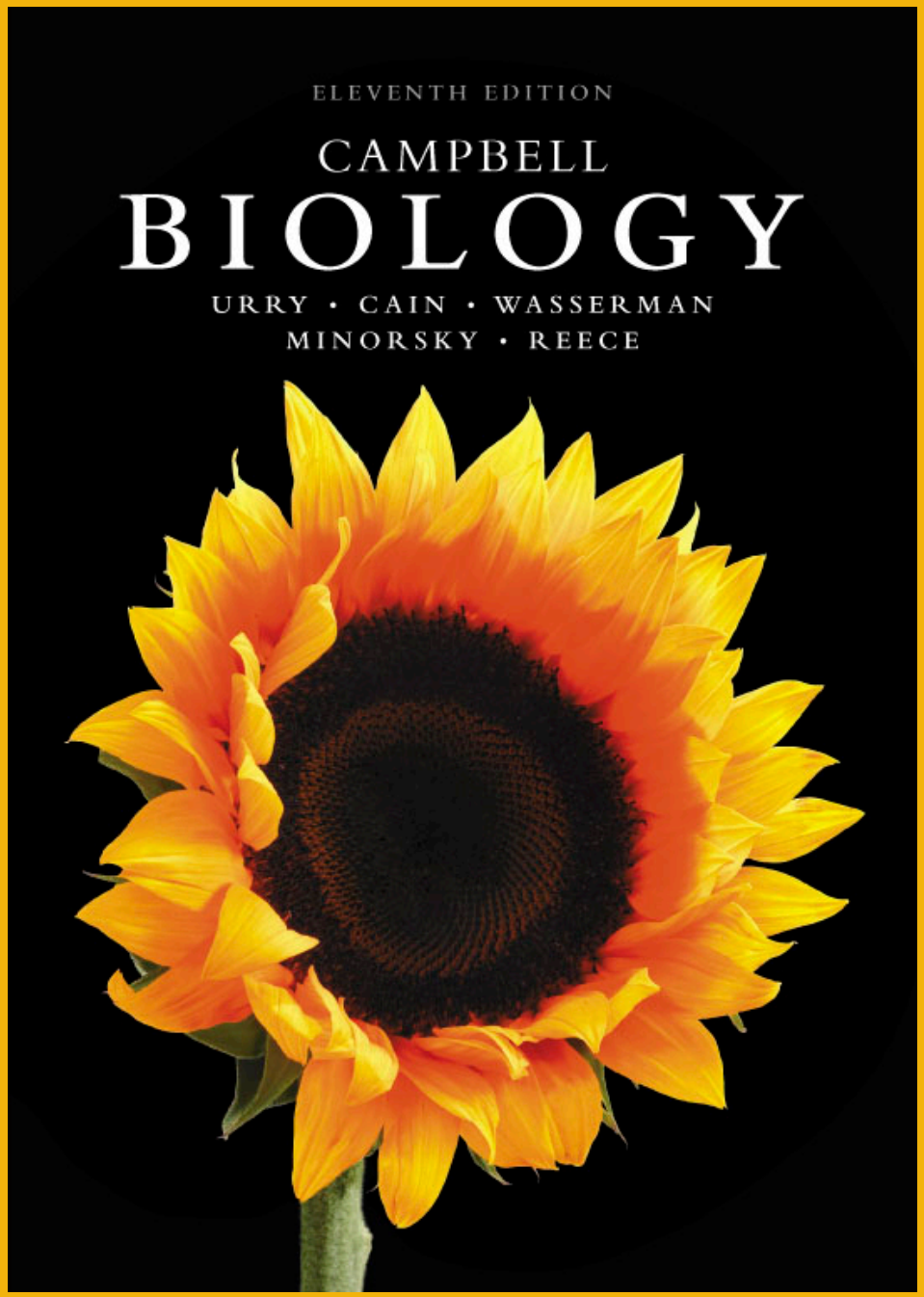


Chapter 24

The Origin of Species

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

That “Mystery of Mysteries”

- In the Galápagos Islands, Darwin discovered plants and animals found nowhere else on Earth

Figure 24.1

Figure 24.1a

Galápagos giant tortoise, another species unique to the islands

- **Speciation**, the process by which one species splits into two or more species, is at the focal point of evolutionary theory
- **Microevolution** consists of changes in allele frequency in a population over time
- **Macroevolution** refers to broad patterns of evolutionary change above the species level
- Speciation forms a conceptual bridge between microevolution and macroevolution

Animation: Macroevolution

Concept 24.1: The biological species concept emphasizes reproductive isolation

- *Species* is a Latin word meaning “kind” or “appearance”
- Biologists compare morphology, physiology, biochemistry, and DNA sequences when grouping organisms

The Biological Species Concept

- The **biological species concept** states that a **species** is a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring; they do not breed successfully 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

Figure 24.2a

(a) Similarity between different species

Figure 24.2aa

Figure 24.2ab

Figure 24.2b

(b) Diversity within a species

Figure 24.2ba

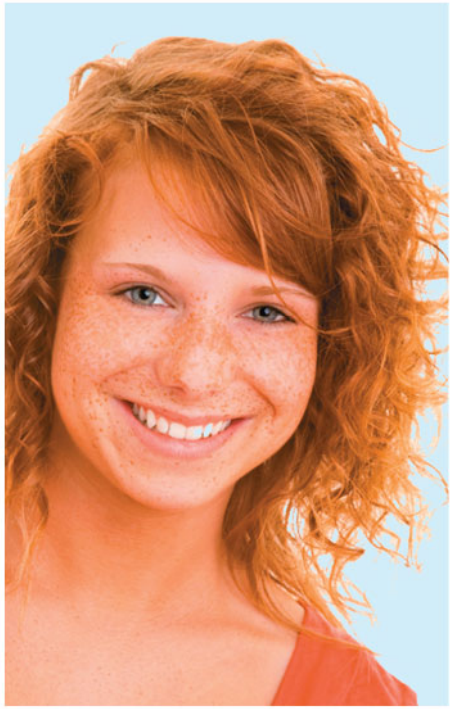


Figure 24.2bb

Figure 24.2bc

Figure 24.2bd

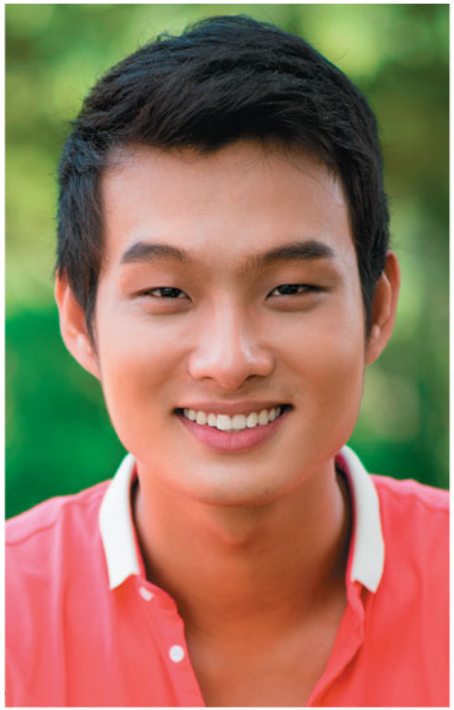


Figure 24.2be

Figure 24.2bf

Video: Galápagos Tortoise

Reproductive Isolation

- **Reproductive isolation** is the existence of biological factors (barriers) that impede two species from producing viable, fertile offspring
- **Hybrids** are the offspring that result from mating between different species
- Reproductive isolation can be classified by whether factors act before or after fertilization

Figure 24.3

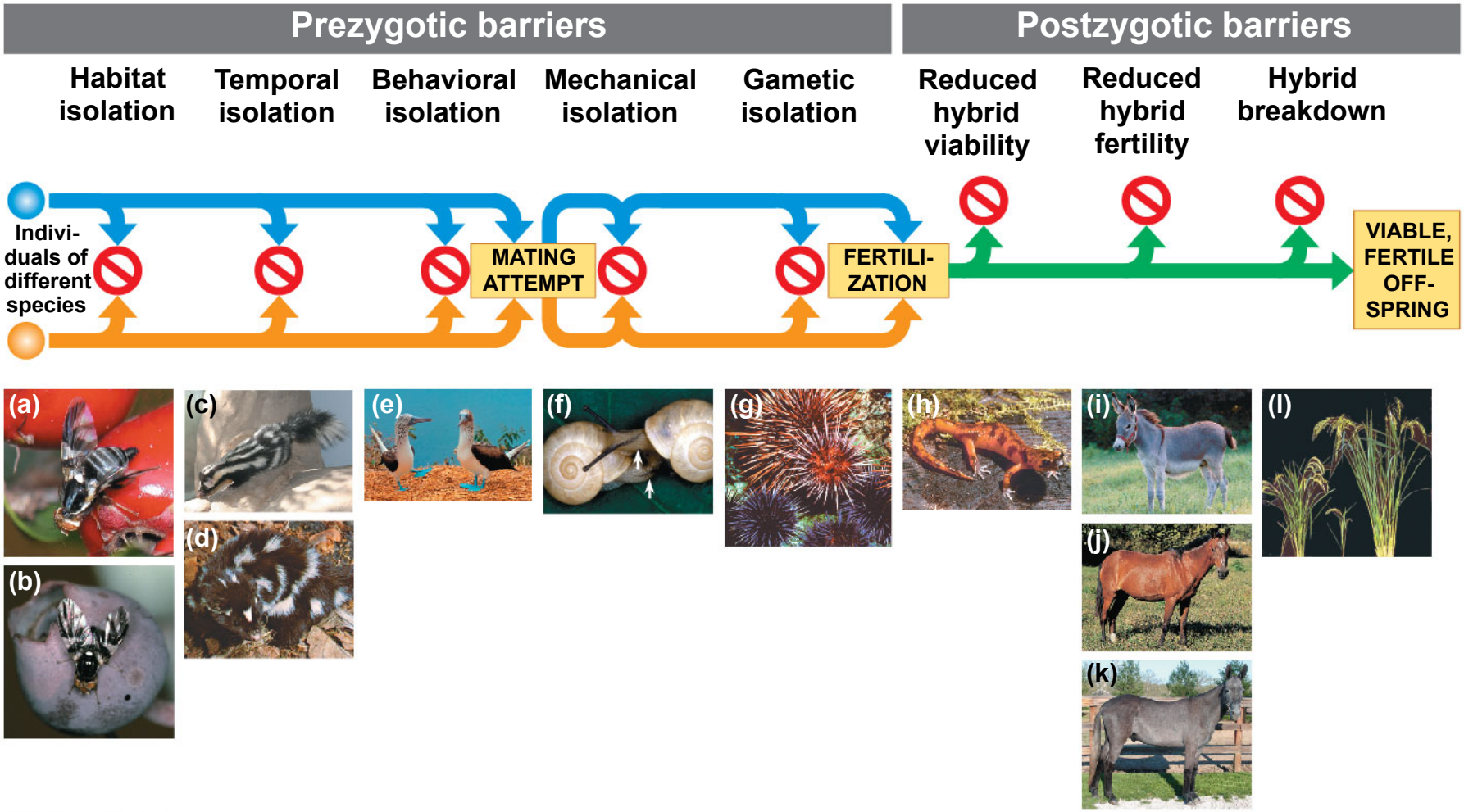
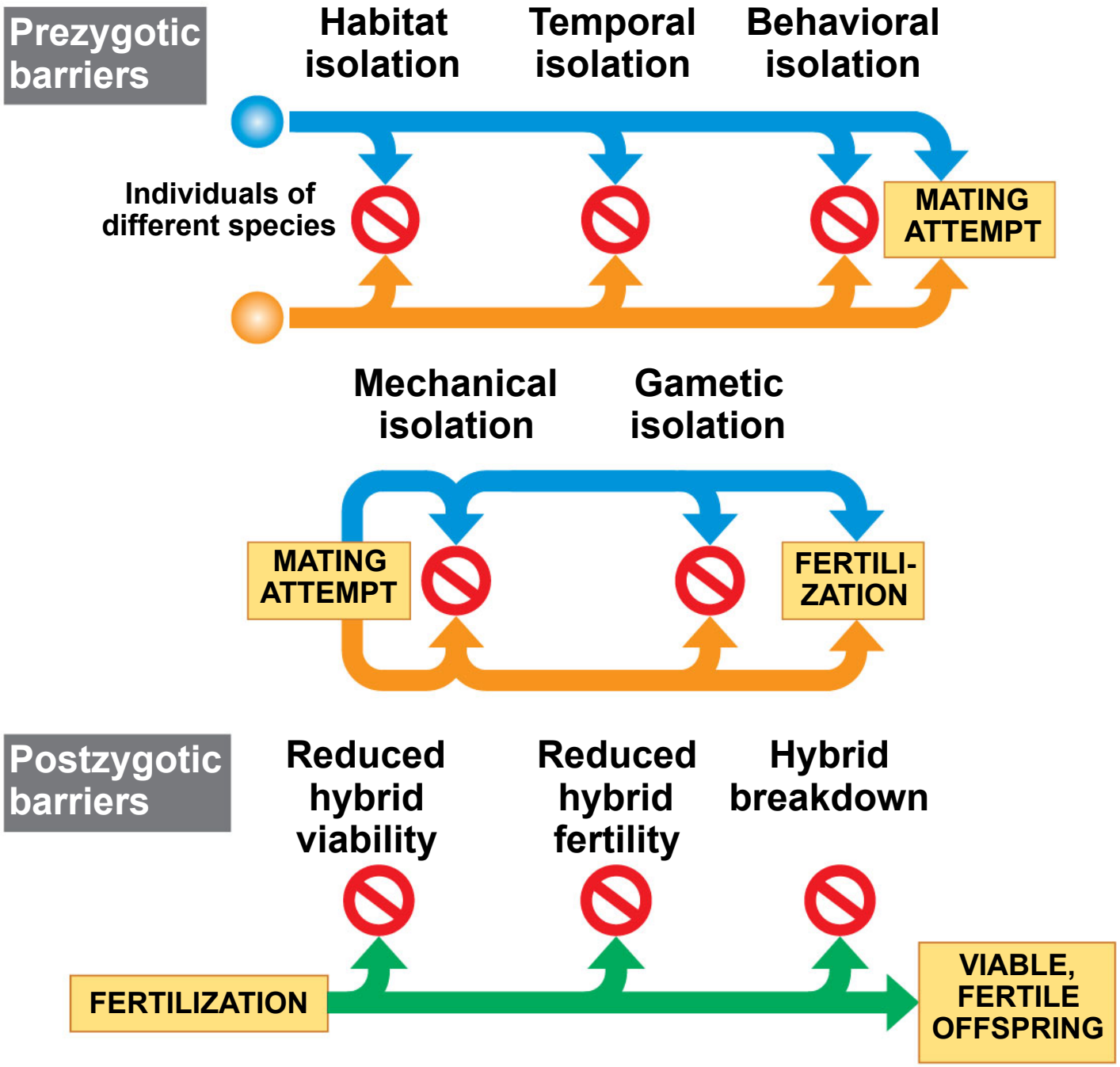
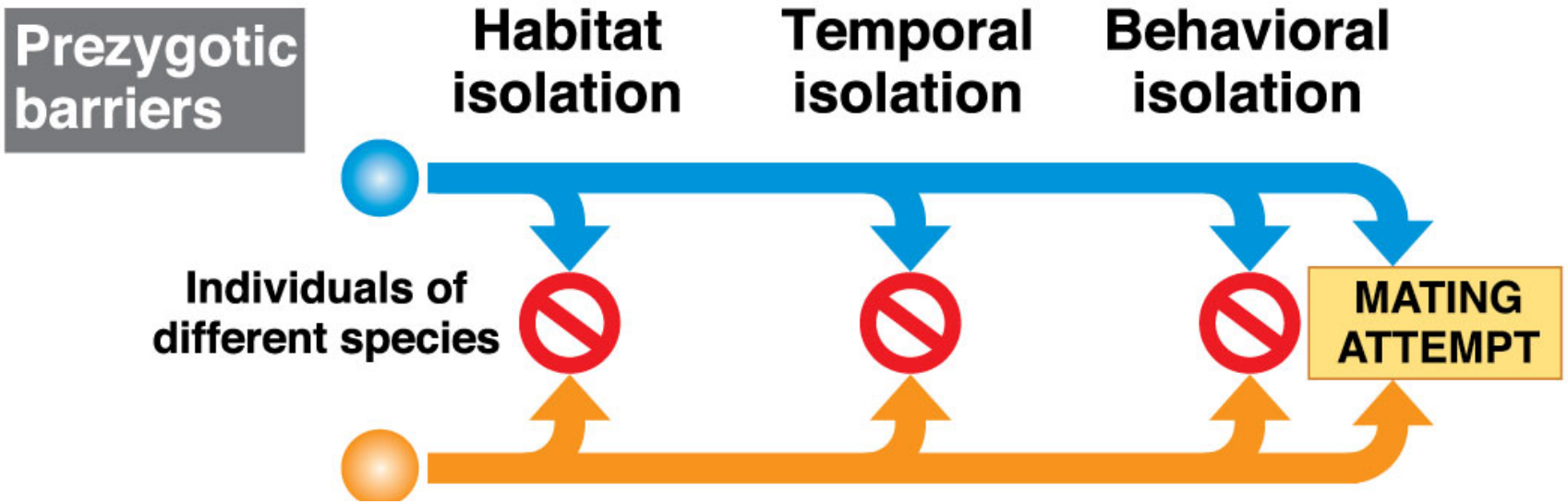


Figure 24.3d



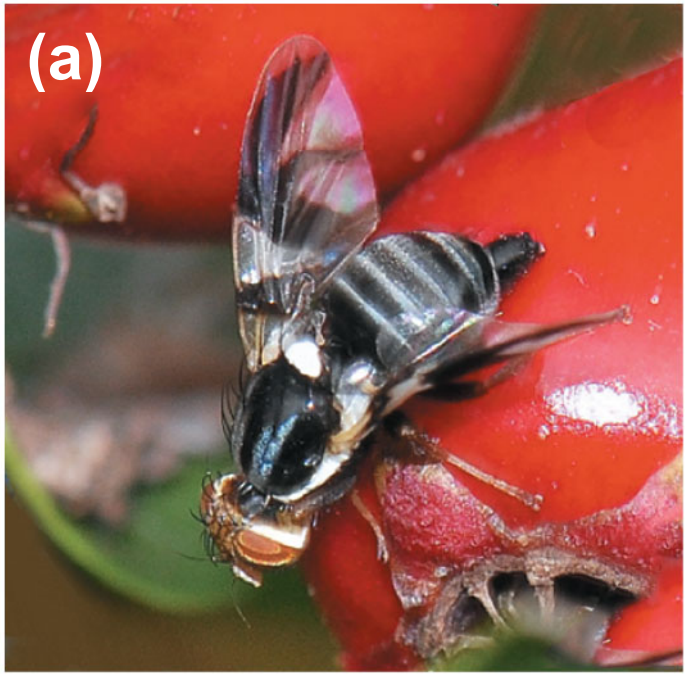
- **Prezygotic barriers** block fertilization from occurring by
  - Impeding different species from attempting to mate
  - Preventing the successful completion of mating
  - Hindering fertilization if mating is successful

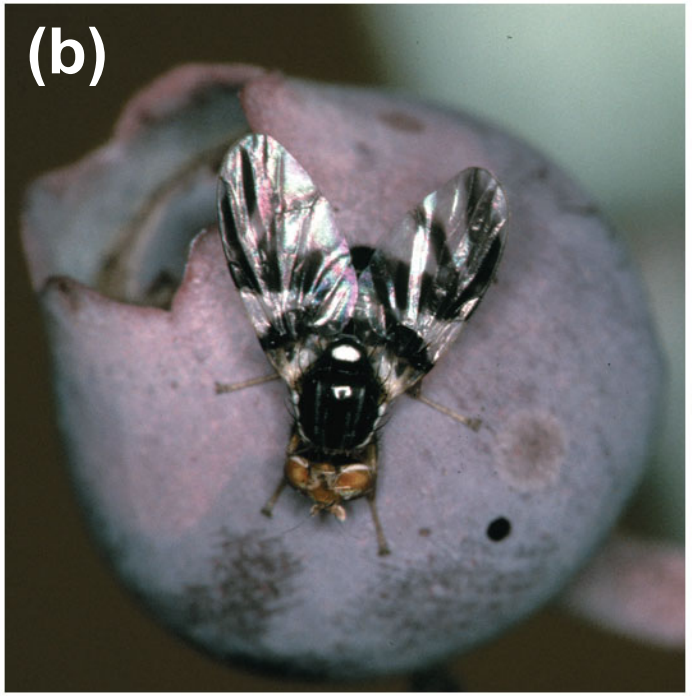
Figure 24.3a



- **Habitat isolation**: Two species encounter each other rarely, or not at all, because they occupy different habitats, even though not isolated by physical barriers

Figure 24.3aa and 23.3ab





- **Temporal isolation**: Species that breed at different times of the day, different seasons, or different years cannot mix their gametes

Figure 24.3ac and 24.3ad

- **Behavioral isolation**: Courtship rituals and other behaviors unique to a species are effective barriers to mating

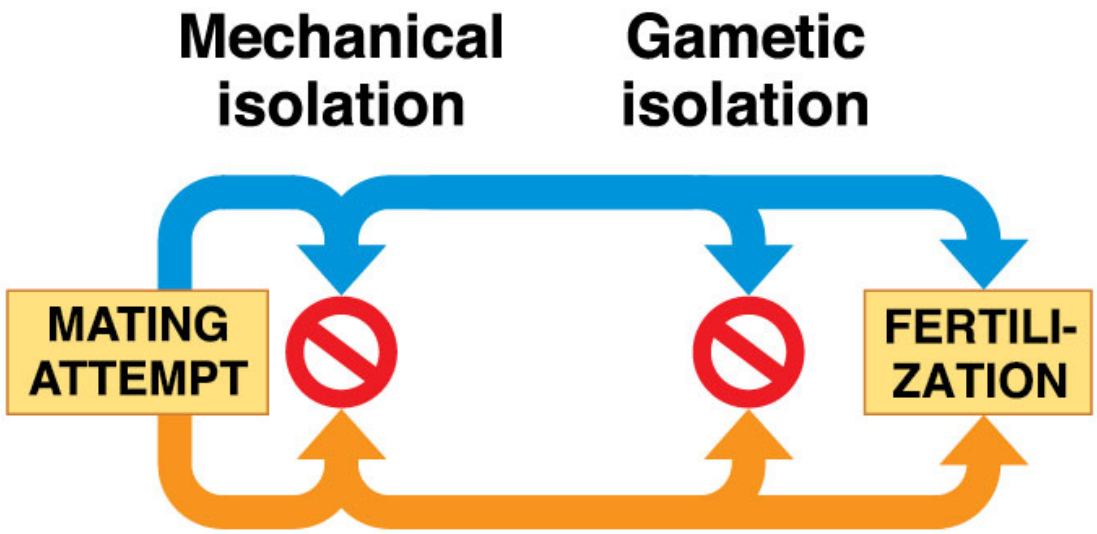
Figure 24.3ae

Video: Blue-footed Boobies Courtship Ritual

Video: Albatross Courtship Ritual

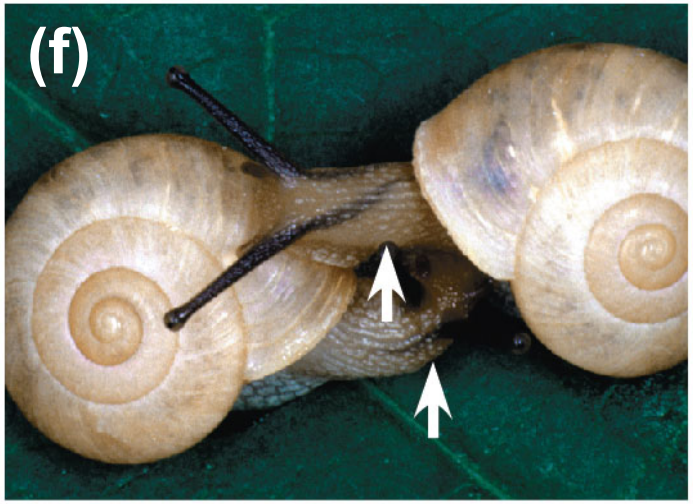
Video: Giraffe Courtship Ritual

Figure 24.3b



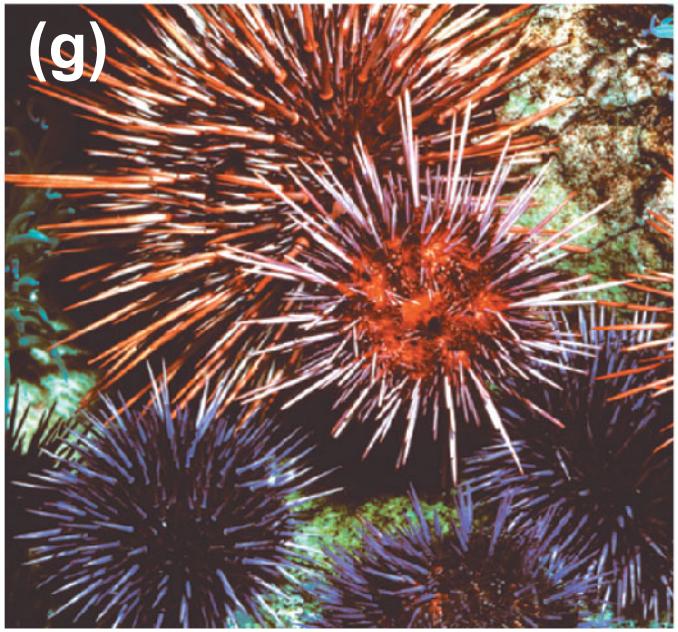
- **Mechanical isolation**: Morphological differences can prevent successful completion of mating

Figure 24.3ba



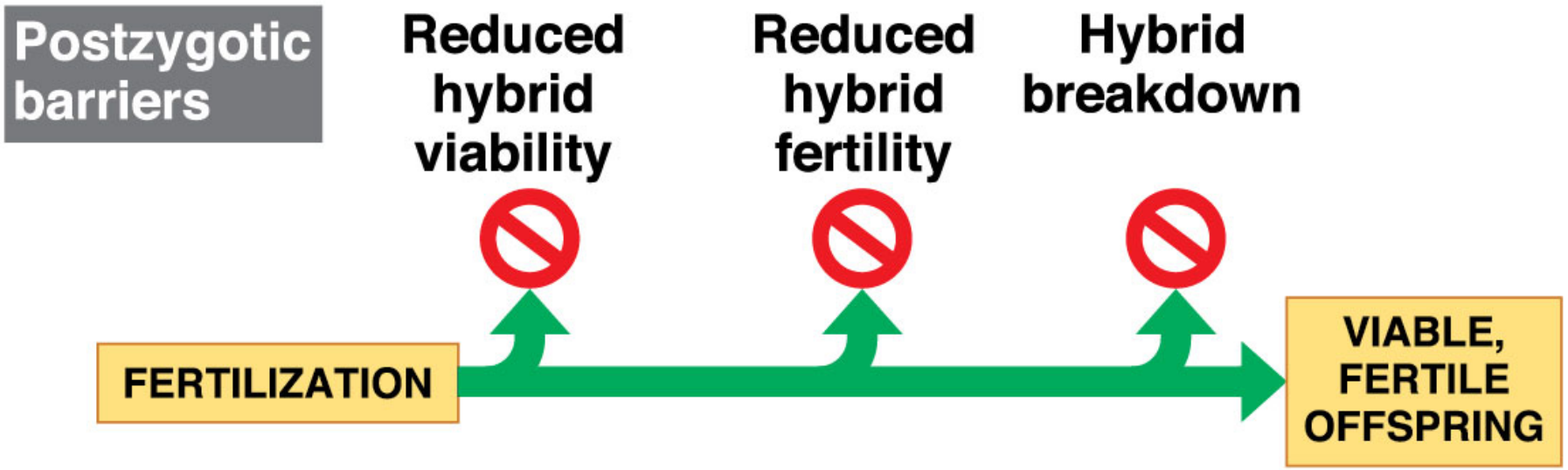
- **Gametic Isolation:** Sperm of one species may not be able to fertilize eggs of another species

Figure 24.3bb



- **Postzygotic barriers** prevent the hybrid zygote from developing into a viable, fertile adult by
  - Reduced hybrid viability
  - Reduced hybrid fertility
  - Hybrid breakdown

Figure 24.3c



- **Reduced hybrid viability**: Genes of the different parent species may interact and impair the hybrid's development or survival in its environment

Figure 24.3ca

- **Reduced hybrid fertility**: Even if hybrids are vigorous, they may be sterile

Figures 24.3cb, 24.3cc, 24.3cd

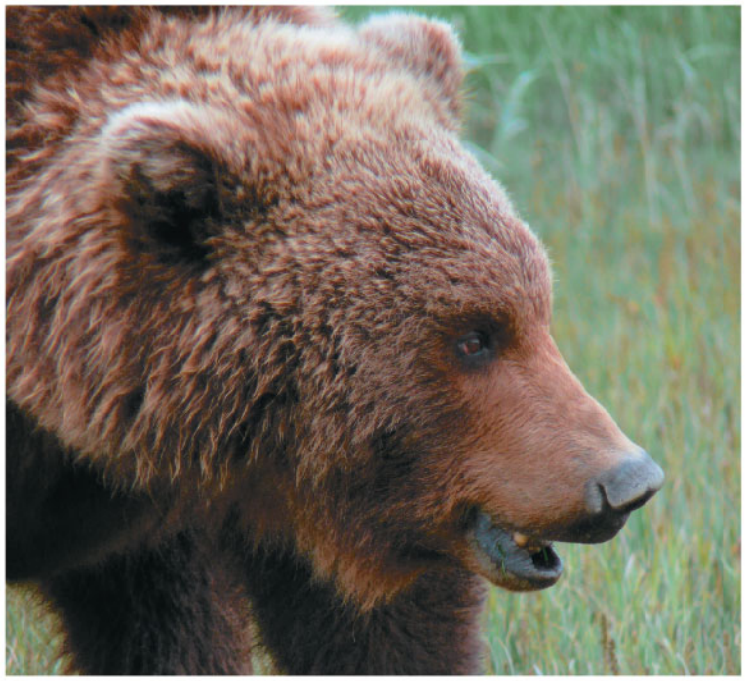
- **Hybrid breakdown**: Some first-generation hybrids are fertile, but when they mate with each other or with either parent species, offspring of the next generation are feeble or sterile

Figure 24.3ce

Limitations of the Biological Species Concept

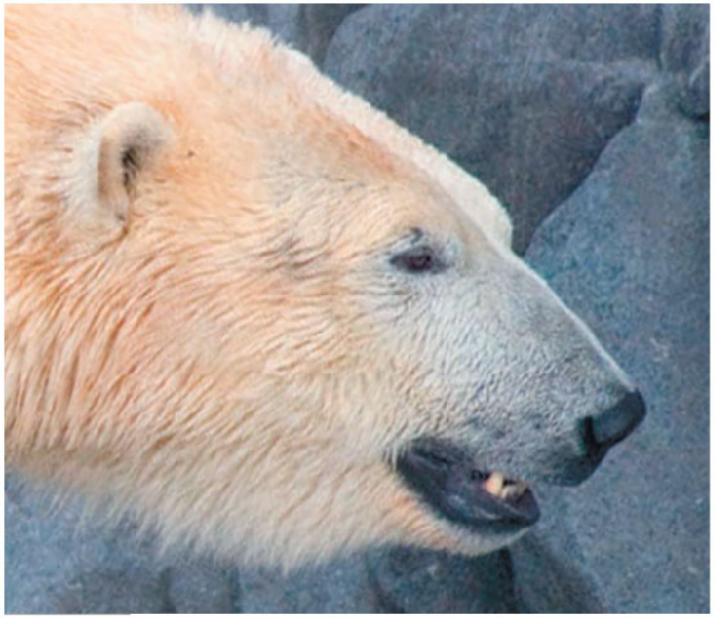
- The biological species concept cannot be applied to fossils or asexual organisms (including all prokaryotes)
- The biological species concept emphasizes absence of gene flow
- However, gene flow can occur between morphologically and ecologically distinct species
  - For example, grizzly bears and polar bears can mate to produce “grolar bears”

Figure 24.4



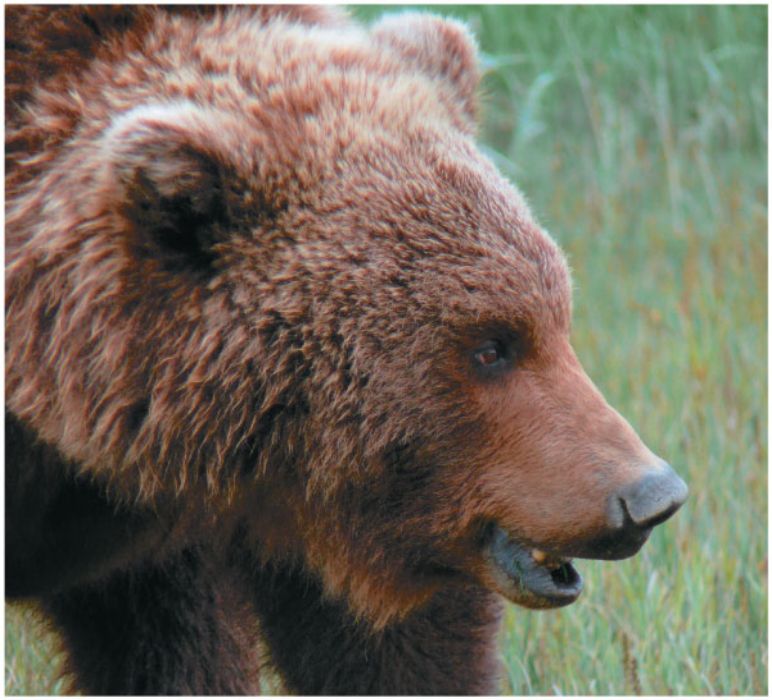
Grizzly bear (*U. arctos*)

Polar bear (*U. maritimus*)



Hybrid "grolar bear"

Figure 24.4a



Grizzly bear (*U. arctos*)

Figure 24.4b

Polar bear (*U. maritimus*)

Figure 24.4c

Hybrid “grolar bear”

Other Definitions of Species

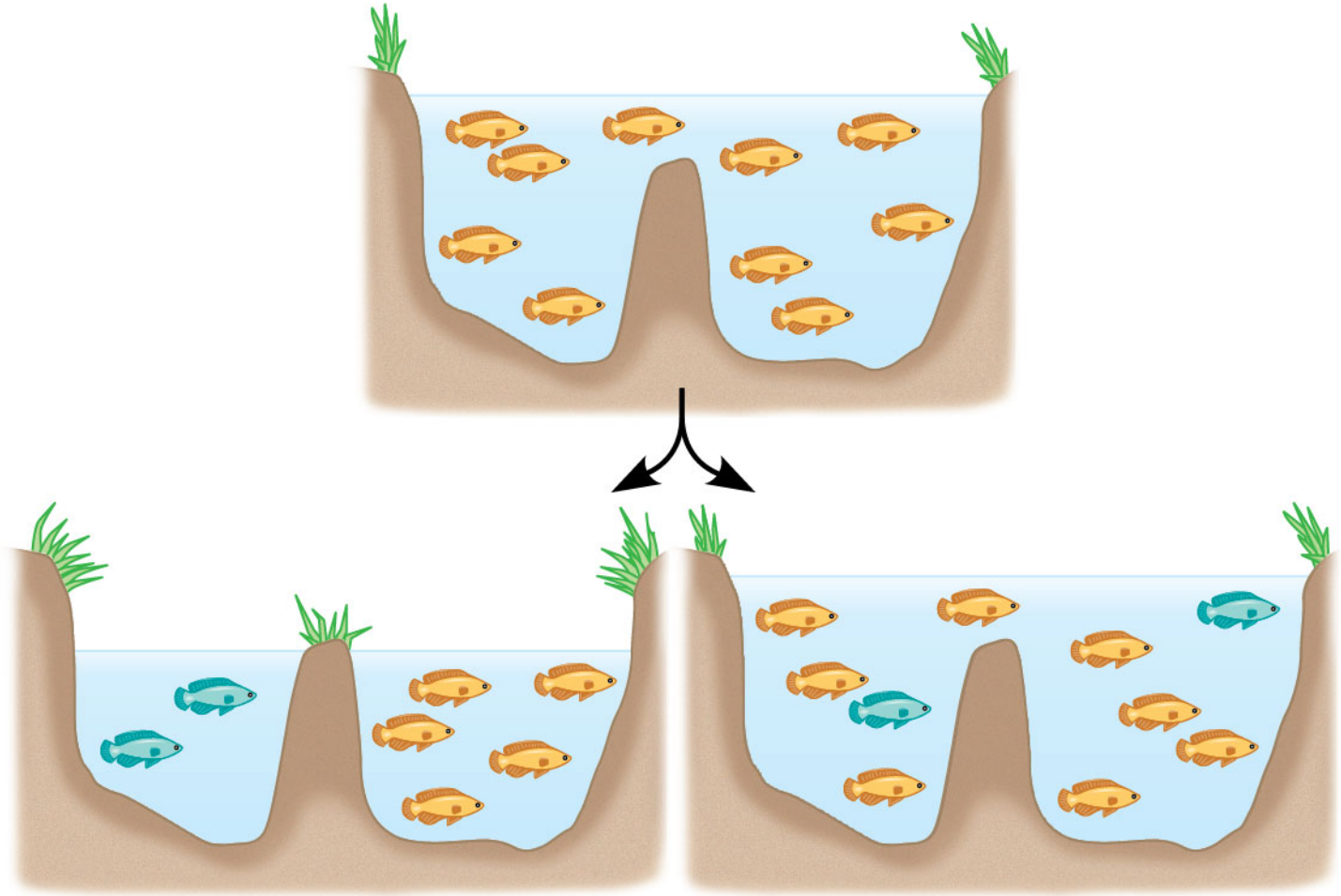
- Other species concepts emphasize the unity within a species rather than the separateness of different species
- The **morphological species concept** defines a species by structural features
  - It applies to sexual and asexual species but relies on subjective criteria

- The **ecological species concept** defines a species in terms of its ecological niche
  - It applies to sexual and asexual species and emphasizes the role of disruptive selection
- Many 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
  - Sympatric speciation

Figure 24.5



(a) Allopatric speciation

(b) Sympatric speciation

Allopatric ("Other Country") Speciation

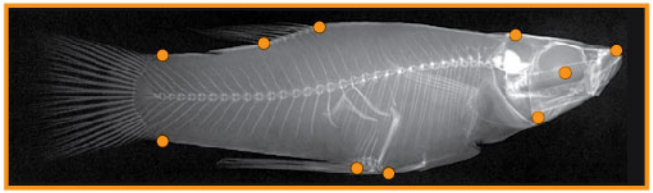
- In **allopatric speciation**, gene flow is interrupted or reduced when a population is divided into geographically isolated subpopulations
  - For example, the flightless cormorant of the Galápagos likely originated from a flying species on the mainland

The Process of Allopatric Speciation

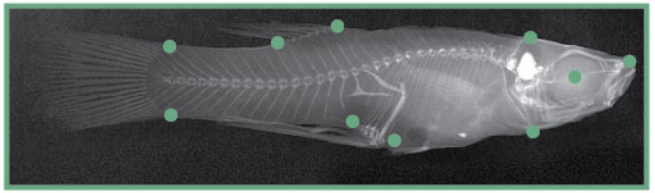
- The definition of barrier depends on the ability of a population to disperse
  - For example, a canyon may create a barrier for small rodents, but not birds, coyotes, or pollen

- Separated populations may evolve independently 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

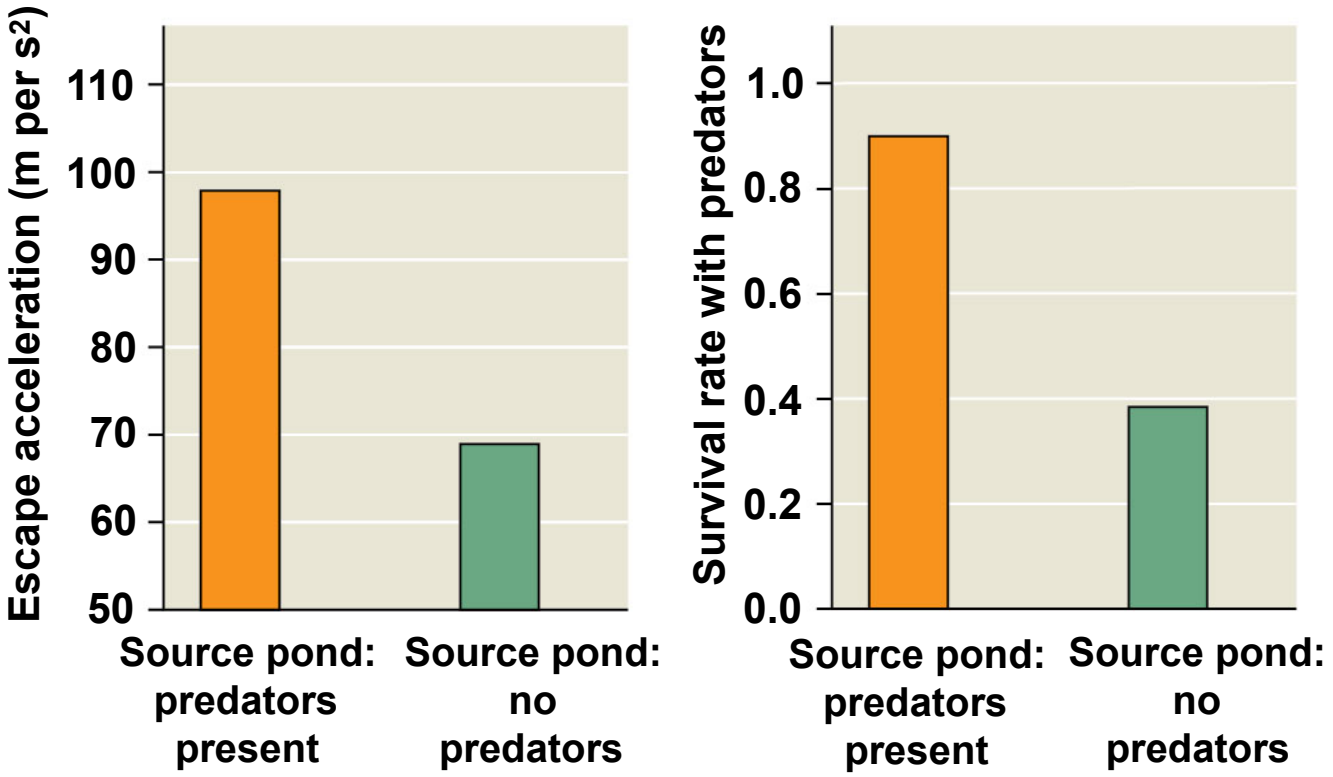


With predators: body shape that enables rapid bursts of speed



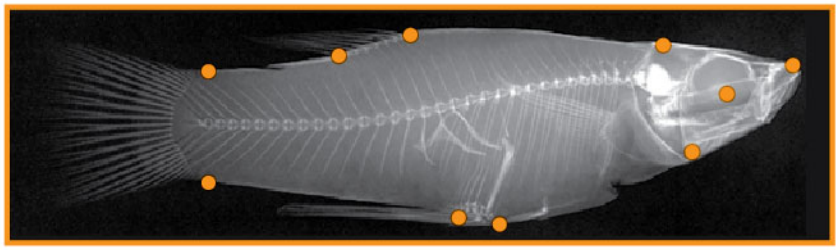
Without predators: body shape that favors long, steady swimming

(a) Differences in body shape

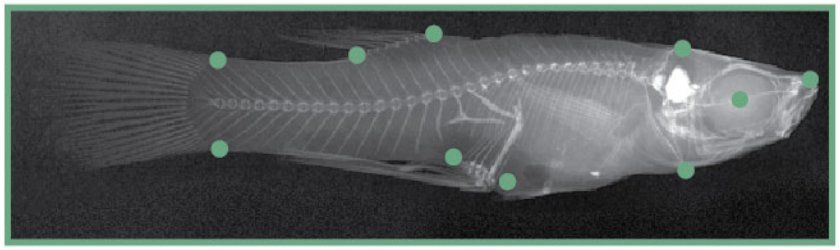


(b) Differences in escape acceleration and survival

Figure 24.6a



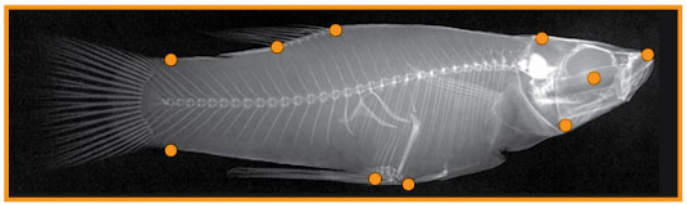
With predators: body shape that enables rapid bursts of speed



Without predators: body shape that favors long, steady swimming

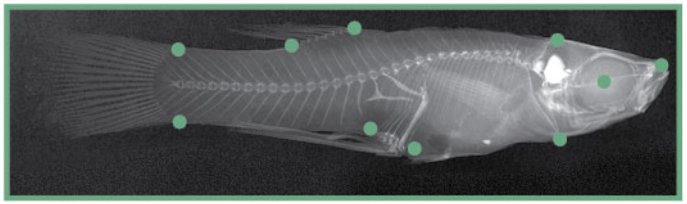
(a) Differences in body shape

Figure 24.6aa



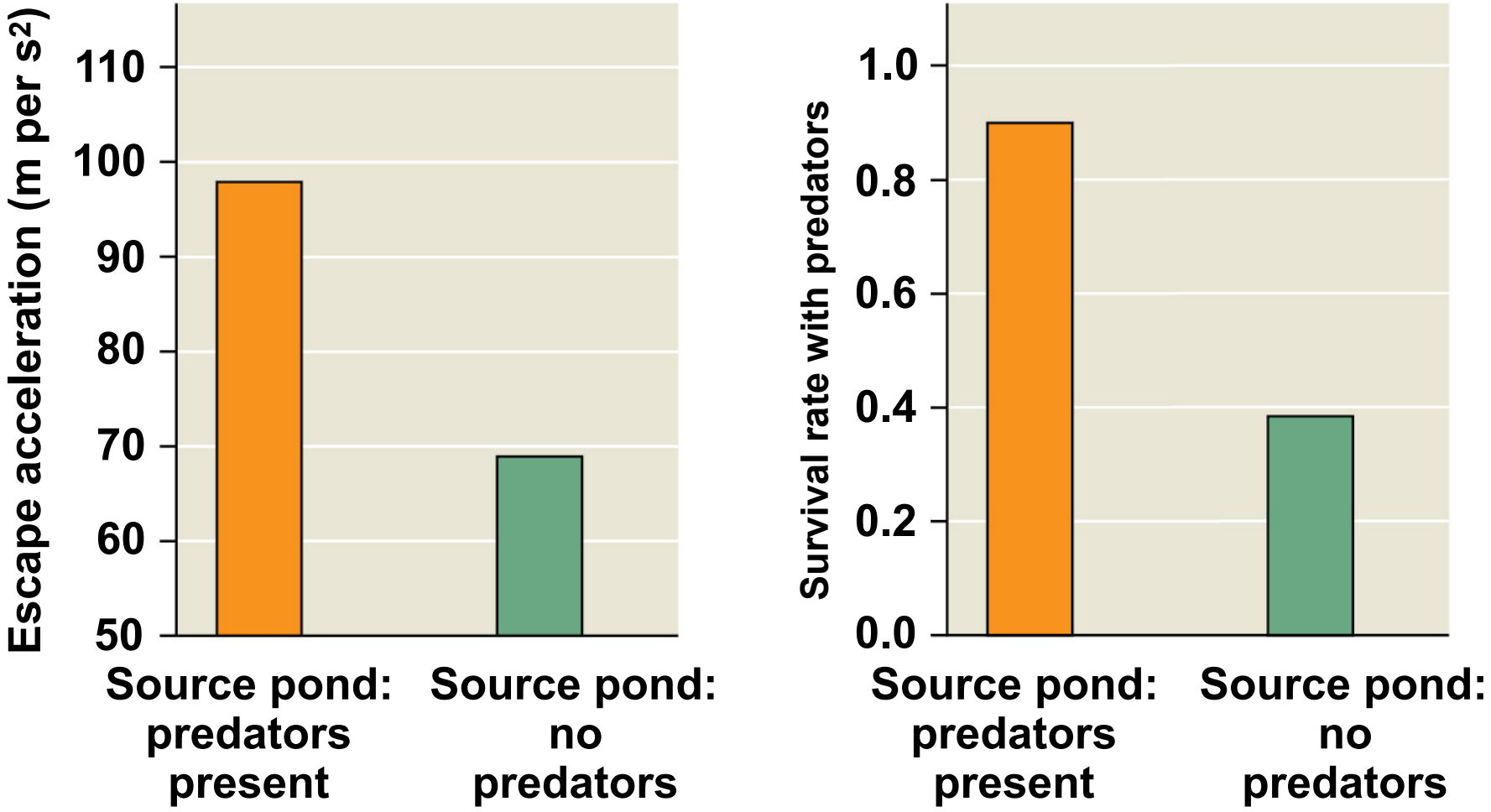
With predators: body shape that enables rapid bursts of speed

Figure 24.6ab



Without predators: body shape that favors long, steady swimming

Figure 24.6b



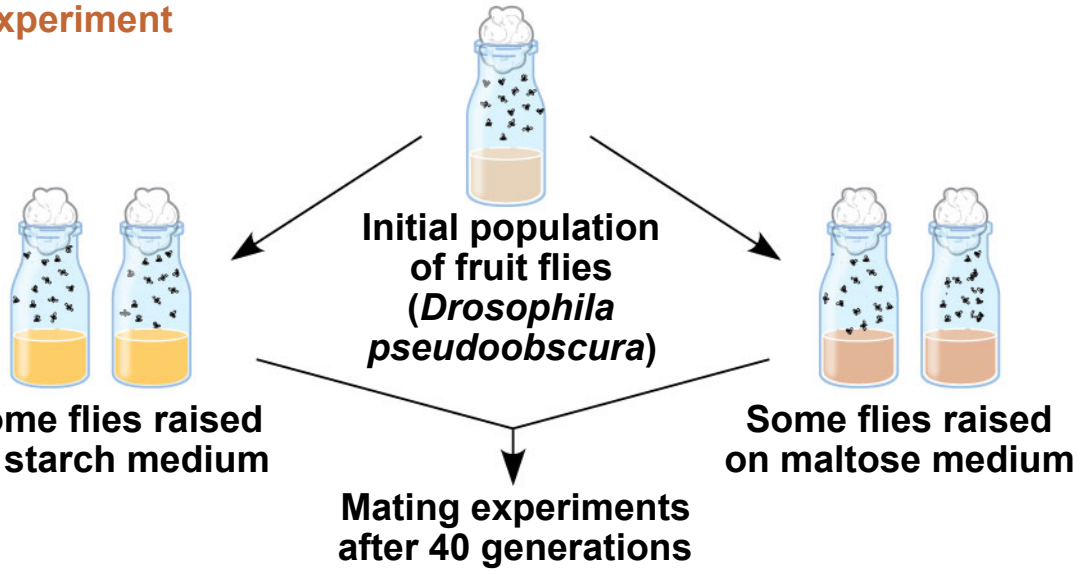
(b) Differences in escape acceleration and survival

Evidence of Allopatric Speciation

- Reproductive barriers can develop between experimentally isolated laboratory populations subjected to different environmental conditions
  - For example, fruit flies taken from the same source population and allowed to adapt to different diets over several generations tend to choose 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).

Figure 24.7a

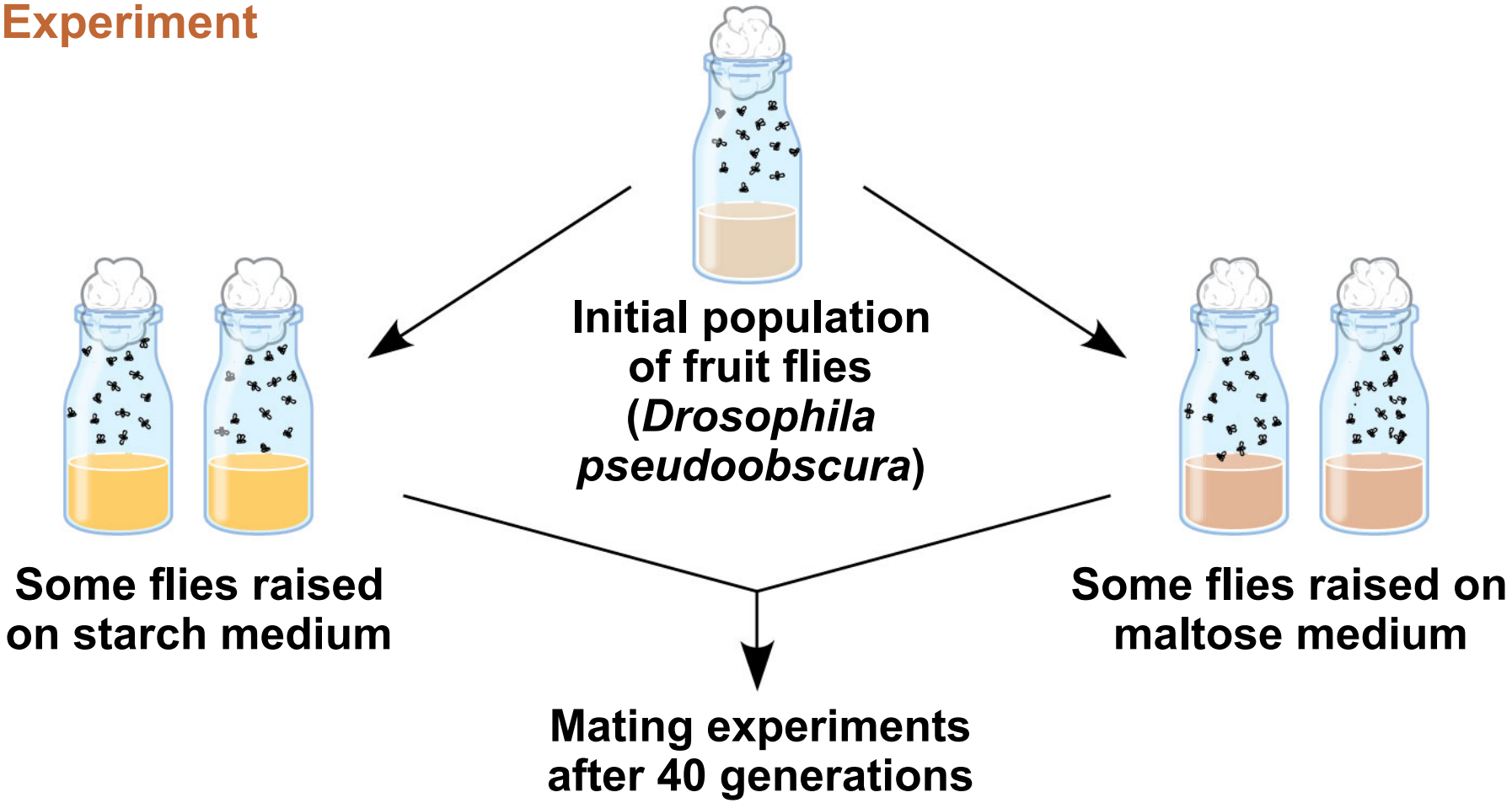


Figure 24.7b

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).

- Allopatric speciation has also been observed in nature
  - For example, sister species of snapping shrimp (*Alpheus*) diverged 3 to 9 million years ago as they became isolated by the formation of the Isthmus of Panama

Figure 24.8

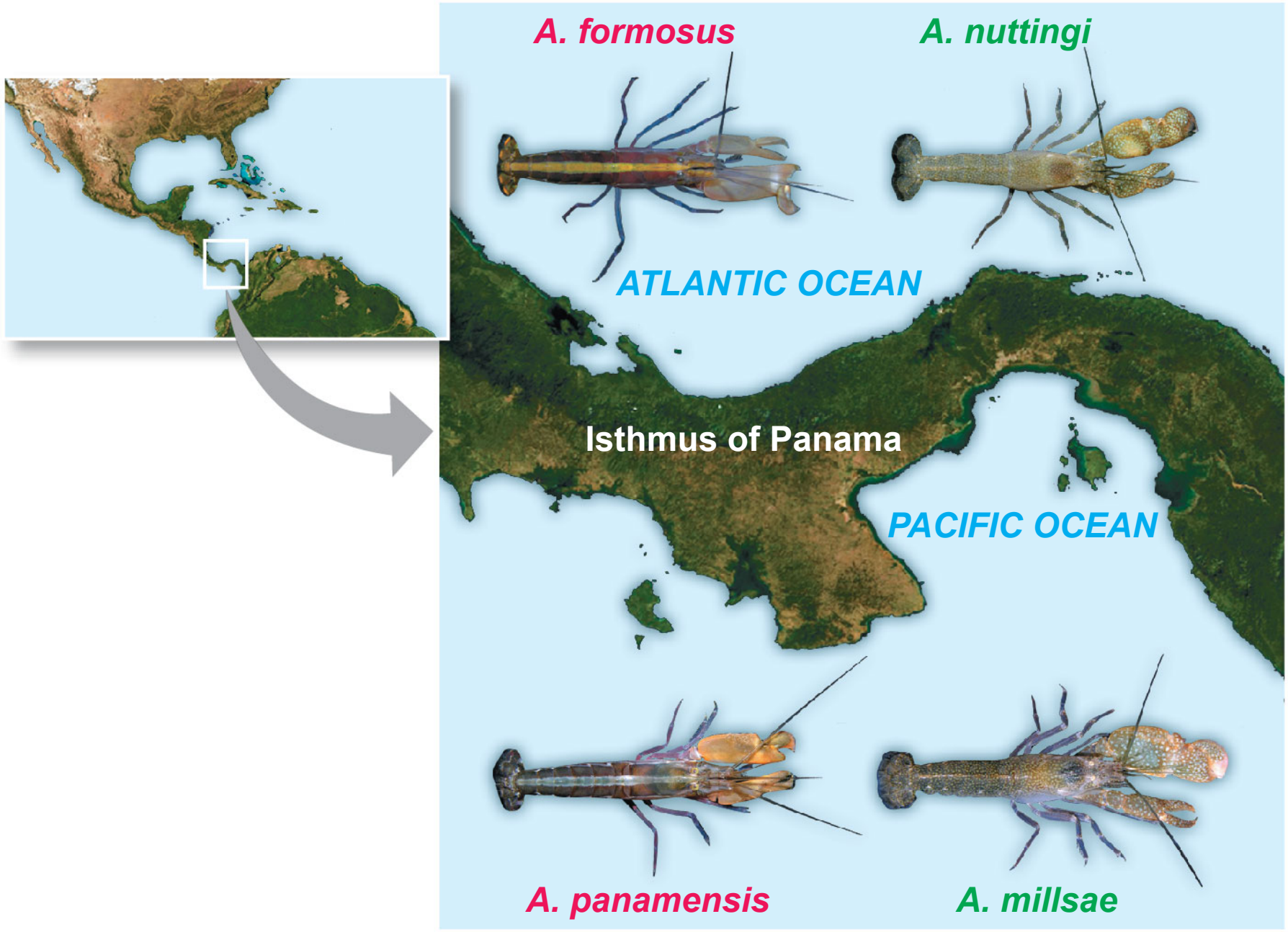
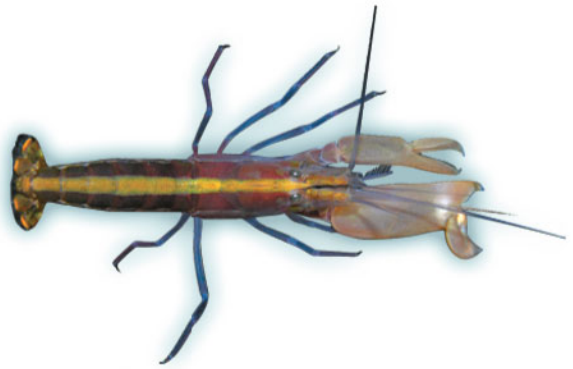


Figure 24.8a



A. formosus

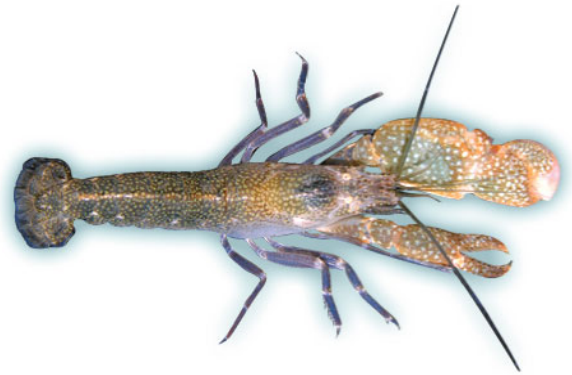
Figure 24.8b

A. nuttingi

Figure 24.8c

A. panamensis

Figure 24.8d



A. millsae

- Regions with many geographic barriers typically have more species than do regions with fewer barriers
- Reproductive isolation between populations generally increases as the distance between them increases

- Reproductive barriers are intrinsic to the organisms themselves; physical separation alone is not a biological barrier

Sympatric ("Same Country") Speciation

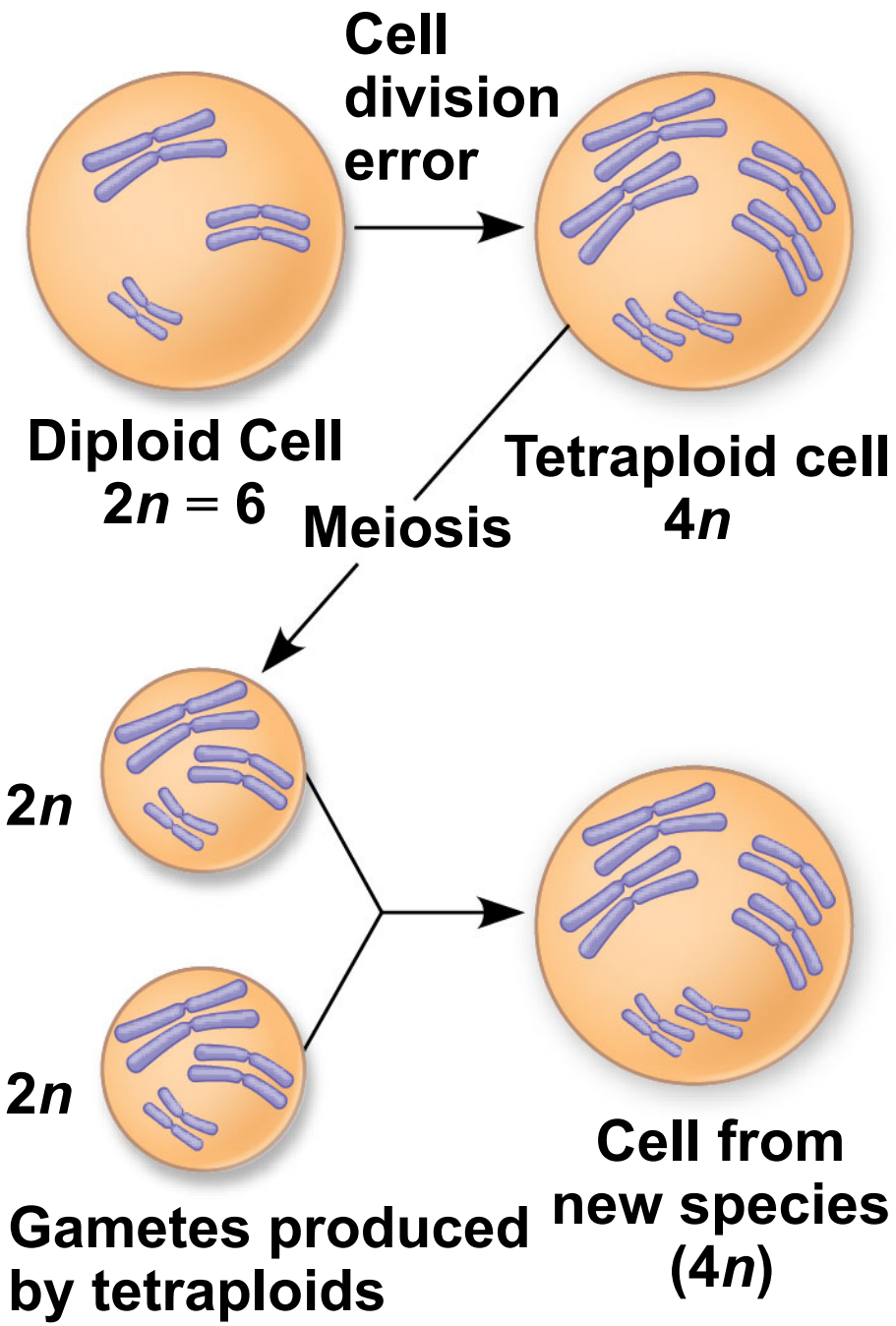
- In **sympatric speciation**, speciation occurs in populations that live in the same geographic area
- Sympatric speciation can occur if gene flow is reduced by factors including
  - Polyploidy
  - Sexual selection
  - Habitat differentiation

Polyploidy

- **Polyploidy** is the presence of extra sets of chromosomes due to accidents during cell division
- Polyploidy is much more common in plants than in animals
- Polyploidy can produce new biological species in sympatry within a single generation

- An **autopolyploid** is an individual with more than two chromosome sets derived from a single species
- The offspring resulting from mating between polyploids and diploids have reduced fertility

Figure 24.9



- An **allopolyploid** is a species with multiple sets of chromosomes derived from different species
- Allopolyploids can successfully mate with each other, but cannot interbreed with either parent species

Figure 24.10_1

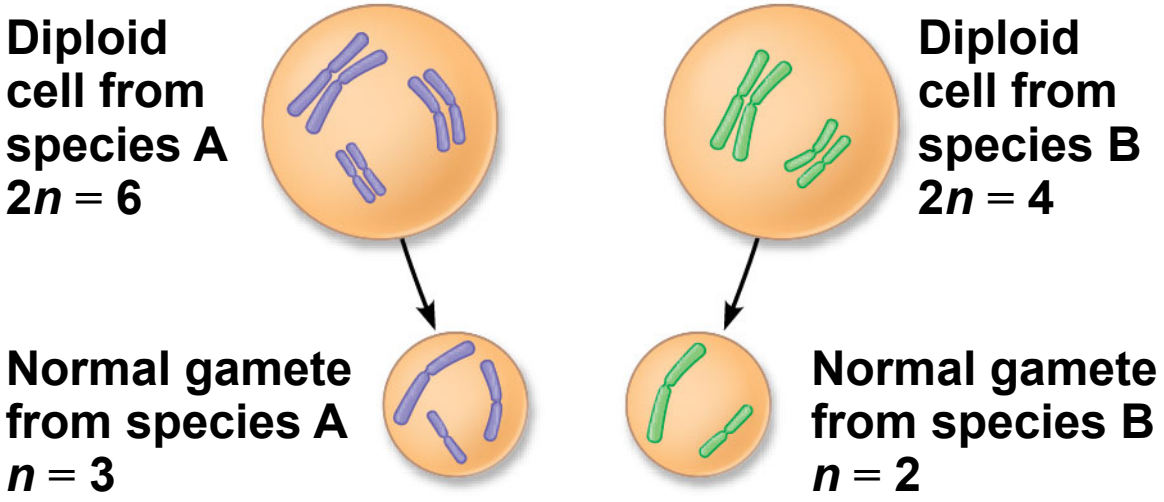


Figure 24.10_2

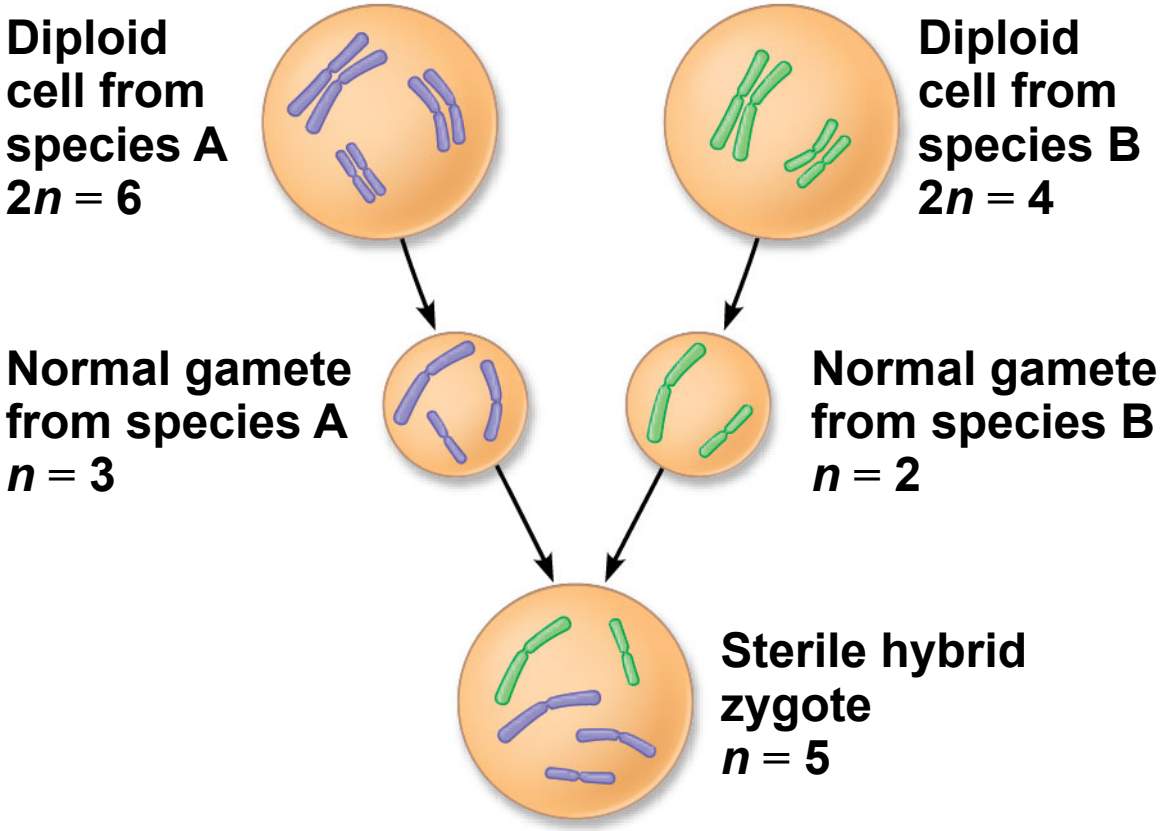
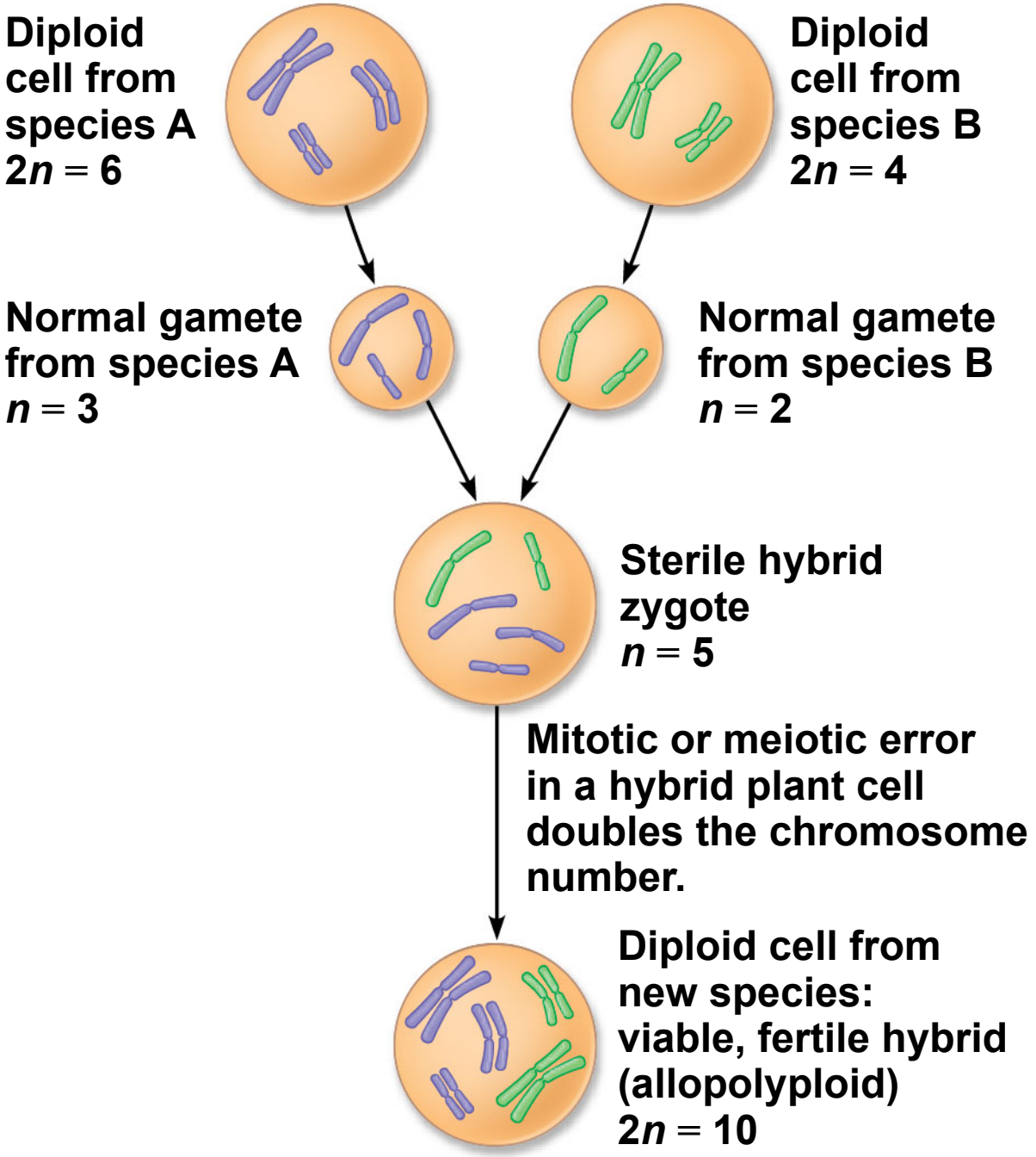
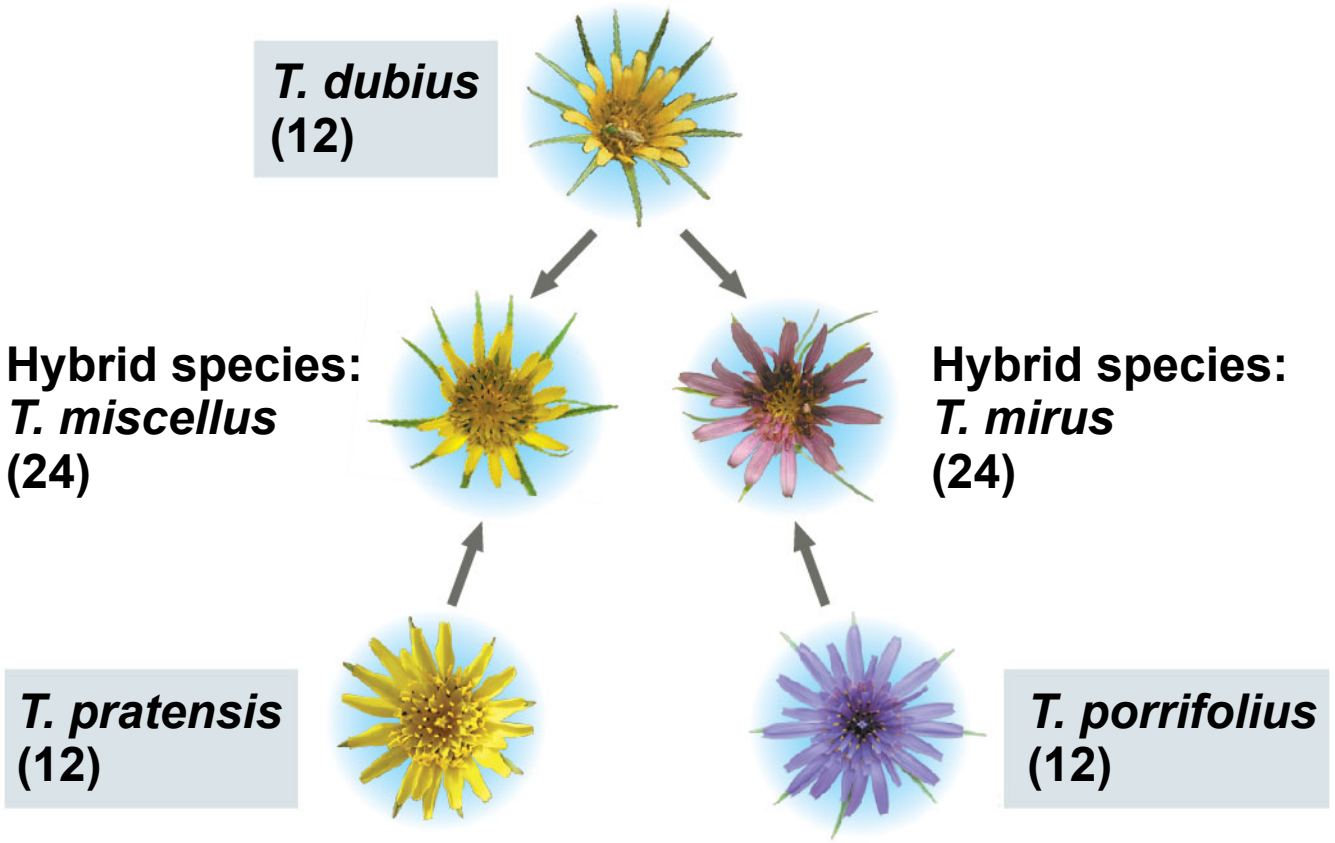


Figure 24.10_3



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

Figure 24.11



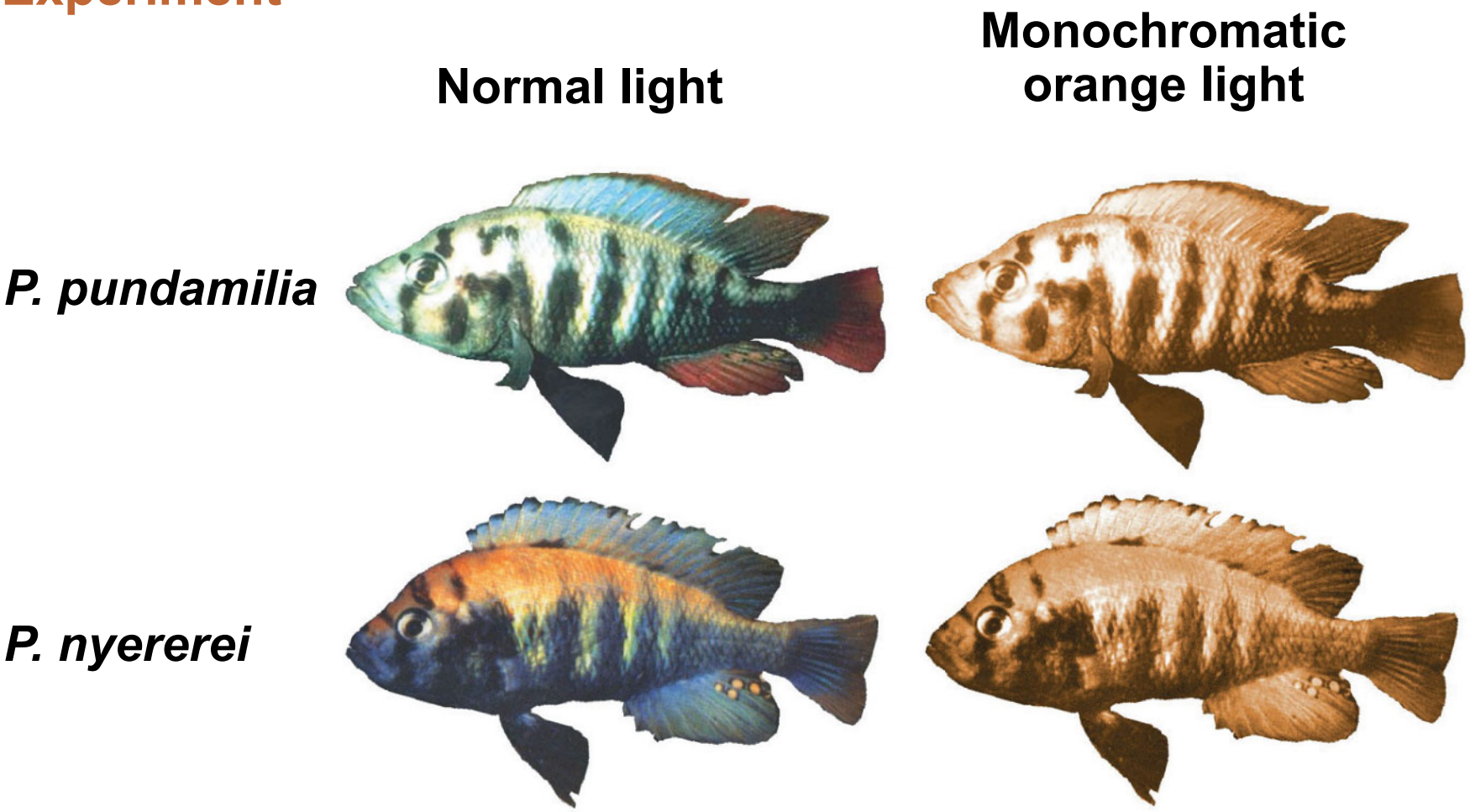
- Many important crops (oats, cotton, potatoes, tobacco, and wheat) are polyploids
- Plant geneticists can produce new polyploid agricultural species using chemicals to induce errors in cell division

Sexual Selection

- Sexual selection can drive sympatric speciation
- Sexual selection for mates of different colors has likely contributed to speciation in cichlid fish in Lake Victoria

Figure 24.12

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).

Figure 24.12a

Normal light

P. pundamilia

Figure 24.12b

Monochromatic orange light

P. pundamilia

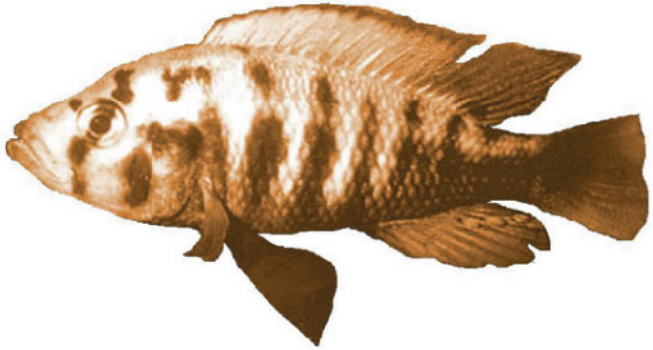


Figure 24.12c

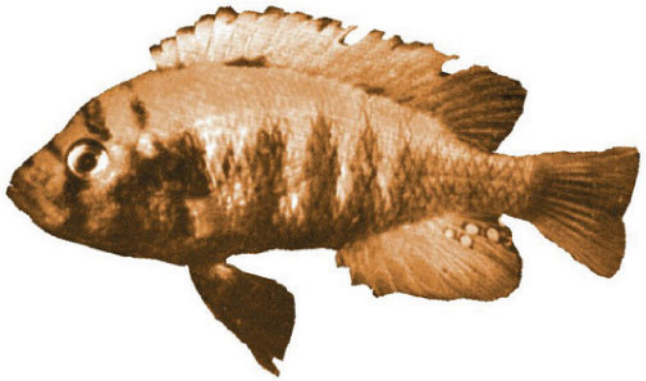
Normal light

P. nyererei

Figure 24.12d

Monochromatic orange light

P. nyererei



Habitat Differentiation

- Sympatric speciation can also result from the appearance of new ecological niches
  - For example, populations of the North American maggot fly (*Rhagoletis pomonella*) can live on native hawthorn trees, as well as more recently introduced apple trees
  - Flies that use different host species experience both habitat and temporal isolation

Allopatric and Sympatric Speciation: *A Review*

- In allopatric speciation, geographic isolation restricts gene flow between populations
- Reproductive isolation may then arise as a by-product of genetic changes resulting from divergent natural selection, genetic drift, or sexual selection
- Even if contact is restored between populations, interbreeding is prevented

- 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, natural selection, or sexual selection

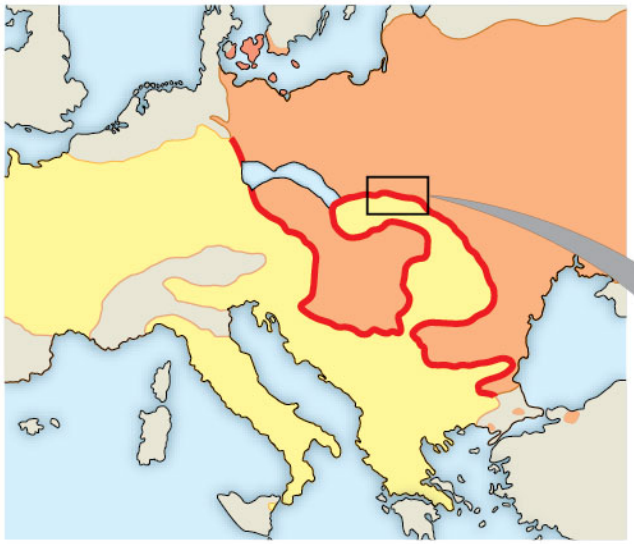
Concept 24.3: Hybrid zones reveal factors that cause reproductive isolation

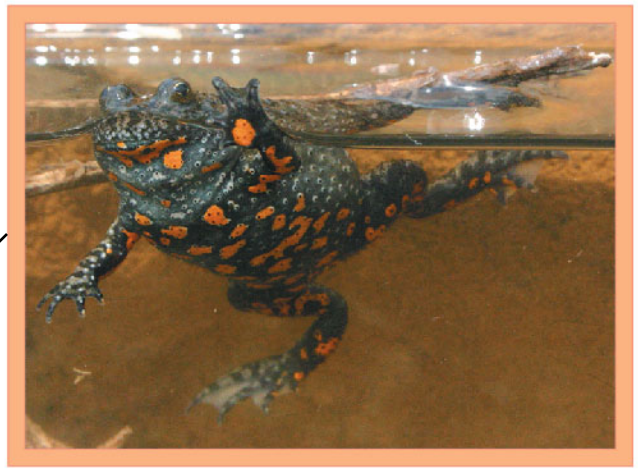
- A **hybrid zone** is a region in which members of different species mate and produce hybrids
- Hybrids are the result of mating between species with incomplete reproductive barriers

Patterns Within Hybrid Zones

- A hybrid zone can occur in a single band where adjacent species meet
  - For example, two species of toad in the genus *Bombina* interbreed in a long and narrow hybrid zone

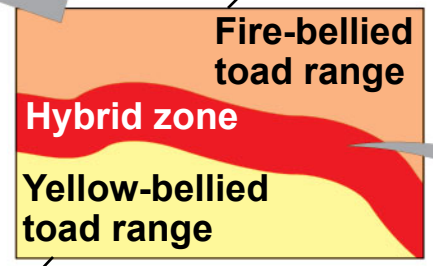
Figure 24.13





Fire-bellied toad, *Bombina bombina*

Yellow-bellied toad, *Bombina variegata*



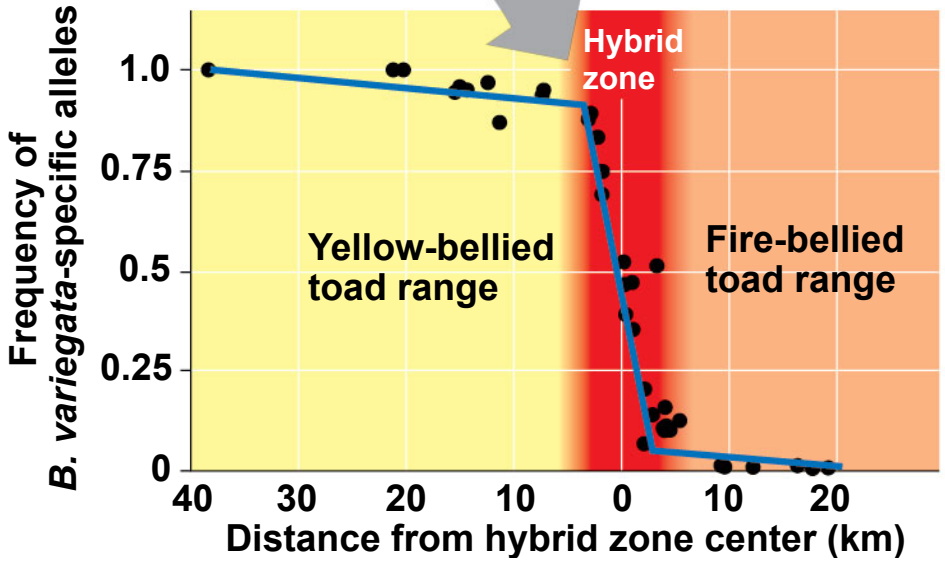


Figure 24.13a

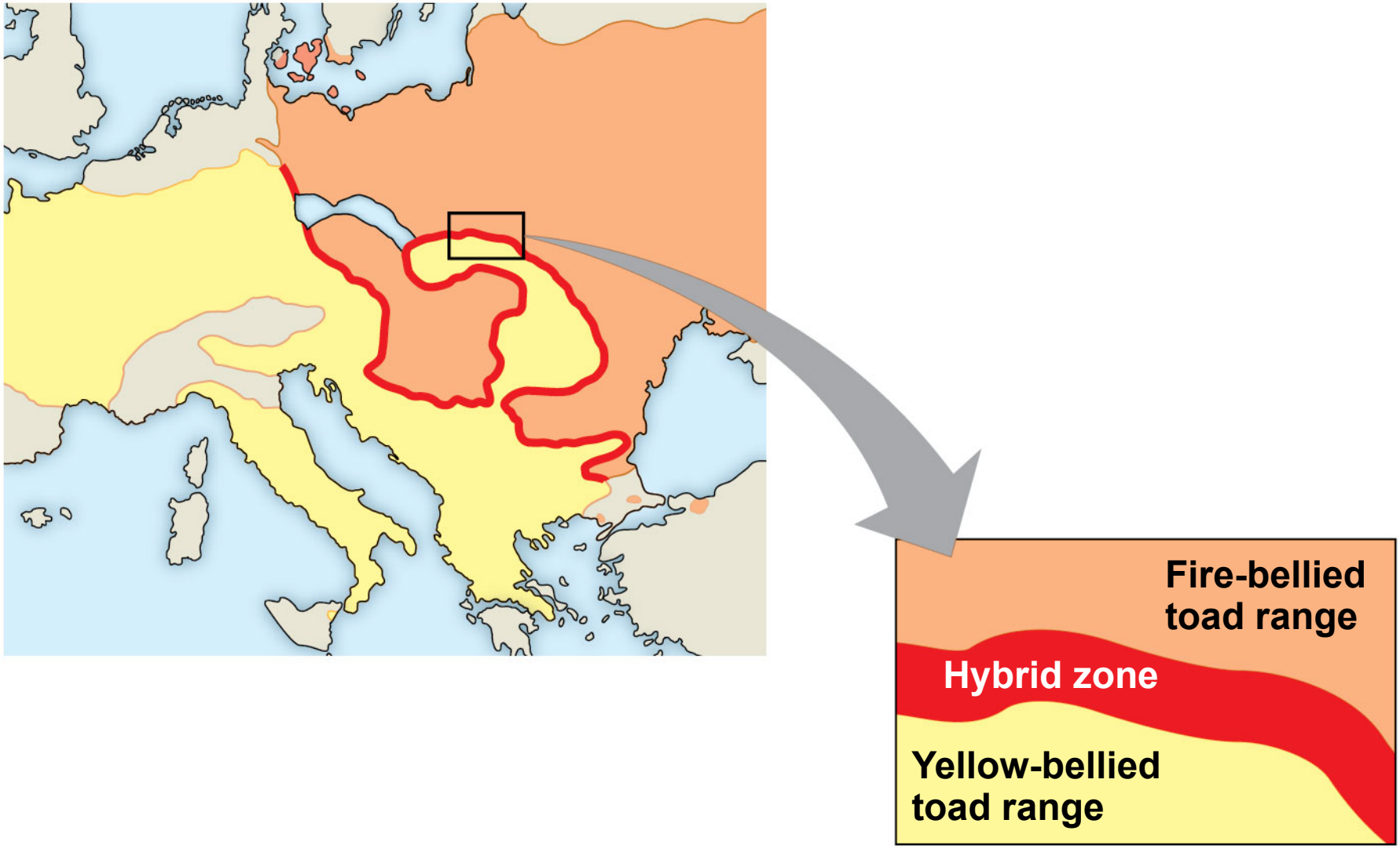


Figure 24.13b

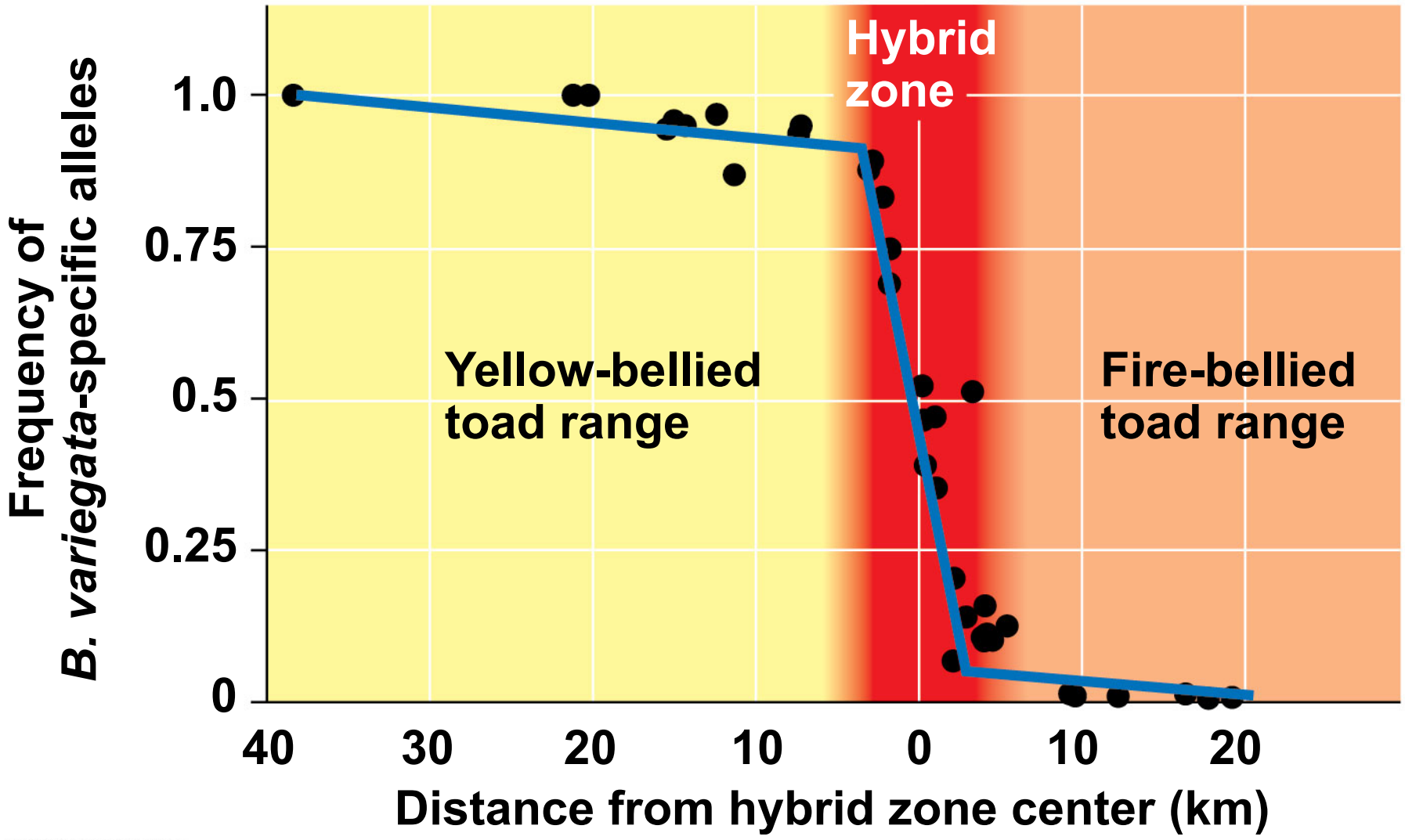
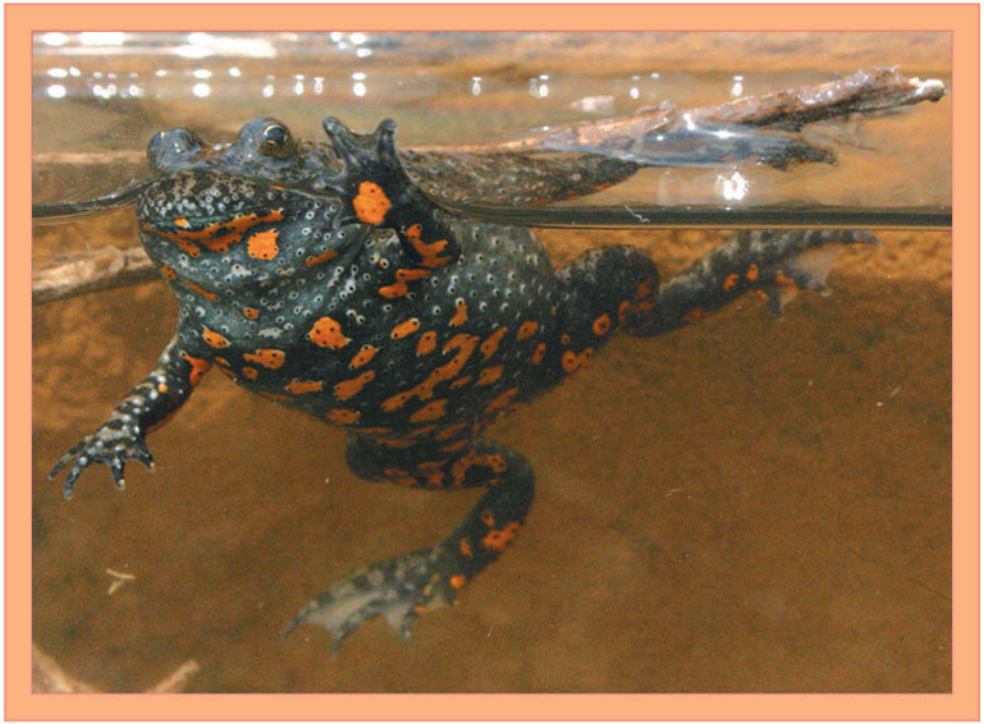


Figure 24.13c

Yellow-bellied toad, *Bombina variegata*

Figure 24.13d



Fire-bellied toad, *Bombina bombina*

- Hybrids often have reduced fitness compared with parent species
- The distribution of hybrid zones can be more complex if parent species are found in patches within the same region

Hybrid Zones and Environmental Change

- Change in environmental conditions can result in the relocation of existing hybrid zones or the production of novel hybrid zones
  - For example, the hybrid zone between black-capped and Carolina chickadees has shifted northward in response to climate change
  - For example, the species range of southern flying squirrels now overlaps with that of the northern flying squirrel

- Breeding between hybrids and parent species can result in the transfer of alleles from one parent species to the other
- 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 24.14_1

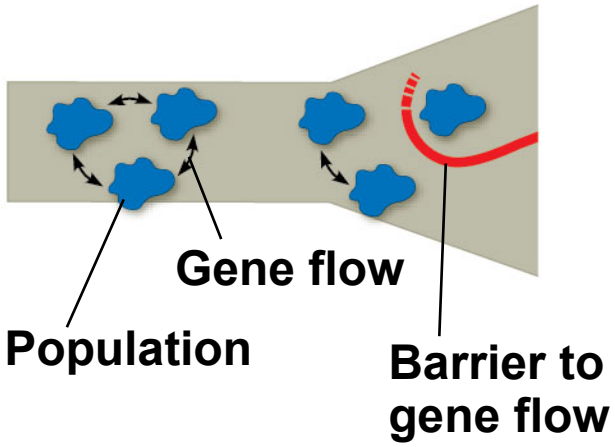


Figure 24.14_2

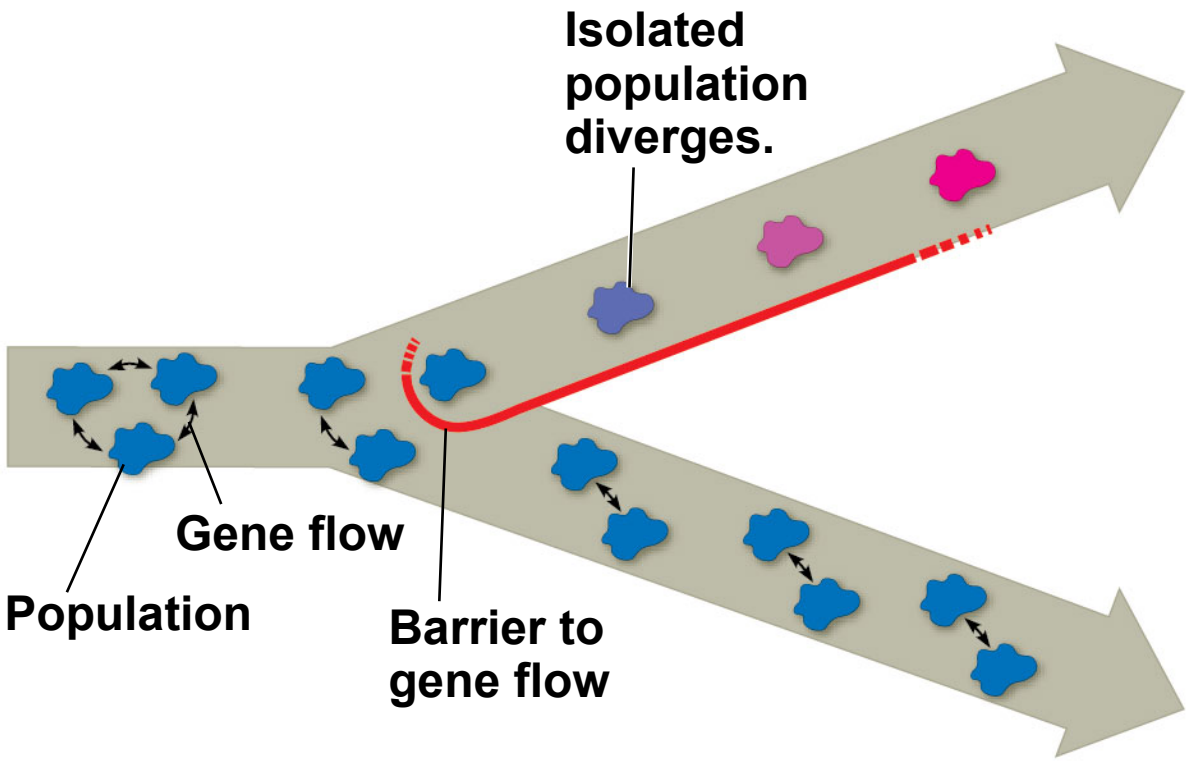


Figure 24.14_3

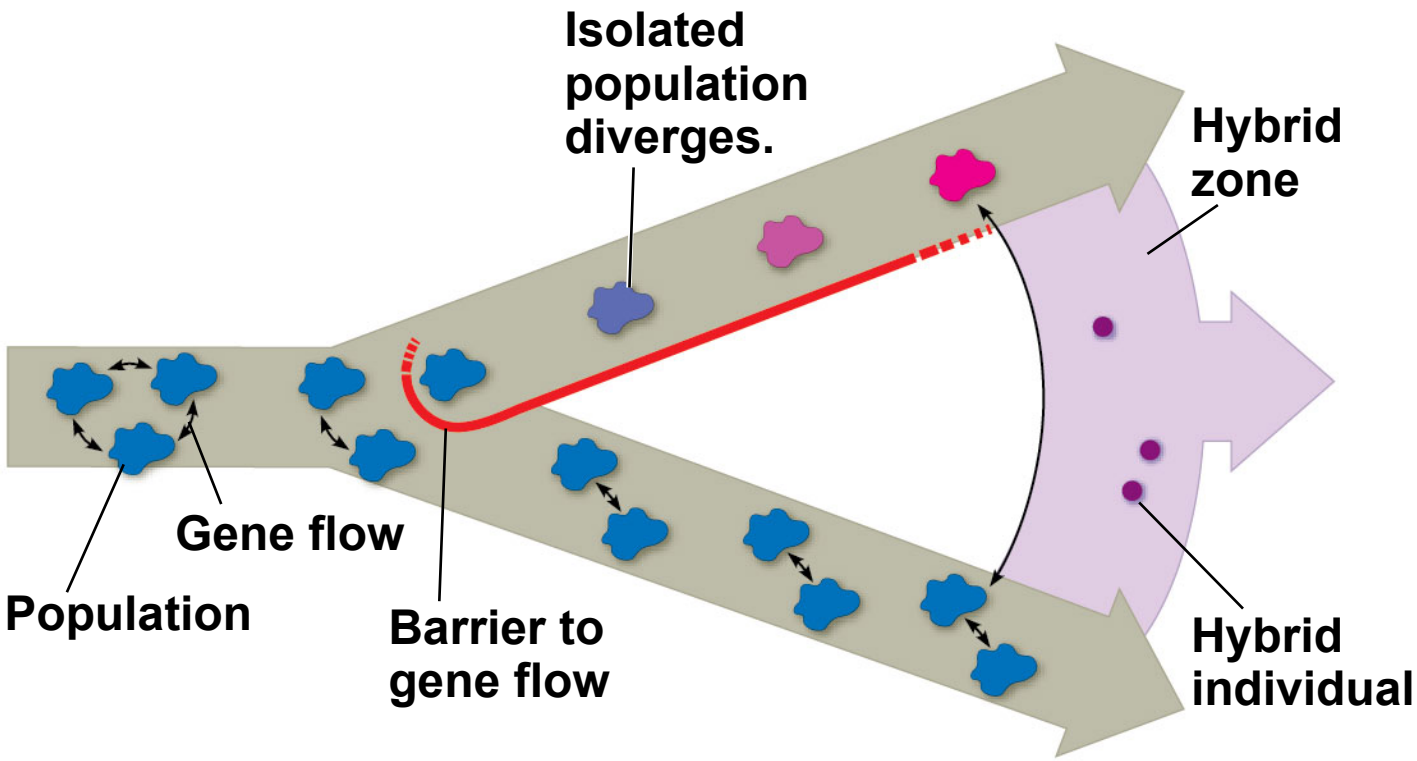
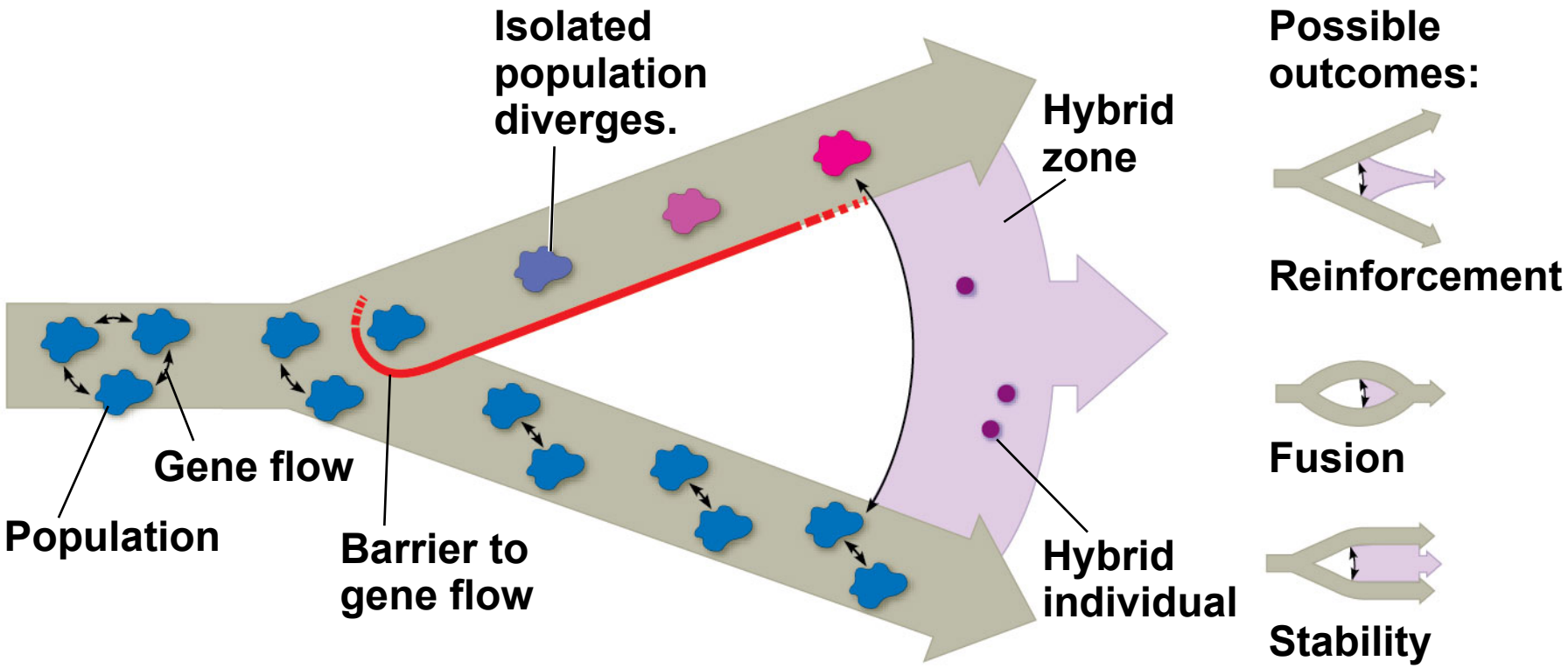


Figure 24.14_4



Reinforcement: Strengthening Reproductive Barriers

- When hybrids are less fit than parent species, **reinforcement** of reproductive barriers may occur through strong selection for prezygotic barriers
- Over time, the rate of hybridization decreases

- Where reinforcement occurs, reproductive barriers should be stronger for sympatric than allopatric species
  - For example, female flycatchers in the genus *Ficedula* recognize and select mates of their own species when choosing between males from sympatric populations
  - Female flycatchers frequently make mistakes when selecting males from the more similar allopatric populations

Fusion: Weakening Reproductive Barriers

- If hybrids are as fit as parents, there can be substantial gene flow between species
- If gene flow is great enough, reproductive barriers weaken and the parent species can fuse into a single species
  - For example, pollution in Lake Victoria has reduced the ability of female cichlids to distinguish males of different species from males of their own species

Figure 24.15

Pundamilia nyererei

Pundamilia pundamilia

***Pundamilia* "turbid water,"**
hybrid offspring from a location with turbid water

Figure 24.15a

Pundamilia nyererei

Figure 24.15b

Pundamilia pundamilia

Figure 24.15c

***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, 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 need to differ between species

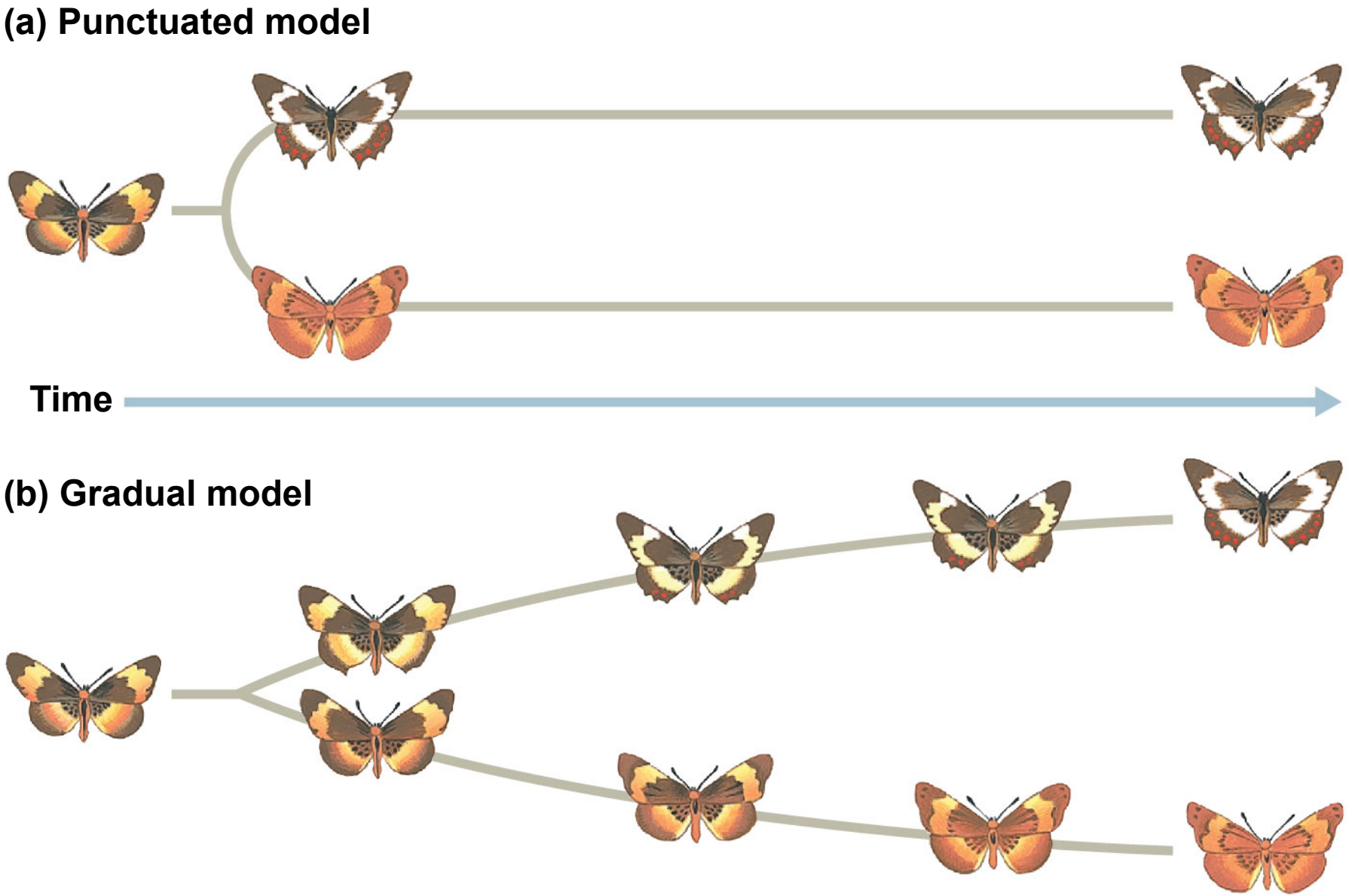
The Time Course of Speciation

- The rate of speciation can be studied using the fossil record, morphological data, or molecular data

Patterns in the Fossil Record

- The fossil record includes examples of species that appear suddenly, persist unchanged for some time, and then disappear
- **Punctuated equilibria** describes these periods of apparent stasis punctuated by sudden change
- The punctuated equilibrium model contrasts with a model of gradual change in a species over time

Figure 24.16

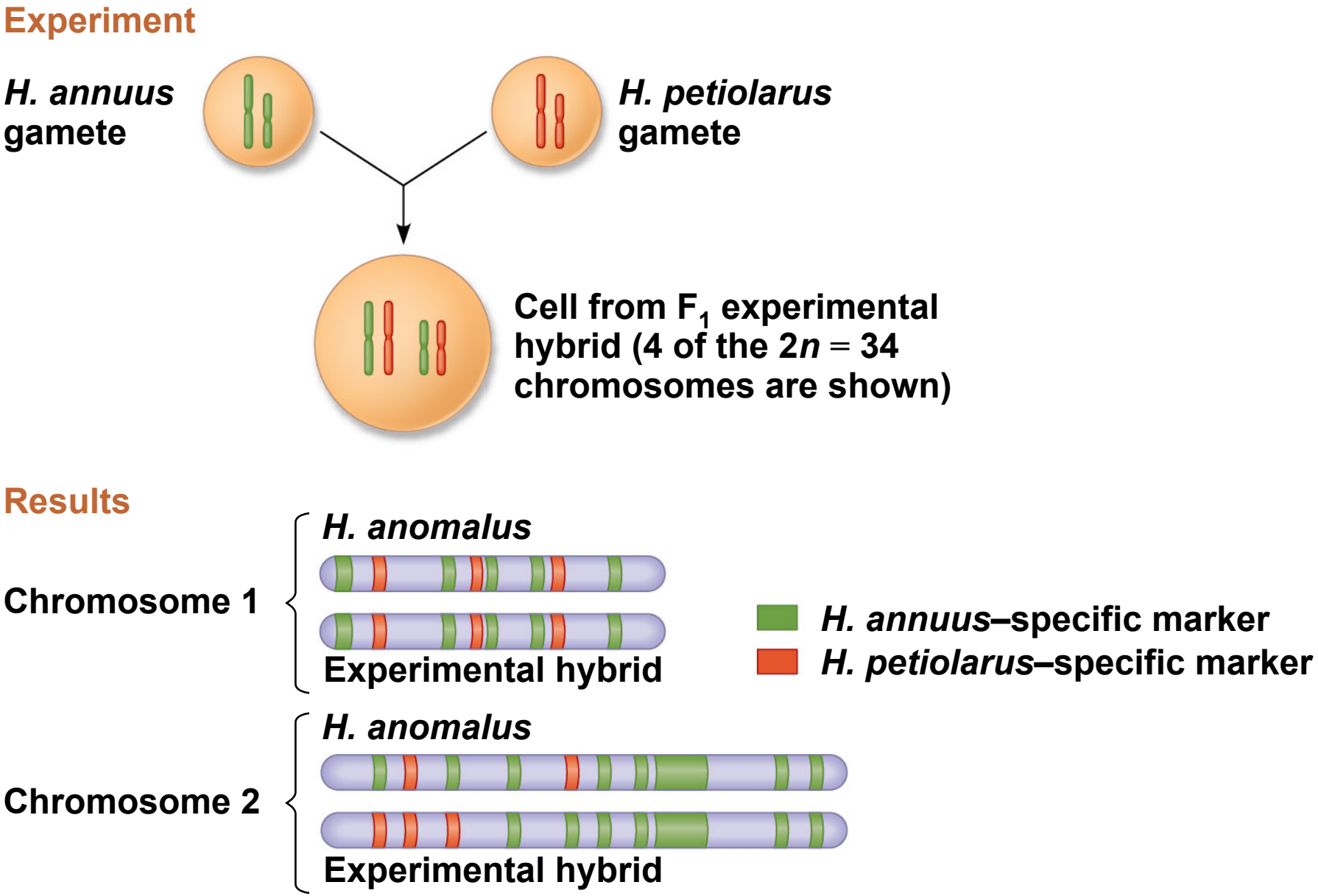


Speciation Rates

- 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 24.17

Figure 24.18



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).

- The interval between speciation events can range from 4,000 years (some cichlids) to 40 million years (some beetles), with an average of 6.5 million years

Studying the Genetics of Speciation

- A fundamental question of evolutionary biology persists: How many genes influence the formation of new species?
- Depending on the species in question, 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 that is 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 24.19

(a) *Mimulus lewisii*

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

(c) *Mimulus cardinalis*

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

Figure 24.19a

(a) *Mimulus lewisii*

Figure 24.19b

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

Figure 24.19c

(c) *Mimulus cardinalis*

Figure 24.19d

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

From Speciation to Macroevolution

- 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

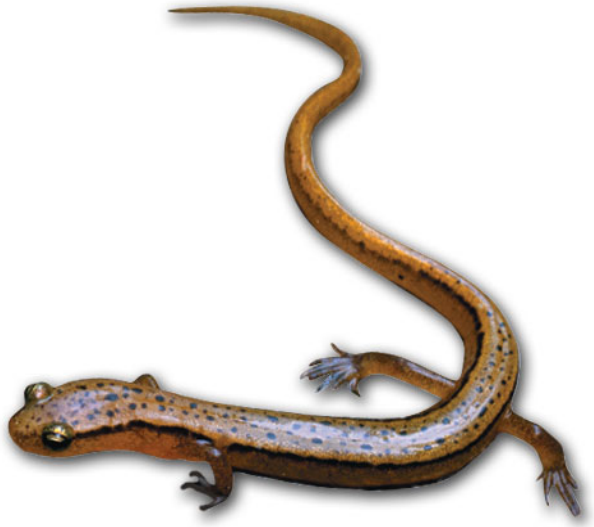


Figure 24.UN02a

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

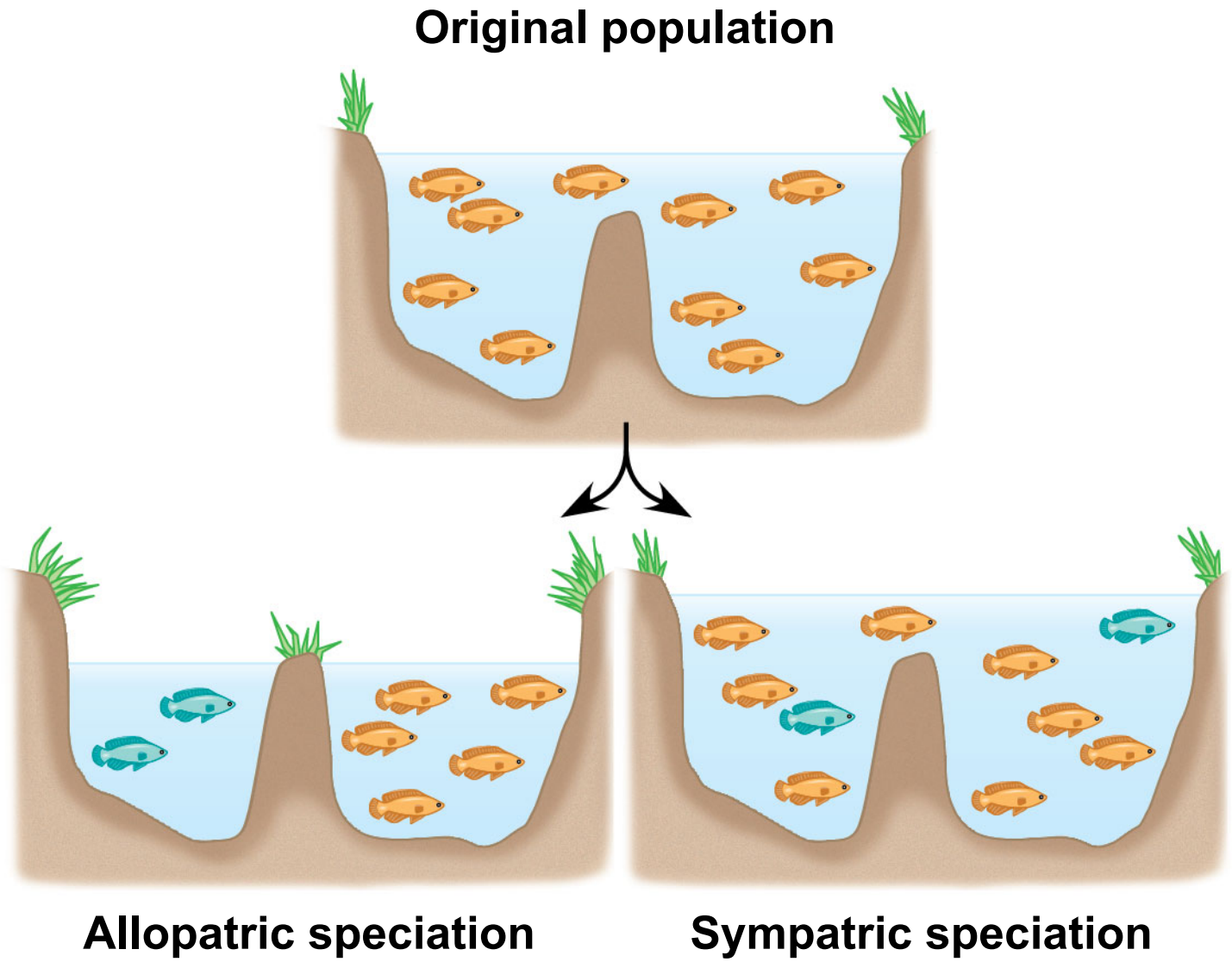


Figure 24.UN04

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