Genetics 453
Evolutionary Genetics

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Outline of lectures 11-13

1. **Group selection and kin selection.** How can we account for the evolution of characters which 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, used to be given in terms of *group selection.*

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 the allele makes a population less likely to go extinct, then this can create a countervailing force to the individual selection. 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 increases the overall frequency of the allele in the species.

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

   - Genetic differentiation between the populations (by forces such as genetic drift)
   - A frequent enough occurrence of extinction of local populations, in a way that is affected by the frequency of this allele.

   It is because of the difficulty of believing in the second condition 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. 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.

4. 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, and his sister, the novelist Naomi Mitchison, outlived him – 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.

5. 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 if

   $$c < rb$$

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

6. It does so because, 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.
7. Another way to think about this is the "personal fitness" approach, which asks what the effect of the allele is. Since the allele occurs both in altruist and in recipient, 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. Hamilton's condition in effect asks the net effect of these two.
8. The coefficient of relatedness r is the probability that a gene copy 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).
9. 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 $r = 0.2$ or more.
10. 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 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.
11. Kin selection 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).
12. 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, which 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.

13. For human behaviors and changes in human behaviors, it is important to realize that 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 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.

14. 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 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.

15. **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.

16. This has 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 a 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.

17. This puts the natural selection at the between-species level. It is *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 as the new peripheral species originate. The selection 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).

18. 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.
19. Empirical studies in the fossil record have given mixed results, although many 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.
20. 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.
21. The perfectly linear, smooth gradualist pattern that punctuated equilibrium theory argued against is a bit of a caricature, though one that neo-Darwinians did perpetrate widely. The zoologists and botanists who established the neo-Darwinian theory included some who in fact did 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.
22. Is species selection part of the neo-Darwinian theory? 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 neo-Darwinian Synthesis emphasized selection at the individual level and was skeptical of mechanisms such as group selection.
23. 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?
24. 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.
25. 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, are are not 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.

26. 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.

27. Owing to Stephen Jay Gould's prowess as a scientific popularizer, most of the public is convinced that a new, sexy theory of evolution has replaced the stuffy, boring old neo-Darwinian one. (They would be less able to tell you what the new theory is). Paleontologists and many 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.