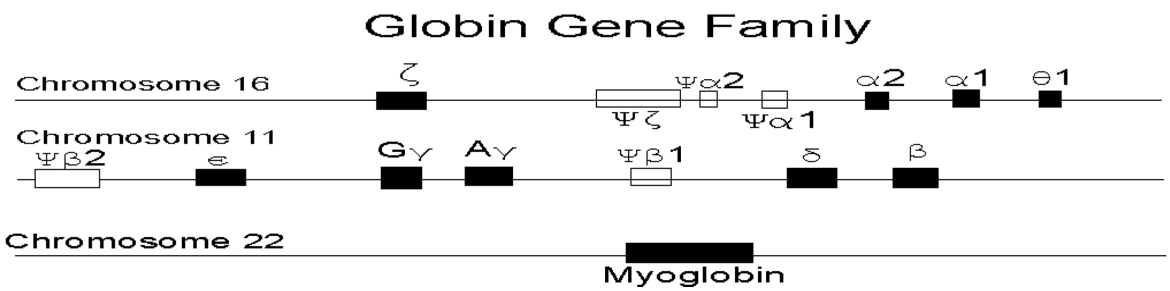
I. Genome Evolution

A. How are genes arranged? They are largely arranged in gene clusters and gene families. In a cluster, related genes are physically next to one another on a chromosome; genes in gene families may be on different chromosomes, but are derived from one another (Hbα on chr 16, Hbβ on chr 11, both descended from myoglobin which is on chr 22). Within the Hbβ cluster are the δ and ε genes.



B. Gene clusters probably originated by unequal crossing over. Pseudogenes (such as Ψβ1) are genes which resemble others in the cluster (in this case, Ψβ1resembles Hbβ), but no longer produce protein.

C. Gene and genome duplication. This is very important for evolution, as one copy of a gene can continue to help the organisms stay alive, while the other copy is free to mutate to take on new function. Obviously this has happened to make gene clusters and families, but it has also happened apparently concurrent with major evolutionary advances. There is evidence, for instance, that the evolution of a backbone was preceded by a whole genome duplication polyploidy).

D. Much DNA does not code for proteins, and much of this non-coding DNA consists of repeated sequences. Several types of repeated sequences have been recognized — short repetitive, middle repetitive, long repetitive. Some of these sequences are transposable elements, which appear to be "parasitic DNA", DNA which replicates for its own sake, and has no coding function.

E. Some repetitive DNA is contained in minisatellites (small pieces of chromosomes appearing at the ends of the chromosomes). Individuals vary in the number of repeats they have of these minisatellite segments, and such genes are called VNTRs — variable number of tandem repeats. Even identical twins will vary in their VNTRs, since the number of repeats is apparently determined as the embryo grows in the first several cell divisions. These VNTRs can be used for "genetic fingerprinting" if one is very careful.

II. Analysis of Adaptation

A. an adaptation is a feature of an organisms which allows it to reproduce better than if it lacked the feature.

B. It is not always obvious how or whether a character is adaptive (see IV: Adaptive Explanation)

C. Adaptation can be studied by one of three methods:

1. comparing the observed form of a character with a theoretical prediction — if something moves fast through a fluid, selection will shape it for the least hydrodynamic drag — or the hip joint of a biped should be different than a quadruped because of the different stresses..
2. experimentally altering the character to see whether reproduction is affected — paint out the bright red throats of male hummingbirds, or alter the tail length of male swallows to see whether reproduction is affected
3. by comparing the form of the character in many species — what is the male/female body size ratio in polygynous species vs. monogamous species.

D. Sex — why does it exist, why do the sexes differ, what sex ratio is selected for?

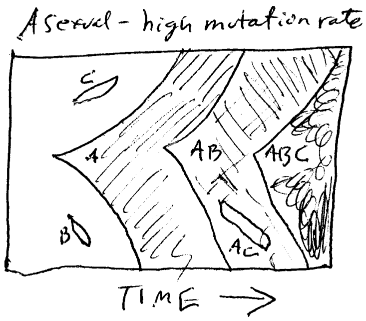
1. what is sex? it is recombination
2. what are the sexes? female is one that produces fewer larger gametes, male is the one that produces more, smaller gametes. Two strategies evolve from one homogametic type.
3. sexual vs. asexual populations in the world — we find that in general, the asexual populations are rare, and recently evolved compared to the sexual populations. Also, many organisms can reproduce both sexually and asexually — and they do so under different conditions.
4. Sex has a 50% fitness cost compared to asexual reproduction. Assume you start with two populations, each with 100 females. Each female produces two offspring (either two female in the asexual population, or one male and one female in the sexual population), then dies. Look what happens to the population sizes through time:

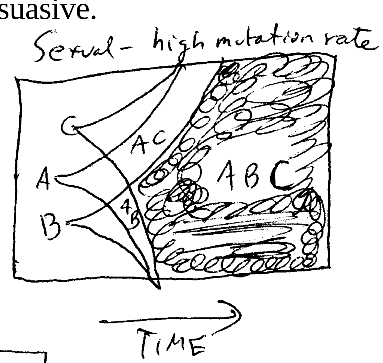
Generations	Asexual Population	Sexual Population
0	100 females, 0 males	100 females, 100 males
1	200 females, 0 males	100 females, 100 males
2	400 females, 0 males	100 females, 100 males
3	800 females, 0 males	100 females, 100 males

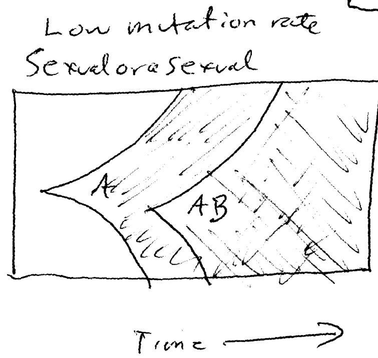
Note that the asexual population rapidly overwhelms the sexual population in size. Thus, it is interesting that there are so few asexual populations, rather than so few sexual populations.

5. Sex has the advantage of recombination, and the standard story is that if there is a reasonably high rate of favorable mutation, sexual populations will incorporate all such mutations in the population faster than an asexual

population will. This is essentially a "group selection" argument for the existence of sex, and is not very persuasive.







6. The individual selection argument for sex: if we look at species that **can** reproduce both asexually and sexually, we find that they generally **do** both, but under different circumstances. Generally, when the offspring are going to be near the parent, the offspring are produced asexually; when the offspring are going to be far from the parent, they are produced sexually. Consider aphids and strawberries. Both reproduce asexually (strawberries produce runners and aphids produce wingless offspring) to establish clones near the parent. Since environments don't usually change much over short distances, and the parent is obviously surviving where she is, it makes sense not to change the genotype of offspring who will share the same environment. However, when offspring are going to be in different environments, a parent will have more surviving offspring by producing a variety of genotypes to strew over a variety of possible environments — and at least one is likely to survive even if the parental environment doesn't exist elsewhere.
7. Coevolution of hosts and parasites. One way to escape parasitism is to change your genotype rapidly enough to keep one step ahead of your parasite's genotype change. This can only be done by sexual populations, since mutation is too slow a mechanism.
8. Sib competition — if there is sibling competition, such that the more similar genotypes are in the most intense competition, sending a bunch of clones into the world practically guarantees that most of them will fail due to competition. Sending out a variety of genotypes lessens such competition.
9. There is apparently no single overwhelming reason why sex is adaptive, but rather a variety of reasons.

E. Why do the sexes differ?

1. It basically all comes down to the difference in gamete size that defines the sexes. The sex producing many small gametes will have the highest reproduction by having the most fertilizations, because each small gamete costs (in energy terms) very little to produce. The sex producing the large gametes has a limited supply of them — each is a heavy investment to begin with, and the way to have the most surviving offspring is to make sure each gamete has the best possible start in life. Thus, males tend to mate indiscriminately, because the more matings, the more offspring. Females tend to mate with much more discretion, choosing only the "best" males so as to give their offspring the best other set of genes.
2. Sexual selection: acts by male competition and by female choice.
   a. males compete for females in a variety of ways — they may physically compete, in which case males tend to be bigger and stronger than females. Males may also compete with various types of displays to prove to females which male is better.
   b. females may choose males which would seem to have reduced fitness — longer tail feathers for instance,. An example is the peacock's tail — the tail makes it more difficult for a male to escape predation, but any male that has such a tail and can still escape predation must be a pretty good male, and thus a good choice for the female. This is the "handicap" theory of female choice. The other main theory of female choice is the "Sexy son" theory — females choose males on some overall "attractiveness" criterion, so that their sons will also be attractive to females.

F. Why is there a 50:50 sex ratio (usually)? The basic reason is that each individual has one father and one mother. If the population contained, say, 75% females and 25% males, each male would get to mate with three females, and thus produce three times as many offspring as each female. There would be selection to produce more sons, since each son would produce three times as many grandchildren as each daughter.

G. What about exceptions to the 50:50 sex ratio? In polygynous breeding systems, with female hierarchies, the offspring of the dominant females get better food and care, and on average grow up to be more dominant animals. Thus, it is advantageous for a high-ranking female to produce more sons, since they will have a better-than-average chance to become a dominant breeding male.

III. Units of Selection — there are arguments about the level at which selection occurs: gene, organism, group

A. selection at the gene level: *SD* and *sr*: these benefit one allele at the expense of another, or one sex at the expense of another. Other alleles can hitchhike if there are inversions, such as in *sr*. These are rare cases of "outlaw alleles", and they will either become fixed, or there will be suppressers of them because they treat other alleles unfairly. However, what about normal alleles? They are what really are the permanent things that change, and, of course, the organisms possessing them show the changes.

B. selection in cell lines: in many organisms, germ lines are not set aside early, and those cell lines that reproduce the most and fastest will increase in frequency.

C. selection on the organismal level — by far the most common level (probably), and the effects are obvious. Features which allow an individual to reproduce more and faster will be passed on in greater proportions.

D. Kin selection: especially in haplodiploid species. Also can be if nonreproductives help their kin, who share their genes, to produce more offspring, which share the same genes. If you reproduce, or help you parents to have two more offspring (each of which, on average, shares 1/2 of your genes) the effect for the genes you carry is the same.

E. classical group selection: can a trait which is good for the group, but bad for the individual, ever increase in frequency. "If trait X is good for the species, it will increase in frequency." Take a species with many groups, some which are homozygous "A" for altruistic, and some homozygous "S" for selfish. Limited food, some groups starve due to lack of food if no reproductive restraint. Depends on rate of group extinction. Selfish individuals can infect altruistic groups and will take over within the group.

F. IN GENERAL, selection operates to produce adaptations at those levels which show heritability. If a lion learns a new trick to hunt, it will have more kids, but the kids will not themselves have more kids unless there is heritability for the new trick. So, at its most basic, :

G. In general, genes are the unit of selection because they show the most heritability. ANY ADAPTATION EXISTS BECAUSE IT INCREASES THE REPRODUCTION OF THE GENES ENCODING IT.

H. Selection works on genes; other levels of organization show adaptations that propagate the genes most efficiently.

IV. Adaptive Explanation

A. We must distinguish current function from adaptive reason for existing when looking at traits.

B. time lags may cause imperfect adaptation — fruits dispersed by the American megafauna, dodos. etc.

C. genetic constraints may cause imperfect adaptation. If the heterozygote is best, homozygotes MUST be produced by meiosis and fertilization.

D. developmental constraints: allometric rules. The size of a body part may be a simple mathematical function of the size of another body part, and not be subject to much independent selection. If the length of the horn of antelope is always the length of the tail squared, then an antelope with a double long tail will automatically have horns 4 times as long. Selection on tail length produces an effect on horn length, but it is tail length, not horn length, that is selected. There may be a single common growth mechanism operating.

E. Historical constraint. If a population is stranded on a local adaptive peak, it may not be able to get off and climb the higher peak some distance away. Recurrent laryngeal nerve. In fish, went straight from brain to a gill arch. In mammals, it goes from brain, to heart, and then back to larynx — in giraffes this is some distance. Why? because as the fish circulatory system transformed into the mammalian one, the nerve stayed in the same relative place, which is now down by the heart.

F. Adaptations can be recognized as characters that are too well fitted to their environment for the fit to have arisen by chance. But there is still room to argue about what is "too well fitted".