

The Concept of Inclusive Fitness¹

Ethology and Behavioral Ecology
Spring 2008

I. The components of Fitness

A. Direct fitness – W_d , darwinian fitness, W gained by increasing ones own reproduction relative to that of others

B. Indirect fitness – fitness gained via kin selection, W_I . This component is rare for most animals but is also very common in others. In some cases it can be the only component of ones fitness. It is the subject of most of this handout.

C. Inclusive fitness – when fitness is obtained by both direct and indirect means (or only by indirect means) we speak of inclusive fitness ($W_{\text{inclusive}}$). Thus:

$$W_{\text{inclusive}} = W_d + W_I$$

Again, remember that in most cases, we will simply talk about W_d and not invoke the inclusive fitness concept.

II. Kin Selection and Evolution

A. NEPOTISM and KIN SELECTION: activities where inclusive fitness is maximized through behaviors directed towards relatives.

1. **Nepotism:** behavior where relatives are favored over non-relatives.

2. **Kin Selection:** as a result of nepotism, where an individual's *inclusive fitness increases primarily as a result of an increase in the INDIRECT FITNESS* component of *inclusive fitness*.

a. Thus, in kin selection W_T must increase

b. However, the principle source of the increase is in W_I

c. It is even possible that W_D might decrease as a result of the action.

? Distinguish between behavior that is "selfish" and behavior that evolved or is maintained by kin selection in terms of relative values of W_T , W_I , and W_D .

B. The idea of OFFSPRING EQUIVALENCE

1. Recall that inclusive fitness is only increased if the individual in question does something that affects the reproduction of some other related individual. Examples would include adopting a relative or helping rear related children or saving the life of a relative that still possesses has some inclusive fitness (i.e., is capable of further reproduction or of helping a relative rear young beyond what they would be able to rear).

2. The gain in fitness realized by each additional must be parceled up according to the number individuals who have helped rear the young and their relatedness. The relatedness is important because it represents the proportion of genes

¹ © 2008. KN Prestwich Department of Biology, College of the Holy Cross, Worcester MA 01610
<mailto:kprestwi@holycross.edu> . For any free non-commercial use, including use in other classes.

shared in common by the altruist and the recipient of the altruism; the gain in inclusive fitness can only be in proportion to that number of genes shared in common.

a. This is the basis of Haldane's famous remark that he would be willing to die in a courageous act only if he could save at least eight cousins (or for instance, at least two siblings).

b. Hamilton summarized this argument succinctly when he stated that in order for an allele to spread by kin selection, the following conditions needed to be met:

1.
$$\frac{B}{C} > \frac{1}{r_{ij}}$$

or as it is also sometimes written:

2.
$$K > \frac{1}{r_{ij}}$$

where **K** is the benefit to cost ratio, also often put as the recipient benefit to altruist (actor) cost in terms of offspring.

Thus, since cousins are on the average 1/8 related to each other, in order for a gain in inclusive fitness to compensate for the loss of ones own life, $K > 8$ or the gain must be more than eight cousins (who would have been lost) in exchange for one's own life.

Equation #1 can be re-arranged in a useful way that emphasizes the size of the benefit to the cost:

3.
$$B * r_{ij} > C$$

Essentially, this version of the equation says that the actual benefit is the number of individuals gained as a result of the altruism times their relatedness to the actor and that for this to be favored by selection, this gain must be greater than the cost to the actor in offspring.

? From the point of view of the success of the altruistic allele (in this case, one that causes its possessor to communicate in such a way that its direct fitness is harmed), why could it be more valuable to direct altruistic acts towards kin (be nepotistic) than to direct these acts towards anyone in the population?

Does an altruist know which other individuals bear the altruistic allele?

C. A potential problems with the kin selection concept and its solution.

1. Shortly after Hamilton published his theory of kin selection (actually, his formalization of kin selection theory -- kin selection as an idea goes back to Darwin) in 1964, a number of individuals came forward with the idea that if an allele for altruism was increased by kin selection to a fairly high frequency in the general population (say 0.5), that it would be increasingly selected for over the alternative. The argument was basically that:

a. If the allele were at high frequency, there would be a high probability that any altruistic act would be directed towards another individual containing a copy of the altruistic allele

b. Essentially, the high frequency of the allele would simulate kinship at that locus -- just as a high value of $r_{i,j}$ means there is a high chance of sharing an altruistic allele and therefore aiming altruism at another copy of the altruistic allele, likewise, a high f will also mean that there is a high chance of directing an altruistic act towards a bearer of the altruistic allele.

c. The result therefore would be that as the frequency of the allele increased in the general population, the chance of an altruistic act being directed towards another altruist would increase. This, argued some, would mean the Hamilton had underestimated the ease with which an altruistic allele could move towards a high frequency.

2. Hamilton shot back the following analysis that showed that no such frequency dependent effect existed -- provided that the altruist could not identify other carriers of the altruism allele. Here is the gist of the argument (refer to the diagram on the next page):

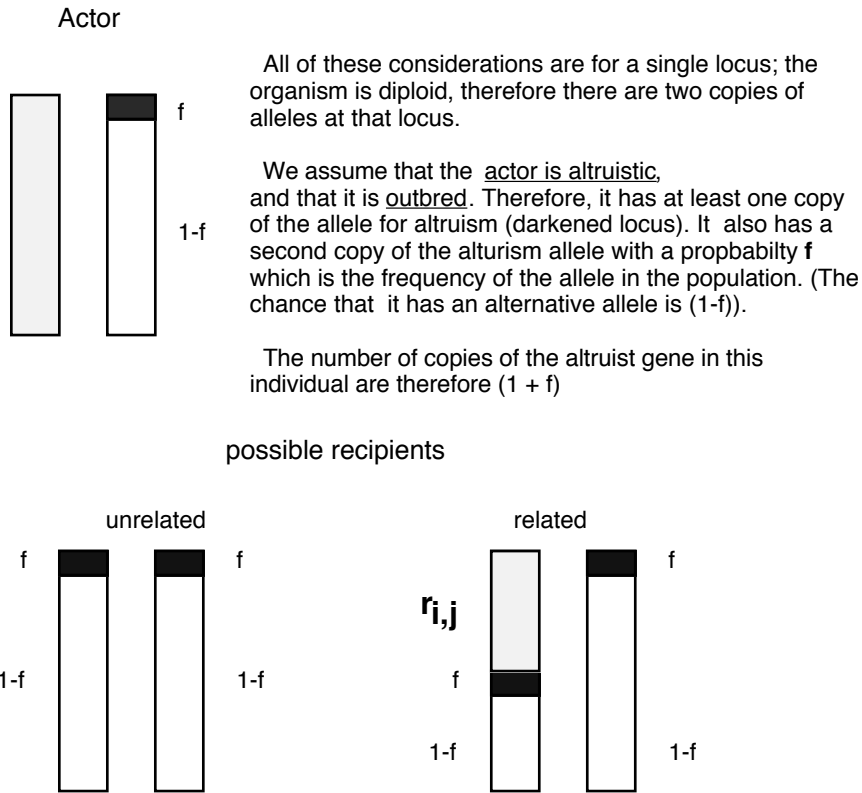
a. Assume that the actor is an altruist who is blindly performing altruistic acts towards other individuals to whom it may or may not be related.

b. In the recipients of the altruism, Hamilton distinguished between two components of the genome:

1. One is the **correlated** portion, that is, the proportion shared by common descent, r_{ij} . In unrelated individuals, this has a value of 0 (and is not shown) while in related individuals it has some value between 0 and 1. Thus the chance that an individual has a copy of an altruistic allele is in part f_{ij} . The correlated genome is normally taken as being a portion of one of the two possible sites since the allele is assumed to be rare and the individual is not a product of inbreeding

2. The remainder is termed the **uncorrelated genome**, the portion that is not of common descent. In it, there is a chance f of the altruistic allele being found. The total number of copies of the allele that are found in any one individual can be either 0, 1 or 2. However, the chance in the general population will equal the chance of finding the allele in the correlated genome (r_{ij}) plus the chance of finding the allele in the uncorrelated genome ($2f$):

Correlated and Uncorrelated Genomes and the Evolution of Altruistic Traits



Here are the "altruism loci" of two individuals **who will receive the benefit of an altruistic act from the actor pictured at the top**. One individual is unrelated to the actor while the other is related.

In the case of the **unrelated individual**, the chance of finding the altruistic allele is f at either of the two sites of the locus. Thus, this individual will contain $2f$ copies of the altruistic gene.

However, in the **relative**, there are two different situations. A certain proportion of its genome is shared with the actor by common descent (marked $r_{i,j}$). This is called the **CORRELATED GENOME** and is shown as the darkly dotted region. The other portion (all that remains), contains the altruistic gene at general population frequency f . This is the **UNCORRELATED GENOME**. (In the unrelated animal, that is the only portion of the genome there is).

The number of copies of the altruistic allele that are present in the relative is $(f_{i,j} + 2f)$.

c. If the altruist aims its actions towards an unrelated individual, it benefits the altruistic allele with a chance f . It benefits the alternative allele with a chance $(1-f)$. The key thing to note here is that since the altruism is being performed blindly and not to kin, the two competing alleles are benefited by altruistic acts exactly in proportion to their frequencies in the population. Thus, neither receives a net benefit over the other and there will be no change in allele frequency.

? What then is the reason that kin selection works?

D. A couple of other notes about kin selection:

1. Note that for the evolution of altruism by kin selection it is not the overall degree of genetic similarity that is crucial, although that is important. The crucial factor is whether or not it is likely that an altruist is preferentially acting altruistically towards others bearing the altruistic allele. What is going on at the other loci is irrelevant. Thus, we use the definition of coefficient of relatedness in the sense of chance of possessing a particular allele (altruistic) in two individuals by common descent. All that kin selection accomplishes is to cause differential benefit to fall on individuals that also possess the altruistic allele.

2. Put another way, a rare allele will only spread if it directs its altruism towards copies of itself. Kin selection is simply **enabling mechanisms** to that end.

3. Keep in mind that in this and in the other examples we want to understand how a single allele can spread through the population after a mutation. We also want to understand how this allele can be maintained in a population when superficially it appears to be disadvantageous to its possessor.

4. Recall that any mechanism that will enable nepotism to occur will be useful in kin selection. There is no reason that the actor must actually be able to recognize its kin -- it must simply act altruistically towards them more than to unrelated individuals.

? What are some proximate mechanisms that allow individuals to primarily bestow altruistic acts on kin?

5. Here are two factors related to indirect fitness that cannot be emphasized too much:

a. A behavior is altruistic only when whatever you expend is unavailable for your own potential reproduction.

b. Both you and the child's biological parents cannot count each extra offspring as your exclusive gain; if you did the gain from the child would count more than from a child who was not adopted.

6. Finally, a caveat about inclusive fitness: never forget that close relatives may also be fierce competitors; when this occurs, altruism will not be favored to evolve by kin selection (the inclusive fitness benefits of altruism towards the allele in some closely related individual are more than offset by the direct fitness losses associated with the competition -- selection will act to cause the individuals not to be altruistic and perhaps also to disperse from each other).

? Assume that one pair of parents produce four offspring while another pair produces only two. For each parent of each pair, give the W_D , W_I , W_T in both absolute and relative terms.

Ans.: absolute measures, pair 1, $W_D = 2$ offspring/parent ; put in genetic terms, 1 copy/parent; $W_I = 0$, $W_T = 2$ or 1 depending on the system of measure; for pair two: $W_D = 1$ offspring/parent ; put in genetic terms, 0.5 copy/parent; $W_I = 0$, $W_T = 1$ or 0.5 depending on the system of measure.

Relative measures, pair 1 is the most fit and has values of W_D and W_T of 1.0; for pair two both measures are 0.5. There is no sense in comparing W_I since it is 0 for both.

Now suppose that you forgo one years reproduction to help your sister rear young with her mate. As a result, they rear two more children than they would have been able to (they would have reared 4 without your help). Give your sister's and your W_D , W_I , W_T in both absolute and relative terms.

*Ans.: W_D for your sister, = 2, for you, = 0; W_I for your sister = 0, for you = $2*0.5 = 1$; W_T for your sister = 2, for you, 1;
relative measures: for your sister = 1.0 for you, 0.5.*

E. Is there any evidence for kin selection and altruism? Ans.-- yes -- plenty. Here are some quick examples:

1. Altruism is most common between relatives (is this proof of kin selection?)
2. in many species which could easily disperse considerable distances, they do not even though you might expect genetically similar individuals to be most alike ecologically and therefore very competitive with each other. If kin selection never mattered, (if W_I is near 0) then one might expect more competition and more dispersal.

3. A Couple of Examples related to Communication:

a. **Aposomatic caterpillars:** in some species of Lepidoptera, the larvae are distasteful and also brightly colored. The bright coloring, quite opposite to the normal **cryptic coloration** of most animals is meant to call attention to its owner -- it warns a predator that its possessor tastes bad, will make you sick or is dangerous. Such a trait (the coloration and or distinctive calls or other behaviors) is called **APOSOMATIC DISPLAYS**.

1. The problem is that the predators often need to be "educated" as to the meaning of the signal. The distinctive coloration (or whatever) aids in this because the predator is more likely to be remember what it was that made it sick and also to generalize to other things like it. However, someone may need to die to educate the predator.
2. Essentially the one that dies is a potential altruist
3. In aposomatic caterpillars (and a number of other examples) the young from a single egg clutch remain together for long periods after they hatch.

? OK -- explain why the caterpillars hang out together. How would a gene for altruism spread quickly in such a situation? Is this a convincing case of kin selection? If not, what else do you think that it could be? (continued)

Is a rattlesnake rattle and example of an aposomatic display? Speculate on the role of kin selection or some other mechanism in the evolution of rattles on snakes

b. The evolution of alarm calls:

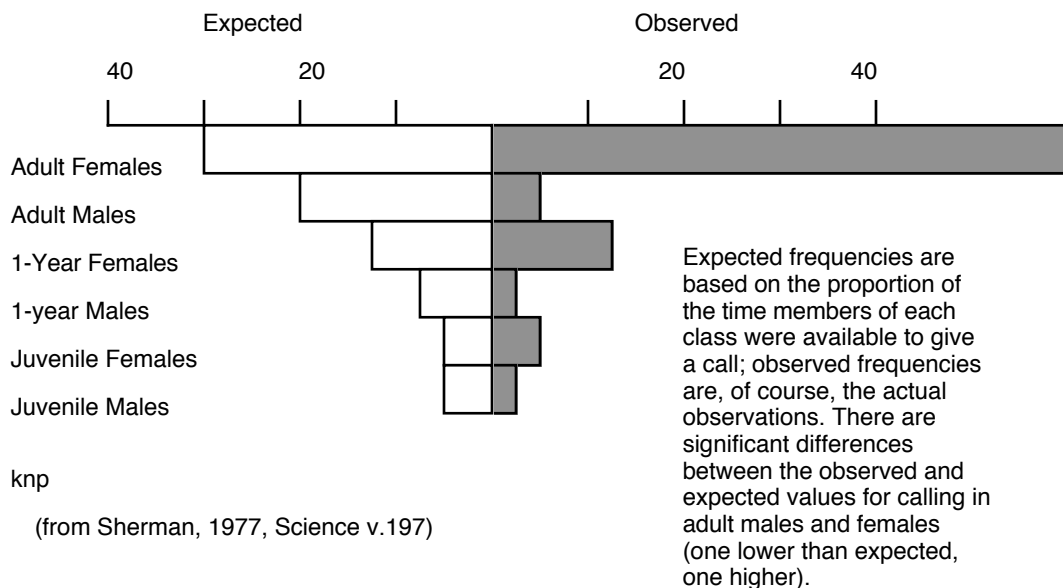
1. Honest alarm calls are given in many species when a predator appears. There are a few of studies that suggest that the call is made at some risk

to the caller. For instance, Sherman (1980, Sociobiology: Beyond Nature/Nurture, an AAAS Symposium) reported that Belding ground squirrels that gave alarm calls were stalked, chased and killed more often than individuals that did not call.

2. Sherman and others have repeatedly reported that these calls tend to be directed primarily in the direction of location of close relatives and that when no relatives are present, the animals are much less likely to call. For instance, males which often enter the colony after traveling some distance are in general much less likely to call than are females which tend not to disperse and to therefore have many close relatives near by. Interestingly enough, the squirrels are less likely to call when they are young than when adult.

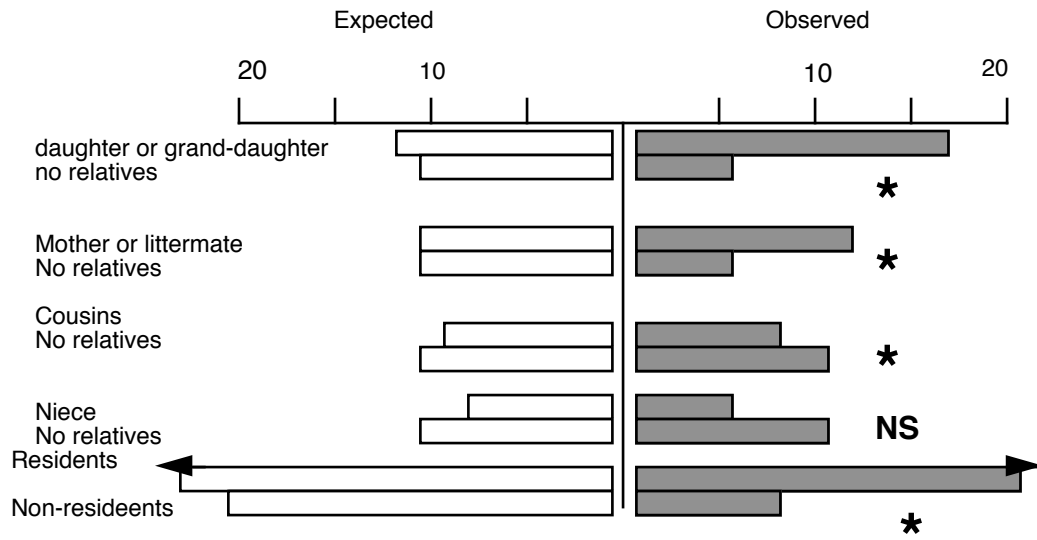
In the next two graphs are data by Sherman for alarm calls in Belding's Ground Squirrels. The first graph suggests that females are much more likely to call than are males and that older individuals are more likely to call than young:

Frequency or Alarm Calls as a Function of the Age and Sex of the Caller



This graph shows that alarm calls are more likely to be directed to near relatives than to non-relatives and that furthermore, calls are no more likely to be directed towards cousins or avunculars than they are to unrelated individuals:

The effect of relationship on the likelihood that an alarm call will be given in Belding's Ground Squirrels



knp
(from Sherman, 1977, Science v.197)

The stars state whether or not there were significant differences between expected and observed values, ns means that no significant difference existed.

? How might kin selection be involved in the evolution of alarm calls? Can you give a likely alternative means whereby these calls could have evolved? Why should older individuals be more likely to call than younger ones -- answer this both in terms of opportunity and fitness? What does this suggest about the relative importance of direct and indirect fitness components to these animals?