CAMPBELL BIOLOGY IN FOCUS

URRY • CAIN • WASSERMAN • MINORSKY • REECE

22

The Origin of Species

Lecture Presentations by
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SECOND EDITION

That "Mystery of Mysteries"

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

Figure 22.1

- **Speciation** is the process by which one species splits into two or more species
- Speciation explains the features shared between organisms due to inheritance from their recent common ancestor

- Speciation forms a conceptual bridge between 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

Concept 22.1: 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 other populations
- Gene flow between populations holds the populations together genetically

Figure 22.2

(a) Similarity between different species **(b) Diversity within a species**

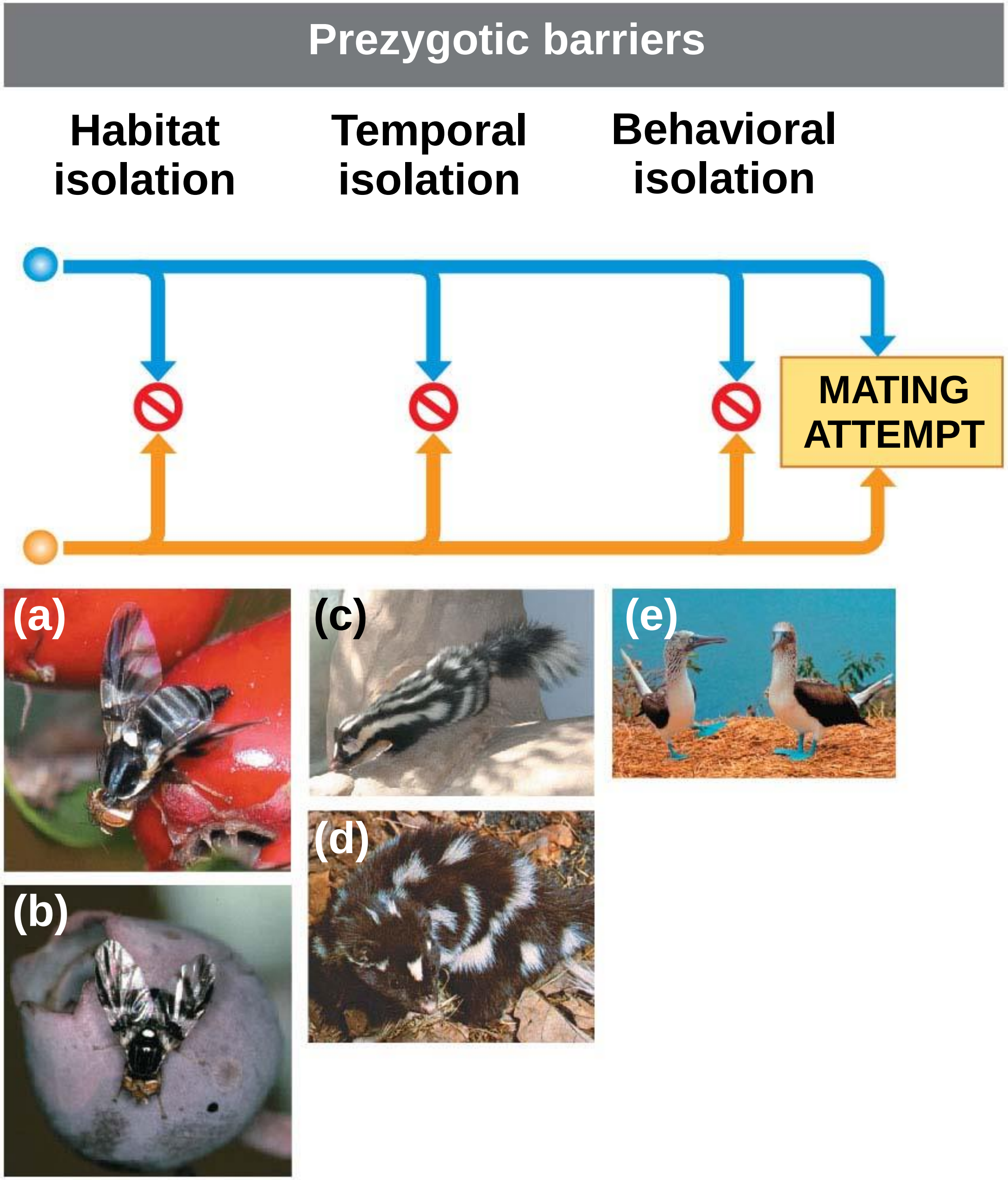
(a) Similarity between different species

Reproductive Isolation

- **Reproductive isolation** is the existence of biological barriers that impede two species from producing viable, fertile offspring
- Sometimes **hybrids**, the offspring of crosses between different species, are successfully produced
- Reproductive barriers can be classified by whether they act before or after fertilization

- **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 22.3-1



Prezygotic barriers
Habitat isolation
Temporal isolation
Behavioral isolation
MATING ATTEMPT
(a)
(b)
(c)
(d)
(e)

- **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 22.3-1a

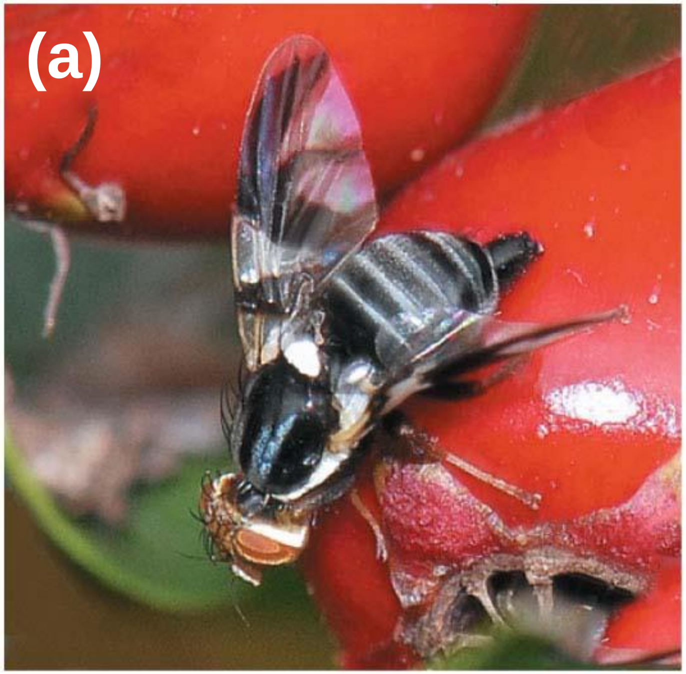
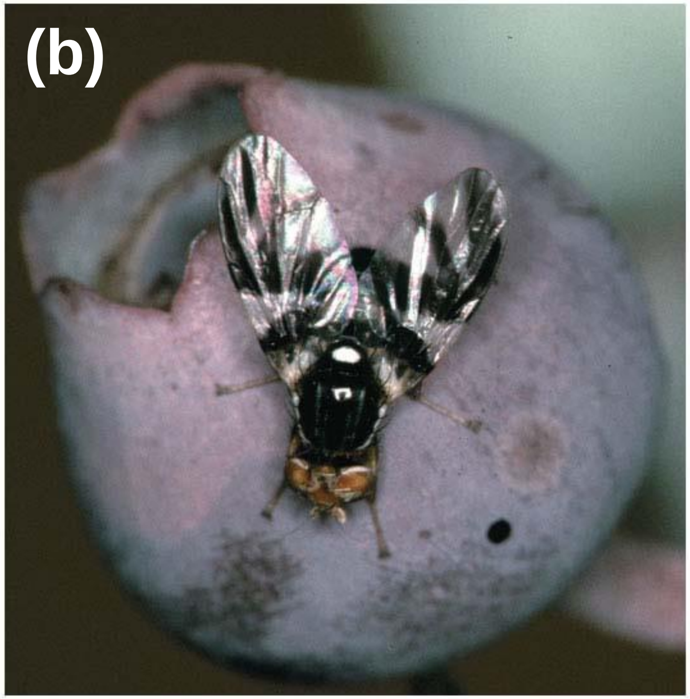


Figure 22.3-1b



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

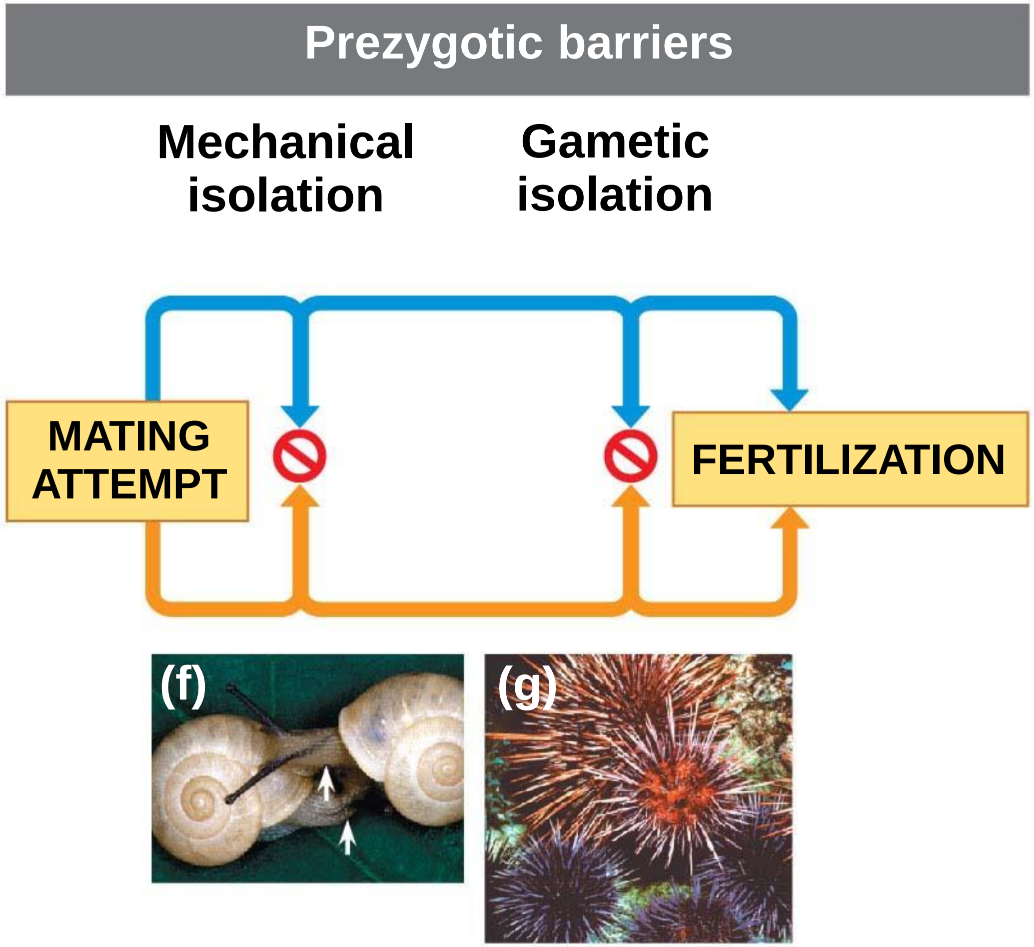
Figure 22.3-1c

Figure 22.3-1d

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

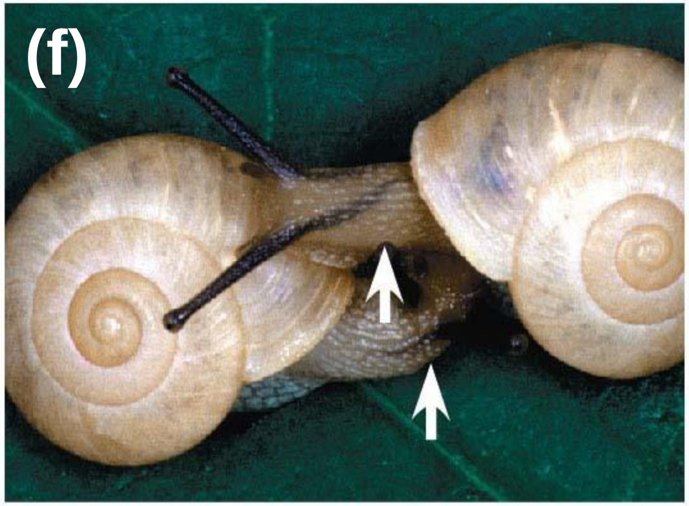
Figure 22.3-1e

Figure 22.3-2


Prezygotic barriers
Mechanical isolation
Gametic isolation
MATING ATTEMPT
FERTILIZATION
(f)
(g)

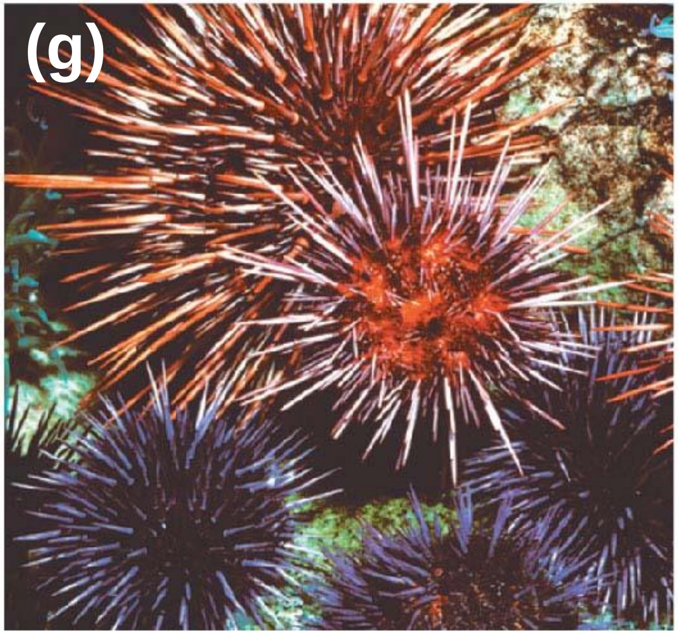
- **Mechanical isolation**: Morphological differences prevent successful mating

Figure 22.3-2f



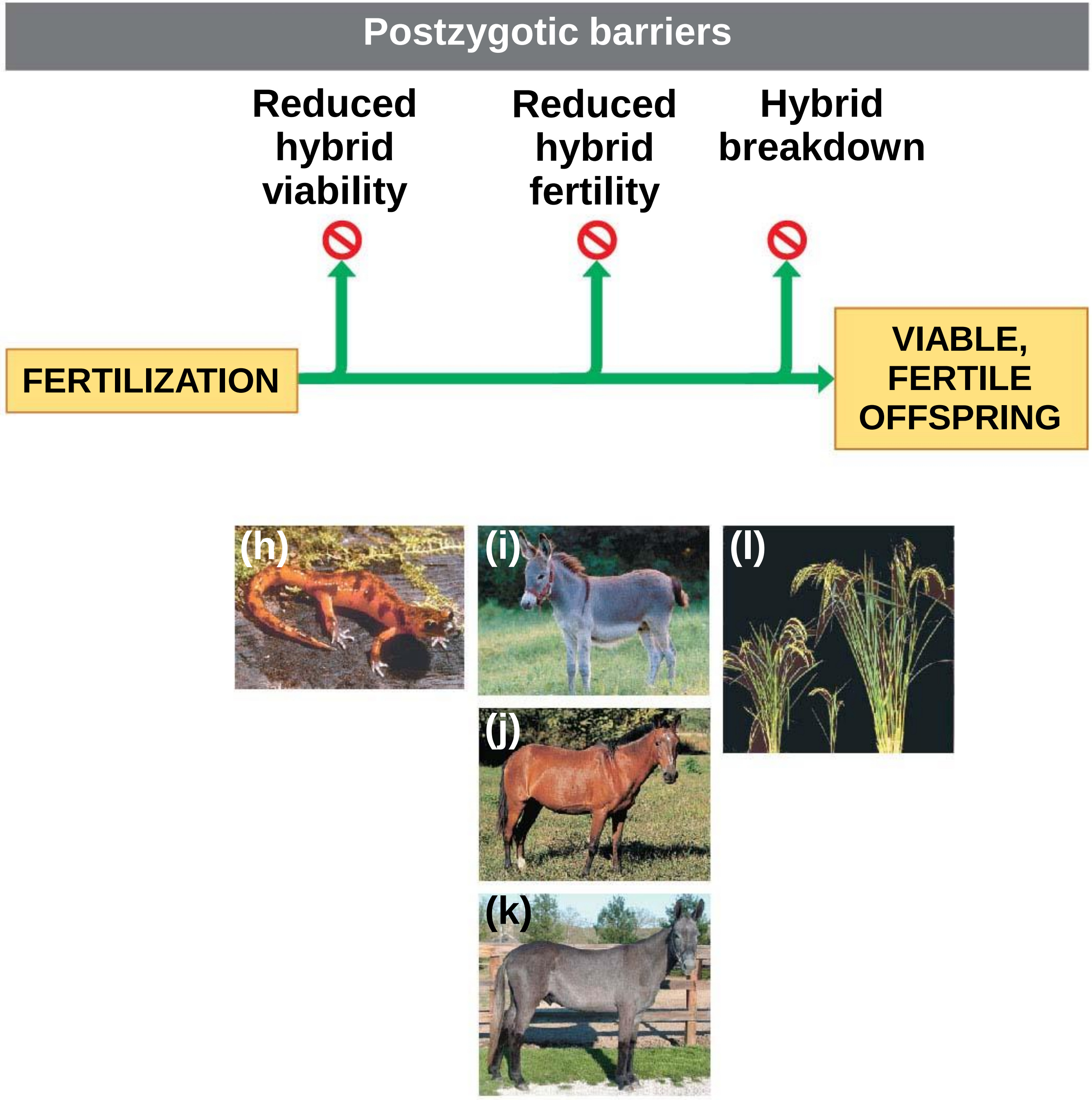
- **Gametic isolation:** Sperm of one species may not be able to fertilize eggs of another species

Figure 22.3-2g



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

Figure 22.3-3



Postzygotic barriers
Reduced hybrid viability
Reduced hybrid fertility
Hybrid breakdown
FERTILIZATION
VIABLE, FERTILE OFFSPRING
(h)
(i)
(l)
(j)
(k)

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

Figure 22.3-3h

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

Figure 22.3-3i

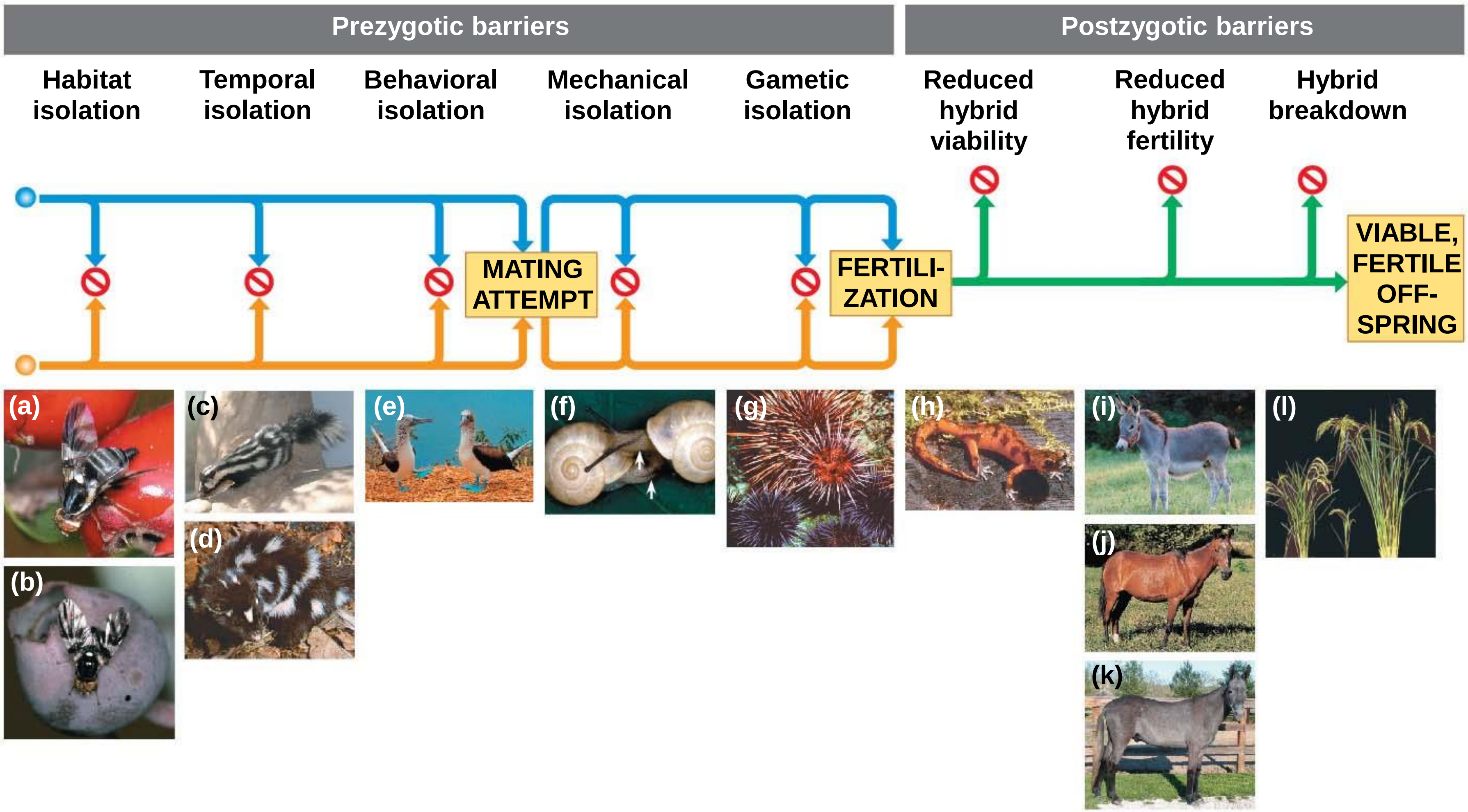
Figure 22.3-3j

Figure 22.3-3k

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

Figure 22.3-3l

Figure 22.3



Prezygotic barriers
Postzygotic barriers
Habitat isolation
Temporal isolation
Behavioral isolation
Mechanical isolation
Gametic isolation
Reduced hybrid viability
Reduced hybrid fertility
Hybrid breakdown
MATING ATTEMPT
FERTILI-ZATION
VIABLE, FERTILE OFF-SPRING
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)

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 distinct species
  - For example, grizzly bears and polar bears can mate to produce "grolar bears"

Figure 22.4

◀ **Grizzly bear (*U. arctos*)**

▼ **Polar bear (*U. maritimus*)**

▲ **Hybrid "grolar bear"**

Figure 22.4-1

▲ **Grizzly bear (*U. arctos*)**

Figure 22.4-2

▲ **Polar bear**
(*U. maritimus*)

Figure 22.4-3

▲ **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 and does not rely on information about gene flow but on subjective criteria

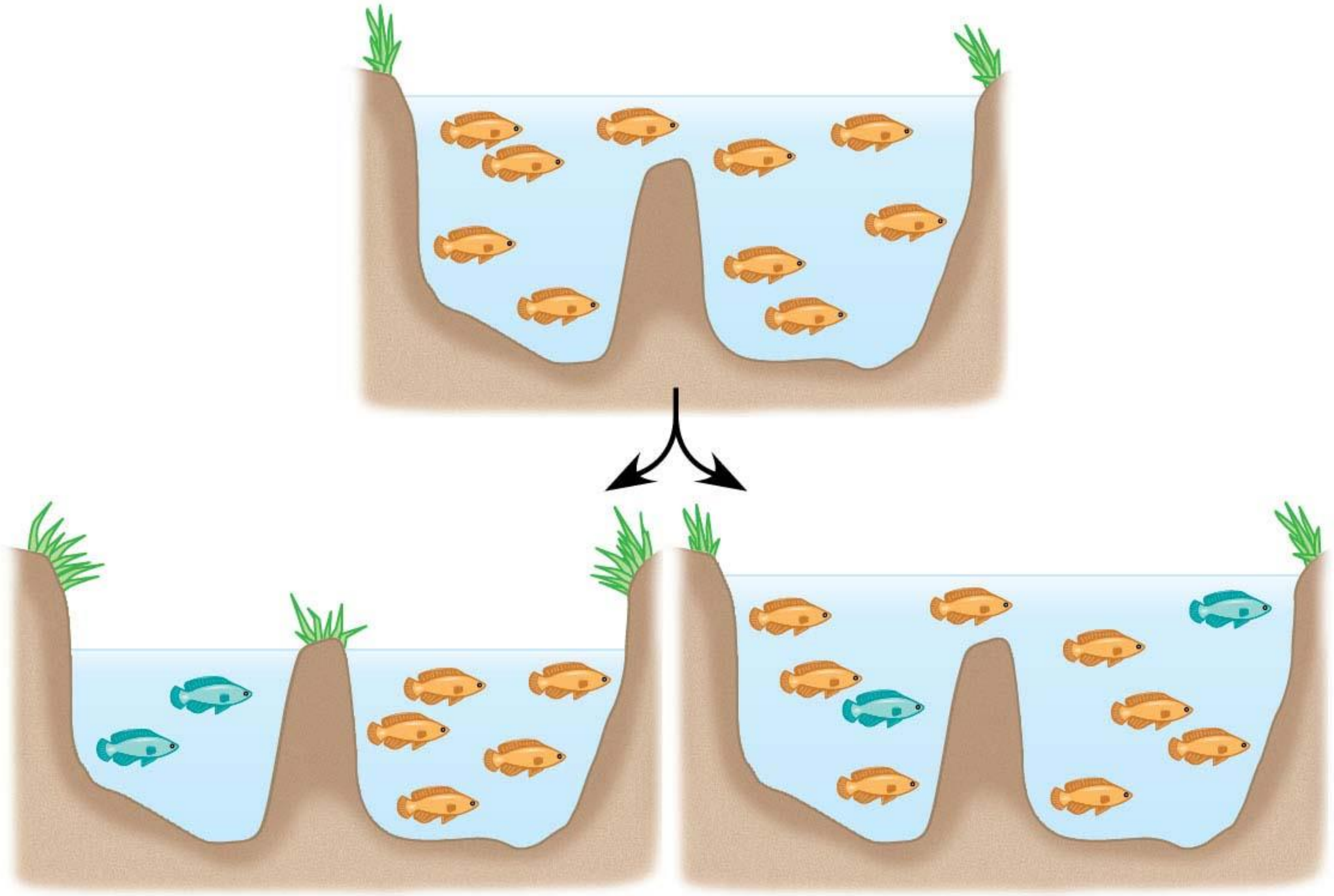
- The **ecological species concept** views a species in terms of its ecological niche
  - It applies to sexual and asexual species and emphasizes the role of disruptive selection

- The **phylogenetic species concept** defines a species as the smallest group of individuals that share a common ancestor, a single branch on a phylogenetic tree
  - It applies to sexual and asexual species, but it can be difficult to determine the degree of difference required for separate species

Concept 22.2: Speciation can take place with or without geographic separation

- Speciation can occur in two ways
  - Allopatric speciation
  - Sympatric speciation

Figure 22.5



(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 flightless cormorant of the Galápagos likely originated from a flying species on the mainland

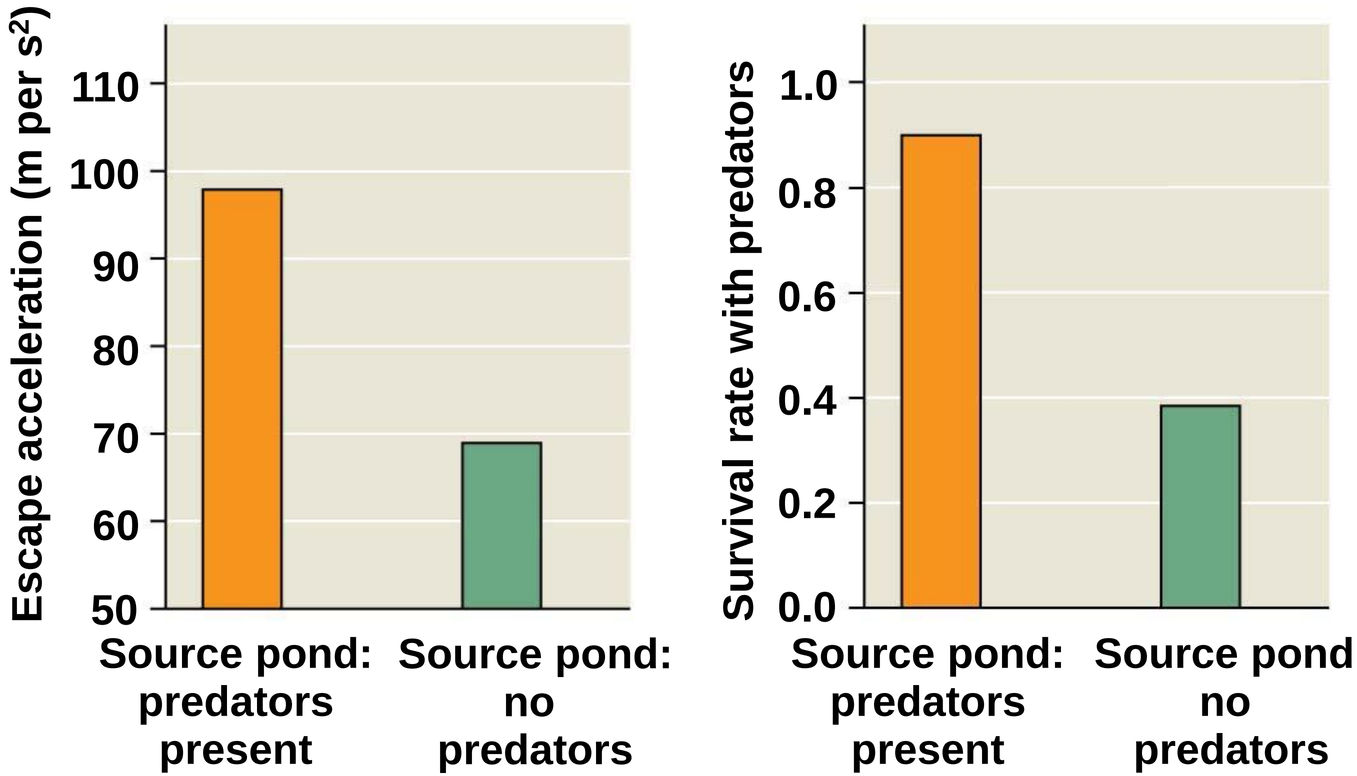
The Process of Allopatric Speciation

- The definition of a geographic 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

- Separate populations may evolve independently through mutation, natural selection, and genetic drift
- Reproductive isolation may arise as a result of genetic divergence
  - For example, mosquitofish in the Bahamas comprise several isolated populations in different ponds
  - Populations in ponds with high predation rates have evolved different body shapes from populations in “low-predation” ponds

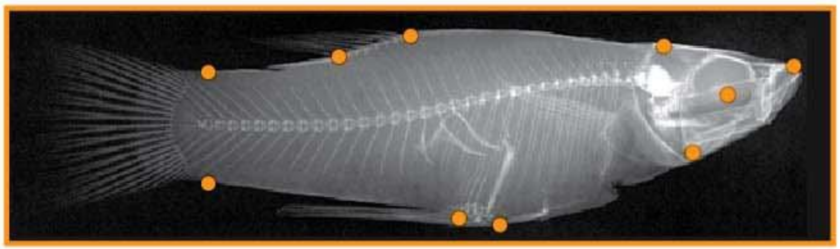
Figure 22.6

(a) Differences in body shape

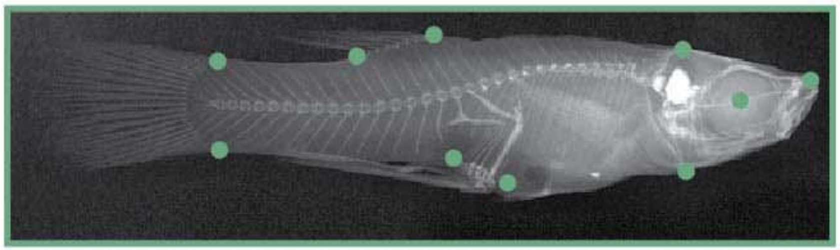


(b) Differences in escape acceleration and survival

Figure 22.6-1



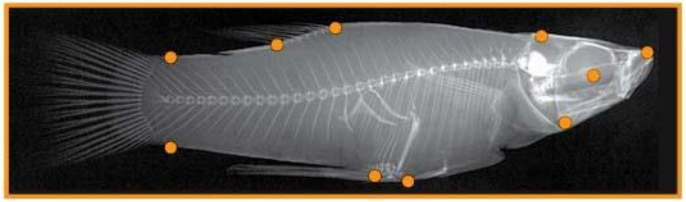
With predators: body shape that enables rapid bursts of speed



Without predators: body shape that favors long, steady swimming

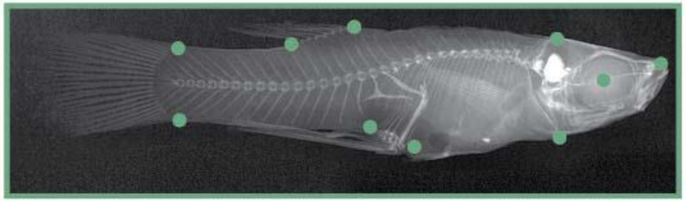
(a) Differences in body shape

Figure 22.6-1a



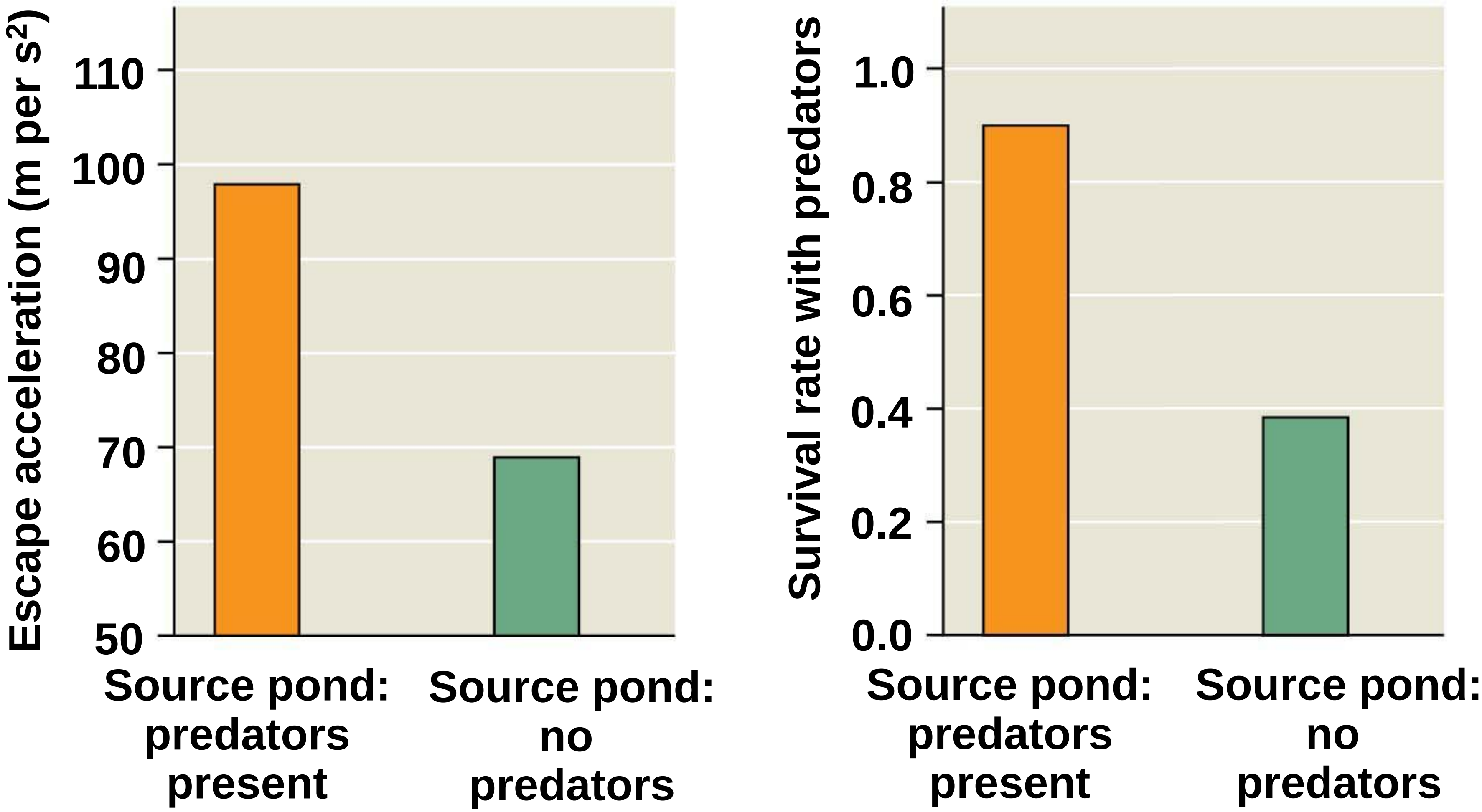
With predators: body shape that enables rapid bursts of speed

Figure 22.6-1b



Without predators: body shape that favors long, steady swimming

Figure 22.6-2



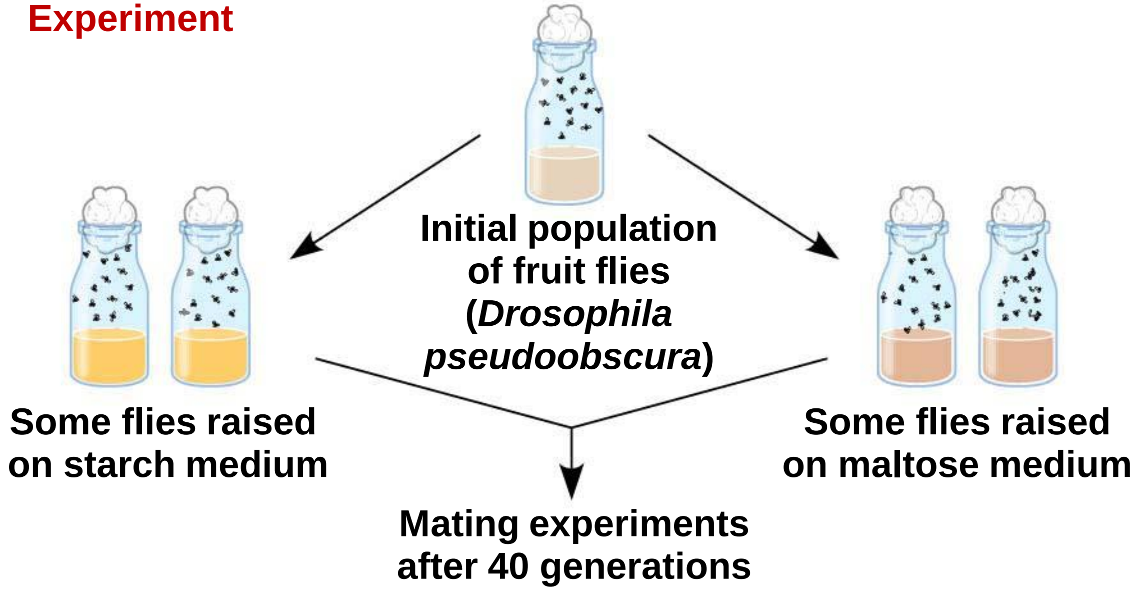
(b) Differences in escape acceleration and survival

Evidence of Allopatric Speciation

- Reproductive barriers can develop in lab populations that are experimentally isolated and subjected to different environmental conditions
  - For example, isolated lab populations of fruit flies raised on different diets evolve to digest their food source more efficiently and prefer to mate with partners adapted to the same food source

Figure 22.7

Experiment



Results

		Female: Starch	Female: Maltose
Male	Starch	22	9
Male	Maltose	8	20

Number of matings in experimental group

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

Number of matings in control group

Figure 22.7-1

Experiment

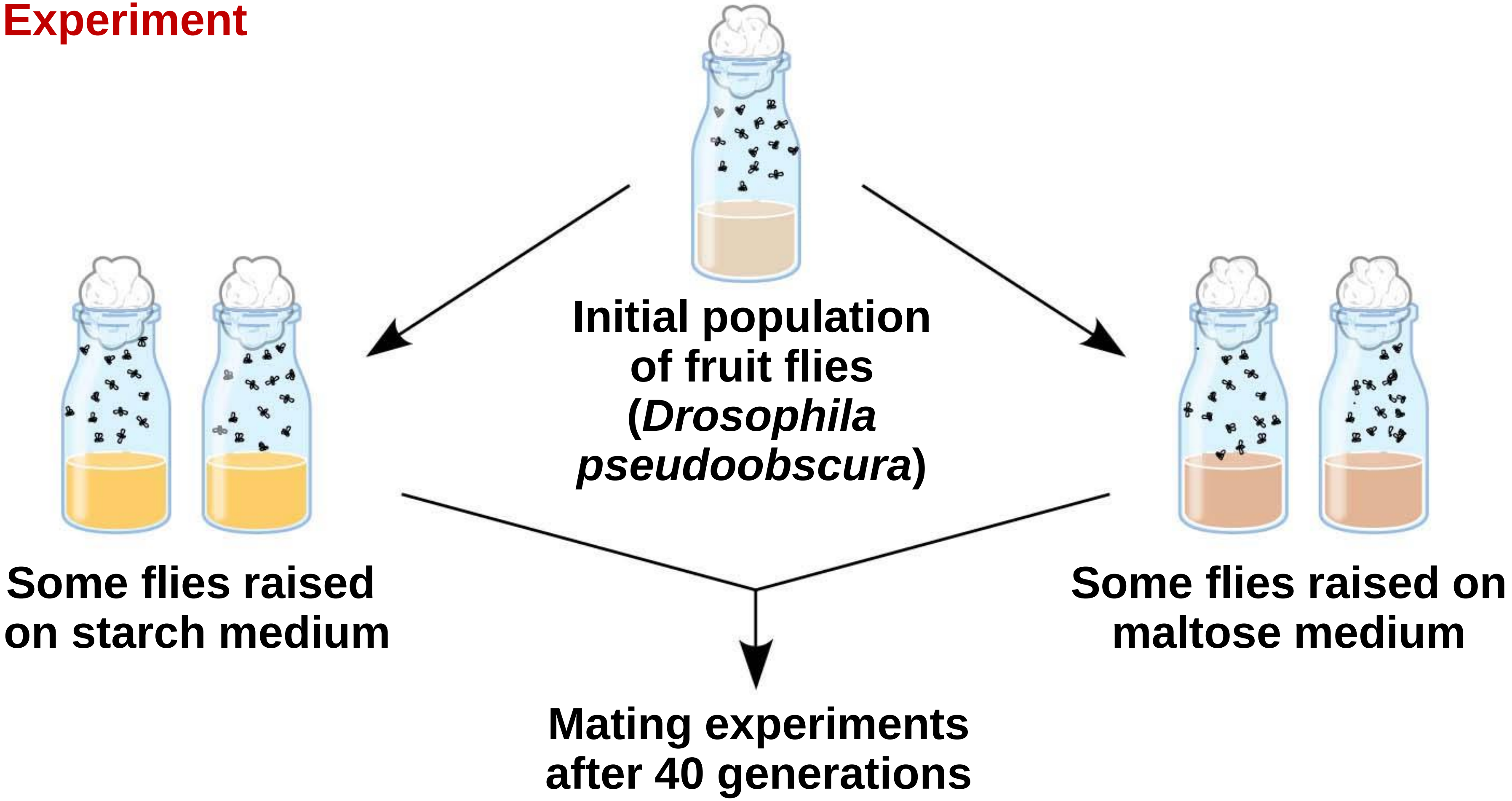


Figure 22.7-2

Results

		Female	
		Starch	Maltose
Male	Starch	22	9
	Maltose	8	20

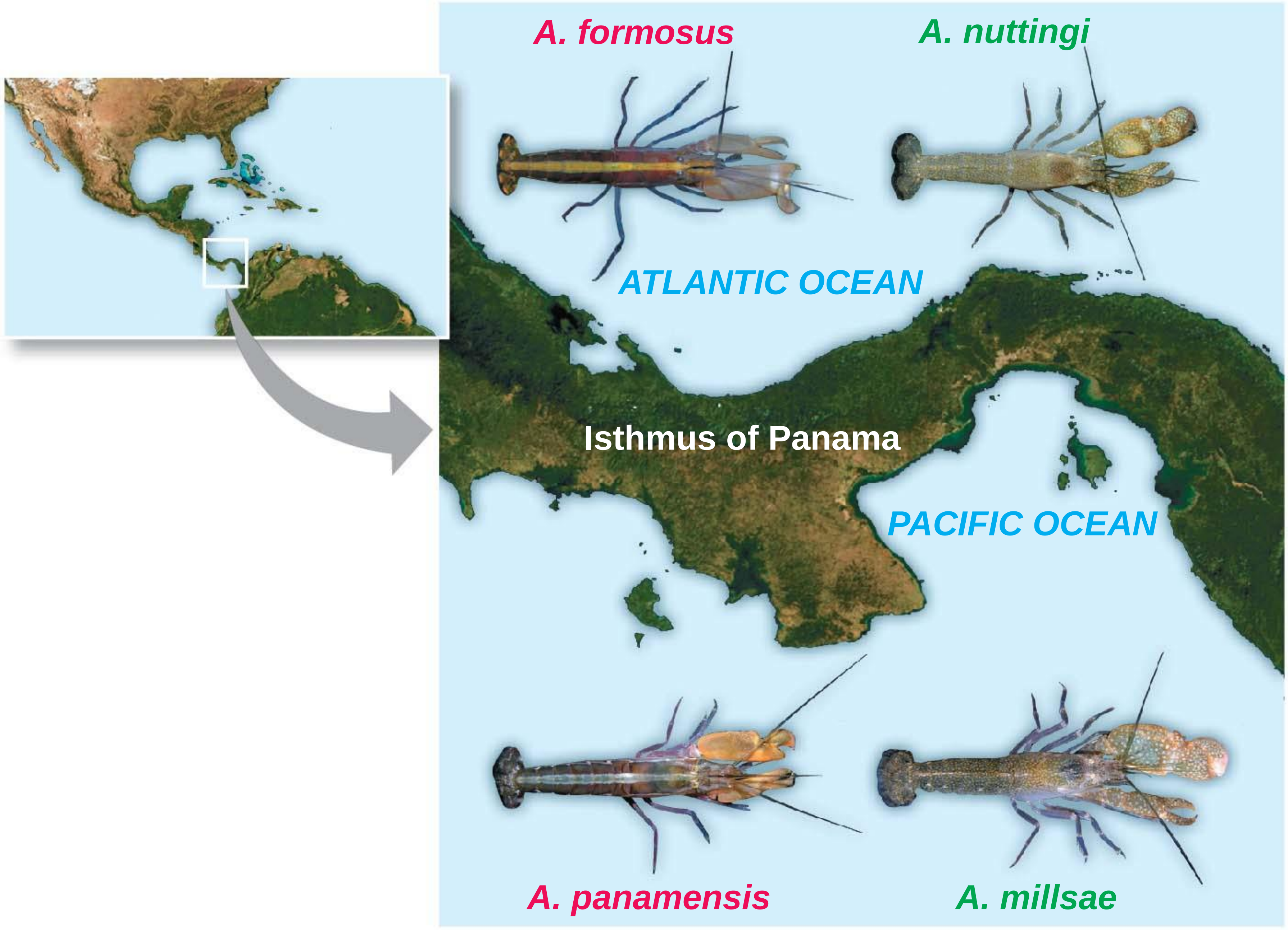
Number of matings in experimental group

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

Number of matings in control group

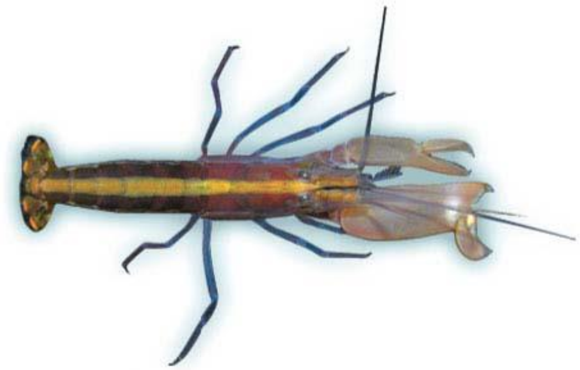
- Allopatric speciation has also been observed in nature
  - For example, sister species of snapping shrimp (*Alpheus*) began to diverge 9 to 3 million years ago when they became isolated by the formation of the Isthmus of Panama

Figure 22.8



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

Figure 22.8-1



A. formosus

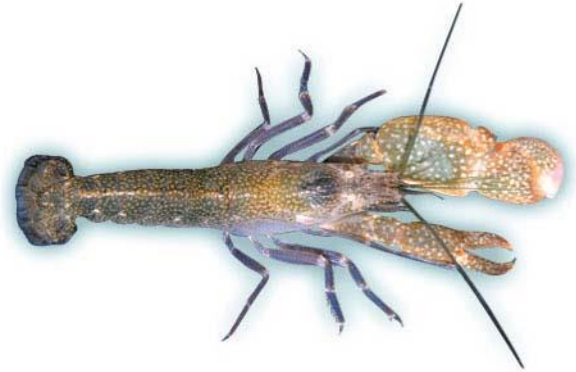
Figure 22.8-2

A. nuttingi

Figure 22.8-3

A. panamensis

Figure 22.8-4



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 geographic distance between them increases
- Reproductive isolation is the result of intrinsic barriers; physical separation is not a biological barrier

Sympatric ("Same Country") Speciation

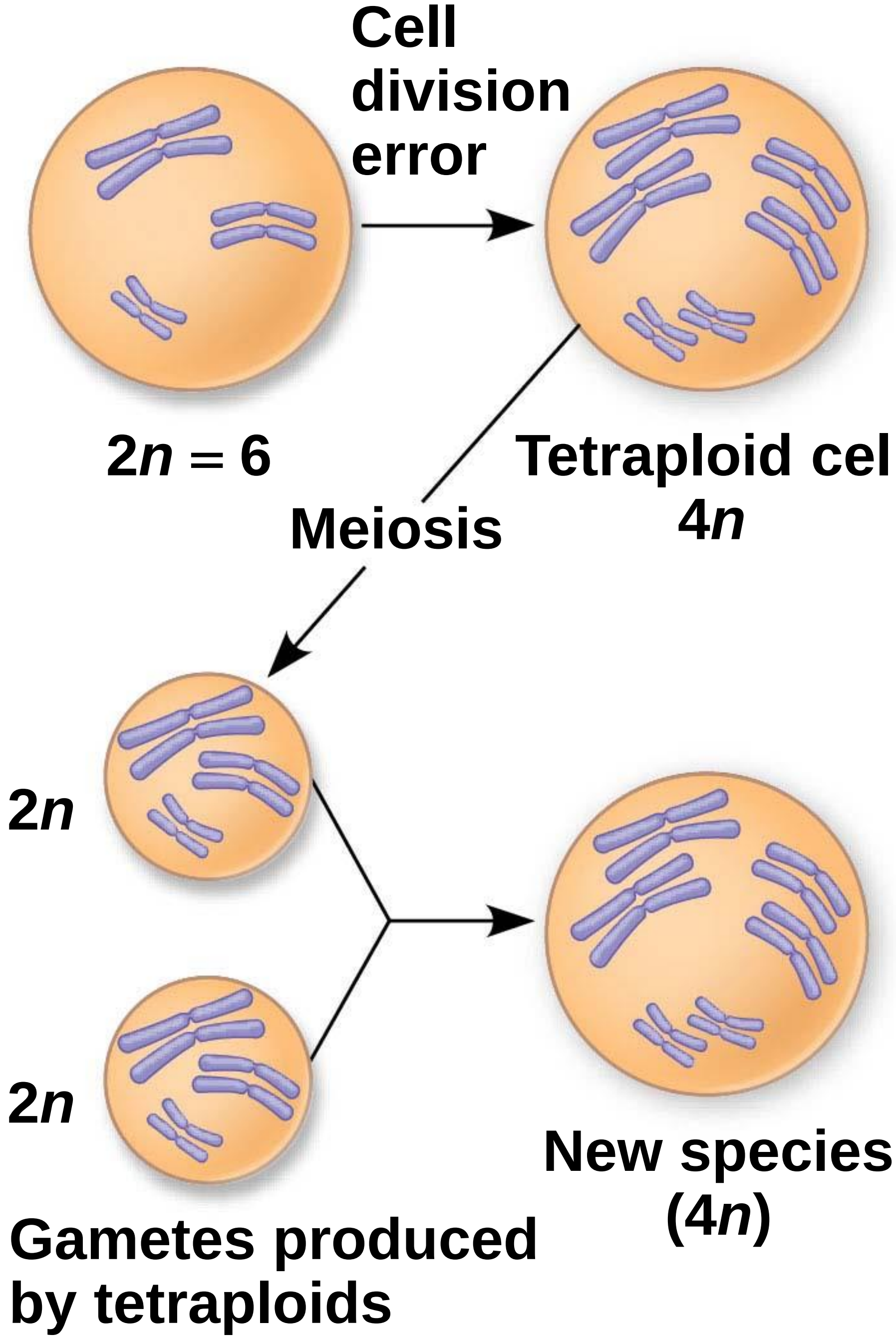
- In **sympatric speciation**, speciation takes place in populations that live in the same geographic area
- Sympatric speciation occurs when gene flow is reduced between groups that remain in contact through factors including
  - Polyploidy
  - Habitat differentiation
  - Sexual selection

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
- An **autopolyploid** is an individual with more than two chromosome sets, derived from one species
- The offspring of mating between autopolyploids and diploids have reduced fertility

- 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 22.9


Cell
division
error
2n = 6
Tetraploid cell
4n
Meiosis
2n
2n
New species
(4n)
Gametes produced
by tetraploids

- At least five new plant species have evolved by polyploidy speciation since 1850
  - For example, three diploid species of goatsbeard plant (*Tragopogon*) have interbred to produce two new tetraploid species

Figure 22.10-s1

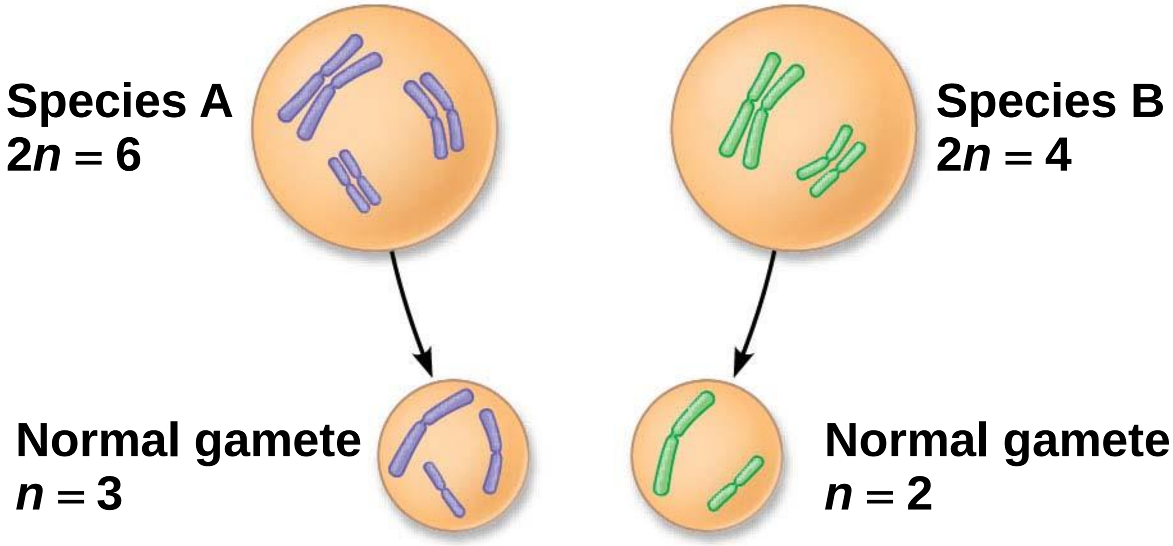


Figure 22.10-s2

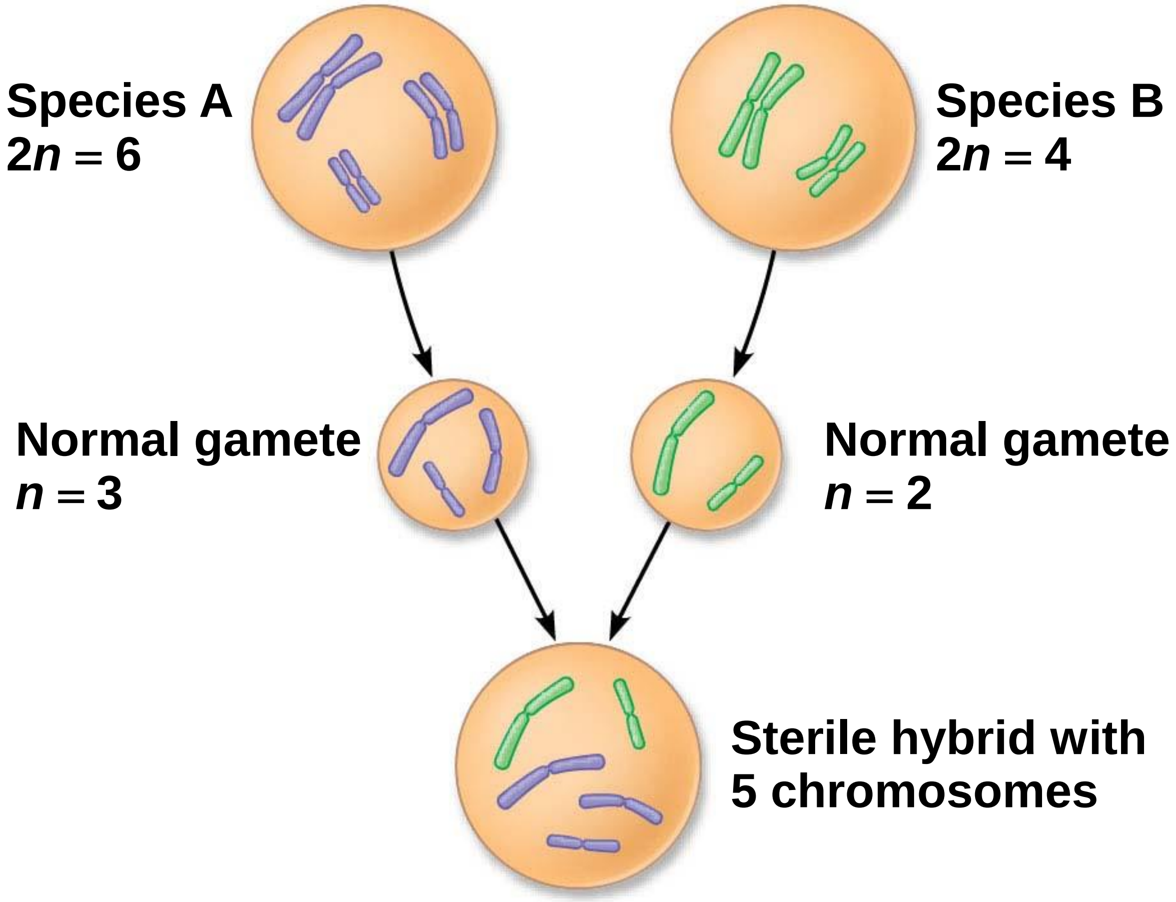
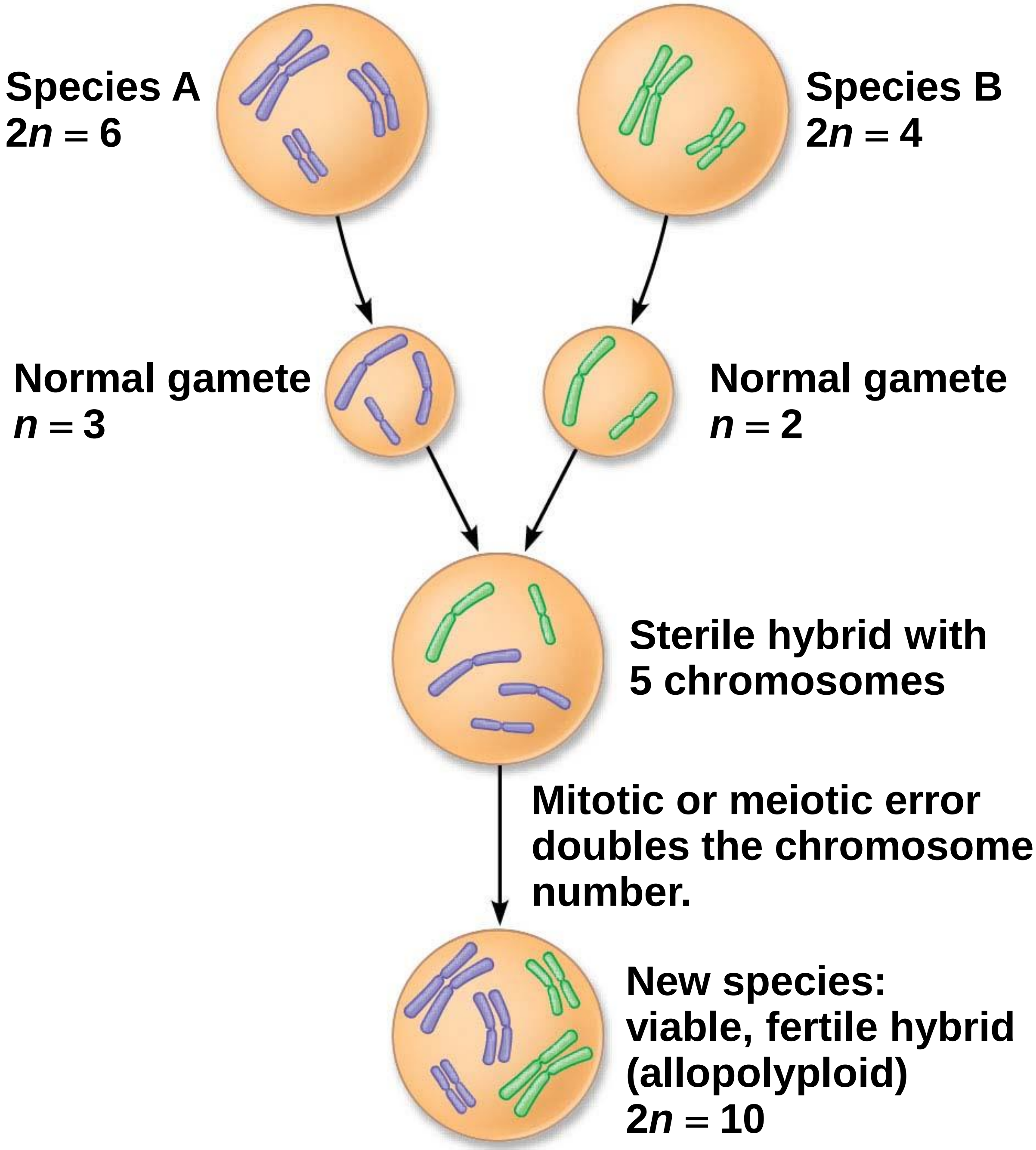


Figure 22.10-s3



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

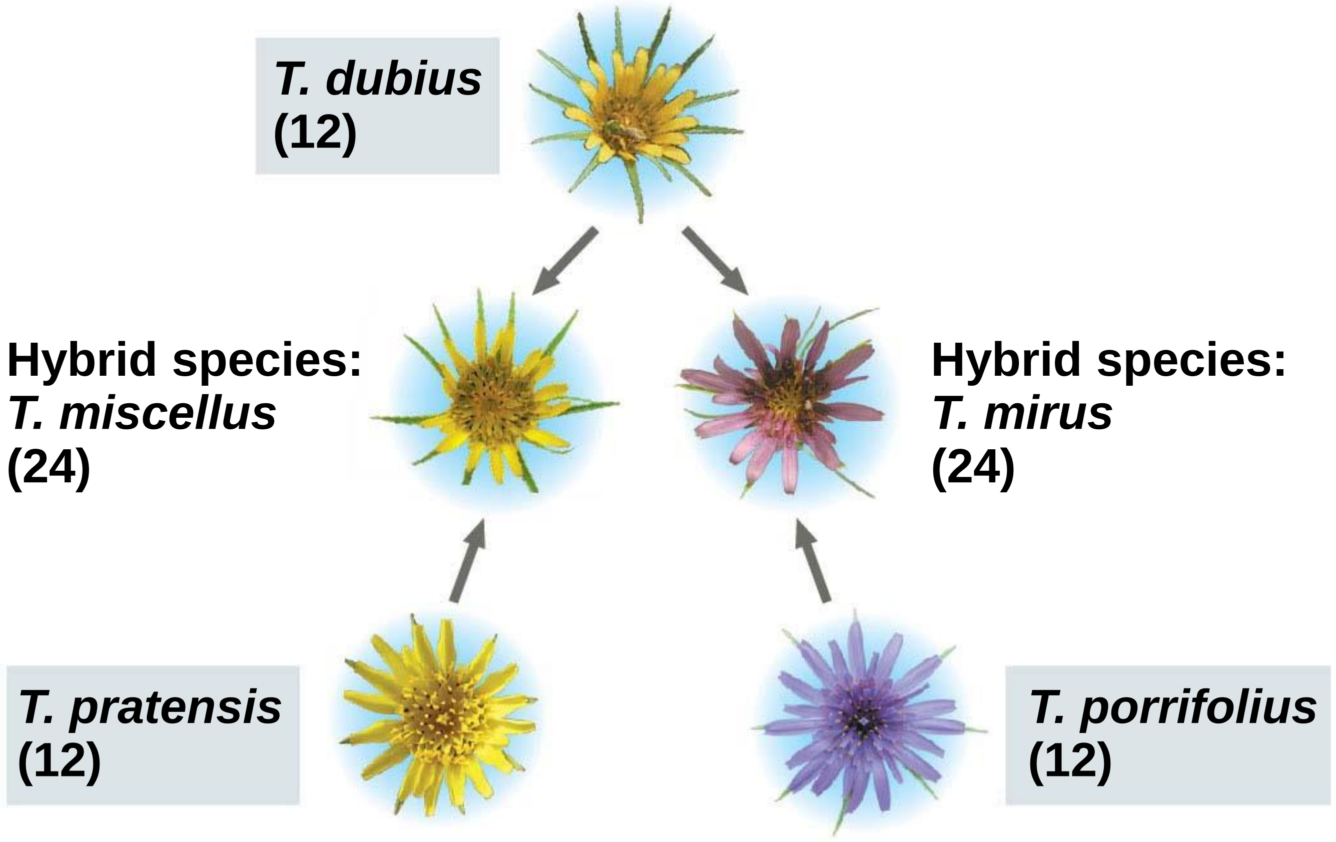
Habitat Differentiation

- Sympatric speciation can also result from the appearance of new ecological niches
  - For example, the North American maggot fly can live on native hawthorn trees as well as more recently introduced apple trees
  - Flies that use different host species are reproductively isolated by both habitat and temporal barriers

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 22.11


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

Allopatric and Sympatric Speciation: *A Review*

- In allopatric speciation, geographic isolation restricts gene flow between populations
- Intrinsic barriers to reproduction may then arise by natural selection, genetic drift, or sexual selection in the isolated populations
- Even if contact is restored between populations, interbreeding is prevented by reproductive barriers

- 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 22.3: 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 22.12

Experiment

Normal light

Monochromatic orange light

P. pundamilia

P. nyererei

Figure 22.12-1

Normal light

P. pundamilia

Monochromatic orange light

P. pundamilia

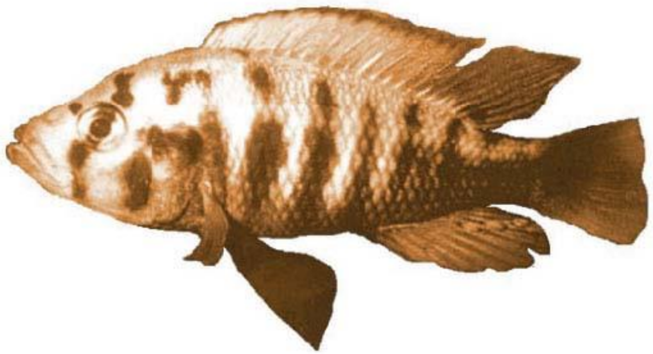


Figure 22.12-3

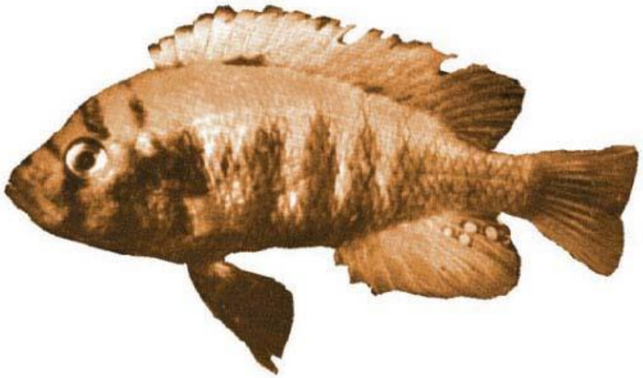
Normal light

P. nyererei

Figure 22.12-4

Monochromatic orange light

P. nyererei



- 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 over Time

- When closely related species meet in a hybrid zone, there are three possible outcomes
  - Reinforcement
  - Fusion
  - Stability

Figure 22.13

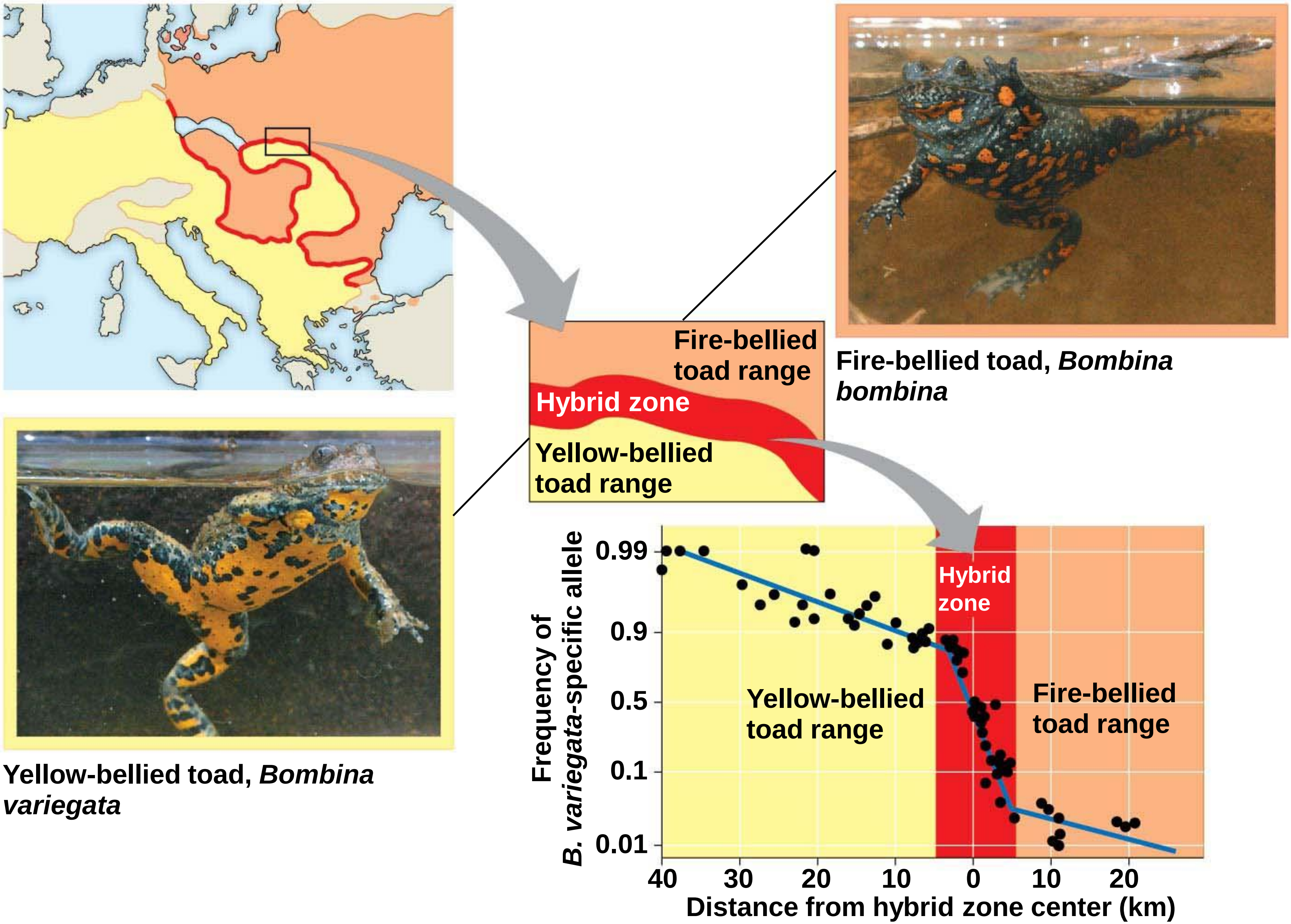

Fire-bellied toad range
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad, *Bombina bombina*
Yellow-bellied toad, *Bombina variegata*
Frequency of *B. variegata*-specific allele
0.99
0.9
0.5
0.1
0.01
Hybrid zone
Yellow-bellied toad range
Fire-bellied toad range
40
30
20
10
0
10
20
Distance from hybrid zone center (km)

Figure 22.13-1

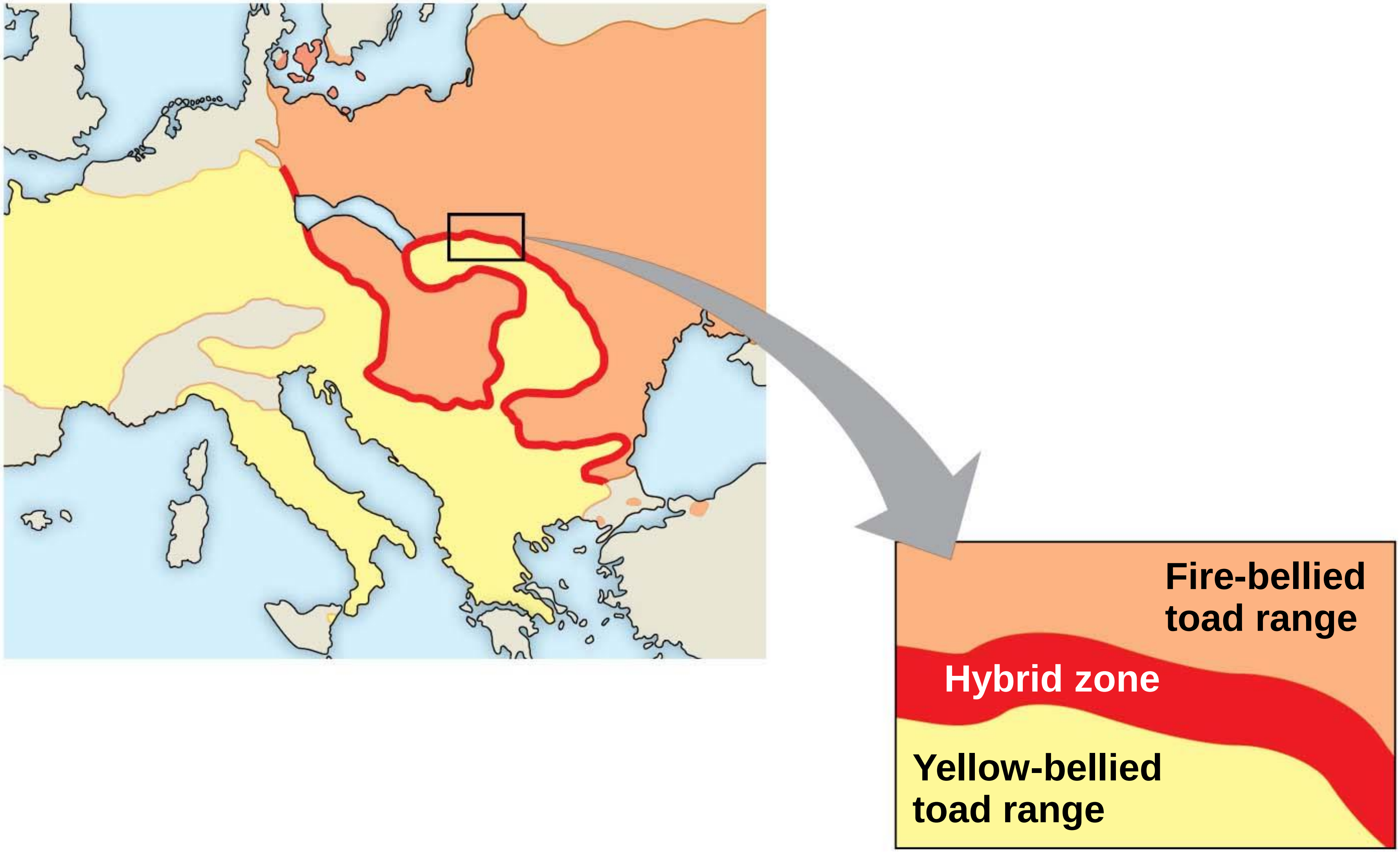


Figure 22.13-2

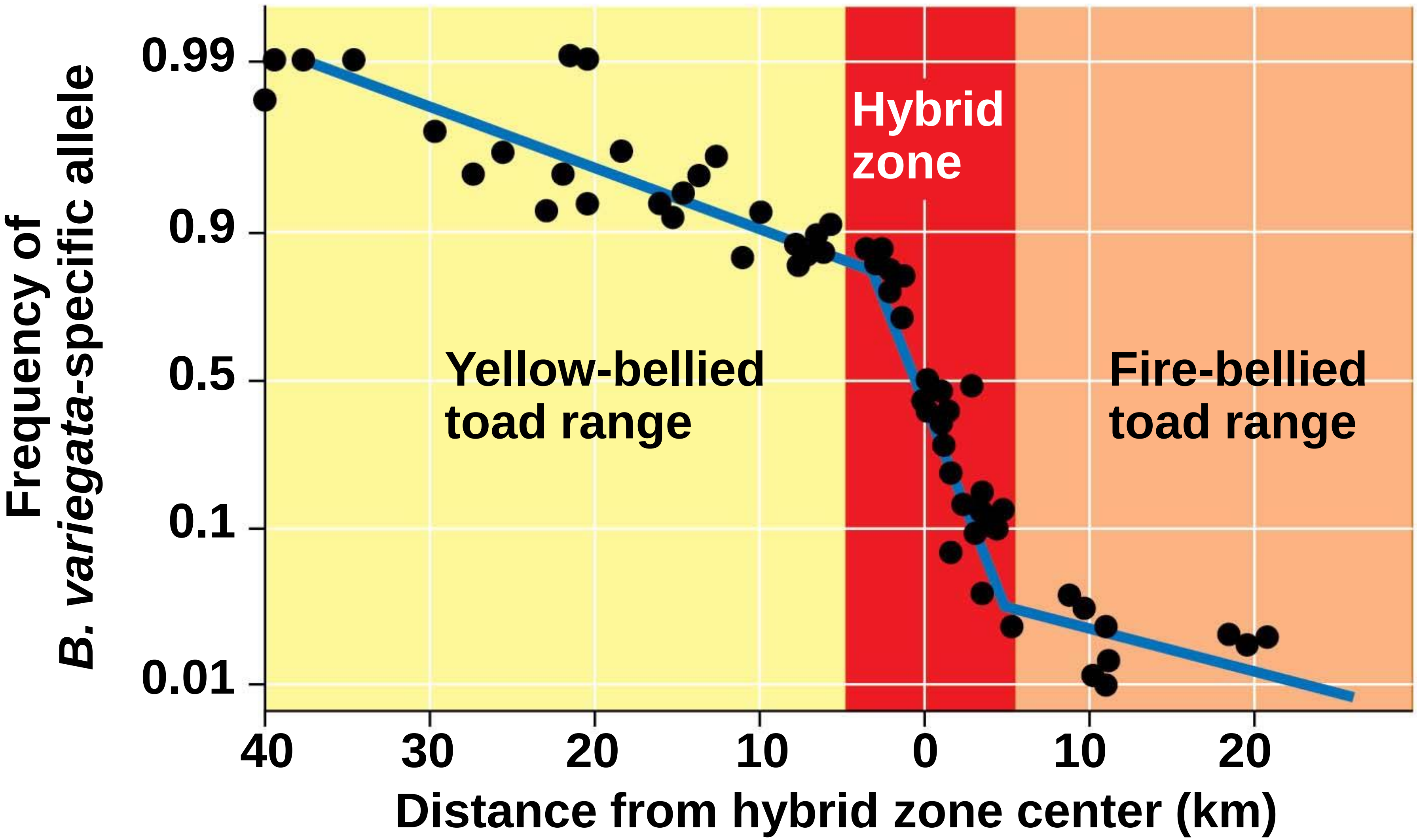


Figure 22.13-3

Yellow-bellied toad, *Bombina variegata*

Fire-bellied toad, *Bombina bombina*

- **Reinforcement** occurs when hybrids are less fit than the parent species
- Natural selection strengthens (reinforces) reproductive barriers, and over time the rate of hybridization decreases
- Where reinforcement occurs, reproductive barriers should be stronger for sympatric than for allopatric species

- **Fusion** of the parent species into a single species may occur if hybrids are as fit as parents, allowing substantial gene flow between species
  - For example, fusion of cichlid species in Lake Victoria may be occurring because water pollution has reduced the ability of female cichlids to distinguish males of different species by color

Figure 22.14-s1

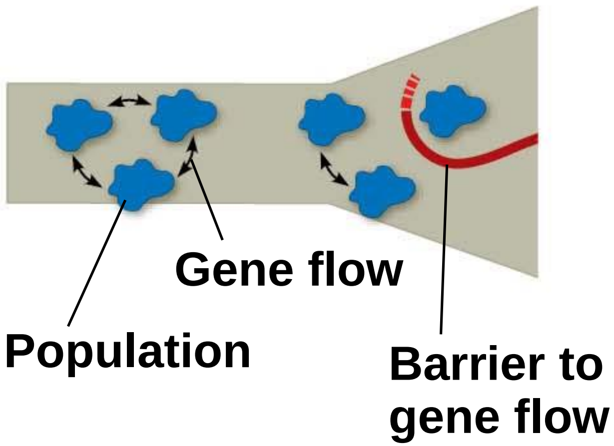


Figure 22.14-s2

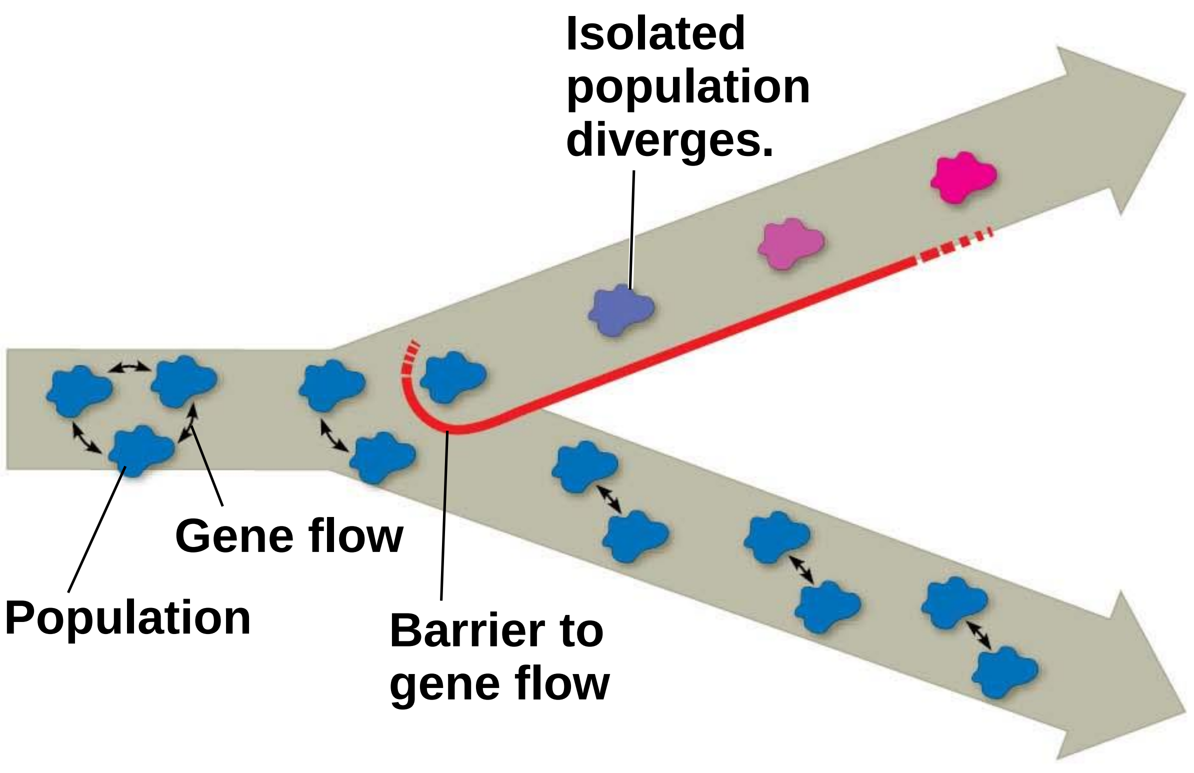


Figure 22.14-s3

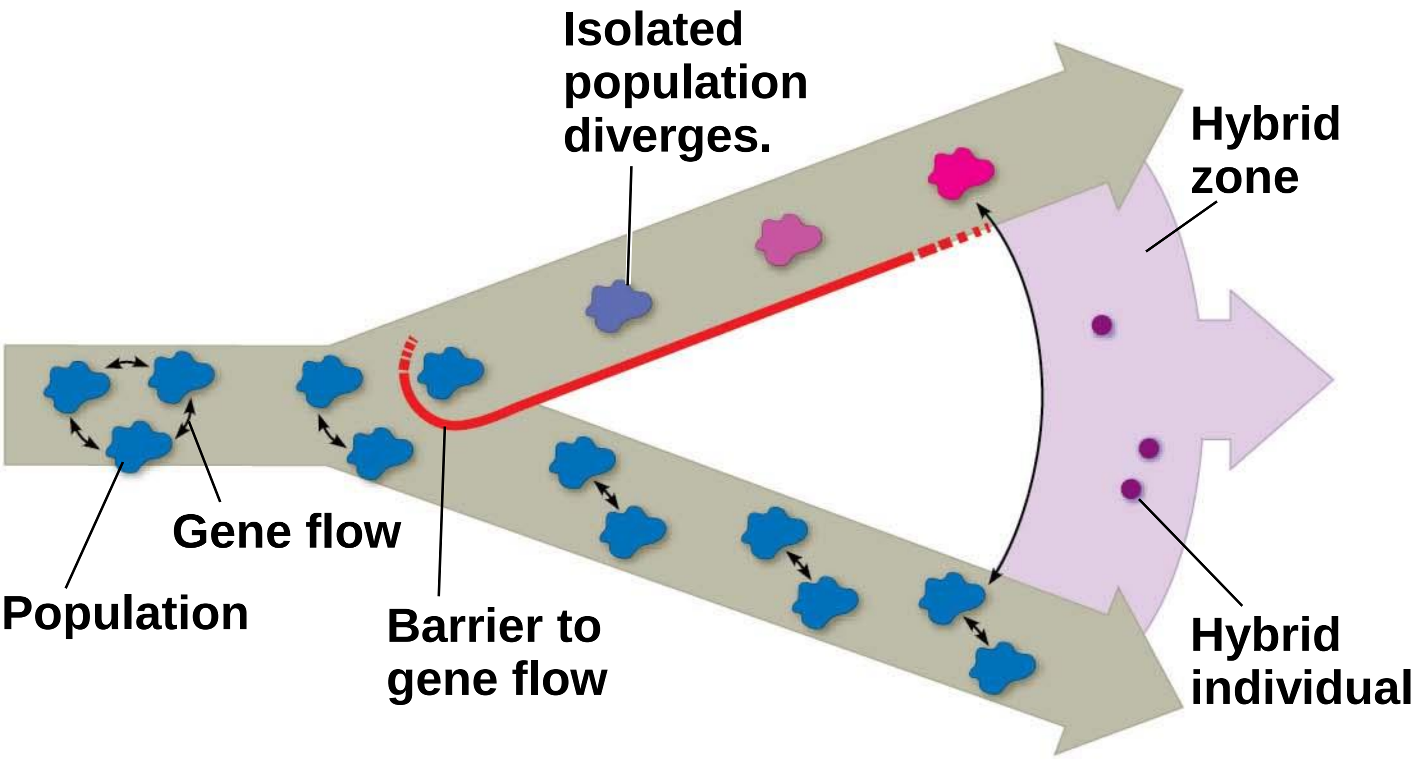
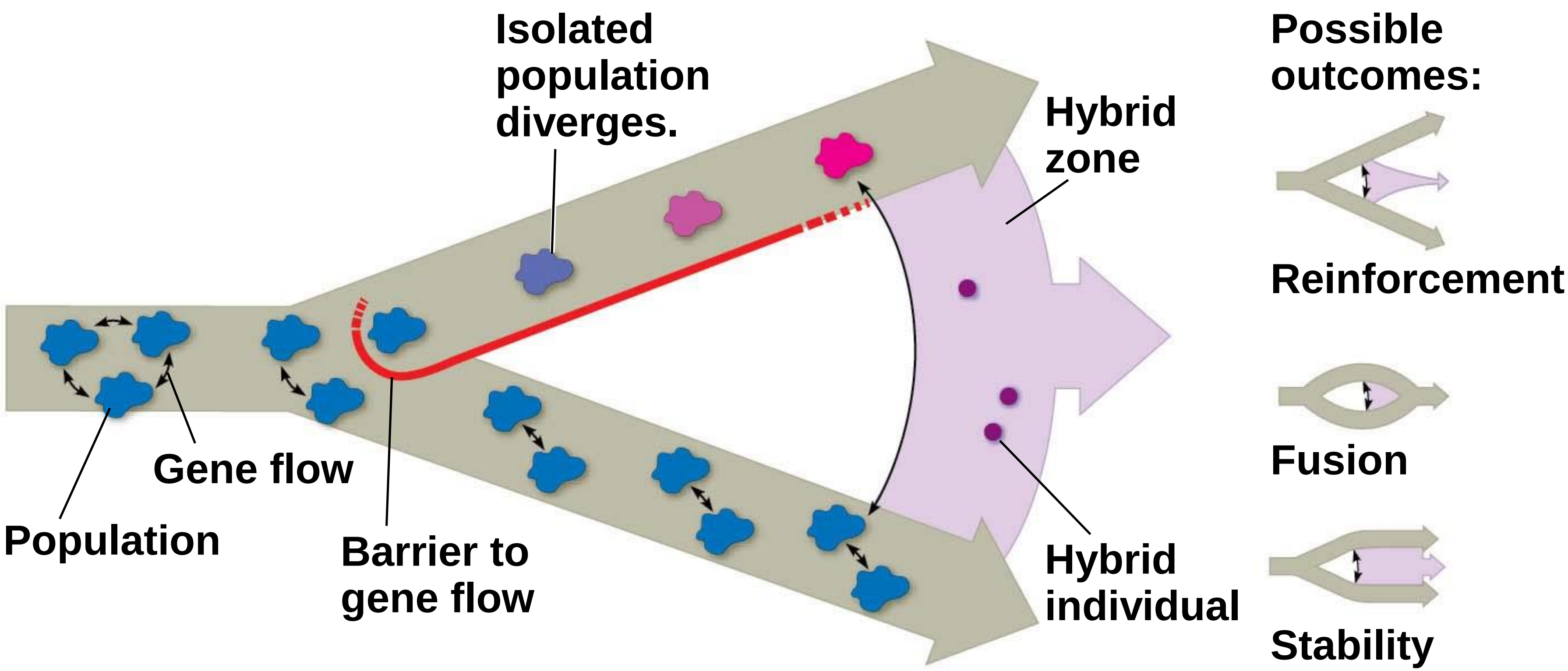


Figure 22.14-s4



- **Stability** of the hybrid zone will result if hybrids continue to be produced over time
- This may occur if hybrids are at least as likely to survive and reproduce as their parent species
- If they are not, gene flow from outside may overwhelm selection for increased reproductive isolation inside the hybrid zone

Concept 22.4: 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, or how many genes need to differ between species

The Time Course of Speciation

- Broad patterns in 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 essentially unchanged for some time, and then disappear
- These periods of apparent stasis punctuated by sudden change are called **punctuated equilibria**
- The punctuated equilibrium model contrasts with a model of gradual change in a species' existence

Figure 22.15

Pundamilia nyererei

Pundamilia pundamilia

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

Figure 22.15-1

Pundamilia nyererei

Figure 22.15-2

Pundamilia pundamilia

Figure 22.15-3

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

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* originated from the hybridization of two other sunflower species and quickly diverged into a new species

Figure 22.16

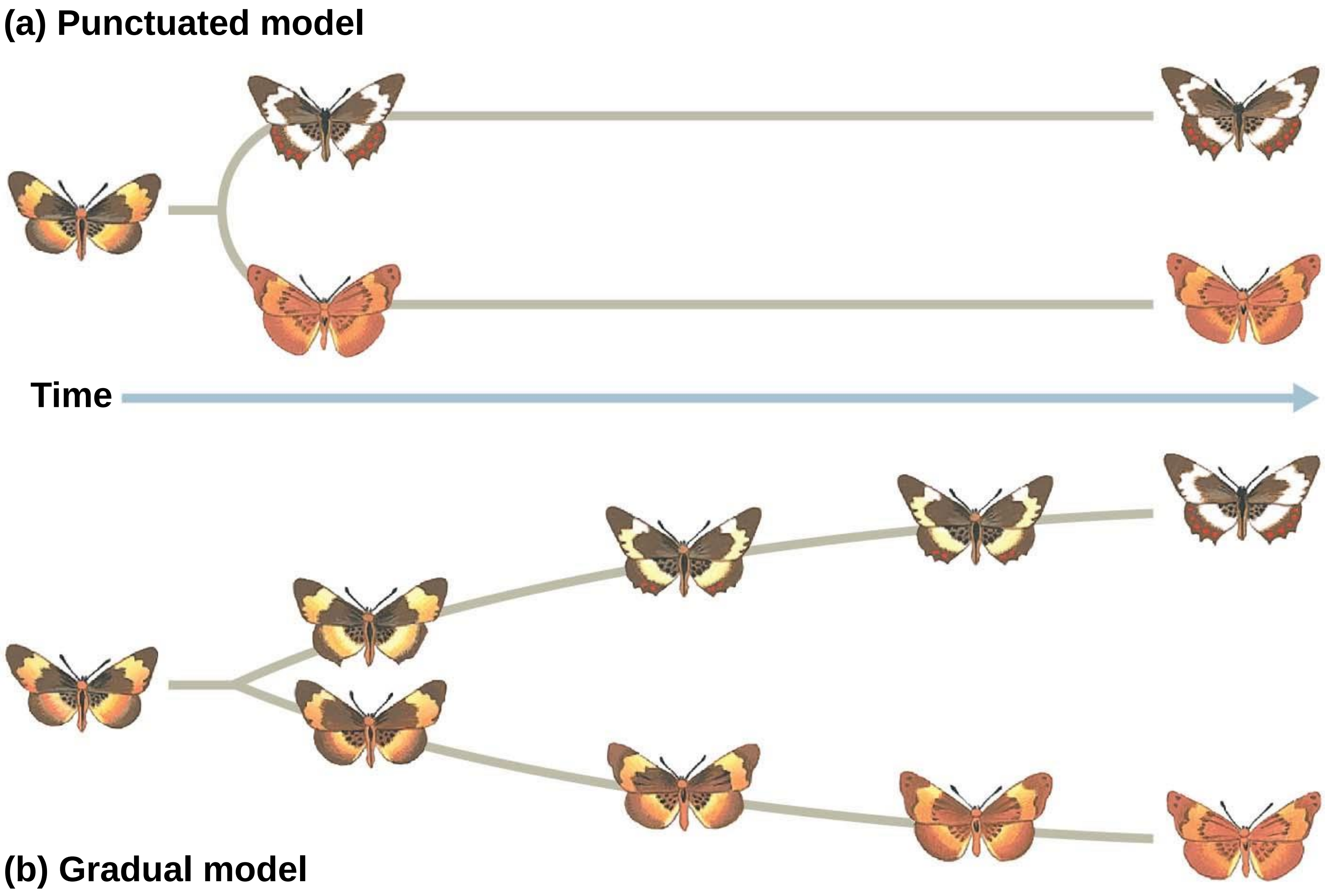


Figure 22.17

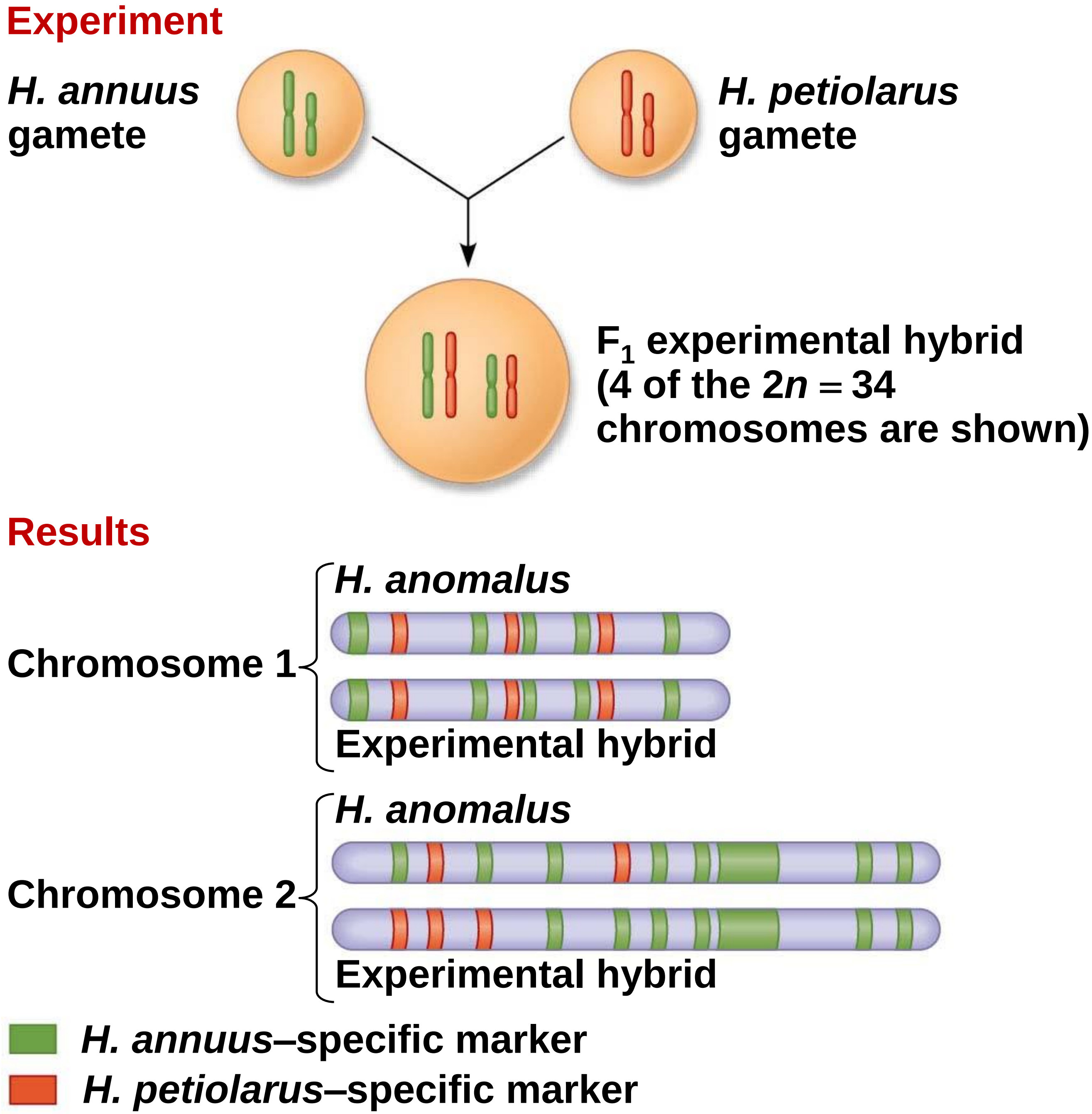
- The interval between documented speciation events ranges from 4,000 years (some cichlids) to 40 million years (some beetles), with an average of 6.5 million years

Studying the Genetics of Speciation

- A fundamental question of evolutionary biology persists: How many genes change when a new species forms?
- Depending on the species in question, speciation might require the change of only 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*), two genes affect flower color, which influences pollinator attraction
- Monkey flowers with different alleles at the flower color loci are less likely to interbreed because they attract different species of pollinators

Figure 22.18


Experiment
H. annuus gamete
H. petiolarus gamete
F1 experimental hybrid (4 of the 2n = 34 chromosomes are shown)
Results
Chromosome 1
H. anomalus
Experimental hybrid
Chromosome 2
H. anomalus
Experimental hybrid
H. annuus–specific marker
H. petiolarus–specific marker

- In other organisms, speciation can be influenced by larger numbers of genes and gene interactions
  - For example, isolation between species of sunflowers in the genus *Helianthus* is influenced by at least 26 chromosome sections (number of genes unknown)

From Speciation to Macroevolution

- Macroevolution is large-scale evolutionary change resulting from the cumulative effect of many speciation and extinction events

Figure 22.19

(a) ***Mimulus lewisii***

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

(c) ***Mimulus cardinalis***

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

Figure 22.19-1

(a) *Mimulus lewisii*

Figure 22.19-2

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

(c) *Mimulus cardinalis*

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

Figure 22.UN01-1

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	1.50	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 et al., 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 22.UN01-2

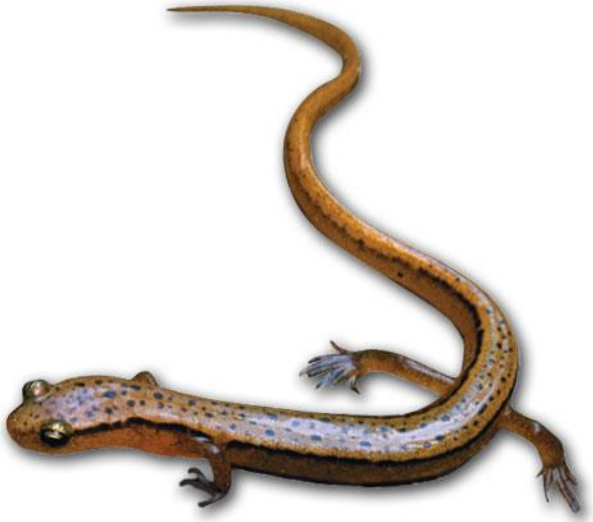


Figure 22.UN02