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Hence, if $\mu_1(\omega^*) > 0$ (i.e., if secondary features of the optimal value are in existence in the initial population), then, since $\chi(\omega)/\chi(\omega^*) < 1$ for all non-optimal values of ω, we get

$$\frac{\mu_n(d\omega)}{\mu_n(d\omega^*)} = \left[\frac{\chi(\omega)}{\chi(\omega^*)}\right]^{n-1} \frac{\mu_1(d\omega)}{\mu_1(d\omega^*)} \to 0 \quad \text{as} \quad n \to \infty. \tag{3.5}$$

Together with (3.2), this becomes

$$E^{(n)}\chi = \int \chi(\omega)\, \mu_n(d\omega) \uparrow \chi(\omega^*) \quad \text{as} \quad n \to \infty. \tag{3.6}$$

As a corollary, we now get the following.

THE SECOND LAW OF INDIRECT SELECTION. *When type-substitutions of the primary feature occur successively with similar intensities of direct selection, an optimal value of the secondary feature tends to become fixed in the population.*

Here again, indirect selection reveals a strong similarity to the classic fitness-selection.

An example of the effect of indirect selection may be the accelerating pace by which pest populations become adapted to the use of new pesticides. Keeping in mind the theoretical possibility of a second-order adaptation of pest populations towards the dynamic process of pesticide introduction, it is suggested that possible changes in the secondary feature of pest populations subjected to repeated use of pesticides be experimentally studied. This includes sexual behavior, demographic mobility, and intrinsic rates of mutation and recombination.

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Let μ_n be the frequency measure of ω in the population after n gene-substitutions. Then the survival probability of a typical clone throughout the $n + 1$-th gene-substitution will be

$$E^{(n)}\chi = \int_\Omega \chi(\omega)\,\mu_n(d\omega).$$

Knowing (see 2.5)

$$\mu_n(d\omega) = \frac{\chi(\omega)\,\mu_{n-1}(d\omega)}{E^{(n-1)}\chi}, \tag{3.1}$$

we readily obtain

$$E^{(n)}\chi = \frac{\int_\Omega [\chi(\omega)]^2\,\mu_{n-1}(d\omega)}{\int_\Omega \chi(\omega)\,\mu_{n-1}(d\omega)} = \frac{\mathrm{Var}^{(n-1)}\,\chi}{E^{(n-1)}\chi} + E^{(n-1)}\chi \geqslant E^{(n-1)}\chi, \tag{3.2}$$

where for all $n = 0, 1, 2, \ldots$

$$\begin{aligned} \mathrm{Var}^{(n)}\,\chi &= \int [\chi(\omega) - E^{(n)}\chi]^2\,\mu_n(d\omega) \\ &= \int_\Omega [\chi(\omega)]^2\,\mu_n(d\omega) - [E^{(n)}\chi]^2 \geqslant 0 \end{aligned} \tag{3.3}$$

is the variance in survival probabilities of clones throughout the $n + 1$-th gene-substitution.

Whenever $\chi(\omega)$ assumes any variation in the initial population (i.e., whenever indirect selection is operating on the ω feature), then inequalities (3.1) and (3.2) become strict.

As a corollary, we get the following.

THE FIRST LAW OF INDIRECT SELECTION. *When type-substitutions occur successively with similar intensities of direct selection, an indirect selection of secondary features (if it occurs) always increases the expected clone-survival-probability in the population.*

Furthermore, the increase in average probability of clone survival being achieved during a single type-substitution in the primary feature is proportional to the standard deviation of clone-survival probabilities in the population.

On a longer scale of time, though not in terms of change through successive generations, this stands in virtual agreement with Fisher's fundamental law of natural selection. (For comparison, see Cavalli-Sforza and Bodmer (1971)).

Furthermore, by an iteration of (3.1), we readily get

$$\mu_n(d\omega) = \frac{[\chi(\omega)]^{n-1}\,\mu_1(d\omega)}{\prod_{k=1}^{n-1} E^{(k)}\chi}. \tag{3.4}$$

For the optimal clone survival probability, we get

$$\chi(\omega^*) \approx 2\alpha_2(1 - \theta)((\omega^*)^2/r)$$

which is of the order of $(1 - \theta)(s/r) \min(s, r)$.

More precisely, it may be shown that up to a multiplication coefficient of order $(1 + 0(s))$, we get the following values of ω^* and $\chi(\omega^*)$ as functions of r and s:

	Intensity of environmental deterioration	Optimal mutation rate	Optimal clone-survival-probability
Case I	$r \ll s$	$(rs)^{1/2}$	$2(1 - \theta)s$ virtually unchanged with r
Case II	$r \approx s$	$(2^{1/2} - 1)s$	$2(2^{1/2} - 1)(1 - \theta)s$
Case III	$r \gg s$	$s/2$ virtually unchanged with r	$[(1 - \theta)s^2]/2r$

Case I represents a situation with insubstantial environmental deterioration. Optimal clone survival probability is essentially not affected; whereas, optimal mutation rate increases as a square root of the intensity of the environmental deterioration.

Case III represents a situation with relatively intensive deterioration. Optimal mutation rate is no longer affected, while a further deterioration results in a substantial increase in the extinction probability of the optimal clones and, thus, of the entire population (see Eshel (1972b)).

3. INDIRECT ADAPTATION

We now take into consideration a succession of gene substitutions caused by repeated changes of the environment. We will see that while fitness selection operates anew each time toward an adaptation of the population to a given, static, environmental condition, indirect selection operates on a longer scale of time towards an adaptation to the dynamics of this repeated process. For this purpose, the dynamics of a change will be measured in terms of the intensities of the selection forces it imposes on primary features. We already know that the survival probability of a clone during gene-substitution depends both on the selection forces operating on the substituted primary features and on the secondary feature which is carried by this clone. Thus, if throughout successive gene-substitutions the dynamics of the process are kept approximately unchanged, then the probability $\chi(\omega)$ of a clone to survive a gene-substitution stays an invariant function of its intrinsic secondary feature ω.

The multitype generating function of the nonlethal progeny born to an individual of a type A_i^{ω} is then

$$\psi_i^{\omega}(\mathbf{u}) = \Phi_i \left\{(1 - \omega) u_i + \omega \sum_j p_{ij} u_j + \omega\theta_i\right\}. \tag{2.6}$$

The Fisherian fitness of this type is given by

$$\alpha_i(\omega) = (1 - \theta_i\omega)\, \Phi_i'(1) = (1 - \theta_i\omega)\, \alpha_i(0),$$

which for all $i = 1,\ldots, n$ is a decreasing function of ω. This reflects the fact that a direct fitness selection always operates toward a zero rate of mutation (see Kimura (1967)). Yet, we know that neither a population nor a clone within it can survive in a changing environment unless it is subjected to some positive rate of mutation.

In terms of our model, let us start with a conservative primary feature A_1, and assume $\alpha_1(0) \leqslant 1$. In this situation, a clone with a zero mutation rate assumes a one dimensional subcritical branching process and, thus, is bound for extinction, i.e., $\chi(0) = 0$. For a general ω, $0 \leqslant \omega \leqslant 1$, it has further been shown (Eshel, 1972b) that the clone-survival-probability $\chi(\omega)$ is a continuous function of ω and is positive only within the open interval,

$$\left(0, \max_i \left\{\frac{\alpha_i(0) - 1}{\theta_i \alpha_i(0)}\right\}\right).$$

An optimal rate of mutation is, thus, obtained for a positive value within this interval.

Assume, moreover, a Poisson distribution of the progeny size, i.e., $\Phi_i(s) = e^{\alpha_i(s-1)}$. (For a validation of this postulate, see Karlin and McGregor (1964, 1968).) Let $n = 2$, $\alpha_1 \leqslant 1$ and $\alpha_2 > 1$. (Here, A_2 may represent the class of all adaptable types.) Let the value $r = 1 - \alpha_1 \geqslant 0$ measure the intensity of environmental deterioration, while $s = \alpha_2 - 1 > 0$ is the Fisherian measure of the selection coefficient in favor of the adaptable type. When these two values are small, it may be shown that clone-survival-probability virtually behaves like

$$\hat{\chi}(\omega) = \begin{cases} 2\alpha_2(1 - \theta)\dfrac{\omega(s - \omega)}{r + (1 - r)\omega} & 0 < \omega < s, \\ 0 & \text{otherwise}, \end{cases}$$

and

$$\omega^* \approx r^{1/2} \frac{(r + (1 - r)s)^{1/2} - r^{1/2}}{1 - r}.$$

This last value, as readily established, is of the order of $\min\{s, (rs)^{1/2}\}$.

DEFINITION 2. If the clone probability $\chi(\omega)$ assumes a maximum at a point $\omega = \omega^*$, then ω^* will be called an *optimal value of the secondary parameter*.

The value $\chi(\omega^*)$ is the survival probability of an optimal clone. From the definition of the optimal value ω^*, it immediately follows that $\chi(\omega^*) \geqslant E^{(1)}\chi$ with a strict inequality unless the frequency-measure of the optimal value in the initial population is already 1. We conclude that in the long run, indirect selection always increases the frequency of the optimal value in the population. A stronger statement will be proved in the next chapter.

In the general case an optimal value ω^* of the secondary feature ω may or may not maximize the individual fitness of its carrier.

EXAMPLE 1. Let

$$\psi_i^{\omega}(\mathbf{u}) = \frac{\psi_i(\omega u_1, \ldots, \omega u_n)}{\psi_i(\omega, \ldots, \omega)},$$

where $\psi_i(\mathbf{u})$ is a probability generating function determining some law of progeny distribution, and the right side of the equation converges. Biologically, this is the simplest case where ω represents a pure fertility parameter, increasing the number of viable offspring born to its carrier by a monotone likelihood ratio (see Karlin (1968a)).

Employing (2.2), the fitness of the A_i^{ω} type is readily given by

$$\alpha_i(\omega) = \omega(d/d\omega)\, l_n \psi_i(\omega, \ldots, \omega).$$

Owing to the logarithmic convexity of generating functions, this is, not surprisingly, a monotone-increasing function of ω. Classic fitness-selection is shown to always operate in favor of high ω values. But it is also not difficult to show that the smallest positive vectorial solution of the system

$$\frac{\psi_i(\omega u_1, \ldots, \omega u_n)}{\psi_i(\omega, \ldots, \omega)} = u_i, \qquad i = 1, \ldots, n,$$

is monotone decreasing with ω. We, thus, conclude that when a contribution in fertility (or viability) does not interfere with other aspects of the process, clone selection leads to the same end result as fitness selection.

EXAMPLE 2. ω is an intrinsic rate of mutation. In this example we assume that the total number of offsprings, either viable or lethal, born to a parent of a type A_i^{ω}, depends only on its primary feature and not on its rate of mutation ω. Thus, the generating function of its total progeny size is denoted by $\Phi_i(s)$. Now, once a primary feature A_i $(i = 1, \ldots, n)$ is mutated, assume a probability $\theta_i > 0$ that it will be mutated to a lethal form, and a probability p_{ij} that it will be mutated to the nonlethal form A_j, $j = 1, 2, \ldots, n$; $\theta_i + \sum_j p_{ij} = 1$.

The expected number of all viable offspring born to an A_i^ω parent is given by

$$\alpha_i(\omega) = [(\partial/\partial u)\, \psi_i^\omega(u,\ldots, u)]_{u=1} . \tag{2.2}$$

Employing the classic Fisherian terminology, this is the *individual fitness* of the type A_i^ω. If for all $i = 1,\ldots, n$ the functions $\alpha_i(\omega)$ are constants—say, $\alpha_i(\omega) = \alpha_i$—then no fitness-selection operates on the secondary feature ω. If, on the other hand, the $\alpha_i(\omega)$ are all monotone increasing (decreasing) with ω, then we say that individual fitness-selection operates in favor of (against) high values of ω.

We will now see that long-run survival of a secondary feature in the population may not depend on short-term forces of fitness-selection operating directly on it.

Let $(u_1 ,\ldots, u_n) = \mathbf{u}(\omega)$ be the smallest positive vectorial solution of the system of equations

$$\psi_i^\omega(u_1 ,\ldots, u_n) = u_i\,; \qquad i = 1,\ldots, n. \tag{2.3}$$

As a general result of the theory of branching processes (e.g., Mode (1971)), we know that the ith component $u_i(\omega)$ of the solution represents the extinction probability of a clone beginning with a single parent of type A_i^ω. As a special case, if the conservative primary feature is represented by A_1, then $\chi(\omega) = 1 - u_1(\omega)$ represents the survival probability of a clone carrying the secondary feature ω. The frequency of the ω-feature within the surviving population, if it exists, will, thus, be multiplied by a coefficient proportional to the clone-survival-probability $\chi(\omega)$.

In a formal way, let μ_1 be the frequency-measure of the value ω in the initial population as distributed over the set Ω of its relevant values. The expected survival probability of a random clone starting with a single parent in the initial A_1-population is

$$E^{(1)}\chi = \int_\Omega \chi(\omega)\, \mu_1(d\omega). \tag{2.4}$$

We assume that this value is positive (otherwise, the whole population is bound for extinction). The frequency-measure of the secondary feature among surviving clones becomes

$$\mu_2(d\omega) = \frac{\chi(\omega)\, \mu_1(d\omega)}{E^{(1)}\chi} . \tag{2.5}$$

We then say that *an indirect (or second order) process of natural selection* alternates the frequency-measure of ω from μ_1 in the initial population to μ_2 in the surviving one.

DEFINITION 1. A value ω_1 of the secondary feature is said to be *favorable* over a value ω_2 if it endows a clone carrying it with a higher probability of survival, i.e., if

$$\chi(\omega_1) > \chi(\omega_2).$$

mental change. The intensity of a change is measured in terms of a decrease in the fitness of the conservative type. This optimal value is shown to maximize the survival probability of the entire population when facing new environmental changes of the *same intensity*. In this sense, second order selection enables the adaptation of a population to the pace of the environmental change, rather then to a static ecological situation. This sort of an indirect adaptation is carried out through modifications in modifying features, which, though not likely to increase individual fitness in any specific environment, facilitate further adaptation to repeated environmental changes of the same intensity. It is speculatively suggested that this aspect of a second order adaptation may be responsible for the accelerating pace by which pest and bacterial populations adapt themselves to newly introduced pesticides and medicines (see Section 3).

Finally, the method of second order selection as well as the concept of biological favorability in the wide, are not restricted to features which are labelled as modifying. For example, when applied to primary features, it is shown that the eventual result of second order selection virtually agrees with classic predictions of fitness selection. In this sense, fitness selection may be interpreted as a case of a clone-selection.

In Sections 2 and 3 we describe the analytic model and basic results of clone-selection in an asexual population. The mathematical analysis of an optimal mutation rate is carried out in a different paper (Eshel, 1972b). A research dealing with some quantitative aspects of second order selection in a sexual population is now in development.

2. DIRECT PRODUCT-BRANCHING-PROCESS AND SECOND-ORDER-SELECTION IN AN ASEXUAL POPULATION

Let ω represent any inherited feature in the population, either continuous or discrete. Ω is the set of all relevant values of ω. Let $A_1, \ldots, A_n$ be the collection of all possible types in respect to another feature in the population. For convenience, we shall call A_i the primary feature of the type A_i^{ω}. This feature generally represents a directly selected trait in the population. ω is called the secondary feature and generally represents a modifier.

An individual in the population may produce offspring of either his own primary feature or another one. The vector-distribution of progeny-sizes of an individual of type A_i^{ω} is given by the multidimensional probability-generating-function $\psi_i^{\omega}(\mathbf{u})$. This function depends both on the primary feature A_i and on the secondary one ω. More specifically, we denote by $p_i^{\omega}(k_1, \ldots, k_n)$ the probability that an individual of type A_i^{ω} produces exactly k_j offspring of the type $A_j (j = 1, \ldots, n)$; then

$$\psi_i^{\omega}(\mathbf{u}) = \psi_i^{\omega}(u_1, \ldots, u_n) = \sum_{k_1, \ldots, k_n = 0}^{\infty} p_i^{\omega}(k_1, \ldots, k_n)\, u_1^{k_1} \cdots u_n^{k_n}. \tag{2.1}$$

about *second order selection* in their favor. For example, clones characterized by a too low rate of mutation are likely to become extinct when environmental conditions become unfavorable to the conservative primary features. On the other hand, a too high mutation rate is likely to cause extinction of a clone even after the establishment of a new, adaptable, mutation. This fact introduces into the model a probabilistic equivalence of fitness selection operating for a favorable modifying feature. Hence, it can be shown that most surviving clones are characterized by a mutation rate which cannot be far away from some optimal value which is small but not zero. A similar process may be responsible for a second order selection for an optimal rate of recombination. In this case, the modifying feature is determined by the geometrical location of genes on the chromosome as well as, possibly, by a specific modifying locus (Simchen, 1967).

In a sexual population, possible recombination between the modifying and the primary genes makes quantitative analysis of second order selection very complicated to carry out. In an asexual population, however, a useful tool for such analysis is offered by the theory of multitype branching processes (with some qualitative results hopefully extended to the sexual case).

Since modifications of primary features in an asexual population can occur only through mutation, the most natural modifying feature to be studied in such a population is the intrinsic mutation rate itself. Yet, assuming a given (nonzero) mutation rate, other features affecting the spread and establishment of a new mutant in a clone may also be regarded as modifying—for example, an intrinsic tendency for migration. Furthermore, in the connotation of a biological type it is sometimes convenient to consider spatial as well as genetic factors. In this case, from the analytic viewpoint, mutation rate may be replaced by the tendency to migrate (Crow and Kimura, 1970).

Note that a crucial prerequisite for application of the theory of branching processes to second order selection is that the success of an individual in the population (measured in terms of progeny size) is independent of the size of its clone. This postulate proves quite acceptable for a large population consisting of many intermingled, small-sized clones, with relatively weak interactions between individuals of the same clone (for a more detailed argument see Mode (1971)). The situation becomes completely different when the size of a surviving clone approaches the capacity of a natural niche or habitat. However, it may be assumed that the clone-size behaves like a respectable branching process up to some critical, not too small size. In this case we know that the more conveniently calculated survival probability of the branching process is quite close to the probability of a clone to approach this critical size and, thus, to become established in some habitat (see Karlin (1966)).

While fitness selection, at any given time, is determined by ecological factors which are prevailing at the moment, it appears that the indirectly selected optimal value of a modifying feature depends on the intensity of the environexample, Williams (1965)). Actually, it is hard to see how biological complexes, like those governing sexual systems, recombination, or even optimal mutation rates, will be spontaneously established in any population without (or even against) selection forces operating within that population. Indeed, without the establishment of a feature, at least within a few populations, interpopulation selection for this feature cannot occur.

From the foregoing it, thus, appears that some mechanism of selection operating in favor of advantageous modifying features at the *population* level is still to be studied. It also appears that this mechanism is not likely to be thoroughly explained by Fisherian methods based on the repeated effect of a direct fitness selection in a completely mixed, normalized-size population. Moreover, if we are not to regard the apparent, long-run biological function of a modifying feature as an evolutionary coincidence, this function should be incoporated into the selection mechanism of the modifying feature in question. To this end we are interested in the long-run survival probabilities of whole, evolving lines of descendents carrying a given modifying feature, rather than in the short term success of individuals in the population.

In an asexual population, such lines are naturally represented by clones. In a sexual population we speak about lines of identity by descent in a given locus ω as *generalized clones* with respect to this locus (see Kempthorn (1960), Karlin (1968a)). More specifically, a generalized clone consists of all individuals descending from a single parent, that carry duplications of a single allele in their ω-locus regardless of their genetic inheritance in other loci. Indeed, all individuals of the generalized clone are offsprings of the original parent but not all offspring of this parent belong to the generalized clone. In a diploid population we respectively speak about generalized clones of haplo-gametes.

Like individuals in an asexual population, all haplo-gametes of a sexual population are divided into mutually exclusive (generalized) clones each carrying a specific ω-gene. Unlike the asexual case, this division is not uniquely determined by the original parents but also depends on the choice of the specific locus in question. Generalized clones are, therefore, difficult to trace empirically. On a theoretical probabilistic level, however, it can be readily shown that clones characterized by different modifying features are likely to become linked with different *primary features* (i.e., genes which determine the fitness of their carrier) or, in a recombinant population, with different combinations of primary genes (see, for comparison, the deterministic analysis of Karlin and McGregor (1972) or Feldman (1972)). Thus, differences in exposure to direct selection forces result in differences in the long-run survival probabilities of these clones. Moreover, under certain conditions, and taking into consideration the pressures of environmental change, it can be shown that modifying features which maximize the survival probability of a clone also maximize the long-run survival probability of the entire population. We call these features *favorable in the broad sense* and speak also been studied in connection with sex and diploidy (Eshel, 1970, 1972a), various mating systems (Karlin, 1968) and optimal mutation rates (Kimura, 1960, 1967). All these features appear to serve long run survival of a population, usually through maintaining a polymorphism at a minimal cost. Yet, in terms of individual fitness, modifying features often prove to be immediately costly for their carrier. Exceptions such as sexual coupling serving as an efficient regulator of team activities among higher vertebrates are from an apparently late, secondary path of adaptation. (For a different view see Scudo 1972.) Consequently it is often difficult to explain many phenomena in the evolution of modifying features based upon a strict analysis of fitness selection within a population.

Thus, for a fairly general condition it can be shown that in the long run, fitness-selection always operates to decrease nonzero rates of mutation (Karlin and McGregor, 1972) or recombination (Nei, 1967; Feldman, 1972). Furthermore, a maximum equilibrium-fitness is obtained in the case of a zero rate of either mutation or recombination (Karlin and McGregor, 1972, 1972a). The readers might note that these results are proved only asymptotically for the duration of the process. In fact, some simple models analysing fitness selection in a changing environment seem to reveal a temporal increase in the rate of mutation (or, with certain prerequisites, also in the rate of recombination). This is the case, for example, when, for mathematical convenience, only one mutant form is allowed which is advantageous in comparison with the conservative type. The situation is completely different, however, if irreversibly deleterious and lethal mutations are incorporated into the model in a higher frequency than the advantageous one is. In this case, despite the necessity of the rare advantageous mutation for future survival of the population, a strict analysis of fitness-selection paradoxically demonstrates a *monotone* decrease of the mutation rate up to a zero level.

Similar phenomena are manifested by applying fitness-selection to problems involving the evolution of intrinsic population controls (Wynne-Edwards, 1962; Lloyd and Christian, 1969), patterns of altruistic behaviour (Haldane, 1932) or tendencies to a negative assortment in mating (Karlin, 1968). Thus, unless a population is very sparce, fitness-selection is shown to favor tendencies to positive assortment while intrinsic tendencies to a negative assortment as well as to self incompatibility are always selected against, their existence being explained on the basis of their advantage in maintenance of polymorphism.

Complementary to the Fisherian approach, there is a natural tendency to explain the evolution of a modifying feature on the basis of some benefit with which it supposedly endows the future population. Yet, if unsupported by analysis of selection forces operating within a population, such a tendency devolves to an explanation of interpopulation selection. This type of selection now faces substantial theoretical objection as being a major force in evolution (see, for

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Clone Selection and the Evolution of Modifying Features

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A statistical mechanism of long-run selection is formulated in order to explain the evolution of modifying features governing mutation, recombination, sexual behavior, demographic mobility, and other factors that do not directly increase the individual fitness of their carrier but which are, supposedly, essential for future evolution of a population. Survival probability of a clone, rather than that of the individual, is shown to play the main role in this mechanism. Changing environment proves to be the main factor affecting it.

A theoretical possibility of a long-run adaptation to the dynamics of an environmental change—rather than to a static situation resulting from it—is demonstrated.

1. MODIFYING FEATURES AND SECOND ORDER SELECTION

The motivation for this work stems from studies concerning the evolution of a variety of traits or features which are commonly labeled as *modifying features* (see, for example, Karlin and McGregor (1972, 1972a) and references therein). When speaking of modifying features we mean inherited features with the following characteristics:

(i) Their main biological function does not involve a direct contribution to the Fisherian fitness of either their carrier or its neighboring individuals. This requirement distinguishes a modifying feature from an altruistic trait (see, for comparison, Haldane (1932), Hamilton (1964), Maynard-Smith (1964), and Eshel (1972)).

(ii) In affecting the process of reproduction within a population, modifying features determine further evolution (or preservation) of other features. These, in turn, may be directly advantageous for the survival of the future population.

Prevalant examples of modifying features are patterns governing sexual reproduction, mating systems, rates of mutation and recombination, and, possibly, also diploidy and polyploidy. In recent years, the long-run evolutionary function of sex and recombination has been extensively studied (e.g., see Crow and Kimura (1965), Bodmer (1970), Eshel and Feldman (1970), Mynard-Smith (1968) and references therein; see also Muller (1932)). Similar effects have

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On the Founder Effect and the Evolution of Altruistic Traits

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1. INTRODUCTION

The possible mechanisms for the establishment of altruistic traits in a population have been discussed by several workers (e.g., Haldane, 1932; Fisher, 1958; Hamilton, 1963, 1964a,b, 1973). In agreement with the terminology of previous authors, we adopt here the term altruist in its biological meaning for any inherited trait which reduces the fitness of its individual carrier but which is beneficial to the neighboring population of this carrier. In this sense, altruistic traits may be either behavioral, physiological, or biochemical. Altruistic traits can be spread and maintained in a population only if the benefit endowed by the altruistic action of an individual altruist benefits other altruistic individuals more than it benefits selfish individuals in the same population (Hamilton, 1963; Maynard-Smith, 1964). Without a kinship structure which is recognizable by the individual, this usually means that the average frequency of altruists in the area near an average altruistic individual must be greater than the frequency of altruists in the population as a whole. In general, this would be the case in any population in which mobility and mixing are not high enough to overcome the local random fluctuations in gene frequency (Wright, 1945). More specifically, whenever a population is naturally divided into (not necessarily isolated) subpopulations or demes, one may measure the demographic mobility of such a population by the probability that an arbitrary individual of an arbitrary deme has been born to parents of other demes. In this case it has been shown (Eshel, 1972) that for any altruistic trait there is a critical level of demographic mobility under which selection would always operate for the establishment of the altruist. If, on the other hand, demographical mobility surpasses another critical value, selection will favor the selfish. Moreover, these two critical values depend on the average size of the deme, both values tending to zero as the standard deme size becomes very large (Eshel, 1976). In other words, when the standard deme size is large, then even a very small immigration among demes will be enough to endow the selfish with a permanent advantage over the altruist (see, for comparison, Levins, 1970 and also, for critical discussion Boorman and Levitt, 1972). Thus, a model based on a permanent deme-structure of a population fails to explain the evolution of certain characters of biochemical altruism in large colonies of nonsocial insects, fungi, bacteria, etc. Such characters, for example, are economic utilization of food resources at the expense of fast growing, passive restraint from overpolluting of the environment (or the host), active cleaning of the habitat or, in some cases, distasefulness of insects (sse the Discussion).

In all these examples, the large number of individuals in a standard colony does not allow local drift within colonies to create a significant and permanent variance among them or to provide the altruist with a sufficient statistical advantage due to the neighbor effect. However, such a variance may be dynamically maintained when colonies are temporal, each being reestablished by a relatively small group of founders.

In our model we consider a specific case of population structure in which the random distribution of altruist and selfish in small founder groups generates subpopulations with different frequencies of altruists and selfish. The selection in the whole population is the balance between selection against the altruist *within* each subpopulation and the advantage that subpopulations with a higher frequency of altruists have over subpopulations with a low frequency of altruists. This model is essentially an extension and generalization of the model of Maynard-Smith (1964), with a special emphasis on the possibility of a stable polymorphism of altruist and selfish in the whole population and on the effect of population density on the number of founders.

We consider several ways in which altruism can be expressed.

1. The fitness of the subpopulation is an increasing function of the *proportion* of altruists. This would correspond, for example, to a situation in which nonaltruists pollute their environment and altruists act to remove the pollution.

2. The fitness of the subpopulation is an increasing function of the *number* of altruists. This would correspond to a situation in which a minimal number of altruists is required to perform some essential service for the whole population.

3. The altruists are more economic in the utilization of a limiting resource. They are also slower, so that the presence of altruists leaves more of the resource for the nonaltruists.

2. A GENERAL SETUP OF THE MODEL

Let us assume a large haploid population of two types, say A and E. The population reproduces in two phases. First, small groups of individuals colonize available habitats, multiply there, and increase in number. Then they get mixed together again to form the next generation of colonizers. More specifically, if p is the proportion of the A type in the population at the time of colonization, then we assume that a fixed proportion $a(m, n; p)$ of all colonies will be founded each by exactly m individuals of the type A and n individuals of the type E. Throughout this work we concentrate on the two simplest cases.

Case I. The initial size of a colony is fixed, say N. Individuals of the different types are equal in their chances of being included in each founding group, independently of the types of other founders. We then get

$$\begin{aligned} a(m, n; p) &= 0 \qquad && m + n \neq N, \\ a(m, n; p) &= \binom{N}{m} p^m q^n \qquad && m + n = N, \end{aligned} \tag{2.1}$$

where $q = 1 - p$.

Case II. The various founding individuals reach the habitat at random, with equal chances and independent of each other. In this case the size of the founding group, as well as the sizes of the subgroups of founders of each type, will be Poisson distributed:

$$a(m, n; p) = e^{-\nu} \frac{\nu^{m+n}}{m!\, n!} p^m q^n, \tag{2.2}$$

where ν is the *density of colonization*, i.e., the average size of a founding group.

Following the phase of colonization, a phase of incubation takes place. During this phase, each individual propagates according to both its own type and the interference of its neighbor colonizers. A type A is said to be *altruist* if:

(i) Its existence in a colony increases the average rate of reproduction within this colony.

(ii) At a given colony, the rate of reproduction of an individual of type A is less than that of its neighbor of type E, if it exists.

More specifically, let $\alpha(m, n)$ and $\beta(m, n)$ be the total value by which altruistic and selfish founders multiply themselves, respectively, during the period of incubation in a colony founded by exactly m altruist and n selfish individuals. Then, (i) can be formally replaced by

$$(m + k)\, \alpha(m + k, n) + n\beta(m + k, n) \geqslant m\alpha(m, n + k) + (n + k)\, \beta(m, n + k) \tag{2.3}$$

for all $m, n, k = 0, 1, 2, \ldots$ with a sharp inequality at least in some cases, i.e.,

$$\alpha(n, 0) > \beta(0, n). \tag{2.3a}$$

In the same way, (ii) may be replaced by

$$\alpha(m, n) \leqslant \beta(m, n) \qquad \text{for all } m, n = 0, 1, 2, \ldots \tag{2.4}$$

with a sharp inequality at least in some cases.

For comparison, see the definitions of altruism in Haldane (1932), Hamilton (1965), and Eshel (1972). In cases where a fixed ratio of fitnesses between altruist and selfish may be assumed throughout a fixed period of incubation, (2.4) may be readily replaced by a stronger condition,

$$\beta(m, n) = \lambda\alpha(m, n) \qquad \text{for all } m, n = 0, 1, 2, \ldots ;\ \lambda > 1. \tag{2.5}$$

Thus, in the discrete situation of k generations of incubation with a fitness ratio of $1 + s$ $(s > 0)$ we get

$$\lambda = (1 + s)^k.$$

In the case of continuous differential growth within the colonies we similarly get

$$\lambda = e^{sT},$$

where T is the length of incubation time.

Example A: The Generalized Haldane's Model

This model (compare Haldane, 1932, Appendix B) corresponds to the situation where

(i) the infinitesimal growth rate of the altruist is smaller than that of the selfish by a fixed ratio of $1/(1 + s)$; and

(ii) the welfare of the entire colony is increased with the relative frequency of the altruist in the colony.

In this postulate we generalize the more specific assumption made by Haldane that the average reproduction of the entire group increases linearly with the relative frequency of the altruist within it. We shall later give further consideration to the linear assumption of Haldane.

In the general case, let $K + B$ $(B > 0)$ be the relative growth rate of a purely altruistic colony. If at a given moment the relative frequency of the altruist in a colony is ξ, $0 < \xi < 1$, then the relative rate of reproduction of the selfish in this colony is denoted by $K + B\psi(\xi)$, where, by definition, $\psi(0) = 0$, $\psi(1) = 1$. $B > 0$ is the supremal advantage endowed to a selfish by its altruistic neighbors.

Assumption (2.3) is equivalent here to a monotone increase in $\psi(\xi)$. (With Haldane's assumption of linearity we get $\psi(\xi) = \xi$.) Finally, assumption (2.5) implies an altruist relative rate of reproduction which is smaller than that of the selfish by a constant, say $s > 0$, at any time and in any colony. Designate $x = x(t)$ and $y = y(t)$ for the respective number of altruistic and selfish individuals existing at a time t $(0 \leqslant t \leqslant T)$ in a given colony; we get

$$\frac{dy}{dt} = \left(K + B\psi\left(\frac{x}{x+y}\right)\right) y \tag{2.6}$$

$$\frac{dx}{dt} = \left(K + B\psi\left(\frac{x}{x+y}\right) - s\right) x. \tag{2.7}$$

With the initial conditions $x(0) = m$, $y(0) = n$ we get

$$\beta(m, n) = \frac{y(T)}{n} = c \exp\left\{KT + B\int_0^T \psi\left(\frac{m}{m + ne^{st}}\right) dt\right\} \tag{2.8}$$

and

$$\alpha(m, n) = x(T)/m = e^{-sT}\beta(m, n). \tag{2.9}$$

For the linear case, (2.8) becomes

$$\beta(m, n) = ce^{KT}\left(\frac{m+n}{me^{-sT} + n}\right)^{B/s}. \tag{2.10}$$

While Haldane's model corresponds to a situation of an active contribution of the altruist to the colony, the following two examples correspond to a situation of passive restraint of the altruist from damaging the colony.

Example B: The Case of a Nonpolluting Altruist

The infinitesimal growth rate of all individuals in the colony is decreasing with the number of the polluting selfish individuals in the colony; the growth rate of the altruist is smaller than that of the selfish by a fixed value s. We get

$$\begin{aligned} dy/dt &= y\psi(y), \\ dx/dt &= x(\psi(y) - s), \end{aligned} \tag{2.11}$$

while $\psi(y)$ is a decreasing function of y. Taking over the simplest linear structure, $\psi(y) = a - y$ (a fixed damage per selfish individual), we get

$$\alpha(m, n) = \frac{ae^{(a-s)T}}{a - n + ne^{aT}} \tag{2.12}$$

$$\beta(m, n) = \frac{ae^{aT}}{a - n + ne^{aT}} = e^{sT}\alpha(m, n). \tag{2.13}$$

Example C: An Altruistic Economy in Exploiting Environmental Resources

In this example we assume a limited rate of supply of resources c for the whole colony per a unit of time. c is measured in units of supply necessary for an altruistic individual in the colony. The amount of supply consumed by a selfish individual in a unit of time is $A > 1$. The colony stops growing when the total amount of resources consumed becomes equal to c; at this moment

$$m\alpha(m, n) + An\beta(m, n) = c. \tag{2.14}$$

If, as a result of its more economical metabolism, the growth rate of the altruist is lower than that of the selfish, we may assume (2.5), which in conjunction with (2.14) renders

$$\alpha(m, n) = c/(m + \lambda An); \qquad \beta(m, n) = \lambda\alpha(m, n). \tag{2.15}$$

We now study the general rules by which the frequency p of the altruist is changed in the entire population from one generation to the next.

Let $h(p)$ and $g(p)$ be the *average* numbers of altruistic and selfish individuals emerging from a single colony at the end of the incubation time. Clearly,

$$h(p) = \sum_{m,n} ma(m, n; p)\,\alpha(m, n), \tag{2.16}$$

$$g(p) = \sum_{m,n} na(m, n; p)\,\beta(m, n). \tag{2.17}$$

The relative frequency of altruistic individuals in the entire population after one generation of colonization and incubation will thus be

$$p' = \frac{h(p)}{h(p) + g(p)} = f(p), \tag{2.18}$$

say.

We know $h(0) = g(1) = 0$; therefore,

$$f(0) = 0 \qquad f(1) = 1 \tag{2.19}$$

and the monomorphic points $p = 0$ and $p = 1$ are obviously equilibria of the system. The point $p = 0$ is stable if $f'(0) < 1$ and only if $f'(0) \leqslant 1$. In order to check the stability of this point we use the equality

$$f'(0) = h'(0)/g(0).$$

Knowing $a(m, n; 0) = 0$ for all $m \geqslant 1$ we obtain

$$g(0) = \sum_{n=0}^{\infty} na(0, n; 0)\,\beta(0, n),$$

whereas

$$h'(0) = \sum_{m,n} m\alpha(m, n) \left\{\frac{d}{dp} a(m, n; p)\right\}_{p=0}.$$

Hence $p = 0$ is a stable equilibrium if

$$\sum_{m,n} m\alpha(m, n) \left\{\frac{d}{dp} a(m, n; p)\right\}_{p=0} < \sum_{n=0}^{\infty} n\beta(0, n)\, a(0, n; 0). \tag{2.20}$$

In this case selection operates against the altruistic trait unless perhaps its frequency surpasses some critical value. If the reverse of inequality (2.20) holds, $p = 0$ is unstable and the altruistic trait is to become established in the population whenever it is introduced into it.

In a similar way, employing the equality $f'(1) = -g'(1)/h(1)$ we find that $p = 1$ is a stable equilibrium if

$$-\sum_{m,n} n\beta(m, n) \left\{\frac{d}{dp} a(m, n; p)\right\}_{p=1} < \sum_{m=0}^{\infty} ma(m, 0; 1)\, \alpha(m, 0). \tag{2.21}$$

We see that with the addition of quite elementary assumptions made about the founding groups, inequalities (2.20) and (2.21) will become much simpler.

Finally, it may be shown that an inner equilibrium $\hat{p} = f(\hat{p})$, if it exists, is stable if

$$(1 - \hat{p})\, h'(\hat{p}) - \hat{p}g'(\hat{p}) < h(\hat{p})/\hat{p}. \tag{2.22}$$

It is unstable if the reverse of (2.22) holds.

We now restrict our study to the two simplest situations of colonization mentioned above: The case of a fixed-size colonizing group with a binomial distribution of types within it and the case of colonization by independent individuals with a two-dimensional Poisson distribution of types in the colonizing group.

3. THE CASE OF A FIXED-SIZE FOUNDING GROUP

With the assumptions of a random sampling of N founders out of a large parental population we get

$$\begin{aligned} a(m, n; p) &= 0 && m + n \neq N, \\ &= a(m, p) && m + n = N, \end{aligned} \tag{3.1}$$

where

$$a(m, p) = \binom{N}{m} p^m q^{N-m} \qquad (q = 1 - p). \tag{3.2}$$

We also denote

$$\begin{aligned} \alpha(m, N-m) &= \alpha_m\,; \qquad m = 1, 2, \ldots, N \\ \beta(m, N-m) &= \beta_m\,; \qquad m = 0, 1, \ldots, N-1. \end{aligned} \tag{3.3}$$

Thus

$$h(p) = \sum_{m=1}^{N} m \binom{N}{m} \alpha_m p^m q^{N-m} \tag{3.4}$$

$$g(p) = \sum_{n=0}^{N-1} (N-n) \binom{N}{n} \beta_n p^n q^{N-n} \tag{3.5}$$

and with assumption (2.5), (3.5) becomes

$$g(p) = \lambda N \sum_{n=0}^{N} \binom{N}{n} p^n q^{N-n} \alpha_n - \lambda h(p). \tag{3.6}$$

Here, by definition, $\alpha_0 = \lambda^{-1}\beta_0$. For convenience we also denote $\beta_N = \lambda\alpha_N$. Condition (2.22) for stability of an inner equilibrium $\hat{p}$ becomes

$$\frac{h'(\hat{p})}{h(\hat{p})} < \frac{1 + (\lambda - 1)\,\hat{p}N}{\hat{p}[1 + (\lambda - 1)\,\hat{p}]}. \tag{3.7}$$

To check the stability of the monomorphic equilibrium $p = 0$ we can readily obtain

$$\sum_{m,n} m\alpha(m, n) \left\{\frac{d}{dp}\, a(m, n; p)\right\}_{p=0} = \alpha_1 N \tag{3.8}$$

and

$$\sum_{n=0} na(0, n; 0)\, \beta(0, n) = \beta_0 N. \tag{3.9}$$

Inserting (3.8) and (3.9) into (2.20), we get

COROLLARY 3.1. *When founding groups are of a fixed size and colonizers are sampled at random then* $f'(0) = \alpha_1/\beta_0$ *and the monomorphic equilibrium* $p = 0$ *is stable if*

$$\alpha_1 < \beta_0. \tag{3.10}$$

It is unstable if $\alpha_1 > \beta_0$.

In a similar way it is shown that

Corollary 3.2. *With the assumptions of Corollary* 3.1, $f'(1) = \beta_{N-1}/\alpha_N$ *and the monomorphic equilibrium* $p = 1$ *is stable if*

$$\alpha_N > \beta_{N-1}. \tag{3.11}$$

It is unstable if $\alpha_N < \beta_{N-1}$.

Note that stability of the point $p = 0$ means that selection will operate against the altruist when it is rare. In this case, almost all altruistic founders will appear as single representatives of their type in the founding groups to which they belong. Thus, during the incubation time, these individuals will multiply by a factor of α_1. Yet, when the altruistic type is very rare, most colonies will lack this type at all, and thus, most founding individuals will multiply during the incubation time by a factor of β_0. Thus, heuristically, the condition $\alpha_1 < \beta_0$ for stability of $p = 0$ asserts that when the altruist is very rare in the population, its growth rate is less than that of the average selfish individual in the population. In the same way, the condition $\alpha_N > \beta_{N-1}$ assures that the growth rate of the selfish, when rare, is less than that of the altruist.

Employing Corollaries 3.1 and 3.2 we now study some of the typical situations described in the previous section.

Example A: The Generalized Haldane's Model

From (2.8), (2.9), and (3.3) we get for a fixed-size founding group

$$\beta_m = c \exp \left\{ KT + B \int_0^T \psi \left(\frac{me^{-st}}{N - m + me^{-st}} \right) dt \right\}$$

$$\alpha_m = e^{-sT} \beta_m .$$

From Corollary 3.1, it thus follows that $p = 0$ is stable if

$$B < \frac{sT}{\int_0^T \psi(1/(1 + (N - 1)\, e^{st}))\, dt} = B_1^*(T), \tag{3.12}$$

say.

From Corollary 3.2 it follows that $p = 1$ is stable if

$$\begin{gathered} \frac{B}{B - s} \int_0^T \psi \left(\frac{N - 1}{N - 1 + e^{sT}} \right) dt < T \\ \text{or} \\ B > \frac{sT}{T - \int_0^T \psi((N - 1)/(N - 1 + e^{st}))\, dt} = B_2^*(T), \end{gathered} \tag{3.13}$$

say. As $0 \leqslant \psi(u) \leqslant 1$ and $\lim_{u\to 0} \psi(u) = 0$, we have

$$\lim_{T\to\infty} B_1^*(T) = \infty$$

$$\lim_{T\to\infty} B_2^*(t) = s.$$

For any $B > s$, we therefore infer that *if the time of incubation is sufficiently long, then both edges are stable and selection favors the majority.* Note that the requirement $B > s$ means that a purely altruistic colony will do better than a purely selfish one (Postulate 2.3a).

With continuity of $\psi(u)$ we have, on the other hand,

$$\lim_{T\to 0} B_1^*(T) = \frac{s}{\psi(1/N)},$$

$$\lim_{T\to 0} B_2^*(T) = \frac{s}{1 - \psi(1 - (1/N))}.$$

If ψ is convex then for values B ann s satisfying

$$1 - \psi\left(1 - \frac{1}{N}\right) < \frac{s}{B} < \psi\left(\frac{1}{N}\right) \tag{3.14}$$

and for a sufficiently short time of incubation, a protected polymorphism of the altruistic and the selfish types will be maintained, i.e., both edges are unstable.

Moreover, it might be shown that $B_1^*(T)$ is a monotone increasing and $B_2^*(T)$ is a monotone decreasing function of T; therefore, convexity of ψ, and a short time of incubation are also necessary conditions for the maintaining of a protected polymorphism.

In the linear case one can directly calculate

$$B_1^*(T) = \frac{NsT}{T + \ln N - \ln[1 + (N - 1)\, e^{sT}]}$$

$$B_2^*(T) = \frac{NsT}{\ln(N - 1 + e^{sT}) - \ln N} < B_1^*(T)$$

for all $T > 0$, and $B_1^*(0) = B_2^*(0) = Ns$.

Conditions for selection near both edges for and against the altruist are depicted in Figure 2.

If $\psi(x)$ is either linear or concave, $B_1^*(T) > B_2^*(T)$ for all $T > 0$ and at least one edge is always stable. No protected polymorphism can be maintained in these cases.

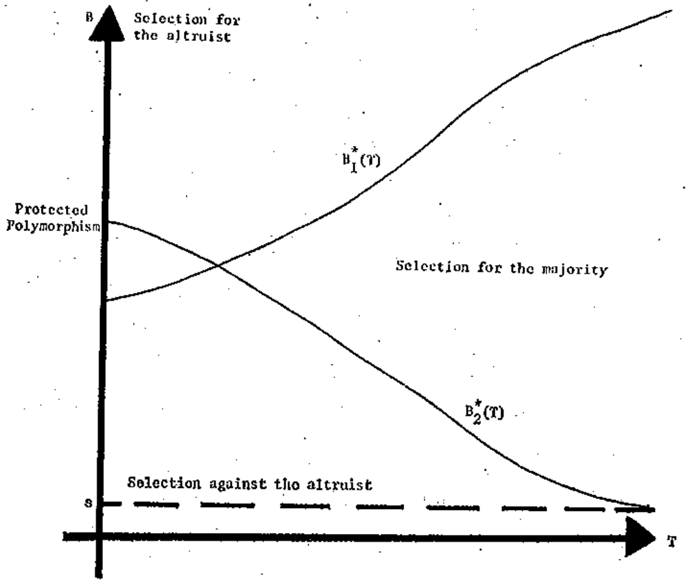

FIG. 1. A convex version of the Haldane's model. Selection for and against the altruist near both edges is manifested as a function of the altruist benefit B and the incubation time T. Note that a protected polymorphism is possible only for a short time of incubation. With long incubation times there is selection for the majority.

Example B: A Nonpolluting Altruist—The Linear Case

In this case (see previous section) we get from (2.12), (2.13), and (3.3)

$$\alpha_m = \frac{ae^{(a-s)T}}{a + (N-m)(e^{aT}-1)}$$

$$\beta_m = e^{sT}\alpha_m$$

and thus

$$f'(0) = \frac{\alpha_1}{\beta_0} = e^{-sT}\,\frac{a + N(e^{aT}-1)}{a + (N-1)(e^{aT}-1)}$$

$$f'(1) = e^{sT}\,\frac{a}{a + e^{aT} - 1}.$$

Here a is the stable capacity of the habitat in terms of number of polluting individuals it can stably support. s is the individual disadvantage of the altruist. In this case it is readily shown that the selfish equilibrium $p = 0$ is stable if

$$s > \frac{1}{T}\ln\left(\frac{a + N(e^{aT}-1)}{a + (N-1)(e^{aT}-1)}\right) = s_1{}^*(T),$$

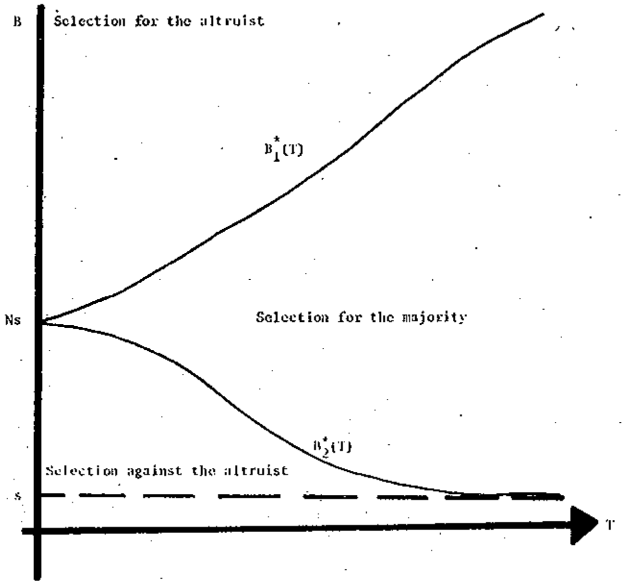

FIG. 2. The linear version of the Haldane's model. Selection for and against the altruist near both edges is manifested as a function of the altruist benefit B and the incubation time T. Note that no protected polymorphism is possible. A long time of incubation is always favorable for the majority.

say. $p = 1$ is stable if

$$s < \frac{1}{T} \ln \left(\frac{a + e^{aT} - 1}{a} \right) = s_2^*(T),$$

say.

It is not difficult to see that for all T:

(i) $s_2^* > s_1^*$ and, therefore, no protected polymorphism can be maintained.

(ii) Both s_1^* and s_2^* are monotone decreasing with T and, thus, a long period of incubation always favors the polluting selfish. Moreover, since $\lim_{\to\infty} s_1^*(T) = 0$, the selfish equilibrium is always stable if T is long enough.

Example C: *Economy in Exploiting Environmental Resources*

In this case we employ (2.15) and (3.3) to get

$$f'(0) = \frac{AN}{1 + \lambda A(N-1)},$$

$$f'(1) = \frac{\lambda N}{N - 1 + \lambda A},$$

where $A > 1$ is the ratio between the amounts of food consumed by the selfish and by the altruist, respectively.

The selfish equilibrium $p = 0$ is stable if

$$N > \frac{A\lambda - 1}{A(\lambda - 1)} = N^*,$$

say. The altruist equilibrium $p = 1$ is stable if

$$N < \frac{A\lambda - 1}{\lambda - 1} = AN^*.$$

Having $A > 1$, we see that at least one edge, and possibly both of them, is always stable with the result of selection in favor of the majority.

We also see that large colony size is always favorable for the selfish (see next section).

We now concentrate on conditions for the maintainence of a polymorphism between altruists and a selfish in the population. First, we know that a condition for a protected polymorphism is that both inequalities $\alpha_N < \beta_{N-1}$ and $\alpha_1 > \beta_0$ hold. With condition (2.5), this requirement becomes

$$\beta_1/\beta_0 > \lambda > \beta_N/\beta_{N-1}. \tag{3.15}$$

For appropriate values of λ, (3.15) holds whenever the benefit endowed on a colony by a single altruistic founder (with all other founders being selfish) is larger than the damage inflicted on a colony by a single selfish founder (with all other founders being altruistic). Here benefit and damage are measured in terms of the total growth of the colony throughout the entire period of incubation. Note that this requirement does not hold in most of the cases being analyzed above, as well as in many other cases studied by the authors.

The reason for this may be the fact that the relative frequency of the altruist in the colony is ever decreasing during the time of incubation; therefore, the accumulated effect of a single altruist founder on the total growth of the colony is generally small. On the other hand, a small group or even a single selfish founder, by ever increasing its relative frequency in the colony, may cause larger damage, especially when the incubation time is long.

It is not difficult, however, to imagine a situation in which the existence of even few altruistic individuals in the colony is crucial for its welfare. In such a situation, condition (3.15) is more likely to be satisfied, with the result of a maintaining of a protected polymorphism.

We end this section by globally analyzing a situation in which, although selection operates against the altruist near both edges, a stable polymorphism is maintained in the interior of the interval (0,1).

Example D

In fig wasps, the males inside the closed syconium of *Ficus sycomorus* work together to make an escape tunnel for the females through the syconium wall (Galil and Eisikowitch, 1968). In such a population it may be of some advantage for a selfish male not to participate in the work, provided that there is a sufficient number of altruistic workers to accomplish the work without his help.

In this example it is reasonable to assume as usual $\beta_n = \lambda\alpha_n$ for all $n = 0, 1,\ldots, N$. We also assume the existence of a critical number K, $1 \leqslant K \leqslant N - 1$ such that

$$\begin{aligned} \alpha_n &= 1 - b < 1 \qquad && n \leqslant K, \\ &= 1 && n > K. \end{aligned} \tag{3.16}$$

We get

$$(\beta_0/\alpha_1) = (\beta_{N-1}/\alpha_N) = \lambda > 1;$$

hence, $p = 0$ is always stable and $p = 1$ is always unstable. Thus, we find that selection favors the selfish near both edges, a theoretical finding that seems to be contradicted by empirical observations. Yet let us consider any frequency $0 < p < 1$ of the altruist in the population.

Employing (3.4), (3.5), and (3.6), we readily get

$$h(p) = Np - b \sum_{m=0}^{K} m \binom{N}{m} p^m q^{N-m}$$

and

$$g(p) = \lambda \left\{ qN - b \sum_{m=0}^{K} (N - m) \binom{N}{m} p^m q^{N-m} \right\}. \tag{3.18}$$

We now show that for λ sufficiently close to 1, $f(p) > p$. This means, that selection favors the altruist whenever its frequency in the population is p.

To show this, we exploit the simple equality

$$\sum_{m=0}^{N} \binom{N}{m} p^m q^{N-m} [pN - m] = 0. \tag{3.19}$$

The sequence $\{pN - m\}$ is decreasing with m and, therefore, the sum of the first K terms of (3.19) is positive since it is positive for $K = N - 1$

$$\begin{aligned} &\sum_{m=0}^{K} \binom{N}{m} p^m q^{N-m} (pN - m) \\ &\qquad = p \sum_{m=0}^{K} \binom{N}{m} p^m q^{N-m} (N - m) - q \sum_{m=0}^{K} \binom{N}{m} p^m q^{N-m} \quad m > 0. \end{aligned}$$

From this, in conjunction with (3.17) and (3.18) we infer

$$\frac{\lambda g h(p)}{p g(p)} = \frac{Npq - bq \sum_{m=0}^{K} m \binom{N}{m} p^m q^{N-m}}{Npq - bp \sum_{m=0}^{K} (N-m) \binom{N}{m} p^m q^{N-m}} > 1$$

and for λ sufficiently close to 1 (depending on p),

$$qh(p) > pg(p).$$

Hence

$$f(p) = \frac{h(p)}{g(p) + h(p)} > p. \tag{3.20}$$

COROLLARY. *For any mixture of altruist and selfish there is a critical value of altruist–disadvantage, below which selection will favor the altruist.*

For any specific value of λ, if it is close enough to 1, it is likely that two points of equilibrium exist in the interior of the interval (0, 1): an unstable equilibrium $\hat{p}_1$ with a low frequency of the altruist, and a stable polymorphism $\hat{p}_2$ $(1 > \hat{p}_2 > \hat{p}_1)$ maintaining a relatively high frequency of the altruist, with a domain of attraction $(\hat{p}_1, 1)$. Furthermore, when $\lambda \downarrow 1$ $\hat{p}_2 \uparrow 1$, the stable frequency of the altruist increases, tending to 1 and $\hat{p}_1 \downarrow 0$ (the domain of attraction of $\hat{p}_2$ increases).

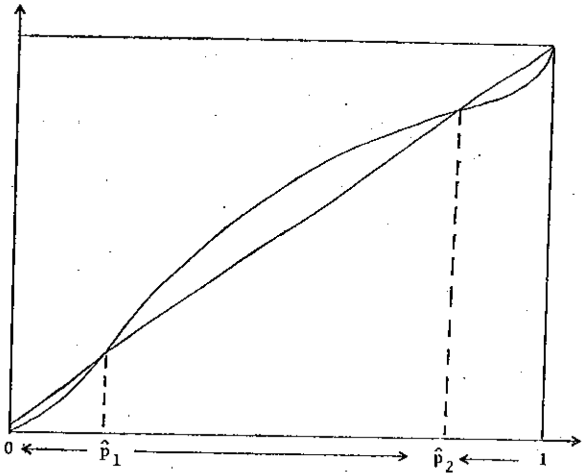

FIG. 3. Points of equilibrium and domains of attraction in an altruist-selfish polymorphism maintained in a population of the fig wasp. The arrows indicate the direction of the selection forces.

4. THE CASE OF TWO-DIMENSIONAL POISSON DISTRIBUTION OF FOUNDING GROUPS

This case corresponds to the situation of a random dispersal of independent individuals of both types over the available habitats. If ν is the expected number of founding individuals, either altruistic or selfish, being settled in a single habitat, then

$$a(m, n; p) = e^{-\nu} \frac{\nu^{m+n}}{n!\, m!} p^m q^n$$

$$h(p) = h_\nu(p) = e^{-\nu} \sum_{m,n} \frac{\nu^{m+n}}{m!\, n!} m\alpha(m, n)\, p^n q^n \tag{4.1}$$

$$g(p) = g_\nu(p) = e^{-\nu} \sum_{m,n} \frac{\nu^{m+n}}{m!\, n!} n\beta(m, n)\, p^m q^n$$

and thus

$$\begin{aligned} f(p) = f_\nu(p) &= \frac{h(p)}{h(p) + g(p)} \\ &= \frac{\sum_{m,n} (\nu^{m+n}/m!\, n!)\, m\alpha(m, n)\, p^m q^n}{\sum_{m,n} (\nu^{m+n}/m!\, n!)[m\alpha(m, n) + n\beta(m, n)]\, p^m q^n}. \end{aligned}$$

We also have

$$\begin{aligned} \left\{\frac{d}{dp} a(m, n; p)\right\}_{p=0} &= -e^{-\nu} \frac{\nu^n}{(n-1)!} && m = 0;\ n \geqslant 1 \\ &= e^{-\nu} \frac{\nu^{n+1}}{n!} && m = 1 \\ &= 0 && \text{otherwise.} \end{aligned}$$

Inserting this into (2.20), we see that $p = 0$ is a stable equilibrium if

$$\sum_{n=0}^{\infty} [\beta(0, n+1) - \alpha(1, n)] \frac{\nu^n}{n!} > 0. \tag{4.3}$$

In a similar way

$$\begin{aligned} -\left\{\frac{d}{dp} a(m, n; p)\right\}_{p=1} &= -e^{-\nu} \frac{\nu^m}{(m-1)!} && n = 0;\ m \geqslant 1 \\ &= e^{-\nu} \frac{\nu^{m+1}}{m!} && n = 1 \\ &= 0 && \text{otherwise.} \end{aligned}$$

Employing (2.21) we see that $p = 1$ is a stable equilibrium if

$$\sum_{m=0}^{\infty} [\alpha(m+1, 0) - \beta(m, 1)] \frac{\nu^{m}}{m!} > 0. \tag{4.4}$$

The parameter ν, namely, the expected number of colonizers settling in a single habitat, may measure the density of the colonizing population. Thus, if the population is very sparce, and ν is very small, the condition (4.3) for stability of the selfish equilibrium becomes

$$\alpha(1, 0) - \beta(0, 1) < 0(\nu).$$

The condition (4.4) for stability of the altruistic equilibrium becomes

$$\alpha(1, 0) - \beta(0, 1) > 0(\nu).$$

However, as a special case of this assumption (2.3) that a purely altruistic colony is better off (in terms of growth rate) than a purely selfish colony of the same size, we have

$$\alpha(1, 0) > \beta(0, 1), \tag{4.5}$$

and thus, when the population is sufficiently sparse, $p = 1$ is always stable and $p = 0$ is always unstable. In other words, selection then favors the altruist near both edges. Furthermore, from (4.2) and (4.5) we get for all $0 < p < 1$.

$$\lim_{\nu \to 0} f_\nu(p) = \frac{\alpha(1, 0)p}{\alpha(1, 0)p + \beta(0, 1)q} > p \tag{4.6}$$

Hence we get

THEOREM 4.1. *In a two-dimensional Poisson process of colonization and selection there is a critical density ν^* of the colonizing population under which selection will always operate in favor of the altruist, whatever its frequency.*

Proof. As we have seen, for any $0 \leqslant p \leqslant 1$ (including the edges) there is a critical density $\nu^*(p) > 0$ under which selection will favor the altruist when its frequency is p, $\nu^*(p)$ being finite or infinite. More specifically, $\nu = \nu^*(p)$ is a positive solution of $f_\nu(p) = p$, if such a solution exists, or ∞ if such a solution does not exist. But $f_\nu(p)$ is a continuous differentiable function of both ν and p; thus, from the theory of the implicit functions we know that $\nu^*(p)$ is a continuous function of p in any interval in which it is finite. Now, for a positive constant $c > 0$,

$$L_c = \{p; \nu^*(p) \leqslant c; 0 \leqslant p \leqslant 1\}$$

is a compact set (maybe empty) and $\nu^*(p)$ is continuous on this set. If $L_c = \phi$, then the chain of the proof of the theorem is complete. If $L_0 \neq \phi$, then $\nu^*(p)$ has its minimum

$$\nu^* = \min_{p \in L_0} \nu^*(p)$$

over L_0. This minimum is positive and satisfies the requirement of the theorem.

Q.E.D.

Under a somewhat less general assumption we now show that if the density of the population becomes sufficiently high, selection will always operate in favor of the selfish type, at least (but, presumably not only) near the edges.

For this, we first take over the assumption

$$\beta(m, n) = \lambda\alpha(m, n) \qquad (\lambda > 1) \tag{2.5}$$

for all $m, n > 0$.

We further assume that the effect of any single founder on the total growth of its colony becomes negligible as the size of the founding group of the colony tends to infinity. More specifically, we assume

$$\lim_{N\to\infty} \max_{0\leqslant m<n} \left| \frac{\beta(m, N-m) - \beta(m+1, N-m-1)}{\beta(0, N)} \right| = 0. \tag{4.7}$$

Finally, dealing with a situation in which the density of the population grows indefinitely, it is natural to assume that $\beta(0, N)$ does not tend to 0 as $N \to \infty$. We assume, less than this, that a value $\delta > 0$ exists such that

$$\beta(0, n) > \delta^n \qquad \text{for all } n = 1, 2, \ldots . \tag{4.8}$$

With these assumptions, we readily get

$$\begin{aligned} &\lim_{\nu\to\infty} \frac{\lambda}{\delta} e^{-\delta\nu} \sum_{n=0}^{\infty} [\beta(0, n+1) - \alpha(1, n)] \frac{\nu^n}{n!} \\ &= \lim_{\nu\to\infty} e^{-\delta\nu} \sum_{n=0}^{\infty} \left[\frac{\lambda\beta(0, n+1) - \beta(1, n)}{\beta(0, n+1)} \right] \frac{\beta(0, n+1)}{\delta^{n+1}} \frac{(\nu\delta)^n}{n!} \\ &\geqslant \lambda - 1 > 0. \end{aligned} \tag{4.9}$$

Hence, for large enough ν,

$$\sum_{n=0}^{\infty} [\beta(0, n+1) - \alpha(1, n)] \frac{\nu^n}{n!} > 0$$

and condition (4.3) for stability of $p = 0$ is satisfied.

In a similar way, we get

$$\sum_{n=0}^{\infty} [\beta(n+1, 0) - \alpha(n, 1)] \frac{\nu^n}{n!} > 0$$

which, being the inverse of (4.4), ensures instability of the altruistic equilibrium $p = 1$. We have thus proved that for a density ν sufficiently high, selection will operate against the altruist near both edges.

Furthermore, for any $0 < p < 1$ it may be shown that for a sufficiently large ν (say, $\nu > \hat{\nu}(p)$), $f(p) < p$ (the proof is technical and will be omitted). Therefore, in the same way as we have proved Theorem 4.1, we get

THEOREM 4.2. *In a two-dimensional Poisson process of colonization and selection with assumptions* (2.5), (4.7), *and* (4.8), *there is a critical density* $\hat{\nu}(\hat{\nu} > \nu^*)$ *of the colonizing population, above which selection will always operate against the altruist.*

Theorems 4.1 and 4.2 may have interesting implications for an ecogenetical model wherein (unlike in our model) not only p, but also ν, changes from one generation to the next (see, for comparison, Motro, 1976). If ecological forces operate to stabilize the population around a value $\nu(p)$, it is likely that such a value will be an increasing function of the frequency of the altruistic type in the population. Thus, any increase in the altruistic type in the population is also likely to increase the density of the population. However, such an increase may, in turn, impose selection forces against the altruist. In some cases, such a situation may lead to a stabilization of a specific density with a polymorphism of altruist and selfish. However, in most examples treated in this work, no stable equilibrium of altruist and selfish may be maintained with any density of the population. In these cases, the population is likely to be fixed on either the altruistic or the selfish type, with a stable density determined thereby. However, it seems possible that a similar situation may lead to a more interesting case of stable fluctuations in the population—starting with a sparse population, the altruistic type becomes fixed in the population, which thereby, increases in density. If the increase is large, selection forces against the altruist may then cause a fixation or at least establishment of a selfish mutant with a resulting decrease in density, and so on. A more rigorous treatment of such a situation is now in development.

For better understanding of the behavior of the population under conditions of neither an extremely low nor an extremely high density, let us treat in more detail some of the examples being treated in the case of a fixed founding group.

Example A: *Haldane's Linear Model*

In this case we know

$$\alpha(m, n) = e^{-sT}\beta(m, n) = e^{(K-s)T}\left(\frac{m+n}{me^{-sT}+n}\right)^{B/s}$$

where $B > s$ (see (2.10) and (2.11), and for comparison, also see the development of this model for a fixed sized founding group in Section 3).

We get

$$e^{-KT}\sum_{n=0}^{\infty}[\beta(0, n+1) - \alpha(1, n)]\frac{\nu^n}{n!} = e^{\nu} - e^{-sT}\sum_{n=0}^{\infty}\left(\frac{n+1}{n+e^{-sT}}\right)^{B/s}\frac{\nu^n}{n!} \tag{4.10}$$

and

$$e^{-(B+K-s)T}\sum_{m=0}^{\infty}[\alpha(m+1, 0) - \beta(m, 1)]\frac{\nu^m}{m!} = e^{\nu} - e^{sT}\sum_{m=0}^{\infty}\left(\frac{m+1}{m+e^{sT}}\right)^{B/s}\frac{\nu^m}{m!}. \tag{4.11}$$

Thus, from (4.3) and (4.10) it follows that $p = 0$ is stable if

$$e^{\nu} > e^{-sT}\sum_{n=0}^{\infty}\left(\frac{n+1}{n+e^{-sT}}\right)^{B/s}\frac{\nu^n}{n!}. \tag{4.12}$$

From (4.4) and (4.11) it follows that $p = 1$ is stable if

$$e^{\nu} > e^{sT}\sum_{n=0}^{\infty}\left(\frac{n+1}{n+e^{sT}}\right)^{B/s}\frac{\nu^n}{n!}. \tag{4.13}$$

Having $B > s$, the right-hand sides of both (4.12) and (4.13) tend to zero as $T \to \infty$ and, therefore, for a long enough time of incubation, selection always favors the majority. For a short time of incubation, (4.12) and (4.13) readily become

$$e^{\nu} > e^{\nu}\left(1 - \frac{\nu^*s - B}{\nu^*}T\right) + O(T), \tag{4.12a}$$

$$e^{\nu} > e^{\nu}\left(1 + \frac{\nu^*s - B}{\nu^*}T\right) + O(T), \tag{4.13a}$$

where, as we recall, $\nu^* = \nu/(1 - e^{-\nu})$ is the expected number of colonizers being settled in a *nonempty* habitat. We, thus, see that for a short enough time of incubation, selection near both edges operates against the altruist if $B < \nu^*s$ and for the altruist if $B > \nu^*s$. With some difficulties, it also may be shown that the value $B_1{}^*(T)$ for which (4.12) becomes an equality is monotone increasing with T and the value $B_2^*(T)$ for which (4.13) becomes an equality is monotone decreasing with T. Therefore, we have

COROLLARY. *Substituting N by ν^*, all the results achieved for the Haldane's linear model with a fixed size of a founding group stays correct for a Poisson distributed founding group.* (See Figure 2 above.)

With few more difficulties, most of the results being obtained for the nonlinear case, also may be generalized for a Poisson-distributed founding group. In this case, the effect of the randomness in the size of the founding group appears to be qualitatively unimportant.

Example B: A Nonpolluting Altruist—The Linear Case

In this case, we know

$$\beta(m, n) = e^{sT} \alpha(m, n) = ae^{aT}/(a - n + ne^{aT}).$$

(See (2.15) and (2.4), and see also the development of this model for a fixed size founding group in Section 3.)

From (4.4) we infer that $p = 1$ is a stable equilibrium if

$$e^{(a-s)T} > ae^{aT}/(a - 1 + e^{aT})$$

or, equivalently if

$$s < \frac{1}{T} \ln \left(\frac{a - 1 + e^{aT}}{a}\right) = s_2^*. \tag{4.14}$$

Note that this condition is again exactly similar to the condition achieved for the case of a fixed-size founding group. Note, moreover, that the condition (4.14) is independent of the density ν of the population. This, however, does not contradict Theorems 4.1 and 4.2 since neither condition (2.3) nor (4.8) is satisfied by this model. (A purely selfish colony, starting with a single colonizer may do better than a purely altruistic colony starting with a single colonizer, provided the period of incubation is short. Indeed, in this case there is no point in wasting energy on avoiding pollution, even from the standpoint of the entire colony.)

It also can be shown that the equilibrium $p = 0$ is stable if

$$a \sum_{n=1}^{\infty} \frac{\nu^{n-1}}{n!} \frac{ne^{sT} - \nu}{a + n(e^{aT} - 1)} > 1. \tag{4.15}$$

Moreover, it is shown that at least one of the conditions (4.14) and (4.15) always holds, and no protected polymorphism can be maintained. These results again stand in agreement with the results more easily obtained for the case of a fixed size founding group.

The same phenomenon is, at least qualitatively, manifested by an analysis of the case of economy in exploiting environmental resources. However, the expected conclusion that randomness in the size of the founding group does not basically affect the evolution of altruistic traits is incorrect.

DISCUSSION

As already mentioned, our model is a more general and analytic form of previously suggested ideas on genetic mechanisms for the maintenance by selection of altruistic characteristics in a population (Maynard-Smith, 1964; Fisher, 1958). We certainly do not suggest that most of the altruistic genes in natural populations are maintained by a mechanism which could be described by this model. The model is, however, a good representation of some quite commonly occurring natural situations, and we shall consider some of them in some detail.

1. *Distasefulness in Insects*

Our model is a good representation of a situation in which adult female moths or butterflies fly large distances and lay all their eggs within a restricted area. The larvae have a limited mobility and stay in the area. A strictly territorial predator (a bird) is the only selective agent. The number of layings within each territory is small. The number of founders is equivalent to twice the number of layings since a fertilized female carries two sets of genes.

The degree of protection conferred on all the larvae in the territory is an increasing function of the relative frequency of larva which have poisonous body fluids. Experimental work with Monarch butterfly larva suggests that a fairly low proportion (25–30 %) of poisonous individuals is sufficient to protect the subpopulations (Brower, 1969).

This situation corresponds, therefore, to the generalized Haldane model with a highly convex benefit function (example A) with a possibility of a stable polymorphism. In fact, the Monarch population in the eastern and central United States is phenotypically polymorphic (only some 25–50 % of the larva contain the poison, which has to be ingested by eating a poisonous food plant).

Note that with respect to our model, a relevant subpopulation is the collection of all larvae within the territory of a single predatory bird. The relevant number of founders in such subpopulations is twice the number of females laying there.

For a given density of layings, the number of founders per subpopulation obviously increases with the size of the territory of the predator. According to the analysis of the model, an increase in the size of the territory will decrease the tendency toward an evolution of distastefulness. The evolution of distastefulness is not expected when the predators are nonterritorial.

Similarly, for a given size of territory and larvae density, a tendency of females to distribute their layings over a wide area, larger than the bird's territory, will also increase the effective number of founders in each subpopulation, and thus, hinder the evolution of distastefulness. This result agrees with the conclusions of Fisher (1958) that, in general, distasteful larvae hatch either from eggs laid in batches by strongly flying moths or from singly laid eggs of poor fliers. The second case implies a slow mixing of the population in adult stage. The evolution of distastefulness in this case cannot be fully explained by our model, and it fits better some form of neighbor effect (Eshel, 1972).

2. *Cooperative Behavior in Bacteria*

Active conditioning of the environment commonly occurs in many bacteria. In general, since individual bacteria are very small, the effect of a single cell on its environment is very limited. Effective conditioning of the medium depends, therefore, on the joint localized action of many cells. This can allow a single selfish cell in a group of altruistic cells to benefit from the conditioning without contributing to it. Such cooperative characteristics can be maintained in a population according to our model if local subpopulations have a small number of founders.

The following examples serve to illustrate the point.

a. Secretion of extracellular hydrolytic digestive enzymes, e.g., in the genera *Bacillus* and *Clostridium*, *Myxococcus*, etc.

b. Secretion of antibiotic substances, e.g., *Bacillus*, *Pseudomonas*, etc., and anti-antibiotics, such as penicillinase by *Bacillus* and others.

c. Preventing the pollution of the medium with harmful metabolic waste products by developing special nonpolluting pathways, e.g., acetyl-methycarbinol formation in *Aerobacter*, *Bacillus*, *Serratia*, etc., when the pH becomes too low or when the concentration of waste products is high (Wood, 1955).

These genera are typical soil bacteria which occur in the soil in microcolonies of possibly a few hundred cells, which are probably started by a small number of founders (Jones and Griffiths, 1964). These conditions would lead to selection for cooperative altruistic characteristics. On the other hand, none of these cooperative characteristics is expected in bacteria which live suspended in water or attached to the solid substrate in flowing water.

3. *Heterogenetic Associations in Fungi*

In heterokaryotic fungi or myxomycetes and in aggregations of slime mold amoeba, there is always the theoretical possibility for an unequal contribution to the next generation by different genetic types within the association. This could lead to domination by those types which are able to contribute more than other types.

The "fitness" of any particular type within an association may very likely be correlated with a decrease in the reproductive success of the association as a whole. When the number of founders of an association is small, the "founder effect" will be able to maintain the altruistic genes in the whole population, in spite of selection against them within each association.

In most heterokaryotic fungi, the optimal nuclear ratio is maintained in the mycelium even when the number of founders is large, and the period of incubation is long. This is the result of localized "hyphal selection" between localized sections which have different nuclear ratios as the result of random assortment during growth. Those hypha in which the nuclear ratios are close to the optimum grow faster than those in which the ratios are further away from the optimum. Thus, the average ratio in the whole mycelium is maintained near the optimum (Davis, 1966). This mechanism is essentially similar to the founder effect, or the neighbor effect, each hypha acting as a local subpopulation within the whole mycelium. A stable polymorphism results when the heterokaryon hypha grow faster than the homokaryon ones.

The founder effect must be important at the level of the whole colony in order to eliminate nuclear types with a tendency to migrate preferentially into forming conidiophores or into other reproductive organs. Some such mechanism must be operating, since there is usually a very close similarity between nuclear ratios in vegatative mycelia and in the conidia which they form (Davis, 1966).

In *Myxomycetes* and in *Neurospora* there is a rapid cytoplasmic streaming which prevents a localized genetic effect. The excessive multiplication of "parasitic" nuclei is prevented by the strict synchronization of nuclear divisions. Thus, the nuclear ratio is maintained at the level it had reached at the initial formation of the plasmodium or mycelium. A few cases of parasitic genes have been described, however (e.g., Pittenger and Brawner, 1961). The founder effect between colonies must be responsible for the maintenance of whatever altruism there is in the whole population.

In the cellular slime molds, the *Acrasiales*, there are pronounced altruistic characteristics in the reproductive cycle, such as the differentiation of the mobile pseudoplasmodium into fertile spore cells and infertile stalk cells. In this case there is a problem, since Filosa (1962) has found that mass subculturing for many generations did not increase the proportion of a mutant of *Dictyostelium discoides* which tended to turn preferentially into a spore above 10–15 %. Under such conditions of mass subculturing, this type of mutant could be expected to completely dominate the population after several generations. It is possible, however, that spores for re-innoculation were always taken from those fruiting bodies which had ripened earlier and those would have had a lower proportion of the mutant cells.

4. *Economic Utilization of Exhaustible Resources by Restricting and Restraining Competition*

Restrained utilization can be expected when the founder effect is effective. A good example of the founder effect is of aphids, in which a colony is often founded by a single fertilized female. It has been shown that regulatory mechanisms maximize the steady production of adult aphids by the colony restraining the full reproductive potential of the insects and avoiding damage to the food plant (Way and Banks, 1967).

Many other examples are known of parasites which do not cause excessive damage to their hosts (Hamilton, 1972). Assuming that restraint may slow the growth of the benign parasites, the benign character may be maintained in the population by the founder effect, since quite often parasitation is initiated by a very small number of founders.

In general, conservative utilization of depletable resources may be expected in territorial animals and not in mobile animals or in large herds.

5. *The Fig Wasps*

These wasps pollinate the fig, and they lay eggs only in the short styled flowers, allowing the other flowers to make seeds, and in some species such as *Ficus sycomorus*, the males have to tunnel through the wall of the syconium to allow the females to escape. Each one of these characters is altruistic, in the sense that not performing any of these functions by an individual decreases the reproductive success of the group or of the whole species, while conferring an advantage to the individual.

Since normal development of the fig syconium in most *Ficus* species depends on the existence of developing seeds, both pollination and the restricting of egg laying to the short styled flowers can be maintained in the population by the founder effect, since each fig is normally entered by a small number of females, and almost each species of *Ficus* has its own specific pollinator (Ramirez, 1970). Tunneling by the males also can be maintained by the founder effect.

Various types of parasites are also found. In *F. sycomorus* in East Africa, *Ceratosolen arabicus* is the pollinator. *Sycophaga sycomori* is parasitic on the fig as it does not pollinate, but its males bore exit tunnels.

Other wasps which lay their eggs through the outer wall into the galls of these two species depend on tunneling by the males of these two species, and thus remain trapped inside if parasitizing too heavily (Galil and Eisikowitch, 1968).

The existence of such parasites suggests that the benefit function is highly convex, for example, that successful tunneling does not require the cooperation of the maximal possible number of males, or that complete pollination can be achieved by a smaller number of females.

Remark. While revising the manuscript, our attention has been called to recent works by Wilson (1975) and Matessi and Jayakar (1975), which are essentially developed on the same line of a temporal group—effect in a seasonally mixed population. The reader is also referred to Matessi and Jayakar (1973) and to Charnov and Krebs (1975). These works, although concentrating on specific biological phenomena, employ the same general principles.

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