

## THE EVOLUTION OF ALTRUISM

In this handout we will consider the problems associated with accounting for the evolution of altruism by natural selection and how those problems can be overcome. Although in many (if not most) cases, altruistic traits will be controlled by several or many genes, we will consider the simplest case in which whether or not an individual displays altruism is determined by genotype at a single locus with two alleles. This simple case is sufficiently tractable algebraically for this course, yet displays the major issues involved in the evolution of an altruistic trait.

The historical difficulty with accounting for the evolution of altruism has been understanding how alleles for altruism can increase in frequency if the trait itself (by definition) reduces the fitness of the individual that carries them. To make this difficulty clear, we first demonstrate that if altruists direct their altruism randomly to all genotypes in a population, then natural selection will eliminate any alleles that produce altruistic behavior.

1. We start out with the following conditions and assumptions:

a. Genotypes AA and Aa are non-altruistic. Genotype aa is potentially altruistic. Altruistic behavior is expressed in any one generation only by a fraction  $k$  of the aa individuals, so that  $(1-k)$  of the individuals of genotype aa do not act altruistically. (Note:  $0 < k < 1$ ).

b. The original gene frequency of the A allele is  $p$ , so that the frequency of a is  $q = 1 - p$ . If there are originally  $N$  individuals in the population, then the number in each genotype is given by the Hardy-Weinberg frequencies:

	AA	Aa	aa
No. of individuals	$p^2N$	$2pqN$	$q^2N$

c. The number of offspring produced by an individual depends only on its status as helper, helped, or unhelped. Helpers, or altruists, produce no offspring. Individuals that are not helpers and that are not helped produce  $M_1$  offspring. Individuals that are helped (*i.e.* recipients) produce  $M_2$  offspring. The definition of altruism implies  $M_1 < M_2$ .

2. Because  $q^2N$  individuals are of genotype aa and a fraction of these are altruistic helpers, the number of altruists is  $kq^2N$ . Therefore, the number of individuals available to be helped is, for each genotype:

genotype	AA	Aa	aa (non-altruists)	aa (altruists)
No. available to be helped	$p^2N$	$2pqN$	$Nq^2 - kNq^2$	0

From this table, the total number of individuals available to be helped is

$$p^2N + 2pqN + Nq^2 - kNq^2 = N(p^2 + 2pq + q^2) - kNq^2 = N(1 - kq^2)$$

3. Because altruists direct their acts randomly at other individuals, the number of individuals of a particular genotype that are helped is given by the following formula (assuming one helper per helped individual):

$$\left[ \frac{\text{No. individuals of genotype available to be helped}}{\text{Total no. individuals available to be helped}} \right] \times [\text{No. of helpers}]$$

For example, for genotype AA, the number of individuals available to be helped is, from (2),  $p^2N$ . The total number of individuals available is, also from (2),  $N[1 - kq^2]$ , while the number of helpers is  $kNq^2$ . Thus,

$$\text{No. AA individuals helped} = \frac{p^2N}{N[1-kq^2]} \times kNq^2 = \frac{Np^2}{[1-kq^2]} \times kq^2 .$$

The values for the other genotypes are determined similarly, giving

	AA	Aa	aa
No. individuals helped	$\frac{Np^2}{[1-kq^2]} kq^2$	$\frac{N2pq}{[1-kq^2]} kq^2$	$\frac{N(1-k)q^2}{[1-kq^2]} kq^2$

4. The number of individuals of each genotype that are not helped are simply determined by subtracting the number helped from the total number available for help. These values are given in Table 1. For example, for the AA genotype,

$$\text{No. not helped} = (\text{No. available for help}) - (\text{No. helped})$$

$$= Np^2 - \frac{Np^2}{[1-kq^2]} kq^2 , \text{ and, multiplying the first term by } \frac{[1-kq^2]}{[1-kq^2]}$$

$$= \frac{Np^2 - kNp^2q^2 - kNp^2q^2}{[1-kq^2]} = \frac{Np^2[1-2kq^2]}{[1-kq^2]}$$

5. Next, we determine the average number of offspring produced by individuals of each genotype. This average is equivalent to a genotype's fitness, and is determined by the following general formula:

$$W = \frac{(\text{No. unassisted individuals}) \times M_1 + (\text{No. helped individ.}) \times M_2}{(\text{No. unassisted individ.}) + (\text{No. helped individ.}) + (\text{no. altruists})},$$

where the denominator is simply the total number of individuals of that particular genotype. Note that the numerator contains no term for altruists because the M value for altruists is zero.

Once again, the following example is for AA individuals:

$$\text{Total No. individuals} = Np^2$$

$$\text{No. unassisted individ.} = \frac{Np^2}{[1-kq^2]} \times [1 - 2kq^2]$$

$$\text{No. helped individ.} = \frac{Np^2}{[1-kq^2]} \times kq^2$$

$$\text{No. altruists} = 0.$$

$$W_{AA} = \frac{\frac{Np^2}{[1-kq^2]} \times [1-2kq^2] \times M_1 + \frac{Np^2}{[1-kq^2]} \times kq^2 \times M_2}{Np^2}$$

$$= \left[ \frac{1-2kq^2}{1-kq^2} \right] M_1 + \left[ \frac{kq^2}{1-kq^2} \right] M_2$$

The value for genotype Aa is determined exactly the same way and yields the same value:

$$W_{Aa} = \left[ \frac{1-2kq^2}{1-kq^2} \right] M_1 + \left[ \frac{kq^2}{1-kq^2} \right] M_2$$

The fitness for genotype aa is determined from the equation

$$W_{aa} = \frac{\frac{N(1-k)q^2}{[1-kq^2]} \times [1-2kq^2] \times M_1 + \frac{N(1-k)q^2}{[1-kq^2]} \times kq^2 \times M_2}{Nq^2}$$

which simplifies to

$$W_{aa} = (1 - k) \left[ \frac{1-2kq^2}{1-kq^2} M_1 + \frac{kq^2}{1-kq^2} M_2 \right]$$

6. From these values for the W's, one can see immediately that  $W_{AA} = W_{Aa}$ . Moreover, by substituting the value of  $W_{AA}$  into the expression for  $W_{aa}$ , one obtains

$$W_{aa} = (1 - k) W_{AA}.$$

Since  $k < 1$ ,  $(1 - k) < 1$ , and hence,  $W_{aa} < W_{AA}$ . Thus, we have the following relationships among the W's:

$$W_{AA} = W_{Aa} > W_{aa} .$$

But we know from the general equation for gene frequency change under natural selection that whenever the fitnesses of genotypes fulfill this condition, the allele a will be eliminated by selection from the population. Thus, altruism, which is associated with the a allele, can not evolve.

We have reached an apparent contradiction. Our model of natural selection tells us that altruism can not evolve. On the other hand, many animals exhibit apparently altruistic behavior. The resolution of this contradiction lies in the realization that we managed to let in an assumption that we did not evaluate. We tacitly assumed that altruistic individuals directed their altruistic acts randomly with respect to genotype. They thus aided AA individuals with the same probability that they aided aa individuals.

Let us now suppose, however, that altruistic individuals are able to discriminate between genotypes and help only other aa individuals. We can then run through the same series of steps, although it is much simpler this time:

1. The original number of individuals in each genotype is given by Hardy-Weinberg:

AA	Aa	aa
$p^2N$	$2pqN$	$q^2N$

We know that  $kq^2N$  individuals of genotype aa are altruists.

2. Consequently, the number of individuals of each genotype available to be helped is

AA	Aa	aa
$p^2N$	$2pqN$	$q^2N - kq^2N$

3. Our new assumption is that each altruist helps one aa individual; no AA or Aa are helped. Then the number of aa individuals helped is  $kq^2N$ , and the number of individuals in each genotype/category is

AA (not helped)	AA (helped)	Aa (not helped)	Aa (helped)	aa (not helped)	aa (helped)	aa (altruists)
$p^2N$	0	$2pqN$	0	$q^2N - 2kq^2N$	$kq^2N$	$kq^2N$

4. The mean number of offspring produced by AA individuals is simply  $M_1$ , since no AA individuals are recipients of altruistic behavior. Hence

$$W_{AA} = M_1$$

Similarly, each individual produces  $M_1$  offspring, so

$$W_{Aa} = M_1$$

The mean number of offspring produced by aa individuals is calculated from the same formula we used before, giving

$$W_{aa} = \frac{(q^2N - 2kq^2N) M_1 + (kq^2N) M_2 + (kq^2N) \times 0}{q^2N}$$

$$= (1 - 2k) M_1 + kM_2 .$$

5. We next ask under what circumstances  $W_{aa} > W_{AA}$ , since when this is true the W's will be related to each other as

$$W_{AA} = W_{Aa} < W_{aa}$$

and the altruistic allele will increase in frequency.

Given  $W_{aa} > W_{AA}$ , we substitute the values for  $W_{AA}$  and  $W_{aa}$  calculated above, and this substitution yields

$$(1 - 2k) M_1 + kM_2 > M_1 .$$

Adding  $(1 - 2k) M_1$  to each side and combining terms gives

$$kM_2 > 2kM_1 ,$$

which, upon dividing each side by  $k$  ( $k$  is positive, remember), gives

$$M_2 > 2M_1 .$$

Thus, whenever helped individuals produce more than twice as many offspring as unaided individuals, the condition

$$W_{AA} = W_{Aa} < W_{aa}$$

will be satisfied and natural selection will lead to the spread of the altruistic trait through the population.

This result reconciles the evolution of altruism with our model of natural selection. It shows that natural selection can promote the evolution of altruistic traits as long as those traits are not directed randomly at other individuals, but are directed differentially toward other individuals carrying the allele associated with altruism.

In nature it is doubtful that organisms can actually distinguish unambiguously among individuals of different genotypes. There are, however, simple ways of distinguishing individuals that have a high probability of carrying the altruistic allele. One such way is to direct altruistic acts only toward close relatives, since close relatives share a large fraction of their genes. For example, full siblings share on average one half of the alleles passed on by their parents (see Table 2 for other

examples). W. D. Hamilton showed that as long as the recipients of altruistic acts are closely related to the donor, natural selection can lead to the fixation of the genes that cause those acts. He also provided the criterion for the evolution of altruistic behavior:

$$\frac{b}{c} > \frac{1}{\bar{r}} .$$

In this equation,  $b$  is the benefit, in terms of increased fitness or increased number of offspring produced, realized by recipients as compared to unassisted individuals. In terms of our  $M$  values,

$$b = M_2 - M_1 .$$

Similarly,  $c$ , the cost to an altruist's reproductive success due to performing altruistic behavior, is given by

$$c = M_1 - M_3 .$$

Here,  $M_3$  is the mean number of offspring produced by an altruistic individual. In our previous example,  $M_3 = 0$ . This may be the case, as for sterile castes in social insects, for example, but need not necessarily be the case.

The value  $\bar{r}$  is simply the average degree of relatedness of the donor and recipients of altruism. Table 2 gives some values of  $\bar{r}$  for some common relationships between two individuals.

Two things are immediately evident from Hamilton's criterion. First, the existence of the criterion demonstrates that there are conditions under which natural selection can lead to the evolution of altruism. Second, the evolution of altruism is easier when the recipients are closely related than when they are distantly related. If recipients are full sibs, for example, then  $\bar{r} = \frac{1}{2}$  and  $\frac{1}{\bar{r}} = 2$ . Hence, altruists that totally sacrifice their ability to reproduce ( $c = 1$ ) must only increase the number of offspring produced by their sibs by a factor of 2.

If recipients are cousins, however,  $\bar{r} = \frac{1}{8}$  and  $\frac{1}{\bar{r}} = 8$ . The same altruistic behavior must then increase the number of offspring produced by cousins by a factor of 8, clearly a much more difficult task. In the extreme case in which recipients are total strangers,  $\bar{r} = 0$  and  $\frac{1}{\bar{r}}$  is infinite. The sterile altruist would then have to increase the reproductive output of the stranger by an infinite amount. This is obviously impossible, and simply demonstrates once again that natural selection can promote the evolution of altruism only if the recipients of altruistic behavior have a high probability of also carrying the gene for that behavior (*i.e.* are close relatives of the donor).

Table 1. Determination of the mean number of offspring produced by individuals of each genotype.

AA and Aa Genotypes

genotype/ category	AA (not helped)	AA (helped)	Aa (not helped)	Aa (helped)
No. individuals	$\frac{Np^2[1-2kq^2]}{[1-kq^2]}$	$\frac{Np^2 kq^2}{[1-kq^2]}$	$\frac{N2pq [1-2kq^2]}{[1-kq^2]}$	$\frac{N2pq kq^2}{[1-kq^2]}$
No. offspring per individual	$M_1$	$M_2$	$M_1$	$M_2$
	↓	↓	↓	↓
Mean number of offspring per individual ( = W)	$\left[ \frac{1-2kq^2}{1-kq^2} \right] M_1 + \left[ \frac{kq^2}{1-kq^2} \right] M_2$		$\left[ \frac{1-2kq^2}{1-kq^2} \right] M_1 + \left[ \frac{kq^2}{1-kq^2} \right] M_2$	

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aa Genotype

genotype/ category	aa (not helped)	aa (helped)	aa (altruist)
No. individuals	$\frac{N(1-k)q^2[1-2kq^2]}{[1-kq^2]}$	$\frac{N(1-k)q^2 kq^2}{[1-kq^2]}$	$Nkq^2$
No. offspring per individual	$M_1$	$M_2$	$M_3 ( = 0)$
	↓	↓	

Mean number of offspring per individual ( $= W$ )

$$(1 - k) \left[ \frac{1 - 2kq^2}{1 - kq^2} \right] M_1 + (1 - k) \left[ \frac{kq^2}{1 - kq^2} \right] M_2$$

Table 2. Coefficients of relatedness ( $r$ ) for several common types of relationships between two individuals. The coefficient of relatedness approximates the fraction of an individual's alleles that are shared by the other individual.

<u>Relationship</u>	$r$
sib – sib	$\frac{1}{2}$
parent – offspring	$\frac{1}{2}$
grandparent – grandchild	$\frac{1}{4}$
uncle – niece	$\frac{1}{4}$
cousin – cousin	$\frac{1}{8}$
half-sib – half-sib	$\frac{1}{4}$
step parent – step child	$\approx 0$
stranger – stranger	$\approx 0$