Outline of lectures 12-14

1. **Group selection and kin selection.** How can we account for the evolution of characters that involve "altruism", in which an individual has a phenotype (such as a behavior) that lowers its own individual fitness but raises the fitness of others? One would think that any allele predisposing the individual to this behavior would be eliminated from the population. The explanation for this, which involves important parts of the evolution of social behavior, was at first given in terms of *group selection*. But with the discovery of *kin selection*, this has changed.

2. Group selection is the change of gene frequencies in a species due to the extinctions (and reappearances) of local populations. If the local populations have different frequencies of the allele, and if a high frequency of one allele gives a population an average property that happens to make it less likely to go extinct, then this can create a change in gene frequency in the species. In cases where there is ordinary selection (*individual selection*) against the allele within the population, group selection can be a countervailing force to the individual selection.

3. In the case of an altruistic behavior, individual selection is gradually reducing the frequency of allele in each population. But the extinction of those populations that have fewer copies of this allele can increase the overall frequency of the allele in the species. Can this be a strong enough force to cause the allele to increase to fixation?

4. Note that for this to work, there must be

   - Genetic differentiation between the populations (by forces such as genetic drift), and

   - a frequent enough occurrence of extinction of local populations, in a way that is affected by the frequency of this allele, so that the populations that have the lowest frequency of that allele are more likely to go extinct.

5. Before 1964, this was used to explain how altruistic behaviors could evolve. The argument was that, the more frequent these behaviors were, the more they reduced the probability of extinction of the whole population.

6. It is because of the difficulty of believing in the second condition (frequent enough extinction) in many cases that many evolutionary biologists are skeptical of the power of group selection. They think that it does occur but is not likely to be a very important evolutionary force. The problem is that individuals die every generation but populations die much less often. This means that it is hard for group selection to be a more important evolutionary force than individual selection. Group selection can occur, but whether it a major evolutionary force is doubtful.

7. The pioneer of theoretical population genetics J. B. S. Haldane is said to once have been asked whether he would lay down his life for his brother. He replied "No, but I would for two brothers or 8 first cousins". (In fact, Haldane didn't have a brother; his sister, the novelist Naomi Mitchison, outlived him and produced children who were well-known biologists – one son was the cell biologist Norman Mitchison and her grandson is the computational molecular biologist Graeme Mitchison). We shall see that, in genetic terms if not in ethical terms, this joke was exactly correct.

8. In 1964, William D. Hamilton published two papers on the theory of *kin selection*. In this scenario, the beneficiaries of the altruistic act are, on average, relatives of the altruist. Hamilton showed that an altruistic behavior can be favored if

$$c \ < \ r\,b$$

where c is the cost to the altruist in fitness terms, b is the benefit (summed over all recipients, and calculated in change of fitness), and r is a coefficient of relatedness between the altruist and the average recipient. The allele that predisposes toward the altruistic act will increase in frequency if this condition holds..

9. The formula comes from a bookkeeping of the number of copies of the allele. The easiest way to see this is to consider an allele which is rare, and whose presence in one copy makes the altruistic behavior more likely.

10. Kin selection works if, for every copy that is eliminated by selection against the altruist, more than one copy in the relatives is saved, for a net increase in the number of copies of the allele in the population.

11. Another way to think about this is the "personal fitness" approach, which asks what the effect of the allele is on the individual carrying it. Since the allele occurs both in altruists and in some recipients, its effect is that (1) you are more likely than others to perform the altruistic act, but (2) you are also more likely to be surrounded by individuals performing altruistic acts toward you. inclusive fitness in effect computes the net effect of these two.

12. The coefficient of relatedness r is the probability that a copy of a rare allele that is found in you is also found in a given relative. For full sibs it is $\frac{1}{2}$, for parents $\frac{1}{2}$, for offspring $\frac{1}{2}$, for half sibs $\frac{1}{4}$, for aunts and nephews $\frac{1}{4}$, and for first cousins $\frac{1}{8}$. (Now consider Haldane's joke).

13. Thus, for example if the altruistic act reduces your fitness by 0.1, but increases the fitness of 10 of your neighbors by 0.05 each, a gene that makes this act more likely can increase, provided that your neighbors are on average related to you by more than $r = 0.2$. That is because $c = 0.1$, $b = 10 \times 0.05 = 0.5$, so if $0.10 < r(0.5)$ then $r > 0.2$.

14. An exactly equivalent way is to think of the allele as affecting "inclusive fitness" (Hamilton's term). It counts your fitness, if you are a bearer of the allele, plus the effects on fitnesses of your relatives, where we weight each one that is affected by its coefficient of relatedness.

15. Note that

    - The gene need not have an absolute effect on the behavior – it could just make it a bit more likely.

    - It need not be a gene that specifically causes a behavior. It could do something else such as make you able to hear better, as long as that something makes the altruistic act more likely.

    - There is no requirement that the altruist know who is their relative, or go around trying to calculate coefficients of relatedness. The altruism could simply be toward the neighbors, who happen to be on average related. (This point is misunderstood by lots of people).

16. Kin selection was widely popularized by E. O. Wilson in his book *Sociobiology: The New Synthesis*. It has been enormously successful in explaining the evolution of social behaviors in animals, plants, and even protists such as slime molds (which aggregate into fruiting bodies, with some cells making up the stalk and capsule but not becoming dispersed as spores).

17. We will consider in class one case, the presence of nest helpers in the Florida Scrub Jay *Aphelocoma coerulescens*. Young scrub jays often stay in the family group for several years, helping bring food to the youg (who are their full sibs since these scrub jays mate for life), and helping defend the nest. It is estimated that a nest that has helpers has on average 1.45 offspring raised per year, while a nest without helpers has only 0.5 offspring raised per year. Does this case satisfy Hamilton's equation? Keep in mind how this behavior affects the count of copies of a rare allele that makes nest helping behavior more likely.

18. Although I have given the argument as if it applies only to alleles when they are rare, it actually works for them when they are common too.

19. In fact, group selection too can be analyzed using Hamilton's equation. The cost is the same, and the benefit can be calculated as the savings in fitness owing to protection of the other individuals in the population by making extinction of the whole population less likely. Group selection requires genetic differences to exist between populations, and that is most easily explained by genetic drift. This causes individuals in the same population to be related. So we have c, b, and r as in kin selection. The condition for an altruistic trait to increase by group selection is the same ($c < rb$) as in kin selection. The difficulty with group selection is that extinction of whole populations may often be so rare that b is not large enough.

20. But for human behaviors and changes in human behaviors, it is important to realize that they do not necessarily arise only by kin selection favoring genetic variation. We do not rely solely on genetic change – there is a massive apparatus of cultural inheritance that transmits information between individuals nongenetically (schools, governments, churches, neighbors, me making you read these notes). Human society also changes so rapidly that genetic change cannot be involved (even with large

selection coefficients of 0.1 or so, genes take tens of generations to change substantially in frequency, and that is hundreds of years. For more realistically weaker selection we are talking in terms of thousands of years). So the rise and fall of (say) the hula hoop or the bicameral legislature is not well explained as a genetic change. Most likely, the French do *not* speak French because they have alleles that predispose them to speak it, while Germans have alternative alleles that predispose them to speak German.

21. In Hymenoptera (ants, bees and wasps) there are multiple occurrences of insect societies. An important predisposing factor is that they are haplo-diploid. Males are haploid, females diploid. In a hive which has one queen and one drone (male), worker females are actually more closely related to their siblings, whom they help raise, than they would be to their own offspring if they flew off to mate outside the hive ($r = 0.75$ instead of 0.5). Termites, however, are "normal" (ordinary diploids) so this does not work as well there.

22. A calculation of the fitness of an allele that predisposes a worker bee to "defect" (some are fertile) is complicated, and involves knowing how much it increases its mother's number of offspring by staying, and how likely it is to successfully find a mate and found a hive if it goes.

23. **Punctuated Equilibrium, Species Selection, and the Shifting Balance Theory** In 1972, Stephen Jay Gould and Niles Eldredge argued that the pattern of evolutionary change seen in the fossil record was not one of gradual change, but was a pattern of stasis with occasional rapid changes. They used the term *punctuated equilibrium* for this pattern of stasis punctuated by occasional shifts to a new equilibrium:

    N. Eldredge and S.J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism, pp. 82-115 in *Models in Paleobiology,* ed. T. J. M. Schopf. Freeman, Cooper, San Francisco.

24. This led to a substantial controversy, particularly because of later papers in which Gould, Eldredge and Steven Stanley argued that the punctuated equilibrium pattern necessitated a different evolutionary process. They argued that large populations show stasis because they rest on a peak of an adaptive surface, which does not change much. They invoked an earlier model of Ernst Mayr in which these large species are continually budding off small peripheral species. A few of these find newer and higher peaks on the adaptive surface. Being separate species, they can then displace the parent species. The result is punctuated change.

25. This puts the natural selection mostly at the between-species level. It is not group selection but *species selection.* Species differ in their ability to resist extinction, and in their ability to form more species. This is very much like individual selection, except that the "individuals" are species. The variability among species originates in random changes, by a combination of random genetic drift (finding new peaks of the adaptive surface) and natural selection (climbing those peaks) as the new peripheral species

originate. Selection then also chooses among the results. In this view of evolutionary change, natural selection within species is mostly doing nothing, and mutation, while the ultimate source of variation, is not the source of differences between species (as those arise from genetic drift and selection on a multi-peak adaptive surface).

26. To understand these arguments, it is important to separate the argument about *pattern* from the argument about *process*. Much of the debate over punctuated equilibrium has confounded the two issues. People see a non-gradualist pattern and jump to the conclusion that species selection must be the mechanism. The issues are (mostly) separate.

27. Empirical studies in the fossil record have given mixed results, although quite a few paleontologists are convinced punctuationists. Studies with fossil protists such as foraminifera show neither punctuation nor gradualism but a pattern that is a bit of both. Other fossils are harder to study in the detail that foraminifera are: some paleontologists argue that they show widespread validity of punctuation.

28. A major difficulty in the examination of the fossil record is that resolution is poor. Often adjacent data points in a time scale are 50,000 years apart. There are exceptions such as layered sediments where spring floods lead to yearly layers. These have attracted some attention. In addition, to see the full proposed pattern of peripheral speciation, we'd have to have simultaneous observations at many places.

29. About the worst organism to study evolutionary processes on is *Tyrannosaurus rex*. There are not enough of them (less than 20, last I heard) to get a statistical sample that allows us to follow change through time. It's much easier to get a sample of forams, or clams, or small mammals, or some fishes. There are many of these around, but they tend not to star in television documentaries, or inspire kids to become paleontologists.

30. The perfectly linear, smooth gradualist pattern that punctuated equilibrium theory argued against is a bit of a caricature, though one that was often invoked in the period after the Modern Synthesis. But the zoologists and botanists who established the that theory included some who did in fact discuss stasis punctuated by rapid change. In particular Ernst Mayr and George Gaylord Simpson, back in the 1940s, discussed scenarios which involved punctuated patterns of change.

31. Is species selection part of the Modern Synthesis? This is a matter of debate. It *is* natural selection, just at a different level. The issue for debate is whether attributing most of the change to species selection is a sufficient shift to merit renaming the theory. It is certainly true that the Modern Synthesis emphasized selection at the individual level and was skeptical of mechanisms such as group selection.

32. Even if species selection were considered to require us to rename the theory and declare the old theory dead, both theories use the same force – natural selection – as the explanation for adaptations. It is just a matter of at what level the natural selection acts.

33. The reasons for being skeptical of species selection are the same as those of being skeptical of group selection: is the mortality of species fast enough to make species selection a forceful enough player?

34. Are there individual selection mechanisms that can achieve a punctuated pattern? Yes. For one, observations 50,000 years apart may make even rather smooth change look punctuated. The origin of dog breeds by artificial selection would look instantaneous if we observed at an interval of even 10,000 years. There are also mechanisms in which an adaptive surface slowly changes shape and a peak subsides while a new one nearby rises. When the first peak becomes low enough, the species will depart for the second, and do so fast enough that in the fossil record this will appear as punctuated change.

35. Sewall Wright in 1932 put forward his *shifting balance theory* in which species are viewed as divided into small populations which have migration between them. Genetic drift can allow one of these populations to climb down off of a peak and reach the bottom of a valley. At that point natural selection may pull it up a nearby, and higher peak. By export of migrants from this new, improved population, its neighbors are drawn towards that peak, and process continues until all populations are converted (it is important to realize that the peaks exist in phenotype space, and may or may not be geographically separated). Wright felt that this was a mechanism that was plausible and allowed species to evolve on a complicated adaptive surface, finding new peaks.

36. The conditions for the shifting balance theory to work are delicate, and may require just the right mix of migration, population size, and shape of the adaptive surface. There is the issue of whether they are met often enough to make it an important scenario. The fact that the theory involves an interaction of multiple evolutionary forces means that it could not be investigated well until the advent of computer simulation.

37. Owing in part to Stephen Jay Gould's prowess as a scientific popularizer, a decade or two ago much of the public became convinced that a new, sexy theory of evolution has replaced the stuffy, boring old one. (They would be less able to tell you what the new theory actually is). Many Paleontologists and some systematists tend to be punctuationists, with exceptions. Evolutionary geneticists, who focus on the mechanisms, tend to be gradualists. For moment the stalemate continues, but more quantitative examination of the fossil record is coming, as is more quantitative consideration of the shapes of multi-species phylogenies. Stay tuned.