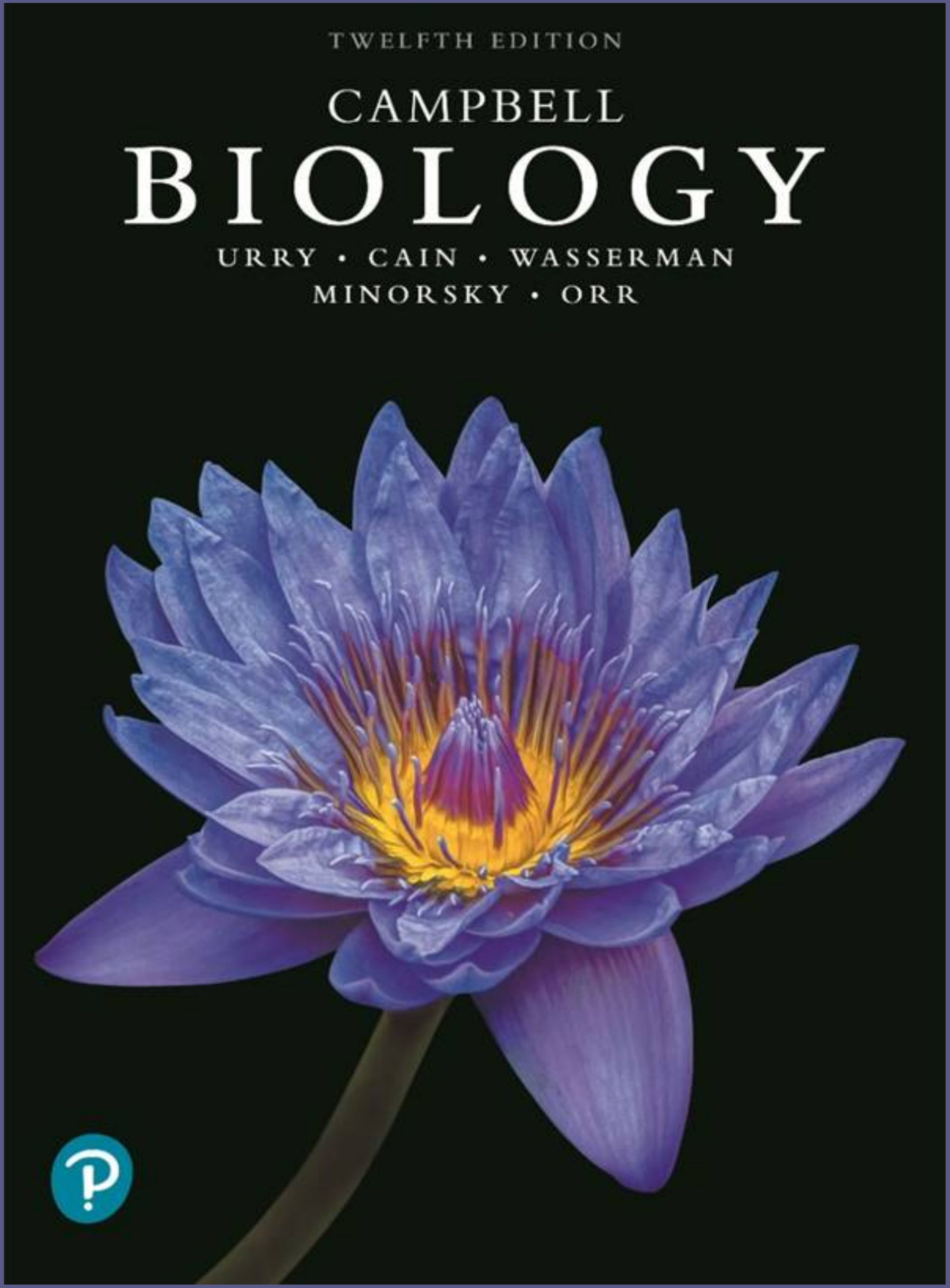


Chapter 24

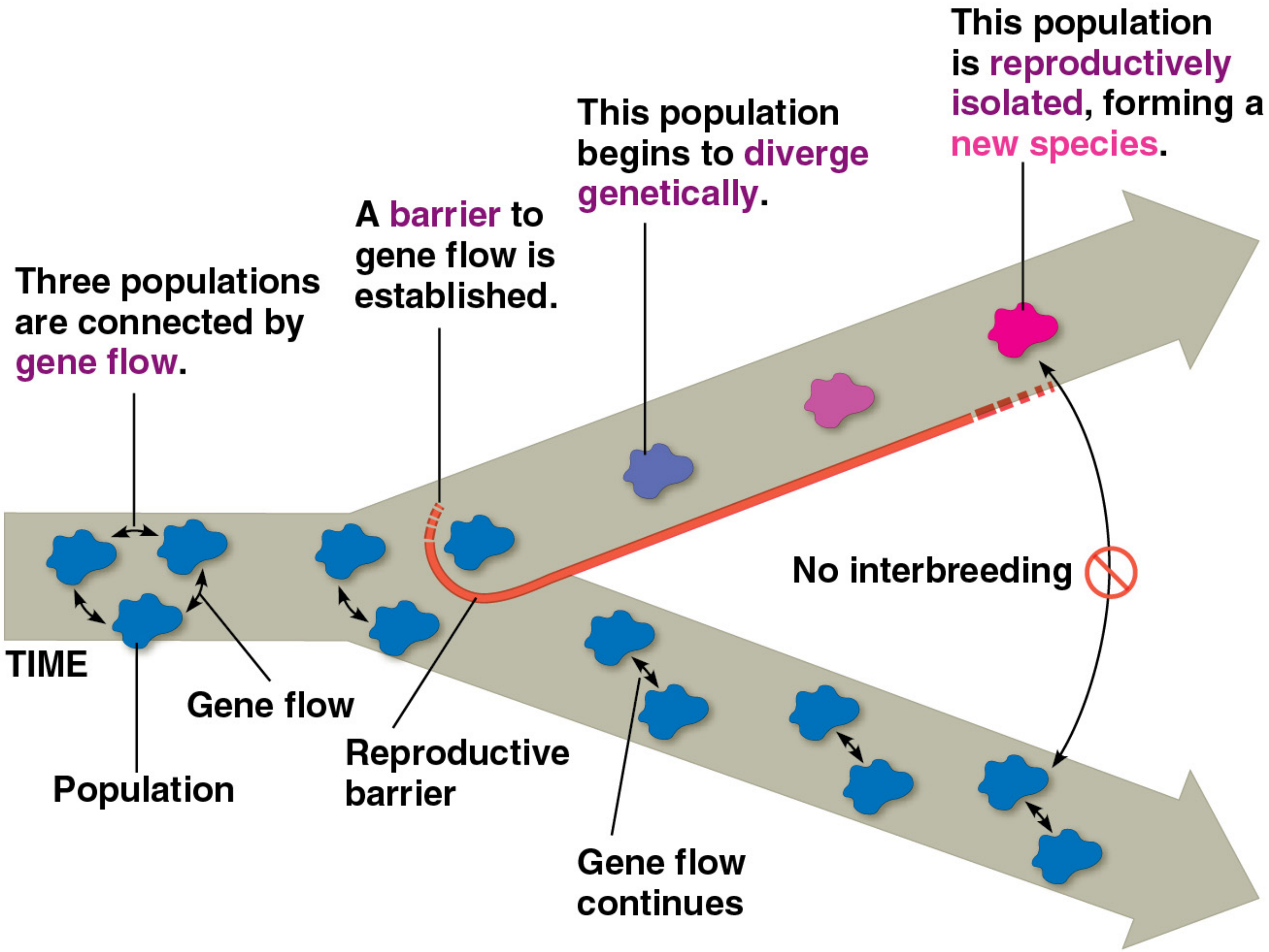
The Origin of Species

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 24.1a

Figure 24.1b

How do new species originate from existing species?



How do new species originate from existing species?

- Darwin was fascinated by **speciation**, the process by which one species splits into two species
- Speciation produced the tremendous diversity of life, and helps to explain the unity of life

- Speciation forms a conceptual bridge between the processes of microevolution and macroevolution
  - **Microevolution** consists of changes in allele frequency in a population over time
  - **Macroevolution** refers to broad patterns of evolutionary change above the species level

Animation: Macroevolution

CONCEPT 24.1: The biological species concept emphasizes reproductive isolation

- The word *species* is Latin for “kind” or “appearance”
- Comparisons of physiology, biochemistry, and DNA sequence generally confirm that morphologically distinct species are discrete groups

The Biological Species Concept

- According to the **biological species concept**, a **species** is a group of populations whose members
  - Have the potential to interbreed in nature
  - Produce viable, fertile offspring
  - Do not produce viable, fertile offspring with members of other such groups
- Gene flow between populations holds a species together genetically

Figure 24.2

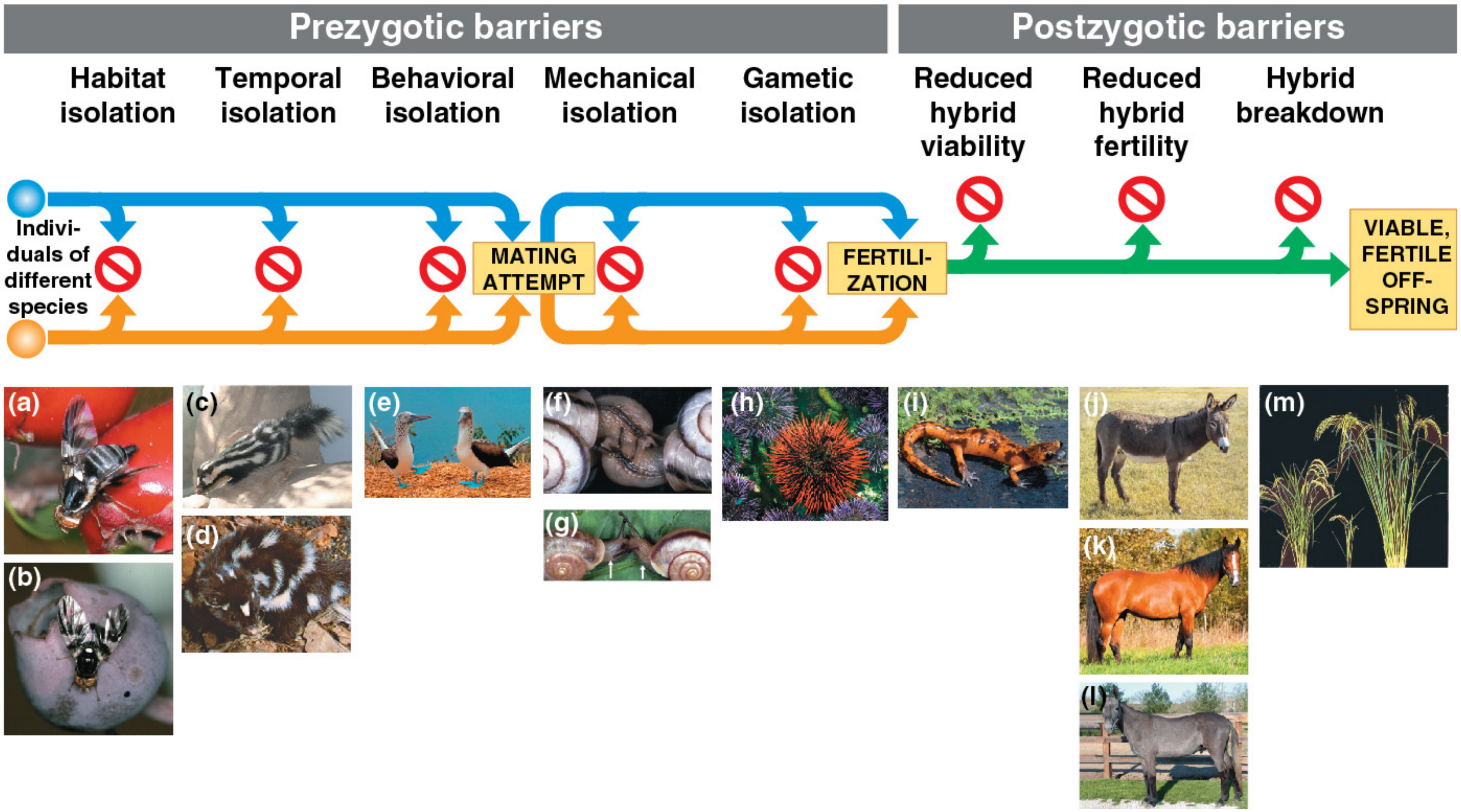
(a) Similarity between different species

(b) Diversity within a species

Reproductive Isolation

- **Reproductive isolation** results when biological barriers impede members of two species from interbreeding and producing viable, fertile offspring
- These barriers limit the formation of **hybrids**, offspring that result from interspecific mating
- Reproductive isolation can be classified by whether factors act before or after fertilization

Figure 24.3



Prezygotic barriers
Postzygotic barriers
Habitat isolation
Temporal isolation
Behavioral isolation
Mechanical isolation
Gametic isolation
Reduced hybrid viability
Reduced hybrid fertility
Hybrid breakdown
Individuals of different species
MATING ATTEMPT
FERTILIZATION
VIABLE, FERTILE OFFSPRING
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)

- **Prezygotic barriers** block fertilization from occurring by
  - Impeding different species from attempting to mate
  - Preventing the successful completion of mating
  - Hindering fertilization if mating is successful

Figure 24.3a

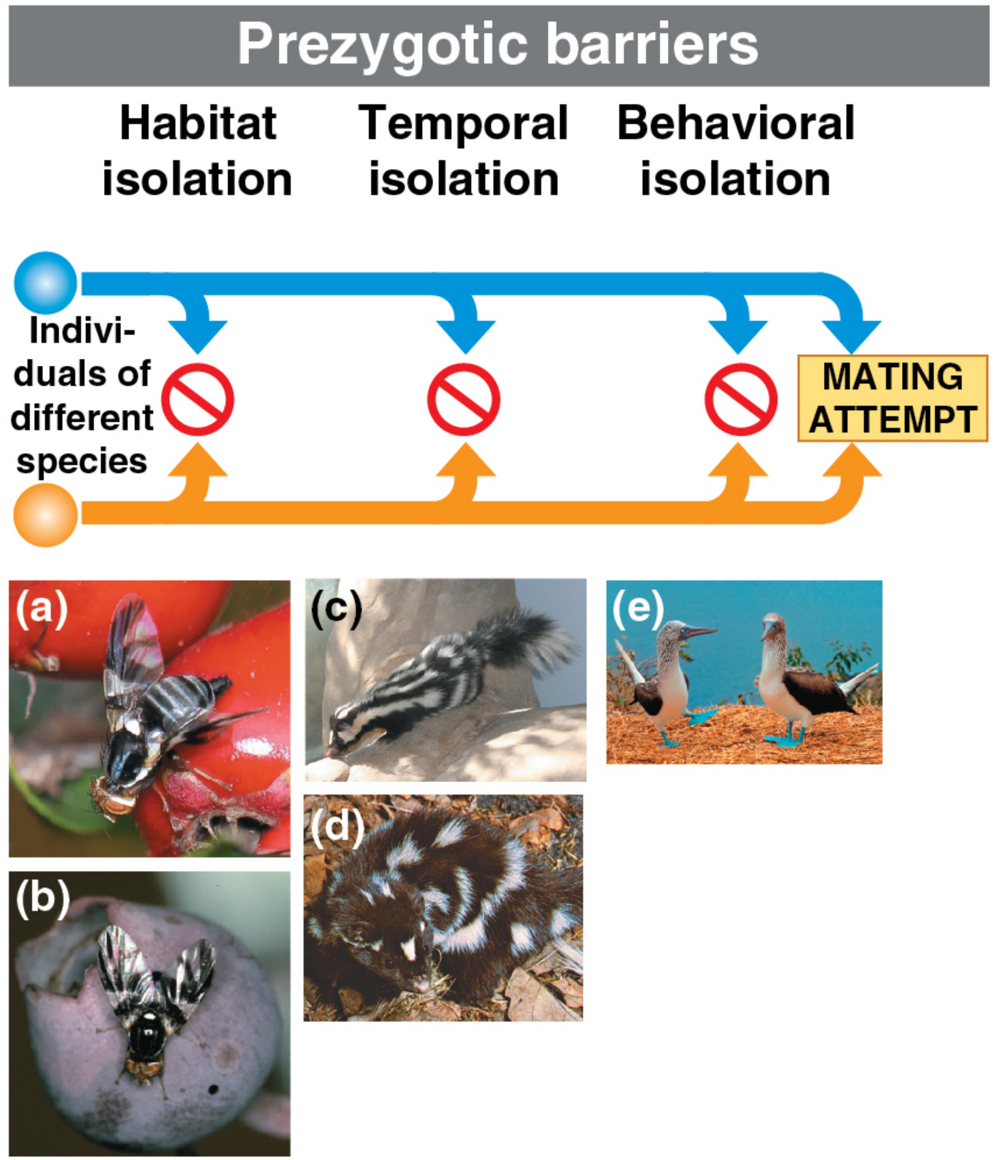

Prezygotic barriers
Habitat isolation
Temporal isolation
Behavioral isolation
Individuals of different species
MATING ATTEMPT
(a)
(b)
(c)
(d)
(e)

Figure 24.3 Exploring Reproductive Barriers (Part 1: Prezygotic Barriers—Habitat Isolation)

Habitat Isolation

- Two species that occupy different habitats within the same area may encounter each other rarely, if at all
  - For example, apple maggot flies are isolated from blueberry maggot flies because they feed and lay eggs on different fruits

Figure 24.3aa and 24.3ab

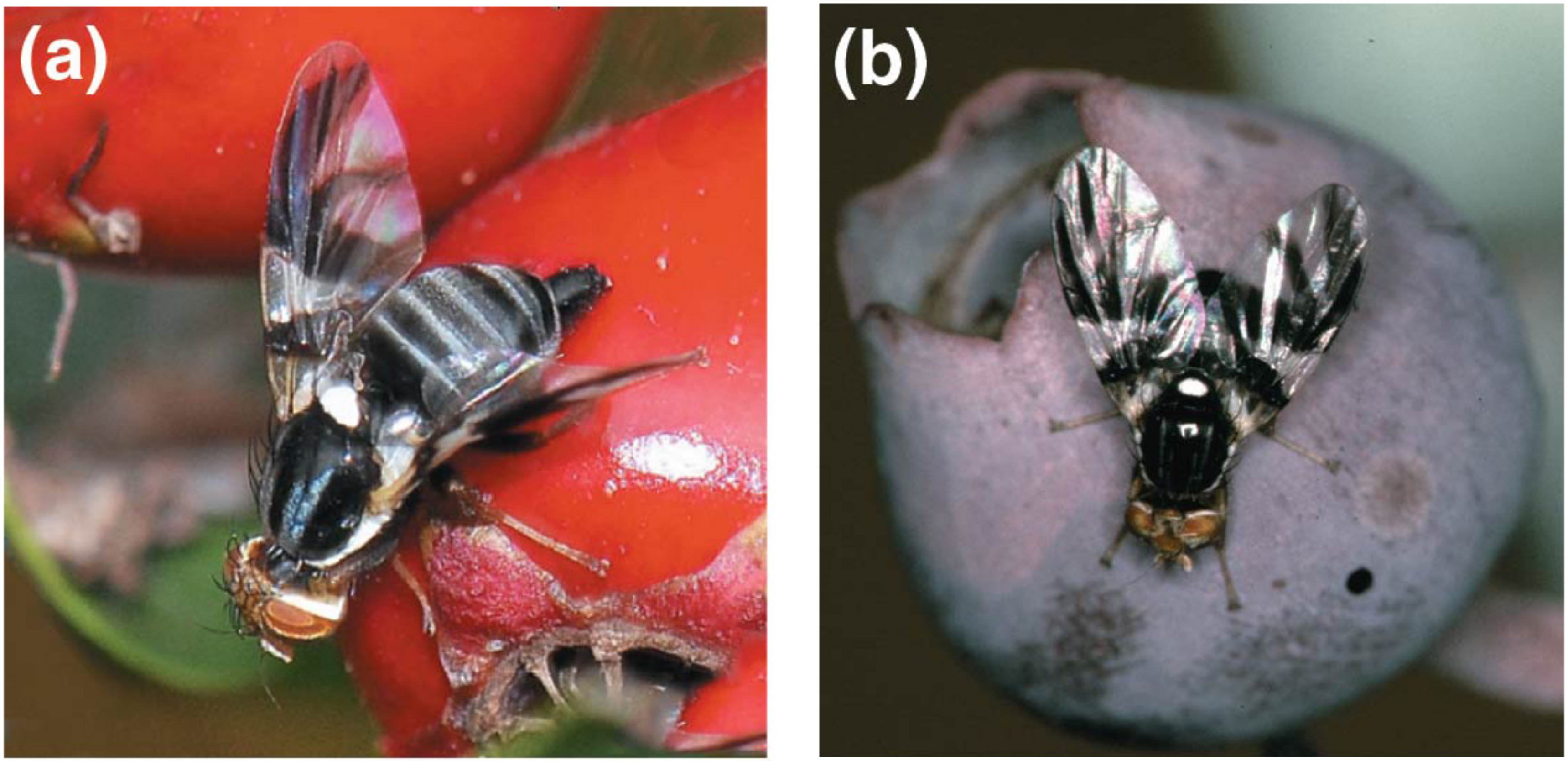


Figure 24.3 Exploring Reproductive Barriers (Part 1: Prezygotic Barriers—Temporal Isolation)

Temporal Isolation

- Species that breed at different times of the day, in different seasons, or different years cannot mix their gametes
  - For example, western spotted skunks mate in summer and eastern spotted skunks mate in winter

Figure 24.3ac and 24.3ad

Figure 24.3 Exploring Reproductive Barriers (Part 1: Prezygotic Barriers—Behavioral Isolation)

Behavioral Isolation

- Courtship rituals and other behaviors unique to a species are effective barriers to mating
  - For example, many species, including blue-footed boobies, mate only after a unique courtship display

Figure 24.3ae

Video: Blue-Footed Boobies Courtship Ritual

Video: Albatross Courtship Ritual

Video: Giraffe Courtship Courtship Ritual

Figure 24.3b

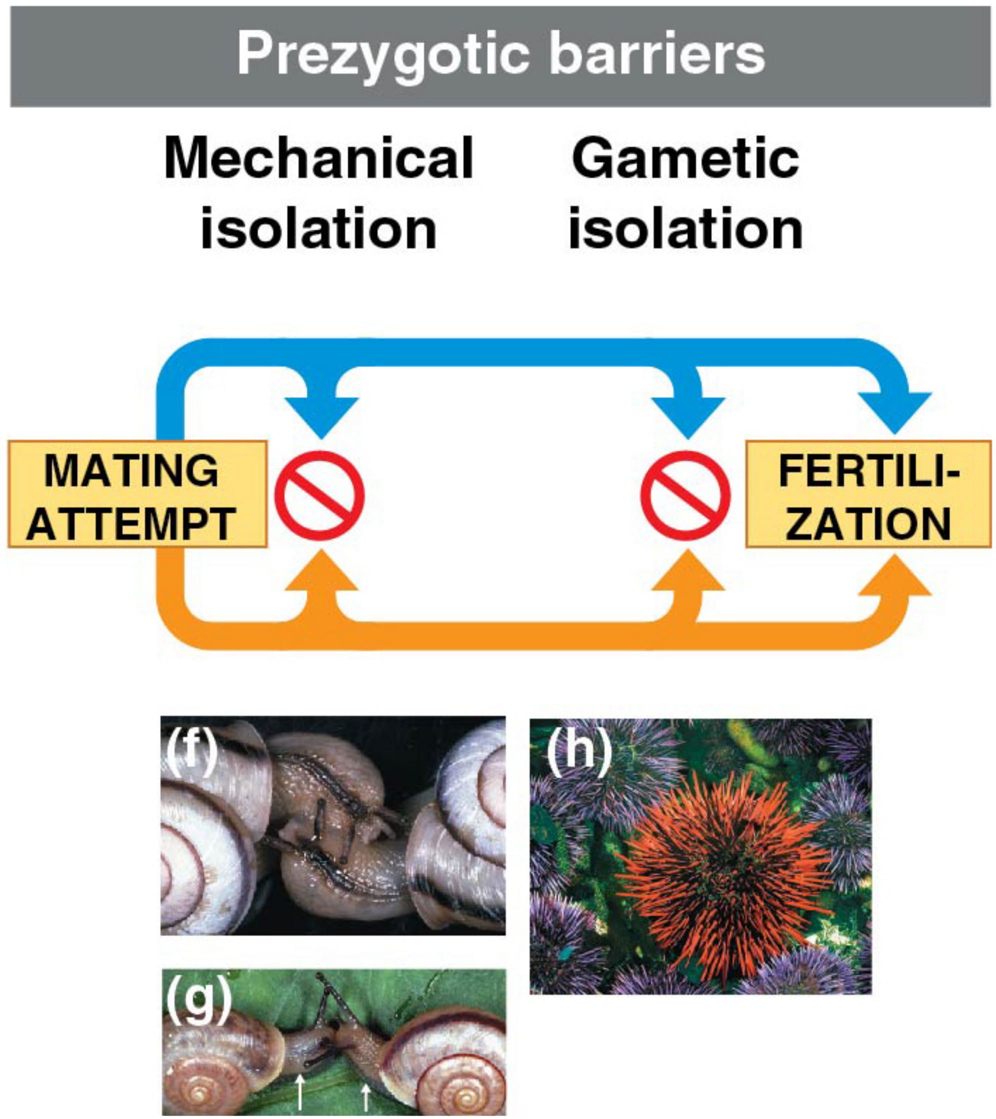

Prezygotic barriers
Mechanical isolation
Gametic isolation
MATING ATTEMPT
FERTILI-ZATION
(f)
(g)
(h)

Figure 24.3 Exploring Reproductive Barriers (Part 2: Prezygotic Barriers—Mechanical Isolation)

Mechanical Isolation

- Mating is attempted, but morphological differences prevent its successful completion
  - For example, the genital openings of snails in the genus *Bradybaena* do not align if their shells spiral in opposite directions

Figure 24.3ba and 24.3bb

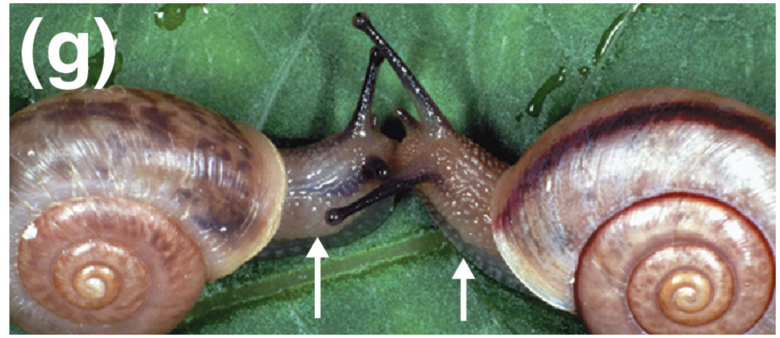
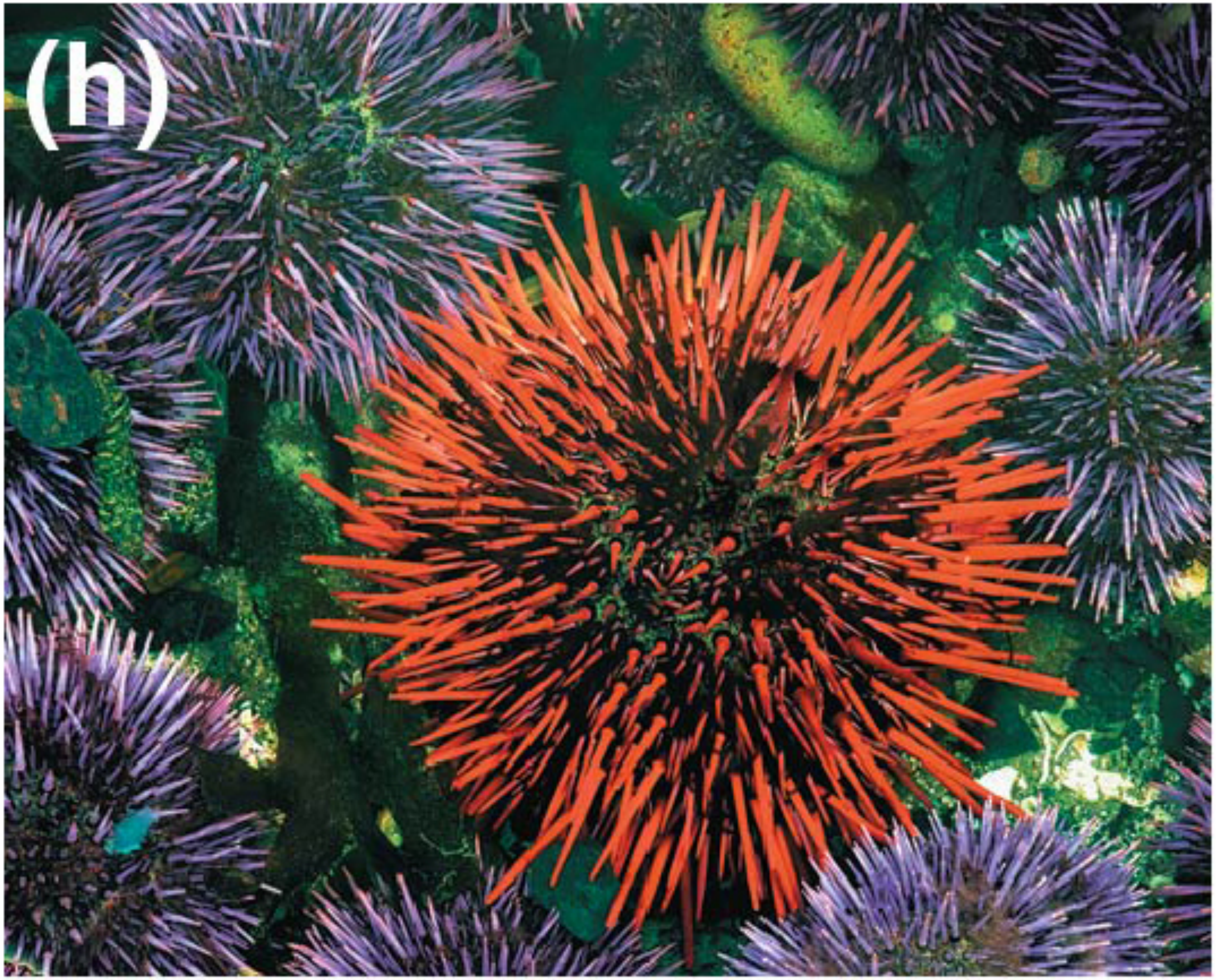


Figure 24.3 Exploring Reproductive Barriers (Part 2: Prezygotic Barriers—Gametic Isolation)

Gametic Isolation

- Sperm of one species may not be able to fertilize eggs of another species
  - For example, surface proteins on the sperm and eggs of different sea urchin species bind poorly to each other, preventing fusion and zygote formation

Figure 24.3bc



Video: Prezygotic Barriers to Mating in Galapagos Finches by Peter and Rosemary Grant

- **Postzygotic barriers** prevent hybrid zygotes from developing into viable, fertile adults through
  - Reduced hybrid viability
  - Reduced hybrid fertility
  - Hybrid breakdown

Figure 24.3c

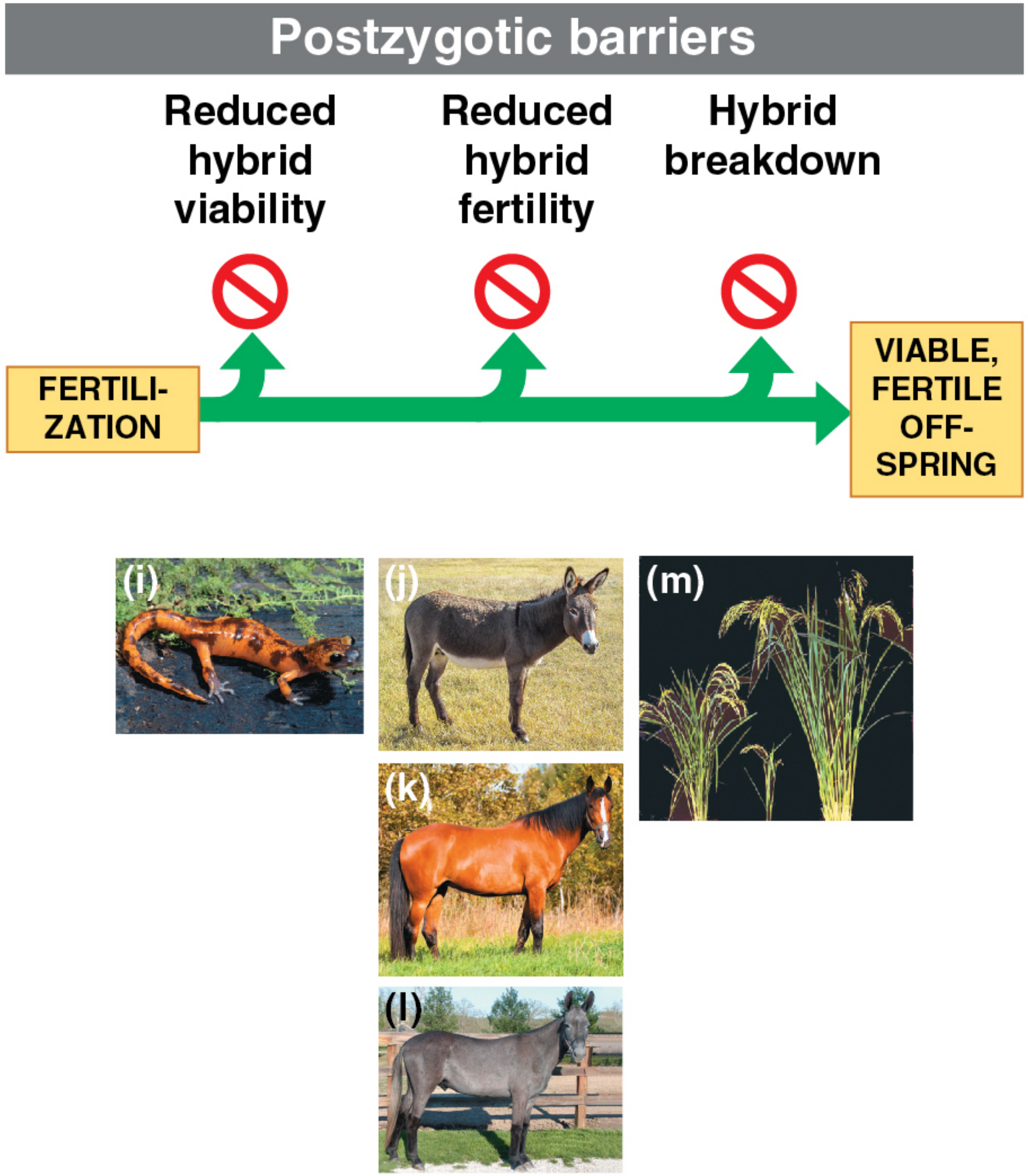

Postzygotic barriers
Reduced hybrid viability
Reduced hybrid fertility
Hybrid breakdown
FERTILI-ZATION
VIABLE, FERTILE OFF-SPRING
(i)
(j)
(k)
(l)
(m)

Figure 24.3 Exploring Reproductive Barriers (Part 3: Postzygotic Barriers—Reduced Hybrid Viability)

Reduced Hybrid Viability

- Genes of different parent species may interact in ways that impair the hybrid's development or survival in its environment
  - For example, the hybrid offspring of different subspecies of salamanders of the genus *Ensatina* do not usually complete development

Figure 24.3ca

Figure 24.3 Exploring Reproductive Barriers (Part 3: Postzygotic Barriers—Reduced Hybrid Fertility)

Reduced Hybrid Fertility

- Meiosis may fail to produce normal gametes, resulting in sterility, if the parent species have chromosomes of different number or structure
  - For example, the hybrid offspring of a male donkey and a female horse, a mule, is robust, but sterile

Figure 24.3cb , 24.3cc and 24.3cd

Figure 24.3 Exploring Reproductive Barriers (Part 3: Postzygotic Barriers—Hybrid Breakdown)

Hybrid Breakdown

- First-generation hybrids are viable and fertile, but offspring in the next generation are feeble or sterile
  - For example, hybrids between certain strains of cultivated rice are vigorous and fertile, but members of the next generation are small and sterile

Figure 24.3ce

Limitations of the Biological Species Concept

- The number of species to which the biological species concept can be usefully applied is limited
  - For example, it cannot be applied to fossils or asexual organisms (including all prokaryotes), because mating cannot be observed

- The biological species concept emphasizes absence of gene flow, but gene flow occurs between many morphologically and ecologically distinct species
  - For example, grizzly bears and polar bears are distinct species, but they can occasionally mate to produce “grolar bears”

Figure 24.4

◀ **Grizzly bear (*U. arctos*)**

▼ **Polar bear (*U. maritimus*)**

◀ **Hybrid "grolar bear"**

Other Definitions of Species

- The biological species concept emphasizes the separateness of different species due to reproductive barriers
- Several other definitions emphasize the unity within a species

- The **morphological species concept** distinguishes a species by its structural features
- It applies to sexual and asexual species and does not require information on the extent of gene flow
- A disadvantage is that it relies on subjective criteria

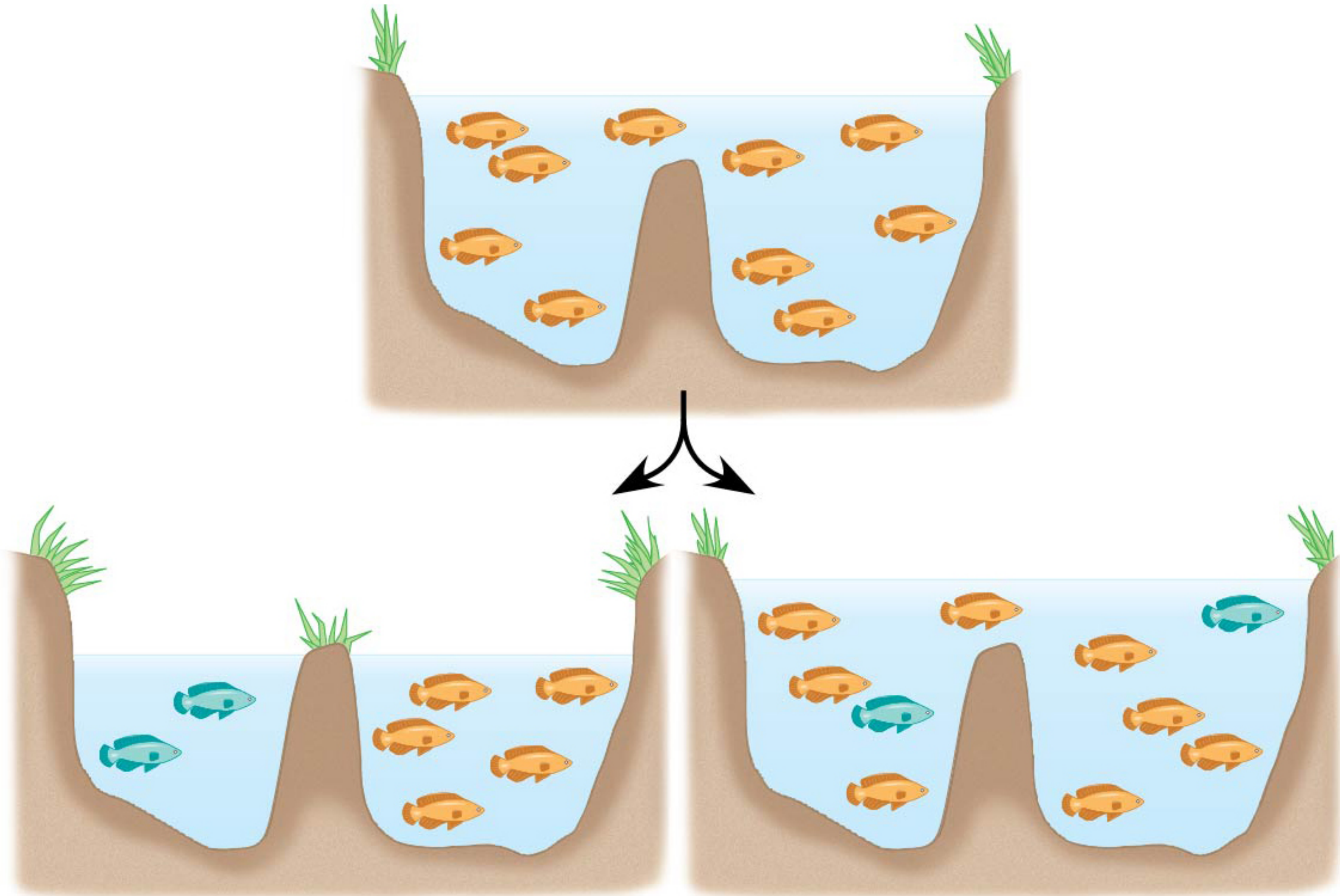
- The **ecological species concept** defines a species by its ecological niche, the sum of its interactions with the nonliving and living parts of the environment
- It applies to sexual and asexual species and emphasizes the role of disruptive selection

- More than 20 other species definitions have been proposed
- The usefulness of each depends on the situation and the research questions being asked

CONCEPT 24.2: Speciation can take place with or without geographic separation

- Speciation can occur in two ways:
  - Allopatric speciation—populations are geographically isolated
  - Sympatric speciation—populations are not geographically isolated

Figure 24.5



(a) Allopatric speciation

(b) Sympatric speciation

Allopatric ("Other Country") Speciation

- In **allopatric speciation**, gene flow is interrupted when a population is divided into geographically isolated subpopulations
  - For example, the water in a lake may subside and form two lakes with separated populations

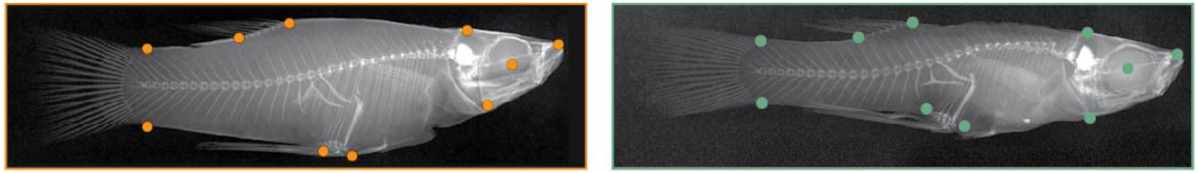
- Allopatric speciation can occur without geographic change when individuals colonize a remote area
  - For example, the flightless cormorant of the Galápagos likely originated from a flying species on the mainland

The Process of Allopatric Speciation

- The effect of a geographic barrier depends on the ability of organisms to move about
  - For example, a canyon may create a barrier for small rodents, but not birds, coyotes, or the pollen and seeds of flowering plants

- The gene pools of isolated populations may diverge through mutation, natural selection, and genetic drift
- Reproductive isolation may arise as a by-product of genetic divergence
  - For example, isolated populations of mosquitofish have become reproductively isolated as a result of selection under different levels of predation

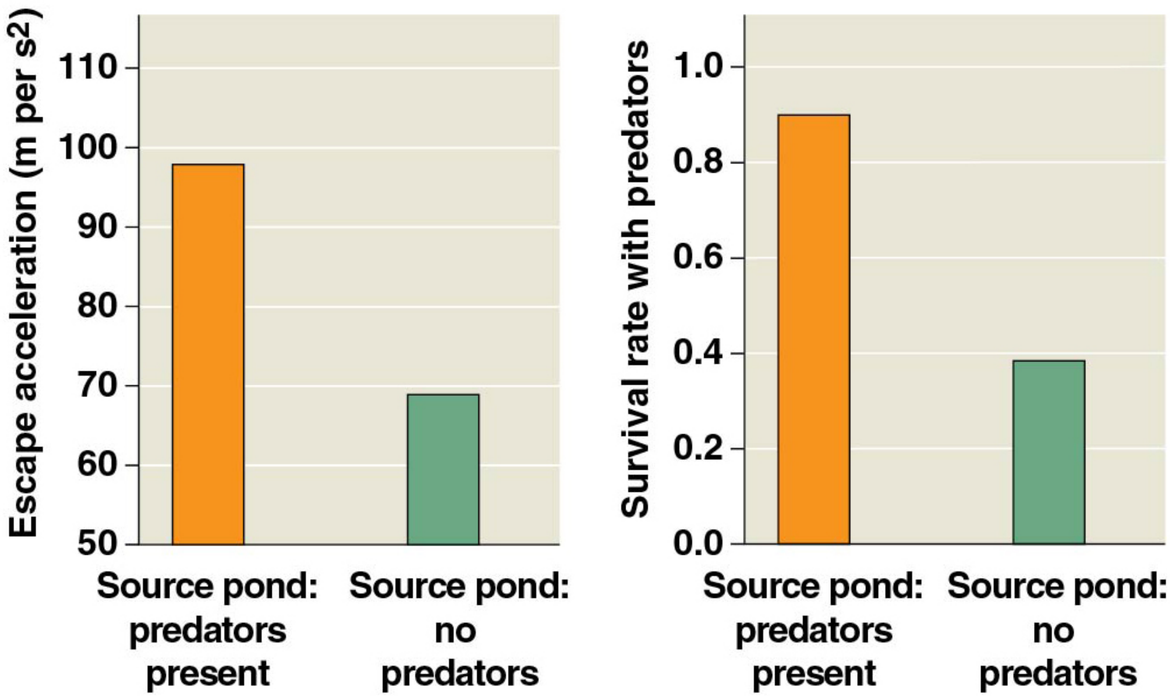
Figure 24.6



With predators: body shape that enables rapid bursts of speed

Without predators: body shape that favors long, steady swimming

(a) Differences in body shape



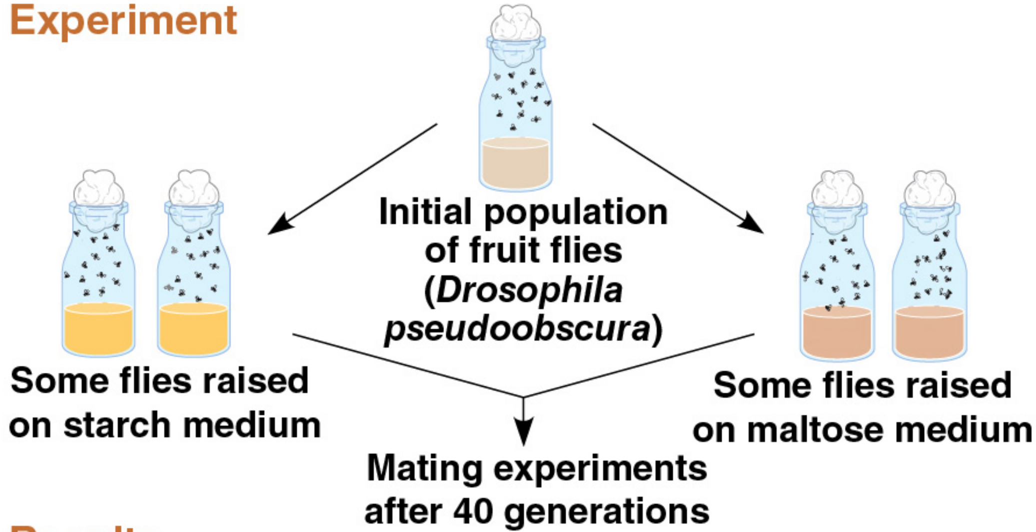
(b) Differences in escape acceleration and survival

Evidence of Allopatric Speciation

- Reproductive barriers develop between isolated laboratory populations subjected to different environmental conditions
  - For example, fruit flies taken from a single parent population, but fed different diets over several generations, prefer mates adapted to the same diet

Figure 24.7

Experiment



Results

		Female	
		Starch	Maltose
Male	Starch	22	9
	Maltose	8	20

Number of matings in experimental group

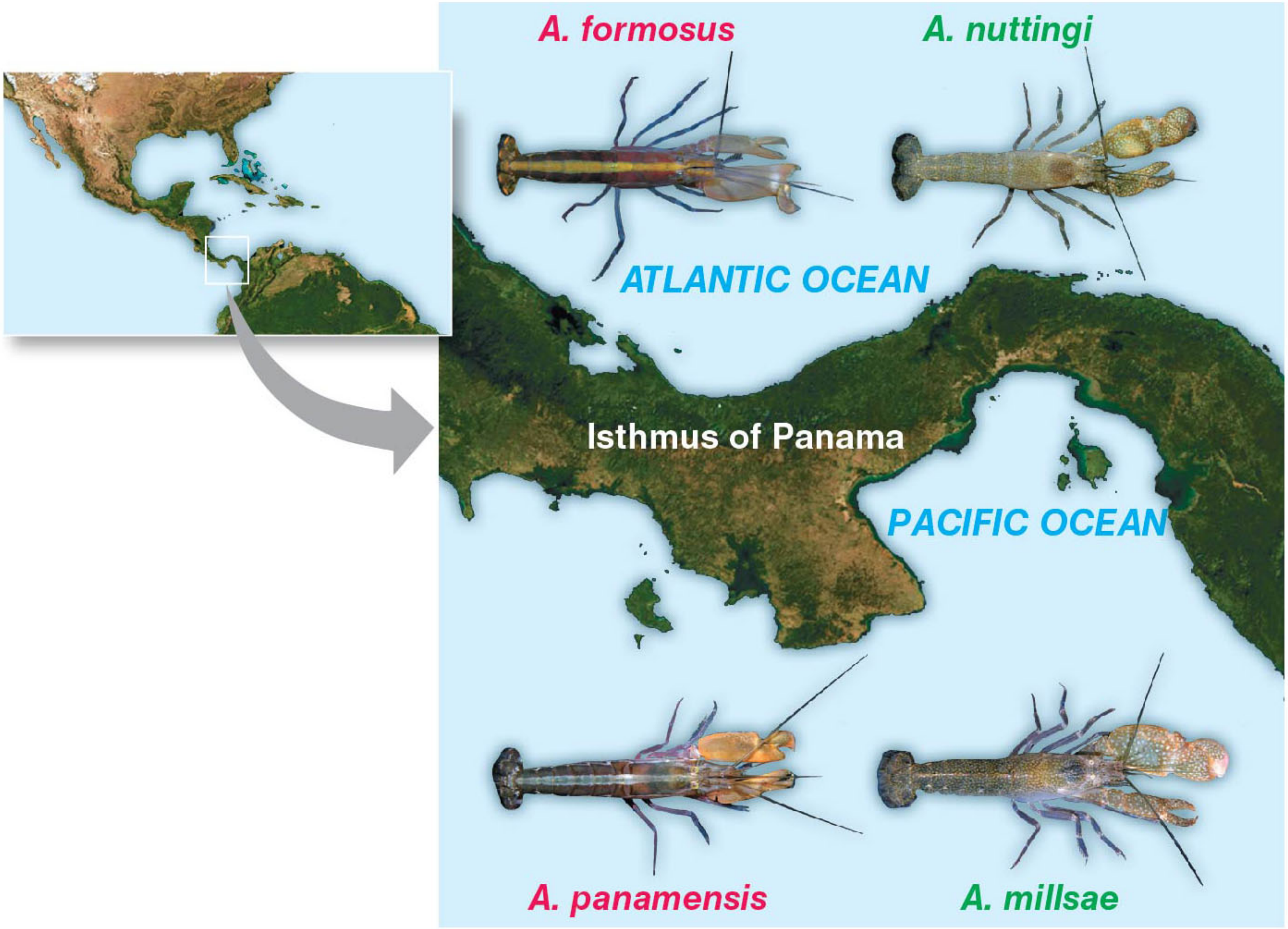
		Female	
		Starch population 1	Starch population 2
Male	Starch population 1	18	15
	Starch population 2	12	15

Number of matings in control group

Data from D. M. B. Dodd, Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*, *Evolution* 43:1308-1311 (1989).

- There is evidence for allopatric speciation in nature
  - For example, sister species of snapping shrimp (*Alpheus*) diverged 9 to 3 million years ago as populations were isolated by the Isthmus of Panama
  - Sister species that lived in deep water diverged first

Figure 24.8


A. formosus
A. nuttingi
ATLANTIC OCEAN
Isthmus of Panama
PACIFIC OCEAN
A. panamensis
A. millsae

- Isolated or highly subdivided regions usually have more species than those with fewer barriers
  - For example, the Hawaiian Islands have many unique plants and animals
- Reproductive isolation between populations generally increases with geographic distance

- Physical separation due to geographic isolation prevents interbreeding, but is not a biological barrier to reproduction
- Biological barriers are intrinsic to the organisms themselves

Sympatric ("Same Country") Speciation

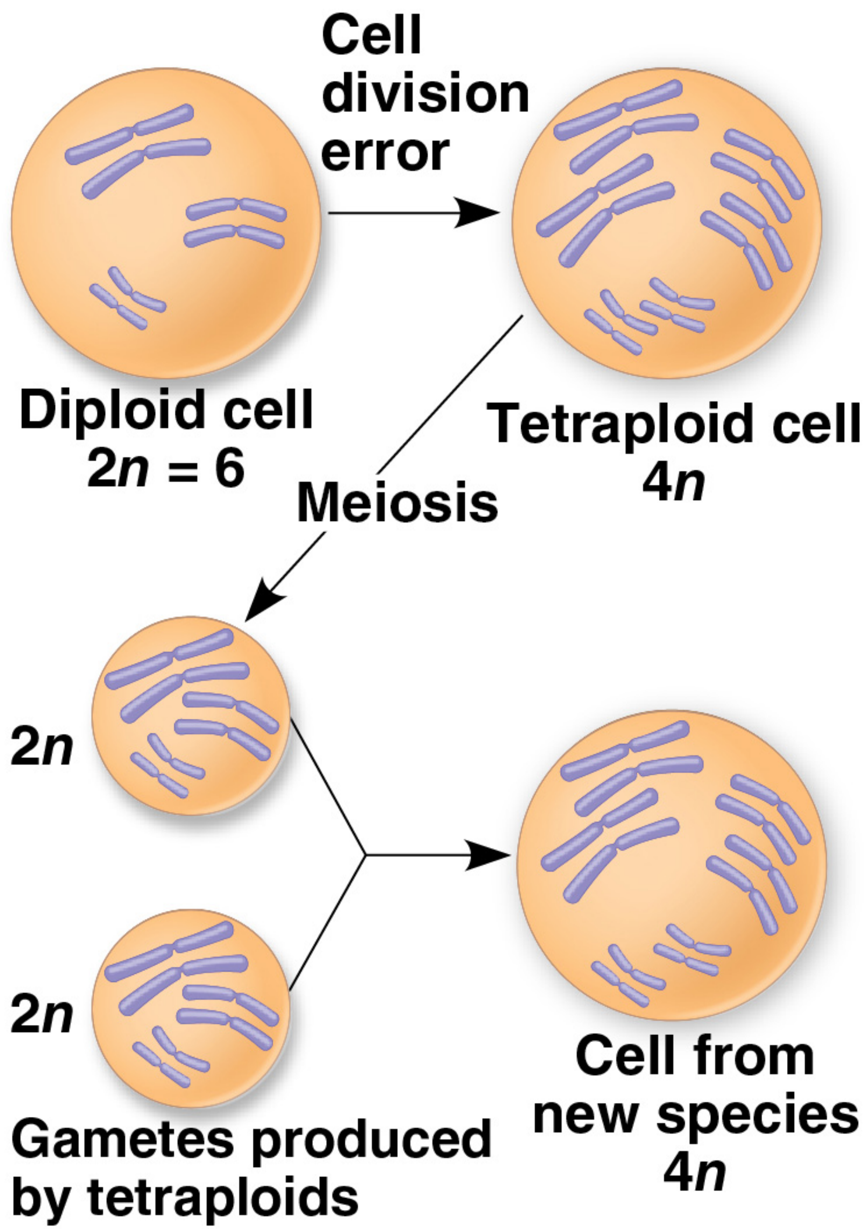
- In **sympatric speciation**, speciation occurs in populations that live in the same geographic area
- Sympatric speciation is less common than allopatric speciation
- It occurs if gene flow is reduced by factors such as
  – Polyploidy
  – Sexual selection
  – Habitat differentiation

Polyploidy

- Accidents during cell division can cause **polyploidy**, the presence of extra sets of chromosomes
- This process can form a new species within a single generation without geographic separation
- Polyploidy is common in plants but rare in animals
- There are two types of polyploids: autopolyploids and allopollyploids

- **Autopolyploids** have more than two sets of chromosomes, all derived from a single species
- In plants, mitotic errors can result in the production of a tetraploid (4*n*) cell from a diploid (2*n*) cell
- Fertile offspring (4*n*) can be produced through self-fertilization or mating with among tetraploids
- Mating between tetraploids and diploids produces triploid (3*n*) offspring with reduced fertility

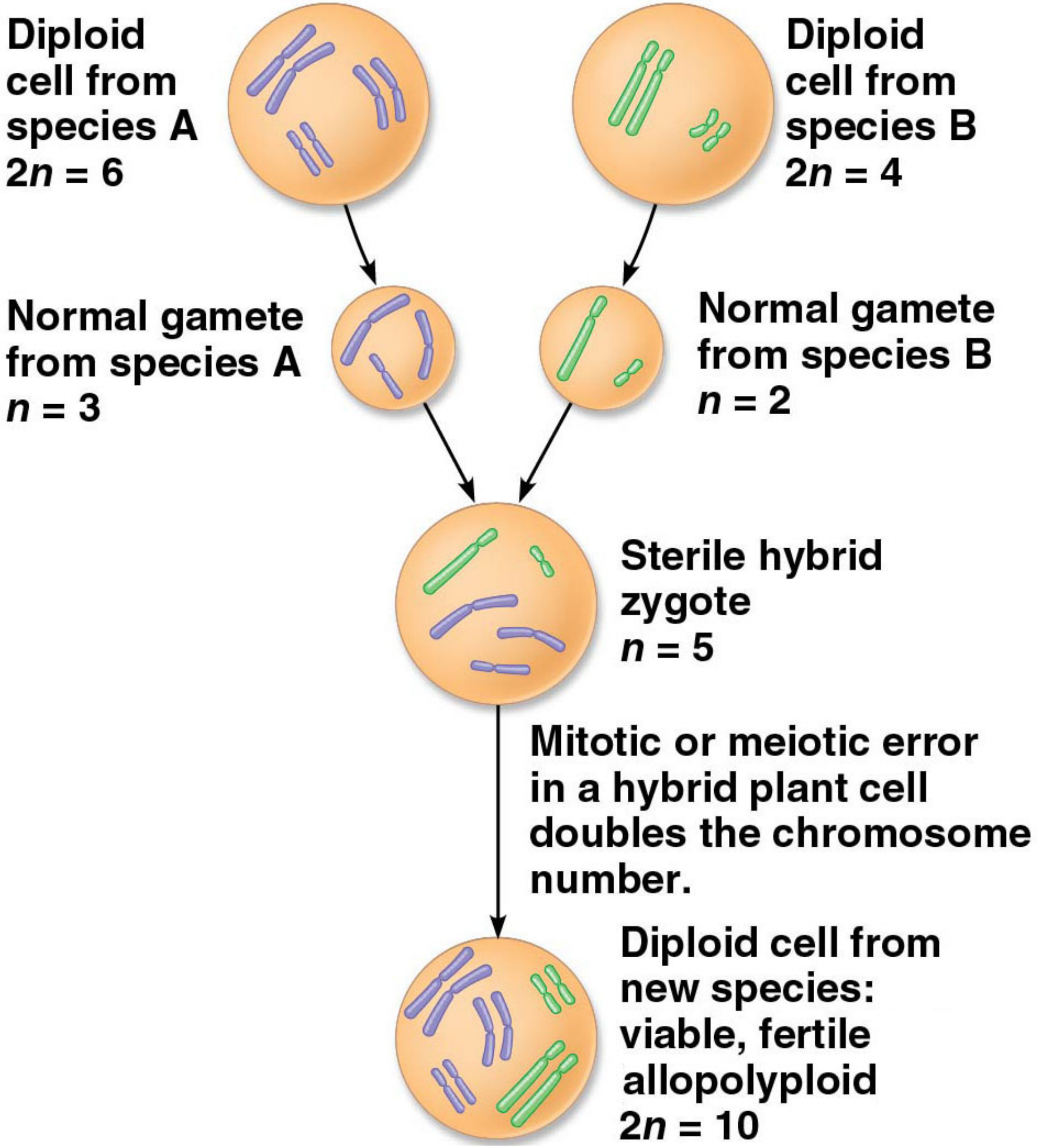
Figure 24.9



Cell division error
Diploid cell
2n = 6
Tetraploid cell
4n
Meiosis
2n
2n
Gametes produced by tetraploids
Cell from new species
4n

- **Allopolyploids** have more than two sets of chromosomes, derived from different species
- Chromosomes from different species do not pair during meiosis, resulting in hybrid sterility
- Sterile hybrids can reproduce asexually
- Allopolyploids are formed if the chromosome number doubles in subsequent generations

Figure 24.10

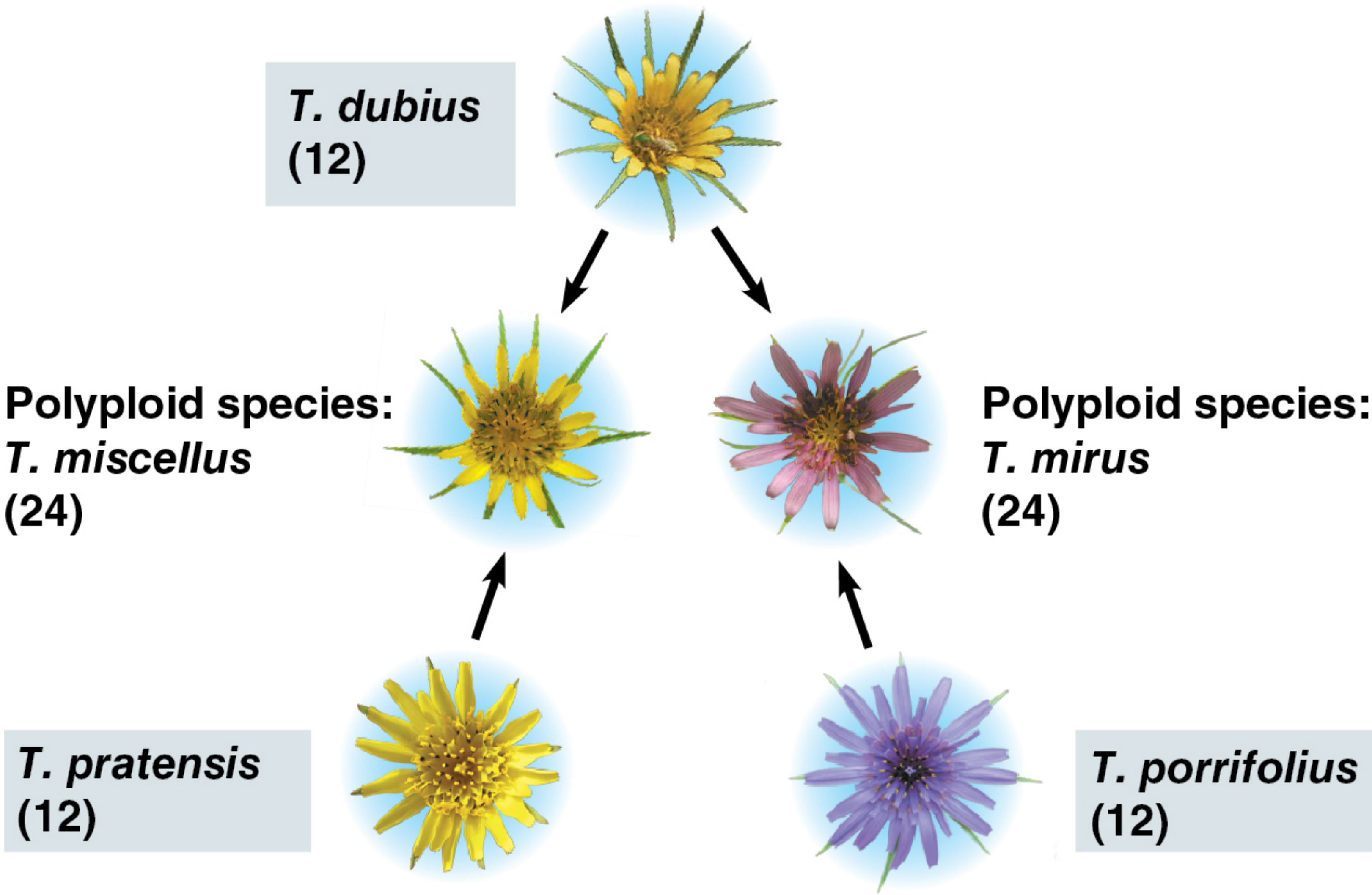


Diploid cell from species A
2n = 6
Diploid cell from species B
2n = 4
Normal gamete from species A
n = 3
Normal gamete from species B
n = 2
Sterile hybrid zygote
n = 5
Mitotic or meiotic error in a hybrid plant cell doubles the chromosome number.
Diploid cell from new species: viable, fertile allopolyploid
2n = 10

- Allopolyploids can successfully interbreed with each other, but not with either parent species
- The diploid number of the new allopolyploid species equals the sum of the diploid number of both parents

- At least five new plant species have originated by polyploid speciation since 1850
  - For example, two allopolyploid species have evolved from three diploid parent species in the genus *Tragopogon*

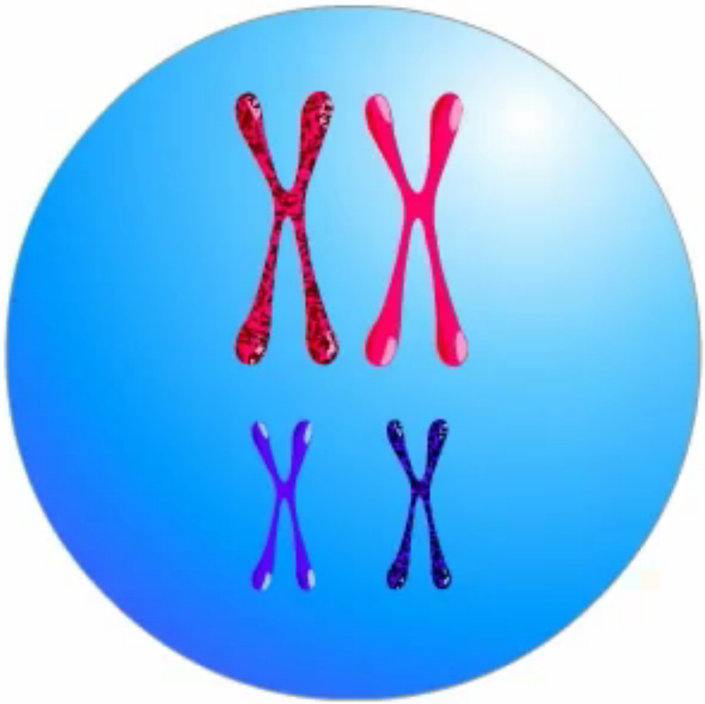
Figure 24.11



T. dubius
(12)
Polyploid species:
T. miscellus
(24)
Polyploid species:
T. mirus
(24)
T. pratensis
(12)
T. porrifolius
(12)

- Many important agricultural crops (oats, cotton, potatoes, tobacco, and wheat) are polyploids
- New polyploid agricultural species are produced using chemicals to induce errors in cell division

Animation: Speciation by Changes in Ploidy



Ploidy

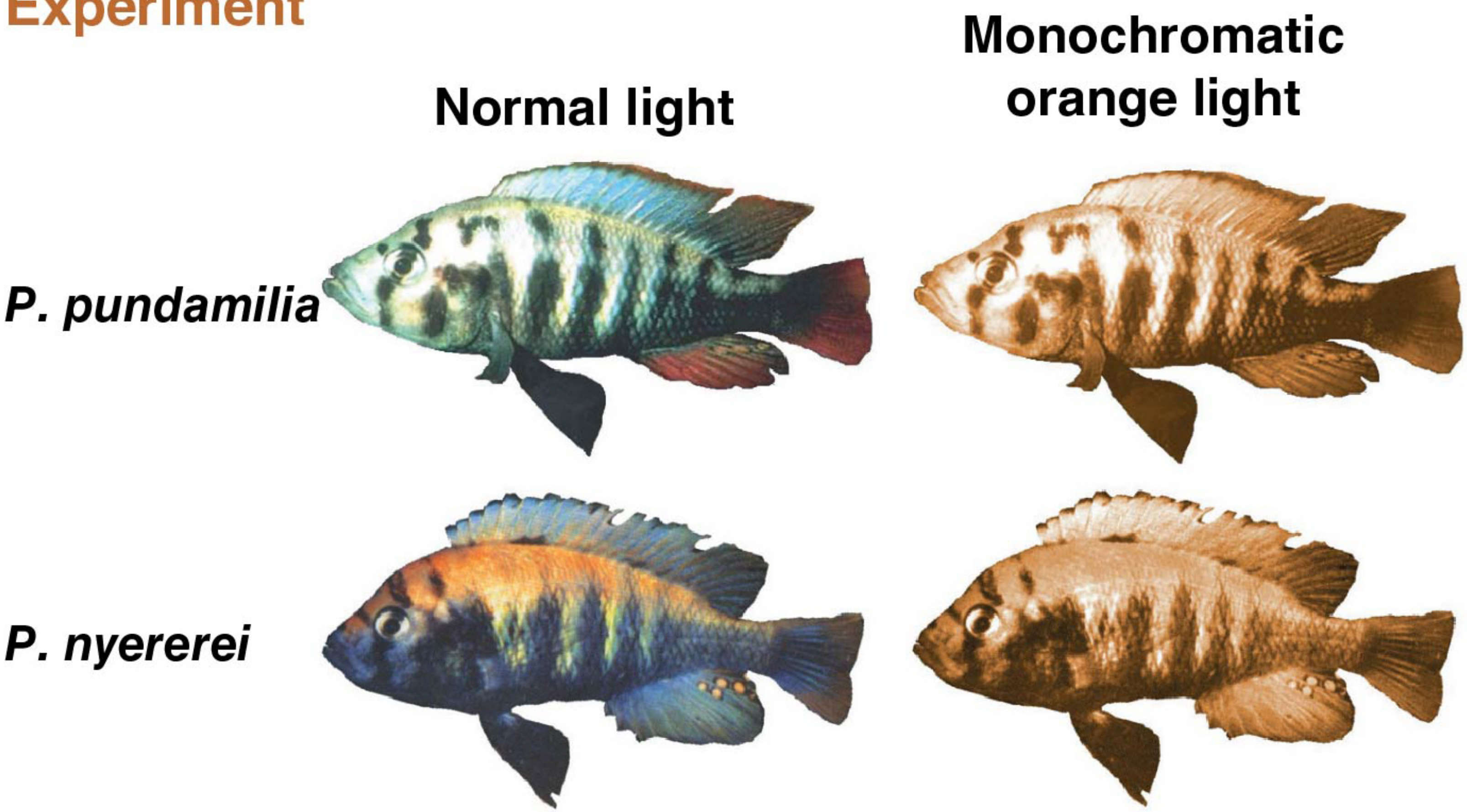
Let's use this simplified cell, which represents a *diploid* plant cell, to examine how changes in a cell's *ploidy* can contribute to the formation of new plant species. This cell has two sets of chromosomes (ploidy = 2*n*), each set consisting of one red and one blue chromosome. In a pair of *homologous chromosomes*, one chromosome originates from the female parent—indicated by the stippling—and the other originates from the male parent.

When a diploid cell undergoes *meiosis*, it normally produces four *haploid* daughter cells, each with one set of chromosomes (ploidy = *n*).

Sexual Selection

- Sympatric speciation can be driven by sexual selection
  - For example, speciation of cichlids in Lake Victoria was likely driven by female mate choice based on male breeding coloration

Experiment



Data from O. Seehausen and J. J. M. van Alphen, The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex), *Behavioral Ecology and Sociobiology* 42:1–8(1998).

Habitat Differentiation

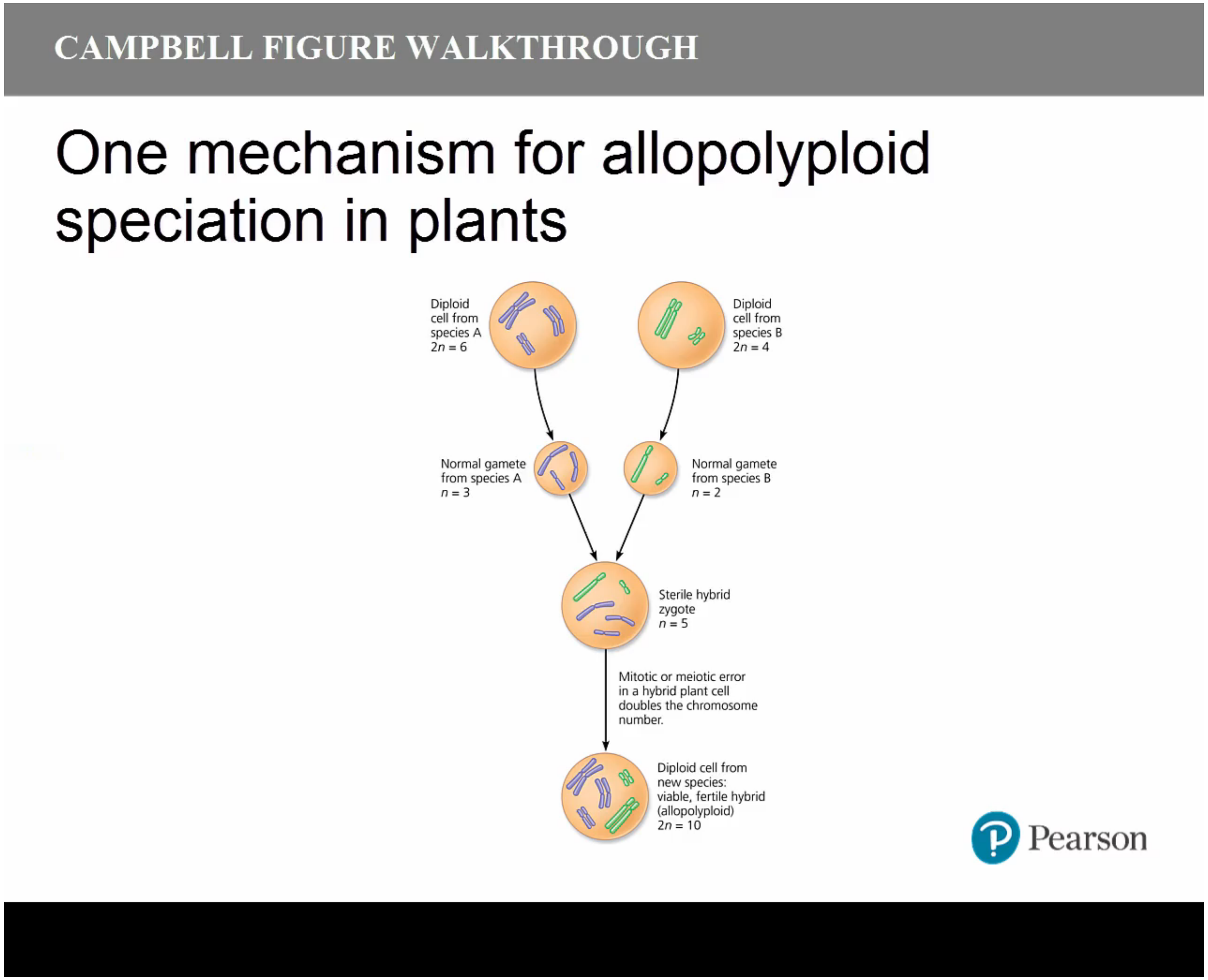
- Sympatric speciation can also result from the exploitation of new habitats or resources
  - For example, apple maggot flies evolved in North America after switching hosts from hawthorn to apple
  - Maggot flies mate on their host plant, resulting in habitat isolation between groups using different hosts
  - Apple-feeding flies develop faster than hawthorn-feeding flies, resulting in temporal isolation
  - Alleles that benefit flies using one host plant harm those using the other, causing post-zygotic isolation

Allopatric and Sympatric Speciation: *A Review*

- In allopatric speciation, geographic isolation restricts gene flow between populations
- Intrinsic barriers to reproduction arise due to genetic change driven by processes including divergent selection and genetic drift
- Reproductive barriers prevent interbreeding even if contact is restored between populations

- In sympatric speciation, a reproductive barrier isolates a subset of a population without geographic separation from the parent species
- Sympatric speciation can result from polyploidy, sexual selection, or natural selection resulting from a switch in food source or habitat

Video: Anole Lizards: An Example of Speciation



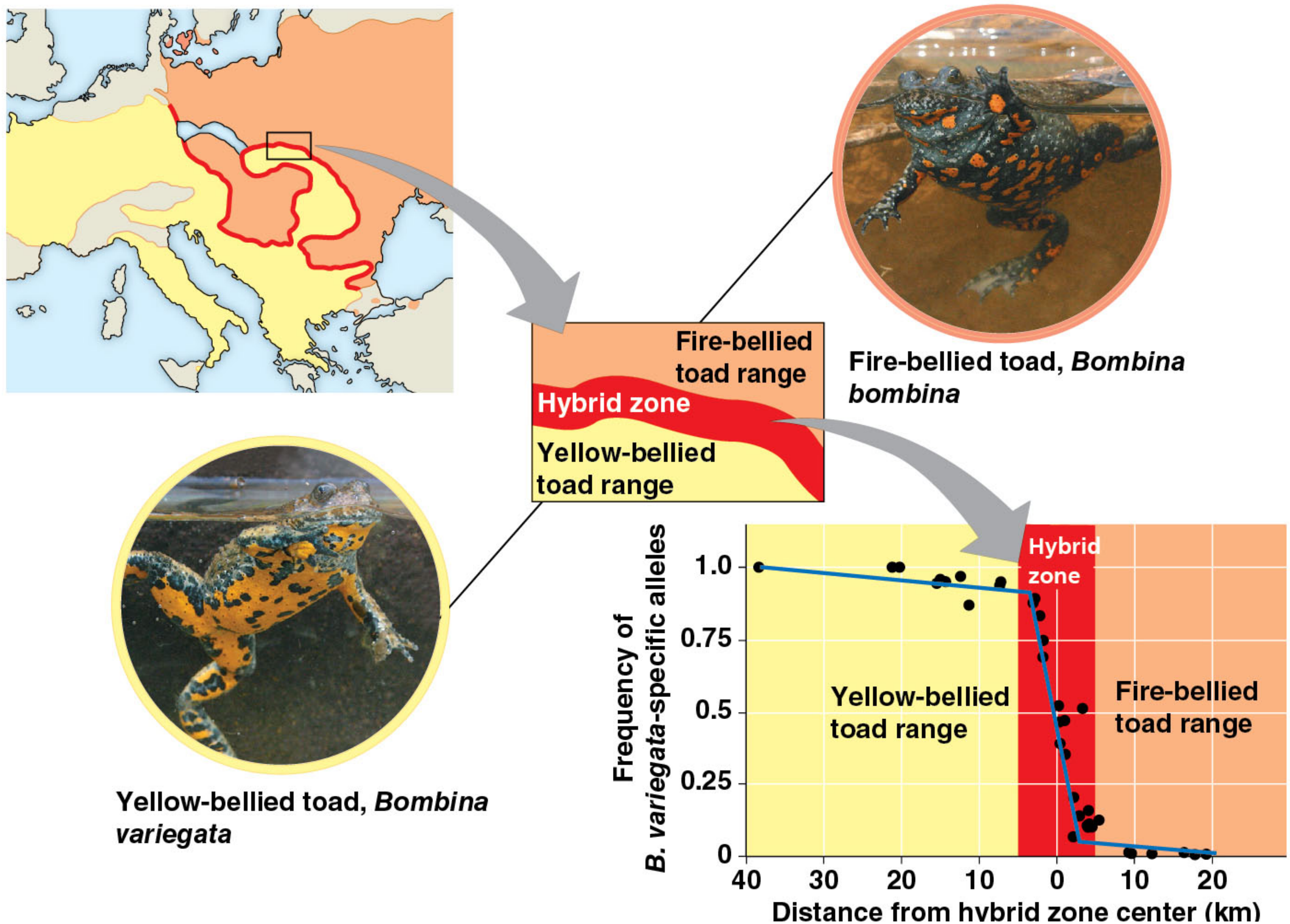
CONCEPT 24.3: Hybrid zones reveal factors that cause reproductive isolation

- A **hybrid zone** is a region in which members of different species mate and produce hybrid offspring
- Hybrids are the result of mating between species with incomplete reproductive barriers

Patterns Within Hybrid Zones

- Some hybrid zones form as narrow bands where habitats of two or more closely related species meet
  - For example, two species of toad in the genus *Bombina* interbreed in a long and narrow hybrid zone

Figure 24.13



Fire-bellied toad range
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad, *Bombina bombina*
Yellow-bellied toad, *Bombina variegata*
Frequency of *B. variegata*-specific alleles
1.0
0.75
0.5
0.25
0
40
30
20
10
0
10
20
Distance from hybrid zone center (km)
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad range

- Hybrids often have reduced survival and reproduction compared with parent species
- Outside the hybrid zone, gene flow may be impeded by obstacles such as natural selection in the different parental habitats

- Hybrid zones are typically located wherever habitats of interbreeding species meet
- This often occurs as isolated patches scattered across the landscape, rather than a continuous band

Hybrid Zones and Environmental Change

- Changing environmental conditions can result in the relocation of existing hybrid zones
  - For example, the hybrid zone between black-capped and Carolina chickadees has shifted northward in response to climate change

Figure 24.14

(a) Black-capped chickadee (*Poecile atricapillus*)

(b) Carolina chickadee (*Poecile carolinensis*)

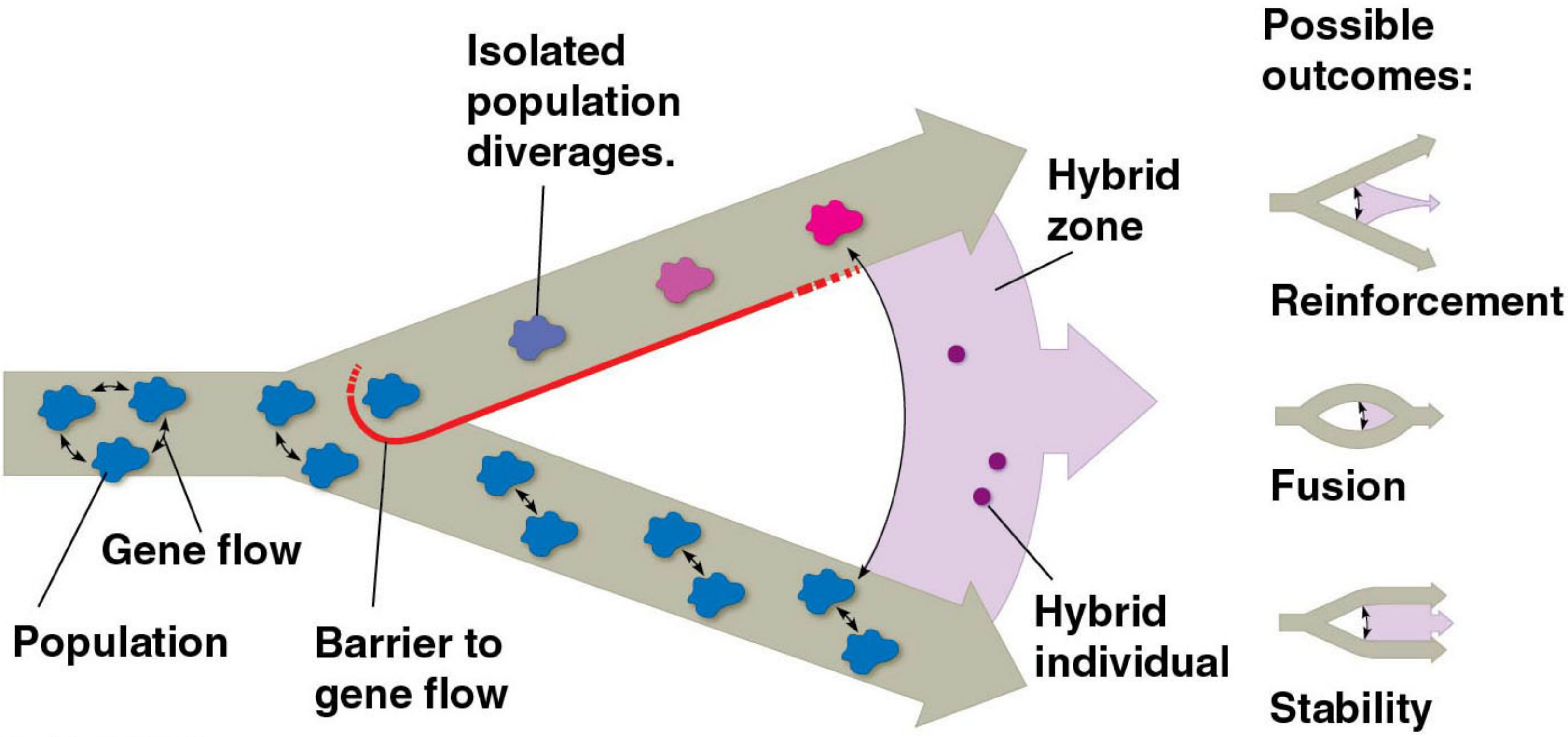
- Changing environmental conditions can drive the production of new hybrid zones
  - For example, the range of the southern flying squirrel expanded northward into the range of the northern flying squirrel in response to a series of warm winters

- Alleles can be transferred from one parent species to the other through breeding between parents and hybrids
- The transfer of novel alleles may help parent species cope with changing environments

Hybrid Zones over Time

- If hybrids do not become reproductively isolated from their parent species, then three alternate outcomes are possible:
  - Reinforcement
  - Fusion
  - Stability

Figure 24.15



Isolated population diverages.
Possible outcomes:
Hybrid zone
Reinforcement
Fusion
Stability
Gene flow
Population
Barrier to gene flow
Hybrid individual

Reinforcement: Strengthening Reproductive Barriers

- If hybrids are less fit than the parent species, then strong selection for prezygotic barriers should reduce hybrid production
- This process is called **reinforcement** because it *reinforces* reproductive barriers
- Reinforcement should be stronger for sympatric than allopatric populations

- Male pied flycatchers closely resemble male collared flycatchers in allopatric, but not sympatric populations
- When given a choice between sympatric males, females select mates of their own species
- When choosing between males from allopatric populations, females often select the other species
- Barriers to reproduction are stronger in flycatchers from sympatric than allopatric populations

Fusion: Weakening Reproductive Barriers

- There can be substantial gene flow between species if hybrids are as fit as their parents
- Reproductive barriers can weaken, and the two parent species may fuse into a single species
  - For example, pollution in Lake Victoria has reduced the ability of female cichlids to visually distinguish between males of their own and different species

Figure 24.16

Pundamilia nyererei

Pundamilia pundamilia

Pundamilia “turbid water,”
hybrid offspring from a location with turbid water

Stability: Continued Formation of Hybrid Individuals

- Extensive gene flow from outside the hybrid zone can overwhelm selection for increased reproductive isolation inside the hybrid zone
  - For example, members of both parent species of *Bombina* routinely migrate into the narrow hybrid zone, resulting in ongoing hybridization

CONCEPT 24.4: Speciation can occur rapidly or slowly and can result from changes in few or many genes

- Many questions remain concerning how long it takes for new species to form and how many genes change when one species splits into two

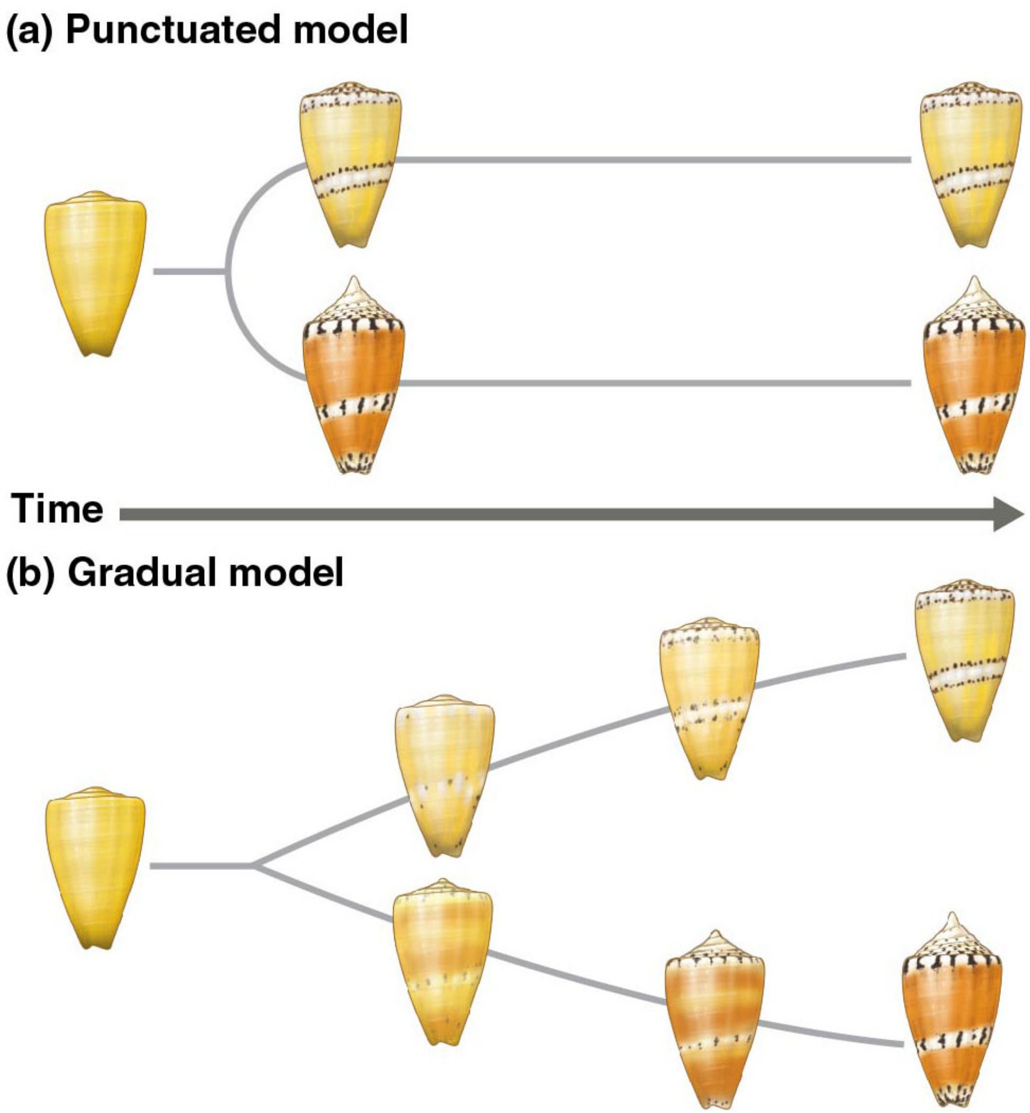
The Time Course of Speciation

- The rate of speciation can be studied by observing broad patterns in the fossil record
- Morphological and molecular data can also be used to asses the time interval between speciation events in particular groups

Patterns in the Fossil Record

- The fossil record includes many episodes where new species appear suddenly, persist unchanged through several strata, and then disappear
- **Punctuated equilibria** describes these periods of apparent stasis punctuated by sudden change
- Rather than a punctuated pattern, other species appear to have changed gradually over time

Figure 24.17



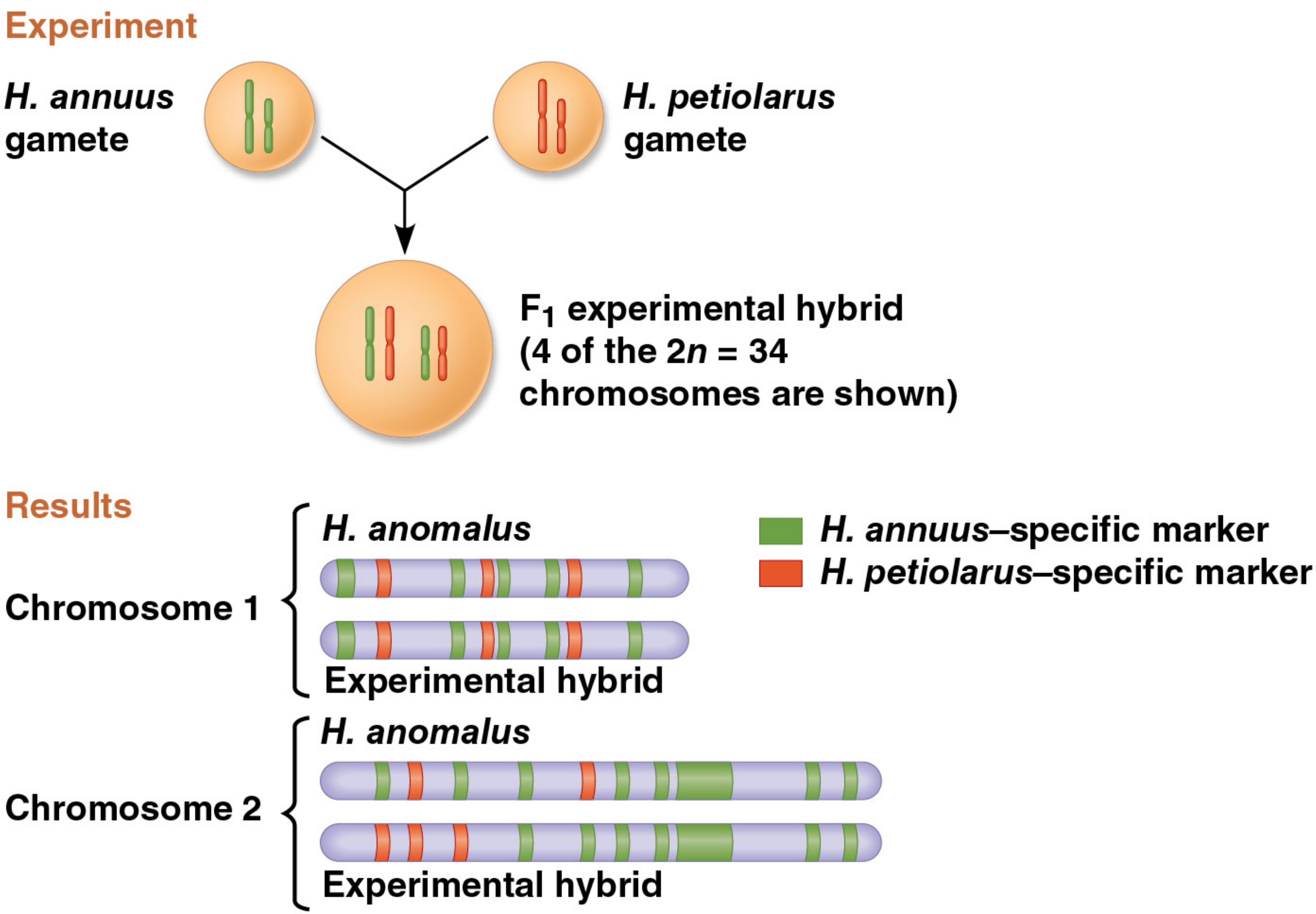
Speciation Rates

- The punctuated pattern in the fossil record and evidence from lab studies suggest that speciation can be rapid
  - For example, the sunflower *Helianthus anomalus* was formed by hybridization between two other sunflower species followed by rapid speciation

Figure 24.18

- The number of chromosomes did not change with the formation of H. *anomalus* (hybrid) sunflowers
- Natural selection produced extensive genetic change in hybrid populations over short periods of time, resulting in reproductive isolation from both parents

Figure 24.19



Data from L. H. Rieseberg et al., Role of gene interactions in hybrid speciation: evidence from ancient and experimental hybrids, *Science* 272:741–745 (1996).

- In a study of 84 groups of plants and animals, the interval between speciation events ranged from 4,000 years (cichlids) to 40 million years (beetles)
- The average time between speciation events was 6.5 million years

Studying the Genetics of Speciation

- Depending on the species, speciation might require change in a single gene or many genes
  - For example, in Japanese *Euhadra* snails, the direction of shell spiral affects mating and is controlled by a single gene

- In monkey flowers (*Mimulus*), at least two loci affect flower color, which influences pollinator preference
- Pollination dominated by either hummingbirds or bees can lead to reproductive isolation of the flowers
- In other organisms, speciation can be influenced by larger numbers of genes and gene interactions

Figure 24.20

(a) *Mimulus lewisii*

(b) *M. lewisii* with *M. cardinalis* allele

(c) *Mimulus cardinalis*

(d) *M. cardinalis* with *M. lewisii* allele

From Speciation to Macroevolution

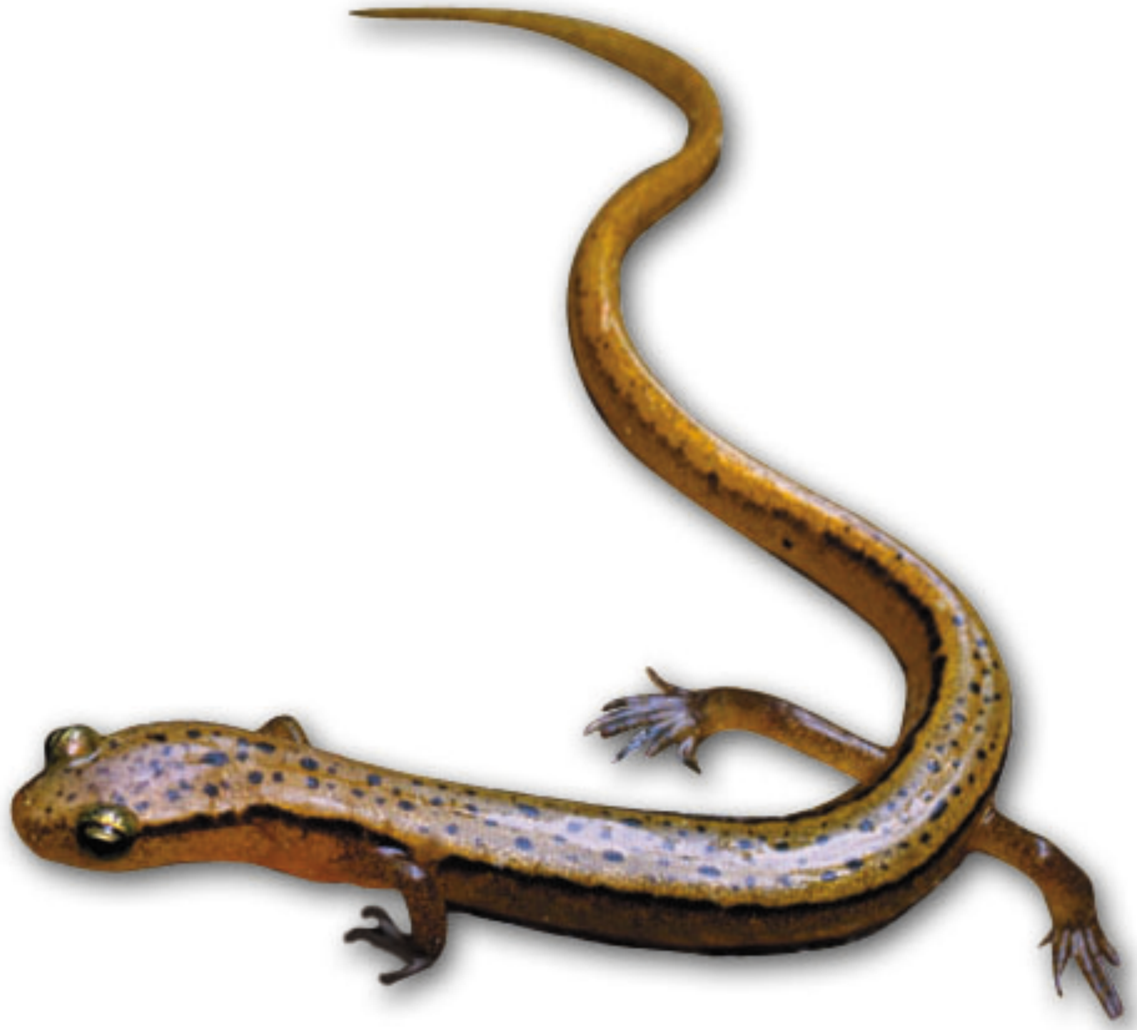
- Differences accumulate with successive speciation events; eventually new groups of organisms form that differ greatly from their ancestors
- Other groups shrink in size as species are lost to extinction
- Macroevolution is the cumulative effect of many speciation and extinction events

Figure 24.UN01a

Geographic Distance (km)	15	32	40	47	42	62	63
Reproductive Isolation Value	0.32	0.54	0.50	0.50	0.82	0.37	0.67
Distance (continued)	81	86	107	107	115	137	147
Isolation (continued)	0.53	1.15	0.73	0.82	0.81	0.87	0.87
Distance (continued)	137	150	165	189	219	239	247
Isolation (continued)	0.50	0.57	0.91	0.93	1.5	1.22	0.82
Distance (continued)	53	55	62	105	179	169	
Isolation (continued)	0.99	0.21	0.56	0.41	0.72	1.15	

Data from S. G. Tilley, A. Verrell, and S. J. Arnold, Correspondence between sexual isolation and allozyme differentiation: a test in the salamander *Desmognathus ochrophaeus, Proceedings of the National Academy of Sciences USA* 87:2715–2719 (1990).

Figure 24.UN01b



Observed numbers of mosquitoes by *kdr* genotype			
	+/+	+/*r*	*r*/*r*
***A. gambiae*:**			
Pre-2006	3	5	2
2006	8	8	7
Post-2006	3	3	57
***Hybrids*:**			
2006	10	7	0
***A. coluzzii*:**			
Pre-2006	226	0	0
2006	70	7	0
Post-2006	79	127	94

Figure 24.UN02b

Figure 24.UN03

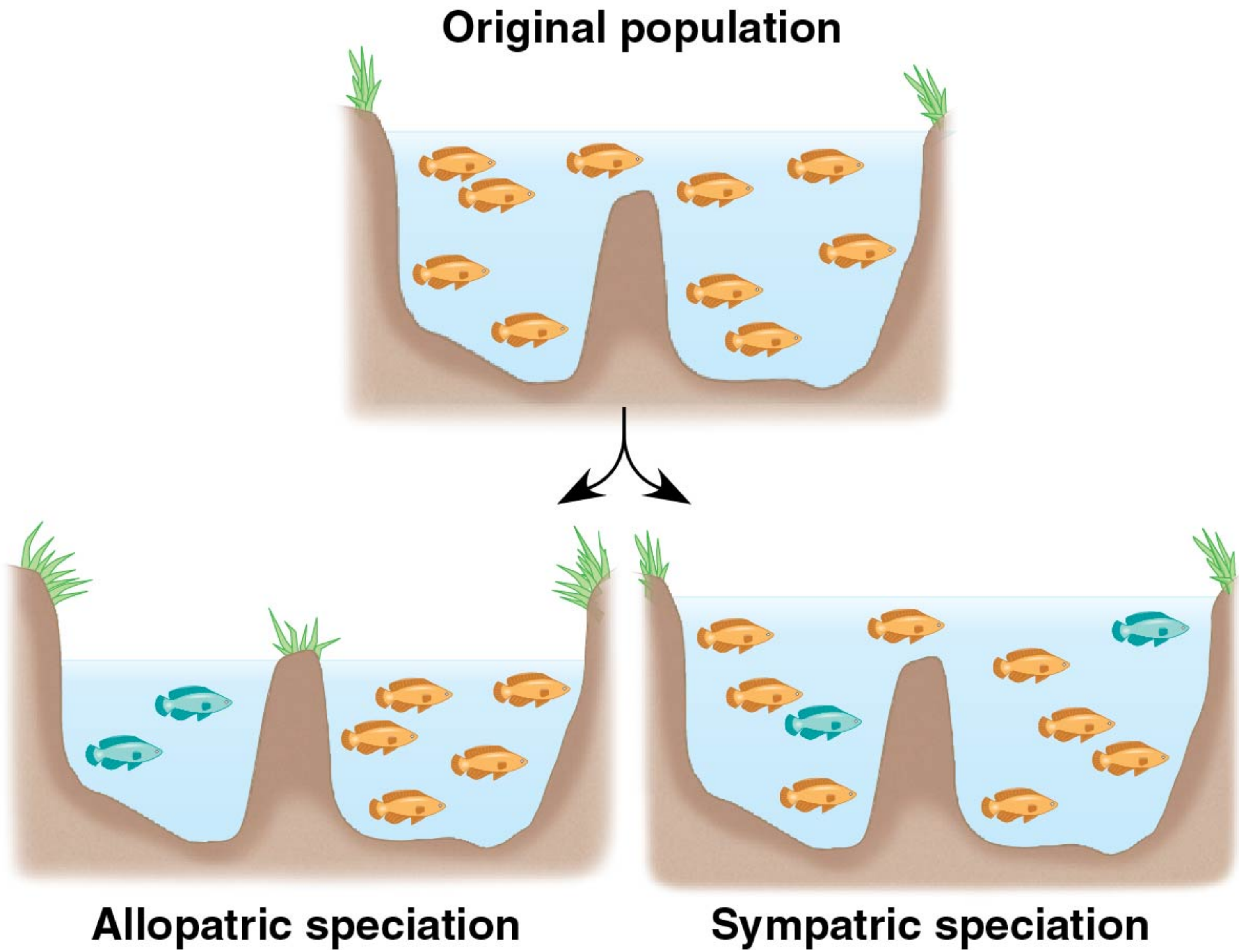


Figure 24.UN04

Ancestral species:

AA

Triticum monococcum
(14)

BB

Wild *Triticum*
(14)

DD

Wild *T. tauschii*
(14)

Product:

AA BB DD

T. aestivum
(bread wheat)
(42)

Figure 24.UN05