

# Brief discussion of the mathematics of kin and group selection

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(Dated: January 22, 2019)

The controversy over group and kin selection has become better understood in recent years as it has been acknowledged that genetic relatedness and group association are both necessary for the evolution of altruism, and their mathematical formulation is the same when averaged across the population. Here we review pedagogically the mathematics underlying kin selection by Hamilton and Price to explain the convergence of these concepts. We further argue that once the role of group association is recognized group association becomes an evolutionary trait, which has to be considered in conjunction with altruism in order for evolutionary models to be meaningful.

Evolutionary biology describes a competition for reproductive success over generations among organisms. An individual that behaves altruistically in this context reduces the number of its offspring while increasing those of another individual. According to Hamilton's rule [1] altruistic traits can arise in evolution if

$$rB > C \quad (1)$$

where  $B$  is the reproductive benefit for the others due to the action of the altruist,  $r$  is genetic relatedness of the individuals that receive the benefit, and  $C$  is reproductive cost to the individual who is the altruist. The reproductive benefit and cost are the number of additional offspring (on average) that an individual will have.

For example, assume there is a rare allele (version of a gene) in a population that makes an individual altruistic. We assume that one of a mating couple has that allele. Each offspring has 50% chance of inheriting that allele. Offspring Bob inherits that allele and his brother Sam has a 50% probability of having the same allele ( $r = 1/2$ ). Then if Bob gives up having  $C = 1$  child to enable Sam to have  $B = 2$  children, according to Hamilton's rule that is an even trade ( $rB = C$ ). The allele can be found in the same number in the next generation. Half of the offspring that are born to Sam's brothers have that allele and since there are two additional offspring ( $B$ ), they make up for the one offspring ( $C$ ) Bob doesn't have. The overall reproductive advantage of the altruistic individual, or of a specific trait or allele that gives that behavior, is:

$$\delta\nu = rB - C \quad (2)$$

i.e. the advantage is given by the relatedness times the benefit minus the cost to the individual. If the altruistic interaction is reciprocated, Sam would help his brothers, including Bob, have offspring and pays the price  $C$  as well. The calculation is the same, so that both brothers have the benefit and the cost. Reciprocation is not always true, but it is convenient mathematically.

This calculation, however, is not the entire story. If Sam's brother has 50% chance of having the altruistic allele, the non-altruistic allele that a brother has the other 50% of the time (Carl, Bob's non-altruistic / bad brother) is also helped to have an additional child on average. The other allele gains extra reproduction. So on average, there is a 50% chance the bad brother gets one other offspring, and the good brother gets one other offspring. So

relative to baseline the bad brother does even better than the good brother among Bob's related individuals. His 'good' allele will survive into the next generation, but the 'bad' allele will expand in number relative to the 'good' one.

For example, consider if there are exactly two brothers for each set of parents. In one out of four cases the two brothers that are born will be altruists, one out of four cases they are both selfish individuals, and two out of four cases one is an altruist and one is a selfish individual. In the first case, the two altruistic brothers help each other to have 2 offspring but give up one, so they have one extra offspring. In the mixed cases, the altruistic brothers lose one offspring. Overall the number of altruistic offspring is the same as without altruism. On the other hand the two selfish individuals have 2 extra offspring from the mixed cases. So among the four families there are the same number of altruistic individuals and two more selfish individuals in the next generation.

In order for there to be an advantage for the altruists, the individuals that an altruistic individual interacts with have to be more likely to be altruists so that the benefits confer on them. However, if the relationship is summarized by a relatedness  $r$ , the individuals are not just the altruists but are those with the specific familial / genetic relatedness—unless we restrict further the individuals beyond just the relatedness. If we restrict the brothers that an altruist helps to also have the same trait / allele, then it really doesn't matter that they are brothers, since we need to detect that trait. If not, we need to compare the benefit given to that other allele to the benefit to the same allele. As in the example of two brothers in each family, if there are a bunch of brothers that interact with each other, while they share alleles in common, some of them are altruistic and some of them are not. Then the altruistic ones gain the benefit of the other altruists but so do the selfish brothers. We have to consider which organisms are interacted with as well as which ones are related to each other.

How does this work more generally? Given a particular way the organisms are organized, the proportion of the altruistic offspring is described by the Price equation [2–5]. Consider a group of  $n$  organisms that interact with each other regularly. They are also on average related to each other. A simple way to describe this is that  $q$  of them share an altruistic allele (for simplicity consider haploid genes so there can be only one copy per individual). As above, the allele causes altruistic behavior with benefit to the other individuals  $B$  and cost to

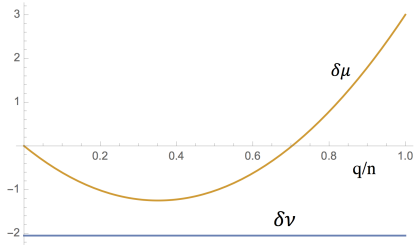


FIG. 1: Example of a plot of the number of altruists born relative to non-altruists per individual (orange) and the relative reproductive advantage of altruists within the group (blue). For no altruists there are no altruists born. If there are a few altruists they help others more than they help their own type. If there are enough altruists in a group, their number increases relative to the non-altruist baseline reproduction by virtue of the altruistic trait. Still, the reproductive advantage of altruists compared to selfish individuals within the group is always negative, as those selfish individuals are helped by the altruists. Altruists can grow more rapidly because of increasing numbers of individuals of a group that has mostly altruists, compared to selfish individuals who are not members of a group that includes altruists. Parameters:  $n = 100$ ,  $B = 5$ ,  $C = 2$ .

self  $C$ . The benefit is distributed among all the group except the individual who is acting altruistically, so each receives  $B/(n-1)$  benefit. There are  $q-1$  organisms that have the altruistic allele that receive the benefit. There are also  $n-q$  non altruistic organisms that receive that benefit. The overall benefit to an altruistic individual  $\nu_1$  and to a non-altruistic individual  $\nu_0$  is

$$\begin{aligned}\delta\nu_1 &= [(q-1)/(n-1)]B - C \\ \delta\nu_0 &= [q/(n-1)]B\end{aligned}\quad (3)$$

In total the number of individuals that receive the first benefit is  $q$  and the number that receive the second benefit is  $n-q$  so we have a difference in number of offspring

$$\begin{aligned}\delta\mu_1 &= [q(q-1)/(n-1)]B - qC \\ \delta\mu_0 &= [(n-q)q/(n-1)]B\end{aligned}\quad (4)$$

The relative growth in the number of individuals of altruistic type is the difference  $\delta\mu = \mu_1 - \mu_0$ :

$$\begin{aligned}\delta\mu &= [q(q-1)/(n-1)]B - qC - [(n-q)q/(n-1)]B \\ &= [(2q^2 - q - nq)/(n-1)]B - qC\end{aligned}\quad (5)$$

Fig. 1 shows how many more altruistic individuals are born for a group relative to the number of non-altruists for a specific example. The general features of the curve are quite general. When there are few altruists, the number of altruists born is smaller than the number of selfish individuals. When there are a lot of altruists, then the altruists are born more than selfish individuals. The advantage of altruism is that when they dominate the group, the growth rate of the group is higher than the

growth rate would be if they weren't altruists.

It will always be true that the benefits are better for the selfish individuals within a group of interacting individuals. The relative growth of an individual that is altruistic in the group compared to that of a selfish individual is  $\nu_1 - \nu_0 = -B/(n-1) - C$ , which is always negative (and independent of  $q$ ). This means that altruists offspring per individual are always less than selfish offspring per individual in the group. The proportion of selfish individuals grows within a group. The number of altruists can grow overall in the population if the groups with altruists are mostly altruists, and therefore those groups grow overall.

The best scenario for altruists is if the groups that they are part of are all altruists, while the groups that include selfish individuals are all selfish. Then altruists benefit the most from their altruism. What doesn't work is if the groups all have the same number of altruists. Then they always lose. In general, groups have to vary in the proportion of altruists, so that altruists are more commonly interacting with other altruists. This gives them a chance. In technical terminology, there has to be variance (defined statistically) in the altruism of groups [3-5]. Variance between groups could result from any of a set of properties including: altruistic individuals recognize altruism and choose to associate with altruists (i.e. to be in the same group with each other); altruists only help altruists; altruists preferentially mate with altruists and their offspring form into groups that are predominantly altruistic; local dispersal and interaction of offspring of altruists results in them being preferentially associated with altruists; non-altruistic behavior is recognized and they are rejected from groups of altruists. Any process that reduces the likelihood that altruists interact with non-altruists is fine. We note that the traditional mathematical treatment of kin selection [4] assumes a variance and calculates its effect but does not specify how that distribution arises (dynamic insufficiency). How the distribution is formed must be specified separately.

We can think about evolution, therefore, as having two processes, dynamics of reproduction and dynamics of association. Only when we combine them together can we understand how altruism fairs. If we keep groups the same size, then there are two extreme cases of association, the first is that the groups are all the same in proportion of altruists, the second is that some are all altruists and others have none. A dynamic process that makes groups non-uniform is called "symmetry breaking" in physics. We can also consider an association dynamic that changes the sizes of the groups. More generally, the dynamics of reproduction and association can depend on variables that are not described by the dynamics of reproduction when treated in isolation. Given that the association dynamics itself is a genetic trait, altruism is not a separable trait from the trait of association and both should be studied together.

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