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On the Neighbor Effect and the Evolution of Altruistic Traits*

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The long-term effects of natural selection are studied in a large population in which survival and fertility of any individual depend not only on its own genotype, but also on the genetic features of neighboring members of its species—a relatively small group of individuals sharing its social community or immediate geographic vicinity and partially separated from similar groups within the population as a whole. Random drift within such local groups or subpopulations, as well as migration among them are taken into account. Conditions for the evolution of altruistic biological traits, are analyzed. Special consideration is given to natural mechanisms of birth control, and possible implications to human evolution are offered. In agreement with Wright (1945), low demographic mobility proves to be the most crucial factor for the evolution of altruistic traits.

1. INTRODUCTION

This study is concerned chiefly with the evolution of biological traits of the sort generally referred to as *altruistic*. These are inherited traits, whether behavioral or physiological, that are at once beneficial to a population as a whole and deleterious to the individual carrier. In this connection, beneficial and deleterious are defined with respect to fitness, i.e., with respect to the expected numbers of viable offspring.

We use the term altruistic for reasons of tradition (see, for example, Haldane, 1932, 1955; Hamilton, 1964, Wynne-Edwards, 1962; Kress, 1970; Trivers, 1971 and references therein). The biological traits falling within this general connotation vary enormously in character, some having very little in common with the more conventional notion of altruism. The inefficiency of some weapons used in mating fights, such as the antlers of bucks or the excessively curved horns of bighorn—both primarily physiological traits—are examples. Obviously restricting the fitness of their carriers, they serve the function of species survival

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by permitting a test of strength without imposing too high a toll of mortality on the population (Lorenz, 1963).

A somewhat similar phenomenon is the development of unpalatability in its relationship to mimicry. Though the trait is ultimately beneficial to the species, it cannot save the individual already killed by the predator who has not yet associated the species' sight with its taste. In such cases, such as the tropical butterflies studied by Blest (1963), Benson (1971), and Fisher (1927), the unpalatable individual, as well as, in many cases, a palatable mimic, is protected by a conspicuous species marker that deters experienced predators. The marked individual is thus directly selected in the population (Fisher, 1927). Indeed the deterrent value of the marker depends on the average unpalatability among individuals in the combined populations of the unpalatable species and the mimicking species. Thus although unpalatability proves essential for the population, a direct selection in its favor may be difficult to recognize. Moreover, because of the possible biochemical costs of unpalatability, the less unpalatable individual may be of a higher fitness (see, for example, Brower, 1969).

The necessary question of what is the selection pattern that enables the evolution of individually disadvantageous traits is of particular interest when it concerns the evolution of inherited mechanisms functioning to reduce fertility in conditions of overpopulation. Nervous tension leading to failure in copulation, as observed in some small mammals (Christian, 1956; Lloyd and Christian, 1969), or the inhibitions to mating in some birds and sea mammals anywhere but in a specific limited area (Wynne-Edwards, 1962) are examples. That such obviously fitness-reducing patterns may be advantageous for the population as a whole offers only part of the answer (see, for example, Christian, 1970). In fact, the problem of population-control mechanisms reduces to a special case of altruist evolution.

From the standpoint of population biology, the crucial question remains how the process of natural selection can favor any inherited trait that by its nature acts to reduce fertility and thus to decrease the frequency of its carrier in the population. The question in fact arises in the evolution of all altruistic traits, however different their manifestation may be. The prevailing explanations of the phenomenon are based upon three factors: kin selection (Haldane, 1932, 1955; Fisher, 1958; Hamilton, 1964); group selection (Wynne-Edwards, 1962); and social compensation (see, for example, Trivers, 1971; Kress, 1970; Hall and DeVore, 1965; and others).

Social compensation may be granted in the form of rank attainment (such as leadership of the group), reciprocation (a kindness returned in kind), or discrimination against the selfish. Though these mechanisms undoubtedly account for many seemingly altruistic behavior patterns, they fall beyond the scope of this work. In fact, patterns fully explained by social compensation are not truly altruistic by our definition, since they do not reduce fitness.

Notwithstanding, it may be that many observed seemingly altruistic behaviors, such as food sharing or cooperation in defense, should be examined more carefully with regard to social compensation for the individual. To avoid this difficulty, I prefer to concentrate our investigation on—though not restrict it to—the more physiologically oriented examples, such as those mentioned previously. In so doing, we also avoid a controversy that has long haunted genetics, a controversy deriving from the theoretical difficulty in applying the term "intrinsic" to behavior patterns (see, for example, Hebb, 1953; Lehrman, 1953; Lorenz, 1965).

The object of this study is to generalize to a single quantitative model both prevailing explanation for the evolution of true altruism, namely, group selection and kin selection. The quantitative findings of our model accord with the basic premise of Wright (1945) that a prerequisite for the evolution of what we have called altruism (Wright does not use the term) is a partial separation of the population into relatively small subpopulations or *demes,* with a low rate of migration among them. In nature, demes are represented by geographic patches or "islands" (compare, for example, Wright, 1949, 1969); but quantitative development of a model based on Wright's premises may be pursued for any partition of a population where the probability of a random offspring's remaining in the parents' deme is sufficiently high. Where mobility is low, perhaps because of a restricted range of dispersal, the model may be valid even for arbitrary subdivisions of an essentially continuously populated area. Moreover, if we consider demes of family-like castes or tribes where deme-to-deme migration is social rather than geographic, the partial-separation model generalizes to include kin selection as a special case. In fact, the distinction between kin selection and group selection is not clear cut in the model, since even with purely geographic subdivision of a population, a low rate of migration among demes tends to increase the rate of identity by descent within them (Wright, 1917, 1952; see also Malecot, 1955; Kimura and Weiss, 1964; Maruyama, 1969). Yet kinship within a subpopulation though common, is not a prerequisite for the development of the model. Partial separation alone may suffice to explain the evolution of an altruistic trait, particularly where the distribution of kinship is difficult to detect (see, for example, Trivers, 1971). In extreme cases it may even explain the co-evolution of such a trait within a multispecies population—for example, the matching warning calls of some bird populations (Williams, 1966; see also Trivers, 1971) or the simultaneous development of unpalatability by identically marked species of butterflies (see above). But in any case, by assuming a well-defined probabilistic process of selection *within* a population, the model seems to avoid most of the objections against over-emphasizing the role of group selection in the theory of natural selection (see, for example, Williams, 1966).

The model attempts to explain and analyze the evolution of altruistic traits chiefly on the basis of the genetic variation from deme to deme resulting from the random character of the reproduction process within each deme. This variation yields differences in local levels of mortality, since subpopulations in which the altruistic type happens to be rare are likely to suffer demographically. For example, in a case where birth control is essential for the population, a total subpopulation may eventually starve because too many of its individuals lack such a control. Thus on a purely statistical basis the nonaltruistic type is more likely to suffer such a disaster, simply because, on the average, it appears with higher frequency in disaster areas. In this sense it is convenient to speak of a selective *neighbor effect*, operating to reduce the frequency of the nonaltruistic type in the population.

It must be emphasized, however, that neighbor selection differs markedly in character from classic fitness selection, which operates to *increase* the frequency of the nonaltruistic trait wherever it exists. Thus in a quantitative situation the long-term effect of these two contradictory forces is difficult to predict without more precise mathematical tools. The process is by its nature multidimensional, being characterized by changes not only in whole-population gene frequencies but also in the distribution of gene frequencies in the various demes.

Our main objective in this study is to answer the crucial question whether, and under what conditions, an altruistic trait is to be maintained or, further, become fixed in the population. For the mathematical development of the model we assume an infinite population partially separated into many finite demes. As a first approximation, to avoid the complications of heterozygosity and mating systems, we ignore effects of sex and diploidy. But in allowing the most general law of reproduction to hold within the demes, a generalization to the sexual diploid case appears to be natural consequence.

The chief quantitative result of this study is the demonstration of the essential role of mobility (which we shall define rigorously in due course) in the evolution of the altruistic type. More specifically we shall show that for any altruistic feature, a sufficiently low rate of mobility will ensure its eventual fixation in the entire population. A sufficiently high demographic mobility, by contrast, results in fixation on the alternative, nonaltruistic type. Actually, the critical mobility rates differ from one altruistic trait to another, depending on intensities of the selection forces within and among subpopulations. If the rate of demographic mobility exceeds the relative fitness of the altruistic trait, it cannot become fixed in the population, however great the advantage it brings to its subpopulation. Yet if this advantage is sufficiently great, a coexistence of types can be established in the population—perhaps a stable polymorphism.

Since a drastic change in the crucial factor of demographic mobility is exclusively typical of the human race (see, for example, Campbell, 1966; Lee and DeVore, 1968), special consideration will be given to the possible impact of these theoretical findings on certain aspects of the evolution of man. Support, from a theoretical point of view, will be accorded the hypothesis (see, for example, Wynne-Edwards, 1965) that the human race might have lost some intrinsic birth-control mechanism sometime prior to the rise of civilization.

Finally, the model suggested in this work, though originally motivated by an interest in altruistic vs. nonaltruistic competition, may be applied to a larger variety of problems in evolution.

2. THE MODEL AND ITS BASIC PROPERTIES

We assume a countable number of demes, each comprising exactly N individuals of type A or B. For a given time t $(t = 0, 1, 2,...)$ let $x_i = x_i^{(t)}$ $(x_i = 0, 1,..., N)$ be the number of A-type (altruistic) individuals in the deme i $(i = 1, 2,...)$. For any $1 \leqslant k \leqslant N$ we assume that a portion $0 \leqslant \xi_k \leqslant 1$ of all the demes includes exactly k A-type individuals $(\sum_{k=0}^{N} \xi_k = 1)$. Formally,

$$\xi_k = \lim_{m\to\infty} \frac{1}{m} \sum_{i=1}^{m} \delta(x_i, k). \tag{2.1}$$

Here $\delta(x_i, k)$ stands for the Kroneker δ. We denote by

$$\bar{x} = \sum_{k=0}^{N} \xi_k k \tag{2.2}$$

the average number of A-type individuals in a typical deme. The portion of the A type in the whole population is $\bar{x}/N$. For most purposes, however, further information is needed about the distribution of the A type among the demes. The genetic composition of the population will thus be characterized by the point $\xi = (\xi_0, \xi_1, ..., \xi_N)$.

From one generation to the next, the population is changed owing to random replacement within demes, migration between them, and possible disasters, which may wipe out the population of some demes. The development of the process is governed by the following rules:

(A) *For a given subpopulation the probability of disaster depends only on its genetic composition, actually on the proportion of A-type individuals within it.*

Formally, let us denote the random variables at a given generation:

$$Y_i = \begin{cases} 0 & \text{if disaster occurs to the subpopulation } i \\ 1 & \text{otherwise} \end{cases} \tag{2.3}$$

$(i = 1, 2,...)$. The survival probability of a subpopulation with r A-type individuals is given by

$$P(Y_i = 1 \mid x_i = r) = q_r > 0. \tag{2.4}$$

The differences among the values $q_0, q_1, \dots, q_N$ indicate group selection based on the frequency of the A type.

(B) *Any surviving subpopulation reproduces according to a random process in which parents are chosen with probability* $1 - \alpha$ $(0 \leqslant \alpha \leqslant 1)$ *from its immediate deme or with probability* α *from any other one.*

The value α indicates the rate of migration or *demographic mobility* in the population. The value

$$x = x(\alpha, r, \bar{x}) = \alpha\bar{x} + (1 - \alpha)r \tag{2.5}$$

represents the average number of A-type individuals in the potential parent population, which is relevant to the reproduction process in a subpopulation originally including r A-type individuals $(r = 0, 1, \dots, N; 0 \leqslant x \leqslant N)$.

(C) *For any value* $0 \leqslant x \leqslant N$ *and any number* $k = 0, 1, \dots, N$, *there is a probability*

$$C_{x,k} = C_{\alpha\bar{x}+(1-\alpha)r,k} \quad \textit{abbreviated as} \quad C^{\alpha}_{r,k}(\bar{x}) \tag{2.6}$$

that the number of A-type offspring in a subpopulation will be k, if the amount of the A type in its potential parent population is x.

The notation $C^{\alpha}_{r,k}(\bar{x})$ is a convenient representation of the transition probability from r to k, in any specific deme when α and $\bar{x}$ are given. Clearly

$$\sum_{k=0}^{N} C_{x,k} = 1; \qquad C_{x,k} \geqslant 0. \tag{2.7}$$

These values, which are determined by the law of reproduction within the subpopulations, will be called the *basic reproduction probabilities.*

(D) *The number of A-type offspring reproduced in any deme increases with the frequency of this type in the potential parent population.*

More specifically we assume that the distribution of A-type offspring in a deme increases in monotone likelihood ratio with the frequency x of this type in the potential parent population. In other words the ratio $C_{x,k+1}/C_{x,k}$ is an increasing function of x (with values on the close interval $[0, \infty]$) for all $k = 0, 1, \dots, N - 1$ so that $C_{x,k}$ is a TP_2 function of x and k (Totally Positive of order 2; see Karlin, 1968).

EXAMPLE. Adapt the standard Wright–Fisher random sampling model with selection to our case (see, for example, Wright, 1969). We obtain

$$C_{x,k} = \binom{N}{k} \frac{(\theta x)^k (N - x)^{N-k}}{[N - (1 - \theta)x]^N}, \tag{2.8}$$

where $\theta > 0$ is the relative fitness of the A type with respect to that of the alternative β type. If A, here, is the altruistic type, clearly $\theta < 1$.

(E) *For each k, $C_{x,k}$ is continuous on $[0, N]$ and has left and right nonzero derivatives at the appropriate edges.*

This is a technical assumption to facilitate proofs.

If we stipulate

$$\text{(F)} \qquad C_{N,N} + C_{0.0} = 1,$$

the process is said to have no mutation.

The fulfillment of (D)–(F) by (2.8) is immediate.

In order to extend the definition of individual advantage to this class of reproduction probabilities, it is useful to introduce the function

$$\psi(x) = E(k \mid x) = \sum_{k=1}^{N} kC_{x,k}, \tag{2.9}$$

which is the expected number of A-type offspring born in a deme, conditioned on the frequency x of this type in the potential parent population.

Assumptions (D) and (E) imply that $\psi(x)$ is a continuous and monotone-increasing function over $[0, N]$, with *positive* derivatives at the edges. Under the assumption (F) of no mutations, we also get

$$\psi(0) = 0; \qquad \psi(N) = N. \tag{2.10}$$

We shall say that the B type is individually advantageous if

$$\text{(G)} \quad \psi(x) < x \quad \textit{for all} \ \ 0 < x < N, \qquad \textit{and} \qquad \psi'(N) > 1 > \psi'(0).$$

For the case of Fisherian selection with a complete mix of the population ($\alpha = 1$), the assumption $\psi(x) < x$ means that the frequency of the B type is ever increasing in the population over successive generations. To see this we denote

$$Q = Q(\xi) = \sum_{r=0}^{n} \xi_r q_r, \tag{2.11}$$

which is the one-generation survival probability of a random subpopulation.

Clearly, we obtain

$$\bar{x}' = \sum_{k=1}^{N} k\xi_k' = Q^{-1} \sum_{k=1}^{N} k \sum_{r=0}^{N} \xi_r q_r C_{\bar{x},k} = \sum_{k=1}^{N} kC_{\bar{x},k} = \psi(\bar{x}) < \bar{x}. \tag{2.12}$$

Under the same argument, the assumption $\psi'(0) < 1 < \psi'(N)$ implies a geometric rate of introducing and fixation of the individualy advantageous type in the population.

For the Wright–Fisher model of random reproduction, (2.9) becomes

$$\psi(x) = \sum_{k=0}^{N} k \binom{N}{k} \frac{(\theta x)^k (N-x)^{N-k}}{(N-x+\theta x)^N} = \frac{N\theta x}{N-x+\theta x} \qquad (2.13)$$

and condition (G) is fulfilled when $\theta < 1$.

The bulk of the mathematical analysis of this work will deal with the no-mutation case. However, most results will be extended, though in a slightly weaker sense, to the situation in which a sufficiently low rate of mutation is allowed.

Independently of the reproduction probabilities, we obtain, from (2.1), (2.3), and (2.4) by using the ergodic theorem,

$$\frac{1}{m} \sum_{i=1}^{m} Y_i \delta(x_i, r) \xrightarrow[(m\to\infty)]{} P(x_i = r)\, P(Y_i = 1 \mid x_i = r) = \xi_r q_r$$

and thus, using again the ergodic theorem,

$$\frac{1}{m} \sum_{i=1}^{m} Y_i = \sum_{r=0}^{N} \frac{1}{m} \sum_{i=1}^{m} Y_i \delta(x_i, r) \xrightarrow[(m\to\infty)]{} \sum_{r=0}^{N} \xi_r q_r = Q(\xi). \qquad (2.14)$$

Denoting by x_i' the number of A-type surviving offspring in the i-th surviving subpopulation ($i = 1, 2, 3, \ldots$), we obtain, in the same way,

$$\frac{1}{m} \sum_{i=1}^{m} Y_i \delta(x_i', k) = \sum_{r=0}^{N} \frac{1}{m} \sum_{i=1}^{m} Y_i \delta(x_i, r)\, \delta(x_i', k) \xrightarrow[(m\to\infty)]{} \sum_{r=0}^{N} \xi_r q_r C^{\alpha}_{r,k}(\bar{x}). \quad (2.15)$$

The existence of the relative frequency of subpopulations with k A-type individuals among the survivors is implied by (2.13) and (2.14) (we use again the ergodic theorem and the interchangeability of the subpopulation index variable i):

$$\begin{aligned}
&\lim_{m\to\infty} \frac{1}{m} \sum_{i=1}^{m} \delta(x_i', k) \lim_{m\to\infty} \left(\sum_{i=1}^{m} Y_i \delta(x_i', k) \Big/ \sum_{i=1}^{m} Y_i \right) \\
&\quad = \sum_{r=0}^{N} \xi_r q_r C^{\alpha}_{r,k}(\bar{x}) \Big/ \sum_{r=0}^{n} \xi_r q_r \\
&\quad = Q^{-1} \sum_{r=0}^{N} \xi_r q_r C^{\alpha}_{r,k}(\bar{x}) = \xi_k'. \qquad (2.16)
\end{aligned}$$

The one-generation change in the population may thus be given by

$$\Delta\xi_k = \xi_k' - \xi_k = Q^{-1} \sum_{r=0}^{N} \xi_r q_r [C^{\alpha}_{r,k}(\bar{x}) - \xi_k]. \tag{2.17}$$

Finally, in order to formulate the general concept of altruism, let us denote the following:

(H) *The A type is said to be* socially favorable *if $q_N \geqslant q_i$ for all $i = 0, 1,\ldots, N-1$ and $q_N > q_0$. The A type is said to be* altruistic *if it is both socially favorable and individually disadvantageous.*

Postulate (H) is manifestly more general than the usual assumption of monotonic (or indeed linear) increase of a deme fitness as a function of the altruist included in the deme (see, for example, Haldane, 1932).

If there is a number i $(0 < i < N)$ such that $q_0 < q_i > q_N$, the types A and B are said to be *cooperative*. This is the case where polymorphic demes may be more successful than monomorphic demes. The value

$$R = R(A, B) = [\max_{0 \leqslant i \leqslant N} q_i - \max(q_0, q_N)] / \max_{0 \leqslant i \leqslant N} q_i \tag{2.18}$$

measures the rate of cooperation between the two types. If one type is completely altruistic, or at least socially favorable, then $R = 0$.

3. Analysis of the Model and Effect of Migration

Theorem 1. *In the case of social vs. nonsocial selection, if the rate of migration is sufficiently low, fixation on the social type occurs with probability* 1, *independent of its individual disadvantage.*

More precisely, if $q_N = q^* > q_0$, then a value $\delta = \delta(\theta, q) > 0$ exists such that, for all $\alpha < \delta$, $\xi \neq e_0 = (1, 0,\ldots, 0)$,

$$\xi_N^{(t)} \xrightarrow{t\to\infty} 1. \tag{3.1}$$

Furthermore, (3.1) *holds even in the case of "weakly" cooperative types, provided $q_N > q_0$ and the rate of cooperation is small.*

The only assumptions needed to prove this theorem are

(D′) *$C_{x,N}$ is a strictly increasing function of x over* $[0, N]$.

(E′) *$C_{x,N}$ is continuous and has a finite left derivative $C'_{N,N} < \infty$ at the edge $x = x_N$.*

(F′) $C_{N,N} = 1$.

The assumptions (E′) and (F′) are clearly implied from the general assumptions (E)–(F). Condition (D′) is implied from the facts that $\sum_{k=0}^{N} C_{x,k} = 1$ and $C_{x,k}$ is a TP_2 function of x and k (*Assumption* D). Note that for the validity of Theorem 1, no restrictions are needed on the rest of the reproduction probabilities.

Proof of the theorem. Set $h = C_{\frac{1}{2},N} > C_{0,N} \geqslant 0$. We know that $q_N > q_0$, and we assume a low rate of cooperation, $R \leqslant h/2$ (clearly $R = 0$ when A is a social type). For $r = 1, 2, \ldots, N (0 \leqslant \bar{x} \leqslant N)$,

$$C^{\alpha}_{r,N}(\bar{x}) = C_{\alpha\bar{x}+(1-\alpha)r,N} \geqslant C_{1-\alpha,N} \geqslant h \tag{3.2}$$

provided α is less than 1/2. Using $\bar{x} = \sum_{r=1}^{N} r\xi_r \geqslant N\xi_N$ with the monotonicity of $C_{x,N}$, we also get $C^{\alpha}_{N,N}(\bar{x}) \geqslant C_{N-\alpha N(1-\xi_N),N}$; and from postulates (E′) and (F′),

$$C^{\alpha}_{N,N}(\bar{x}) = 1 - C_{N,N}\alpha_N(1 - \xi_N) + 0[\alpha(1 - \xi_N)].$$

Denoting $\lambda = NC'_{N,N} + 1 < \infty$, the last identity implies that for α small enough, say $0 < \alpha < \delta_1 \leqslant \frac{1}{2}$,

$$C^{\alpha}_{N,N}(\bar{x}) > 1 - \lambda\alpha(1 - \xi_N). \tag{3.3}$$

From (2.15), (3.2), and (3.3),

$$\xi_N' = Q^{-1} \sum_{r=0}^{N} \xi_r q_r C^{\alpha}_{r,N}(\bar{x}) \geqslant Q^{-1} \left\{ \xi_N q_N [1 - \lambda\alpha(1 - \xi_N)] + h \sum_{r=1}^{N-1} \xi_r q_r \right\}$$

and a sharp inequality is obtained when $\xi_0 < 1$. Thus

$$\begin{aligned} Q\Delta\xi_N = Q(\xi_N' - \xi_N) &\geqslant q_N\xi_N[1 - \lambda\alpha(1 - \xi_N)] + h \sum_{r=1}^{N-1} \xi_r q_r - \xi_N \sum_{r=0}^{N} \xi_r q_r \\ &\geqslant \xi_N q_N (1 - \xi_N)(1 - \alpha\lambda) - \xi_0 \xi_N q_0 + (h - \xi_N) \sum_{r=1}^{N-1} \xi_r q_r . \end{aligned} \tag{3.4}$$

Let us denote $q^* = \max_{0<i\leqslant m} q_i$, and let us divide our discussion into two cases, the first when $\xi_N \leqslant q^* h/(q^* - q_0)$ and the second the alternative case. In the first case we have $h - \xi_N \geqslant -q_0\xi_N/q^*$ and thus

$$\begin{aligned} Q\Delta\xi_N &\geqslant \xi_N q_N (1 - \xi_N)(1 - \alpha\lambda) - \xi_0 \xi_N q_0 - \frac{q_0}{q^*} \xi_N \sum_{r=1}^{N-1} \xi_r q_r \\ &\geqslant \xi_N q_N (1 - \xi_N)(1 - \alpha\lambda) - q_0 \sum_{r=0}^{N-1} \xi_r = \xi_N(1 - \xi_N)(q_N(1 - \alpha\lambda) - q_0]. \end{aligned} \tag{3.5}$$

Define, thus $\delta_2 = [(q_n - q_0)/\lambda q_N] > 0$ and for $\alpha < \delta_2$ we get $Q\Delta\xi_N \geqslant 0$ with a sharp inequality when $0 < \xi_N < 1$.

When, on the other hand, $\xi_N > q^*h/(q^* - q_0)$, then $h - \xi_N < 0$, and since $\sum_{r=1}^{N-1} \xi_r q_r \leqslant q^*(1 - \xi_0 - \xi_N)$, (3.4) becomes

$$\begin{aligned} Q\Delta\xi_N &\geqslant \xi_N(1 - \xi_N)(1 - \lambda\alpha) - \xi_0\xi_n q_0 - (\xi_N - h)\, q^*(1 - \xi_0 - \xi_N) \\ &= (1 - \xi_N)[q^*h - \xi_N(q^* - q_n) - \lambda\alpha\xi_N q_N] + [(q^* - q_0)\, \xi_N - q^*h]\, \xi_0 . \end{aligned}$$

Dealing with $\xi_N > q^*h/(q^* - q_0)$ the second term is nonnegative. As for the first term, using $R \leqslant h/2$ so that $q^* - q_N < q^*h/2$ and $q^* \geqslant q_N$, we readily get

$$Q\Delta\xi_N \geqslant (1 - \xi_N)\, q^*(h/2 - \lambda\alpha).$$

This again, is positive if $\alpha < \delta_3$, where we define $\delta_3 = h/2\lambda > 0$ (strictly positive if $\xi_N < 1$).

For any $\xi \neq e_0, e_N$ [here $e_N = (0,..., 0, 1)$] we thus conclude that if $\alpha < \delta = \min(\delta_1, \delta_2, \delta_3)$ then $\xi_N' > \xi_N$ and (3.1) immediately follows. Q.E.D.

COROLLARY 1. *With the prerequisites* (D′) *through* (F′) *of Theorem* 1, *if only* $q_N > q_0$ *and the rate of migration is low enough, then the monomorphic equilibrium* e_0 *is* unstable. *In other words, the A type is* maintained in the population (*though perhaps not fixed*) whatever the values $q_1, q_2,..., q_{N-1}$ *and the reproduction probabilities* $C_{x,0}, C_{x,1},..., C_{x,N-1}$. *In this case the theorem can clearly be applied for strongly cooperative types.*

Proof. From (3.5) it immediately follows that if $0 \leqslant \alpha < \min(\delta_1, \delta_2)$, then $\xi_N' > \xi_N$ for all $\xi_N \leqslant g^*h/(q^* - q_0)$ and for $\xi_0 < 1$. Moreover, δ_1 is positive whenever $C'_{x,N} < \infty$, whereas $\delta_2 = (q_N - q_0)/\lambda q_N > 0$, if, in addition $q_N > q_0$. For α smaller than these two values, the corner e_0 is thus unstable. Q.E.D.

COROLLARY 2. *Under the conditions of Theorem* 1, *the frequency* ξ_N *of pure-A demes monotonically increases in time. It is, furthermore, both introduced into the population and fixed in it geometrically fast.*

Proof. Immediate from the proof of the theorem. The geometrical rates of fixation and introduction follow from (3.5).

Remark. This is not the case with the frequency $\bar{x}/N$ of the A type in the entire population. Even if it is completely altruistic and the subpopulations are completely isolated it is not difficult to show that when the initial variation between subpopulations is small and the individual disadvantage of the social type is high, then for a certain period both $\bar{x}$ and $Q(\xi)$ are monotonically *decreasing*. Thus, statistical compensation for the social type can be expressed only in long-run terms, and its selective advantage under conditions of partial isolation, as shown in Theorem 1, cannot be represented by any equivalent of a *fitness parameter* in the classic generation-to-generation sense. As a matter of fact, inherited social patterns are not unique in this respect (see Discussion; see also Eshel, 1971).

THEOREM 2. *If the rate of migration is sufficiently high, fixation occurs on the individually profitable type, whether social, nonsocial or cooperative.*

More precisely, for any set of values $q_0, q_1, ..., q_N$ *(given the reproduction probabilities), there is a value* $\delta = \delta(q_0, q_1, ..., q_N) > 0$ *such that if* $1 - \alpha \leqslant \delta$, *then*

$$\xi^{(t)} \xrightarrow[\text{a.s.}]{(t\to\infty)} e_0 \qquad \text{for all } \xi^{(0)} \neq e_N \tag{3.6}$$

and (with probability 1*) fixation occurs geometrically fast.*

Proof. For all $0 \leqslant \alpha \leqslant 1$, and $\xi \in S^N$, (ξ in the N-dimensional simplex S^N), using (2.16) we obtain

$$\begin{aligned}\Delta\bar{x} = \sum_{k=1}^{N} k\Delta\xi_k &= Q^{-1} \sum_{k=1}^{N} \xi_r q_r[C^{\alpha}_{r,k}(\bar{x}) - \xi_k] \\ &= Q^{-1} \sum_{r=0}^{N} \xi_r q_r\{\psi(\alpha\bar{x} + (1 - \alpha)r) - \bar{x}\}.\end{aligned}$$

From (2.9) and the TP$_2$ property of the $C_{x,k}$, monotonicity of $\psi(x)$ follows. Denote $\psi(\alpha\bar{x} + (1 - \alpha)N) = \Gamma(\alpha, \bar{x})$; we thus get

$$\Delta\bar{x} \leqslant \Gamma(\alpha, \bar{x}) - \bar{x} \xrightarrow{\alpha\to 1} \psi(\bar{x}) - \bar{x} \leqslant 0 \tag{3.7}$$

with a strict inequality if $0 < \bar{x} < N$. Since $\Gamma(\alpha, \bar{x}) - \bar{x}$ is continuous in both variables, then for all $\epsilon_1, \epsilon_2 > 0$ there exists a value $\delta_1 = \delta_1(\epsilon_1, \epsilon_2) > 0$ such that, if $1 - \alpha < \delta_1$, then

$$\epsilon_2 < \bar{x} \leqslant N - \epsilon_1 \Rightarrow \Delta\bar{x} < 0. \tag{3.8}$$

Furthermore, for all $0 \leqslant \alpha \leqslant 1$,

$$\Gamma(\alpha, N) = \psi(N) = N. \tag{3.9}$$

Moreover $\Gamma(\alpha, x)$, taken as a function of x, has a left derivative at $x = N$ given by

$$(\partial/\partial x)\, \Gamma(\alpha, N) = \alpha\psi'(N)$$

and for $\alpha > 1/\psi'(N)$, $(\partial/\partial x)\, \Gamma(\alpha, N) > 1$ [we know that $\psi'(N) > 1$; see assumption (G), Section 2]. This inequality together with (3.9) implies that the value

$\epsilon_1 > 0$ on the right-hand side of (3.8) may be chosen in such a way that, for all $N > \bar{x} > N - \epsilon_1$, $\Gamma(\alpha, \bar{x}) < \bar{x}$. From (3.7), we then get

$$N > \bar{x} > N - \epsilon_1 \Rightarrow \Delta\bar{x} < 0. \tag{3.10}$$

Now, from the basic assumptions (E) and (F) (Section 2) it follows that $C'_{0,k} > 0$ for all $k \geqslant 1$, and a positive value $\sigma > 0$ exists such that $C_{x,k}$ is monotone increasing on the interval $[0, \sigma]$ for all $k = 1, 2, \ldots, N$. Now choose any positive values ϵ_2, δ_2 such that

$$\epsilon_2 + N\delta_2 < \sigma. \tag{3.11}$$

For $\bar{x} < \epsilon_2$, if we require $1 - \alpha < \delta_2$, then for all $r, k \geqslant 1$,

$$\alpha\bar{x} + (1 - \alpha)r \leqslant \alpha\bar{x} + (1 - \alpha)N \leqslant \epsilon_2 + N\delta_2 < \sigma$$

and thus $C^{\alpha}_{r,k}(\bar{x}) \leqslant C^{\alpha}_{N,k}(\bar{x})$. Using this we get

$$\begin{aligned} \bar{x}' &= \sum_{k=1}^{N} kQ^{-1} \sum_{r=0}^{N} \xi_r q_r C^{\alpha}_{r,k}(\bar{x}) \leqslant \frac{1}{\xi_0 q_0} \sum_{r=0}^{N} \xi_r q_r \sum_{k=1}^{N} kC^{\alpha}_{r,k}(\bar{x}) \\ &\leqslant \sum_{k=1}^{N} kC_{\alpha\bar{x},k} + \frac{q^*}{q_0}\frac{1 - \xi_0}{\xi_0} \sum_{k=1}^{N} kC^{\alpha}_{N,k}(\bar{x}). \end{aligned} \tag{3.12}$$

Since $\bar{x} \geqslant 1 - \xi_0$, we have

$$(1 - \xi_0)/\xi_0 \leqslant \bar{x}/(1 - \bar{x}) \leqslant \bar{x}/(1 - \epsilon_2).$$

From this by writing $C = q^*/(1 - \epsilon_2)\, q_0$, (3.12) becomes

$$\begin{aligned} \bar{x}' &\leqslant \sum_{k=1}^{N} kC_{\alpha\bar{x},k} + C\bar{x} \sum_{k=1}^{N} kC_{\alpha\bar{x}+(1-\alpha)N,k} \\ &= \psi(\alpha\bar{x}) + C\bar{x}\psi(\alpha\bar{x} + (1 - \alpha)N). \end{aligned} \tag{3.13}$$

For abbreviation we denote the right-hand side of (3.13) $\phi(\alpha, \bar{x})$.

For all α we have $\Phi(\alpha, 0) = 0$ and

$$[(\partial/\partial x)\, \Phi(\alpha, x)]_{x=0} = \alpha\psi'(0) + C\psi((1 - \alpha)N) \leqslant \psi'(0) + C\psi(\delta_2 N).$$

But $\psi(\delta_2 N) \to 0$ as $\delta_2 \to 0$ and from the basic assumption (G) we know that $\psi'(0) < 1$. Thus, choosing δ_2 small enough we obtain $[(\partial/\partial x)\, \Phi(\alpha, x)]_{x=0} < 1$. Without affecting the requirement (3.11), the value ϵ_2 may be chosen such that, for all $\bar{x} < \epsilon_2$, $\Phi(\alpha, \bar{x}) < \bar{x}$; and from (3.13) we get

$$0 < \bar{x} < \epsilon_2 \Rightarrow \Delta\bar{x} \leqslant \Phi(\alpha, \bar{x}) - \bar{x} < 0. \tag{3.14}$$

Using (3.8), (3.10), and (3.14) we now conclude that if $\alpha > 1 - \delta$, where $\delta = \min(\delta_1, \delta_2) > 0$, then $\Delta\bar{x} < 0$ for all $\xi \neq e_0, e_N$.

Furthermore, (3.14) immediately implies that in the vicinity of e_0, $\Delta\bar{x} \leqslant -\theta\bar{x} + 0(\bar{x})$, where $\theta = 1 - \psi'(0) - C\psi(\delta_2 N) > 0$, and fixation on type B occurs geometrically fast. Q.E.D.

Remark. Unlike the long-range selective advantage of the altruistic type in the case of low migration, the selective advantage of the individually profitable type under conditions of high migration is immediate, and its proportion $[1 - (\bar{x}/N)]$ in the population is monotonically increasing. Theorems 1 and 2 do not specify the crucial rates of migration needed for fixation on either the altruistic or the individually profitable type. A more specific result is given by the following:

COROLLARY 3. *If the B type is individually advantageous in a broad sense assumed in this study, and if*

$$\alpha > 1/\psi'(N), \tag{3.15}$$

then the altruistic equilibrium e_N is unstable.

The proof follows from (3.10) (see the proof of the theorem).

Remark. If reproduction within subpopulations occurs according to the Wright–Fisher model, we know that $\psi(x) = n\theta x/(N - x + \theta x)$ [see (2.7)] and (3.15) clearly becomes $\alpha > \theta$. In other words, if the rate of migration exceeds the relative fitness of *the altruist, this type cannot become established in the population, however much it benefits the deme.* In this case one may also establish

$$\varlimsup_{t\to\infty} \bar{x}^{(t)} \leqslant (1 - \alpha)/(1 - \theta),$$

which forms an upper bound on the proportion of the altruistic type that may be maintained in the population.

Altruistic–Nonaltruistic Polymorphism

By use of local analysis at corner e_0 it is not difficult to verify that for any reproduction probabilities, any set of values $q_1, q_2, \dots, q_N$, and any rate of migration, if q_0 is small enough (but still positive), this "socially unfavorable" equilibrium is unstable.

Together with Corollary 3, this result shows that, at least under certain circumstances, a type coexistence may be maintained for some moderate rate of migration between altruistic and nonaltruistic types. Take, for example, a population reproducing according to the Wright–Fisher model with $\alpha > \theta$. Its altruistic corner e_N is unstable, independently of $q_0, q_1, \dots, q_N$. If, in addition,

q_0 is sufficiently small, the nonaltruistic corner is also unstable and neither type may become fixed in the population.

Yet an unsettled question is whether for any altruistic–nonaltruistic situation a long-term coexistence may be maintained for some moderate migration rate.

Effect of Mutation

Let us introduce a new parameter $1 > \mu \geqslant 0$, *the rate of mutation.* We assume that before reproduction, any individual has a probability μ to alter its type. Let the previously defined functions $C_{x,k} = C^0_{x,k}$ stand for the reproduction probabilities without mutation. With mutation present, these probabilities are altered to

$$C^{\mu}_{x,k} = C_{(1-\mu)x+\mu(N-x),k}\,. \tag{3.16}$$

As before

$$C^{\alpha,\mu}_{r,k}(\bar{x}) = C^{\mu}_{\alpha\bar{x}+(1-\alpha)r,k}\,. \tag{3.17}$$

are the local transition probabilities from r to k A-type individuals in a subpopulation where μ, α, and $\bar{x}$ are the rates of mutation and migration and the average number of A-type individuals per subpopulation, respectively.

The transformation

$$T\colon S^N x[0,1]^2 \to S^N$$

given by

$$T(\mu, \alpha, \xi) = \xi'$$

is well defined by inserting (3.17) into (2.16). Clearly it is continuous in all variables.

From Theorem 1, using the Karlin–McGregor (1971a,b) principle of small perturbations, it is not difficult to prove that *for any $\epsilon > 0$, if the rates of cooperation, migration, and mutation are small enough, a locally stable equilibrium ξ^* is maintained in an ϵ vicinity of the altruistic corner e_N* such that, for all ξ^0 with $\xi_N > 1 - \epsilon$,

$$\xi^{(t)} \xrightarrow[t\to\infty]{} \xi^*. \tag{3.18}$$

We shall further show that the following holds:

Proposition. *The equilibrium ξ^* is also* globally stable; *i.e.,* (3.18) *holds for all $\xi^{(0)} \in S^N$.*

Moreover, for all $\epsilon > 0$, if μ and α are sufficiently small (but $\mu > 0$), ξ_N is monotone increasing in time, as far as $\xi_N < 1 - \epsilon$.

Proof. From the Karlin–McGregor theorem we already know that there exists an $\epsilon > 0$ such that for $\xi^{(0)}_N > 1 - \epsilon$, $\xi^{(m)} \xrightarrow{(m\to\infty)} e_N$. It is thus sufficient to prove that if $\xi_N \leqslant 1-\epsilon$, then $\xi_N' > \xi_N$. This is trivially so in the case $\xi_N = 0$ (for we then have $\xi_N' \geqslant \mu^N > 0$). For $0 < \xi_N \leqslant 1-\epsilon$, denote

$$(\xi_N' - \xi_N)/\xi_N = f_{\mu,\alpha}(\xi),$$

which is a continuous function on the domain $\{\xi \mid 0 < \xi_N \leqslant 1-\epsilon\}$. From Corollary 2 of Theorem 1 it follows that, for sufficiently small α, $f_{0,\alpha}(\xi) > 0$. Furthermore, using the geometrical rate of introduction of ξ_N into the population (same corollary), we know that

$$\varliminf_{\xi \to e_0} f_{0,\alpha}(\xi) > 0.$$

A positive value $\delta > 0$ thus exists, so that for all $\xi \in S^N$, with $0 < \xi_N \leqslant 1-\epsilon$,

$$f_{0,\alpha}(\xi) \geqslant \delta. \tag{3.19}$$

Under the effect of mutation, nonaltruistic types appear in a portion $1-(1-\mu)^N$ of the pure altruistic demes. By contrast, other demes may become pure socially favorable. We thus have

$$\xi_N^{(\mu)} - \xi_N \geqslant (1-\mu)^N \xi_N, \tag{3.20}$$

where $\xi_N^{(\mu)}$ represents the frequency of pure socially favorable demes after mutation. For $0 < \xi_N \leqslant 1-\epsilon$, having α sufficiently small, we thus obtain, from (3.19) and (3.20),

$$f_{\mu,\alpha}(\xi) \geqslant (1-\mu)^N f_{0,\alpha}(\xi) - [1-(1-\mu)^N] \geqslant (1-\mu N)\delta - 2\mu N$$

and for $\mu < \delta/(2N+\delta)$ this is a positive value. Q.E.D.

In exactly the same way we obtain, from Theorem 2, the following:

If the rate of migration is close enough to 1 *and the rate of mutation is sufficiently small, then a globally stable equilibrium is maintained in the vicinity of the nonaltruistic corner* e_0. *Moreover, the frequency of the altruistic type in the population is monotonically decreasing in time, up to a certain small value* $\epsilon(\mu) > 0$ *which tends to* 0 *as* $\mu \to 0$.

Generally, if a stable equilibrium is maintained without mutation, there is a stable equilibrium in its ϵ vicinity maintained by a sufficiently small rate of mutation (Karlin and McGregor, 1971a). We thus conclude that (except, indeed, for the first appearance) the effect of mutation on the evolution of the altruistic type is practically negligible.

4. Discussion and Possible Implications for Human Evolution

The model we have developed attempts to explain and analyze the evolution of altruistic traits on the basis of interaction between neighbors or individuals that happen to share a common deme. As we have seen, this *neighbor effect* depends essentially on the dispersal of the altruistic and nonaltruistic individuals among the demes, rather than on their genetic frequencies within the entire population. The dispersal of types is governed in turn by the random processes of reproduction within demes. When the number of demes is large, the effects of these locally unpredictable factors on the population as a whole may become predictable by the laws of large numbers. In this situation, presumably the prevailing one in nature, the long-term fate of an altruistic trait is determined (with probability 1) by the law of reproduction and by the demographic conditions in the population.

A quantitative analysis of this process suggests, in agreement with Wright (1945), that a certain restriction on demographic mobility in the population is the main—though not the sole—factor in the evolution of the altruistic trait. This result is also qualitatively consistent with previous findings obtained under the assumption either of pure kin selection (Hamilton, 1964) or of reciprocal altruism (Trivers, 1971). As we have seen, the statistical effect of kin selection may be regarded as a special case of the neighbor effect, and it is thus not surprising to find the population behaving similarly under the two effects. Reciprocation, by contrast, as well as other forms of social compensation, usually yields different forms of quasialtruistic behavioral patterns that are essentially confined to populations of specific social structures. Yet it is of interest that within such a restriction, both true altruism and socially compensated ones seem likely to evolve under the same conditions of low mobility and partial partitioning of the population.

A drastic situation of deme subdivision is manifestable by clans or troops of various high vertebrates. It is thus of no surprise that some of the most extreme examples of altruism—food sharing, a complete inhibition of competitive fights, even for sexual ends, and, possibly an intrinsic mechanism of birth control—have been observed within the practically closed clans of rats (see, for example, Lorenz, 1963 and references therein). Self-sacrificial behavior of baboons in defence of their troops may be explained on the same basis (Washburn and DeVore, 1961; Hall and DeVore, 1965; Crook, 1969). Yet it is shown that a less drastic subdivision naturally imparted by distance may be sufficient to create the same evolutionary effect—the establishment of altruistic features in the population—provided the demographic mobility of this population is sufficiently low.

In agreement with the theoretical model, a significant difference in demographic mobility has recently been observed between palatable and unpalatable butterflies dwelling in the same area, and the role of low mobility in the evolution of the unpalatable type has already been suggested, on an empirical basis, by Benson (1971).

Differences in mobility level may also account for the difference in population control between the highly mobile meadow vole, *Microtus Pennsylvenicus*, which virtually lacks such a control, and the less mobile voles, such as *Microtus Cherogaster* (see Asdell, 1946 and also Christian, 1970, for an ecological treatment of the subject, establishing the advantage of population-size control for the *entire populations* of the less mobile voles).

Finally, in view of the theoretical conclusion of this study, it may be worthwhile postulating the evolutionary effects imposed on a population by a drastic change in its demographic mobility. Though it may be assumed that the development of a new altruistic trait requires a considerable span of time (see, for example, Simpson, 1945), the *extinction* of such a trait under a newly imposed condition of high mobility may occur at a higher rate (see a comment on Simpson's work by Wright, 1945). And a rapid increase in demographic mobility is a factor no doubt exclusive to human evolution. Thus, from a theoretical point of view, the quantitative understanding of the effects imposed by this factor on the selection of altruistic traits may add to our knowledge of human evolution.

As it has already been suggested by Trivers (1971; and see also Campbell, 1966; Lee and DeVore, 1968), the demographic conditions that prevailed in pre-Neolithic human populations were likely to favor the evolution of altruistic patterns. These patterns may in turn have been prerequisites for the subsequent development and maintenance of human societies. Yet because of the tremendous increase in human mobility during only the last ten thousand years or so, it may be that natural selection no longer favors such altruistic traits, however favorable for human society some of them may still be.

A question repeatedly raised by ethologically oriented authors (Lorenz, 1963; Morris, 1967; and others) is to what extent the relatively short period of human civilization has been sufficient for man to adapt biologically to his new environment. Attempts have been made to explain the malfunctioning of modern society on the basis of the still-persisting "australopithecine" drives of man. But perhaps a more crucial question is whether human evolution is in fact headed toward a desirable social adaptation, i.e., whether present fertility selection necessarily favors traits that are beneficial to human society as presently constituted. The theoretical conlusion of this study suggests that the opposite may be true. It may be that some intrinsic human drives, altruistic in nature, that are fundamental for the establishment of any human civilization, could possibly evolve only under precivilization demographic conditions. And it is possible that just those selection forces imposed by civilization itself act to reduce the frequency of these fundamental drives within human population, thus leading it into the course of misadaptation.

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