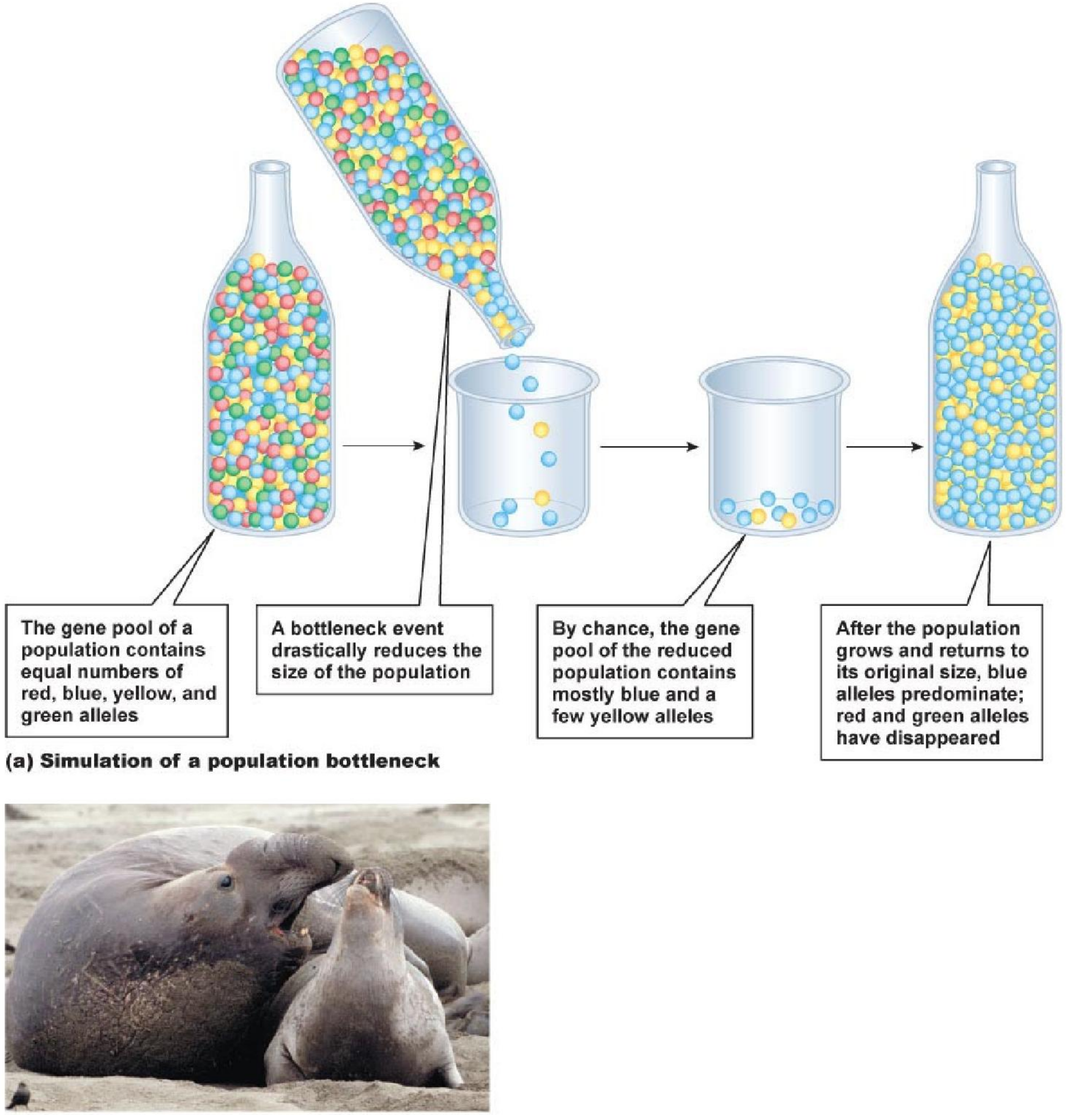
15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations (continued)**
  - A **population bottleneck** is a drastic reduction in population size brought about by a natural catastrophe or overhunting
  - A population bottleneck can rapidly change allele frequencies and reduce genetic variation

15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations (continued)**
  - A bottleneck has been documented in the northern elephant seal
    - Hunted almost to extinction in the 1800s, the elephant seals had been reduced to only 20 individuals by the 1890s
    - A hunting ban allowed the population to increase to 30,000
    - Biochemical analysis shows that present-day northern elephant seals are almost genetically identical
    - Despite their numbers, their lack of genetic variation leaves them little flexibility to evolve if their environmental circumstances change

Population Bottlenecks Reduce Variation



(b) Elephant seals

Fig. 15-7

15.2 What Causes Evolution?

- **Allele frequencies may drift in small populations (continued)**
  - The **founder effect** occurs when a small number of individuals leave a large population and establish a new isolated population
  - By chance, the allele frequencies of founders may differ from those of the original population
  - Over time, the new population may exhibit allele frequencies that differ from the original population

A Human Example of the Founder Effect

(a) A child with Ellis–van Creveld syndrome

(b) A six-fingered hand

Fig. 15-8

15.2 What Causes Evolution?

- **Mating within a population is almost never random**
  – Nonrandom mating will not change the overall frequency of alleles in a population
  – Nonrandom mating, however, will change the distribution of genotypes and, therefore, of phenotypes in a population

15.2 What Causes Evolution?

- **Mating within a population is almost never random (continued)**
  - Organisms within a population rarely mate randomly
    - Many organisms have limited mobility and tend to remain near their place of birth, hatching, or germination, thus increasing the likelihood of inbreeding
    - In animals, nonrandom mating can also arise if individuals have preferences or biases that influence their choice of mates, as is the case for snow geese, which favor mates of the same color
    - A preference for mates that are similar is known as assortative mating
  - Nonrandom mating may lead to inbreeding, increasing the chance of producing homozygous offspring with two copies of harmful alleles

Nonrandom Mating Among Snow Geese

Fig. 15-9

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial**
  - Natural selection favors certain alleles at the expense of others
    - Those individuals with the selective advantage have higher reproductive success, so their alleles are passed on to the next generation
  - The evolution of penicillin-resistant bacteria illustrates the relationship between natural selection and evolution

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial (continued)**
  - The first widespread use of penicillin occurred during World War II
  - Penicillin killed almost all infection-causing bacteria
  - Penicillin did not affect bacteria possessing a rare allele that destroyed penicillin on contact
  - Bacteria carrying the rare allele survived and reproduced

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial (continued)**
  - Natural selection does not cause genetic changes in individuals
    - Penicillin did not cause the allele for resistance to appear
    - The allele for penicillin resistance arose spontaneously (before exposure to penicillin)
    - The presence of penicillin caused bacteria possessing the rare allele to be favored (have greater reproductive success) over bacteria lacking the allele

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial (continued)**
  - Natural selection acts on individuals, yet changes populations
    - Penicillin (the agent of natural selection) acted on individual bacteria
    - The bacterial population evolved as its allele frequencies changed

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial (continued)**
  - Evolution is the change in allele frequencies of a population, owing to unequal reproductive success among organisms bearing different alleles
    - Penicillin-resistant bacteria had greater **fitness(适合度)** (reproductive success) than nonresistant bacteria because the resistant bacteria produced greater numbers of viable offspring

15.2 What Causes Evolution?

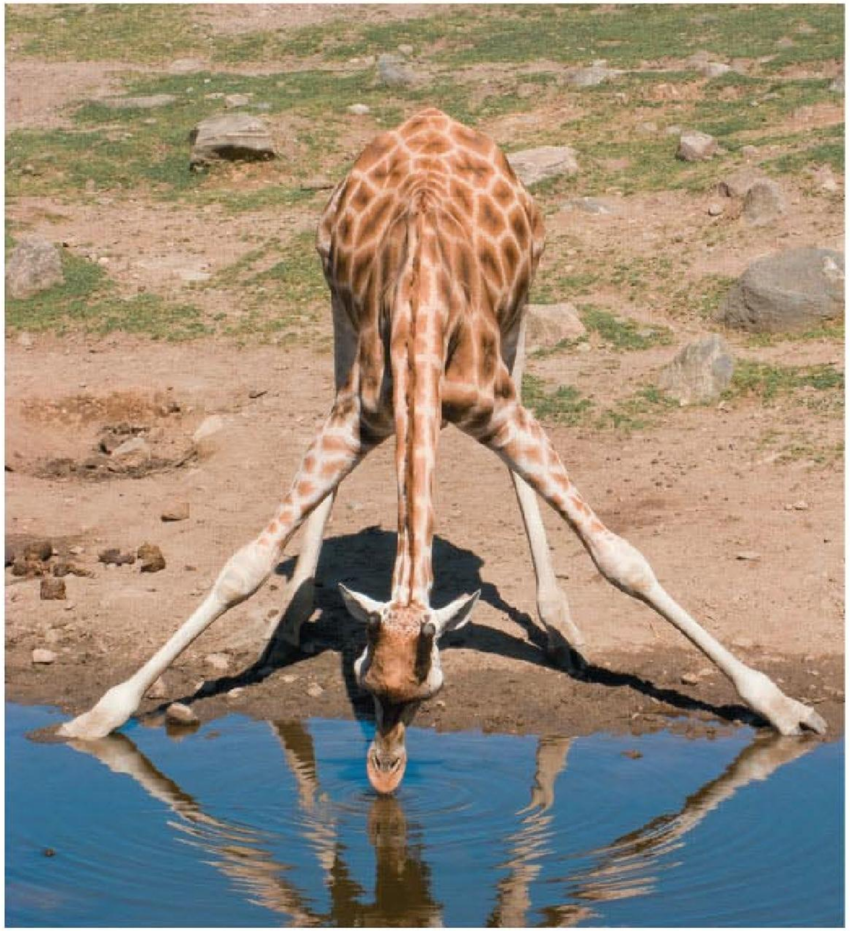
- **All genotypes are not equally beneficial (continued)**
  - Evolutionary changes are not "good" or "progressive" in any absolute sense
    - Penicillin-resistant bacteria were favored only because of the presence of penicillin
    - In an environment free of penicillin, the allele for resistance confers no selective advantage and the bacteria containing it may be less fit, depending on what other agents of selection are present

15.2 What Causes Evolution?

- **All genotypes are not equally beneficial (continued)**
  - Evolution is a compromise between opposing pressures
    - The long neck of male giraffes was favored only because it confers a distinct advantage in combat to establish dominance
    - The long neck of a giraffe is a compromise between the advantage of being able to win contests with other males and a disadvantage of vulnerability while drinking water

A Compromise Between Opposing Environmental Pressures

(a) A contest for dominance



(b) Drinking at a water hole

Fig. 15-10

Table 15-1 Causes of Evolution

Process	Consequence
Mutation	Creates new alleles; increases variability
Gene flow	Increases similarity of different populations
Genetic drift	Causes random change of allele frequencies; can eliminate alleles
Nonrandom mating	Changes genotype frequencies but not allele frequencies
Natural and sexual selection	Increases frequency of favored alleles; produces adaptations

Table 15-1

15.3 How Does Natural Selection Work?

- **Natural selection stems from unequal reproduction**
  - **Natural selection** (自然选择)is often associated with the phrase "survival of the fittest"
  - The fittest individuals are those that not only survive, but are able to leave the most offspring behind
    - Ultimately, it is reproductive success that determines the future of an individual's alleles

15.3 How Does Natural Selection Work?

- **Natural selection acts on phenotypes**
  - Natural selection does not act directly on the genotypes of individual organisms
  - Instead, natural selection acts on phenotypes, the structures and behaviors displayed by the members of a population
  - Natural selection acts on the genotype only indirectly, but crucially, through the phenotype by determining which organisms survive to pass their alleles on

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others**
  - Successful phenotypes are those that have the best adaptations to their particular environment
  - **Adaptations(适应)** are characteristics that help an individual survive and reproduce

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - Adaptations arise from the interactions of organisms with both the nonliving and the living parts of their environment
    - Nonliving (abiotic) environmental components include such things as climate, the availability of water, and the concentration of minerals in the soil
    - Living (biotic) environmental components consist of other organisms

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - Interactions with other organisms include competition, coevolution (协同进化), and sexual selection

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - **Competition(竞争)** is an interaction among individuals who attempt to utilize a limited resource
    - The competition may be among individuals of the same species or of different species
    - It is most intense among members of the same species because they all require the same things

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - When two species interact extensively, each exerts strong selective pressures on the other
  - When one evolves a new feature or modifies an old one, the other typically evolves new adaptations in response
  - This constant, mutual feedback between two species is called **coevolution**
    - Predator-prey relationships generate strong coevolutionary forces

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - **Predation(捕食行为)** is an interaction in which one organism (the predator(捕食者)) kills and eats another organism (the prey(被食者))
  - Coevolution between predators and prey is akin to a "biological arms race"
    - Wolf predation selects against slow, careless deer
    - Alert swift deer select against slow, clumsy wolves

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - **Sexual selection(性选择)** is a type of selection that favors traits that help an organism acquire a mate
  - Examples of traits that help males acquire mates include the following
    - Conspicuous features (bright colors, long feathers or fins, elaborate antlers)
    - Bizarre courtship behaviors
    - Loud, complex courting songs

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - Darwin recognized that sexual selection could be driven either (1) by sexual contests among males or (2) by female preference for particular male phenotypes
    - Male–male competition for access to females can favor the evolution of features that provide an advantage in fights or ritual displays of aggression

15.3 How Does Natural Selection Work?

- **Some phenotypes reproduce more successfully than others (continued)**
  - Where females actively choose their mates, males often develop elaborate ornamentation and displays that often leave them more vulnerable to predation
  - Even though they expose a male to predation, elaborate displays may signal to females that the male is especially worthy of mating because he is healthy and vigorous enough to overcome the selective disadvantages of his conspicuous appearance

Competition Between Males Favors the Evolution, Through Sexual Selection, of Structures for Ritual Combat

Fig. 15-11

The Peacock's Showy Tail Has Evolved Through Sexual Selection

Fig. 15-12

15.3 How Does Natural Selection Work?

- **Natural selection and sexual selection can lead to various patterns of evolutionary change in three ways**
  - Directional selection(方向性选择)
  - Stabilizing selection (稳定化选择)
  - Disruptive selection (分化选择)

15.3 How Does Natural Selection Work?

- **Directional selection favors individuals with an extreme-value trait and selects against both average individuals and individuals at the opposite extreme**
  - If environmental conditions change in a consistent way, a species may respond by evolving in a consistent direction
    - For example, if the climate becomes colder, mammal species may evolve thicker fur

15.3 How Does Natural Selection Work?

- **Stabilizing selection favors individuals with the average value of a trait, such as intermediate body size, and selects against individuals with extreme values**
  - Stabilizing selection commonly occurs when a trait is under opposing environmental pressures from two different sources
  - For example, *Aristelliger* lizards of intermediate body size are favored over the extremes
    - The smallest lizards have difficulty defending territory
    - The largest lizards are more likely to be eaten by owls

15.3 How Does Natural Selection Work?

- **Disruptive selection favors individuals at both extremes of a trait, and individuals with intermediate values are selected against**
  - The population divides into two phenotypic groups over time
  - Disruptive selection adapts individuals within a population to different habitats

Three Ways That Selection Affects a Population Over Time

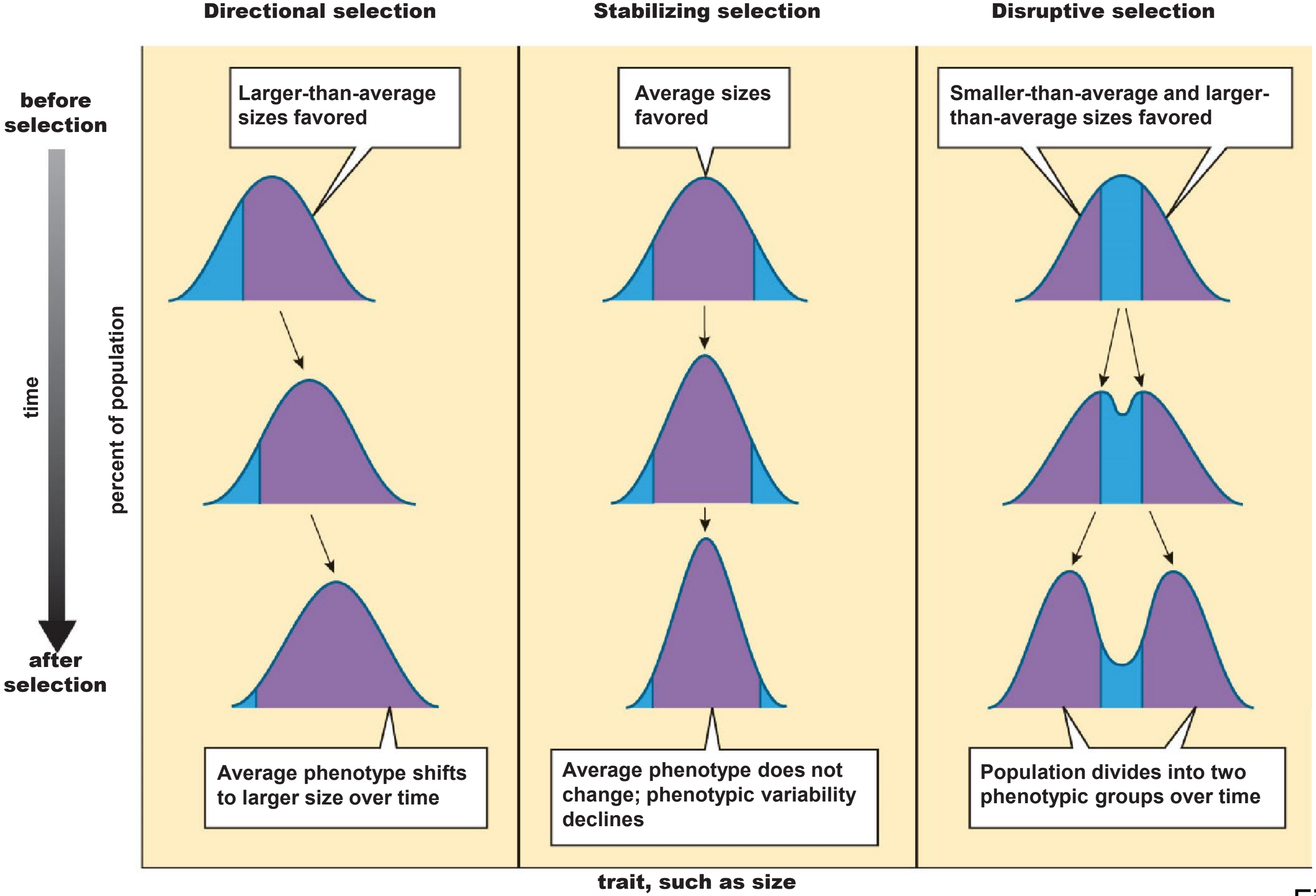


Fig. 15-13

15.3 How Does Natural Selection Work?

- **Beak size in black-bellied seedcrackers is subject to disruptive selection**
  – Birds with large, stout beaks are able to crack the hard seeds found in their habitat
  – Birds with small, pointy beaks are better adapted to process the soft seeds of the habitat
  – Birds with intermediate-size beaks have a lower survival rate than individuals with either large or small beaks

Black-bellied Seedcrackers

Fig. 15-14

15.3 How Does Natural Selection Work?

- **Black-bellied seedcrackers represent an example of balanced polymorphism, in which two or more phenotypes are maintained in a population**
  - Each phenotype is favored by a separate environmental factor

15.3 How Does Natural Selection Work?

- **Balanced polymorphism(多态性) often occurs when environmental conditions favor heterozygotes**
  - For example, normal and sickle-cell hemoglobin alleles coexist in malaria-prone regions of Africa
  - Homozygotes for the sickle-cell allele suffer from severe anemia caused by clumping of the defective hemoglobin in their red blood cells and often die

15.3 How Does Natural Selection Work?

- **Balanced polymorphism often occurs when environmental conditions favor heterozygotes (continued)**
  – Ironically, the sickling of the red blood cells confers increased resistance to malaria, a deadly disease affecting red blood cells that is widespread in equatorial Africa
  – Heterozygotes have one allele for defective hemoglobin, which gives them increased resistance to malaria, and one allele for normal hemoglobin, which moderates their anemia, giving them a selective advantage over either type of homozygote