TAWP LECTURES:
THE MANY FACETS OF ALTRUISM

Day 2, January 20th, 2011

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Agenda

- The History of Group Selection
- Reciprocal Altruism
- Inclusive Fitness Theory
- Multi-Level Selection Theory

Darwin in the Origin

...we can perhaps understand how it is that the use of the sting should so often cause the insects own death: for if on the whole the power of stinging be useful to the community, it will fulfil all the requirements of natural selection, though it may cause the death of some few members (pg 202)

How the workers have been rendered sterile is a difficulty... for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being affected by natural selection (pg. 236)

Darwin in The Descent of Man

Finally, the social instincts which no doubt were acquired by man, as by the lower animals, for the good of the community, will from the first have given him some wish to aid his fellows, and some feeling of sympathy (pg 103)

Darwin in The Descent of Man

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and in increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection.

(Darwin 1871, 166)

The History of Group Selection

The probability of survival of individual living things, or of populations, increases with the degree with which they harmoniously adjust themselves to each other and to their environment. This principle is basic to the concept of the balance of nature, orders the subject matter of ecology and evolution, underlies organismic and developmental biology, and is the foundation for all sociology.

Allee et al. (1946) The Principles of Animal Ecology

The History of Group Selection

- From Darwin through the 1960's, group selection was commonly invoked to explain altruistic behaviors. No special explanation was needed.

- But in 1966 George C. Williams published Adaptation and Natural Selection which was very popular and very harsh on group selection. Group selection was basically never invoked after this.

The History of Group Selection

- The obvious problems were that you need competition between groups for a process of group selection (like in Darwin's morality case). But lots of 'for the good of the species' reasoning didn't seem to have the right group structure.

- More importantly, there is a serious problem of 'subversion from within'. While altruistic individuals do help the groups they are in, within those groups, selfish individuals will be relatively more fit and so selfishness will spread in that group and in fact, in every group.

Apparent altruism in nature

--Meerkat sentinel behavior--

How could altruism evolve

- It is just a fact that lots of organisms (across all taxa - animals, plants, bacteria) exhibit behavioral traits that are apparently altruistic. How can this be explained?

- Strategy 1: they aren't really altruistic. Perhaps alarm calls confuse predators rather than draw attention to the caller.

- Strategy 2: they aren't really altruistic. 'Altruistic' behaviors now (like food sharing) lead to being on the receiving end in the future. So lifetime fitness is enhanced.

    - Obviously neither is helpful in cases like sterile insect castes or cellular smile molds.

Reciprocal Altruism

- Robert Trivers first carefully analyzed the conditions under which apparently altruistic behavior could be explained by positing that such behaviors are in the long-run interest of the altruist.

- Instructive cases include grouper fish who don't eat cleaner fish. They expect to have many future interactions with the cleaner.

- The iterated prisoner's dilemma is a useful example to think about.

Prisoner's Dilemmas?

- Arms race - this assumes you are better off with more weapons than the opponent, but worse off absolutely with more weapons.
- Paying taxes - this assumes that there is no possibility of being punished for not paying.
- Closed bag exchange

Prisoner's Dilemma

- In the one-shot prisoner's dilemma, defecting is rational.
- In biological 'games' that have this structure where the payoffs represent fitness, it would seem impossible for anything but the defect strategy to evolve. For example, if you were sure you will never meet this cleaner fish again, you are better off eating it.
- But if we think of an organism's whole lifetime as the game, it may be that cooperating can be part of a good strategy since it might lead you to being on the receiving end of cooperation in the future.

Tit for Tat

- The basic structure of an iterated prisoner's dilemma is that the players player some number of prisoner's dilemmas. Their strategies can depend on the past behavior of the other player.
- Tit for Tat is the strategy that plays 'cooperate' first then plays what the other player did on the previous move.
- TFT does better against TFT that AllD does against TFT.

TIT FOR TAT AND RECIPROCAL ALTRUISM

- TFT and other strategies in the iterated prisoner's dilemma and other games are examples of behaviors that appear temporarily altruistic (sacrificing short term gains) but aren't altruistic from the long run prospective.

- These kinds of behaviors can evolve by natural selection (though actually there are really tricky dynamics involved). Importantly, unconditional cooperation can (sometimes) evolve too for similar reasons.

Evolutionarily Stable Strategies

- An evolutionarily stable strategy is one that if popular, can't be invaded by mutants.
    - S is an ESS iff: For all other strategies T, either

1) $E(S,S) > E(T,S)$ or

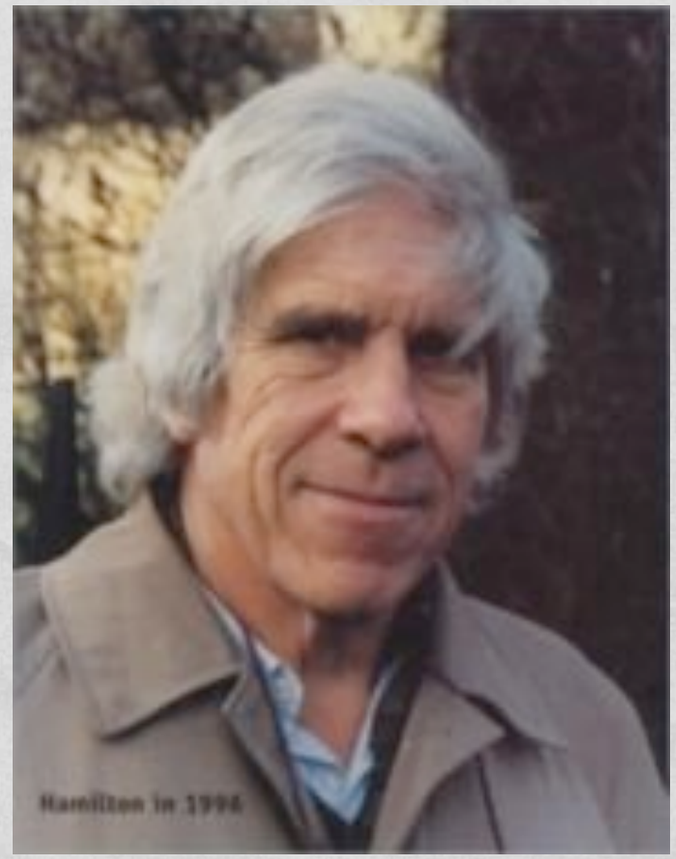
2) $E(S,S) = E(T,S)$ and $E(S,T) > E(T,T)$

- Tit For Tat is evolutionarily stable under some conditions (All D is always stable). Other evolutionary considerations favor it over always defect.

Kin Selection

- But there are clear cases of altruistic behavior that can't be explained by reciprocation (like sacrificing your life or sterility). Same for sentinel behavior which affects everyone.

Here, W. D. Hamilton (1963/4) pointed out that such behaviors can evolve by benefiting close relatives.

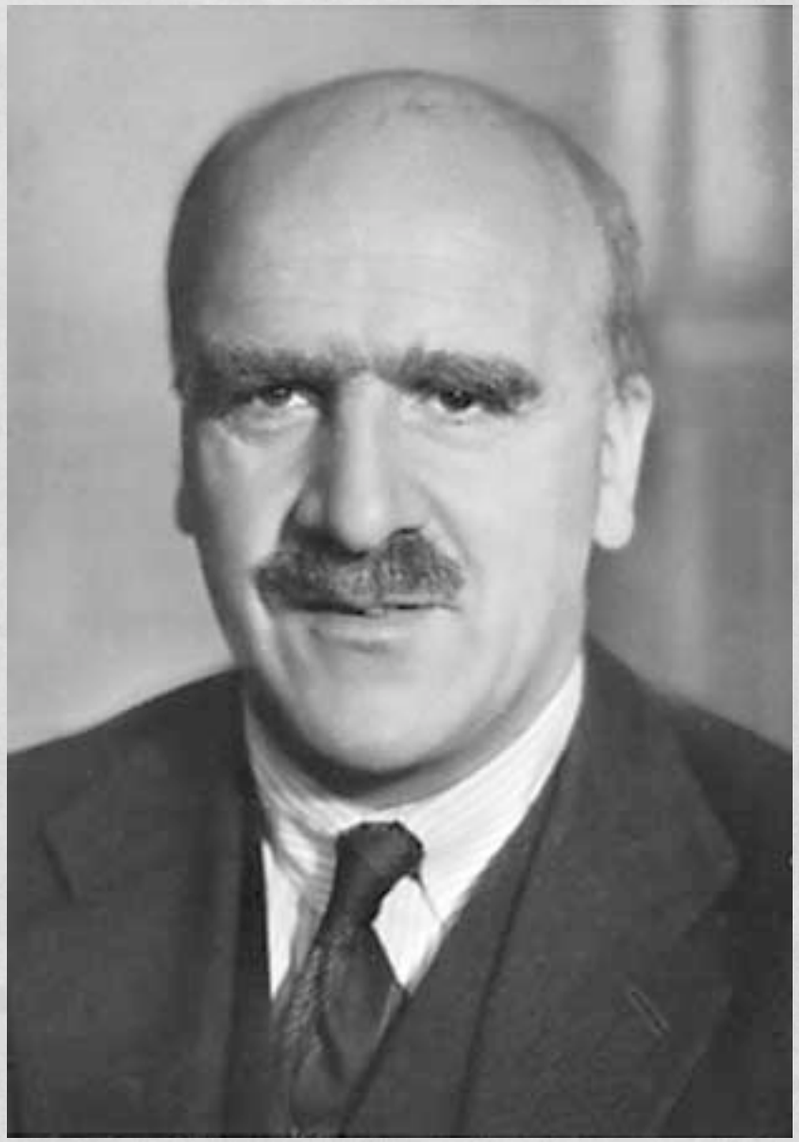


Hamilton's Rule

- Lets call 'c' the cost in direct fitness to the actor and 'b' the benefit to the recipient of the behavior.
- The benefit to the recipient, weighted by the 'coefficient of relatedness' (r) represents the benefit to the actor's genes.
- So a behavior will evolve if r x b > c
  - This is called Hamilton's Rule

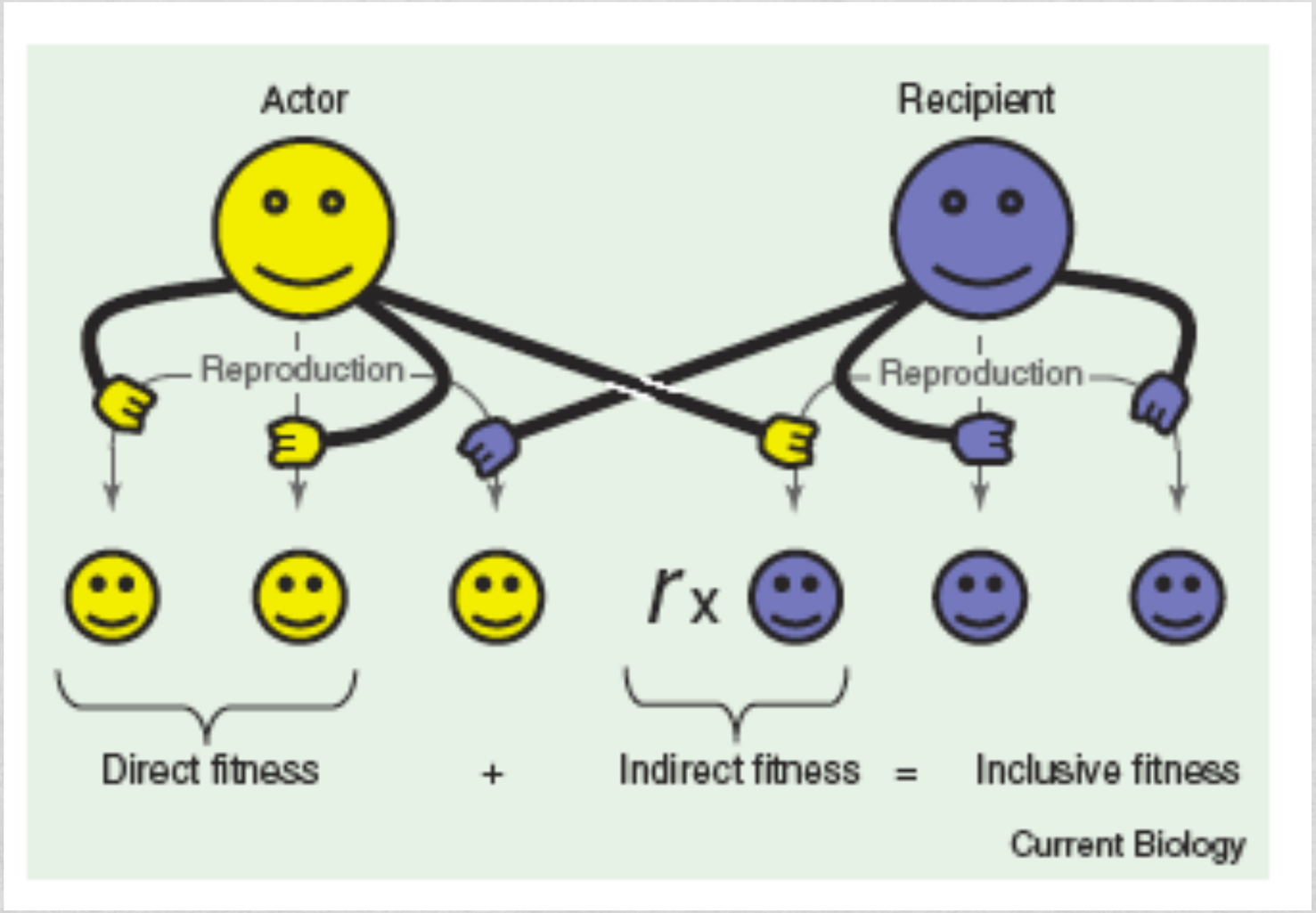
Hamilton's Rule

J.B.S. Haldane once quipped "I would gladly lay down my life for two brothers or eight cousins".



Inclusive Fitness

The correct version of natural selection is thus 'traits will evolve that maximize a gene's inclusive fitness'.



Altruism Requires Correlation

- Actually, calling r the 'coefficient of relatedness' or describing it as 'the percent of genes identical by descent' is a mistake.
  - For any pair of humans more than 99% of their genes are 'identical by descent'
  - And what matters for r is not genealogical relatedness, but the correlation of altruistic pairs.

Altruism Requires Correlation

- If altruists are equally likely to meet other altruists or other selfish players, the altruistic gene will not evolve.
- But if there is a correlation, altruism can evolve depending on the details.
  - Genealogy is one obvious way to get correlations.
  - Also, for dispersal reasons, alarm calls, food sharing, etc. is just more likely to help kin in most cases.

Simpson's Paradox

- The problem of subversion from within still seems to threaten altruism.
- For any single interaction, altruism does worse then selfishness would. Within any group, selfishness does better than altruism.
- But it can still be true that averaged across groups altruism can do better.

Berkeley Discrimination Case

- In 1973, Women had a lower acceptance rate into graduate school then men did across the university.
- An investigation was done to see if there was significant gender bias and it was found than in no departments were woman worse off (significantly). In fact, in many they did significantly better.
- But women tended to apply to departments with higher rejection rates (english and psychology rather than engineering and chemistry)

Simpson's Paradox

In general, Simpson's paradox allows that:

$Pr(E|C \,\&\, B_i) > Pr(E|{\sim}C \,\&\, B_i)$
for every subpopulation B_i

But still, $Pr(E|C) < (\text{or} =) Pr(E|{\sim}C)$
[the average effect of C across backgrounds]

Simpson's Paradox

- All of the following are possible:
  - Drug A cured women more frequently than drug B and cured men more frequently, but did worse overall.
  - Batter A has a higher batting average on grass than B and higher on turf, but worse overall.
  - The percentage of democrats is rising in every single state but declining overall.

Simpson's Paradox and Altruism

- The same happens with the evolution of altruism
  - There are a number of groups which vary with respect to how frequent altruism is in the group.
  - In each group, the frequency of altruists goes down over time.
  - Averaged across groups, the frequency of altruism goes up since altruistic groups grow at a faster rate.

Multi-Level Selection Theory

- Current defenders of group selection (Sober and Wilson, but now increasingly others too) subscribe to "Multi-level selection theory"

- Selection acts simultaneously at many levels. Anytime there is heritable variation in fitness - between genes in an organism, between organisms in a population, between populations in a species, etc. there will be natural selection.

- Altruism is selected against at one level and selected for at another level. If the parameters are right, it will evolve.

Multi-Level Selection Theory

- Calling inclusive fitness effects "multi-level selection" or especially "group selection" is still very controversial.

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The Major Transitions

- It is now common to allow that group selection can be involved in the "major transitions" like moving from asexuality to sexuality, independent replicators to chromosomes and organisms, unicellular to multicellular

- Here, the collection of genes in a chromosome is the group. Genes within the same chromosome now are (usually) not in competition. Similarly, cells in your body (usually) don't compete with each other.

- Some people think of eusociality as a major transition (a colony of ants has a fitness, individual ants are just parts).

Human Sociality as a major transition

- David Sloan Wilson and others have argued (tentatively in some cases) that human sociality could be the result of a major transition as well.

- Perhaps group selection (human groups directly competing with other humans groups) resulted in the 'most social' groups surviving.

For tomorrow

- On day 3, we focus explicitly on humans.
- Humans appear to be behaviorally altruistic quite often -- though much of this behavior can be explained via norms which is sometimes thought to undermine its altruistic nature.
  - Is there a biological explanation for these behaviors such as group selection or cultural selection?
  - Does this shed any light on our question about psychological egoism and motivational altruism?