

## EXPECTATIONS

- Define the concept of speciation and explain the mechanisms of speciation.
- Explain biological barriers to reproduction.
- Describe alternative concepts of species.

The meadowlarks in Figure 12.7 look remarkably similar, yet they are different species. How is a species defined? Historically, species were described in terms of their physical form. But obviously physical similarity does not necessarily mean organisms are the same species. To this end, scientists now also consider physiology, biochemistry, behaviour, and genetics when distinguishing one species from another.

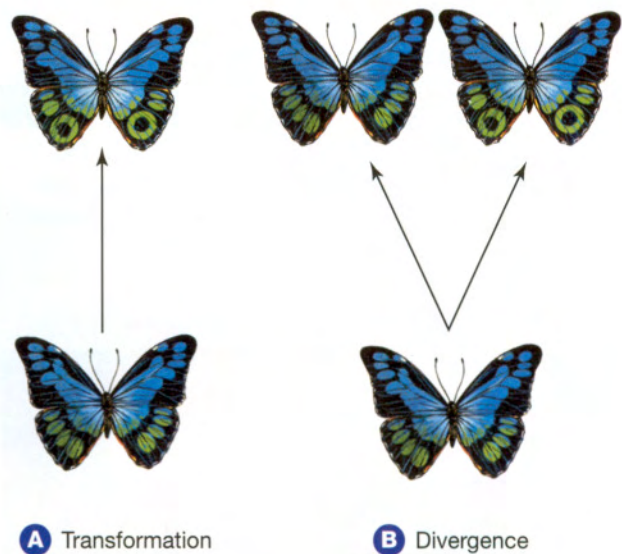
The most common definition of a species describes a **biological species** concept. In this context, a species consists of a reproductively compatible population; that is, a population that can interbreed and produce viable, fertile offspring. To accomplish this, the populations must be able to interbreed in the same time period. If one population breeds in the spring and one in the fall, the two populations would generally not interbreed. The concept of a biological species, therefore, centres on the inability of two species to hybridize. (A hybrid is the offspring of a cross between individuals of two species.) In those cases where hybrids can form, they are usually infertile or the gametes produced are not viable. A well-known example of two biological species are the horse and the donkey. According to the biological species concept, the

horse and the donkey are two separate species. They may interbreed, but the offspring of a horse and donkey (called a mule or hinny) is almost always infertile.

There are two general pathways that lead to the formation of new species: transformation and divergence. Figure 12.8 illustrates the two pathways. A species can be the result of accumulated changes over long periods of time such that one species is transformed into another (**transformation**). The alternative is **divergence**, in which one or more species arise from a parent species that continues to exist. Both pathways are the result of natural selection. Divergence promotes biological diversity because it increases the number of species. In transformation, however, a new species is gradually created while the old species is gradually lost. Identifying instances of transformation is subjective, since it is difficult to determine when the new species became reproductively isolated from the original species, which no longer exists.



**Figure 12.7** Even though eastern and western meadowlarks (*Sturnella magna* and *S. neglecta*, respectively) overlap in parts of their range, they are separate species.



**Figure 12.8** There are two patterns of speciation: (A) transformation (or anagenesis), in which one species evolves into another; and (B) divergence (cladogenesis), in which one or more species arise from a parent species.



**Speciation**, the formation of species, is a continuous process. Examples of speciation occurring today are often difficult to pinpoint because there are so many factors affecting the natural selection of individuals within a species. It is challenging to determine exactly when a species becomes a new species, or whether two different populations are the same species. For example, bird species such as the Baltimore oriole (*Icterus galbula*) and the Bullock's oriole (*I. bullockii*) in North America were once considered to be one species, called the northern oriole. After more research, the northern oriole (*Icterus galbula*) was again separated into the two species. Modern DNA analysis helps scientists to determine which populations may be a single species and which ones (such as the Baltimore oriole and the Bullock's oriole) may be two or more species.

## Biological Barriers to Reproduction

In order for species to remain distinct, they must remain reproductively isolated. Various barriers prevent interbreeding and restrict genetic mixing between species, and species are generally separated by more than one type of barrier.

**Geographical barriers** such as rivers prohibit interbreeding because they keep populations physically separated. However, there are many **biological barriers** that keep species reproductively isolated even when their ranges overlap.

It is clear that a bat will not mate with a squirrel, nor will a fern fertilize a rose, but what biological barriers keep species that are closely related to each other from interbreeding? Reproductive barriers are one example — they can act before or after fertilization to isolate gene pools.

### Pre-zygotic Barriers

**Pre-zygotic barriers** (also known as pre-fertilization barriers) either impede mating between species or prevent fertilization of the ova if individuals from different species attempt to mate.

■ **Behavioural isolation** The songs of birds, the courtship rituals of elk, and the chemical signals (called pheromones) of insects are all examples of behavioural barriers to reproduction. Any special signals or behaviours that are species-specific prevent interbreeding with closely related species. For example, even bird species that look virtually identical (such as the meadowlarks in Figure 12.7) and have overlapping ranges can remain separate biological species, largely because of differences

in their songs. The songs allow them to recognize individuals of their own species. Another example of behavioural isolation is that females of some species release powerful, species-specific pheromones to attract males.

■ **Habitat isolation** Although two species may live in the same general region, they may live in different habitats and therefore encounter each other rarely, if at all. For example, two species of North American garter snakes — the common garter snake and the northwest garter snake — live in the same area, but the northwest garter snake prefers open areas (such as meadows) and rarely enters water, while the common garter snake is most commonly found near water. These snakes are shown in Figure 12.9.



**Figure 12.9** The northwest garter snake (*Thamnophis ordinoides*) (A) and the common garter snake (*T. sirtalis*) (B) occupy different habitats in a similar geographical area. This keeps the two species reproductively isolated.



- Temporal isolation** Many species are kept separate by temporal (timing) barriers. For example, two species may occupy the same habitat but mate or flower at different times of day, in different seasons, or in different years (not all species mate every year). In a dramatic example, three tropical orchid species in the genus *Dendrobium* bloom for a single day, with the flowers opening at dawn and withering in the evening. Flowering in all three species occurs in response to various stimuli in the weather. However, the lapse between the stimulus and flowering is eight days in one species, nine in another, and 10 in the third. Because of this difference in timing, the three species remain reproductively isolated even though they live in the same habitat. As another example of temporal isolation, species of giant silkworm moths fly and mate at different times during the day.

- Mechanical isolation** Species that are closely related may attempt to mate but fail to achieve fertilization because they are anatomically incompatible. For example, the genitals of some insects operate in a kind of lock-and-key system. If a male and female of different species attempt to breed, their genitals will not fit together. Genital anatomy is so distinctive in many organisms (particularly insects) that it is often used to classify species based on morphology.

In plants, variations in flower structure may impede pollination if the flower and the pollinator are incompatible. In two species of sage, for example, the flowers have different arrangements of stamen and style. One species is pollinated by bees that carry pollen on their backs and the other species is pollinated by bees that carry pollen on their wings. If the “wrong” pollinator visits a flower, pollination cannot occur because the pollen does not come into contact with the stigma of the other species.

- Gametic isolation** If gametes from different species do meet, gametic isolation ensures they will rarely fuse to form a zygote. The methods of gametic isolation vary among species. For example, in species in which the eggs are fertilized within the female reproductive tract, the sperm of one species may not be able to survive in the environment of the female reproductive tract of another species. In plants, pollen grains of one species typically fail to germinate on the stigma of another species, so fertilization is prevented.

Many aquatic animals, such as the sea urchin in Figure 12.10, broadcast their gametes into the

surrounding water and the eggs are fertilized in the water column. If gametes from two different species meet, chemicals on the surface of the eggs will recognize and reject sperm cells from another species.



### ELECTRONIC LEARNING PARTNER

Refer to your Electronic Learning Partner for more information on how a geographical barrier can isolate populations.

### Post-zygotic Barriers

In some cases, the sperm of one species successfully fertilizes an ovum of another species and a zygote is produced. There are several **post-zygotic** (post-fertilization) **barriers** that prevent these hybrid zygotes from developing into normal, fertile individuals.

- Hybrid inviability** Genetic incompatibility of the interbred species may stop development of the hybrid zygote at some stage during embryonic development. For example, hybrid embryos created artificially between sheep and goats die in their early developmental stages before birth. Hybrid inviability is usually due to genetic incompatibility, which prevents normal mitosis after fusion of the nuclei in the gametes.



**Figure 12.10** Chemicals on the surface of this sea urchin's eggs prevent sperm from a different species from successfully fertilizing them.



## BIO FACT

The concept of reproductive isolation as a determinant of biological species applies to natural systems. In artificial situations such as labs and zoos, species that are reproductively isolated in natural situations can and sometimes do have viable, fertile offspring.

- **Hybrid sterility** Sometimes, two species can mate and produce hybrid offspring (such as a horse and donkey producing a mule or hinny, as discussed earlier). However, a reproductive barrier still exists between the two species if the hybrid offspring is sterile. If meiosis fails to produce normal gametes in the hybrid (because the chromosomes of the two parent species differ in number or structure), this barrier may come into effect.
- **Hybrid breakdown** In some cases, the first-generation hybrids of crossed species *are* viable and fertile. However, when these hybrids mate with each other or with an individual from either parent species, offspring of the next generation

are sterile or weak. For example, different cotton species can produce fertile hybrids, but the offspring of the hybrids die as seeds or early in development.

## Limitations of the Concept of Biological Species

The situations listed above are based on a concept of biological species, which is based on the fact that individuals cannot interbreed and produce viable, fertile offspring. There are limitations to this idea, however, so evolutionary biologists are beginning to look at different models for delineating species.

The biological species concept does not work in all situations. For instance, this definition cannot be applied with absolute certainty to species known only as fossils. In addition, many organisms (such as prokaryotes, protists, and some fungi, plants, and even some animals) are asexual. While bacteria do transfer genes to a certain extent, bacteria do not have anything equivalent to the genetic recombination that occurs during sexual

## THINKING LAB

### Leopard Frogs — One Species or Seven?



(A) Northern leopard frog (*Rana pipiens*)  
(B) Southern leopard frog (*Rana sphenocephala*)

#### Background

Leopard frogs were once believed to be a single, extremely variable species (*Rana pipiens*) that ranged across North America. Today, however, scientists know that what they thought of as the “leopard frog” is actually at least seven different, but related, species in North America. This was determined using the biological species concept.

#### You Try It

1. Listen to the calls of two different species of leopard frogs supplied by your instructor or by using the

connections on the Web Link. Analyses of frog calls were one of the clues that led biologists to realize that there were more than one species of leopard frog. What type of biological barrier is a mating call? Explain how this type of biological barrier keeps species separate.

2. Choose two species of leopard frogs and describe in point form the differences that result in them being regarded as closely related but separate species. (They are referred to as sibling species.) Use connections on the Web Link or library resources. Leopard frogs in North America include the northern, southern, Rio Grande, plains, relict, Florida, Ramsey Canyon, and lowland leopard frogs.
3. Populations of amphibians, including frogs, are on the decline in North America, and scientists are tracking population numbers to try to determine the cause of the decline. When it comes to conservation and monitoring of species, why is it important to know that there are seven species of leopard frog rather than just one, wide-ranging species?

#### WEB LINK

[www.mcgrawhill.ca/links/biology12](http://www.mcgrawhill.ca/links/biology12)

To listen to the calls and view photographs of the northern leopard frog and the southern leopard frog, go to the web site above, and click on **Web Links**.



reproduction by two parents. As a consequence, defining species based on their inability to interbreed does not fit well with asexual organisms.

In other cases, the definition of biological species may be too rigid to apply directly. For example, coyotes can interbreed with domestic dogs and wolves to produce fertile hybrid offspring, yet all three remain distinct species. As well, other

populations seem to be in the midst of evolving into two species, where it is difficult to distinguish the exact point at which adjacent and closely related species start to interbreed and where, or if, they stop. This inability to fit all organisms into the biological species concept has led evolutionary biologists to propose some alternative concepts to define species.

## Canadians in Biology

### Sticklebacks and Speciation

A three-spined stickleback is a scaleless fish with a row of three spines on its back. Dr. Dolph Schluter believes this little fish may provide evidence that natural selection can create new species. This view of speciation, which is central to the theory of evolution, is widely accepted by scientists. However, actual examples from living animals have not been easy to find. Dr. Schluter is also looking at the possibility that the “same” species may arise more than once.

The Montréal-born Dr. Schluter, who received his BSc from the University of Guelph and his PhD from the University of Michigan, is a zoology professor at the University of British Columbia. Dr. Schluter’s earliest work included studying the Galápagos finches with Peter and Rosemary Grant (whose research on the Galápagos finches is discussed in section 10.1). Since then, his studies have included the three-spined sticklebacks in coastal B.C. lakes.

When the last ice age ended some 13 000 years ago, three-spined sticklebacks lived in ocean waters throughout much of the northern hemisphere. They ate microscopic plankton near the surface of the water. As the ice retreated and the ocean level dropped, some three-spined sticklebacks became stranded in newly formed lakes along the coasts. In the fresh-water lakes, these three-spined sticklebacks found plankton near the surfaces of deep, open areas. They also found a new source of food — insect larvae, snails, and other invertebrates near the bottoms of shallower areas.

A number of years later, according to Dr. Schluter’s hypothesis, the ocean rose again, depositing more water and more three-spined sticklebacks in some of the coastal lakes. The newly arrived sticklebacks and those already in the lakes then had to compete for food. In a few lakes, two forms of sticklebacks evolved. One form, the limnetics (inhabitants of open water in fresh-water lakes), became very good at feeding on plankton near the surface. For example, they developed smaller mouths, smaller bodies, and longer gill rakers, which they used to strain food out of the water. Meanwhile, the bottom

feeders, or benthics, were developing better adaptations as well. For example, because their food was bigger than the plankton they had previously eaten, benthics developed wider mouths and bigger bodies. Their gill rakers, which were no longer so useful to them, became shorter and less numerous. The limnetics and benthics each lived in their own separate parts of the lakes.



Dr. Dolph Schluter

Dr. Schluter and his colleagues regard the limnetics and benthics as separate species. “By calling them species,” he says, “we imply that they don’t interbreed — or interbreed so rarely that their differences in mating behaviour, genetics, and so on are maintained by natural selection against hybrids.” But their definition of a species is a “soft” one, with which some scientists would disagree. Laboratory studies have shown that while limnetics and benthics that come from the same lake do not mate readily, they do nevertheless mate. On the other hand, limnetics from one lake willingly mate with limnetics from other lakes, and benthics from one lake willingly mate with benthics from other lakes.

People tend to think of the origin of a species as a unique, unrepeatable event in evolution. “One of the most exciting implications of this work,” says Dr. Schluter, “is that the same ‘species’ (defined by mating compatibility) can actually arise more than once.”



## Alternative Concepts of Species

The biological species concept requires almost complete isolation of the gene pool. Alternative concepts of what defines species generally recognize that there is often some degree of genetic exchange between species. No single concept gives the perfect definition for species and, in reality, different concepts fit better in particular situations.

Historically, and still to a large extent today, organisms have been classified into separate species based on measurable physical features (essentially, the phenotype). This is called the **morphological species concept**. This model can be applied to both fossils and living organisms. Other models emphasize species-specific mating adaptations (*recognition species concept*); the fact that species have distinct clusters of genetic traits (*cohesion species concept*); the ecological role of a species within the environment (*ecological species concept*); and the evolutionary history and ecological role of a species (*evolutionary species concept*).

Regardless of how species are specifically defined, it is important to remember that speciation requires populations of organisms to become, and to largely remain, genetically isolated from others. The next section explores the mechanisms that lead to genetic isolation of a gene pool from that of a parent species.

### BIO FACT

Part of the difficulty in applying the morphological species concept is that individuals within a species can be very different at different stages in their life history. Indeed, the juvenile and adult stages of some organisms have been considered separate species for long periods of time before their life cycle became better understood. Another difficulty is that there is slight variety in size, shape, and other morphological characteristics within a population; therefore, misclassification can result. For example, approximately 600 species of snails in the genus *Cerion* have been identified in the Caribbean islands based primarily on differences in size, shape, and coloration. It has since been shown that almost all of these differences result from slight variations in genes that regulate growth and that there may be, in fact, only two species of *Cerion*.

## SECTION REVIEW

- K/U** Explain how biological diversity contributes to speciation.
- K/U** Explain the difference between habitat isolation and geographical barriers.
- K/U** If two species produce a hybrid offspring that is infertile, is reproductive isolation between the two species still maintained? Explain your answer.
- MC** Plant breeders have artificially created new species and varieties of plants such as roses, cotton, apples, day lilies, and chrysanthemums. Give some reasons why these plants were developed. List some other species that have also been created by plant breeders.
- K/U** Explain why it is difficult to fit all organisms into the biological species concept.
- C** Using a flow diagram, describe the two pathways that can lead to the formation of a new species. Which pathway leads to an increase in biodiversity?
- C** Prepare a chart that lists the five types of pre-zygotic barriers, provides a brief description of each barrier, and gives an example of a species or group of species that shows the result of this type of barrier.
- K/U** Identify the type of reproductive barrier each of the following situations describe, and note in each case whether the barrier is pre-zygotic or post-zygotic.
  - fireflies use distinctive patterns of flashes
  - crossing frogs from two different populations produces frogs that never produce any offspring
  - two species of grass flower at different times of year, yet live in the same habitat
  - two species of flycatcher overlap in range, but one lives in open woods and farmland while the other lives in swampy areas
  - the crossing of two species of fly produces a fertile hybrid offspring, whose offspring is weak and infertile
- K/U** List the advantages and disadvantages of basing classification only on morphological characteristics.

### UNIT PROJECT PREP

Keep track of information in this chapter that is related to the Unit Project on Searching for the Common Ancestor. Pay particular attention to terminology and the use of illustrations such as phylogenetic trees, charts, and tables.