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Source: *Evolution*, Vol. 42, No. 1 (Jan., 1988), pp. 193-196

Published by: Society for the Study of Evolution

Stable URL: <http://www.jstor.org/stable/2409127>

Accessed: 10-09-2016 02:28 UTC

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NOTES AND COMMENTS

Evolution, 42(1), 1988, pp. 193–196

A MATHEMATICAL MODEL FOR ALTRUISM IN HAYSTACKS

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Received December 2, 1986. Accepted August 3, 1987

Our purpose is to provide an inclusive-fitness model for Wilson's (1987) simulation model of altruism in haystacks. In Wilson's population, groups are founded by single mated females and grow in isolation for a sequence of G nonoverlapping random-mating generations, at which point they disperse. Females either mate in the group before dispersal (with probability m), or mate at random in the whole population after dispersal (probability $1 - m$). All mated females then compete to be the foundresses for the next cycle. This situation was first studied in a model of altruism by Maynard Smith (1964) who represented it as a population of mice living in haystacks.

We suppose that, between two individuals in the dispersal generation of the same group, there is the possibility of an altruistic act controlled by a pair of alleles at a single locus. The standard inclusive-fitness condition that the altruistic behavior be selectively favored is that

$$bR > c$$

where b is the benefit to the recipient, c is the cost to the donor, and R is the coefficient of relatedness between them. We will discuss the conditions under which this condition will correspond to the increase in frequency of the "altruistic" allele and will show how R can be calculated under assumptions of weak selection and additive gene action.

If there is no within-group mating and $G = 1$, then offspring dispersing from the same group are outbred sibs and $R = 1/2$; but if $G > 1$, then R exceeds $1/2$, and, in general, the smaller is the group size (N) and the larger is G , the larger will be R , though it is difficult to obtain an exact formula for R in terms of G and N . We obtain formulas for R for $G = 1$ and $G = 2$, and we perform some numerical calculations for large values of G , assuming both a constant group size and an exponentially growing group. We compare our results with Maynard Smith's (1964) model and with Wilson's (1987) simulations, though both models differ from ours in some respects.

The Inclusive-Fitness Model

We begin by looking at a general model of altruism. Suppose we have a population with a periodic life cycle (which may or may not be a single generation) and at some point in this cycle, individuals find themselves in groups, possibly formed at random, or more likely derived from some local or family structure in the pop-

ulation. Suppose each individual x performs, with probability H_x , an altruistic act towards a random member y of the same group. If the act is performed, we suppose the fitness of x is decreased by c and the fitness of y is increased by b . The question to be answered is, when will such behavior be selectively favored?

The first thing to note is that b and c are usually taken as immediate measures of fitness, but natural selection acts on the way in which these translate into contributions to the next cycle. In our haystack model, what counts are contributions to the next foundress generation, and, if the altruistic act occurs early in the life of the group, this may be difficult to calculate and will depend on the nature of the forces limiting the growth rate or the final size of the group. It is for this reason that we restrict attention to altruistic acts in the dispersal generation, so that b and c can be taken to measure changes in probability of founding a new group.

As an extreme example, suppose that there is some maximum group size and that every group attains that size at some point. Then an altruistic act will not result in an altered number of dispersing individuals from the group but can only change the genetic composition of the dispersers; in fact, the effect of the act will be to change the expected number of dispersing descendants, not only of the donor and recipient, but of every individual in the group. Under these circumstances, the ultimate total benefit to the recipient and other group members must be equal to the ultimate cost to the donor, and it would seem that altruism could never be favored unless the group was completely inbred. Wilson (1983) and Grafen (1984) have discussions of this matter.

The second thing to note is that there are two different types of altruism that may be described by this model. In the first type, the beneficiary is a single, randomly chosen, recipient (for example, a grooming act), and, in the second type, the act is directed towards the group as a whole (for example, a warning call). In the second case, the average benefit will be the same for all members of the group, other than x , and b will be chosen so that this is $b/(N - 1)$, where N is the size of the group.

In summary, for the purpose of the general condition (1) below, we will assume that b and c measure changes in contributions to the next cycle and that b measures the total change in benefit of a single act of x to all his group mates.

Now we consider a simple genetic model for describing this behavior. We suppose that we have an infinite diploid population, in which the behavior is controlled at a single locus with two alleles, one designated "altruistic" and the other "normal." If we define the genotypic value P_x of x to be the frequency in x of the altruistic allele, then the condition for the population-wide frequency of this allele to increase is

$$bR > c \tag{1}$$

where

$$R = \frac{\text{Cov}(P_y, H_x)}{\text{Cov}(P_x, H_x)}, \tag{2}$$

provided the denominator of R is positive. Condition (1) was first provided by Hamilton (1964a, 1964b), and, since that time, a considerable amount of discussion has focused on the correct and most general definition of R (Crozier, 1970; Hamilton, 1972; Michod and Hamilton, 1980; Pamilo and Crozier, 1982; Charlesworth, 1980; Seger, 1981; Uyenoyama, 1984; Grafen, 1985; Taylor, 1988). It was first noticed by Seger (1981) that the most direct way to obtain (1) and (2) is from Price's (1970) covariance formula for gene-frequency change.

To calculate R we have to know how H_x , which we call the phenotypic value of x , depends on genotype. One thing to note is that it is possible that H_x will depend on the genotypic value not only of x , but perhaps of y (if x is able to recognize the extent to which y is altruistic and modify his actions accordingly), or even of some third individual z (perhaps the groups are sib groups, and it is the mother of x who can control whether her offspring are altruistic towards one another). Therefore, in the most general case, H_x is a function of several genotypic values P_x , P_y , and P_z , and to calculate R we will have to know this function. Seger (1981) had an interesting example in which H_x is a function of P_x and P_y : H_x is 1, 1/2, or 0 depending on whether P_x is greater than, equal to, or less than P_y .

We will assume, as did Wilson (1987), that H_x depends only on P_x and is 1, h , or 0, depending on whether P_x is 1, 1/2, or 0. In fact, we will perform our calculations of R for the special case $h = 1/2$ of "additive gene action," because in this case R can be calculated from recursion formulas, at least when selection is weak. We note that Wilson (1987), in his simulations, took $h = 1$, the case of dominance of the altruistic allele.

Thus, assuming $h = 1/2$, $H_x = P_x$, and the numerator and denominator of (2) are covariances of genotypic values:

$$R = \frac{\text{Cov}(P_y, P_x)}{\text{Cov}(P_x, P_x)}.$$

If the alleles are neutral, that is, if $b = c = 0$, then

$$R = \frac{2f_{xy}}{1 + f_x} \tag{3}$$

(Michod and Hamilton, 1980), which is the coefficient proposed by Hamilton (1972). Here, f_{xy} is the coefficient of consanguinity between x and y (Crow and Kimura, 1970 p. 68) and is defined as the probability that random alleles from x and y are identical by descent, and f_x is the inbreeding coefficient of x . These coefficients, f_{xy} and f_x , can be expressed in terms of the "con-

densed identity state probabilities" Δ_i (Jacquard, 1974; Michod and Hamilton, 1980), which are independent of allele frequency, and so, in this case (of neutral alleles), R is independent of allele frequency. Of course, in practice, the alleles will not be neutral, but if selection is weak, R should be almost independent of allele frequency. In practice, f_{xy} and f_x are calculated recursively, assuming the population is at equilibrium. This is how we shall calculate R .

Calculation of R

Now we focus attention on the "haystack" life cycle described at the beginning, and let x and y be random individuals of the same generation in the same group. The coefficients of consanguinity and inbreeding will change with each generation, so we will index them with the generation number. Thus, we let f_0 be the inbreeding coefficient of the founding generation and let g_0 be the coefficient of consanguinity between the foundress and her mate (we assume that she is singly mated); for each $t \geq 1$, we let f_t be the inbreeding coefficient and let g_t be the coefficient of consanguinity between two different individuals of the same group in generation t . For altruism in the dispersal generation, we will have, from (3),

$$R = \frac{2g_0}{1 + f_0}. \tag{4}$$

Under the assumption of random mating in the group, the values of f_t and g_t can be recursively calculated from the formulas

$$\begin{aligned} f_{t+1} &= g_t \\ g_{t+1} &= \frac{1}{2N_t}(1 + f_t) + \frac{N_t - 1}{N_t}g_t \end{aligned} \tag{5}$$

(Crow and Kimura, 1970 p. 102), where N_t is the effective size of generation t in the group (Crow and Kimura, 1970 p. 103). These formulas are valid for all $t \geq 0$ provided we use $N_0 = 2$. By solving these recursively we can find each f_t and g_t in terms of the starting values f_0 and g_0 .

It remains to calculate f_0 and g_0 , and these will, of course, depend on the past history of the population. The usual thing to do is to suppose that the population is in equilibrium, that is, the values of f and g do not change from one cycle to the next. Using the fact that the dispersal generation (generation G) of one cycle is the founding generation of the next, we find the equilibrium equations to be

$$\begin{aligned} f_0 &= f_G \\ g_0 &= mg_G, \end{aligned} \tag{6}$$

noting that the foundress has a probability m of choosing her mate from her dispersal group. This gives us a set of two equations, which can be solved for f_0 and g_0 . Finally, having found f_0 and g_0 , we can find f_G and g_G from (6).

As examples, we do the calculations for $G = 1$ and $G = 2$. When $G = 1$, the dispersal generation is the sib generation, and we have a standard model for discrete, nonoverlapping generations with partial sib-mating. The equilibrium calculation gives us

$$f_0 = f_1 = \frac{m}{4 - 3m}$$

$$g_0 = mg_1 = \frac{m}{4 - 3m}, \tag{7}$$

and, for altruism in the dispersal generation (which is sib-altruism), (4) gives us

$$R = \frac{1}{2 - m}, \tag{8}$$

a standard result for sib-altruism under partial sib-mating (Uyenoyama, 1984 eq. 10). If $m = 0$, there is no inbreeding, and we get the classical result, $R = 1/2$.

For $G = 2$ we get

$$f_0 = f_2 = \frac{2N + m}{6N - 4mN + m}$$

$$g_0 = mg_2 = \frac{m(2N + 1)}{6N - 4mN + m} \tag{9}$$

where $N = N_1$ is the size of the sib generation. For altruism in the dispersal generation, we get

$$R = \frac{2N + 1}{4N - 2mN + m}. \tag{10}$$

If $m = 0$ this equals $(2N + 1)/4N$, which is slightly less than two. The effect of the extra generation in the group is to increase the advantage of altruism in the dispersal generation.

In both (8) and (10), R increases with m . This certainly makes sense; larger m means more inbreeding and higher relatedness between members of the same group. In the extreme case of $m = 1$, all mating takes place before dispersal, and both the above equations give $R = 1$. It is not hard to argue that this will happen for all G . If there is no population-wide mating, the only equilibrium is $f_0 = g_0 = 1$, and any two individuals in the same group are genetically identical.

We now compare these results with Wilson's (1987) simulations, though it is important to note that his model differs from ours in three different aspects. First of all, as we have mentioned, Wilson (1987) assumed the altruistic allele was dominant ($h = 1$), whereas we assume no dominance ($h = 1/2$). Second, Wilson (1987) used nonzero b and c (of course), whereas our calculations of R assume $b = c = 0$. Third, although Wilson (1987) had many generations in the group, he did not build in any change in gene frequency due to sampling error after generation 2. This is a somewhat artificial situation, but it would seem that if the variance in gene frequency between stacks does not change, then neither should f and g , and the effect of the extra generations on the value of R should be minor. It is perhaps not unreasonable then to compare our results for $G = 2$ to his version 6 (Wilson, 1987 fig. 2d), with N equal to his clutch size which he took to be $C = 5$. Setting $N = 5$ and $m = 0$ in (10), we get $R = 11/20 \approx 0.55$, and so the threshold value of b/c is approximately 1.8; Wilson's graph shows a rapid increase in the equilibrium frequency of A at just about this value (Wilson, 1987 fig. 2d [$m = 0$]). Setting $N = 5$ and $m = 0.5$ in (10), we get $R = 22/31 \approx 0.71$, giving a threshold b/c of 1.4, which also agrees well with Wilson's graph.

DISCUSSION

What we have called a group is a colony, founded by a single mated female and existing for a sequence of G nonoverlapping random-mating generations with

effective size N_t in generation t . We have supposed that generation G females mate at random in the group with probability m and then disperse to found the groups for the next cycle, the unmated females mating at random in the whole population.

For any particular neutral locus, the foundress and her mate contribute four alleles to the group, and in each generation every individual possesses two copies from this set of four. As each generation is formed, the new allele pool is obtained by sampling at random from the old. Sampling error will cause the four original alleles to be unequally represented in the group. In fact, the distribution of these four alleles will tend to become lopsided with one or two, (and ultimately just one) allele remaining. This process of "genetic drift" will proceed more quickly when the effective group sizes N_t are small, and will proceed farther for greater G . The effect of this will be to increase the size of the genetic identity coefficients f_{xy} and f_x of the dispersal generation, and these are our g_G and f_G .

There are two general questions one might ask: 1) how does the selective advantage of altruism change over the life of the group, that is, is altruism more likely to occur in a young or in a mature group? and 2) how does this advantage in a fixed (say the dispersal) generation, depend on the important group parameters G and N_t . The first question is partly answered by the above discussion. As t increases, so, on the whole, do the coefficients f and g , and altruistic genes are more likely to find themselves in the company of other altruistic genes and are more likely to flourish. But the situation is complicated by the fact that, at different times, b and c may translate differently into contributions to the next cycle.

To avoid this problem, we have restricted attention to altruism in the dispersal generation, and so it is the second question that our model really addresses, though even here we run into some mathematical difficulties. Certainly our intuition tells us that as the number G of generations in the life of the group increases, so should the equilibrium values of f_G and g_G , and this is borne out by our results for $G = 1$ and $G = 2$. But a general analytic result is not easy to obtain, mainly because the recursion formulas (5) cannot be solved in any simple way, and we leave it as an open problem. It appears to be also true that smaller group sizes (N_t) will result in higher equilibrium values for f_G and g_G and, therefore, probably a higher R , but this is also hard to show.

As a check on our intuition, we have calculated some equilibrium values of f_G and g_G for large values of G under two scenarios: constant group size ($N_t = C$ for all $t \geq 1$) and exponentially growing group size ($N_t = 2(C/2)^t$ for all t), assuming no mating before dispersal ($m = 0$).

For the case of constant group size, the equilibrium values of f_G and g_G increase to 1 as G increases, and so R increases to 1. For $C = 20$, the values of R for $G = 1, 10, 20, 40$, and 80 are 0.50, 0.66, 0.77, 0.88, and 0.96, respectively. For $C = 50$, the same values are 0.50, 0.58, 0.64, 0.74, and 0.85. When the group is allowed to grow exponentially, the equilibrium values of f_G and g_G appear to be independent of G for reasonably large G . For $C = 6$, R stays close to 0.56 for all G between 30 and 50. For $C = 10$, R is close to 0.54 for the same values of G .

It is interesting to compare our results to Maynard Smith's (1964) original haystack paper. In his model, selection is strong (b and c are large), and the number of generations G in the group is large. These parameters are large enough that any group whose founders possess at least one nonaltruistic allele, will, by generation G , have lost all altruistic alleles, due to the combined forces of drift and selection. In this case, he showed that the selective advantage of altruism was highly frequency-dependent and, if the probability m of within-group mating was fairly low, selection could only favor altruism if it had a two-fold advantage and was the common allele in the population. If the allele for altruism was rare, it could never be favored unless m were close to one. Thus, our numerical calculations for constant group size, reported above, which had R increasing nearly to one as G increased to 80, could only be expected to reflect the action of selection [in Equation (1)] if b and c were extremely small, so that the process of drift has far more influence on the change in genetic composition of the groups than does selection.

Wilson's (1987) simulations also show a small amount of frequency dependence. His graphs of ESS (evolutionarily stable strategy) allele frequency against b/c show stable polymorphisms for small b/c intervals. The difference between these results and our frequency-independent values of R can be due to any (and probably to all) of the three ways in which his model differs from ours: nonzero selection instead of neutral alleles, dominance instead of no dominance, and his accounting of genetic drift only at the beginning of the life of the group.

ACKNOWLEDGMENTS

We are grateful to J. Seger for a number of helpful comments on the manuscript. This work was partially supported by grants from the Natural Sciences and Engineering Research Council of Canada, and from the National Science Foundation (BSR 8320457).

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