

***Recombination***

- *Diploid organisms*: The first step in sexual reproduction is the production of gametes, each of which has half the chromosomes of the parent. Chromosomes assort independent into gametes (Mendel's second law). Crossing over occurs within chromosomes, creating chromosomes that differ from chromosomes in the parents.
- *Fertilization* creates individuals that have genotypes different from either of their parents. Siblings differ in genotype from one another.
- *Bacteria and viruses*: Although sexual reproduction occurs only in eukaryotes, bacteria and viruses have other mechanisms that result in new combinations of alleles.

***Sexual reproduction is an evolved trait***

- *There is great variety in modes of sexual reproduction*
- *Isogamy vs. anisogamy*: isogamous species produce gametes of the same size and form; anisogamous species produce gametes that differ in size and form. Some fungi and algae are isogamous. All other sexually reproducing species are anisogamous. The sex that produces the larger gamete is defined to be the female.
- *Hermaphroditic individuals vs. separate males and females*: most plants are hermaphroditic; most animals have separate sexes. Some hermaphrodites, for example peas, can self-fertilize; some, for example slugs, cannot.
- *Genetic vs. environmental sex determination*: in humans, as in many other species with separate sexes, sex is determined by genotype. In mammals, XX individuals are female; XY individuals are male. In birds, males are ZZ and females are ZW. Other genetic mechanisms are found in other groups. For example, in bees, ants and wasps, males are haploid and females are diploid. In some species of plants and animals, sex is determined by the environment. For example, in most species of turtles and in all crocodilians, the sex of an individual depends on the temperature of the egg during a critical period of development. Usually males are produced when eggs are incubated at low temperatures and females are produced when eggs are incubated at higher temperatures.
- *Capable or incapable of asexual reproduction*: Some plants and animals can produce new genetically identical individuals by budding or fission. Some plants can produce seeds asexually (apomixis). Some animals can produce diploid eggs asexually (parthenogenesis). Both apomixis and parthenogenesis result in offspring that are genetically identical to their mother. Some species never engage in sexual reproduction. For example, several species of whiptail lizards, including the endangered California species, *Cnemidophorus hyperythrus*, are comprised of females that reproduce only by parthenogenesis.
- *Many species, including aphids, can reproduce both sexually and asexually*: Typically they undergo several generations of asexual reproduction followed by one generation of sexual reproduction.

- *Do not confuse self-fertilization with parthenogenesis or apomixes:* Self-fertilization occurs when a female gamete is fertilized by a male gamete from the same individual. Siblings produced by self-fertilization have genotypes that differ from one another and from their parent. In contrast, offspring produced by parthenogenesis or apomixis are (except for mutation) identical to one another and to their parent.

### ***Sexual modes of reproduction persist despite the two-fold cost of sex***

- Because sexual reproduction requires that equal numbers of sons and daughters be produced, females who reproduce asexually will on average produce twice as many daughters as females who reproduce sexually. This is the two-fold cost of sexual reproduction.
- The fact that many species retain the capacity for both sexual and asexual reproduction tells us that sexual reproduction could be eliminated by natural selection. The question is why sexual reproduction persists.
- One answer is that genetically diverse offspring are better able to survive in different conditions. Sexual reproduction is often associated with dispersal, as in *Pilobolus* mushroom discussed by Dr. Feldman. Dispersing individuals would be expected to encounter environmental conditions different from those experienced by their parents.
- A second answer is that asexually reproducing species are not able to eliminate deleterious mutations as efficiently as sexually reproducing species. Although completely asexual species have evolved, they do not seem to be very successful and do not have large geographic ranges.

### ***Sexual selection***

- *Darwin's theory of sexual selection explains sexual dimorphism:* Darwin recognized that some features of plants and animals cannot be explained by natural selection because they do not make species better adapted to their environments. Instead, sexually dimorphic characters such as the peacock's tail, the antlers of a deer, or the horn of a stag beetle, seem to reduce chances of survival.
- Darwin recognized that the struggle for existence was both a struggle to survive and a struggle to reproduce.
- *Darwin noted that sexual dimorphism was associated with male-male competition and female choice.*
- In birds of paradise, sexual dimorphism is associated with female choice. The extravagant plumage of males serves no purpose other than being attractive to females.
- Big-horn sheep are an example of sexual dimorphism associated with male-male competition. The large horns of males are used in fights with other males. Females mate with the winners.
- *Anisogamy explains Darwin's generalization that sexual dimorphism results from competition by males for females:* In anisogamous species, many more male gametes than female gametes are produced. The reproductive capacity of females

- is limited by their ability to produce eggs; all the eggs they produce can be fertilized. The reproductive capacity of males is limited by their ability to fertilize eggs, not by the number of gametes they produce. Therefore, sexual selection results from a struggle among males for access to females.
- *Examples of male-male competition* include within group dominance, female-defense polygyny, territorial polygyny, and lekking (where the males compete for a position in the lek).
  - *Female choice can be broken into two broad categories*: resource based, where the female chooses the male that brings the most resources; and non-resource based choosiness, where the female chooses the male based on some inherent property of the male (such as good genes). An example of a direct benefit (resource based choosiness) is the bush cricket, where the male provides a spermatophore to the female that is energy rich. The good genes hypothesis is a model for choosiness in which the female chooses the male that is “best” in terms of the genes he carries. The quality of the male is indicated by some secondary character. An example of the good genes hypothesis was the Gray Tree Frog (*Hyla versicolor*), that has long or short calls. The length of the call indicates the quality of the male.
  - *Leks are aggregations of males* which females visit only for the purpose of mating. An example of a lekking species is the bower bird.
  - *The sensory bias/exploitation hypothesis states* that latent preferences in females are used by males to gain greater reproductive success. The hypothesis predicts that the female sensory bias should evolve before the male trait (that exploits the sensory bias). Two examples supported this hypothesis: first, the evolution of the chuck call in *Physaleumus* frogs occurred after the female sensory bias for chucks evolved; second, swords (extensions of the tails in Swordtail fish) evolved after the female preference for swords evolved.

### ***Evolution of altruism***

- *Helpful behaviors* are instances where an actor performs some action that benefits another individual (the recipient). Numerous examples of helpful behaviors exist in nature, and include alarm calls (as in the Belding ground squirrel), sentinel behavior (as in meerkats), nest helping, and eusocial behavior (as in ants and bees).
- *How can helpful behavior be explained?* It presents something of a puzzle, because natural selection acts on individuals, so one individual should not help another if the behavior potentially decreases its fitness. The evolutionary explanation of helpful behavior is as follows: The actor benefits, in which case the helpful behavior is termed mutualism; the actor eventually benefits, in which case the helpful behavior is termed reciprocal altruism; or the actor helps close relatives, in which case the helpful behavior is termed kin selection.
- *Vampire bats provide an example of reciprocal altruism.* The bats hang out together in groups of about 10. They feed at night, and sometimes will fail to find a meal. Individuals will share meals by regurgitating blood meals to others. They share more frequently with those with whom they exchanged a meal earlier.

- *Kin selection* is the idea that a helpful behavior can spread evolve if the behavior is likely to help close relatives. The actor performs an action at some cost,  $C$ , to itself that provides a benefit,  $B$ , to some other individual that is related to the actor by a relatedness,  $r$ . The helpful behavior can spread if  $Br - C > 0$ .
- *Inclusive fitness*: Inclusive fitness is an organism's personal reproductive success (i.e., the number of children the individual has) plus the amount of fitness an individual induces in its close relatives (i.e., the number of offspring the close relatives of the individual has).
- *Eusocial behavior in insects* (such as ants and bees) may be partly explained by the unusual sex determining mechanism in these insects. Fertilized eggs become females (which are diploid) whereas unfertilized eggs become males (which are haploid). The result is that sisters are very related to one another ( $3/4$ ) but less related to their brothers ( $1/4$ ). The asymmetry in relatedness also means that sisters should want to invest more energy in sisters, than in brothers.

### *Example test questions*

Q1. Which answers best fill the blanks in the following sentence? In animals, parthenogenesis results in siblings that are genetically \_\_\_\_\_ one another, while mating of males and females results in siblings that are genetically \_\_\_\_\_ one another.

- A. related to; unrelated to
- B. polyploidy to; haploid to
- C. larger than; smaller than
- D. the same as; different from
- E. different from; the same as

Q2. Which one of the following provides the best definition of isogamy?

- A. Isogamous species have temperature-dependent sex determination
- B. Isogamous species produce gametes of the same size
- C. Isogamous species are haploid
- D. Isogamous species are polyploid
- E. Isogamous species produce gametes of different sizes

Q3. Which one of the following best fills the blanks in the following statement? Darwin described two kinds of sexual selection, \_\_\_\_\_ and \_\_\_\_\_.

- A. isogamous; anisogamous
- B. competition of males for females; competition of females for males
- C. competition of males for females; female choice
- D. haploid; diploid
- E. early; late

Answers: D, B, C