

Outline of lectures 26-28

Evolution of Genetic Systems

1. Features of our genetic systems are explained to various degrees by evolutionary biology. Starting with the most well-explained and proceeding to the least, they are:
 - Sex ratios
 - Degeneration of Y chromosomes,
 - anisogamy (unequal-sized male and female gametes)
 - outcrossing and recombination
 - Diploidy
 - mutation rates.
2. Sex determination mechanisms vary widely. They include (see the overhead for more): XX-XY, ZW-ZZ, XX-XO, XX-XY₁Y₂, arrhenotoky (haplo-diploidy), environmental sex determination, self-sterility systems, and sequential hermaphroditism.
3. Sex ratios are often near 1:1, even when there is no good ecological reason why that would help the species. Often a species would produce more offspring if there were more females and fewer males. Nevertheless the sex ratio stays near 50% males.
4. Carl Düsing in 1883-4 gave an explanation of this which is the standard modern theory. It is usually attributed to R. A. Fisher, in 1930, who mentioned it. It depends fundamentally on the fact that each offspring has one female and one male parent. If there is an excess of one sex (say females), then a gene that causes its bearers to become males more often will have an advantage. It will have it because the males as a whole are having as many offspring as the females as a whole have. So the average male has more offspring than the average female. Therefore by producing more males, the gene will be more represented in the next generation.
5. This is not just an impressionistic verbal argument – it can be quantitated by working out the gene frequencies in males and females in future generations. The gene will increase as long as there is a deficiency of males, and as long as it produces more males. If a gene produces more than 50% males in its bearers, it will increase until it reaches a frequency where the population has a 50:50 sex ratio.

6. The same argument works in haplo-diploids, in environmental sex determination systems, in sequential hermaphrodites, where it predicts equal effort put into being a male and into being a female, and in simultaneous hermaphrodites such as many flowers, where it predicts equal reproductive allocation to ovules and pollen.
7. Y chromosomes can have some unusual evolutionary phenomena. If one has a “driven” Y which gets into gametes more than 50% of the time, it will increase in frequency. If a Y gets into 100% of gametes, it will increase to fixation *even though as it does so the population goes extinct!* Has this happened? It is hard to know, as what is left are the species that do not have such a driven Y. In any case modifiers of the X or autosomes that resist this will be favored too.
8. (*This was not covered in lecture but is worth mentioning*). Y chromosomes commonly have few functional loci. This degeneration of the Y was finally explained in 1978 by Brian Charlesworth, using the phenomenon of “Muller’s Ratchet”, which was invented by H. J. Muller (and worked on later by me, too).
9. Y chromosomes have no recombination through most of their length, for a simple reason: to avoid producing chromosomes that have some but not all of the essential male-determining signals.
10. Muller pointed out that such recombinationless chromosomes would degenerate. They pick up mutants, at various loci. If the population gets into a state where each copy of the chromosome has at least one mutant, then without recombination it can never get a chromosome which has no mutants. The ratchet has moved one notch. This process continues, and mutations pile up on the chromosome, though the rate at which this happens may be slow if selection against the mutants is strong, mutation weak, and/or population size large.
11. Back mutation can actually reverse the ratchet, but it is a rare phenomenon and will not do so until it is far advanced. Recombination could produce a mutant-free chromosome, but it is absent.
12. The evolution of recombination with outcrossing is also to some extent explained by Muller’s Ratchet. This is often called the “evolution of sex” to attract more attention, although it has nothing to do with the evolution of the differentiation between the sexes. Outcrossing allows genes from different parents to be recombined into the same offspring. This is not in and of itself an advantage (contrary to a lot of ill-considered statements).
13. Outcrossing with recombination allows the Ratchet to be unsprung. If we did not outcross all our chromosomes would be subject to the Ratchet.

14. An alternative explanation, due to Fisher (1930) and Muller (1932), is that an advantage of recombination is that it allows advantageous mutants that arise in different parents to both be fixed in the same population. (In a sense the Ratchet is a similar phenomenon, except that the advantageous alleles start out at high frequency instead of as mutants; recombination allows the favored nonmutant alleles to be combined).
15. A second major class of explanations for recombination is the theory of Sturtevant and Mather (1942) who imagined a case in which in some generations selection favors gene combinations AB and ab , but in others the combinations Ab and aB . The presence of recombination helps the population rapidly switch between these states, and can be used as the basis of an argument that modifier genes that encourage recombination will be favored.
16. The late W. D. Hamilton (of kin selection fame) pushed the idea that the evolutionary pressure caused by rapidly evolving parasites could select for some gene combinations in some generations, and different ones only a few generations later. This biological scenario uses the Sturtevant/Mather explanation. It is usually called the “sex and parasites” explanation.
17. The problem with all of these explanations is that John Maynard Smith has shown that there is a Cost of Meiosis, which is the 50% loss of fertility of the species due to wasting effort on making males (it is really a Cost of Males). This will select strongly against sexual lineages.
18. That 50% of the effort will be spent on males is a consequence of Düsing’s sex ratio argument. It means that the Cost of Meiosis is just as serious in, say, hermaphrodite plants as a cost of pollen production.
19. A clonally-reproducing organism will have a twofold advantage. The exisating arguments for the evolution of recombination are hard-pressed to overcome this.
20. There are other explanations (the sex-and-parasites argument and an argument that recombination is needed only for repairing double-stranded DNA breaks are the main ones). At the moment we have lots of explanations and too few ways of telling which might be important. We also have the pesky Cost of Meiosis.
21. It is not that evolutionary biology cannot explain “sex” (as is sometimes implied) but that it has too many explanations.