**Chapter 11  
Sex: causes and consequences**

Mechanisms of reproduction are diverse

There are several advantages and disadvantages to sexual reproduction:

(see table in ppt)

Sex creates new genotypes

A variety of theories have been proposed over the years to explain **why sexual reproduction may be more advantageous than asexual reproduction**, and, for that matter, why sexual reproduction even exists at all.

For years everyone accepted the general proposition that sex is good for evolution because it creates genetic variety, which, in turn, is useful in adapting to constantly changing and challenging environments. But it may give organisms a very different kind of edge.

By the late 1980s, in the **contest to explain sex**, only two hypotheses remained in contention.

* One, the deleterious mutation hypothesis, was the idea that sex exists to purge a species of damaging genetic mutations: Alexey Kondrashov, now at the National Center for Biotechnology Information, has been its principal champion.
  + He argues that in an asexual population, every time a creature dies because of a mutation, that mutation dies with it. In a sexual population, some of the creatures born have lots of mutations and some have few.
  + If the ones with lots of mutations die, **then sex purges the species of mutations**. Since most mutations are harmful, this gives sex a great advantage
  + But why eliminate mutations in this way, rather than correcting more of them by better proofreading?
  + Kondrashov has an ingenious explanation of why this makes sense: **It may be cheaper to allow some mistakes through and remove them later.** The cost of perfecting proofreading mechanisms escalates as you near perfection.
  + According to Kondrashov's calculations, the rate of deleterious mutations must exceed one per individual per generation if sex is to earn its keep eliminating them; if less than one, then his idea is in trouble.
  + The evidence so far is that the deleterious mutation rate teeters on the edge: it is about one per individual per generation in most creatures. But even if the rate is high enough, all that proves is that **sex can perhaps play a role in purging mutations**. It does not explain why sex persists.
  + The main defect in Kondrashov's hypothesis is that it works too slowly. Pitted against a clone of asexual individuals, **a sexual population must inevitably be driven extinct by the clone's greater productivity**, unless the clone's genetic drawbacks can appear in time.
  + Currently, a great deal of effort is going into the testing of this model by measuring the deleterious mutation rate, in a range of organisms from yeast to mouse. But the answer is still not entirely clear.
* In the late 1980s the Red Queen hypothesis emerged, and it has been steadily gaining popularity. First coined by Leigh Van Valen of the University of Chicago, it refers to Lewis Carroll's *Through the Looking Glass*, in which the Red Queen tells Alice, "**[I]t takes all the running you can do, to keep in the same place.**"
  + This never-ending evolutionary cycle describes many natural interactions between hosts and disease, or between predators and prey: As species that live at each other's expense coevolve, they are engaged in a constant evolutionary struggle for a survival advantage. They need "all the running they can do" because the landscape around them is constantly changing.
  + The Red Queen hypothesis for sex is simple: **Sex is needed to fight disease.** Diseases specialize in breaking into cells, either to eat them, as fungi and bacteria do, or, like viruses, to subvert their genetic machinery for the purpose of making new viruses. To do that they use protein molecules that bind to other molecules on cell surfaces.
  + The arms races between parasites and their hosts are all about these binding proteins. **Parasites invent new keys; hosts change the locks.** For if one lock is common in one generation, the key that fits it will spread like wildfire. So you can be sure that it is the very lock not to have a few generations later.
  + According to the Red Queen hypothesis, sexual reproduction persists because it enables host species to evolve new genetic defenses against parasites that attempt to live off them
  + Sexual species can call on a "library" of locks unavailable to asexual species. This library is defined by two terms: **heterozygosity** and **polymorphism**. Both are lost when a lineage becomes inbred. What is the function of heterozygosity?
  + In the late 1970s, with the help of two colleagues from the University of Michigan, Hamilton built **a computer model of sex** and disease, a slice of artificial life. It began with an imaginary population of 200 creatures, some sexual and some asexual. Death was random. As expected, the sexual race quickly died out. **In a game between sex and "asex," asex always wins -- other things being equal.** That's because asexual reproduction is easier, and it's guaranteed to pass genes on to one's offspring. Next they introduced several species of parasite, 200 of each, whose power depended on "virulence genes" matched by "resistance genes" in the hosts. The least resistant hosts and the least virulent parasites were killed in each generation. Now the asexual population no longer had an automatic advantage -- **sex often won the game**. It won most often if there were lots of genes that determined resistance and virulence in each creature. In the model, as resistance genes that worked would become more common, then so too would the virulence genes. Then those resistance genes would grow rare again, followed by the virulence genes. As Hamilton put it, "antiparasite adaptations are in constant obsolescence." **But in contrast to asexual species, the sexual species retain unfavored genes for future use.**
  + "The essence of sex in our theory," wrote Hamilton, "is that it stores genes that are currently bad but have promise for reuse. It continually tries them in combination, waiting for the time when the focus of disadvantage has moved elsewhere."
* Some species, such as strawberry plants, aphids, sponges, rotifers, and water fleas (Cladocera), can reproduce both sexually or asexually according to the conditions. These species are called heterogonic.
* Many heterogonic species time their sexual reproduction for periods of environmental uncertainty, and reproduce asexually when conditions are more stable; but that is not the important point here. What matters is that an individual can reproduce in either way.
* Therefore, when an aphid reproduces sexually, it must be advantageous to the individual, because if it was not the aphid could have reproduced asexually. Both sexual and asexual reproduction must have 'balanced' advantages to maintain them in the species' life cycle: otherwise the inferior one would be lost.

Persistence of asexual reproduction in Bdelloid rotifers

* Enter dormant phase during difficult conditions
  + Horizontal gene transfer
  + Shedding of parasites

**Anisogamy** results in differential investment in reproduction

**Anisogamy** (also called **heterogamy**) refers to a form of sexual reproduction involving the union or fusion of two dissimilar gametes (differing either in size alone or in size and form). The smaller gamete is considered to be male (sperm cell), whereas the larger gamete is regarded as female (egg cell).

Limitations on reproductive success differ for the sexes

* Females are limited by **fecundity**
* Males are limited by the number of mates they can obtain

Investment differences can extend past fertilization

Uncertain paternity may explain why male parental care is rare

* Females have certain paternity
* Males have uncertain paternity
  + Parental care could be directed toward offspring not their own

Asymmetrical parental care alters operational sex ratio

* **Operational sex ratio:** ratio of males to females capable of reproducing at a given time
* Slower rate of reproduction by females leads to male biased OSR

**Sexual selection**

* Differential reproductive success resulting from competition for mates
  + Intrasexual selection
  + Intersexual selection
* Sexual selection typically stronger on males
  + Maximize fitness by mating multiply
  + Male biased OSR

Sexually dimorphic result from sexual selection

* **Ornaments:** attractive traits that increase mating success
* **Armaments:** weaponry used to outcompete other individuals

Male-male competition leads to extreme variance in reproductive success

Benefits of female choice

* **Direct benefits:** benefit the female directly
  + e.g. food, nest sites, protection
* **Indirect benefits:** benefits that affect the genetic quality of the female’s offspring

See table in notes.

**Types of mating systems**

* **Monogamy:** one male pairs with one female
  + Sexual: partners mate with each other exclusively
  + Social: partner pair but may cheat
* **Polygyny:** males mate with multiple females
* **Polyandry:** females mate with multiple males

Polyandry selects for male traits that increase paternity

Sperm competition drives evolution of larger testes

Sexual conflict results in antagonistic coevolution

* **Sexual conflict:** traits that confer a fitness benefit on one sex but cost to the other
  + Traits coevolve antagonistically