BIO 45 - Lect. 3 -5 - ALTRUISM AND INCLUSIVE FITNESS

I. ALTRUISM - The "big" Problem with being social

A) Altruism (genotypic altruism) is sacrificing some or all of one's own fitness to increase that of others.

B) <u>Helping (phenotypic altruism)</u> is aid giving behavior that directly benefits the donor's own survival and reproduction

II. What is inclusive fitness?

A. 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.

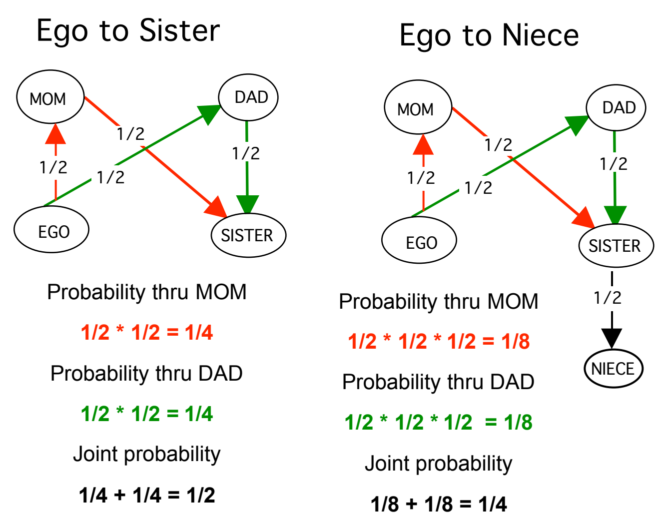
$$\textbf{Inclusive fitness} = [N_1 + N_2 - N_4] + [N_3 \times r]$$

N_1, N_2, and N_3 as defined in Alcock, $\mathbf{N_4}$ = number of your offspring due to help of others. r = your relatedness to your relative.

B. **What is Relatedness?** A lot of confusion about inclusive fitness comes from how one defines relatedness **-"r".** It can have several definitions. <u>Our definition is the probability that two individuals share the same allele through common decent</u>. But why common descent and not actual genes shared?

Obviously you and I share <u>all</u> the genes in the human population that are fixed for one allele. We also share 90% or so of these with chimpanzees! We aren't really interested in these shared genes.

Hamilton's model was asking when a <u>rare</u> altruistic allele could spread in the population. We focus on who else might have a copy of that rare allele. Close relatives are most likely to carry the rare allele at first. That's the definition of relatedness we use = **the coefficient of relatedness**. See figure at right for probability of shared alleles between EGO and sibs in diploid species (we will do haplo-diploid ones later).



III. Inclusive Fitness ==> HAMILTON'S RULE

A) The accounting for inclusive fitness we just went through actually simplifies into a general rule of thumb that we can use to determine whether helping is adaptive in any given situation. What the rule says is: "Since you share genes with both your own offspring and with relatives and their offspring, if you help relatives enough and don't hurt yourself too much in the process, you could gain fitness through helping them produce their kids."

Hamilton's rule is **rb - c > 0.** Here **c** is the **cost** to the giver's fitness (c fewer offspring because of helping), and **b** is the **benefit** to the recipient's fitness (offspring gained by the recipient from the help). Here again, "r" is a measure of the relatedness between giver and the receiver [we no longer tracking alleles like Alcock was and thus do not need to add relatedness of parents to their own young]

IV. Using Hamilton's Rule

Hamilton's rule says that for unrelated individuals (r = 0) no benefit can overcome the cost of loss of the altruist's fitness (0 - c can't be greater than 0) and aid giving is selected against. If the giver and receiver are identical twins (r = 1) then as long as the receiver gains more offspring than the giver loses (b > c) giving will be favored.

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Now consider two full sibs (r = 1/2). Here b/2-c must be greater than 0 in order for selection to favor helping. The gain to a brother or sister must be more than twice the cost in fitness to the giver. The inclusive fitness advantage soon disappears as relatedness decreases. So the point is, helping close relatives may be favored by selection when the costs and benefits balance.

V. Examples of using inclusive fitness reasoning to explain helping.

A) ground squirrel alarm calls - See Alcock for the results of Sherman's study on alarm calling. Sherman didn't actually calculate Hamilton's rule for alarm calling. Instead he reasoned that if alarm calling evolved because of inclusive fitness, then individuals with close relatives should call and ones without close relatives should not.

B) helpers at the nest in birds and mammals. See Alcock for details. We can apply Hamilton's rule to helping if we know the following: 1) how many **more** offspring are raised due to having help (**b**), 2) how many offspring the helpers could have raised by breeding on their own (**c**), and the relatedness (**r**) of helpers to those helped (often their parents). When Hamilton's rule is applied to helping (young remain with parents to help rear siblings) it often shows that the helper's choice is between no chance of reproduction on its own versus some inclusive fitness by staying and helping. In a sense, that would mean c = 0 in Hamilton's rule. The inclusive fitness gain from helping is generally not equal to what the individual's fitness would be if it **could** breed on its own. This points us to ecological and social factors that limit breeding opportunities for young adults - ecology is a large part of behavioral ecology. There are also other reasons for helping besides gaining inclusive fitness. For example, birds usually do better at raising young once they have had experience -- why not practice on siblings before you go it on your own?

C) Sterile workers in the Hymenoptera (ants, bees and wasps) puzzled Darwin. How could selection favor these workers who were sacrificing their own reproduction to help their mother produce new queens and drones? Darwin viewed the workers as a sort of extended individual (workers = external cells of the queen's body). Hamilton's inclusive fitness theory offered a great solution to the problem. He pointed out a neat feature of the biology of Hymenoptera that enhanced the inclusive fitness effect (made Hamilton's rule more likely to work). Males are haploid; they come from unfertilized eggs - and thus they have no fathers. That leads to sisters being 3/4 related (as long as they have the same father). Given that high degree of relatedness it is easy to see why extreme helping by daughters might be more likely in these kinds of insects. Here workers are sacrificing their reproduction to help their sisters reproduce.

Should workers help their brothers? Sisters and brothers have no father in common so r =.25. Therefore we would not expect them to gain much from taking care of brothers - they don't! Instead they try to produce sons of their own (r = 0.5). This they can sometimes do since males are haploid and workers do not need to have mated to produce sons. That brings workers into conflict with the queen over who produces the males -- something we will discuss. Hamilton's theory really got a lot of attention as a result of how well it seemed to fit social insects. The real story is more complex. For example, what happens if queens mate with several males? We now know that they often do. As a way of thinking about aid giving behavior, Hamilton's theory has been very important. It may not , however, explain the social behavior of termites. Why? Look for alternative explanations in Alcock.

D) Inclusive fitness will not work in nature unless individuals "know" who their kin are. They don't have to calculate relationships or consciously know - only act appropriately. It turns out that when organisms are given the chance to choose between kin and non-kin they tend to choose kin - even if they have been raised apart since birth. This has been shown for animals from fruitflies and tadpoles to rhesus monkeys.