BIO 45 – Lect. 3-3 - The Costs and Benefits of Being Social

I. Why Live In Groups? -- See Alcock Chs. 14 For Details

A. Kinds Of Groups: Think about groups with different combinations of the following attributes:

1. **Size and composition** - 2 to many, one sex or mixed sexes, and one age or all ages
2. **Permanence** - momentary aggregations, seasonal, or permanent
3. **Structure or organization** - accidental aggregation, structured (by size, sex, age), or organized (hierarchies, castes..)
4. **Relatedness** - random, extended families, family, clone...

How do differences affect what happens - interactions, degree of cooperation or competition, and coordination of interactions?

B. Costs and Benefits of Living in Groups- see Alcock for similar list and details

1. **Disadvantages**
   - increased competition for mates, food, and shelter
   - increased chance of disease or parasitism
   - increased chance of. inbreeding, crowding and stress, exploitation, infanticide and altruism
   - increased attraction of predators
2. **Advantages**
   - increased protection from predation - cooperative or not
   - help in finding or catching food
   - defense of resources from others
   - cooperation in care of young
   - increased protection against infanticide or harassment by males
   - modification of environment (nests, dams, V's of geese)

II. Group Dynamics – cooperative organization or selfish herd?

III. Altruism - The "Big" Problem With Being Social

A) Problem: Altruism is sacrificing some or all of one's own fitness to increase that of others. Any genetic tendency towards altruism should soon disappear since altruistic individuals will be less fit than those they help. Yet we often see cooperative, aid giving behavior in nature -- why?

B) Partial Solution: What looks like altruism may not really be altruism. Helping behavior can be reproductively selfish. For example, in ostriches one female takes care of her eggs and those of other females. She isn't really helping the others since she uses their eggs to protect hers. It is important to distinguish between apparent (phenotypic) altruism and real (genotypic) altruism:

- Phenotypic altruism = **helping** = aid giving behavior that directly benefits the donor's own survival and reproduction. This would include things like parental care and reciprocation.
- Genotypic altruism = **altruism** = aid giving behavior at a cost to a donor's immediate fitness.

IV. Can An Altruism "Allele" Be Spread Via Natural Selection?

The problem: When an altruism allele is rare, a new mutation in the population, it will tend to help other alleles and not itself. It can only spread if bearers of the allele aid only others who also carry the same allele. Altruism could theoretically evolve if it could overcome this problem.

A) One solution (called the 'green beard' effect) is to have the 'altruist gene' linked to a phenotypic trait so that altruists can recognize each other. If altruists only aid altruists, then the altruism allele could increase in the population. What is the problem with this approach to evolving altruism?

B) A second solution is to have altruism evolve by group selection. Those social groups with widespread altruism might survive and reproduce better than groups without it. Members of 'altruist groups' could then colonize areas where 'selfish groups' have gone extinct and altruism would spread. There are several models for the evolution of altruism by group selection. However, they would over-ride the loss of the trait due to individual selection. Note, this is not the same as "good for the group" or "good for the species" thinking. It is a model of selection at the level of groups with some strict requirements.

C. A third solution is due to W.D. Hamilton (1964). What if bearers of the altruist allele only help close relatives? The allele could spread by helping close relatives because they are the most likely to share copies of a new mutant. This is the basic idea behind inclusive fitness and Hamilton's rule. It sounds like the first solution but with two interesting twists. First, recognition of close relatives should not be easily invaded by deception. Second, by extending an individual's fitness to include helping copies of its own alleles which are in the bodies of others, genotypic altruism becomes reproductive selfishness!

V. What is inclusive fitness? What did Hamilton say? How does Alcock describe it?

Let's start with what Hamilton did in 1964 and 1972. His concern was how a rare altruism allele might be able to spread in a population. He felt that since close relatives were most likely to bear copies of the same allele, helping relatives would solve the problem (see IV. C. above). He went through a lot of population genetics modeling to show that he was correct. He then derived a cost-benefit rule of thumb that could be used to figure out when selection would favor helping. He found that, with some assumptions, his simple rule of accounting for fitness by tracking phenotypes gave basically the same answer as the more complex models that tracked the spread of alleles in a population.

The only way his rule of thumb will work is if we do the fitness accounting correctly. We are comparing the average, relative fitness of helpers and non-helpers. Thus we cannot count the same offspring for the fitness of more than one individual. That means we have to divide up offspring (conceptually) and assign the parts to the fitness of those responsible for the parts. Sounds gruesome, but it works. Another way to say this is that we have switched to looking at the fitness of individuals based on the fitness of the alleles they carry. Thus copies of the allele in the next generation have to be assigned to the individuals who made it possible for them to get there.

Alcock (following Brown) calls inclusive fitness the sum of direct and indirect fitness. Alcock does the inclusive fitness accounting by tracking a parent's alleles (pp. 435-437). When calculating direct fitness (figure 15) he discounts the number of kids an individual has (N_1 and N_2) by **r.** Here **r** = 0.5 -- the chance any kid has a particular allele that the parent has. He also does this discounting for indirect fitness (Fig. 15). Remember he is tracking the fitness of alleles. The kids of a helped relative result in N_3 x "r" copies of the helper's allele. The "r" is A's relationship to B's kids. There are two relationships involved: 1) A's relatedness to B, and 2) B's relatedness to its kids (=0.5). B's relatedness to its kids (0.5) has to be the same as A to its kids (= 0.5). Of course this assumes that they really are their kids (if not, r = 0). So, what's the problem? Not much really, we just don't need the 0.5s.

Hamilton and most behavioral ecologists use "r" as the relatedness between A and the relative (B) whose reproduction is being helped -- not B's kids. Thus we ignore the extra parent-offspring "0.5"s. The two accounting methods will give the same answer to the question "should A help B?" because the only thing that changes due to A's help are the number of kids B has.

Let me say the last two paragraphs in another way: Alcock's inclusive fitness formula (Figure 15 is: $(N_1 \times r) + (N_2 \times r) + N_3 \times r$. His equation really is: $(N_1 \times 0.5) + (N_2 \times 0.5) + N_3 \times (0.5 \times r)$. Hamilton and I are interested in the relatedness to helped relatives. We remove all of the parent-offspring 0.5s to get: $N_1 + N_2 + N_3 \times r$.

But there is another problem. Alcock doesn't clearly show where to subtract any of the helper's offspring that were due to help received from others. He notes that this must be done (p.435, …"that owe their existence to the parent's actions, not to the efforts of others") but the equations in Fig. 15 do not clearly show it. Why does he have to do that? We are asking, "Can helping be adaptive and spread in a population?" Thus we compare the fitness of helpers and non-helpers (in order to see if the helping allele can spread). To do that accurately, we have to make sure that we don't give a helper credit for offspring it could not have had without help. Thus we have to subtract any offspring that A would not have had without the help of others from A's direct fitness. We will replace Alcock's formula with:

Inclusive fitness = Direct fitness, **minus** any due to help from others, **plus** any Indirect fitness of relatives **due to your actions**, **adjusted by** your relatedness to them.

$$\textbf{Inclusive fitness} = [N_1 + N_2 - N_4] + [N_3 \times r]$$

where N_4 = number of your offspring due to help of others. r = your relatedness to your relative.