6

Evolution and Ecology

- *Case Study:* Trophy Hunting and Inadvertent Evolution
- What Is Evolution?
- Mechanisms of Evolution
- Adaptive Evolution
- The Evolutionary History of Life

- Joint Effects of Ecology and Evolution
- *Case Study Revisited*
- *Connections in Nature*: The Human Impact on Evolution

Case Study: Trophy Hunting and Inadvertent Evolution

Bighorn sheep populations have been reduced by 90% as a result of hunting, habitat loss, and introduction of domestic cattle.

Hunting is now restricted in North America; permits to take a large "trophy ram" cost over $100,000.

Figure 6.1 Fighting over the Right to Mate

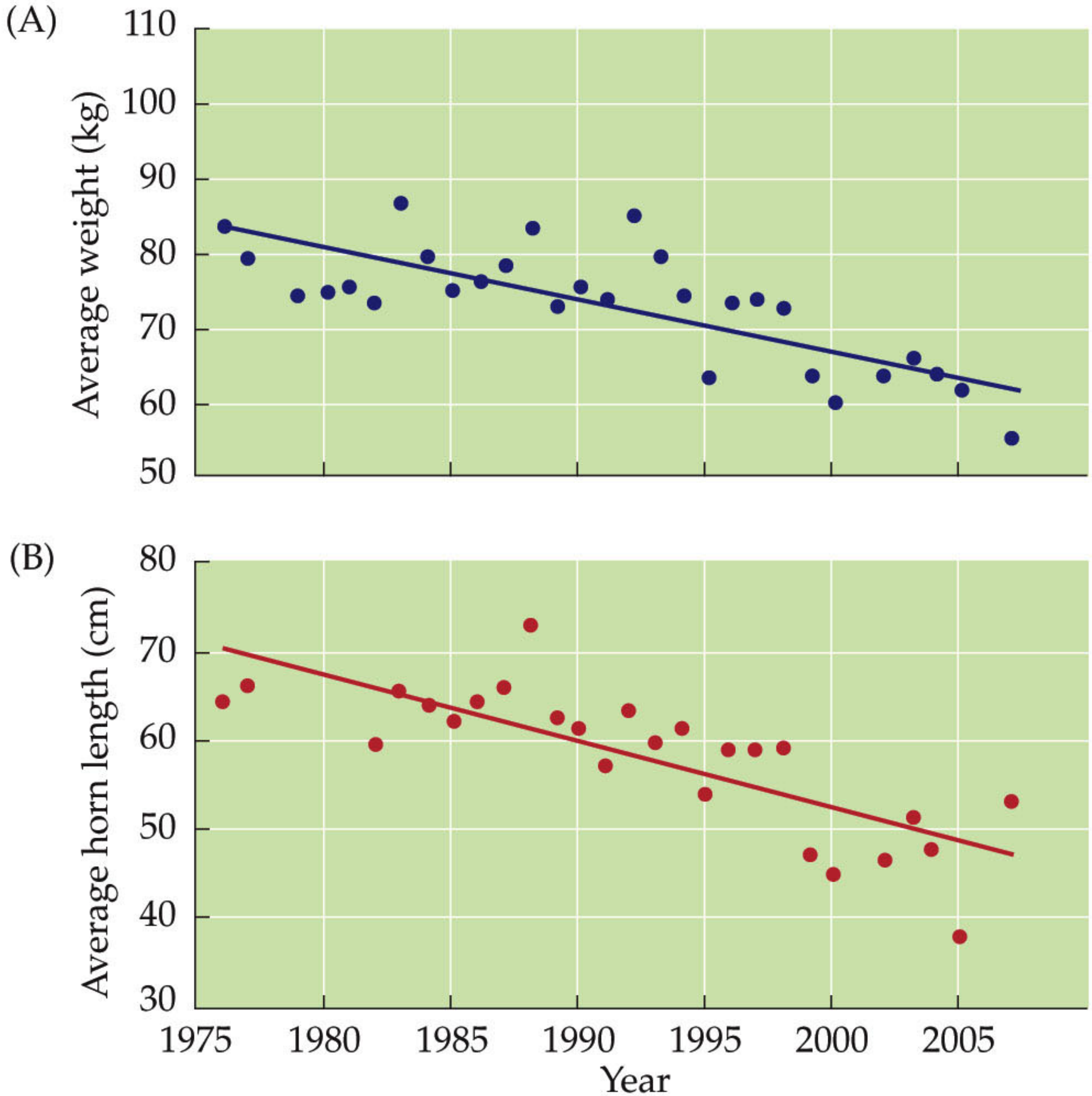
Case Study: Trophy Hunting and Inadvertent Evolution

Trophy hunting has negative impacts on bighorn sheep populations.

It removes the largest and strongest males—the very males that would sire large numbers of healthy offspring.

Coltman et al. (2003) found that over a 30-year period, when about 10% of the males were removed by hunting each year, the average size of males and the average size of their horns decreased.

Figure 6.2 Trophy Hunting Decreases Ram Body and Horn Size



ECOLOGY, Figure 6.2

This is also being observed in other species.

- African elephants are poached for ivory; the proportion of the population that have tusks is decreasing.
- By targeting older, larger fish, commercial fishing for cod has led to a reduction in the age and size at which these fish mature.

Case Study: Trophy Hunting and Inadvertent Evolution

- In rock shrimp, all individuals are born male, and become females when they are large enough to carry eggs.

Commercial harvesting takes the largest individuals—all females for this species.

The genes for switching sex at a smaller size spread in the population, resulting in more females, but small females lay fewer eggs.

Introduction

We know that humans have a large impact on the environment—pollution, land use change, climate change, etc.

We are just beginning to realize that we also cause evolutionary change, and the consequences of this.

Ecology and evolution are strongly connected.

Concept 6.1: Evolution can be viewed as genetic change over time or as a process of descent with modification.

Biological evolution is change in organisms over time.

It includes small fluctuations that occur continually within populations, and also the larger changes that occur as species gradually become increasingly different from their ancestors.

What Is Evolution?

Horn size in bighorn sheep is a heritable trait. Because trophy hunting selectively eliminates rams with large horns, it favors rams with genes for small horns.

It seems likely that trophy hunting is causing the genetic characteristics of the bighorn sheep population to change, or evolve, over time.

- Genes are composed of DNA. They specify (encode) proteins.
- Genes can have two or more forms called **alleles**.
- The **genotype** is the genetic makeup, and is represented by letters, one for each allele.
- Example: for two alleles, *A* and *a*; individuals could be *AA*, *Aa*, or *aa*.

Evolution is change in allele *frequency* (proportion) over time.

Example: In a population of 1,000, 360 are *AA*, 480 are *Aa*, 160 are *aa*.

Frequency of *a* is 0.4 or 40%; frequency of *A* is 0.6 or 60%.

If the frequency of *a* changed to 71%, the population would have evolved at that gene.

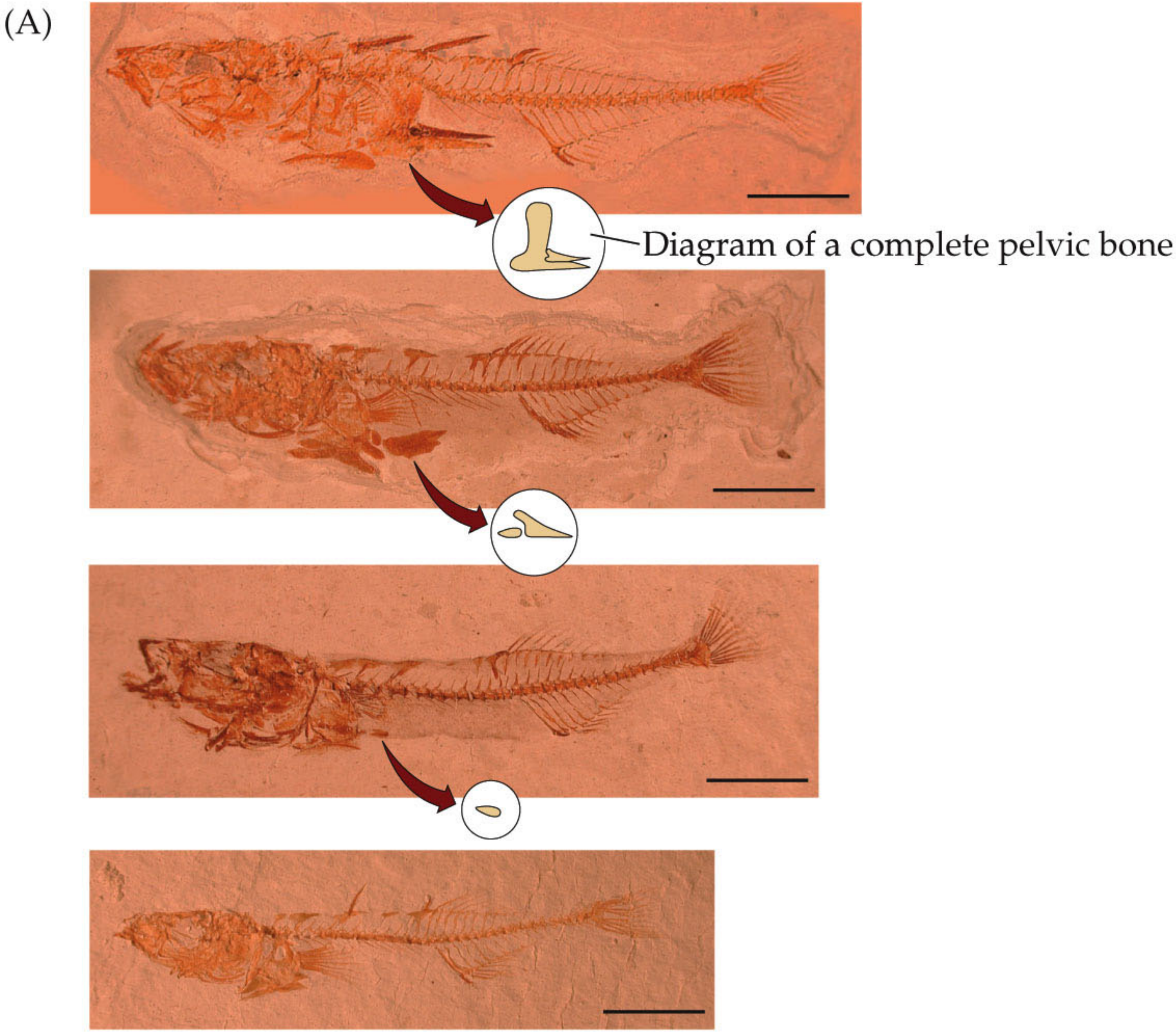
What Is Evolution?

Evolution can be defined more broadly as *descent with modification*.

As populations accumulate differences over time, and when a new species forms, it is different from its ancestors.

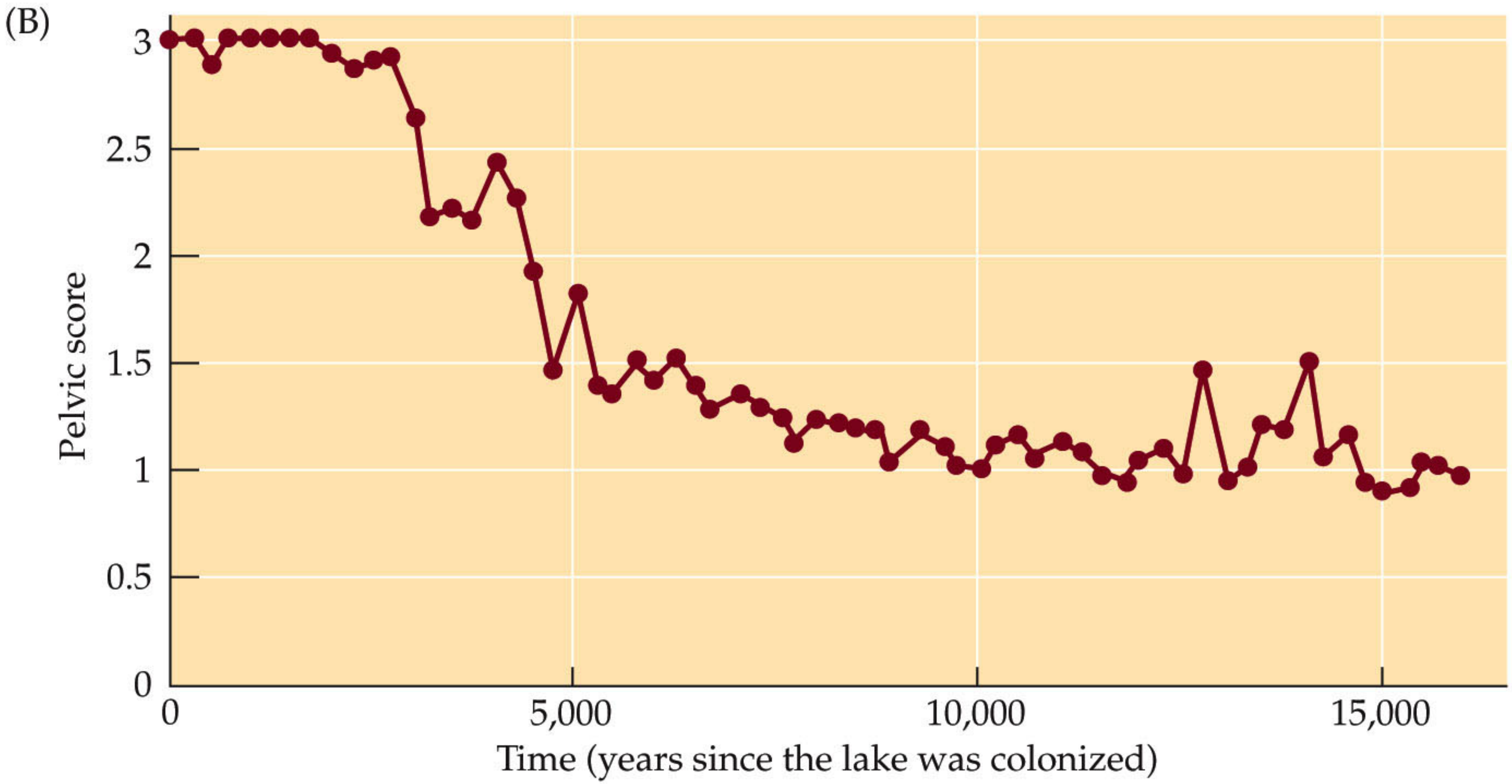
A new species will retain many of the same characteristics of its ancestors, and resemble them.

Figure 6.3 Descent with Modification (Part 1)



ECOLOGY, Figure 6.3 (Part 1)

Figure 6.3 Descent with Modification (Part 2)



What Is Evolution?

Charles Darwin used the phrase "descent with modification."

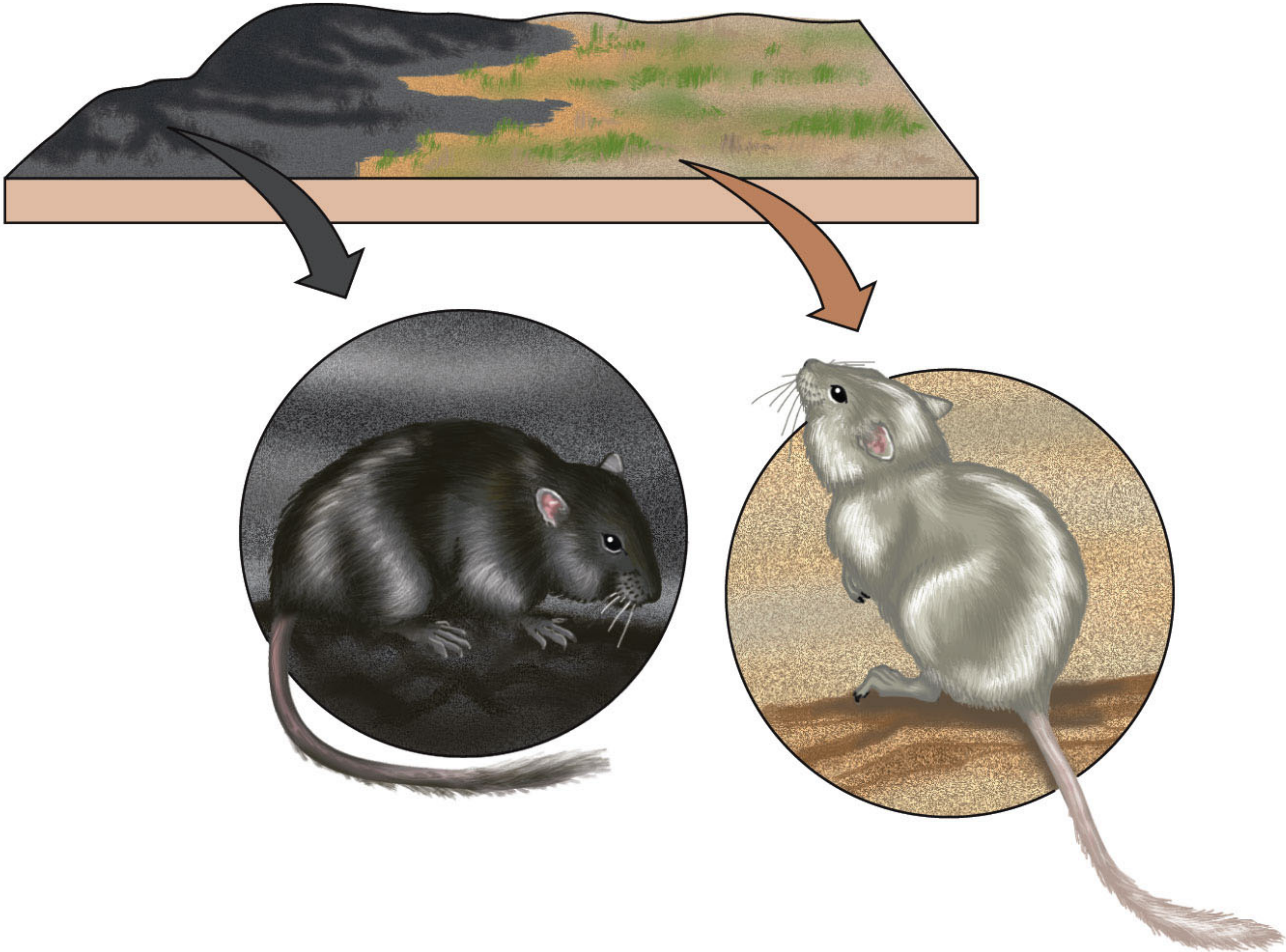
He proposed that populations become different over time through **natural selection**: Individuals with certain heritable characteristics survive and reproduce more successfully than individuals with other heritable characteristics.

What Is Evolution?

If two populations experience different environmental conditions, individuals with one set of characteristics may be favored in one population, while individuals with a different set of characteristics may be favored in the other population.

Natural selection causes the populations to diverge genetically over time.

Figure 6.4 Natural Selection Can Result In Differences Between Populations



ECOLOGY, Figure 6.4

What Is Evolution?

Natural selection acts as a sorting process.

Individuals with favored traits have more offspring, and their alleles will increase in frequency in the population.

The population will evolve, but individuals do not evolve.

Concept 6.2: Natural selection, genetic drift, and gene flow can cause allele frequencies in a population to change over time.

Four key processes influence evolution:

- Mutation
- Natural selection
- Genetic drift
- Gene flow

Phenotype—the observable characteristics of individuals that are determined by the genotype.

Individuals differ from one another in part because they have different alleles for genes.

Figure 6.5 Individuals in Populations Differ from One Another

ECOLOGY, Figure 6.5

Different alleles arise by **mutation**.

Mutations are changes in the DNA of a gene that can result from copying errors during cell division, mechanical damage, exposure to certain chemicals (mutagens), or exposure to high-energy radiation.

Mechanisms of Evolution

Environment can also influence phenotype.

For example, in the case of two plants with the same genotype growing in different soils, the plant in nutrient-rich soil will be larger.

Formation of new alleles by mutation is critical to evolution.

If mutation did not produce new alleles, all members of a population would have identical genotypes.

Individuals in a population differ because of mutation, and *recombination*—production of offspring that have combinations of alleles that differ from those of their parents.

Mutation occurs too rarely to be the direct cause of allele frequency change.

Mutations occur at rates of 10^{-4} to 10^{-6} new mutations per gene per generation. In each generation, one mutation would occur in every 10,000 to 1,000,000 copies of a gene.

At these rates, in one generation, mutation causes virtually no change in the allele frequencies of a population.

Natural selection occurs when individuals with particular heritable traits tend to leave more offspring than individuals with other heritable traits.

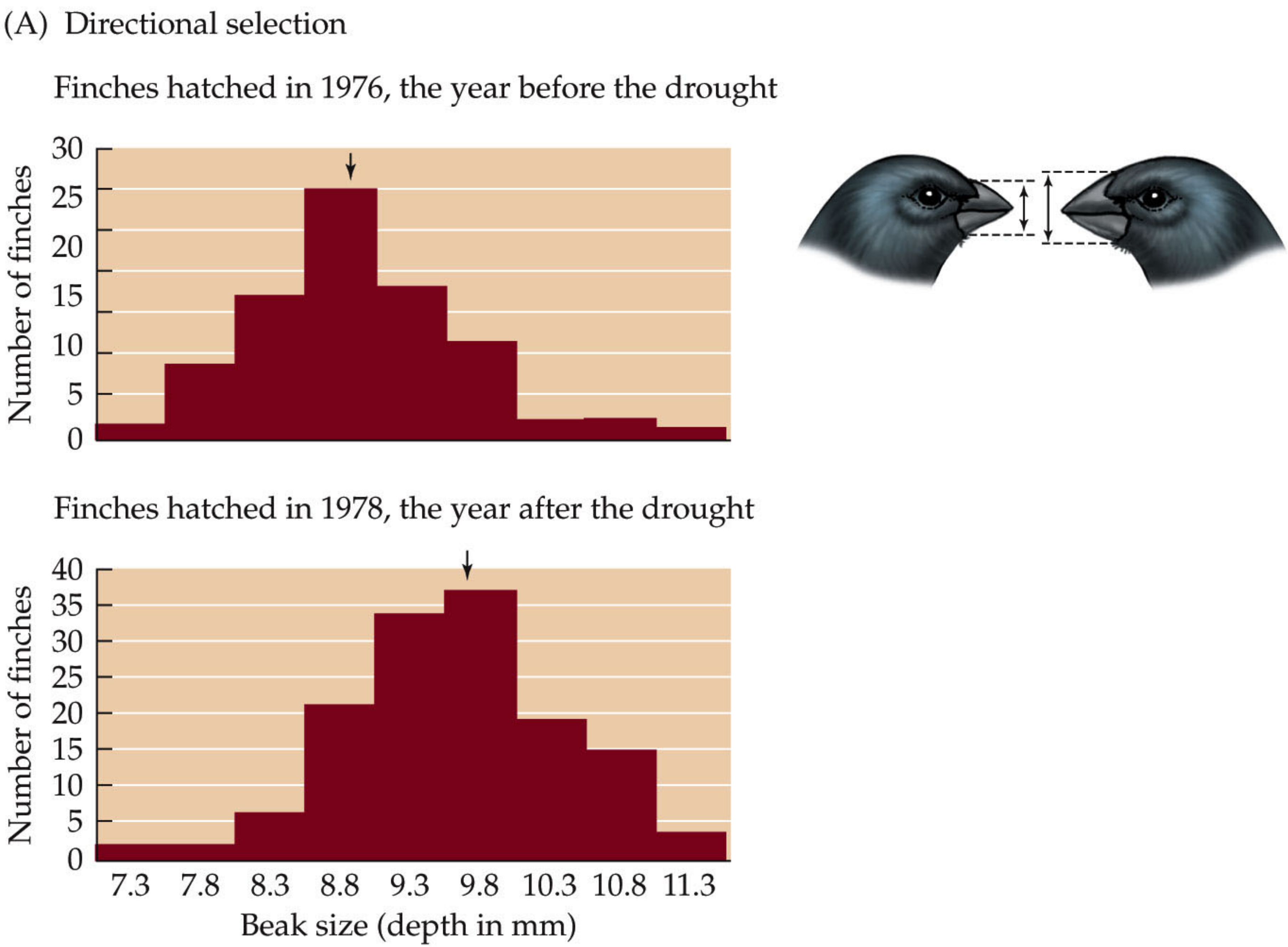
Darwin's view of natural selection as the most important agent of evolutionary change is well-supported by genetic and ecological studies.

Natural selection can be categorized into three types:

Directional selection: Individuals with one extreme of a heritable phenotypic trait (for example, large size) are favored.

Example: Drought favored large beak size in medium ground finches.

Figure 6.6 A Three Types of Natural Selection

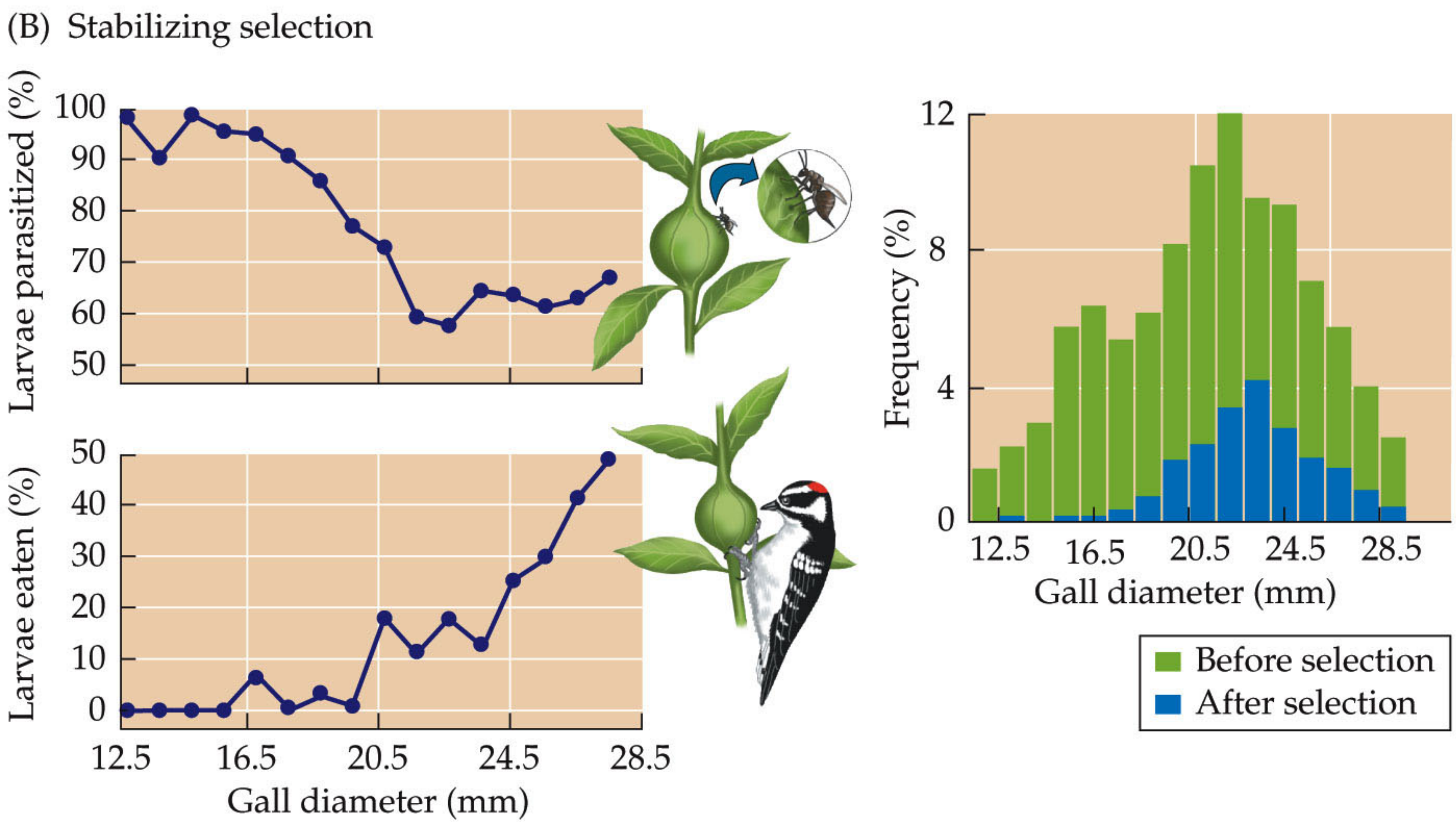


ECOLOGY, Figure 6.6 (Part 1)

Stabilizing selection: Individuals with an intermediate phenotype are favored.

Example: Parasites and predators of *Eurosta* flies result in stabilizing selection. Parasitic wasps select for small gall size; birds select for large gall size.

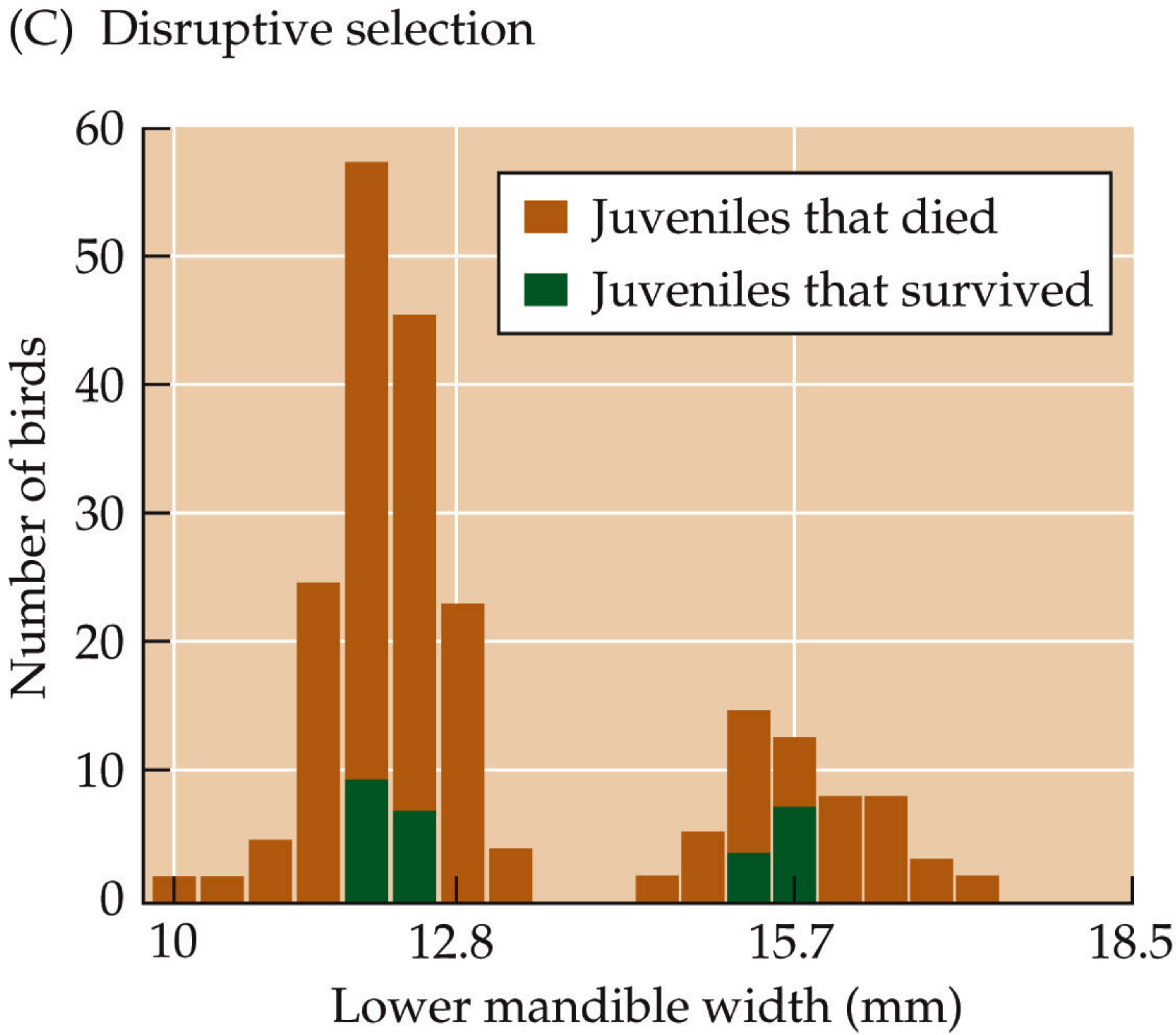
Figure 6.6 B Three Types of Natural Selection



Disruptive selection: Individuals at both phenotypic extremes are favored.

Example: African seedcrackers (birds) have two food sources—hard seeds that large beaks are needed to crack, and smaller, softer seeds that smaller beaks are more suited to.

Figure 6.6 C Three Types of Natural Selection



ECOLOGY, Figure 6.6 (Part 3)

Natural selection operates only on aspects of the phenotype that have a genetic basis.

This can result in populations in which all individuals have the favored allele.

Example: Bar-headed geese migrate over the Himalayas, and have evolved hemoglobin with a very high affinity for oxygen.

Genetic drift occurs when chance events determine which alleles are passed to the next generation.

Example: A population of ten wildflowers in a field; three are *AA*, four are *Aa*, three are *aa*. Frequency of both alleles is 50%.

A moose walks through, killing two *AA* and two *Aa* plants. Frequency of the *a* allele would increase to 67%.

Genetic drift is significant only for small populations.

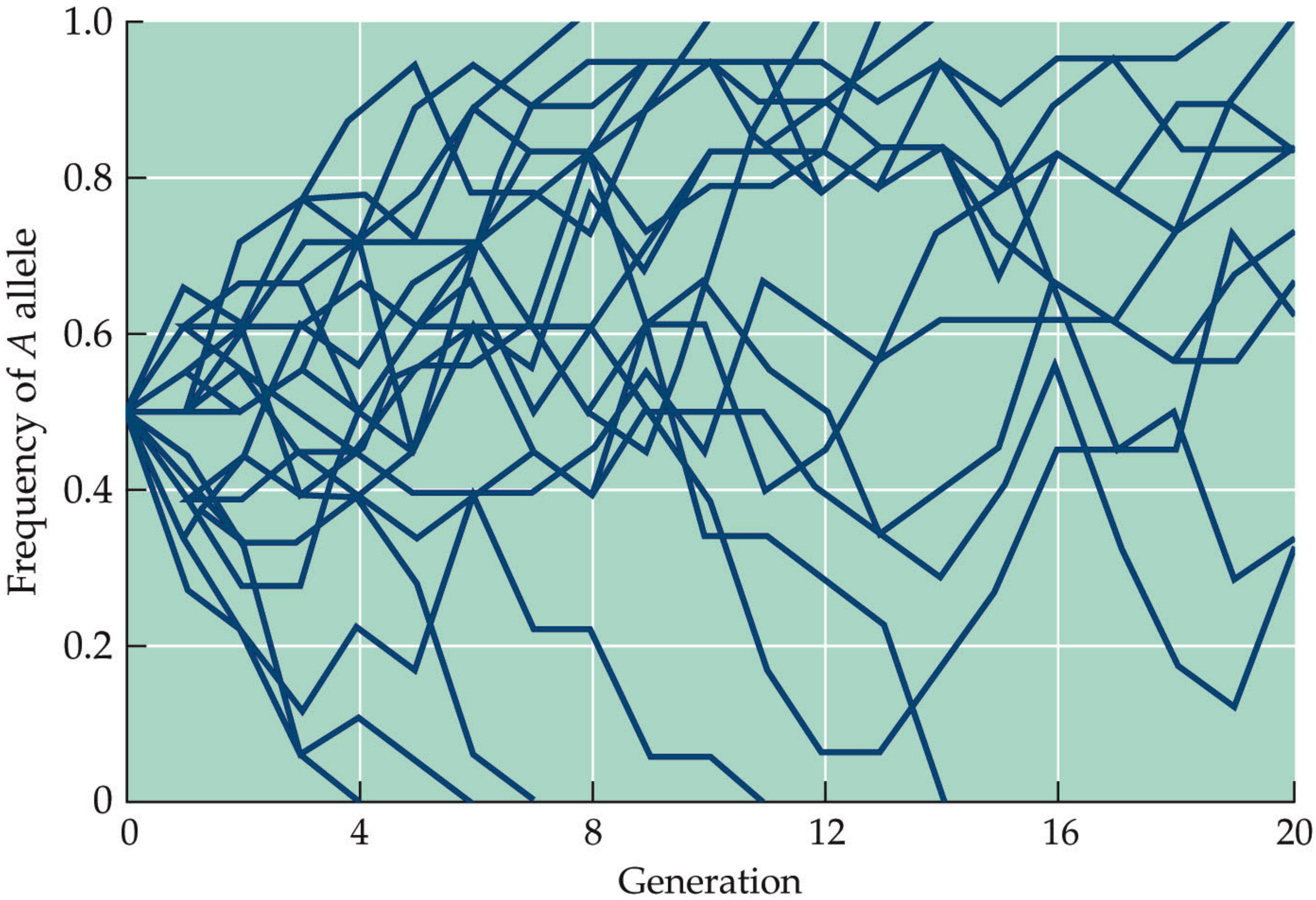
If the wildflower population had 10,000 individuals, the chance of the moose killing 40% of the population without killing any *aa* plants is essentially zero.

It is more likely that individuals of all genotypes would be killed, and allele frequency would stay the same.

Genetic drift has four effects on small populations:

1. Because it acts by chance alone, it causes allele frequencies to fluctuate at random. Some alleles may disappear, other may reach 100% frequency (**fixation**).

Figure 6.7 Genetic Drift Causes Allele Frequencies to Fluctuate at Random



ECOLOGY, Figure 6.7

2. Because some alleles are lost, genetic drift reduces genetic variation of the population.

3. Frequency of harmful alleles can increase. If the allele has only mildly deleterious effects, genetic drift can “overrule” natural selection.

4. Differences between populations can increase.

The second and third effects can have dire consequences.

Loss of genetic variation reduces the ability of the population to respond to changing environmental conditions.

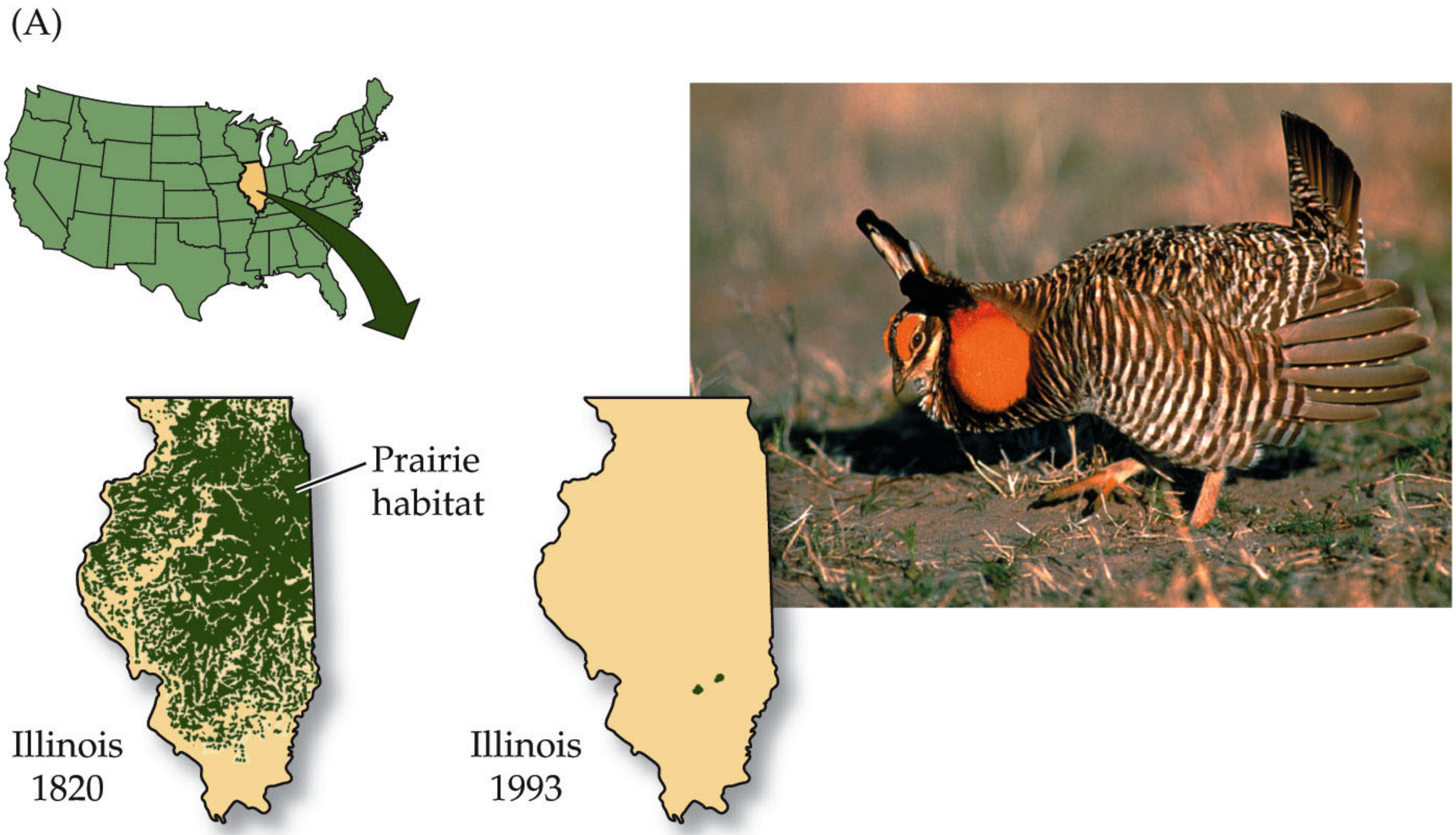
Increase of harmful alleles can reduce survival and reproduction.

These effects are important for species that are near extinction.

Greater prairie chicken populations in Illinois have been reduced by loss of habitat to farmland.

1993 population was <50. DNA from this population compared with museum specimens from the 1930s showed a decrease in genetic variation.

50% of eggs failed to hatch, suggesting fixation of harmful alleles.


(A)
Prairie
habitat
Illinois
1820
Illinois
1993

(B)

	Illinois 1933	Illinois 1993	Kansas	Nebraska	Minnesota
Population size	25,000	<50	750,000	75,000–200,000	4,000
No. of alleles at six genes	31	22	35	35	32
Percentage of eggs that hatch	93	<50	99	96	85

Gene flow occurs when alleles are transferred from one population to another via movement of individuals or gametes.

Gene flow has two effects:

1. Populations become more similar.

2. New alleles can be introduced into a population.

Example: The mosquito *Culex pipiens* can carry malaria and West Nile virus.

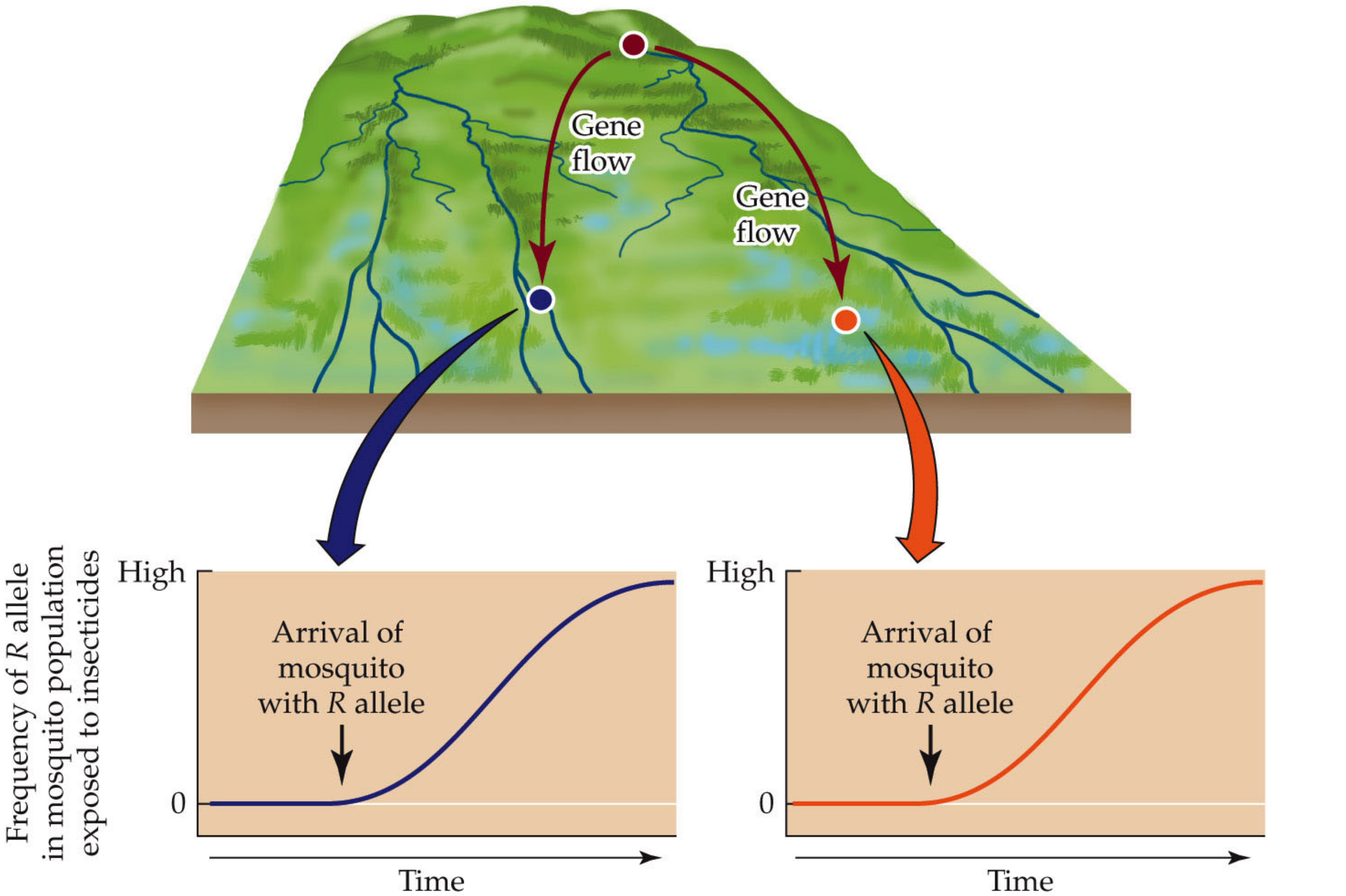
Organophosphate insecticides are used to control the mosquitos.

In the 1960s, new alleles that provided resistance to the pesticides arose by mutation in Africa or Asia.

Mosquitos carrying the new alleles were blown by winds or transported by humans to new locations.

Once in a new population, the allele frequency increased rapidly because insecticide resistance was favored by natural selection.

Figure 6.9 Gene Flow: Setting the Stage for Selection for Insecticide Resistance



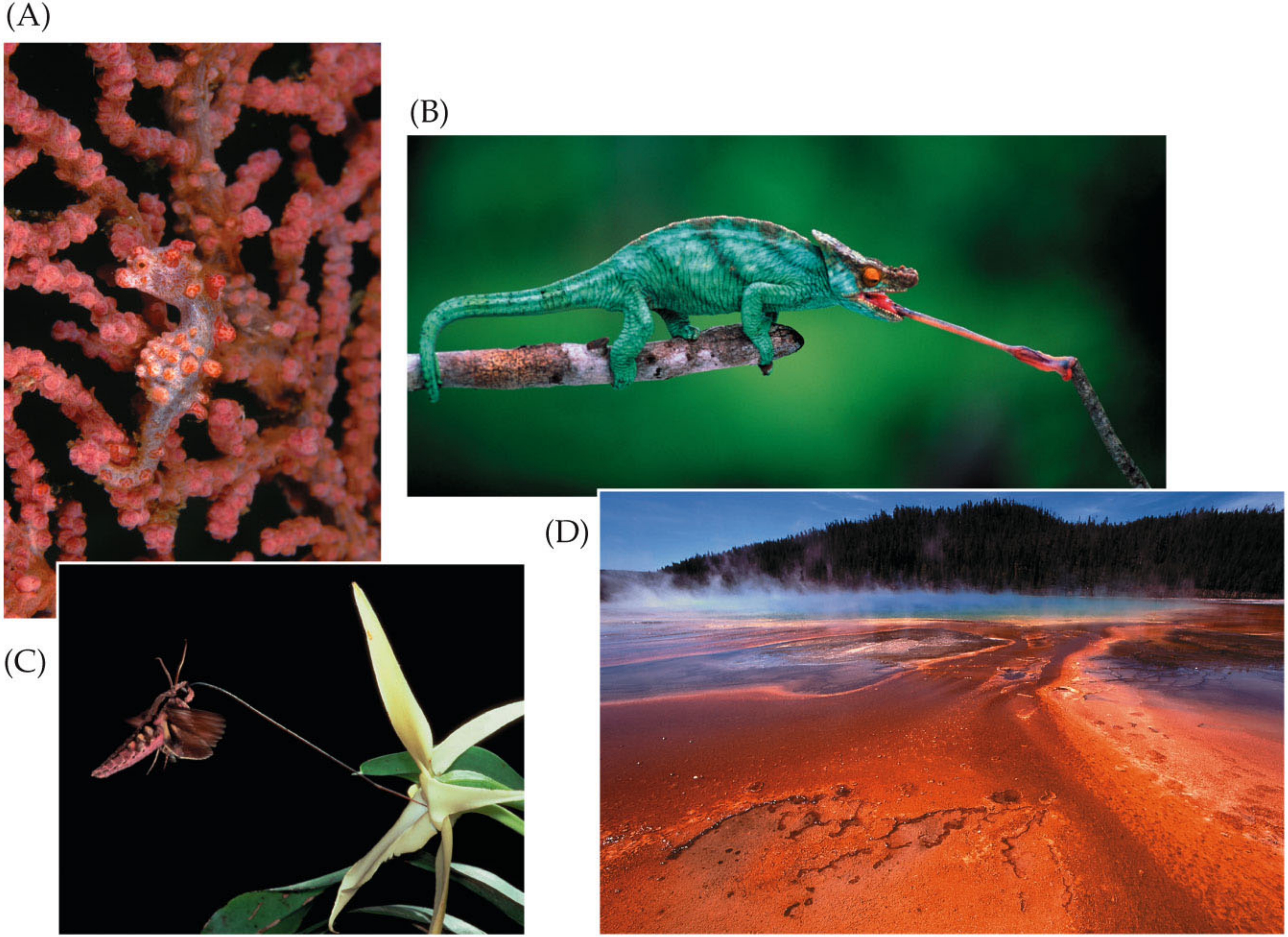
ECOLOGY, Figure 6.9

Concept 6.3: Natural selection is the only evolutionary mechanism that consistently causes adaptive evolution.

There are many examples of organisms that are well suited for life in their environments.

Adaptations are features of organisms that improve their ability to survive and reproduce in their environments.

Figure 6.10 A Gallery of Adaptations



Adaptive Evolution

Natural selection is not a random process.

By consistently favoring individuals with certain alleles, natural selection causes **adaptive evolution**, in which traits that confer advantages tend to increase in frequency over time.

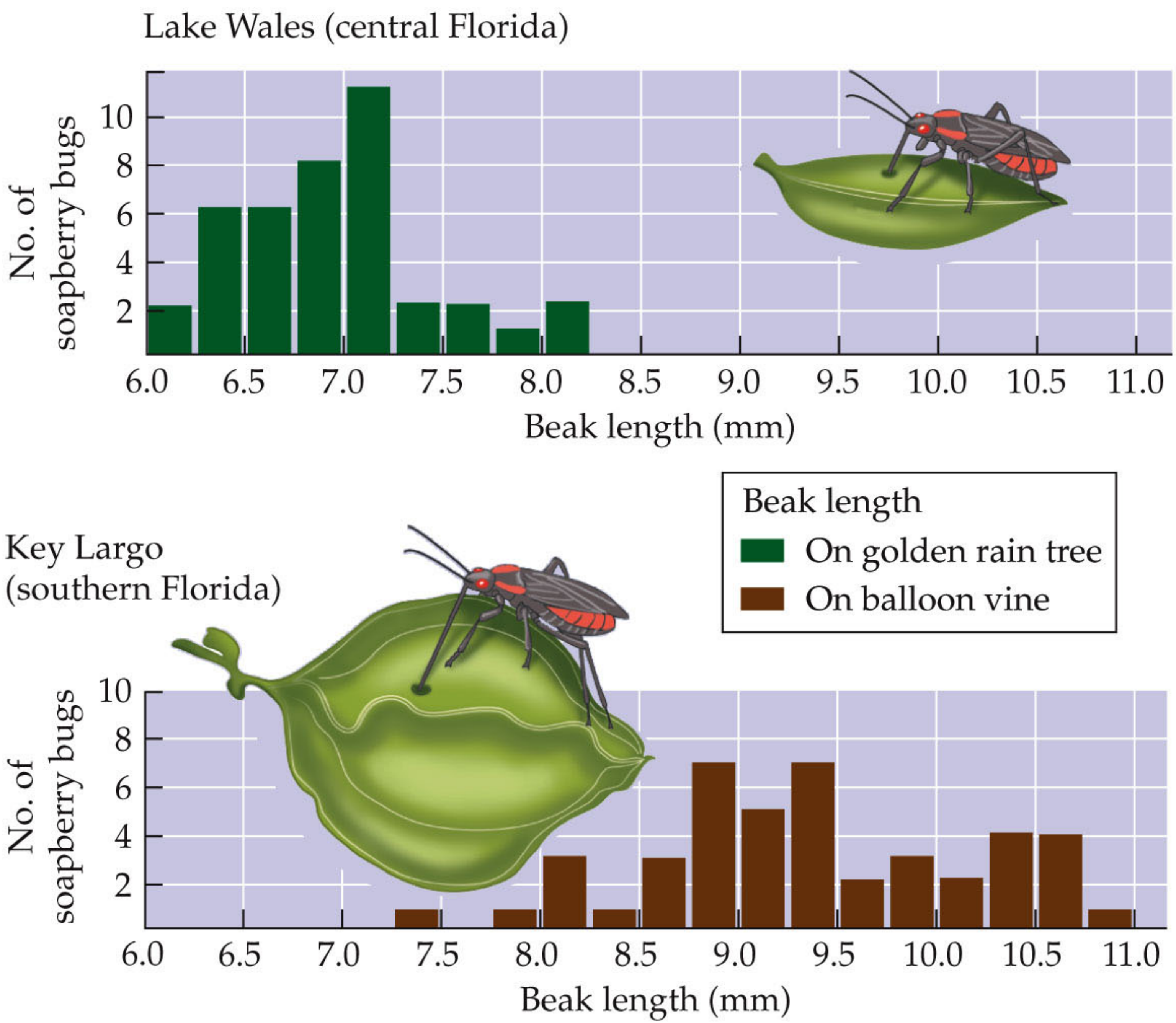
Example: The soapberry bug feeds on seeds of the balloon vine in southern Florida by piercing the fruits with its beak.

In central Florida they feed on seeds of the golden rain tree, introduced from Asia. The oldest golden rain trees in central Florida are 35 years old. The fruits are smaller than balloon vine fruits.

Carroll and Boyd (1992) predicted that in central Florida populations, beak length would evolve to be shorter, because the bugs were feeding on smaller fruits.

In Oklahoma and Louisiana, the bugs fed on fruits larger than balloon vine fruits, and the researchers predicted longer beak lengths.

Figure 6.11 Rapid Adaptive Evolution in Soapberry Bugs



ECOLOGY, Figure 6.11

Beak length is a heritable characteristic so the observed changes in beak length must have been due to changes in the frequencies of alleles.

In a relatively short time (35–100 years), natural selection caused adaptive evolution in which a characteristic (beak length) evolved to match an aspect of the environment (fruit size) more closely.

Adaptive Evolution

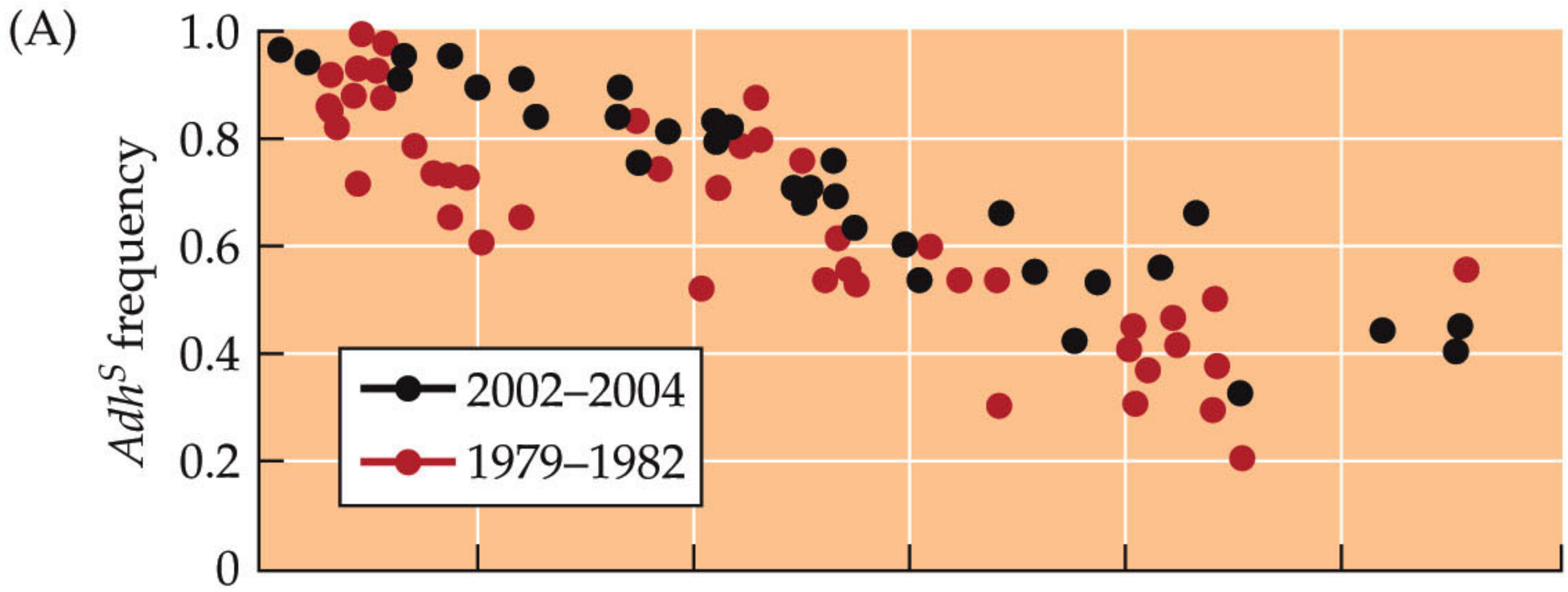
There are many examples of rapid adaptive evolution, including increased antibiotic resistance in bacteria; increased insecticide resistance in insects; drab coloration in guppies, which makes them harder for predators to see; and increased beak size in *Geospiza* finches.

Rapid adaptive evolution can happen on a continental scale.

Clines are gradual changes in a characteristic over a geographic region.

Example: In the fruit fly *Drosophila*, the alcohol dehydrogenase (*Adh*) gene exhibits a cline in which the Adh^S allele decreases in frequency as latitude increases.

Figure 6.12 A Rapid Adaptive Evolution on a Continental Scale

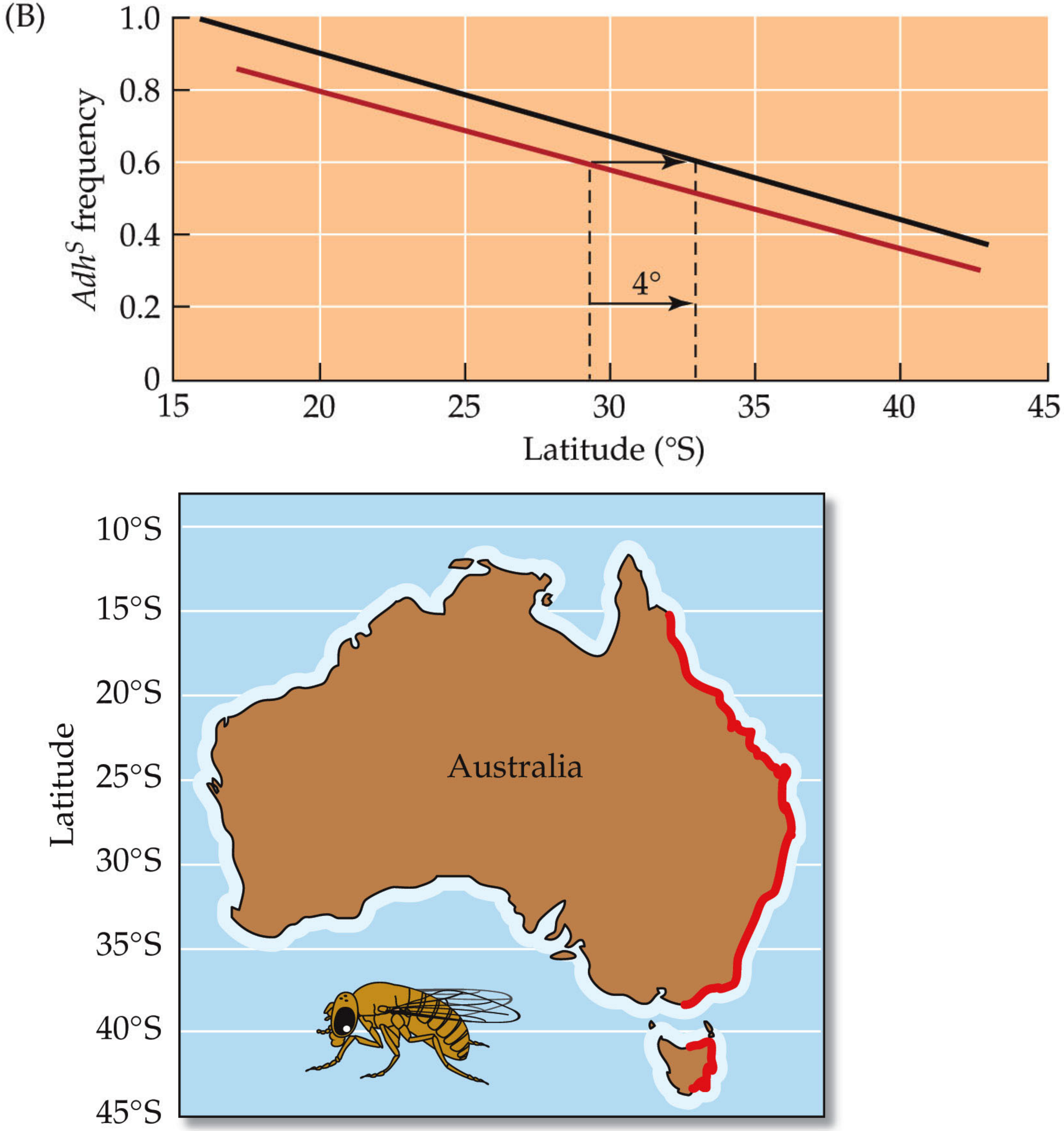


The *Adh*^{S} allele is less effective in colder temperatures, so natural selection resulted in this cline with latitude.

In the past 20 years in Australia, the *Adh*^{S} cline has shifted about 4° latitude toward the South Pole, as mean temperature has increased 0.5°C.

This shift indicates an adaptive change in allele frequency in response to climate change.

Figure 6.12 B Rapid Adaptive Evolution on a Continental Scale



Adaptive Evolution

Gene flow can limit how well a population is adapted to its environment.

Some plant species, such as bentgrass, have genotypes that allow them to grow in soils contaminated with heavy metals in former mine sites.

Research at mine sites found the tolerant genotypes to be dominant.

But downwind of the mine site there were more of the tolerant genotypes than expected.

Because bentgrass is wind-pollinated, alleles were carried into the downwind region with normal soils.

Adaptive Evolution

Allele frequency at the downwind site didn’t change because there was strong selection against the plants that were not suited to growing in normal soils.

In this case, natural selection was strong enough to overcome the effects of ongoing gene flow.

Adaptive Evolution

Natural selection does not result in a perfect match between organisms and their environments, partly because environments are constantly changing.

Also, there are several constraints on evolution:

- Lack of genetic variation
- Evolutionary history
- Ecological trade-offs

Adaptive Evolution

1. Lack of genetic variation: If there is no beneficial allele, adaptive evolution at that gene can not occur.

Example: Initially, the mosquito population lacked alleles that provided resistance to pesticides, so the pesticides were effective.

Advantageous alleles arise by chance, not “on demand.”

2. Evolutionary history: Natural selection works on the traits already existing in organisms.

Organisms have certain characteristics and lack others because of their ancestry.

Example: Dolphins evolved from terrestrial mammals; they have lungs and cannot “breathe” underwater.

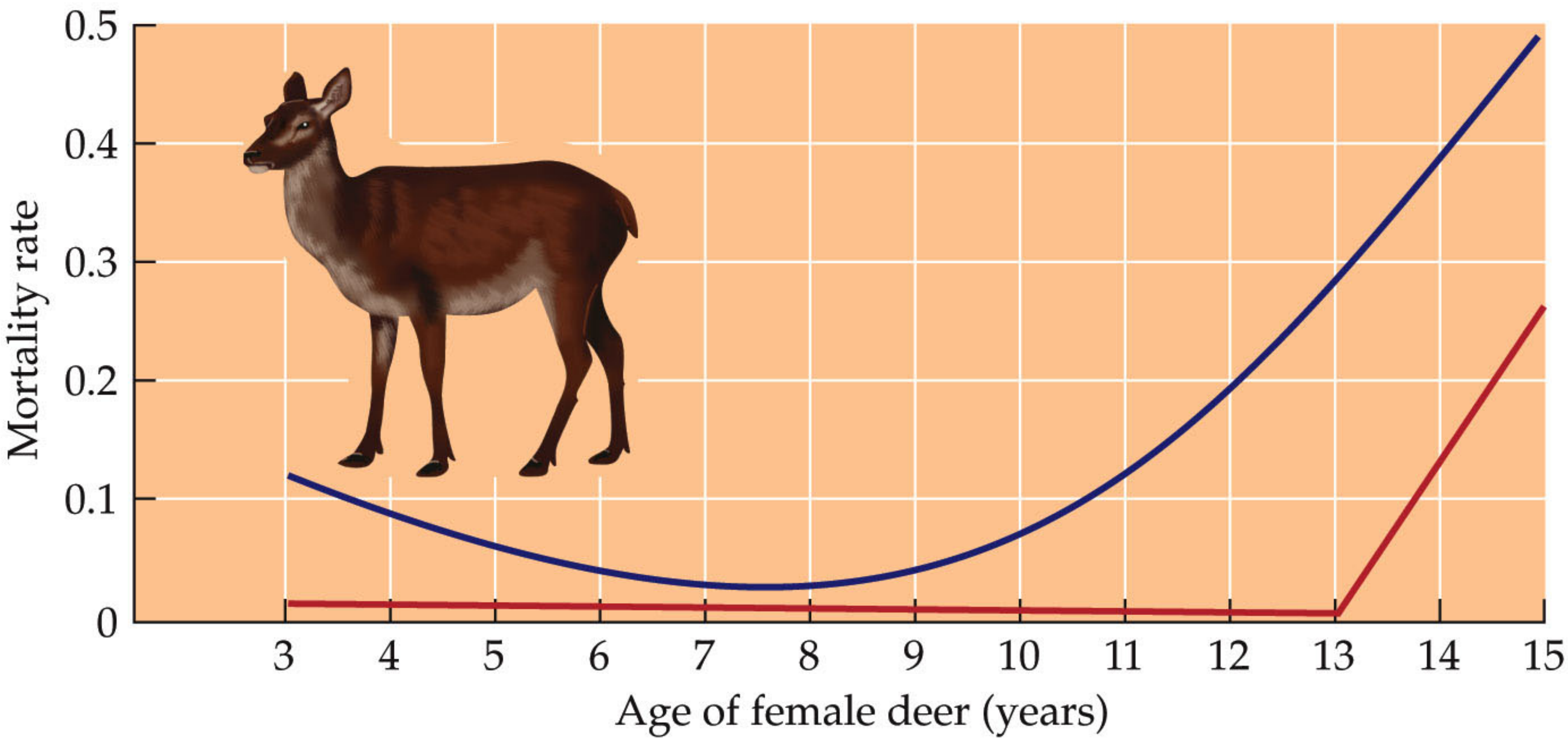
Adaptive Evolution

Natural selection can bring about great changes, such as the mode of life and streamlined body form of the dolphin.

But it does so by modifying traits that are already present, not by creating advantageous traits de novo.

3. Ecological trade-offs: All organisms face trade-offs in allocation of energy and resources to growth, reproduction, and survival.

Adaptations represent compromises in the abilities of organisms to perform different and sometimes conflicting functions.



0.5
0.4
0.3
0.2
0.1
0
Mortality rate
3
4
5
6
7
8
9
10
11
12
13
14
15
Age of female deer (years)

Adaptive Evolution

Adaptive evolution highlights the connection between ecology and evolution.

Adaptive evolution is driven by ecological interactions, the interactions of organisms with one another and with their environment.

Ecology is a basis for understanding evolution.

Concept 6.4: Long-term patterns of evolution are shaped by large-scale processes such as speciation, mass extinction, and adaptive radiation.

Species are groups of organisms whose members have similar characteristics and can interbreed.

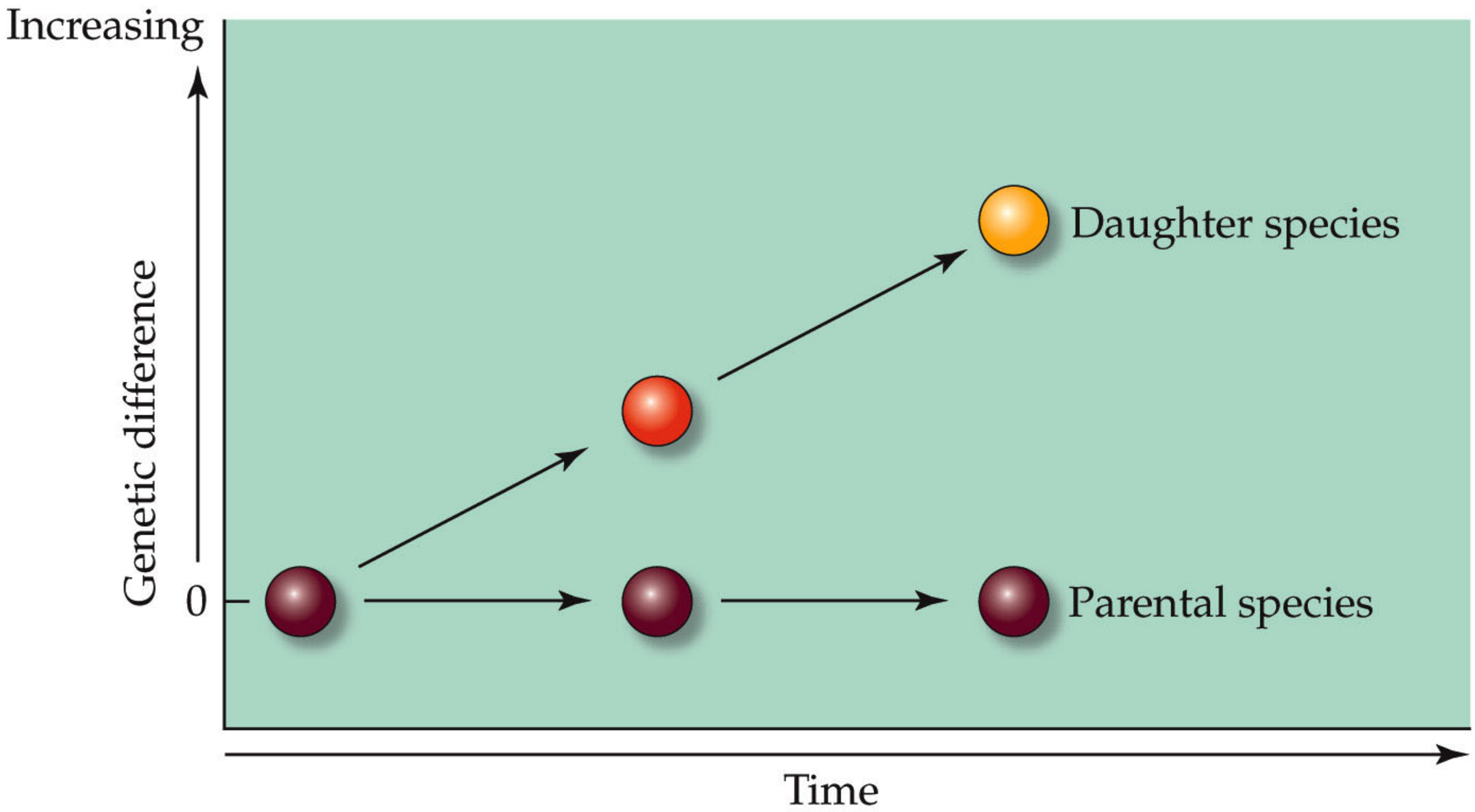
Ecological interactions influence the number of species alive today.

Speciation—the process by which one species splits into two or more species.

Most commonly occurs when a barrier prevents gene flow between two or more populations of a species.

Barriers can be geographic or ecological. The populations then diverge genetically over time.

Figure 6.14 Speciation by Genetic Divergence



ECOLOGY, Figure 6.14

New species can also arise when members of two different species mate to produce fertile hybrid offspring.

The key step in speciation is the evolution of barriers that prevent breeding with the parental species.

This occurs when a population accumulates so many genetic differences that they cannot produce viable, fertile offspring if they mate with the parental species.

Accumulation of differences that lead to speciation can be an accidental by-product of natural selection.

Example: In experiments with fruit flies being grown on different food sources, the beginning of reproductive barriers was also observed.

Most matings occurred between flies selected to feed on the same food source.

Figure 6.15 Reproductive Barriers Can Be a By-product of Selection

		Female	
		Starch	Maltose
Male	Starch	22	9
	Maltose	8	20

Mating frequencies in experimental group

		Female	
		Starch population 1	Starch population 2
Male	Starch population 1	18	15
	Starch population 2	12	15

Mating frequencies in control group

In some cases, the trait favored by selection is the same trait that drives speciation.

Example: Mosquitofish that live in pools with fish predators have evolved a body shape for high-speed escape swimming.

Female mosquitofish prefer to mate with these streamlined males.

Thus, natural selection favors different body shapes in mosquitofish, depending on the presence or absence of predators.

These different body shapes drive the early stages of speciation through their effects on mate choice.

Genetic drift can also lead to evolution of reproductive barriers, and hence to the formation of new species.

But gene flow *always* acts to slow down or prevent speciation. Populations that exchange many alleles tend to remain genetically similar, making it less likely that reproductive barriers will evolve.

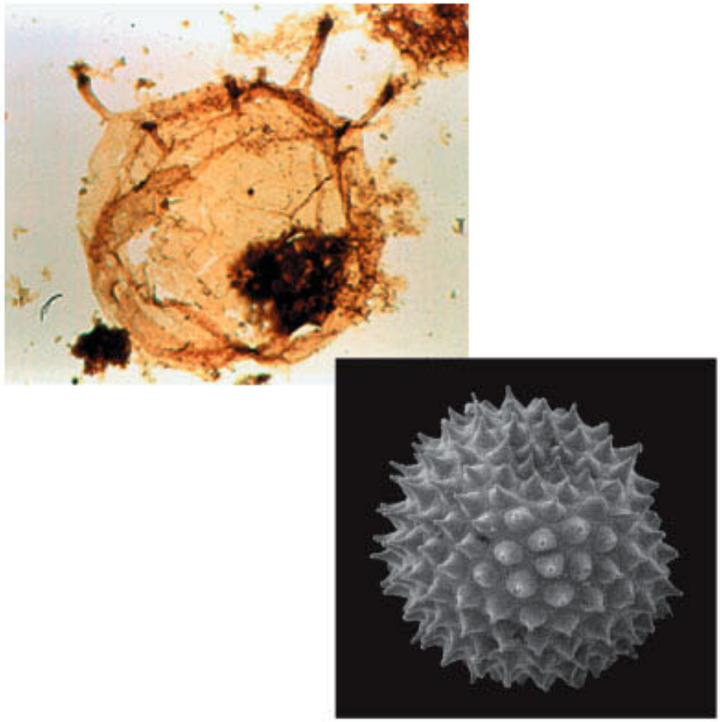
Evolution can also be viewed as an observed pattern of change.

To observe patterns of evolution over long time scales, we turn to the fossil record.

Life on Earth has changed greatly over time.

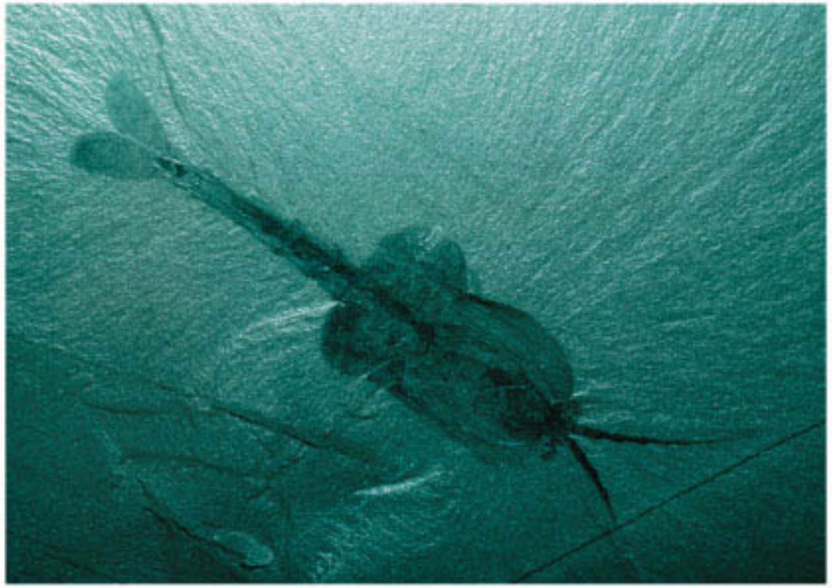
(A)

(B)



The first organisms were prokaryotes (bacteria and archaea).

(C)



Complex animals with bilateral symmetry appeared about 600 million years ago.

Figure 6.16 D,E,F Life Has Evolved Greatly over Time

(F)

(E)

(D)

Over millions of years, evolution resulted in the formation of major new groups of organisms, such as terrestrial plants, amphibians, reptiles, and mammals.

The Evolutionary History of Life

The rise to prominence of one group was often associated with the decline of another group.

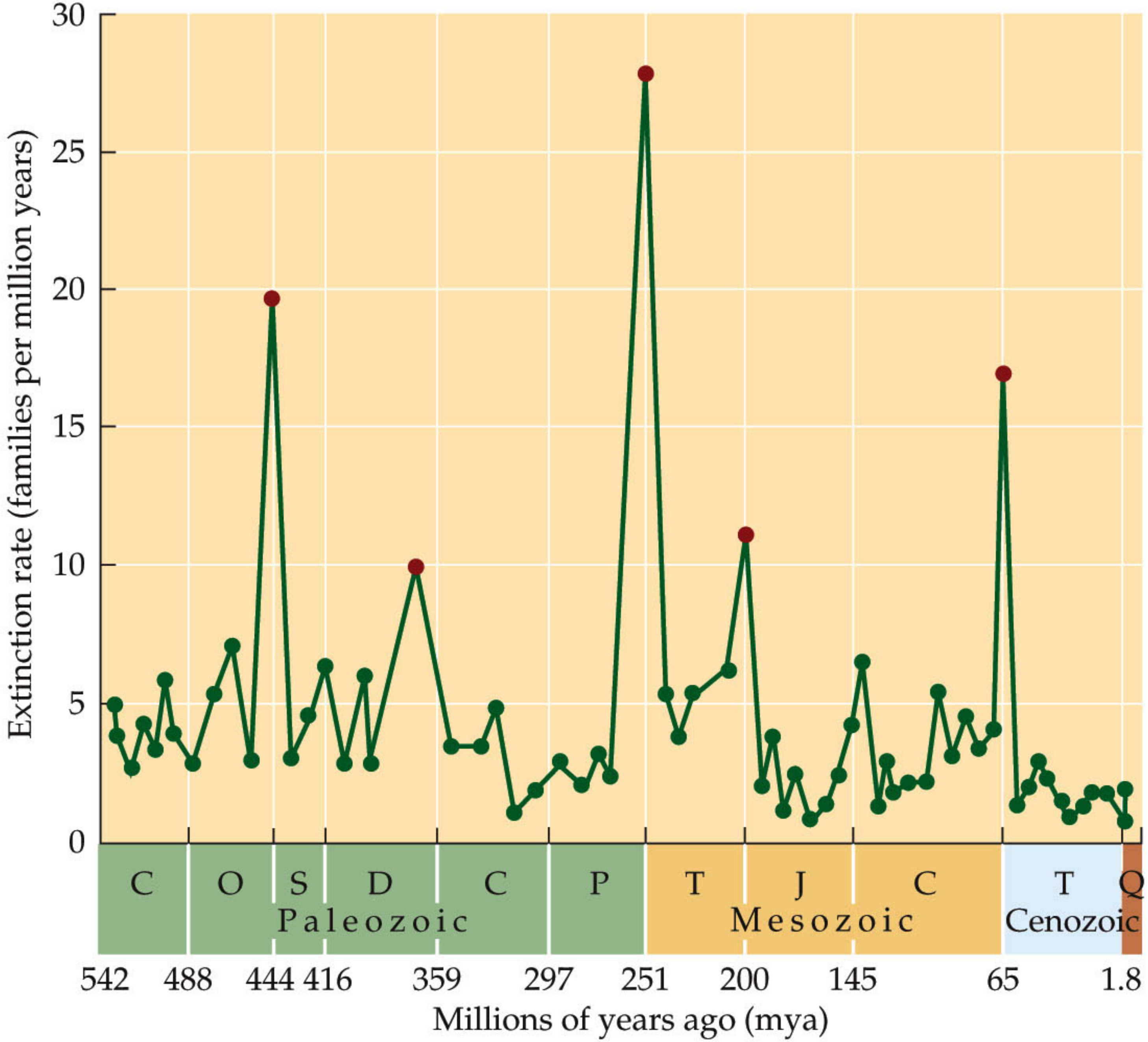
Example: 265 million years ago, reptiles replaced amphibians as the dominant group of terrestrial vertebrates.

65 million years ago, the reptiles were replaced in turn by the mammals.

The fossil record documents five **mass extinction** events.

Large proportions of Earth’s species were driven to extinction worldwide in a relatively short time—a few million years or less.

Figure 6.17 The “Big Five” Mass Extinctions



Each mass extinction was followed by great increases in the diversity of some of the surviving groups.

Mass extinctions remove competitor groups, allowing survivors to expand into new habitats or new ways of life.

Great increases in diversity can also occur when a group of organisms evolves major new adaptations.

Stems and waxy cuticles provided early terrestrial plants with support against gravity and protection from desiccation.

These increases in diversity over a short time period are called **adaptive radiations**.

Biological communities are devastated by mass extinction events.

After a mass extinction, it takes millions of years for adaptive radiations to increase the diversity of life to the levels seen prior to the mass extinction.

This has great implications if human activities cause a sixth mass extinction.

Figure 6.18 Devastating Effects of a Mass Extinction

Ecological factors seem to have been the cause of many of the greatest changes in the history of life.

The first complex life forms were all small or soft-bodied, or both.

Ten million years later, this safe, soft-bodied world disappeared forever with the appearance of large, well-armed, mobile predators and large, well-defended prey.

This major step appears to have resulted from an “arms race” between predators and prey.

Early predators equipped with adaptations for capturing large prey provided powerful selection pressure that favored heavily armored prey species.

That armor, in turn, promoted further increases in the effectiveness of the predators.

The rise to prominence of one new group of organisms has often led to increase in the diversity of other organisms.

Example: In flowering plants, the flowers have either radial or bilateral symmetry.

Sargent (2004) found that plant species with bilaterally symmetrical flowers gave rise to new species more rapidly than did closely related species with radially symmetrical flowers.

Sargent attributed this to the greater specificity of plant–pollinator interaction in bilaterally symmetrical flowers.

Gene flow in diverging populations may be reduced by this specificity, leading to higher speciation rates.

Concept 6.5: Ecological interactions and evolution exert a profound influence on one another.

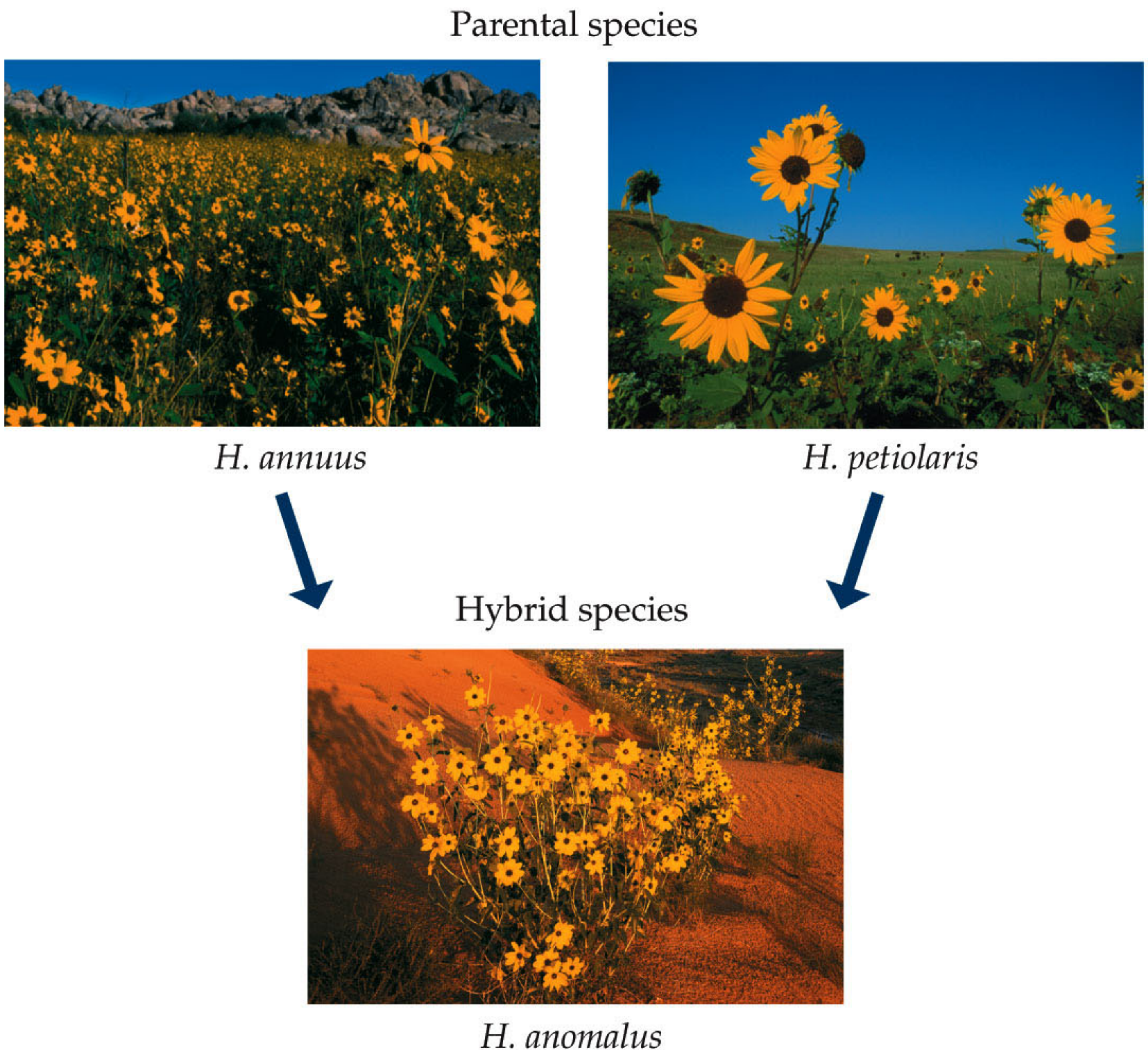
While ecological interactions influence evolution, evolution also influences ecological interactions.

The sunflower *Helianthus anomalus* originated from two other sunflowers, *H. annuus* and *H. petiolaris,* which produced hybrid offspring.

Rieseberg et al. (2003) showed that the new gene combinations appear to have facilitated a major ecological shift.

H. anomalus grows in a different and more extreme environment than the parent species.

Figure 6.19 Hybrids That Live in New Environments



Joint Effects of Ecology and Evolution

Evolution can also result from a broad range of ecological interactions, including predation, competition, herbivory, parasitism, and mutualism.

Ecology also influences small evolutionary changes (e.g., loss of habitat for greater prairie chickens resulted in genetic drift.)

Joint Effects of Ecology and Evolution

When an organism evolves a new adaptation, the outcome of ecological interactions may change, and have a ripple effect that alters the entire community.

Example: If a predator evolves a new way of capturing prey, some prey species may go extinct, others may decrease in abundance, migrate to other areas, or evolve new ways to cope with the more efficient predator.

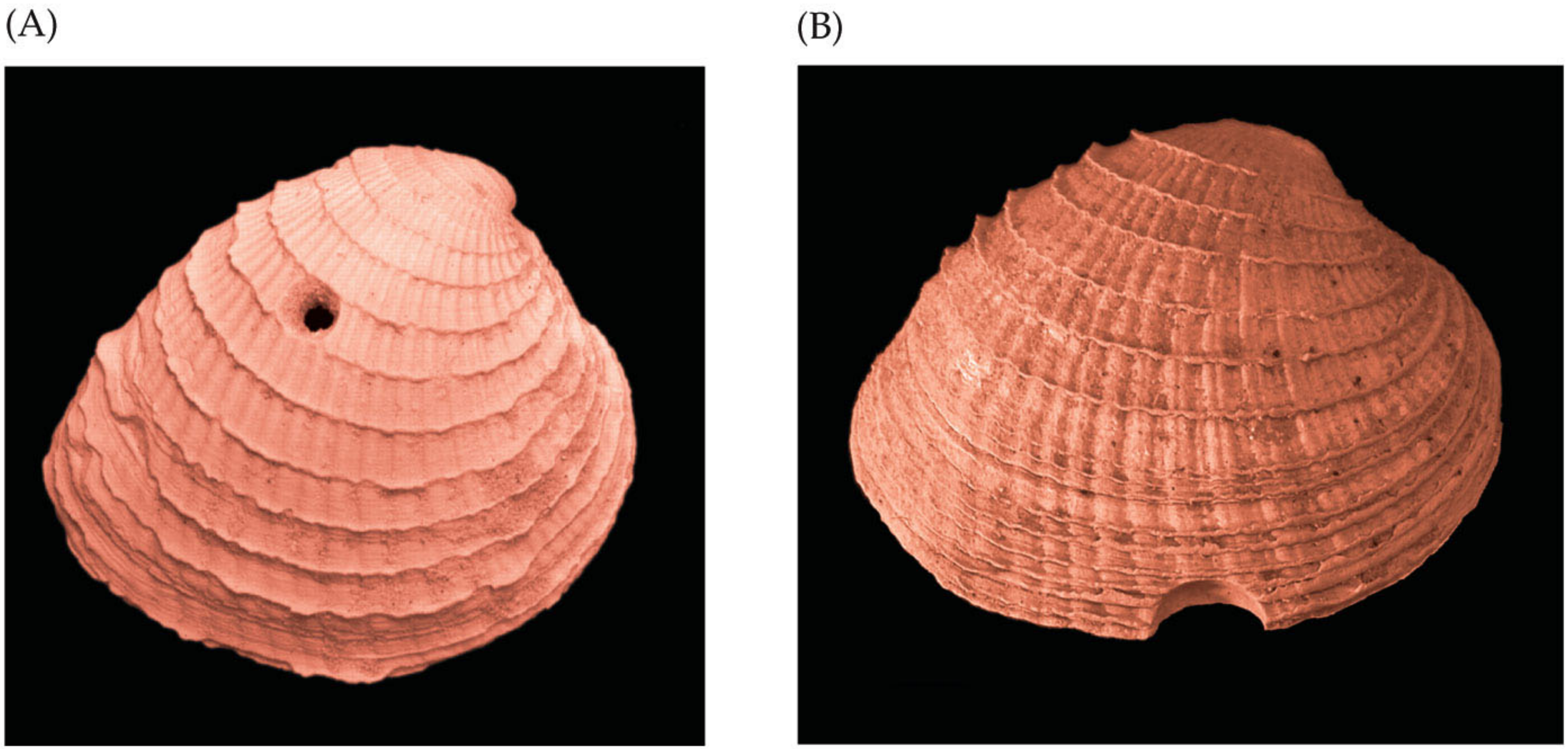
Joint Effects of Ecology and Evolution

In the mass extinction of 200 million years ago, 70% of marine species were lost.

Dietl et al. (2004) studied the effect of this extinction event on predatory snails that drill through the shells of clams.

For modern snails, it takes a week to drill into the clam shell; during this time the snail is vulnerable to other predators and competitors.

Figure 6.20 Evidence of Ancient Predatory Behavior



Drilling through the edge of the shell takes less time, but the clam may close on the drilling snail and injure it.

Dietl et al. predicted that edge drilling would be uncommon after the mass extinction, because snails would face fewer competitor and predator species.

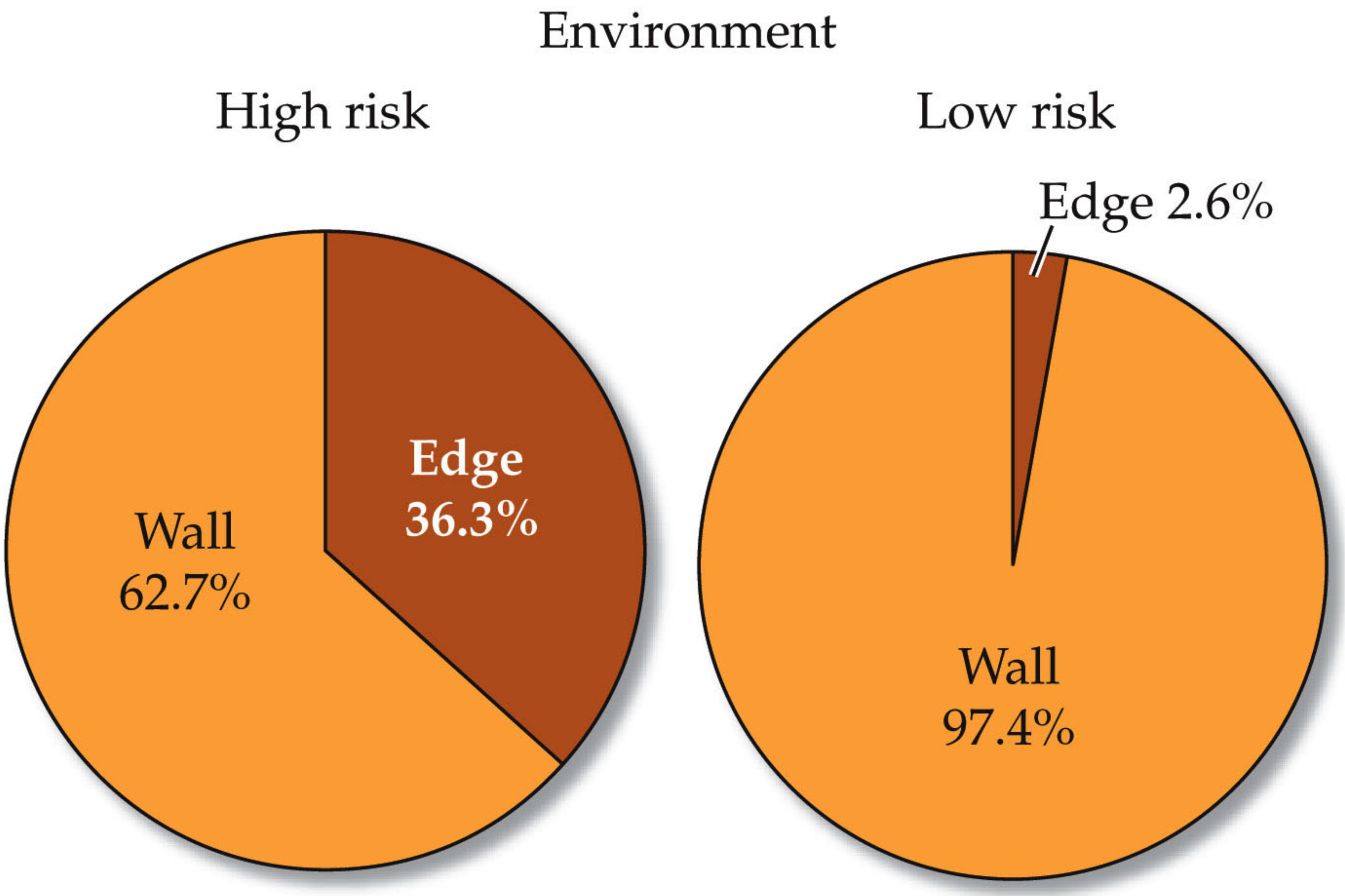
This was confirmed by fossil surveys. Edge drilling stopped completely after the mass extinction.

Joint Effects of Ecology and Evolution

These results were strengthened by experiments on modern snails.

Edge drilling increased when densities of competitor species were increased.

Figure 6.21 Edge Drilling Increases in High-Risk Environments



ECOLOGY, Figure 6.21

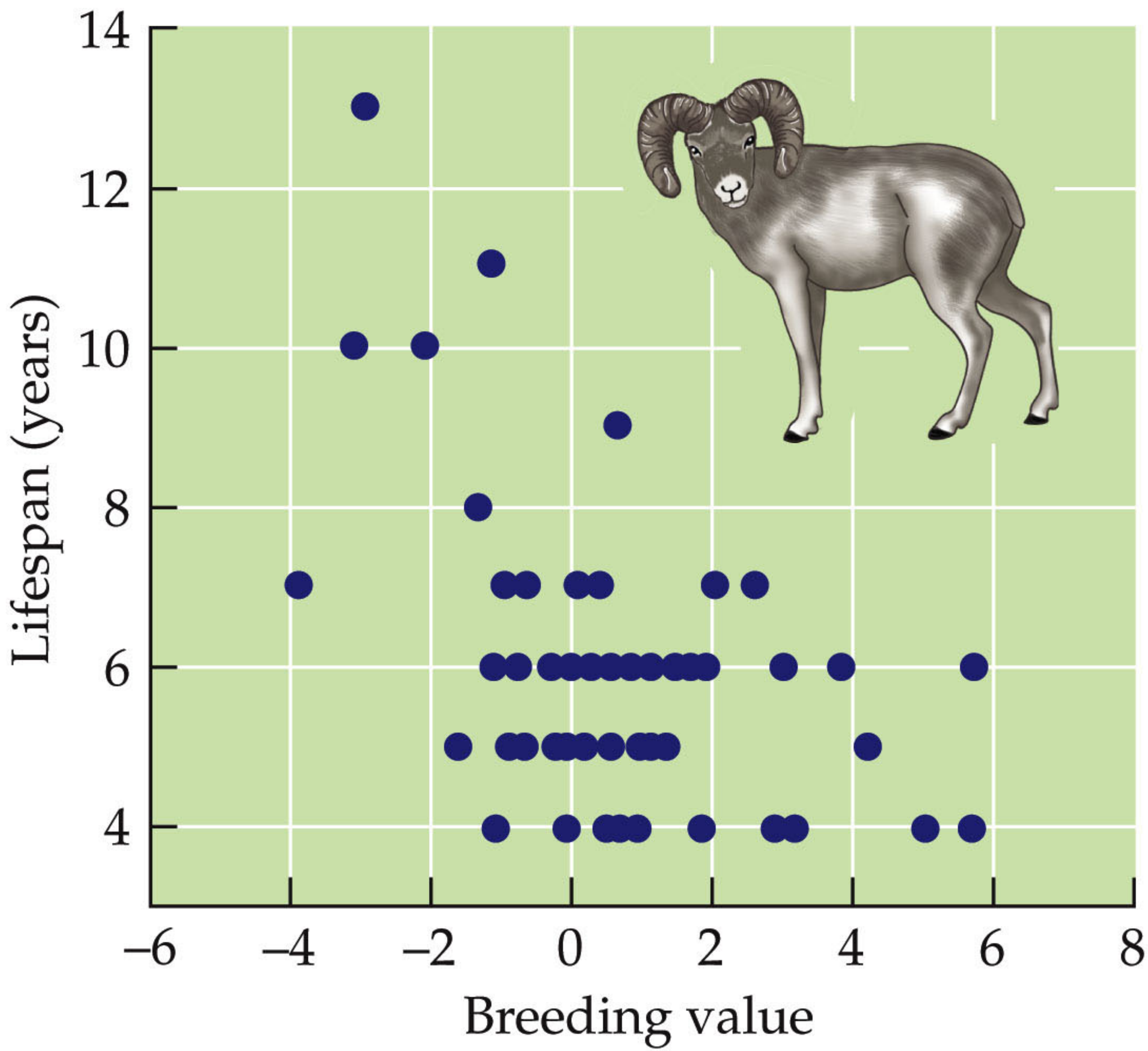
Case Study Revisited

The bighorn sheep taken by trophy hunters are between 4 and 6 years old, before they have sired many offspring.

Hunting thus decreases the chance that alleles for large horns are passed to the next generation.

Horn sizes have decreased over the last 30 years. Trophy hunting has caused directional selection.

Figure 6.22 Longevity and Breeding Value in Bighorn Sheep



Case Study Revisited: Trophy Hunting and Inadvertent Evolution

Humans have caused evolutionary changes in many organisms.

Example: Antibiotics used to control disease bacteria are a strong source of directional selection, leading to evolution of antibiotic resistance.

This has become a difficult and expensive problem in medicine.

One way to slow the evolution of antibiotic resistance is to decrease our use of antibiotics, especially unnecessary prescriptions.

This will reduce the extent to which bacterial populations are exposed to antibiotics and hence selected for resistance.

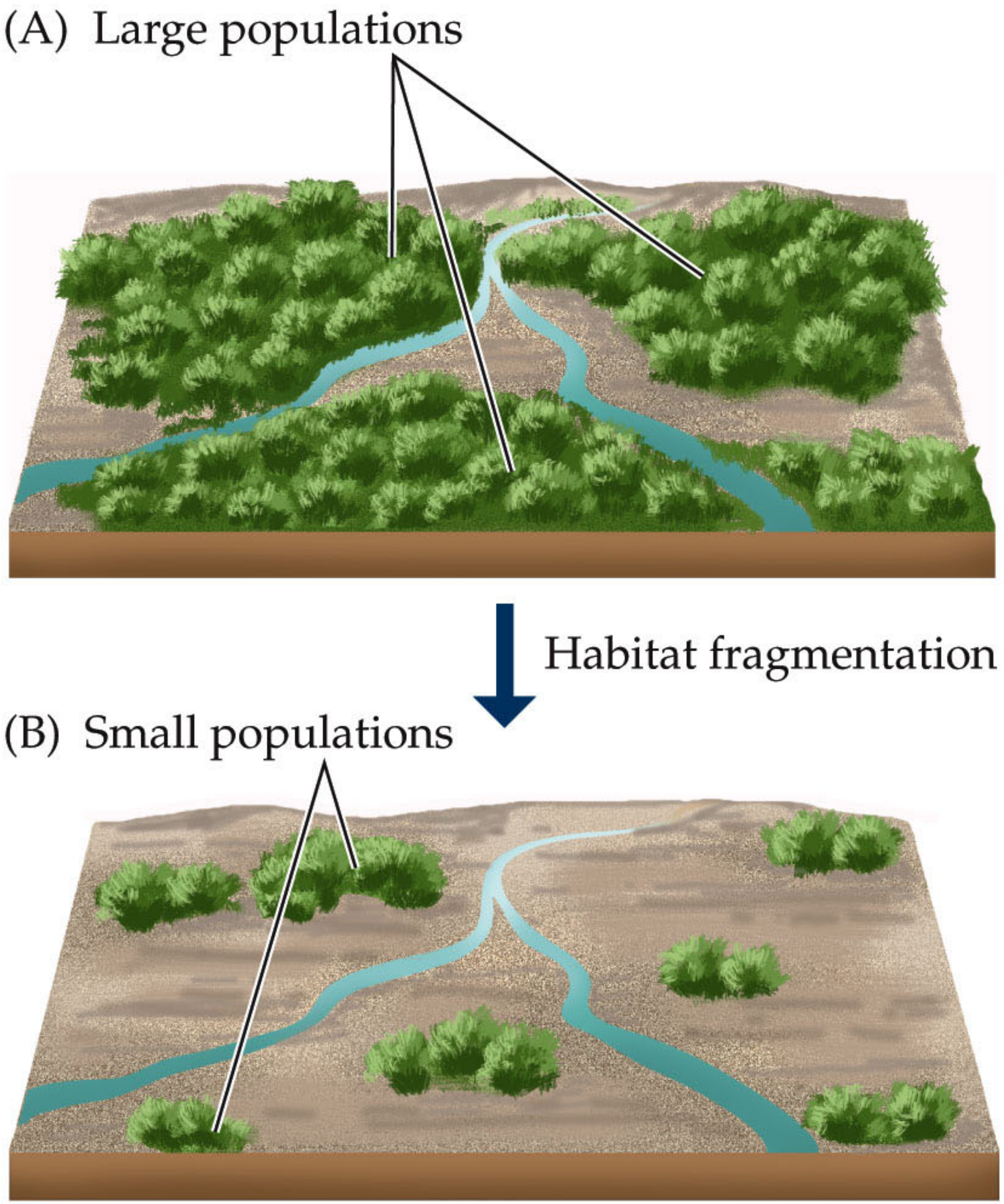
Connections in Nature: The Human Impact on Evolution

Many human actions can alter the course of evolution.

Emissions of pollutants or introductions of invasive species change aspects of the environment and alter selection pressures.

Habitat fragmentation leaves spatially isolated patches that can affect evolutionary processes.

Figure 6.23 Evolutionary Effects of Habitat Fragmentation on a Hypothetical Species (Part 1)



ECOLOGY, Figure 6.23 (Part 1)

Figure 6.23 Evolutionary Effects of Habitat Fragmentation on a Hypothetical Species (Part 2)

	Unfragmented habitat	Fragmented habitat
Population size	Large	Small
Distance between populations	Short	Long
Genetic drift	Low impact	High impact
Genetic variation within populations	High	Low
Gene flow	High	Low

Connections in Nature: The Human Impact on Evolution

Human actions that affect the environment can alter the three main mechanisms of evolution: Natural selection, genetic drift, and gene flow.

We know with certainty that our actions cause major environmental changes; we can infer that they are also causing evolutionary changes.

Connections in Nature: The Human Impact on Evolution

Habitat fragmentation, overharvesting, and introductions of invasive species are among the main reasons why Earth is undergoing a biodiversity crisis.

The extinction rate today is 100 to 1,000 times higher than the “background” extinction rate seen in the fossil record.

Connections in Nature: The Human Impact on Evolution

When human actions drive a species to extinction, the future course of evolution is altered.

Many scientists think that if current trends continue, humans will cause a sixth mass extinction.

If that happens, our actions will greatly and irreversibly change the evolutionary history of life on Earth.