

12 SEX AND RECOMBINATION

These notes are a supplement to the material covered on pp. 274-278 of your text. You should be familiar with all this material.

12.1 SEXUAL AND ASEXUAL REPRODUCTION

There are really only two features that distinguish sexual from asexual reproduction: **meiosis** and **syngamy**. **Meiosis** is the process by which a diploid organism produces haploid gametes. **Syngamy** is the fusion of two haploid gametes to produce a diploid zygote.

During meiosis, the genes of each parent are “shuffled” such that each gamete, while possessing half of the parental genotype, carries a unique combination of parental genes. This “shuffling” arises by **recombination** which includes two components; independent assortment and crossing-over. As a consequence, sexual reproduction is capable of generating a wide variance of phenotypes, even in the absence of mutation.

Asexual reproduction can be **vegetative** or **parthenogenetic apomixis**. In parthenogenesis, a single cell can give rise to a new diploid individual. In **apomixis**, meiosis is suppressed so that offspring develop from a single diploid cell produced by their parent. In some organisms, females can give rise to only female offspring, but the offspring are produced by meiosis. This is sexual reproduction, even though no males are involved. In the absence of mutation, asexual offspring are genetically identical to their parent.

Sexual reproduction is often (but not always) accompanied by **anisogamy** (differences in size of two kinds of gametes). In yeast and in many algae, two haploid cells of the same size (**isogamous**) unite to produce a diploid zygote. The two cells must be of different mating types (+/-) to be able to unite. Anisogamous organisms have large gametes (defined as ‘eggs’) and small gametes (defined as ‘sperm’).

In some species (mammals, arthropods, many angiosperms), an individual can produce either eggs or sperm, but not both. That is, the sexes are separate (**dioecious**). However, many kinds of plants and animals can produce both eggs and sperm, either at the same time (**simultaneous hermaphrodites**), or at different times (**sequential hermaphrodites**). Finally, some organisms have some individuals that are hermaphroditic, and some individuals that are only female (or only male).

12.2 THE PROBLEM WITH SEX

12.2.1 *The cost of sex*

For organisms where the sexes are clearly distinct (dioecious), there is a “**cost of males**”. John Maynard-Smith (1978 *The evolution of sex*) provided an illustrative example. Imagine a polymorphic population containing both sexual and asexual individuals. Imagine further that there is a single gene controlling the reproductive mode. Both sexual and asexual individuals produce equal numbers of offspring, but the asexual individuals produce only females (which are capable of reproducing asexually), while

sexual individuals produce both males and females. The sexual females will therefore only have half as many grandchildren as the asexual female. **The rate of increase of an asexual genotype is twice that of a sexual genotype, all else being equal.** Thus there is a two-fold cost in terms of number of progeny in each generation. Thus asexual reproduction should quickly take over.

More generally, there is a “**cost of meiosis**”. Imagine an asexual population of females. In this population a mutation arises that causes meiosis. Initially, this allele will be found only in heterozygous individuals. **Therefore a female will pass on this gene for meiosis to only half her offspring while asexual females will pass on the allele for asexual reproduction to all her offspring.** Assuming that the mean number of offspring is the same regardless of the parental genotype, the rate of increase for the allele causing meiosis is only half that of the allele for asexual reproduction. Under these conditions, the allele for meiosis should not persist.

12.2.2 Recombination breaks up favorable gene combinations.

First, consider an asexual organism with no recombination. Any lineage (e.g. cell lineage in *E. coli*) that acquires a beneficial mutation will increase in frequency, while any cell lineage that acquires a deleterious mutation will go extinct. Thus beneficial mutations accumulate in the population of asexually reproducing organisms and soon are fixed. Over a long enough period a whole series of beneficial mutations may become fixed in a population. Now consider what happens with recombination. Beneficial combinations of genes are broken up with each act of recombination.

12.3 POSSIBLE ADVANTAGES TO SEXUAL REPRODUCTION

12.3.1 Recombination is for DNA repair.

Errors in DNA can be repaired by copying from an undamaged strand on a homologous chromosome. Eukaryotes have sophisticated DNA repair mechanisms, suggesting that repair is an important component of genetic homeostasis. According to the DNA-repair hypothesis, the formation of new gene combinations is simply a side effect of DNA repair and not the reason for recombination or sexual reproduction.

Critique: (Maynard-Smith, Kondrashov) argue that this hypothesis does not explain meiosis and syngamy - DNA repair does not require the complicated mechanisms of meiosis and syngamy. Permanently asexual diploid organisms could repair DNA in the same way without the cost of meiosis and sex. So the **origin** of recombination may be due to its role in DNA repair, but the **evolution** of meiosis and separate mating types, and the maintenance of sexual reproduction, may be attributed to other causes involving

12.3.2 Asexual populations accumulate deleterious mutations

i) **Muller's ratchet (H.J. Muller).** In asexual populations (if most mutations deleterious and back mutations are rare) there will be a distribution of the numbers of deleterious mutations per individual. Due to continued mutation and genetic drift, the class of individuals with 0 mutations (most fit) will eventually disappear. Then the most fit genotype will be those with 1 mutation. This class will also disappear eventually. Asexual populations cannot regenerate individuals with low numbers of mutant alleles so the loss of superior genotypes is an irreversible process - a ratchet. With each loss of

superior genotypes, the ratchet advances and the fitness of the population declines. As population fitness declines, population size might also decline, leading to faster drift, and a faster ratchet. Eventually population may experience a “**mutational meltdown**”, leading to extinction. An asexual population has no way to re-generate the 0-mutation class, while a sexual population can regenerate this class through meiosis, recombination, and syngamy.

Evidence: Bacterial populations do seem to accumulate deleterious mutations over many generations.

Critique: Most powerful in small populations, might not be very important in large populations. It confers a long-term but not a short-term advantage. However, asexual species are generally young, so these could be populations that have not been asexual long enough to suffer from the ratchet.

ii) Synergistic epistasis (**Kondrashov’s “hatchet”**). Does not require genetic drift, so can work in large populations. Sex purges mutations because recombination will produce individuals with many mutations who then die, eliminating many mutations at once. If rates of deleterious mutations per diploid genome per generation are high enough, and mutations interact synergistically, then sexuals can overcome their inherent 2-fold disadvantage. This happens because selection will tend to create negative linkage disequilibrium among deleterious alleles by eliminating genotypes with combinations of deleterious alleles. In asexual populations selection then becomes less effective at removing deleterious alleles as negative linkage disequilibrium (LD) increases. However, sexual reproduction and recombination break down this negative LD and allow selection to more effectively remove alleles. **With a sufficiently high mutation rate per genome ($U > 1$), this process can provide a strong short-term advantage for sex and recombination.**

Evidence: Evidence for high mutation rates and synergistic interactions exists, but is not universal.

Critique: Hatchet still requires 1000s of generations to do its work. Might be too slow to outweigh the short-term advantage of asexuality. This model is still attractive because of its universality.

12.3.3 Faster adaptive evolution.

There are several different kinds of models that propose that the advantage of sex is that it increases the rate of adaptive evolution. To understand this concept imagine that a different beneficial mutation occurs in two different families in a population. If the population is sexual, the two different mutations can end up in the same organism through meiosis and syngamy. In an asexual population, the only way the mutations can end up in the same organism is if the same lineage experiences both mutations.

Evidence: Dunbrach et al. (1995), Otto and Lenormand 2002.

A general critique: If populations are ‘waiting’ for new mutations in order to adapt to an environment, this mechanism will only confer a substantial advantage in a large population. In a small population, beneficial mutations are so rare that the first mutation is likely to be fixed or lost before the second arises. However mutation, gene flow, and variable selection will maintain at least some variation within populations. Populations may gain as much or more from generating new combinations of alleles as from a new mutation. The basic idea is that recombination reduces the frequency of non-optimal combinations of alleles and can potentially increase the frequency of superior combinations.

i) **Temporally fluctuating selection.** Selection for an intermediate optimum in a polygenic trait tends to create negative linkage disequilibrium (see Chapter 7 in Freeman and Herron). As an example, consider four different loci, each with two alleles. One allele at each locus (A, B, C, D) increases the size of the organism and the alternate alleles (a, b, c, d) decrease size. Stabilizing selection for an intermediate size will create an excess of combinations such as *AbcD* and *abCD*, while combinations like *abcd* and *ABCD* will become rare. These low-fitness allele combinations will be produced each generation in a sexual population, but will disappear in an asexual population. If the environment changes to favor small individuals then some individuals will produce gametes of type *abcd* in a sexual population and therefore produce high-fitness offspring. But asexual individuals will not be able to produce these gametes. Thus there is a short-term advantage of sexual reproduction in a situation like this.

Evidence: Some evidence that populations with restricted recombination do not evolve as fast to a changing environment (Carson 1959).

ii) **Different genotypes are favored in different habitats.** If different habitats favor different genotypes, and the offspring of a single female will disperse to different habitats, a sexual female will produce offspring with greater range of genotypes and thus have a better chance of producing an offspring with high fitness in some habitat.

Evidence: Asexual populations often found in extreme environments (e.g., high altitude/latitude), but this might be due to reproductive assurance.

iii) Similarly, if different genotypes use slightly different resources, individuals with similar genotypes will **compete** more with each other than they will with individuals with different genotypes. So a sexual female will have offspring that compete less with each other, and therefore her offspring will have higher average fitness.

Evidence: Antonovics found that grass plants had higher fitness and suffered less from predation if grown in competition w/ other genotypes rather than with the same genotype.

iv) **Red Queen Hypothesis.** This is the best well-known of the 'variable-environment' hypotheses. The name of this hypothesis comes from Lewis Carroll's novel "Through the looking glass". Alice and the Red Queen find themselves running across a chessboard but don't seem to be moving anywhere. Similarly, species populations are viewed as having to continuously "run" (read evolve) to track changing environments just to keep even. If they fail to adapt to the changing conditions, they are liable to go extinct. In addition to changing abiotic conditions, the biotic environment is always going to be changing. Predators are becoming better predators, competitors are becoming better competitors, parasites are becoming better parasites. If a species does not continuously keep up it is likely to be displaced by a competing species. This is where the advantage to sexual reproduction is believed to lie. Sexually reproducing populations, by virtue of their enhanced ability to generate variation quickly, are able to track changing environments more effectively than asexual species.

Evidence: Host-parasite arms race might lead to a Red Queen situation. Curt Lively - snails and trematode infection in New Zealand. *Potamopyrgus antipodarum* is freshwater snail that has parthenogenetic and sexual individuals at varying frequency in different populations. Trematode parasite eats gonads, and so should impose strong selection on the snails. Prediction of the Red Queen is that sex should be more prevalent in populations with high infection rates. This prediction was supported by a comparative study of different populations of snails.