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Evolution of Social Behavior Through Interpopulation Selection

(spite/selfishness/group selection/altruism)

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ABSTRACT Under certain special conditions natural selection can be effective at the level of local populations, or demes. Such interpopulation selection will favor genotypes that reduce the probability of extinction of their parent population even at the cost of a lowered inclusive fitness. Such genotypes may be characterized by altruistic traits only in a viscous population, i.e., in a population in which neighbors tend to be closely related. In a nonviscous population the interpopulation selection will instead favor spiteful traits when the populations are susceptible to extinction through the overutilization of the habitat, and cooperative traits when it is the newly established populations that are in the greatest danger of extinction.

Recent theory has established that natural selection can be effective at the level of local populations, or demes, under certain rather restricted conditions (1–3). When these conditions obtain, interpopulation selection may result in the persistence of genotypes that reduce the probability of extinction of their parent population, even when such genotypes possess an inclusive fitness lower than that of the alternative selfish genotypes. It has been generally assumed that such "patriotic" genotypes would be characterized by the so-called altruistic traits. I will show that this may be the case only in a viscous population, i.e., in a population in which neighbors tend to be closely related individuals. In a nonviscous population the interpopulation selection will instead tend to favor spiteful traits when the populations are likely to become extinct through over-population and the consequent overutilization of the habitat, and cooperative traits when the populations tend to be wiped out when newly established and below a critical minimum size.

The outcome of natural selection will depend on an interplay between the interpopulation and the intrapopulation selection. Interpopulation selection will favor genotypes that reduce the population growth when the populations are susceptible to extinction through overpopulation, and will favor genotypes that enhance the population growth when the populations are liable to extinction when below a critical minimum size. Intrapopulation selection, on the other hand, will favor the genotype with the highest inclusive fitness irrespective of the effect of such a genotype on the chances of extinction of its parent population. I will investigate these selective pressures in the context of a model of a very simple genetic system which takes account of social effects of genotypes.

Consider an asexual organism with nonoverlapping generations. For such an organism, the genetic fitness W is equivalent to the net reproductive rate R given by

$$N(t + 1) = RN(t),$$

where $N(t)$ is the population size at time t. The net reproductive rate R may be decomposed into three components: a base rate v, a neighbor effect x, and a self-effect resulting from the social interaction y. Social traits may be distinguished into selfish, cooperative, altruistic, and spiteful on the basis of signs of x and y. A selfish individual achieves a positive self-effect y at the cost of a negative social effect x. Both the social and self-effects are positive for a cooperative individual, while they are both negative for a spiteful individual. An altruist sacrifices its own fitness, i.e., has a negative y in order to achieve a positive social effect x. To sum up:

$$x_{sl} < 0, \qquad y_{sl} > 0 \qquad [1a]$$

$$x_{co} > 0, \qquad y_{co} > 0 \qquad [1b]$$

$$x_{sp} < 0, \qquad y_{sp} < 0 \qquad [1c]$$

$$x_{al} > 0, \qquad y_{al} < 0 \qquad [1d]$$

$$x_{as} = 0, \qquad y_{as} = 0 \qquad [1e]$$

Here the subscripts are: *sl* for selfish, *co* for cooperative, *sp* for spiteful, *al* for altruistic, and *as* for asocial. The subscript *so* will also be used below to denote any of the four social traits with nonzero x and y.

Consider a large, thoroughly mixed, i.e., fully nonviscous population of such an organism comprising N_1 individuals of genotype 1 and N_2 of genotype 2. The total social effect generated in the population will be $x_1N_1 + x_2N_2$. This will be shared equally by all individuals so that the social effect per individual is $(x_1N_1 + x_2N_2)/(N_1 + N_2)$. If p is the frequency of genotype 1 and $1 - p$ that of genotype 2, then the social effect per individual is $px_1 + (1 - p)x_2$. The magnitude of self-effect is independent of frequency and will be y_1 for an individual of genotype 1 and y_2 for an individual of genotype 2. Then:

$$N_1(t + 1) = N_1(t)(v + px_1 + (1 - p)x_2 + y_1)$$

$$N_2(t + 1) = N_2(t)(v + px_1 + (1 - p)x_2 + y_2)$$

and

$$W_1 = v + px_1 + (1 - p)x_2 + y_1 \qquad [2a]$$

$$W_2 = v + px_1 + (1 - p)x_2 + y_2 \qquad [2b]$$

where W_1 and W_2 are absolute fitnesses of genotypes 1 and 2, respectively. The relative fitness of genotype 1 with respect to genotype 2, designated $U_{1,2}$ is:

$$U_{1,2} = (z + y_1)/(z + y_2) \qquad [3]$$

where

$$z = v + px_1 + (1 - p)x_2$$

For the case where one of the genotypes is asocial, and the other social, the relative fitness of the social genotype is

$$U_{so,as} = 1 + [y_{so}/(v + px_{so})] \quad [4]$$

These fitnesses take explicit account of neighbor-modulated effects and are equivalent to the inclusive fitness introduced by Hamilton (4). Intrapopulation selection would favor the particular social or asocial trait with the highest relative fitness U. Eq. **4** shows that intrapopulation selection would favor a social trait over asociality only if the former has a positive self-effect y. Note that $v + px$, the denominator, is the absolute fitness of the asocial type, and therefore can never be negative, being defined as the ratio of two positive numbers. Therefore, asociality will prevail over altruism and spite, but not over selfishness and cooperation. Eq. **3** further suggests that amongst the last two, intrapopulation selection would favor the trait with the larger self-effect, irrespective of the magnitude of the social effects.

These results depend on the assumption of complete mixing in the population and will be changed if the social effect is preferentially directed to individuals with more or less than the average degree of relatedness. This could happen, for example, through a tendency for the relatives to remain together or through an ability to distinguish kin from nonkin. In particular, both altruism and spite, ruled out above, may then evolve. Altruism may evolve if the recipients of the social benefit are related more than average to the donor of the benefit, and spite may evolve if the recipients of the social harm are related less than average to the dispenser of the harm (4, 5). Thus all the four social traits considered may be shown to evolve without reference to interpopulation selection. Nevertheless, whenever effective, interpopulation selection must have social consequences and I intend to explore these.

Interpopulation selection, with its tendency to favor genotypes that reduce the probability of extinction of their parent populations, may operate under two very different regimes (6). If the populations are in the greatest danger of extinction when newly formed and below a critical size, interpopulation selection would favor "patriotic" genotypes which enhance the population growth rate so that the populations remain below the critical minimum size for the shortest possible duration. "Patriotic" genotypes that thus enhance the population growth rate are termed "pioneers". If, on the other hand, the populations are susceptible to extinction through overpopulation and the consequent overutilization of the habitat, interpopulation selection would favor genotypes that depress the population growth rate. Such "patriotic" genotypes have been termed "urbans". In either case the selective pressures exerted by the interpopulation selection will be proportional to the efficacy of a genotype in either enhancing or depressing the population growth rate, as the case may be.

From Eqs. **2a** and **2b** the growth rate of a population comprising two genotypes 1 and 2 is given as:

$$\begin{aligned} \overline{W} &= pW_1 + (1 - p)W_2 \\ &= v + p(x_1 + y_1) + (1 - p)(x_2 + y_2) \end{aligned} \quad [5]$$

The contribution to population growth of genotype i is thus given by $x_i + y_i$, the sum of its self- and social effects. Interpopulation selection for pioneer patriots would favor high positive values of $x + y$ and that for urban patriots would favor high negative values of $x + y$. Obviously cooperative individuals can be pioneers, but not urbans, and spiteful individuals can be urbans but not pioneers. In theory, selfish and altruistic individuals can be both pioneers and urbans. However, selfish individuals are unlikely to be effective either as pioneer or as urban patriots. This is because their positive self-effect is achieved at the cost of a negative social effect. The individual and its neighbors will then be in a situation of conflict, and this should generate selective pressures for minimizing x as well as y. As the social and self-effects are of opposite signs and unlikely to be very large in magnitude, the resultant sum is unlikely to reach high positive or high negative values.

The altruists achieve a positive social effect by sacrificing their own fitness. There will then be no conflict with the neighbor and it may be possible to achieve a high social effect at the cost of a relatively small self-sacrifice, i.e., a high positive x for a small negative y, and hence a high positive $x + y$. Altruists can then be effective as pioneers. Cooperative traits achieve a positive self- as well as social effect, and should also be effective as pioneers. No statement, however, seems possible about cooperators' effectiveness relative to the altruists without more detailed models of social behavior.

On the other hand, altruists should be rather ineffective as urbans, and it is possible to argue that spiteful individuals would be much more effective in this regime. By definition, altruists have a positive x, and hence can achieve high negative values of $x + y$ only through a very negative self-effect y, i.e., by very substantially reducing their own survivorship and reproductive output, but without actively benefiting others so that x also remains low. Spiteful individuals, on the other hand, should be much more effective urbans, as they achieve negative values of both x and y. Thus spiteful individuals may not only reduce their own survivorship and reproductive output below the maximum possible, which is the only recourse open to the altruists, but may also channel the resources thus saved towards reducing the survivorship and the reproductive output of their neighbors as well. For example, birds may hold excessively large breeding territories so that the demands of territorial defense actually depress their own reproductive output below that achieved by holding a somewhat smaller territory. This may simultaneously depress the reproductive output of neighbors by either throwing them out of the category of territory holders who may breed, or by reducing the size of their territories below the optimum size for reproductive success. Poisoning of the environment by the secretion of noxious metabolites and cannibalism are other possible examples of spiteful behavior. Such behavior must obviously be more effective than altruistic behavior in depressing the population growth rate.

In addition to interpopulation selection, the social traits will also be subject to intrapopulation selection for the maximization of inclusive fitness. If two traits are equally favored by interpopulation selection, then clearly the trait with a higher inclusive fitness will be favored through the combined influence of inter- and intrapopulation selection pressures. The extent of interpopulation selection pressure depends on the effectiveness of a social trait in enhancing or depressing the population growth rate, i.e., on the value of $x + y$. It is therefore of interest to consider the relative inclusive fitness of the various social traits, assuming that they achieve the same value of $x + y$. Then for the pioneers:

$$x_{al} + y_{al} = x_{co} + y_{co} = x_{sl} + y_{sl} > 0 \quad [6]$$

From **1a**, **1b**, and **1d**, and **6**

$$x_{al} > x_{co} > x_{sl}$$

$$y_{sl} > y_{co} > y_{al}$$

These inequalities allow the computation of the relative fitnesses of the social traits either when they are competing with asocial individuals or with each other. In the first case:

$$1 + \frac{y_{sl}}{v + px_{sl}} > 1 + \frac{y_{co}}{v + px_{co}} > 1 + \frac{y_{al}}{v + px_{al}}$$

and hence

$$U_{sl,as} > U_{co,as} > U_{al,as}$$

This follows from the fact that the denominators must all be positive as shown above, and from the inequalities of x and y. Also:

$$U_{sl,co} = (y_{sl} + z)/(y_{co} + z) > 1$$

$$U_{sl,al} = (y_{sl} + z)/(y_{al} + z) > 1$$

$$U_{co,al} = (y_{co} + z)/(y_{al} + z) > 1$$

Thus, assuming that the alternative genotypes are equally effective in enhancing the population growth rate, the selfish trait has the highest, the cooperative trait the intermediate, and the altruistic trait the lowest inclusive fitness. However, it was argued above that only the last two will in fact be effective in enhancing population growth, and hence need be considered in the context of interpopulation selection. Since of these the cooperative traits will be favored over altruistic traits by intrapopulation selection, cooperative traits are the more likely to characterize pioneer patriots.

A similar analysis may be applied to the urbans by assuming that the altruistic, spiteful, and selfish traits are equally effective in depressing the population growth, i.e.,

$$x_{al} + y_{al} = x_{sp} + y_{sp} = x_{sl} + y_{sl} < 0 \qquad [7]$$

From **1a**, **1c**, and **1d**, and **7**

$$x_{al} > x_{sp} > x_{sl}$$

$$y_{sl} > y_{sp} > y_{al}$$

From these the relative fitnesses of social traits may be computed as above. When they are competing with asocial individuals:

$$1 + \frac{y_{sl}}{v + px_{sl}} > 1 + \frac{y_{sp}}{v + px_{sp}} > 1 + \frac{y_{al}}{v + px_{al}}$$

and hence

$$U_{sl,as} > U_{sp,as} > U_{al,as}$$

When the social traits are competing with each other:

$$U_{sl,sp} = (y_{sl} + z)/(y_{sp} + z) > 1$$

$$U_{sl,al} = (y_{sl} + z)/(y_{al} + z) > 1$$

$$U_{sp,al} = (y_{sp} + z)/(y_{al} + z) > 1$$

Thus, assuming the three types to be equally effective in reducing population growth, the selfish trait has the highest, the spiteful trait the intermediate, and the altruistic trait the lowest relative fitness. However, it was argued that the selfish trait would not be able to achieve high negative values of $x + y$ and hence only the last two may be considered in the context of the evolution of urban traits. Of these, it was shown that spite should be more effective in terms of reducing population growth. It is also the trait with a higher inclusive fitness even if altruism were to be equally effective in depressing population growth. Hence both inter- and intrapopulation selection would favor spite over altruism in the case of populations susceptible to extinction through an overutilization of the habitat. Behavior patterns often invoked in discussions of self-regulation of populations such as maintenance of excessively large territories are then interpretable as instances of spiteful behavior evolving through interpopulation selection for urbans. It is of course possible, and probably likely, that much of this behavior is simply selfish; however, the possibility of its evolution through interpopulation selection must also be kept open.

Our entire analysis is based on the assumption of a non-viscous population. Viscosity of the population results in an enhancement of the inclusive fitness value of altruistic traits, and a reduction in the inclusive fitness value of spiteful traits, leaving the inclusive fitness of cooperative traits relatively unaffected. Such a change in intrapopulation selection pressures could reverse the balance suggested for thoroughly mixed populations, and could lead to the evolution of altruism as both pioneer and urban traits through interpopulation selection. More sophisticated models will be required for an analysis of this situation, which will not be attempted here.

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1. Levins, R. (1970) in *Some Mathematical Questions in Biology* (Lectures on Mathematics in the Life Science, American Mathematical Society, Providence, R.I.), Vol. 2, pp. 75–108.
2. Eshel, I. (1972) "On the neighbour effect and the evolution of altruistic traits," *Theor. Pop. Biol.* **3**, 258–277.
3. Boorman, S. A. & Levitt, P. R. (1972) "Group selection on the boundary of a stable population," *Proc. Nat. Acad. Sci. USA* **69**, 2711–2713.
4. Hamilton, W. D. (1964) "The genetical evolution of social behaviour I," *J. Theor. Biol.* **7**, 1–16.
5. Hamilton, W. D. (1970) "Selfish and spiteful behaviour in an evolutionary model," *Nature* **228**, 1218–1220.
6. Wilson, E. O. (1973) "Group selection and its significance for ecology," *Bioscience* **23**, 631–638.