Polygenic Models of Group Selection for Altruism

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It is undoubtedly an interesting question whether man is by nature altruistic. Darwin (1871) was inclined to the view that man's altruistic tendencies were partly the product of evolution, and even suggested a mechanism by which they could have evolved. On the other hand, his contemporary T.H. Huxley (1893) was convinced of man's innate selfishness. Altruistic behaviors are widely observed among diverse species of animals (Wilson, 1975). Despite the possible pitfalls of arguing from analogy, and although human altruism is undoubtedly modified by culture, I believe that the underlying emotion is genetically determined. I should qualify genetic determinism to mean that the behavior is expressed in the usual environments in which man finds himself, which includes social interaction with his fellows.

Altruistic behavior is defined as behavior which reduces the fitness of the actor and improves the fitness of the beneficiary. All other things being equal, altruism is subject to adverse natural selection. In many animals, including such primates as the chimpanzee, olive baboon, and Japanese monkey, however, the species comprises many partially isolated groups. Reproduction occurs within the group, and a number of individ-

uals are exchanged each generation between the groups. The ancestral hominids most probably possessed such a population structure at least until the advent of the Neolithic revolution. With such a population structure, it is possible that selection between groups overrides countervailing selection between individuals, provided of course that the expression of altruism within a group is positively correlated with increased group proliferation or reduced group extinction. In the early hominid hunting bands, altruistic cooperation between members must have been extremely valuable for the success of the group (Morris, 1967).

The purpose of this report is to describe some models of group selection and to state the conditions for evolution of altruism by this mechanism. Detailed derivations are given elsewhere (Aoki, 1982a, 1982b; Crow and Aoki, 1982). References to the relevant background literature can also be found in these papers.

It is widely believed that most behavioral traits are multifactorial. To fix ideas, we consider as our trait the propensity to perform altruism or the intensity of altruism performed. The trait is assumed to be determined by a large number of unlinked or loosely linked genes, acting additively within and between loci, and an independent environmental component with zero mean within each group. We assume discrete non-overlapping generations. We assume Hardy-Weinberg proportions within each random mating group, and linkage equilibrium

within each group and within the whole population. We further
assume that each group, regardless of its size, exchanges an
effective number

$$M_e = 2kM_f + 2(1-k)M_m \tag{1}$$

of individuals per generation with the whole population, where
k is the proportion of males within each group at the time of
migration, and M_f and M_m are the numbers of females and males
actually exchanged. The groups themselves can be of variable
and varying sizes. These assumptions apply throughout. We
now consider some models of group selection.

Differential Proliferation Model

Although the trait is selected against within each group,
the growth rate of a group is positively correlated with the
mean value of the trait within that group. Let $\bar{C}$ be the popu-
lation (species) mean value of the trait. Then the change in
$\bar{C}$ per generation due to selection is given by

$$\Delta\bar{C} = (-\gamma V_w + \beta V_b)/\bar{W} \tag{2}$$

Here, V_w and V_b are the within- and between-group genetic
variances, $-\gamma$ is the within-group regression of the average
excess of fitness on the average effect of the trait, β is
the (between-group) regression of group mean fitness on the

group mean value of the trait, and $\bar{W}$ is the population mean

fitness. The relative importance of within- and between-

group selection is given by the two terms, $-\gamma V_w$ and βV_b. By

definition, γ and β are both positive.

The intraclass correlation between genotypic trait values

in a group is

$$r = V_b/(V_b + V_w) \tag{3}.$$

From (2) and (3), we see that the condition for the increase

of $\bar{C}$, i.e. the evolution of altruism, is

$$r > \gamma/(\gamma+\beta) \tag{4}.$$

In the balance between the island model type migration

assumed here (Wright, 1940) and random drift, we have

$$r \simeq 1/(1+2M_e) \tag{5},$$

provided M_e is sufficiently small compared to the minimum group

size. By combining (4) and (5), we can obtain an upper limit

on M_e for altruism to evolve. Strictly speaking, the relation

(5) is valid only for genes not subject to selection, but our

assumptions insure weak selection at each contributing locus,

and thus the approximation should be good. Since we are

assuming the existence of a large number (to be precise an

infinite number) of groups, there will be no change in $\bar{C}$ due to migration and random drift.

Groups that grow too large tend to split into new sub-populations. $\bar{C}$ is unaffected by the process, as is r if the split is random. If the split is assortative, r increases, and this is favorable to our model. Studies of the Yanomamo Indians (Chagnon, 1979) and macaques (Furuya, 1969; Cheverud et al., 1978) show that group fission is such that relatives stay together. On the other hand, groups that grow too small are expected to go extinct for nongenetic as well as genetic reasons. Since a smaller group usually has a smaller mean value of the trait, this should contribute to an increase of $\bar{C}$. These processes are not explicitly modeled.

Differential Extinction Model

A group with a lower mean value of the trait suffers a higher probability of extinction. The change in $\bar{C}$ per generation due to selection is

$$\Delta\bar{C} \simeq (-\gamma V_w + \beta V_b/\bar{\alpha})/\bar{W} \qquad (6).$$

Here, V_w, V_b, $\bar{W}$, and γ are as before; β is the regression of group survival probability (i.e., 1 minus the extinction probability) on the group mean value of the trait, and $\bar{\alpha}$ is the mean survivorship of the whole population. Equation (6) is approximately valid for weak selection. In terms of r, the

condition for group selection to prevail over individual selection is

$$r > \gamma/(\gamma + \beta/\bar{\alpha}) \qquad (7)$$

Replacement of an extinct group can occur by the splitting of a large surviving group. If we picture a new group as being formed by the association of colonists from many groups, then we must assume that extinction is generally rare, i.e. $\bar{\alpha} \simeq 1$. In either case, the effect of recolonization on r can be neglected, and to a first order of approximation r is determined by migration and random drift (equation (5)). Also, group growth can occur in this model, provided it is uncorrelated with the altruistic trait.

Hamilton's Model of Benefit Dispensation

Hamilton (1975) assumed that an altruist suffers a cost in fitness c, while donating a total benefit b which is distributed evenly among the group members; each member experiences its share of the benefit as an increment to its fitness, and the total benefit to each member is the sum of increments received from all sources within the group. This scheme of benefit dispensation is a special case of the differential proliferation model.

It is straightforward to show (Aoki, 1982c) that

$$\gamma = c \qquad\qquad (8)$$

and

$$\beta = b-c \qquad\qquad (9).$$

Substituting (8) and (9) into (4), we obtain

$$r > c/b \qquad\qquad (10),$$

which is commonly called Hamilton's inequality.

We note in passing that (10) can be derived without the assumptions of Hardy-Weinberg proportions and linkage equilibrium within each group. Thus (10) is also valid in a kin selection model (Aoki, 1982c). In fact, Hamilton's model and inequality were originally proposed in the context of kin selection (Hamilton, 1964).

Discussion

The costs and benefits associated with altruism are generally quite difficult to measure. See Maynard Smith and Ridpath (1972) for a rare example in which these selection parameters have been successfully measured. Here, however, the form of selection is kin selection and not group selection.

It is perhaps a more straightforward matter (but still

quite arduous) to estimate r. For example, the average value
of r in troops of Japanese monkeys, as estimated from variation
at 16 (neutral) polymorphic loci in 33 troops, is a little less
than 1/6 (based on data from Nozawa et al., 1982). The value
falls between the genetic correlation values of 1/4 for half
sibs and 1/8 for cousins in a large random mating population.
We can at least say that if group selection is to be invoked to
explain the existence of an altruistic behavior in the Japanese
monkey (see Kurland (1976) for examples), then the cost and
benefit must be such that the relevant inequality (2), (6), or
(10) is satisfied with r ≃ 1/6.

When protein or isozyme electrophoretic data are not avail-
able, observation of the number of migrants per generation can
be used to estimate r (equation (5)). Equation (5) is based on
the island model which assumes that the immigrants are a random
sample of the whole species. In reality, migration is usually
restricted to adjacent groups. In this case, we must apply a
correction factor to equation (5); it is appropriate to multi-
ply the observed M_e by 1/3 to 1/4 before substituting it into
the equation (Crow and Aoki, 1982).

In considering the repertoire of altruistic behaviors
demonstrated by man, one is struck by the many examples of
alruism performed with the expectation of future reciprocation.
Perhaps heroism in war (or on the hunt) is a rare example of
"unconditional" altruism, although even in this case the motive
appears to be not entirely free of baser feelings. Certainly,

heroism, either done or perceived, invokes strong emotions in man, and this is probably not so much a result of our upbringing as our biological heritage. The cost and benefit of heroism in our hunter-gatherer days were possibly such that it was favored by group selection. It has even been suggested that recent improvements in the means of travel are responsible for a decline in our altruistic tendencies by having caused a drop in r. Although this observation may apply to heroism, it is probably a reduced expectation of reciprocation in an alienated society which has led to the general decline.

Summary

Conditions are derived for altruism to evolve under various models of group selection. The altruism is assumed to be determined by many additively acting genes and an independent environmental component.

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