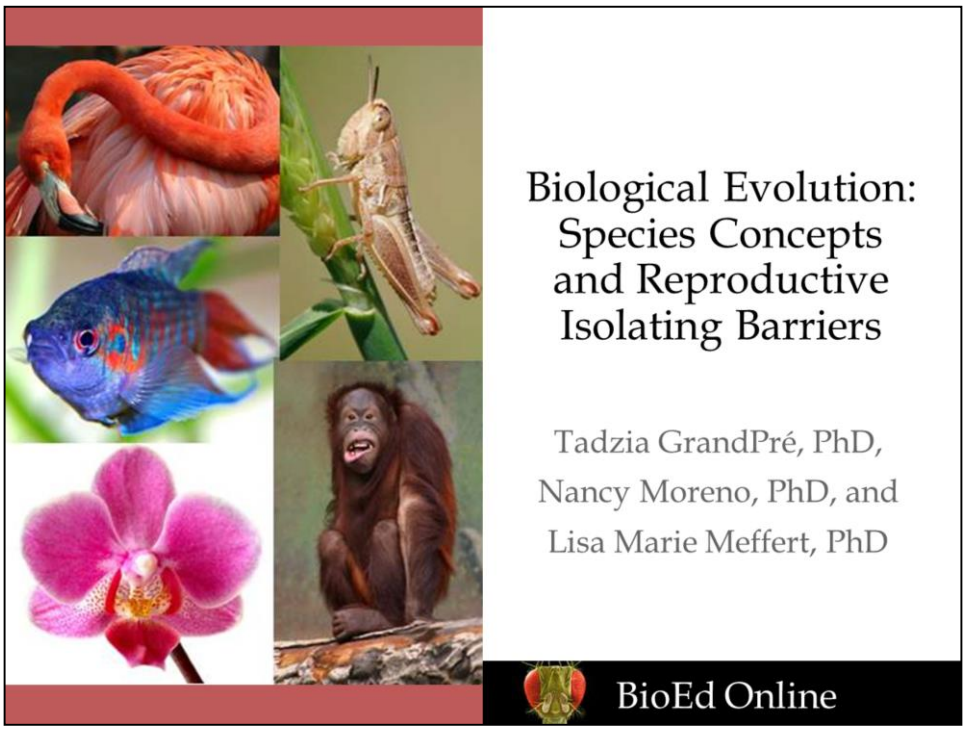

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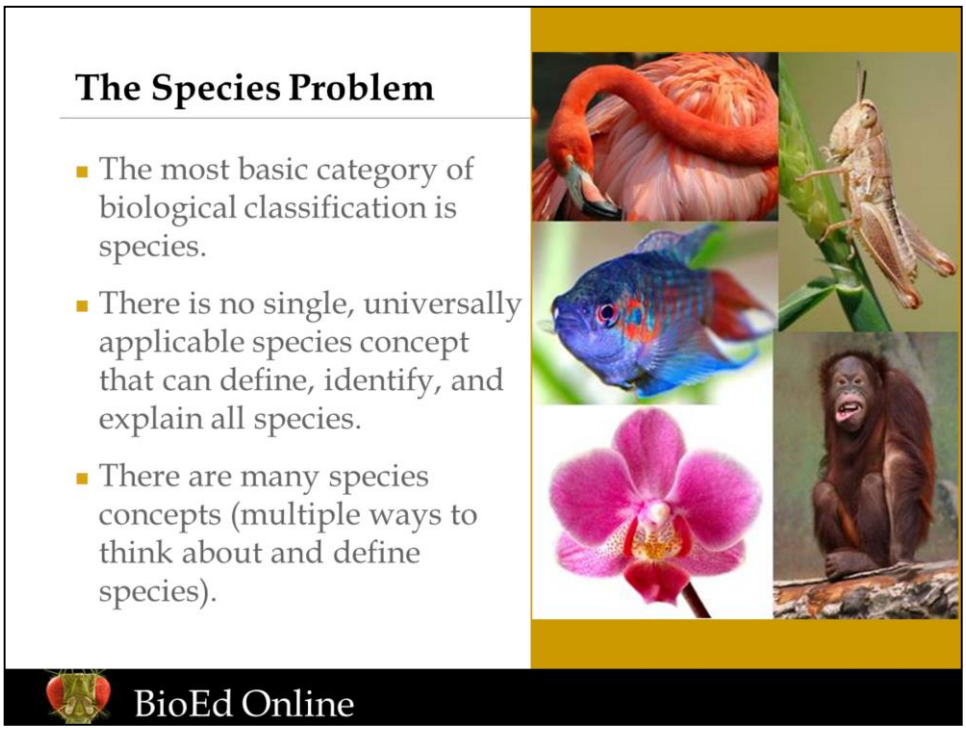

The Species Problem

Although scientists generally agree that species represent the most basic and fundamental groups into which living and extinct organisms are classified, there is debate over how species should be identified as well as the precise definition of the word "species." This controversy, known as the **species problem**, stems from the quest for a single, universal, and functional conception of species. This "essential species concept" would have to identify species unambiguously as discreet, natural units in addition to explaining the existence of species and how they arise in nature. While a number of different species concepts have been proposed, none are able to meet these requirements for all species.

In response to this problem, many scientists recommend a pluralistic approach, that is, the recognition that there are multiple ways to think about and define species. Investigators must therefore choose an appropriate species concept based on their needs. For example, a paleontologist who tries to understand prehistoric vertebrates by studying fossils is likely to require and apply a different conceptualization of species than a microbiologist who studies heredity and variation in populations of bacteria.

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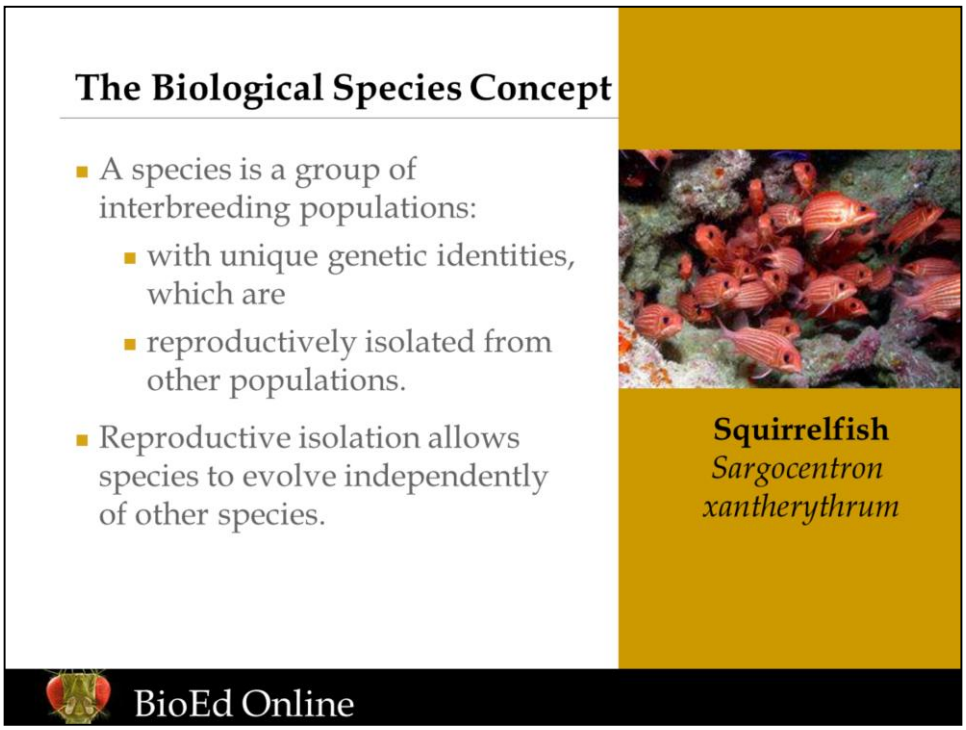

The Biological Species Concept

Scientists working to understand evolution and speciation (the processes by which species arise), frequently apply **the biological species concept**. Ernst Mayr, one of the leading evolutionary biologists of the 20th century, provided the most commonly accepted version of the biological species concept, which posits that "species are groups of interbreeding natural populations that are reproductively isolated from other such groups."

Mayer's work focused on vertebrate animals, a group for which the biological species concept is particularly useful. It also has been applied to plants and other populations. However, most plant biologists also consider evolutionary history and morphology in their species definitions. The **biological species concept** defines species in terms of interbreeding populations, and is therefore most useful for understanding organisms that reproduce sexually. For these organisms, the formation of a new species involves the accumulation of enough genetic differences within individuals of a population to prevent them from breeding with individuals of other populations – a condition referred to as reproductive isolation. When reproductively isolated, species accumulate genetic changes and evolve along independent trajectories. Without reproductive isolation, populations merge in a genetic sense (they share a common gene pool), and thus converge (become similar) in an evolutionary sense.

Many biologists do not interpret the biological species concept rigidly, and characterize species as populations with "substantial but not necessarily complete reproductive isolation" (Coyne and Orr, 2004).

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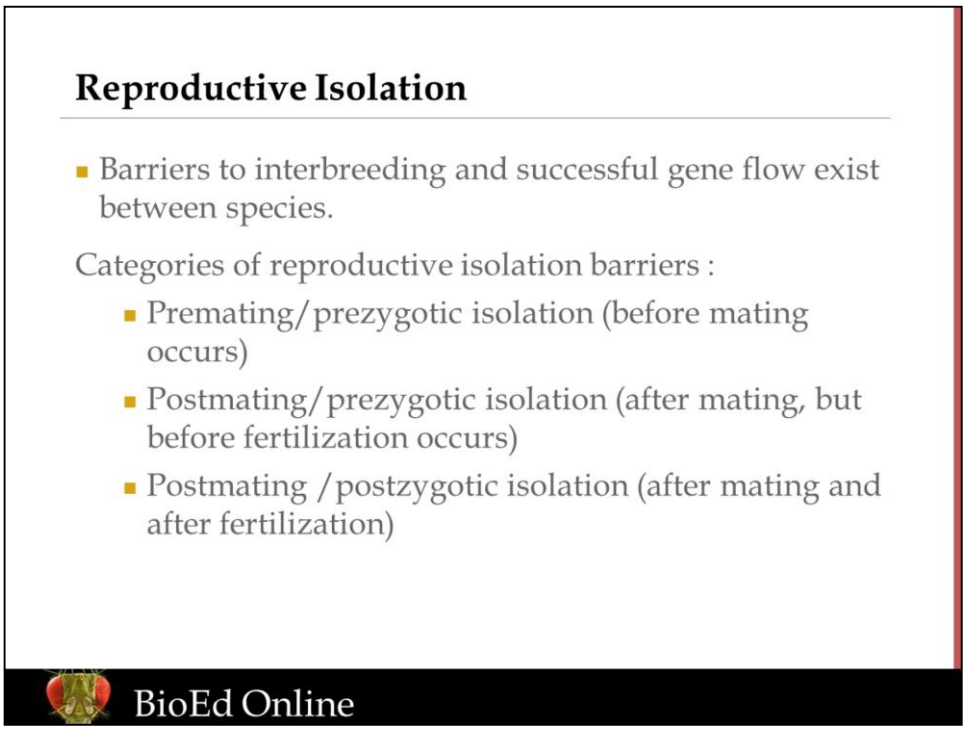


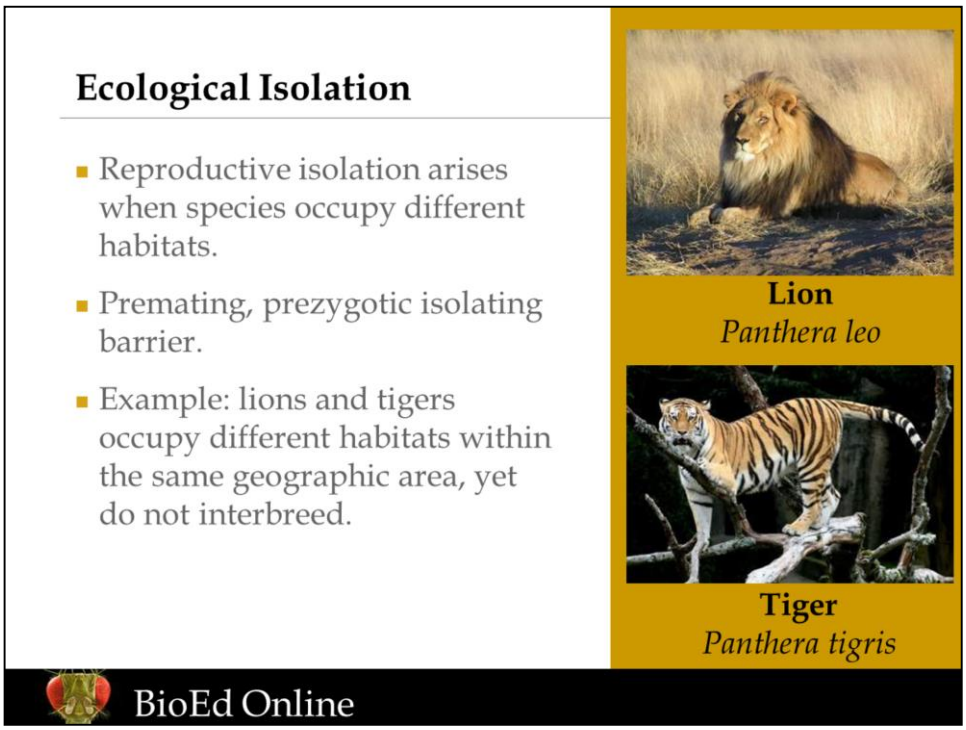
Reproductive Isolation

The divergence of species from parent or ancestral populations is reinforced by reproductive barriers that limit exchange of genes with members of other populations. These isolating barriers, originally described by Dobzhanky (1937) as isolation mechanisms, are defined as biological properties of individual organisms that impede gene exchange with members of other populations. External factors, such as geographic barriers are not considered to be reproductive isolating barriers.

Reproductive isolation barriers can be categorized in different ways: relative to the act of mating or relative to the production of zygotes. Premating/prezygotic isolation barriers impede mating between members of different species. However, if members of different species do mate, postmating/prezygotic isolation barriers prevent the formation of a zygote. If these isolating barriers fail and a zygote is formed after the members of two species mate, postmating/postzygotic isolation barriers reduce the viability and/or fertility of the zygote.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.



Ecological Isolation

Ecological isolation occurs when different species live in the same geographic area but occupy different habitats within that area. These barriers are byproducts of different adaptations to local environments. Under these circumstances, individuals of different species do not hybridize simply because they rarely encounter one another.

For example, until recently, the natural ranges of lions and tigers in India overlapped. However, these two species have different habitats: lions live and breed in the open grasslands while tigers generally stay in the forest. Thus, even though lions and tigers technically can mate and produce viable offspring, this rarely, if ever occurs in natural settings.

Ecological isolation is a premating and prezygotic isolating barrier.

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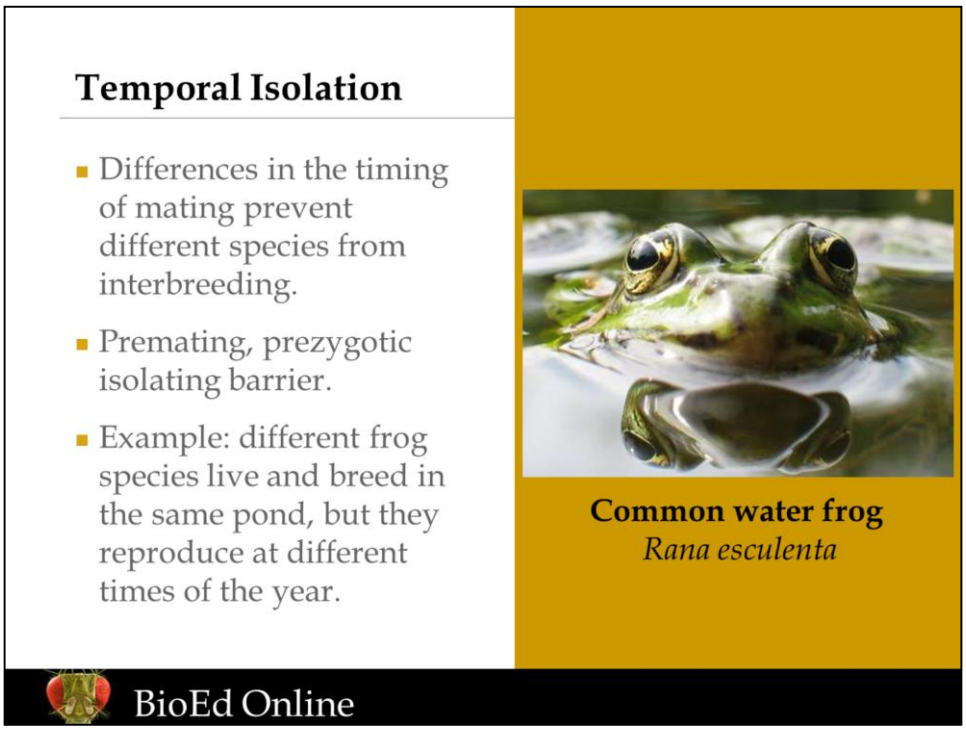

Temporal Isolation

Temporal isolation occurs when members of two species occupy similar habitats, but breed at different times. Thus, gene flow between populations is impeded even when the species populations occupy the same habitat within the same geographic area.

Different species of frogs, for example, may share the same pond for reproduction, but will not hybridize because they use the pond at different times of the year. Similarly, differences in the flowering times of two closely related species of plants can keep them from being cross-pollinated by one another.

Temporal isolation prevents mating between different species, and therefore also prevents the formation of a zygote, so it is a premating isolating barrier as well as a prezygotic isolating barrier.

Reference:

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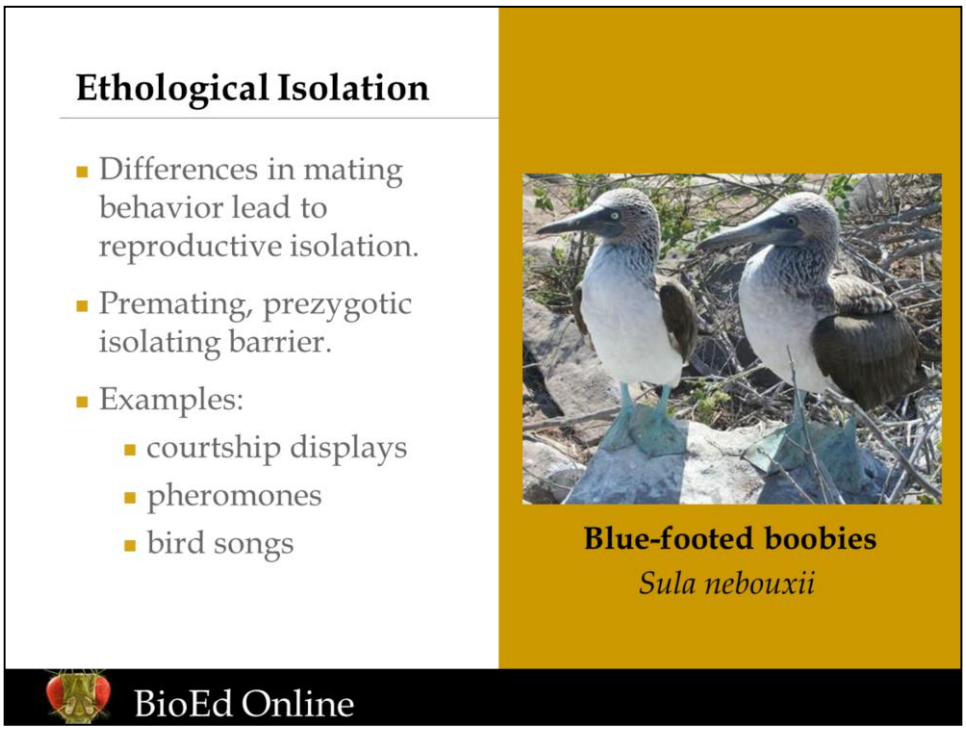

Ethological Isolation

Ethological (behavioral) isolation results from differences in courtship or mating behavior that keep members of different species from mating, even when they inhabit the same geographic area. These barriers often consist of special signals or elaborate behaviors that are used by members of a species to attract or recognize and accept mates. Examples include courtship displays (such as with the blue-footed boobies in this photo), pheromones (chemical signals), and the songs of birds.

Ethological isolation specifically prevents mating between different species and therefore also prevents the formation of a zygote. It is a premating isolating barrier as well as a prezygotic isolating barrier.

Reference:

Campbell, N.E. & Reece, J.B. (2002). *Biology* (6th ed.). San Francisco: Benjamin Cummings.

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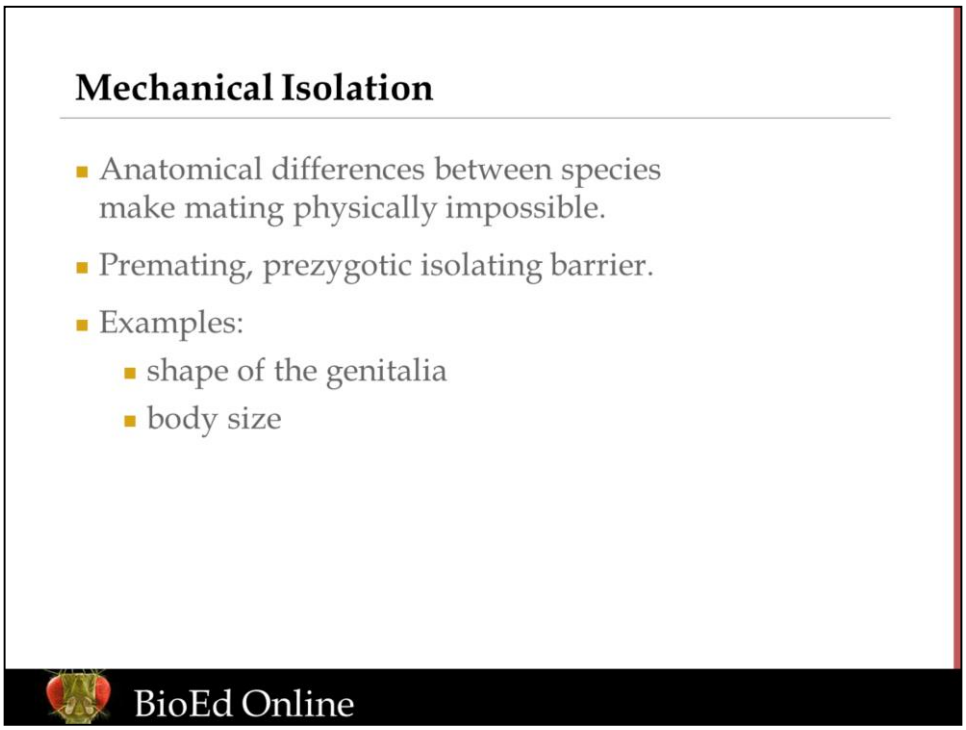

Mechanical Isolation

Even if there are no temporal or behavioral cues to keep individuals of two species from hybridizing, it may simply be physically impossible for mating to take place. **Mechanical isolation** occurs when two species have significant anatomical differences that prevent them from mating.

For example, many species of the fly genus *Drosophila* are virtually indistinguishable except for differences in the male and female genitalia. Similar to the workings of a lock and key, males cannot copulate successfully with females from the wrong species. Mechanical isolation is a premating isolating barrier as well as a prezygotic isolating barrier.

Reference:
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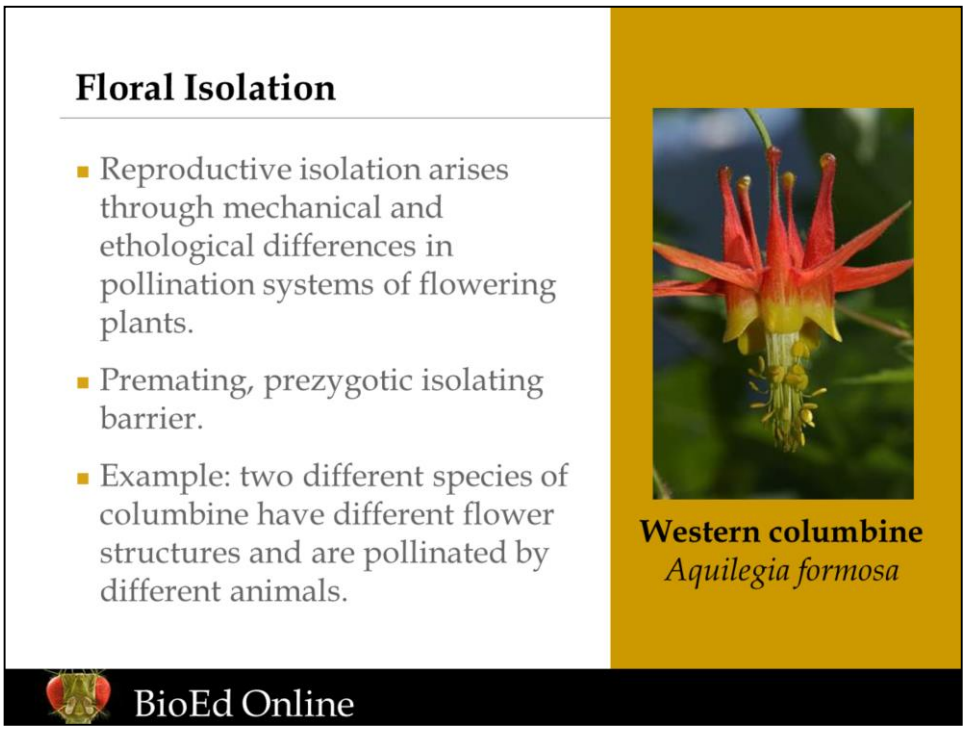

Floral Isolation

Floral isolation (pollinator isolation) occurs when gene flow between flowering plant species is reduced due to mechanical and ethological differences in pollination systems. Mechanical isolation occurs when the transfer of pollen between individuals of different species is impossible because of different flower structures. Ethological isolation occurs when pollinators preferentially visit one type of flower at the exclusion others, even if they exist in the same geographical location.

Two species of columbine provide an example of floral isolation. The two species, western columbine (Aquilegia formosa) and hairy columbine (Aquilegia pubescens) have different flower structures and different pollinators: western columbine is pollinated by hummingbirds, and the hairy columbine is primarily pollinated by hawkmoths. The two species have morphologies that have evolved to suit a particular kind of pollination. The western columbine has long, nectar-containing tubes that only can be reached by the beak of a hovering hummingbird. The hairy columbine provides a landing platform, and is fragrant in the evening to attract its moth pollinators. The two species also are ecologically isolated: the hairy columbine is generally found at higher elevations than the western columbine.

Floral isolation is a premating isolating barrier as well as a prezygotic isolating barrier.

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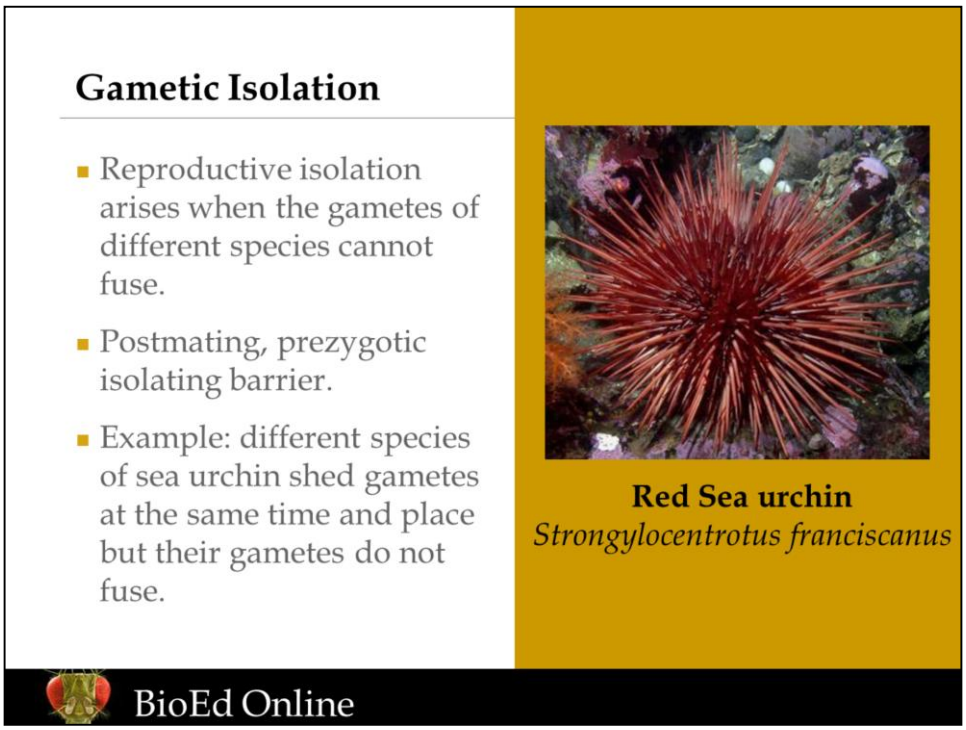

Gametic Isolation

When the gametes of one species cannot fuse with the gametes of another species to form a zygote, **gametic isolation** has occurred. This is a kind of "lock-and-key" isolating mechanism in which, despite successful mating or pollination, hybridization will not occur because the gametes of one species function poorly with the gametes or reproductive tract of another species.

Sea urchins provide a good example of this type of reproductive isolating barrier. Many sea urchin species live in sympatry (within the same geographic region) and shed their gametes at the same time (no temporal isolation), but remain evolutionarily distinct. In this case, the formation of hybrid zygotes is prevented because the surface proteins of the ovule (the "lock") and sperm, or male gametes (the "keys") of different species do not fit together.

Gametic isolation is a postmating isolating barrier while still a prezygotic isolating barrier.

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Hybrids

The reproductive isolation mechanisms discussed so far are all examples of prezygotic isolation, where gene flow between species is prevented often before mating can occur and before a zygote can form.. In contrast, postzygotic isolation occurs after members of two different species have mated and fertilization has occurred. The offspring of such crosses are called **hybrids**. In most cases, the viability or fertility is reduced, and can be considered a postzygotic isolating barrier. Sometimes, however, hybrid offspring and their progeny are viable and fertile. When successful hybrid populations arise, the lines between existing natural species or new species (particularly in plants) can become blurred.

For example, as we discussed previously, lions and tigers rarely meet in their natural environments. However, if held together in captivity, they will interbreed. A liger is the offspring of a male lion and a female tiger, and a tigon is a hybrid between a male tiger and a female lion.

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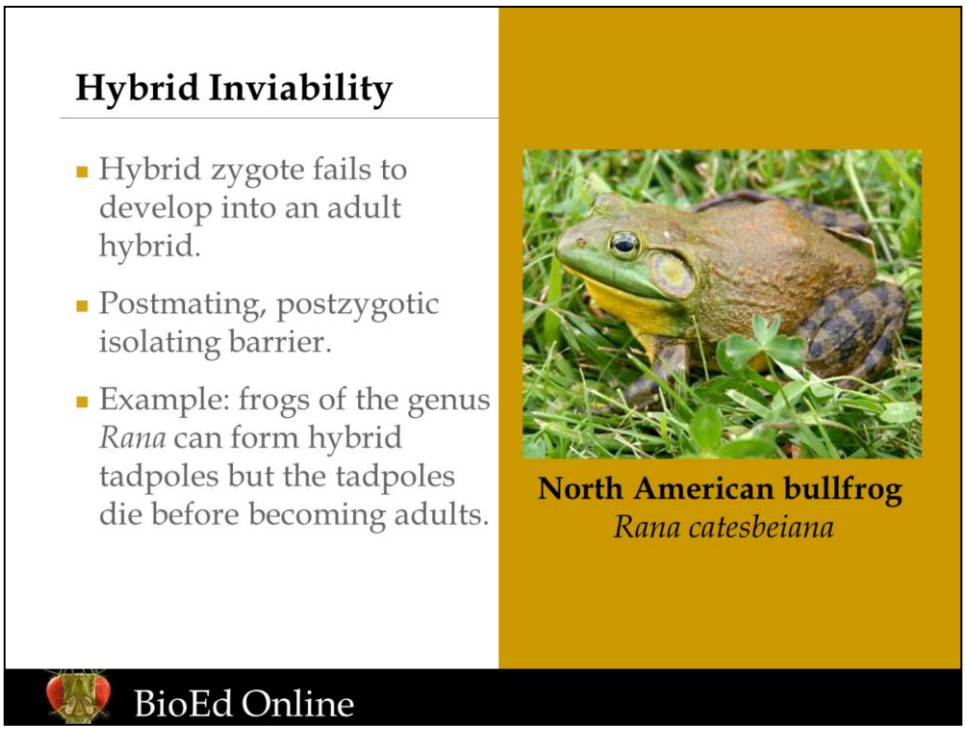

Hybrid Inviability

When hybrid zygotes are formed, they frequently die at some point during their development due to genetic incompatibility between the two parent species. This isolation mechanism, known as **hybrid inviability**, prevents the genomes of the two species from mixing. In this way, the gene flow between the two populations is impeded.

One example of hybrid inviability occurs in the frog genus, *Rana*. Interbreeding between some species of *Rana* results in the formation of hybrid tadpoles, but the tadpoles die before they become reproductive adults. Thus, the populations corresponding to different species remain genetically isolated.

Hybrid inviability is a postmating isolating barrier and also a postzygotic isolating barrier.

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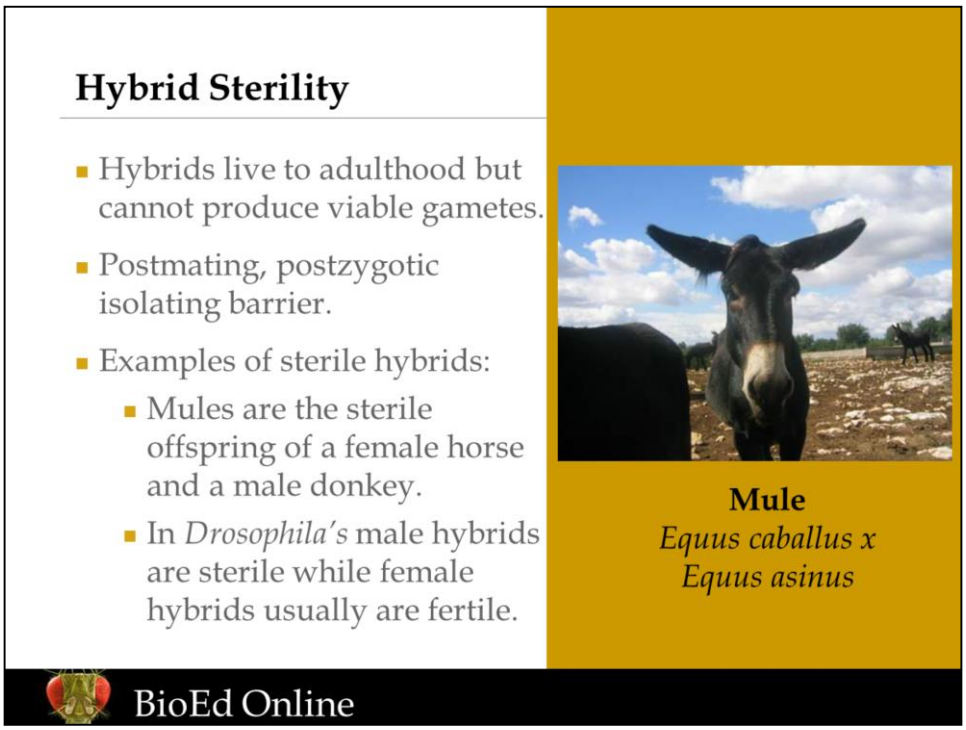

Hybrid Sterility

In some cases, hybrid zygotes successfully develop into adults but the adult individuals do not produce viable gametes. This isolating barrier, known as **hybrid sterility**, restricts the amount of genome mixing that can occur across two species.

A classic example of a sterile hybrid is the mule, the offspring of a female horse and a male donkey. All mules typically are sterile. However, within other taxonomic groups, hybrid sterility is displayed in only one sex. For example, in the fly genus *Drosophila*, crosses between different species produce sterile male hybrids and female hybrids that usually are fertile.

When hybrid sterility affects one sex preferentially, it is generally the heterogametic sex (the sex with two different sex chromosomes) that is sterile, while the homogametic sex (the sex with a matching pair of sex chromosomes) is fertile. This is known as "Haldane's rule." In most mammals and insects, including flies, the males are heterogametic and the females are homogametic. Birds and reptiles are the opposite. That is, the males are homogametic and the females are heterogametic.

Hybrid sterility is both a postmating and a postzygotic isolating barrier.

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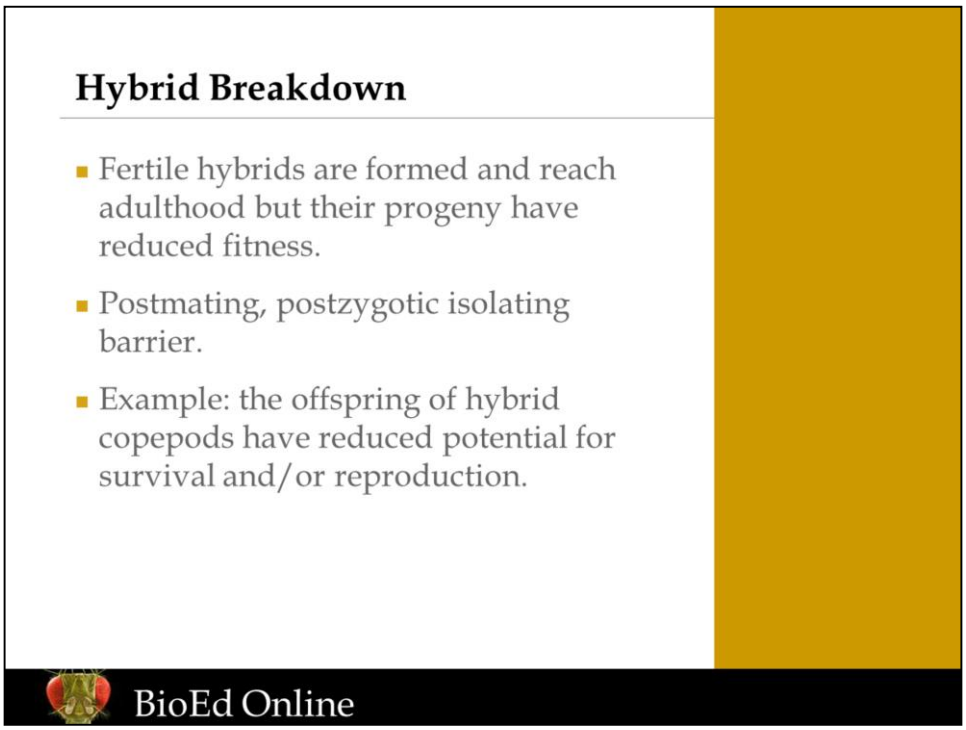

Hybrid Breakdown

In some cases, the first generation of hybrids (the F_1 generation) are fully viable and fertile, but their progeny have reduced fitness (reproductive success). This isolating barrier, known as **hybrid breakdown,** limits the amount of genome mixing that will occur between two populations.

A proposed explanation for hybrid breakdown is that different species evolve different combinations of genes, or "gene assemblages" that work together synergistically to create maximum levels of fitness. Because individuals in the F_1 generation inherit these complementary assemblages, they exhibit fitness levels that are comparable to those in the pure-bred species. In subsequent generations, however, recombination breaks up the assemblages, producing incompatible gene associations, resulting in reduced fitness.

Intertidal copepods on the Pacific coast exhibit hybrid breakdown. The F_1 hybrids can have fitness levels comparable to pure-bred members of the parental species, but the F_2 generation (formed by crossing the F_1) is frail and exhibits a greatly reduced potential for survival and reproduction.

References:

Burton, Ronald S. (1990.) Hybrid breakdown in development time in the copepod *Tigriopus californicus*. Evolution 44:1814-1822.

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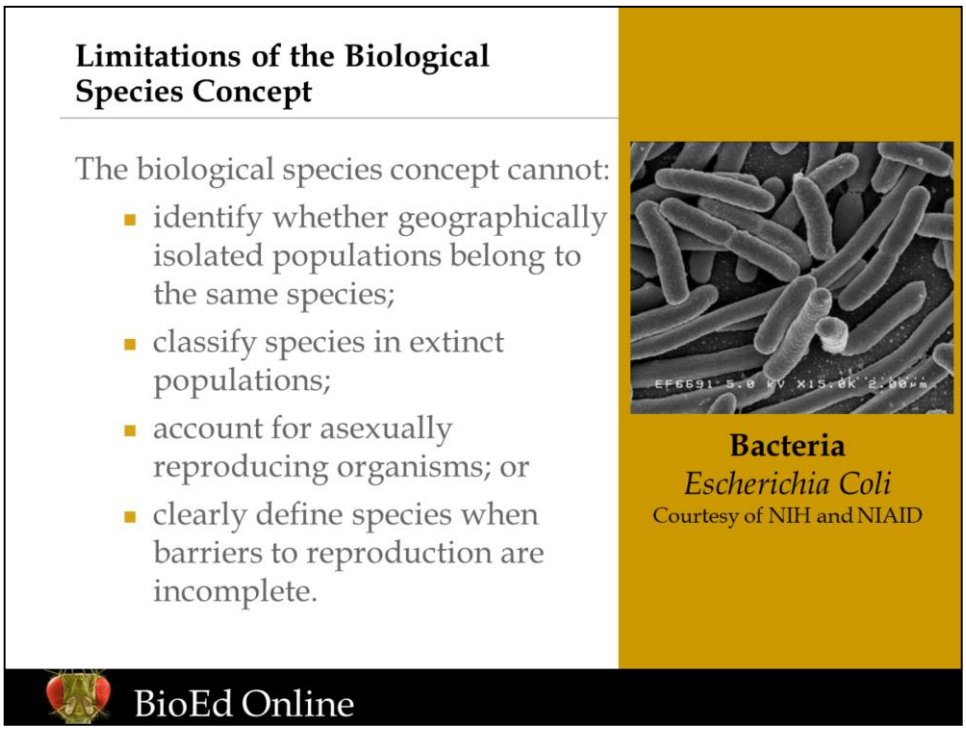

Limitations of the Biological Species Concept

While the biological species concept has had a profound influence on the development of current evolutionary theory, it has limitations. For example, because the biological species concept defines species in terms of interbreeding, it cannot be used to determine if similar populations that are geographically separated belong to the same species, nor is it useful for the classification of species in extinct populations. In addition, the biological species concept is most applicable to organisms that reproduce sexually and is less useful for the classification of organisms that reproduce asexually, including single-celled organisms like bacteria, many plant species, and even some vertebrates. The biological species concept also can be problematic when reproductive isolating barriers are incomplete. Biologists would consider this strong evidence of reproductive isolation. For example, some estimates suggest that 10% of bird species hybridize. Hybridization is even more common among flowering plants. These limitations of the biological species concept have led scientists to propose alternative species concepts.

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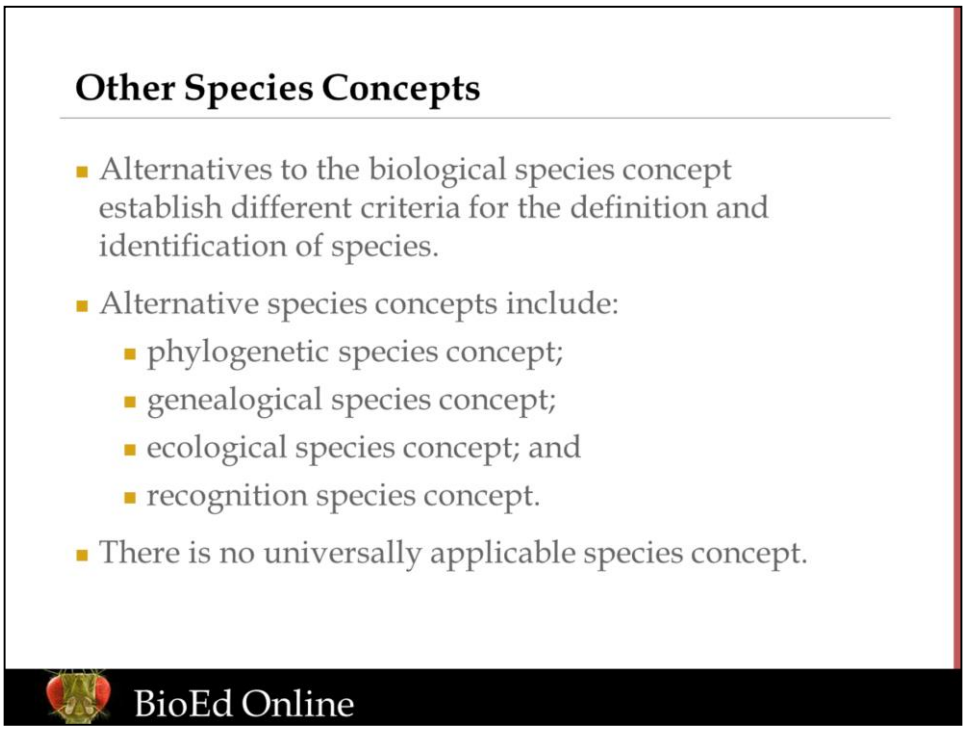

Other Species Concepts

Alternatives to the biological species concept establish different criteria for the definition and identification of species. One alternative is the phylogenetic species concept, which defines species as discreet, irreducible groups of organisms that are "diagnosably different" from other groups and share a common ancestor. Subtle variations of this idea have been proposed, such as the genealogical species concept that defines a species as a group whose members are more closely related to one another than to any organism outside the group. Together, these concepts highlight the role of evolutionary history and genetic divergence in the process of speciation. Phylogenetic relationships are often inferred through the use of quantitative methods. For example, current molecular techniques now permit the direct comparison of genetic information to create groupings or to assign individuals to specific species groups. Before the advent and wide use of DNA, and other sequencing information, phylogenetic relationships were inferred from morphology, geographical distribution, and other characteristics related to phenotype.

While the phylogenetic species concepts are concerned with the identification of historically related groups, a number of alternative species concepts emphasize the origins of the discreet groups seen in nature. For example, the ecological species concept defines species as a group of organisms that has adapted to a particular niche in an environment and evolves independently from all groups outside of its range. Thus, species are identified by the use of a common set of environmental resources. In contrast, the recognition species concept defines a species as a group of "biparental organisms that share a common fertilization system." According to this species concept, species are identified as a group of organisms that only recognize other members of the group as potential mates.

These, and other species concepts, have been proposed to address some of the limitations of the biological species concept. For example, both the ecological and phenotypic species concepts are used to define species in groups that reproduce asexually, for which the biological species concept is not useful.

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Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sunderland, MA: Sinauer Associates.
Futuyma, D.J. (2005). *Evolution*. Sunderland, MA: Sinauer Associates.

Summary: Species Concepts

- The most basic category of biological classification is species.
- There is no universal species concept that can define, identify, and explain all species.
- The biological species concept:
  - is one of the most widely used and accepted ways of delimiting species;
  - defines species as interbreeding, reproductively isolated populations; and
  - has limitations, which have led to the proposal of alternative species concepts.

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