10

All About Sex

Many of nature's greatest wonders are about sex. It is impossible not to be astonished by the mating display of a male peacock. Plants are equally remarkable: the flowers of an orchid are to the plant what the peacock's feathers are to the bird.

Animals and plants reproduce in a staggering diversity of ways (**FIGURE 10.1**). Many species are **hermaphroditic**: each individual has both male and female gonads, and mating involves exchanging eggs and sperm (in animals) or mutual pollination (in plants). When a pair of leopard slugs mate, their intimate moment begins as they hang together from a long thread of mucus (see Figure 10.1A).

SUGGESTIONS FOR FURTHER READING

As with so many topics in evolutionary biology, Charles Darwin wrote not only the first but also some of the most insightful thoughts on sexual selection. He laid out the principles of sexual selection in *On the Origin of Species* (John Murray, London, 1859), then elaborated them in his longest book, *The Descent of Man and Selection in Relation to Sex* (John Murray, London, 1871). Both books have many important ideas that still have not been fully explored.

Insects are by far the most diverse group of animals, so it is not surprising that they have a remarkable range of strange and fascinating forms of sexual selection. The book by D. M. Shuker and L. W. Simmons, *The Evolution of Insect Mating Systems* (Oxford University Press, Oxford, 2014) is a recent collection of articles by leading researchers in that field.

Males have evolved a remarkable variety of weapons to fight each other. These weapons, and their implications for humans, are explored (and beautifully illustrated) in a book by D. J. Emlen, *Animal Weapons: The Evolution of Battle* (Henry Holt, New York NY, 2014).

An overview of the diversity and evolution of sex determination mechanisms is given by D. Bachtrog and colleagues in "Sex determination: Why so many ways of doing it?" (*PLOS Biology* 12: e1001899, 2014).

A witty yet scholarly exploration of some of the more interesting and unusual sides of sex in the animal kingdom is Olivia Judson's popular book, *Dr. Tatiana's Sex Advice to All Creation* (Henry Holt, New York NY, 2013).

The definitive work on the evolution of sex ratios and sex allocation is S. West's *Sex Allocation* (Princeton University Press, Princeton NJ, 2009).

The evolution of sexual reproduction and recombination is one of the most fascinating but difficult topics in evolutionary genetics. Lucid introductions have been written by several of the leading researchers in the field: S. P. Otto ("The evolutionary enigma of sex," *Amer. Nat.* 174: S1–S14, 2009), N. H. Barton ("Why sex and recombination?", *Cold Spring Harbor Symp. Quant. Biol.* 74: 187–195, 2009), and C. M. Lively and L. T. Morran ("The ecology of sexual reproduction," *J. Evol. Biol.* 27: 1292–1303).

11

How to Be Fit

Who has not dreamed of living forever? We know we won't. Someone born in Japan today has a life expectancy of about 83 years. A white American born in 2010 is projected to live about 79 years on average, a black American 75 years. A French woman, Jeanne Calment, is said to have been mentally fully competent when she died in 1997 at the age of 122 years.

But some other species live much longer. Greenland sharks (*Somniosus microcephalus*) were recently found to live for at least 272 years, and the largest individuals are estimated to be almost 400 years old [41]. This is impressive

Life histories and mating strategies

Males as well as females are subject to costs of reproduction, and that fact underlies some interesting variations in life histories. For example, some plants, annelid worms, fishes, and other organisms change sex over the course of the life span (a phenomenon called sequential hermaphroditism). In species that grow in size throughout reproductive life, a sex change can be advantageous if reproductive success increases with size to a greater extent in one sex than in the other (**FIGURE 11.14**). For example, the pollen required to fertilize many ovules requires much less energy to produce than an equivalent number of seeds. Many species of squashes (Cucurbitaceae) and other plants produce male flowers when they are small, and switch to producing female flowers when they become larger and can obtain enough energy to develop more seeds. A female slipper shell (*Crepidula fornicata*) carries a stack of smaller males; when she dies, the biggest male changes sex, having become large enough to produce abundant eggs (see Figure 11.14C). Conversely, many sex-changing fishes are females first. In the bluehead wrasse (*Thalassoma bifasciatum*), some individuals start life as females and later become brightly colored "terminal-phase males" that defend territories and achieve high reproductive success by mating with many females (see Figure 11.14B) [60]. Almost all species of sex-changing fishes, as well as other sex-changing animals, change sex when they have reached about 70 per cent of their maximum size [1], as predicted by mathematical theory [12].

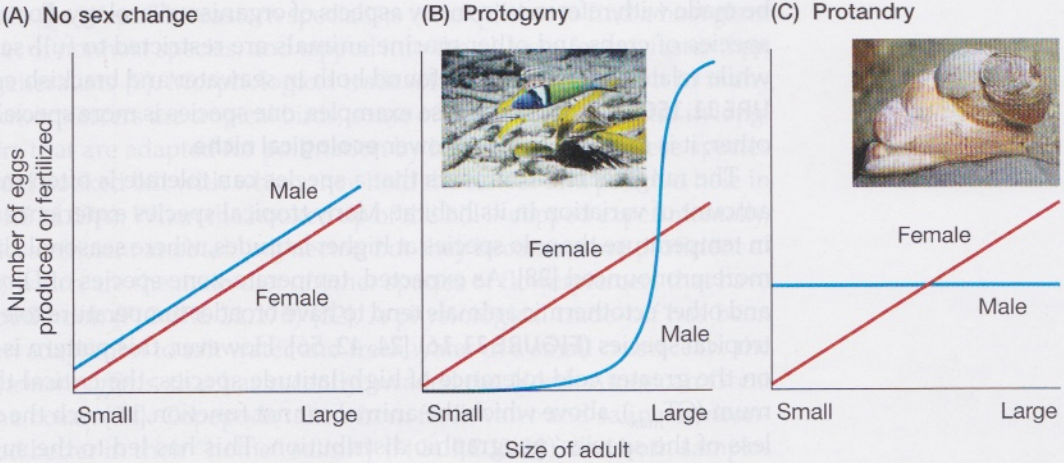
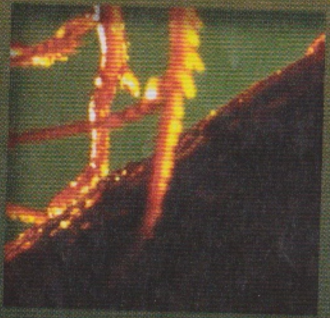


FIGURE 11.14 A model for the evolution of sequential hermaphroditism. (A) When reproductive success increases equally with body size in both sexes, there is no selection for sex change. (B) A switch from female to male (protogyny) is optimal if male reproductive success increases more steeply with size than female reproductive success does. This is the case in the bluehead wrasse (*Thalassoma bifasciatum*) shown here: females are yellow; males are blue, white, and green. (C) The opposite relationship favors the evolution of protandry, in which males become females when they grow to a large size. For example, a female slipper shell (*Crepidula fornicata*) carries a stack of males; when she dies, the lower-most male becomes female. (After [60].)

12

Cooperation and Conflict



Look at an ant nest. It is familiar, yet utterly remarkable. Hundreds to millions of individuals—a mother and her many, many nonreproducing daughters—perform a complex ballet of cooperative behaviors to gather food, raise offspring, and defend the nest. Leafcutter ant nests can include tens of millions of individuals, all daughters of a single queen that mated once and then stored sperm in her reproductive tract so that she could fertilize eggs for years afterward. These workers differ in size and form and are specialized for different tasks. Some are soldiers that defend the nest, some cut and bring home pieces of leaves, and some are farmers that chop up the leaves and use them to grow a fungus that provides the colony's food. All these individuals sacrifice their own reproduction to increase the fitness of their queen.

But not all ants are so unselfish. In some species, female workers kill their brothers and nephews, and sometimes even kill their mother [64]. What could possibly lead to the evolution of such extreme forms of altruism and aggression in ants?

aggregation in species without sperm competition. That prediction is confirmed: the sperm from the same male do not preferentially aggregate in a closely related monogamous species (*P. polionotus*) [25].

Even bacteria can cooperate. *Pseudomonas aeruginosa* requires iron, which it takes up from its environment by binding iron atoms with proteins called siderophores that the bacteria excrete into their environment. Bacterial cheaters, however, take up iron bound with the siderophores produced by others, and they avoid paying the cost of producing siderophores themselves [34]. The outcome of competition between genotypes that excrete siderophores (cooperators) and genotypes that do not (cheaters) depends on the environment they grow in (**FIGURE 12.5**). The bacteria can be maintained in the lab under conditions to produce either high or low relatedness between them, and either strong or weak competition between relatives. When the bacteria have low relatedness and are in a strongly competitive environment, the cheaters win. But when the bacteria are closely related and are in a weakly competitive environment, the cooperators can drive the cheaters to extinction.

Another pathway to the evolution of altruism is by the "green beard" effect, which occurs when a single gene codes for a phenotypic trait that enables its carrier to recognize and help other individuals with the same trait (for example, a green beard) [20]. This situation is uncommon in nature, but a few cases have been described [31]. One comes from the slime mold that we discussed earlier (see Figure 12.1). The *csA* gene encodes a cell adhesion protein that binds to the same protein in the membrane of other cells. This acts as a green-beard recognition system: cells with *csA* adhere to each other and pull themselves into aggregations. Cells that have the *csA* gene knocked out act as cheaters. If they manage to get into an aggregation with cells that have *csA*, their lower adhesion makes it more likely that

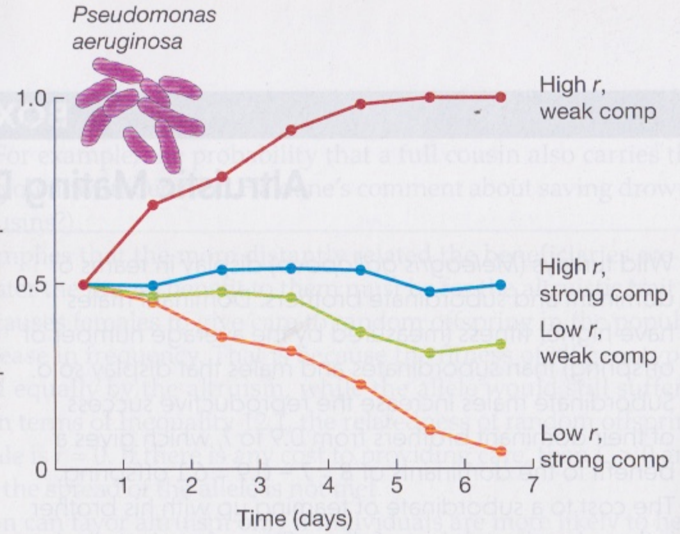


FIGURE 12.5 Evolution of cooperation in an experiment with the bacterium *Pseudomonas aeruginosa*. The cooperator genotype excretes siderophores, which are used by neighboring bacteria to take up iron from the medium. The cheater genotype does not excrete siderophores, but benefits from the siderophores made by others. Bacteria evolved in cultures that were maintained with either low relatedness (low *r*) or high relatedness (high *r*), and with either weak competition (weak comp) or strong competition (strong comp) between relatives. The cooperator genotype increased in frequency when there was high relatedness and weak competition. (After [34].)

they will end up as spores. Cells with the *csA* gene are more altruistic, and they are able to prevent the cheaters from spreading in the population because they are more effective at recognizing each other and forming aggregations [62].

Spite

A behavior is spiteful if it harms both the actor and the recipient. Spite is the antithesis of altruism, but inclusive fitness theory predicts that spiteful traits can evolve. The conditions needed are that the actor be *less* closely related to the recipient than to an average member of the population, and that *harming* the recipient enhance the fitness of other individuals in the population that are more closely related to the actor [82].

An example of spite comes from bacteriocins, toxins that are secreted by many bacteria and that kill susceptible bacteria [67]. Bacteriocin-producing genotypes are resistant to the toxin because of a resistance gene that is tightly linked to the gene for the toxin. Producing bacteriocin reduces growth. However, genotypes that make bacteriocins increase in laboratory cultures [41]. By killing susceptible cells, they free up resources and enhance the growth of relatives that also carry the producer gene.

SUGGESTIONS FOR FURTHER READING

An Introduction to Behavioural Ecology (Wiley-Blackwell, Oxford, 2012) by N. B. Davies and colleagues is an outstanding introduction to that field. A more general introduction to animal behavior is *Animal Behavior: An Evolutionary Approach* by J. Alcock (Sinauer Associates, Sunderland, MA, 2013).

The evolution of social behavior and its implications for major transitions in evolution are comprehensively treated by A. F. G. Bourke in *Principles of Social Evolution* (Oxford University Press, Oxford, 2011). An excellent set of essays on many aspects of cooperation and conflict is *Levels of Selection*, edited by L. Keller (Princeton University Press, Princeton, NJ, 1999). J. A. R. Marshall's *Social Evolution and Inclusive Fitness Theory* (Princeton University Press, Princeton, NJ, 2015) is a comprehensive synthesis of that topic.

Genetic conflict and selfish genes are reviewed in a book by A. R. Burt and R. Trivers, *Genes in Conflict: The Biology of Selfish Genetic Elements* (Harvard University Press, Cambridge, MA, 2006). Much shorter but excellent are the review articles by J. H. Werren, "Selfish genetic elements, genetic conflict, and evolutionary innovation" (*Proc. Natl. Acad. Sci. USA* 108: 10863–10870, 2011) and W. R. Rice, "Nothing in genetics makes sense except in light of genomic conflict" (*Annu. Rev. Ecol. Evol. Syst.* 44: 217–237, 2013).

The evolutionary "battle of the sexes" is an area of active research. We recommend *Sexual Conflict* by G. Arnqvist and L. Rowe (Princeton University Press, Princeton, NJ, 2005). A concise overview that focuses on genetic aspects is the article by R. Bonduriansky and S. F. Chenoweth, "Intralocus sexual conflict" (*Trends Ecol. Evol.* 24: 280–288, 2009).

The topic of group selection has a rich history. One of the most important contributions to this subject is the famous book by G. C. Williams, *Adaptation and Natural Selection* (Princeton University Press, Princeton, NJ, 1966), which has stimulating thoughts on many other topics as well. More recent discussions include a book by E. Sober and D. S. Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Harvard University Press, Cambridge, MA, 1988), which takes a positive view of group selection, and an article by S. A. West and colleagues ("Evolutionary explanations for cooperation," *Current Biology* 17: R661–R672, 2007), who instead emphasize kin selection.