microevolution changes in gene (allele) frequencies and phenotypic traits within a population and species

speciation the formation of new species



Figure 1 Recent genetic evidence suggests there are at least three species of orcas.

reproductive isolating mechanism any behavioural, structural, or biochemical trait that prevents individuals of different species from reproducing successfully together

prezygotic mechanism a reproductive isolating mechanism that prevents interspecies mating and fertilization (for example, ecological isolation, temporal isolation, and behavioural isolation)

postzygotic mechanism a reproductive isolating mechanism that prevents maturation and reproduction in offspring from interspecies reproduction

Speciation

Scientists know that species continuously evolve. This knowledge is based on a wide range of evidence, including the direct observations of evolution in nature and the dramatic examples of change in domesticated species of plants and animals. Changes that occur within species, sometimes referred to as **microevolution**, are often relatively easy to understand. Natural selection favours faster-running cheetahs, colourful displays of male songbirds, and larger brains in humans. But what factors lead to **speciation**—how does an entirely new species evolve? How did cheetahs, giraffes, and humans evolve in the first place?

What Is a Species?

A biological species, according to one definition, includes all the members of a population that can interbreed under natural conditions. Individuals of different species cannot interbreed under natural conditions and are described as being reproductively isolated from one another. Populations of different species do not exchange genetic information—they have different gene pools. Defining a species as all members of a population with a common gene pool has advantages.

Evidence of interbreeding between individuals and groups can be difficult or impossible to examine and cannot be applied to species that rarely or never reproduce sexually. Some species are quite distinct from all others and can be readily identified based on their morphology or physical appearance, while two other species might be outwardly indistinguishable from each other. As a result, biologists must employ a variety of methods to help distinguish species.

Today the ability of biologists to sample and compare the genetic makeup of different populations has led to some surprising results. Until very recently, orcas were thought to be a single species, but genetic comparisons suggest they represent at least three species (**Figure 1**).

Modes of Speciation

New species can evolve under a variety of circumstances. However, this process always includes the evolution of distinct features that isolate the new species reproductively, and therefore genetically, from other species.

Mechanisms of Reproductive Isolation

For a new species to form, individuals from the original species must evolve to become reproductively isolated from the remainder of the population and they must establish a new interbreeding population. A **reproductive isolating mechanism** is any biological factor that prevents the two populations from interbreeding when living in the same region. Reproductive isolating mechanisms can operate in any number of ways. For example, they may be differences in breeding season, physical or behavioural traits, habitat preferences, or the incompatibility of gametes. These are all **prezygotic mechanisms** because they prevent fertilization and zygote formation. Still others, called **postzygotic mechanisms**, can prevent a fertilized egg from growing into a viable and reproducing adult. **Table 1** (next page) lists and provides examples of each of these mechanisms. As you will learn, any mechanism that prevents two populations from interbreeding can give rise to new species, but how do such reproductive isolating mechanisms evolve?

Reproductive isolating mechanisms are often quite subtle, and organisms that appear very similar to each other may not interbreed. Some bird species, for example, are notoriously difficult to distinguish. The willow and alder flycatchers, small songbirds native to Ontario, appear virtually identical and, short of genetic testing, even experts can tell them apart only by their song and the nests they build.

Table 1 Reproductive Isolating Mechanisms

Mechanism	Description	Example
Prezygotic	I	I
behavioural isolation	Different species use different courtship and other mating clues to find and attract a mate.	Male frogs of different species have unique calls that attract only females of their own species.
temporal isolation	Different species breed at different times of the year.	Pussy willows produce flowers in the early spring. They are reproductively isolated from plant species that produces flowers at a different time of year.
ecological isolation	Very similar species may occupy different habitats within a region.	The mountain bluebird (<i>Sialia currucoides</i>) lives at high elevations, while the eastern bluebird (<i>Sialia sialis</i>) prefers lower elevations and does not encounter the mountain species.
mechanical isolation	Differences in morphological features may make two species incompatible.	Male damselflies transfer sperm during an unusual mating flight. The male and female genitalia of each species are uniquely shaped and are physically incompatible with other species (Figure 2).
gametic isolation	Male gametes may not be able to recognize and fertilize an egg of a different species.	Many marine animals including corals, clams, and sea cucumbers release their sperm and eggs into open water. The sperm recognize eggs of their own species through chemical markers on the surface of the eggs (Figure 3).
Postzygotic		
zygotic mortality	Mating and fertilization are possible, but genetic differences result in a zygote that is unable to develop properly.	Some species of sheep and goat are able to mate, but the zygote is not viable (Figure 4).
hybrid inviability	A hybrid individual develops but either dies before birth or, if born alive, cannot survive to maturity.	When tigers and leopards are crossed, the zygote begins to develop but the pregnancy ends in a miscarriage or stillborn offspring.
hybrid infertility	Hybrid offspring remain healthy and viable but are sterile.	Mules are the sterile hybrid offspring of a horse-donkey cross.



Figure 2 Damselfly individuals of one species are physically incompatible with individuals of other species.



Figure 3 Sea cucumbers have gametic isolation from other marine animals.

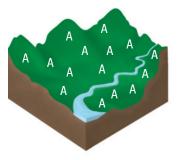


Figure 4 The zygote produced by a goat and sheep cross is not viable.

Allopatric Speciation

Most new species form when a single species is separated into two geographically isolated populations. This is called **allopatric speciation**. Once populations are physically separated, they can no longer exchange genetic information. Over many generations the populations will gradually become less and less alike. Any mutation that arises in one population is not shared with the other population. Any differences in the environments of the two populations will lead to different forms of natural selection. Changes that result from genetic drift may also cause the populations to become increasingly different. Once enough time has passed, there is a good chance that the two populations will have evolved some sort of reproductive isolating mechanism. Perhaps their courtship rituals will have changed, the time of year they breed or produce pollen will have shifted, or they may no longer be physically compatible.

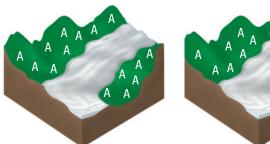
allopatric speciation the formation of a new species as a result of evolutionary changes following a period of geographic isolation



At first, a population is distrubuted over a large geographical area.

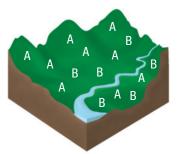


Figure 6 The Galapagos cormorants lost their ability to fly.



A geographical change, such as the advance of a glacier, separates the original population, creating a barrier to gene flow.

In the absence of gene flow, the separated populations evolve independently and diverge into different species.



When the glacier later melts, allowing individuals of the two species to come into secondary contact, they do not interbreed.

Figure 5 Geographic separation leads to allopatric speciation.

Figure 5 shows how geographical separation can lead to allopatric speciation. The geographic splitting of a species into two populations can occur in a number of ways. Populations may become isolated on remote islands where they are far from the original population. New selective pressures can then cause them to evolve dramatically new features like that of the flightless cormorant of the Galapagos Islands (Figure 6). Mountain ranges may form, separating populations of species whose members do not travel over mountains. Continental drift has split apart entire continents and separated countless species into separate populations.

A clear example of allopatric speciation followed the formation of the Isthmus of Panama-a thin strip of land that now separates the Caribbean Sea from the Pacific Ocean. Prior to its formation, the Caribbean Sea was connected by a wide channel to the Pacific Ocean. Many species of marine organisms inhabited this region. Two million years ago, the isthmus formed, permanently dividing species such as the wrasse into separate

species have evolved into 14 different species.

Pacific and Caribbean populations (Figure 7). Now, the species on

both sides are distinct and cannot successfully interbreed, even when placed together. Perhaps the best examples are the seven different

species of snapper shrimp on each side of the isthmus-each having

its closest relative on the other side. Since being separated, 7 original

sures on species. Consider the effect that the formation of the Rocky

Mountains had on the evolution of species. As this mountain range

formed, it divided many widely distributed species into separate western and eastern populations and also produced profound changes

in their environments. West of the Rocky Mountains, the climate is generally moderate with cool summers, mild winters, and heavy precipitation. East of the mountains, there are hot summers, cold winters, and little precipitation. As a result, the western and eastern populations of the original species experienced different environmental

conditions and different selective pressures. Plants, for example, would be selected for their ability to thrive in wet conditions on the

coast and arid conditions in the prairies (Figure 8). Over millions of

Geologic changes can directly influence the natural selection pres-

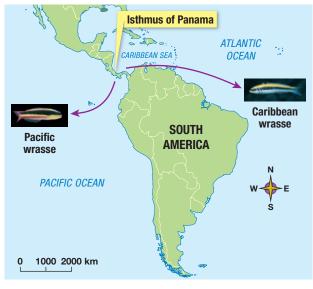
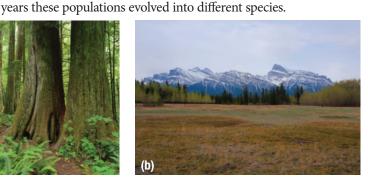


Figure 7 The Pacific and Caribbean wrasse species evolved from a single species that became separated into two populations by the isthmus.

Figure 8 The mountain ranges in Western Canada create two strikingly different environments. (a) On the west coast, natural selection favours species that thrive in a wet, mild climate. (b) On the eastern side of the mountains, natural selection favours species able to survive a dry climate.





338 Chapter 8 • The Origin of Species

A USEFUL ANALOGY

It is often useful, in trying to understand a difficult concept, to consider an analogous process that is more familiar. Understanding speciation is difficult in part because of the long times involved and the formation of isolating mechanisms with which we are unfamiliar. However, consider how the process of speciation is analogous to the formation of a new language. In a non-biological but analogous way, we inherit our language from our parents and pass it on to our children. When a human population becomes geographically separated into two groups, their spoken languages start to diverge. Regional accents and slang develop and spellings change, as do common phrases. New words are also introduced in each population. You have no doubt noticed these differences yourself in the English spoken by people from Australia, England, the United States, and Canada. Given enough time and continued isolation, languages become distinct and individuals from the different regions are no longer able to understand each other. The earliest Germanic language, for example, spoken in northern Europe during the first millennium BCE, has since given rise to more than 50 distinct languages.

Sympatric Speciation

A new species can also evolve from within a large population. This process, called **sympatric speciation**, occurs when individuals within a population become genetically isolated from the larger population. Such isolation may occur gradually or suddenly.

One example of gradual sympatric speciation appears to be under way as a direct result of human action. The hawthorn fly is native to North America. The original population of hawthorn flies laid their eggs in the small fruits of hawthorn trees (**Figure 9**). Between 1800 and 1850, after the introduction of apple trees to North America, some of these flies began laying their eggs on apples. Today, the species consists of two populations. One population, now called apple maggot flies, feeds almost exclusively on apples, while the other feeds almost exclusively on hawthorns. Disruptive selection likely favoured mutations that enhanced each feeding behaviour. There is still a small amount of interbreeding between the populations, but they are on their way to becoming reproductively isolated and separate species.

Sudden sympatric speciation is also possible. Even a single mutation can render an individual unable to reproduce with other members of the population. If two such individuals share the same mutation or if a single individual is able to reproduce asexually, a reproductively isolated population, a new species, may result. This is thought to have occurred many times in the evolution of plants. Many plants are able to reproduce both sexually and asexually. If an individual plant has a mutation that prevents successful sexual reproduction, it might still be able to produce large numbers of offspring asexually. These offspring would be sexually compatible with each other.

POLYPLOIDY AND HYBRID SPECIES

Polyploidy can result in sympatric speciation. Mutations causing polyploidy double the number of chromosomes in an individual. Polyploids produce fertile offspring when mated with each other but produce sterile offspring when mated with the original species. The evolution of 30 % to 70 % of all flowering plant species has involved polyploidy. Ontario's eastern gray treefrog (*Hyla versicolor*) is a polyploid species that evolved from the Cope's gray treefrog (*Hyla chrysoscelis*), which is virtually identical in appearance (**Figure 10**). *H. versicolor* is a tetraploid species with four sets of chromosomes (4*n*), while *H. chrysoscelis* is diploid (2*n*). The chromosomes of both species are near-perfect matches, indicating that the eastern treefrog evolved as a result of a polyploidy mutation of the Cope's species.

An interesting quality of polyploids is that they may be fertile when hybridized with other polyploids. This occurs because each of their gametes carries two copies of each chromosome (2n), which then act as typical homologous pairs in the hybrid. The hybrid effectively becomes a diploid individual with a mix of chromosomes from two original species. The hybrid can form a new species that will not produce fertile offspring when crossed with either of the two parent species.

sympatric speciation the evolution of populations within the same geographic area into separate species



Figure 9 Disruptive selection is resulting in the sympatric evolution of a new species of fly. The original species now consists of two distinct populations. The original form, seen here, mates and lays eggs on native hawthorn fruit. The recently evolved form lays eggs on the fruit of introduced apple trees.



Figure 10 Ontario's eastern gray treefrog is a tetraploid species that is almost indistinguishable from the diploid Cope's gray treefrog.

Human Influence on Speciation

The separation of a single population into two isolated populations can lead to speciation, but it can also threaten the survival of species. Many human activities, such as agricultural expansion and the construction of roads, are causing once large habitats to be fragmented into smaller areas that effectively isolate populations. A recent study of timber rattlesnake populations in the state of New York revealed that roadways are a significant barrier to gene flow and that genetic diversity within each isolated population was low. Similar research in China has shown that the survival of giant pandas, a critically endangered species, is threatened by their separation into small isolated populations in patches of bamboo forest. Populations with low genetic diversity are at greater risk when threatened by disease or changing environmental conditions such as climate change.

These concerns can be addressed by conservation practices. Gene flow can be maintained and enhanced if the connectivity between habitats is ensured. For example, fragmented habitats can be joined by wildlife corridors such as highway overpasses with strips of connecting forest that are left standing (**Figure 11**).

8.2 Summary

- New species can form as a result of the evolution of a reproductive isolating mechanism that prevents members of two populations from interbreeding.
- Populations of the same species evolve independently when separated by a geographic barrier.
- Differences in selective pressures and genetic drift can lead to the evolution of reproductive isolating mechanisms and the formation of new species.
- New species evolve when mutations result in immediate reproductive isolation or when disruptive selective pressures cause one species to gradually separate into reproductively isolated populations.
- Human activities influence the evolution of new species.

8.2 Questions

- It is not possible to know if two similar fossils represent individuals that were reproductively isolated from each other. Suggest other methods or characteristics that paleontologists might use to determine if two specimens represent different species.
- 2. Explain which type of reproductive isolating mechanism is at work in each of the following situations: **K**
 - (a) Zebroids, the hybrid offspring of matings between horses and zebras, are sterile.
 - (b) Asian lions were once common and lived in open grasslands, while Asian tigers preferred forests.
 - (c) Female fireflies identify males by the pattern of light flashes they produce. Each species has a unique pattern of flashes.
 - (d) Male geese have a penis, while male herons do not. Male herons are unable to fertilize female geese.
 - (e) When pollen grains from white pine trees land on the female cones of red pine trees, fertilization does not occur.
- 3. Plant and animal breeders try to keep their breeding lines "pure" to prevent unwanted crosses with their breeding stock. How is this human activity analogous to the conditions that cause allopatric speciation?

- 4. Would you expect to find more unique species on a large remote island or on a smaller island that is close to a large continent? Explain your reasoning.
- 5. How can the separation of two populations lead to
 - (a) the formation of a new species?
 - (b) a reduction in genetic diversity of the populations and a possible threat to their survival?
- 6. An unusual and endangered Tasmanian plant, *Lomatia tasmanica*, is a triploid plant (3n = 33 chromosomes) and is completely sterile. It can reproduce only asexually, and all known individuals are genetically identical clones of one another. Fossil evidence suggests this clone has existed for more than 43 000 years.
 - (a) How many chromosomes do you think would be found in the plant species from which it evolved?
 - (b) Do you think this species arose by allopatric or sympatric speciation? Explain.
 - (c) In what way does this plant not fit a typical definition of a species?



Figure 11 Wildlife corridors prevent isolation, increasing gene flow and maintaining genetic diversity.