

Some Means Through Which Altruistic Behavior Could Evolve

Ethology and Behavioral Ecology

Summary: *This set of notes reviews five mechanisms that are likely means whereby an altruistic allele could increase in frequency. Primary among them are cooperative mechanisms that require that all involved individuals (both recipients and actors) benefit in terms of direct fitness and kin selection that posits that the main gain in fitness comes from the indirect component. We will take a critical view of all of these mechanisms and you are expected to remain critical throughout the course whenever these are brought up. The last section of the notes will deal with a critical look at an actual test of the kin selection hypothesis in Florida Scrub Jays .*

I. Overview

A. If we accept the idea that altruism cannot evolve by group selection except in the most unusual of cases, then what alternatives does that leave us? Obviously, altruistic behavior has evolved a number of times

B. Other possible mechanisms: There are **five** we will consider:

1. **Pleiotropy**
2. **Parental Manipulation**
3. **Kin Selection**

4. **Cooperation** (two forms):

- (a) **Reciprocal altruism**
- (b) **Mutualism**

? Why are we so concerned with trying to figure out how apparently altruistic behavior evolved? In what way is it a special problem for evolutionary theory? Why is it so important in social behavioral theory?

II. Pleiotropy and Parental Manipulation:

A. **Pleiotropy** is of course the phenomenon whereby an allele affects several traits. Dawkins envisioned the following scenario whereby it could be the mechanism that allowed an altruistic allele to spread:

1. Suppose that an "allele" has two phenotypic effects:

- a. It predisposes its possessor to act altruistically towards other individuals that it is around
- b. It causes its possessor to seek out and remain in a certain area of the environment -- it causes aggregations in certain well-defined places.

2. The effect of (b) is to bring animals that possess the altruistic allele together in a common area. Thus, many of the individuals present in this area, certainly a higher proportion than in other areas) will possess the altruistic allele. Altruistic behavior is thus more likely to be aimed at other individuals who also possess the allele than it is to be aimed at selfish individuals. This will favor the increase of the altruistic allele.

? Why will the altruistic allele be favored over the alternative? Frame your answer in terms of benefits to the two competing genotypes.

In what ways is this similar to kin selection (see below)? How is it different?

B. Parental Manipulation. Richard Alexander proposed this mechanism.

1. Basically, the idea is that when there are fitness conflicts between parents and offspring, the parents must always win (lower offspring fitness to the benefit of the parent -- for instance by becoming a worker for the parents) because if the offspring had a genetically influenced tendency to win instead of the parents, they will be at a disadvantage when they themselves become parents and are faced with their own offspring.

2. Dawkins pointed out that this is a fallacious argument by turning it on its head: offspring that win would be advantageous since parents that produced offspring that always won would produce more successful offspring than would parents that always won.

3. Nevertheless, there is some evidence that parental manipulation is a valid force in the evolution of altruistic behavior. It seems a possible partial explanation for some insect societies, although we will see that this idea has been tested by Trivers and Hare (in a later class):

a. The parents force their offspring to behave altruistically. There are a number of ways which this could be accomplished -- for instance, by discipline (as in humans) or by withholding food from young if the result was to produce adults that were less capable of reproduction and predisposed, for instance, to helping their parents rear the parent's young.

b. Put another way, the parents pass on a gene that makes the offspring susceptible to the manipulation.

c. To make this example clear, you should imagine a case where the parents produce two types of young -- those that help and act altruistically and those that benefit from the altruism --- an example would be worker and reproductive offspring in social insect.

d. From this, Alexander would argue that parents who were able to successfully manipulate their offspring into acting altruistically will in certain circumstances increase their inclusive fitness over parents that do not manipulate their offspring, since they will be able to rear more young. Again, we will see a direct test of this notion later in the course.

? From what you know, do you feel that either of these mechanisms would likely be common means whereby altruism could evolve?

III. Kin Selection

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**

Earlier in the course during the evolution and ecology overview, we considered relatedness. This is a review of what we considered then; you may want to get those notes out again and review them as you go through this section.

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 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, 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):

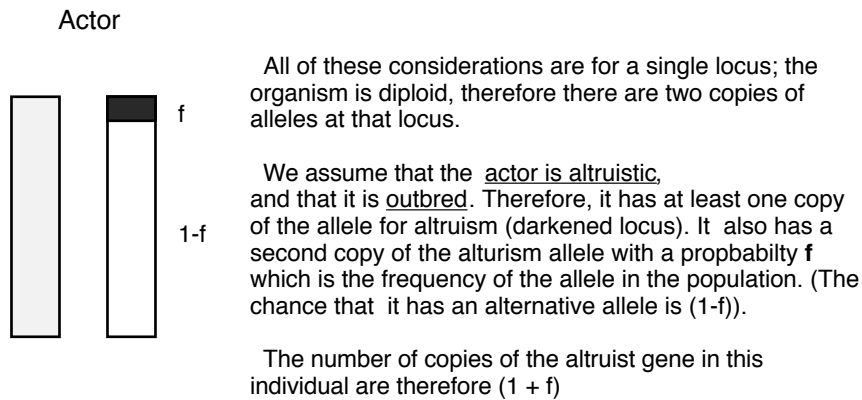
a. Assume that the actor is an altruist who is blindly performing altruistic acts towards other individuals to whom it may or may not be related.

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

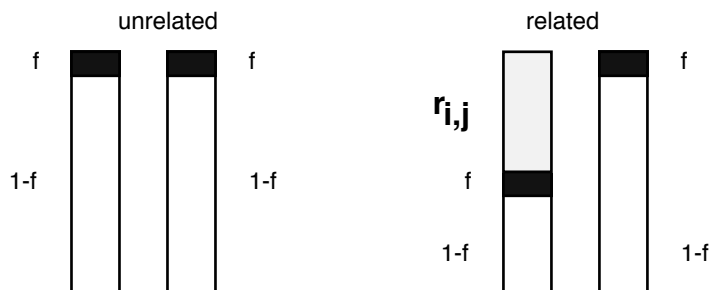
1. One is the **correlated** portion, that is, the proportion shared by common descent, r_{ij} . In unrelated individuals, this has a value of 0 (and is not shown) while in related individuals it has some value between 0 and 1. Thus the chance that an individual has a copy of an altruistic allele is 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



possible recipients



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 altruist 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, like the pleiotropy example of Dawkins, 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:

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. Brotherhoods:

1. Here a group of brothers will band together in an effort to assist their most dominant member obtain matings (and they might well increase their own chances too).

2. There are many examples; they are quite common among some primates, in lions, and in some birds. One of the best-studied examples is in turkeys where brothers assist each other at lekking sites.

? Where is the altruism here? Is there more than kin selection involved? How would you test for whether or not kin selection was the most important factor in the evolution of these brotherly groups?

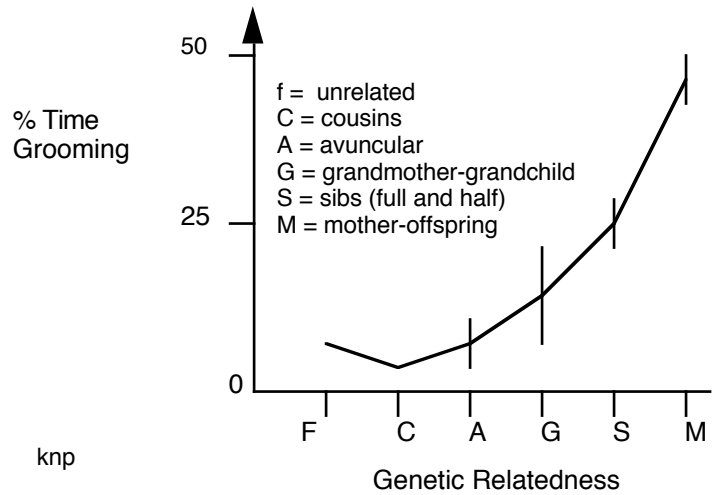
c. Macaques (and many other primates):

1. These primates live in rather large bands. Within these bands it is found that the relatedness between individuals is rather high. Behaviorally a number of unusual behaviors are observed that include:

- a. sharing of food
- b. mutual grooming
- c. less aggression within matriline

On the following pages are two graphs that depict the relationship between r and grooming -- the first gives the % of time which individuals of different degrees of relatedness groomed each other:

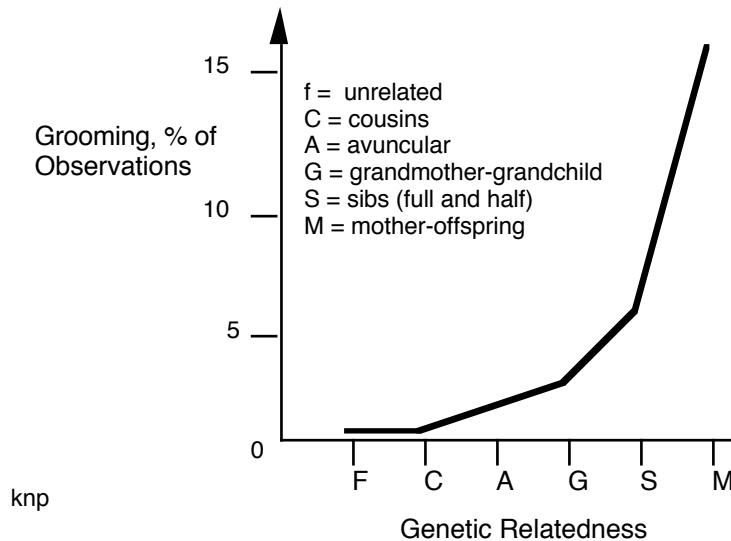
Grooming in Japanese Macaques as a Function of Relatedness



from Kurland, 1977, *Contributions to Primatology*, vol 35

and the second shows the frequency with which grooming events occurred between individuals of different relatedness:

Grooming as a Function of Relatedness



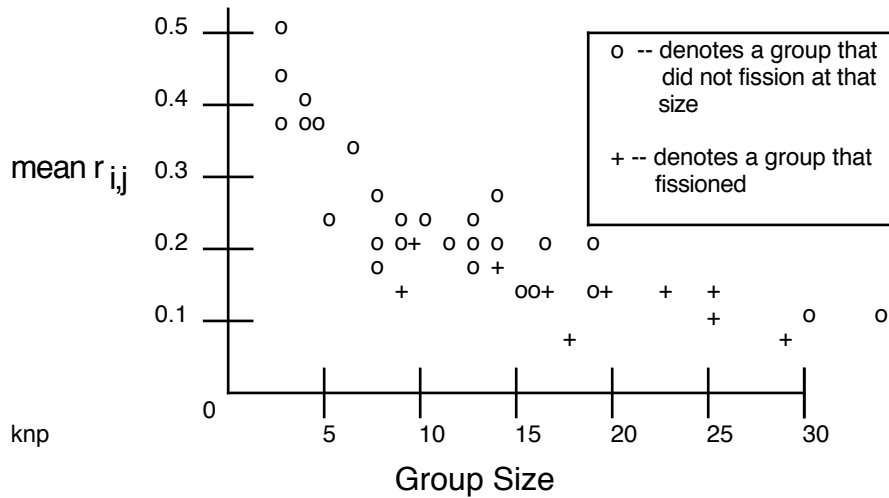
from Kurland, 1977, *Contributions to Primatology*, vol 35

If we accept the idea that grooming is an altruistic act, are you satisfied that this sort of data proves that it has evolved via kin selection? Is there an alternative view to the idea that grooming is directed towards relatives largely as the result of kin selection? Explain.

As groups get large, not surprisingly, the average relatedness of the group's members decreases. What is more interesting is that as the relatedness decreases, the groups are

more likely to fission. This is shown in the graph below for a different species of macaque

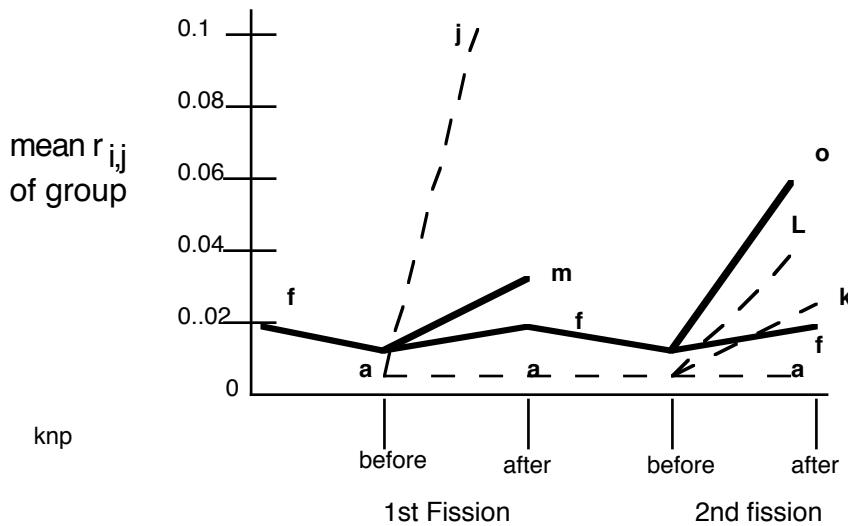
Mean Relatedness and the Chance of Group Fission in Rhesus Macaques



(approximate point position, taken from Chepko-Sade and Oliver, 1979, Behav. Ecol & Sociobio)

Furthermore, the groups tend to fission in such a way as to produce groups where the mean relatedness between individuals is raised (the groups could also have divided in such a way as to maintain a low degree of relatedness):

The effect of fission on the mean relatedness of members of groups of rhesus macaques



Fission points are where the lines branch. Each time a group fissions, a smaller group with a relatively high r is created. These groups are given new names. The r of the remaining group is less affected since it is large. (from Chepko-Sade and Oliver, 1979, Behav. Ecol & Sociobio)

? One interpretation of these graphs is that fissioning is a means to maintain a high mean value of r_{ij} within a group and this will encourage kin selection. Provide an alternative to the notion that the reason the groups are fissioning is to maintain a large mean r_{ij} . Hint -- could the increase in mean r_{ij} simply be a consequence rather than a purpose of the fission? What would this imply about kin selection as compared to individual selection? What other factors could easily be as important as degree of relatedness in terms of influencing whether a group split or not? If those factors were the only that mattered, why would you still expect to see r_{ij} rise?

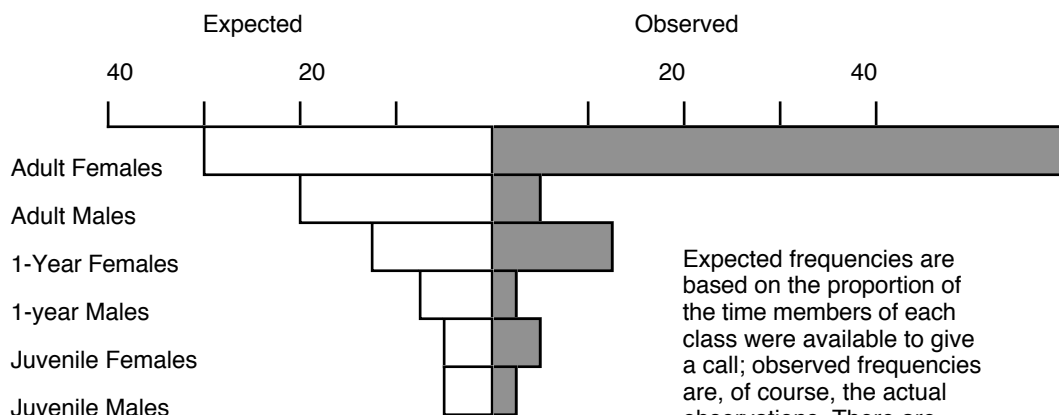
d. The evolution of alarm calls:

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



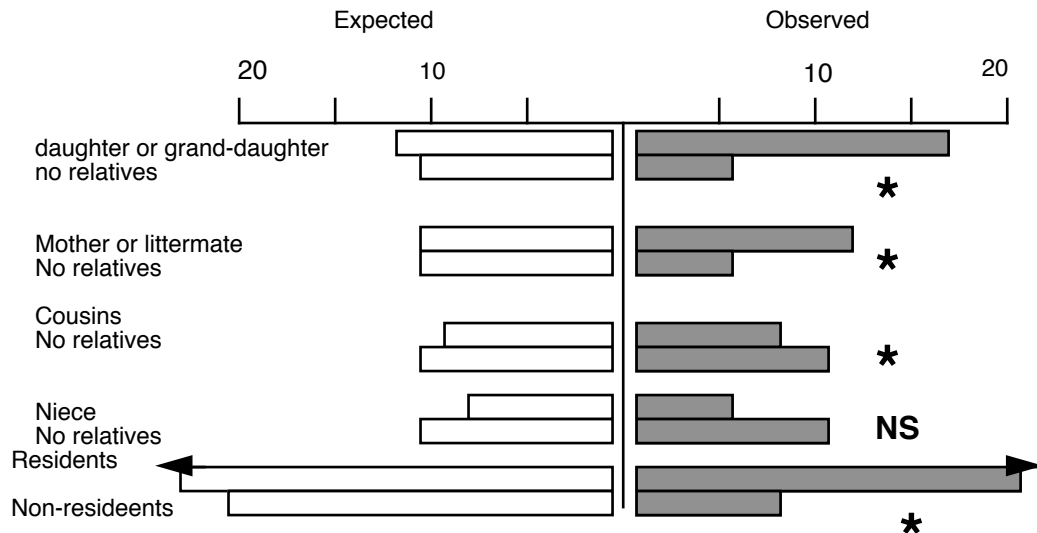
Expected frequencies are based on the proportion of the time members of each class were available to give a call; observed frequencies are, of course, the actual observations. There are significant differences between the observed and expected values for calling in adult males and females (one lower than expected, one higher).

knp

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

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?

IV. Cooperation: reciprocal altruism and mutualism

A. **General:** both of these mechanisms involve the evolution of altruism via gains in direct fitness; what distinguishes them from kin selection is that if they are the mechanism whereby social behavior evolves, then **gains in direct fitness are by themselves sufficient to explain the occurrence.** Thus, the actor and altruist do not need to be related; however, even if they are, that does not mean that kin selection and not cooperation is the explanation for the behavior.

B. **Mutualism:** we will use this term in a limited sense (it

can be used more broadly). For us, mutualism will involve:

1. **Long-term relationship**
2. Where **both partners benefit**
3. Mutualistic interactions often imply very intimate inter-relationships,

even to the extent that they may become largely **obligatory**.

C. **Reciprocal Altruism**: "you scratch my back, I'll scratch yours" -- the idea that an altruistic act is bestowed on an individual with the expectation that the other will reciprocate at the appropriate time. There are some very specific conditions that must be met for this mechanism to work and they will be discussed below.

We will concentrate on the evolution of cooperative or altruistic behavior by reciprocal altruism because the conditions for its evolution are interesting and it is the form of "altruism" practiced most often by humans and certain other primates.

D. A Technique that has been very useful in gaining an understanding of reciprocal altruism is **GAME THEORY**.

This section is review from earlier in the course, you will probably be able to read through it rapidly but if you are weak on game theory, use it as a review. **The specific example is new, however, and so pay close attention to it.**

1. Recall that Game Theory can be defined as a technique whereby we can discover the likely outcome of contests that involve two or more different behavioral strategies ("behaviors"). Thus, it is a means to predict which type or mix of behaviors is best given a certain set of conditions. This will be in contrast to another technique which we will cover soon called optimality modeling or optimality theory where we will attempt to predict the best way to perform a specific behavior given a certain set of conditions.

2. Review of the Basics of Game Theory: The following steps are involved in applying game theory

- a. the alternative behaviors must be named and defined -- what will someone "playing" each strategy do.
- b. all possible encounters must be listed. The way this is done typically is to construct a grid (matrix) that shows all possible encounters between the strategies (see below).

c. **payoffs must be assigned** to each strategy as the result of each possible interaction. They are typically abbreviated as P(A,A) which is read as the payoff to individual playing A against A; thus, P(B,A) is the payoff to an individual playing b against a. The payoffs and the possible encounters are summarized in the matrix mentioned above. Here is an example where two individuals, each of whom could either potentially play strategy A or B against the other:

	individual #2	
individual #1 V	altruist	cheater
altruist	P(A,A)	P(A,C)
cheater	P(C,A)	P(C,C)

sometimes this is written a bit differently where each cell of the matrix lists the payoff to each individual in each encounter by dividing the cell with a diagonal line:

	A ₂	C ₂
A ₁	payoff to A ₁ \ to A ₂	payoff to A ₁ \ to C ₂
C ₁	payoff to C ₁ \ to A ₂	payoff to C ₁ \ to C ₂

(Note that the slash, \, is not a division sign)

d. the fitness of each strategy is then determined as the sum of its gains as a result of all of the interactions it finds itself in. Thus, the frequency of each type of encounter must be calculated and multiplied by the payoff for that encounter;

payoff to a = $(P(A,A) * \text{freq. of AA encounters} + P(A,B) * \text{freq. of AB encounters})$ (where the order of whether A moves on B or vice versa does not matter)

These are then summed for each strategy and compared with the strategy having the highest average payoff being the one that is most fit.

e. often the game is then played a number of times

4. An example of game theory: Discovering the conditions where reciprocal altruism might be expected to evolve using the "prisoner's dilemma" game.

Assume that two individuals are arrested for a crime. Each is interrogated separately by the police who are endeavoring to get them to implicate the other person in the crime. They have a choice to either remain silent or implicate the other. They do not know what the other prisoner has done

:

a. the strategies:

1. **A = altruistic behavior** -- don't implicate the other, essentially, offer cooperation with the other prisoner (although you are not actually communicating with them nor do you know what they are doing you are cooperating by not implicating them)

2. **C = cheating behavior** -- implicate the other -- selfish behavior (its not spite because you do not know if they have implicated you). Why this is selfish will be more clear when we look at the payoffs below:

b. the payoffs

1. R= reward if neither cheats
2. P= punishment if both cheat
3. S= sucker's payoff
4. T= payoff if the other is the altruist and you cheat , the

temptation factor

For this game we will assume that **T>R>P>S** and for simplicity we will assign each the value of **T = 3, R = 2, P = 1, S = 0.**

(T is given the greatest value since we assume that the police not only simply release you when you have not been implicated but they also provide you with some sort of a reward for implicating the other player; if both walk (due to

"cooperation"), reward R is given -- you get to leave but no other special reward is given. The reason that P is greater than S is that we assume that all the blame (and pain) is then shouldered by one instead of two.)

Here is the payoff matrix for our game:

	altruist	cheater
altruist	$R \setminus R$	$S \setminus T$
cheater	$T \setminus S$	$P \setminus P$

or:

	altruist	cheater
altruist	$2 \setminus 2$	$0 \setminus 3$
cheater	$3 \setminus 0$	$1 \setminus 1$

It should be obvious that if you believe that the other person is going to cheat, it is best for you to cheat since $P > S$. But what if you are not sure?

If you do not know what the other prisoner is doing, you must assume an equal likelihood that the other could be playing either strategy; thus all outcomes are equally likely. The resulting payoffs of a consistent strategist against an unknown opponent is:

for a consistent altruist = $(R + R + S + S) = 2 + 2 + 0 + 0 = 4$
 for a consistent cheater = $(T + P + P + T) = 3 + 1 + 1 + 3 = 8$

Once again, obviously the **best thing is to cheat**. This is even truer because *if the other player also analyzes the problem, she will conclude that it is best to cheat if there is only one encounter*. In other words, if the other player might cheat, there is absolutely no sense in being altruistic since you will be worse off than even if you both cheat.¹ Thus, for single games with the payoffs given immediately above:

$$W_{\text{cheat}} > W_{\text{cooperate}}$$

Also notice that the values of the payoffs are crucial in deciding how to play the game. For our example, the closer the value of R is to T , the less the likelihood of cheating.

? Explain why it is that if R approaches T that cheating becomes less likely. Is it still the best strategy?

¹ Note that this is not exactly the same thing as a "sucker's payoff". What is being addressed here is simply the likely payoff if you don't know what the other might do and if, taken over many instances of this game against a large number of similar players, it is equally likely that your opponent might play any of the four strategies.

5. Now, what happens if the game is played multiple times. This is essentially the same thing as saying that there is individual recognition since you know you will be playing the game with the same other person even if you don't actually meet or talk to them.

? Why is it significant to imply that something that acts just like individual recognition can occur without you actually meeting the other player?

When the game is played repeatedly, the result is that rather quickly, both players begin to cooperate with each other. However, if they know the total number of games that are to be played, they start to cheat near the end.

? Qualitatively explain why this should be the case -- why should the players learn to cooperate and why should they cheat when they know that they are approaching the end?

E. Conditions that favor the evolution of reciprocal altruism: From these types of analysis, it has been learned that reciprocal altruism will be most favored if:

1. You have a means to keep track of the actions of the other players: there is a means to recognize the other player and keep track of its behavior, this prevents cheating. This usually will mean that **individual recognition** and a **long-term memory** is required.

2. There is a low risk to the actor

3. There is a large benefit for the recipient

4. If there is a high probability of the situation being reversed in the future

5. If the future is likely to be very soon instead of a very long time hence.

? How do humans keep individuals from cheating in reciprocal interactions? Does this list look like a series of things you might think about in deciding whether or not to do a favor (assuming there was time to think and the favor was not totally trivial)? Explain.

IV. Methodology: Can we experimentally determine how an "altruistic" behavior evolved?

A. We will review an example of a study of the evolution of "helping at the nest".

1. Helpers are individuals who do not breed themselves but who engage in caring for the young of others and the defense of the nest. Thus, it would seem that the actions of helpers are altruistic in that helping is done instead of investing in one's own direct reproduction.

2. Most importantly, they are individuals who are physiologically able to reproduce; this distinguishes them from many alloparents seen in primates, many of whom are not sexually mature and in any case do not make a large contribution to the rearing of the young.

3. Helpers (see below) often make a very significant difference in the number of young that can be successfully reared.

B. the experiments that will be done fall under the category of **natural experiment** -- the investigators simply measured the inclusive fitness of birds that helped

as compared to those that nested on their own -- each of these two natural behavioral strategies can be viewed as analogs to experimental treatments.

B. General Information:

1. Helping at the nest, while not extremely common, does occur in a number of species.

2. One of the best studied is the Florida Scrub Jay -- these are bluish-grey birds that are related to blue jays (but they don't have a head crest or black wing bars -- there is a very closely related species in California and parts of the Southwest).

3. More importantly for us, they are very social birds. They live in groups consisting of a one or more breeding pairs, their unfledged young and a number of other birds (that often are their young but may also be unrelated).

4. They are restricted to a very challenging habitat -- the Florida scrub. This is a dry sandy community centered around low evergreen oaks, palmettos and other short woody plants and grasses.

a. Predators abound, in particular snakes that eat eggs and young (black, yellow rat and indigo snakes) and raptors (principally hawks). Mice and rats may also raid the nests.

b. The birds often forage outside of the scrub and therefore must travel considerable distances to get food. It should be obvious how helpers could be useful.

5. helpers are usually close relatives (often but not always offspring or siblings) of the nesting birds.

Dr. Glenn Woolfenden and his students have studied these birds extensively in central Florida. The techniques they use are observation (every local bird is banded and can therefore be identified -- a task made easier by the fact that they do not disperse great distances) and experiment.

C. There are two general questions that we need to answer about helping. The first is less interesting, but is important nonetheless:

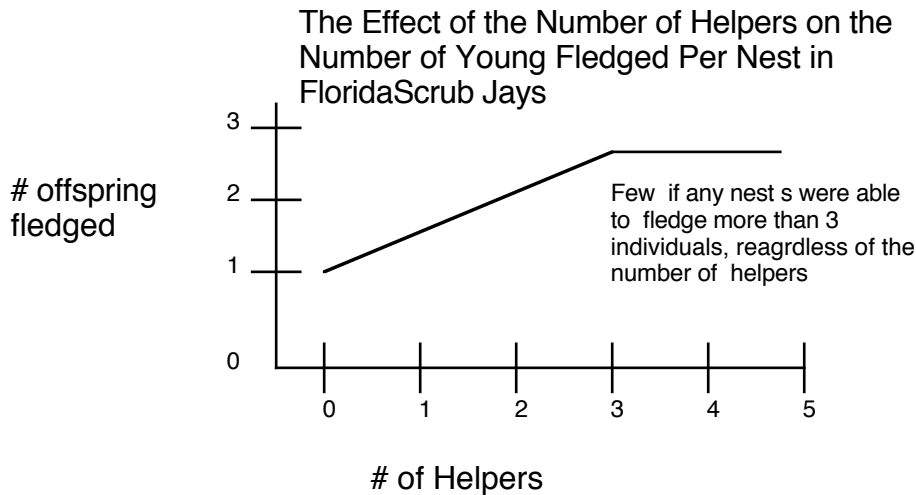
1. **Do helpers help:** This is rather easy to answer. Woolfenden found the following when he compared inexperienced parents (had never raised young before) and experienced parents who in both cases either had or lacked helpers. His results, based on many nests give the average number of young fledged per nest:

parents\ helpers?	without helpers	with helpers	mean # helpers
neither or one experienced	1.03	2.06	1.7
both parents experienced	1.26	2.20	1.9

Obviously, helpers increase the number of young fledged over the success of a solitary pair. Also, it is obvious and not too surprising that experienced parents do better than pairs where one or both birds are inexperienced.

? What does this suggest to you about the role of inheritance in parental care in these birds?

In another study, Woolfenden was able to demonstrate that adding more helpers increased the number of successfully fledged young per nest, up to a limit:



Thus, it is fair to conclude that helpers do indeed help and therefore are not having no effect or a negative effect

2. This then brings us to a more interesting question -- **Why and When Should Helpers Help?**

a. We should be able to produce a number of hypotheses as to the reasons for helping.

i. Keep in mind that for helping to evolve we must assume that helping must somehow increase the inclusive fitness of the actor. That is, when a "decision" is made to help or not to help, the criteria on which it must be based if it is to succeed by natural selection is :

$$W_T \text{ for helpers} > W_T \text{ for breeders}$$

ii. Put another way, the bird is making a "decision" to either help or breed and selection will favor the evolution of helping ("altruism") once that "allele" is present if it confers greater inclusive fitness than the alternative "selfish allele" to breed.

Notice that I have placed the terms decision, altruism, and allele in quotes. What do you think that I am trying to convey? In what sense is a decision being made? Are the genetic bases of these traits necessarily single alleles? (think back to early in the course). Are the genes really altruistic and selfish in the human sense or are we simply using those terms for convenience?

b. In terms of the actual reasons that helping might have evolved over individual breeding, there are two main categories of explanations:

i. Reasons associated primarily with an increase in individual (direct) fitness, W_D

a. Perhaps the helpers are primarily young and not likely to succeed in rearing young. Furthermore, it was shown above that experience increases the success of a jay in fledging young. Therefore, if helping is less dangerous and physiologically less demanding, birds could easily be selected to wait and help if they gained valuable experience over birds that simply waited or chose to breed.

b. Territories are very important to breeding success in these birds. By helping, perhaps the chance of gaining a favorable territory or a territory period is enhanced. For instance, the birds could gain the territory if one or both of the parents died (and perhaps gain a mate if unrelated)

c. The kin selection argument: helping could evolve via kin selection if:

$$W_{i, H} > W_{D, S}$$

where $W_{i, H}$ is the indirect fitness of a helper (since it is assumed that they have no young of their own while helping and therefore have no direct fitness gain) and $W_{D, S}$ is the direct fitness of a non-helper (since it is assumed that these birds do not help and therefore have no indirect fitness gain)

Be able to write an inclusive fitness equation for helpers and non-helper breeders -- what are the values of direct and indirect fitness in these respective cases?

d. Woolfenden decided to test the kin selection hypothesis. His reason for this was that it would be relatively easy to do if certain assumptions were made and the fact that the helpers were usually very close relatives made the kin selection hypothesis an attractive one to start with.

1. he assumed that: over the rest of their lives (when they were breeding) the inclusive fitness of birds that had at one time been helpers was no different than that of birds who had never helped.

2. this meant that if he simply measured the difference (if any) in inclusive fitness for birds that helped vs. those of the same age that did not help, he would know whether or not kin selection was a likely mechanism for the evolution of helping.

e. Here are the things that were measured (symbols are my own, not his):

Table of relevant variables:

N_{ib}	offspring for inexperienced individuals without helpers
N_{eb}	" experienced " "
N_H	" nests with helpers
r_s	relatedness between parents and offspring
r_h	relatedness <u>between helpers and offspring of hosts</u>
n	= number of helpers

f. As usual: **payoff in W_T for non-helpers = $N_{ib} * r_s$ for an inexperienced pair.** That is:

$$W_{T, ib} = N_{ib} r_s$$

Note that this is all direct fitness

Note that not helping to raise young is not considered an alternative. Why? Should it be? Under what circumstances?
 Why inexperienced? Should we use experienced birds?
 Why should we also assume that birds that do not help are raising young without helpers? (Hint: remember -- we are asking how this trait could evolve).

likewise:

payoff in W_T for helpers = difference between payoff with helpers and payoff without helpers.

(The reason is that this difference represents the additional birds that can be reared only with helpers -- the data presented earlier showed that helpers do help -- that they can, up to a limit, increase the total number of young fledged. Thus, a portion of the fitness gain must go to any helper who is related to the young) Therefore:

payoff in W_T for helpers = $(N_h - N_{eb})$ where N_e refers to the number that can be raised by experienced parents

? Why is the figure for non-helped experienced breeders subtracted from the number reared by birds with helpers?

however, we also need to take into account the number of helpers -- recall the earlier table that showed that most nests had almost two helpers. Incidentally, Woolfenden did not do this and was roundly criticized for it. Thus, the equation becomes:

$$W_T = \frac{(N_h - N_{eb})}{H} r_H$$

where H is the number of helpers.

You should help when you do better than by trying on your own (since you can only do one or the other). Thus:

$$W_{T, \text{helpers}} > W_{T, \text{ib}}$$

by substitution:

$$\frac{(N_h - N_{eb})}{H} r_h > r_s N_{ib}$$

g. if helpers are helping their parents, then

i. $r_h = 0.5$ since the offspring will be sibs.

ii. Likewise, between parents and offspring $r_s = 0.5$, as

usual. Thus, r_h and r_s cancel in this case and the expression becomes:

$$\frac{(N_h - N_{eb})}{H} > N_{ib}$$

h. Woolfenden et al. collected the following data for two different

years

N_h	Year #1 fledged	Year #2 fledged	# helpers (yr. 1,2)
N_h	1.3	2.2	1.7, 1.9
N_{eb}	0.5	1.26	---
N_{ib}	0.5	1.03	---

Thus, for year #1: $\frac{(1.3 - 0.5)}{1.7} (>, <, +?) 0.5$

$$0.47 < 0.5$$

And for year #2:

$$\frac{(2.2 - 1.26)}{1.9} (>, <, +?) 1.03$$

$$0.49 < 1.03$$

i. The data show that at best helping is an even proposition as or should not occur, if kin selection is the only means by which it evolves.

One other thing that must be kept in mind is that the value of N_{IB} in one sense probably over-estimates the success of individual birds breeding alone. In most cases parents w/o helpers are mixes of experienced and inexperienced parents (thus, if both were inexperienced, new parent success would probably be lower)

j. The fact remains that it does occur. There are two possible paths:
i. we stick with the kin selection argument by supposing that what must really be measured is the lifetime differences in W_T for helpers vs., non-helpers.

? What do you think about this argument? Why might it be reasonable to assume that there would be such differences?

ii. or we tentatively accept the idea that helping evolved for essentially selfish reasons that have nothing to do with kin selection. We outlined these earlier and there is some observational and experimental evidence in their favor. They are:

- a. obtain experience
- b. gain status
- c. territorial budding -- gain a piece of the resident bird's territory -- helping may increase tolerance from the territory owners
- d. gain the territory as the result of the death of one or both of the resident birds, especially if you are not related to the surviving owner.

Additional evidence is that unrelated helpers sometimes occur.

? Do you think the evolution of helping in scrub jays is settled? What additional evidence do you think needs to be gathered -- list what would be needed for a number of strong tests of competing hypotheses.

If the fitness of those who help vs. those that don't is similar, is there another possible way that helping could have evolved? What is it?

Reflect on the fact that beautiful ideas may not have much to do with the way that things really work and that multiple causes are often more common than single ones, even if we find them less tidy!

Later in the course we will look at another example of helping where the kin selection argument may hold more water -- in an African bird with a wonderfully haughty name -- the superb blue wren. We will also learn more about helping.