Author's Notes: In this paper we developed a "stochastic" description of the population dynamics of a predator-prey ecosystem. This is because mutants are initially single individuals that therefore do not obey laws of statistical averages – but instead survive or not depending on luck as well as ability. Expressions for their probability of survival are found and the results generalized to arbitrary ecosystems. The results of these calculations reveal the importance of neutral or near neutral mutations, and indicate the limited ability of 'selection' to eliminate less effective members of the population. Evolution appears as a complex dialogue between mutation and selective forces where neither is necessarily dominant and both the extremes of Neo-Darwinism and of Neutral drift are refuted. A calculation of the non-linear effects of the spatial interaction between individuals of a mutant population shows how altruism and a division of labour can evolve because of spatial inhomogeneity and how the 'unit' of selection can thereby change from individuals to social groups.

Key words: Stochastics; Master Equation; Neo-Darwinism; Neutral drift; Evolutionary Stable Strategies.

EVOLUTION AND THE STOCHASTIC DESCRIPTION OF SIMPLE ECOSYSTEMS

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1. Introduction

In an earlier paper, one of us (Allen, 1976), has studied the evolution of simple ecosystems. It was assumed that mutations leading to phenotypes which were hitherto absent in the population occur with a frequency much smaller than that of normal births and deaths of the populations, and hence that the evolution can be regarded as being due to the stochastic appearance of "new population types" in a system that has attained its steady state consistent with the "normal" dynamics.

In this paper we shall examine some aspects concerning the initial appearance of a mutant population, when its numbers are small and require a stochastic description (Allen, 1975), and shall show that the probability of extinction of new mutants is non-negligible and plays a significant role in the evolutionary process. An evolutionary step is only considered to occur when the populations of a significant part of our system have been modified by the growth of a mutant type.

Let us suppose that our simple ecosystem consists of n interacting populations governed by the equations,

$$\frac{dx_i}{dt} = G_i(x_1, x_2, \cdots x_n) \quad 1 \leqslant i \leqslant n \qquad (1)$$

and that the system has attained a stable steady state, $x_1^0, x_2^0 \ldots\ldots x_n^0$

$$G_1(x_1^0, x_2^0 \cdots x_n^0) = 0$$

$$G_2(x_1^0, x_2 \cdots x_n^0) = 0$$

$$G_n(x_1^0, x_2^0 \cdots x_n^0) = 0$$

Let us consider what happens in a small

region, when a new population type appears. Only if it succeeds in attaining a significant population will it be possible to describe it by a "deterministic", average value equation. This deterministic equation will either describe its rejection or its amplification. Thus an evolutionary step will only occur if the mutant population survives the initial period of "stochastic" dynamics, reaches macroscopic numbers permitting a deterministic description, and is then amplified by this latter towards some state characterised by its presence as a finite fraction of the population. Perhaps we should make some remarks here about the relation of this work to that of the theory of Evolutionary Stable Strategies (ESS) developed by Maynard-Smith. Firstly, the basic intuition behind both is very similar, that is that evolution occurs not because of a change for the "good" of the species, but simply if a gene had properties such that it could invade the system. The statement of this idea was (Allen, 1975, 1976) that in order for an evolutionary step to occur, the system must be **unstable** to the appearance of a small number of the new mutant types. In other words evolution does not occur in order to "optimize" some global parameter for the species, but corresponds to a local phenomena of instability. As we shall see in the latter section of this paper, however, the instability of the system can be due to nonlinear genetic terms which take into account the 'inclusive fitness' of a new gene.

The popularisation and success of ESS, particularly as expressed in the splendidly clear book of Dawkins (Dawkins, 1976), has given considerable insight into many aspects of evolution such as aggressiveness, parental investment, sexual behaviour etc., and of course this is largely due to the brilliant, intuitive approach that Maynard-Smith has introduced. However, while sharing considerable enthusiasm for such simple intuitive methods, we believe that many questions such as the calculation of the stable ratios of "hawk" and "dove" genes for example, and other more complicated balanced polymorphisms, the question of neutral drift in

populations and of the stochastic aspects which are the subject of this paper, cannot in fact be studied, or properly understood without treating the full equations governing the population dynamics of the genotypes in the ecosystem.

Let us now return to our formulation of the "selfish-gene" idea and consider the initial phase of any evolutionary step, when only a few examples of the new mutant exist in some small sub-volume of the system. We wish to find the probability of their stochastic extinction during this phase. In order to do this it is necessary to write down the so-called "master equation", which governs the evolution in time of the probability distribution for. finding a population x, at time t (Ebeling and Feistel, 1974, 1976, 1977; Ebeling and Mahnke, 1979). We must also take into account the fact that this small sub-volume is embedded in the surrounding system, which we shall suppose is characterized by the steady state concentrations of the previously existing populations $x_1^0 .... x_n^0 ..$

2. The master equation formulation

In order to describe the stochastic dynamics taking place within our sub-volume, V, we need to consider the basic processes that must be included in our description that increase or decrease the numbers of any particular population present. Also, we must take into account that "potentially" there are many different types of each population that could, in theory, exist or come into existence. Which ones actually exist in the system will depend precisely on the evolutionary path the system follows.

The processes which are present in the system, and which cause the time change of the probability distribution are of three basic types: "birth" "death" and "diffusion" across the boundaries of the small volume V. In our study we shall also distinguish between "normal births" and the occurrence of a mutation in

which reproduction of one population gives rise to an individual of another. In general the dynamics of any simple ecosystem can be written in these basic terms and we shall give some general equations later. However, in order to make the details of the method clear, let us write down the Master Equation for a system which is neither the simplest, nor the most complicated imaginable, and which, therefore, should permit the reader to perform a similar analysis for other cases. The example which we shall study here is that of a predator-prey ecosystem.

We have a "prey" species, x_i, and a predator y_k, where the index corresponds to the phenotype i and k, respectively. As we shall show later this can be generalized (at the cost of a great many more indices) to the equations governing the genotypes. We may suppose that we have the macroscopic equations for the whole system,

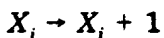$$\frac{dx_i}{dt} = a_i x_i (1 - x_i/N_i) - s_{ik} x_i y_k \qquad (2)$$

$$\frac{dy_k}{dt} = s_{ik} x_i y_k - d_k y_k$$

with stationary states:

$$x_i^0 = \frac{d_k}{s_{ik}} \qquad y_k^0 = \frac{a_i}{s_{ik}}\left(1 - \frac{d_k}{s_{ik}N_i}\right) \qquad (2'$$

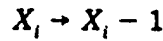Let us examine the microscopic processes which give rise to this equation. We have:

   (a) the normal replication of species x,

$$X_i \rightarrow X_i + 1$$

with probability

$$a_i X_i \left(1 - \sum_j \frac{X_j}{N}\right)$$

   (b) the capture and destruction of prey x_i by predator y_k,

$$X_i \rightarrow X_i - 1$$

with probability

$$\sum_k \frac{s_{ik}}{V} X_i Y_k$$

   (c) the normal reproduction of predator y_k,

$$Y_k \rightarrow Y_k + 1$$
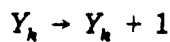
with probability,

$$\sum_i \frac{s_{ik}}{V} X_i Y_k$$

   (d) the death of a predator, y.

$$Y_k \rightarrow Y_k - 1$$
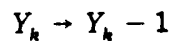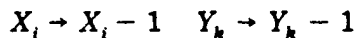
with probability, $d_k Y_k$,

   (e) the "diffusion" of a prey or predator into the sub-volume from the outside,

$$X_i \rightarrow X_i + 1 \quad Y_k \rightarrow Y_k + 1$$

with probability, $D_i x_1^0$, and $D_k y_k^0$

   (f) the "diffusion" of a prey or predator out of the system,

$$X_i \rightarrow X_i - 1 \quad Y_k \rightarrow Y_k - 1$$

with probabilities $D_i x_i$ and $D_k y_k$
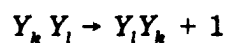
   In addition to these normal processes, we have also those concerning the mutation of predator and prey.

   (g) the "abnormal" reproduction of x_i,

$$X_i, X_j \rightarrow X_i X_j + 1$$
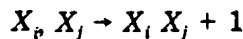
with probability $\quad M_{ij} X_i \left(1 - \sum_j X_j/N\right)$

   (h) the abnormal reproduction of the predator, Y_k.

$$Y_k Y_l \rightarrow Y_l Y_k + 1$$

with probability $\quad \sum_l M_{ki} X_i Y_l / V$

It is necessary, and as we shall see interesting, to include the two "diffusion" terms coupling the stochastic sub-volume with its surroundings, in order to avoid the existence of absorbing states: $X_i = 0$, Y_k, $= 0$ and $X_i = N$, $Y_k = 0$.

We can now write down the equation governing the probability distribution at time t.

$$\frac{dP(X_1 \cdot \cdot \cdot \cdot \cdot Y_m, t)}{dt} =$$

$$A_i(X_i - 1)P(X_i - 1) - A_i X_i P(X_i)$$

$$+ \left(D_i + \sum_k \frac{s_{ik}}{V} Y_k \right)(X_i + 1)P(X_i + 1)$$

$$- \left(D_i + \sum_k \frac{s_{ik}}{V} Y_k \right) X_i P(X_i)$$

$$+ (D_k Y_k^0 + \sum_i \frac{s_{ik}}{V} X_i (Y_k - 1))P(Y_k - 1)$$

$$- (D_k Y_k^0 + \sum_i \frac{s_{ik}}{V} X_i Y_k)P(Y_k)$$

$$+ \sum_i \frac{M_{ik}}{V} X_i Y_l P(Y_k - 1)$$

$$- \sum_i \frac{M_{ik}}{V} X_i Y_k P(Y_k) \tag{3}$$

where,

$$A_i = a_i(1 - \sum_j X_j/N) + D_i x_i^0$$

$$+ \sum_j \frac{M_{ji}}{V} X_j \left(1 - \sum_j \frac{X_j}{N}\right)$$

and where we have dropped all the occupation numbers in $P(X_1 \ldots Y_{,,,})$ which remain unchanged during the process considered.

We may easily verify that under the usual approximations this master equation leads to the very reasonable first moment approximation equation,

$$\frac{dx_i}{dt} = a_i x_i \left(1 - \sum_j \frac{x_j}{N}\right) - \sum_n s_{ik} x_i y_k$$

$$+ \sum_j M_{ij} x_j \left(1 - \sum_j \frac{x_j}{N}\right) + D_i(x_i^0 - x_i)$$

$$\frac{dy_k}{dt} = \sum_j s_{ik} x_i y_k - d_k y_k - \sum_k M_{ik} x_i y_k$$

$$+ D_k(y_k^0 - y_k) \tag{4}$$

but of course these are not of central interest since we are particularly interested in the stochastic behaviour of a mutant population when it is present in only very small quantities, and cannot be successfully or correctly described by a deterministic equation. Let us therefore return to the correct description of such a situation, which is equation (3) and look and its solution.

3. The stochastic behaviour of mutants

Let us assume that the frequency of mutation is small compared to that of "normal" births and deaths. Furthermore, let us consider the simplest case that there is only a single type of prey present and a single type of predator, and that the system has attained a stationary state. Let us now examine what will occur according to equation (3) when n_2 mutants (where n_2 is small) of the prey species x, appear in our small volume V. We know that the steady state (2') can only be changed if an evolutionary step occurs in the system as a whole. This requires that the mutant should survive and multiply within the small sub-volume first. Thus, the initial survival problem can be discussed supposing that the state (2') remains unperturbed outside V, and this allows a considerable simplification to be made in equation (3). If x_2 is the mutant population and x_1 the pre-existing type, we have,

$$\frac{dP(x_2,t)}{dt} = a_2\left(1 - \frac{x_1^0}{N}\right)((x_2 - 1)P(x_2 - 1) - x_2 P(x_2)) + s_{21}$$
$$y_1^0((x_2 + 1)P(x_2 + 1) - x_2 P(x_2)) \tag{5}$$

which is the linearized birth and death equation for the small population x_2 around the steady state x_{1}^{o}, y_{1}^{o}. Let us study its solution for the initial conditions,

$$P(x_2, t = 0) = 1, \quad \text{for } x_2 = n_2$$
$$P(x_2, t = 0) = 0, \quad \text{for } x_2 \neq n_2 \tag{6}$$

This is a well known result however, (Bartholomay, 1958) and the probability of extinction of the initial population n_2 after a time t is given by,

$$P(0,t) = \left\{ \frac{e^{(a_2(1 - x_1^0/N) - s_2 y_1^0)t} - 1}{\left(\frac{a_2(1 - x_1^0/N)}{s_2 y_1^0}\right)} \times e^{(a_2(1 - x_1^0/N) - s_2 y_1^0)t} - 1 \right\} \tag{7}$$

and substituting the values of $x_1^0 = d_1/s_1$ and $y_1^0 = a_1/s_1 * (1 - d_1/Ns_1,)$ then we find for the case where we start initially with a single mutant,

$$P(0,t) = \frac{e^{(a_2 - (a_1 s_2/s_1))(1 - d_1/Ns_1)t} - 1}{\frac{a_2 s_1}{s_2 a_1} \ e^{(a_2 - (a_1 s_2/s_1))(1 - d_1/Ns_1)t} - 1} \tag{8}$$

and clearly, as t tends to infinity, the probability of extinction is:

$$P_{ext} = \lim_{t \to \alpha} P(0,t) = 1 \quad \text{if } a_2/s_2 < a_1/s_1$$
$$= \frac{a_1/s_1}{a_2/s_2} \quad \text{if } a_2/s_2 > a_1/s_1$$

Now let us return to the more general situation of any simple ecosystem. We may always follow the procedure above and construct the linearised birth and death equation governing the probability distribution of some new mutant population, which is a small perturbation of the pre-existing situation. We have,

$$\frac{dP(x_2,t)}{dt} = A(x_1^0, y_1^0 \cdots)((x_2 - 1)P(x_2 - 1) - x_2 P(x_2)) + D(x_1^0, y_1^0 \cdots)$$
$$\times ((x_2 + 1)P(x_2 + 1) - x_2 P(x_2)) \tag{9}$$

where $A(x_1^0, y_1^0 \ldots)$ contains all the processes tending to increase x_2, linearized in x_2, and evaluated at the old stationary state x_1^0, $y_1^0 \ldots$
and of course $D(x_1^0, y_1^0 \ldots)$ contains all the terms tending to decrease x_2 evaluated in a similar approximation. We may solve this equation quite generally for all times t, giving a probability of extinction for x_2. Thus in general, if $A < D$, then the probability of extinction is 1, while for $A > D$, the probability of extinction is still, D/A, which means nevertheless that a mutation with a 10% increase in "fitness" $(A/D = 1.1)$ has only a 1 in 10 chance of surviving.

In fact this interpretation is a little simple, since what is really significant is the probability of a mutant surviving long enough to reproduce on average. Thus if we write,

$$A/D = 1 + \delta \tag{10}$$

where δ measures the increase or decrease in efficiency of the mutant type, then the probability of survival for a time t is.

$$P_{sur}(t) = 1 - P_{ext}(t) = \frac{\delta}{1 + \delta - e^{-(A-D)t}}$$

If now we evaluate this expression for a time t, which is the average time to reproduce n generations,

$$t = A^{-1} \times n$$

The probability of a mutant population, initially of size 1, which is 6 % better or worse (δ can be negative) surviving for n generations is:

$$P_{sur}(n) = \frac{\delta}{1 + \delta - e^{-n\delta/1+\delta}}$$ (12)

This quite general form, true for any mutant arriving in any simple ecosystem is shown as a function of δ in Fig. 1.

The curves shown in Fig. 1 confirm the conclusion that the very sharp distinction that appears in the deterministic analysis between favourable and unfavourable mutations, is smoothed out in-this more correct stochastic picture. In fact, it should be pointed out that the above result is nevertheless foreshadowed in the deterministic approach (Allen, 1975, 1976). If we take the predator prey problem for example and look at the case when a mutant prey x2 has appeared in small, macroscopic quan-

tities in the previously stable system, $x_1^0 = d_1/s_1$, and $y_1^0 = a_1/s_1 * (1 - d_1/Ns_1,)$ then deterministically we have that:

$$\frac{dx_2}{dt} = a_2 x_2 \left(1 - \frac{x_2 + x_1^0}{N}\right) - s_2 x_2 y_1^0$$

and if

$$\frac{a_2/s_2}{a_1/s_1} = (1 + \delta) \quad \frac{dx_2}{dt} = x_2 \left[\frac{s_2 a_1}{s_1}\left(1 - \frac{d_1}{Ns_1}\right)\right]\delta$$

$$x_2(t) = x_2(0) e^{\delta[(s_2 a_1/s_1)(1-(d_1/Ns_1))]}$$ (13)

Thus, although we have in this case definitely either growth or decay depending on whether δ is positive or negative, we see that the characteristic time of this growth or decay tends to infinity as δ tends to zero.

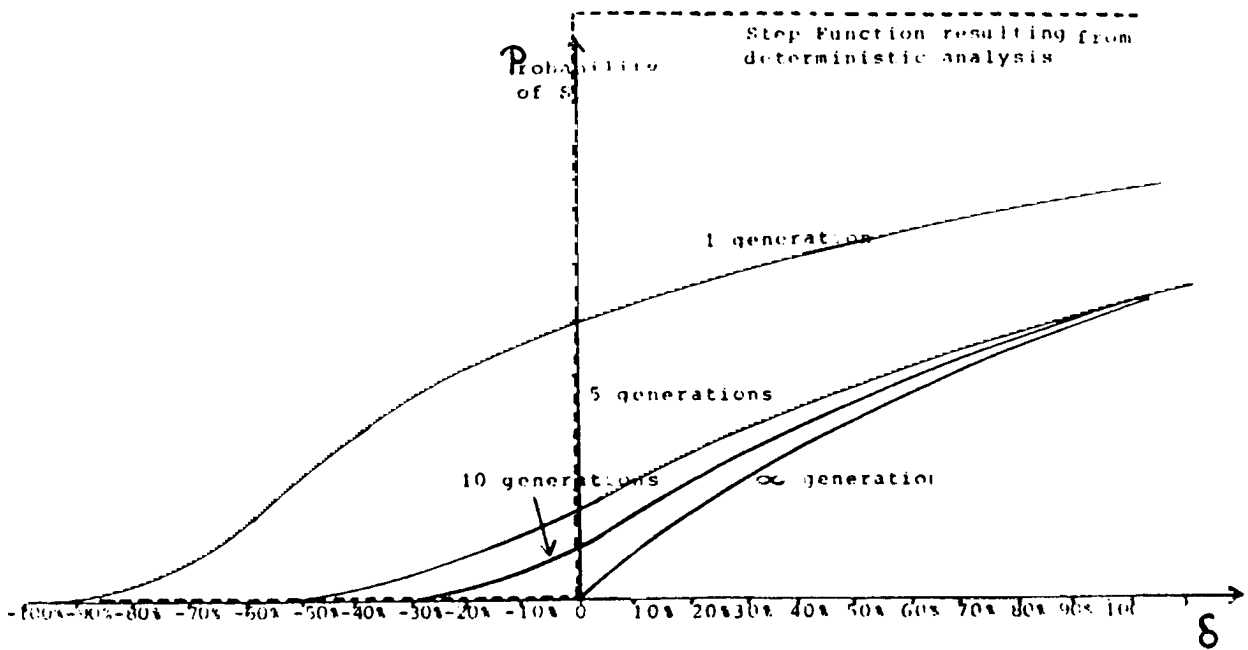Our stochastic analysis thus enables us to clarify the behaviour of mutants which are

Fig. 1. Probability of survival of a mutant of fitness δ, for a number of generations, n.

nearly neutral. Let us examine in more detail the effect on the evolutionary process of the period of stochastic dynamics that must necessarily precede the establishment of a mutant in sufficiently large numbers to be described by a deterministic equation. If the probability of the appearance of a mutant of given effectiveness, δ compared to its "parent", is given by a Gaussian distribution,

$$M(\delta) = \left(\frac{2\pi}{\sigma}\right) e^{-\delta^2/2\sigma^2} \qquad (14)$$

then we can write down the joint probability density that a mutant of type δ **will appear, and then survive** n generations. It is,

$$P(\delta, n) = M(\delta) \cdot P_{sur}(n \text{ gen.})$$

$$= \left(\frac{2\pi}{\sigma}\right) e^{-\delta^2/2\sigma^2} \frac{\delta}{1 + \delta - e^{-n\delta/1+\delta}}$$

$$\qquad (15)$$

This function is illustrated in Fig. 2 and depends of course on the variance of the Gaussian. However, it is clear that the relative probabilities of the appearance and survival of mutants which are slightly retrograde, neutral or slightly positive, for at least 10 or 20 generations is of the same order. As the

generations of survival specified is increased, so the probability decreases, and the peak moves to the right of the $\delta = 0$ axis. Thus the probability of survival 1 generation is very nearly symmetric about the zero axis, but as n increases, the probability of survival of the negative mutants decreases quicker than that of positive ones, and the maximum of the probability function shifts to the right. We may calculate the "most frequent" evolutionary event which will persist for long times, and change the macroscopic state of the system. It is given by,

$$\frac{d}{d\delta} \left(\left(\frac{2\pi}{\sigma}\right) e^{-\delta^2/2\sigma^2} \frac{\delta}{1+\delta} \right) = 0$$

$$\delta^2_{max} - \delta^3_{max} = \sigma^2$$

and solving this for example for the case where a $= 0.1$, we find δmax.. $= 0.09554$ where δmax. is the δ of the most frequent evolutionary event. In fact, at n = 0 the peak is of course at $\delta = 0$, and as the time of survival is increased so the maximum moves to the right until approximately δmax $= \sigma$. Although this describes the most frequent evolutionary event which we may expect, if we calculate the probability density of this
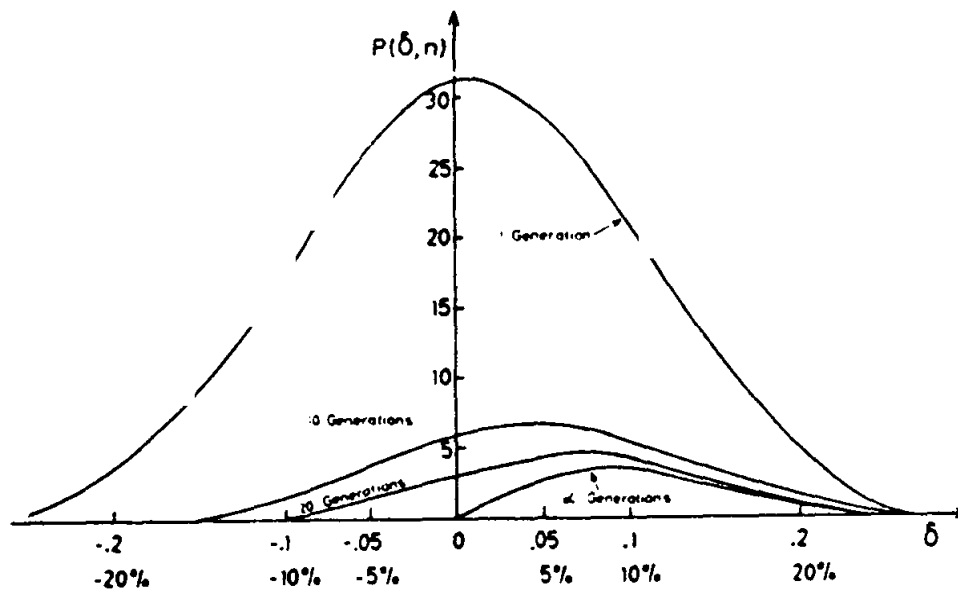

Fig. 2. Probability of the appearance and survival of a mutant of fitness δ.

peak and compare it with that corresponding to the appearance and survival for 20 generations of a neutral mutation, or even of a mutation which is 5% less fit than its parents,
we find for $P(\delta, n)$; $\sigma = 0.1$ $\delta_{max} = 0.07$

$$n = 20.$$

$$P(\delta_{max}, 20) = 4.3; \qquad P(\delta = 0, 20) = 2.992$$

$$P(\delta = -0.05, 20) = 1.447$$

Thus, in general we see that such events will in fact occur really quite often, and that the system will break up into localities characterised by some particular quasi-neutral drift (mutations of - 5% to + 5% are frequently occurring and retained). However, from time to time a really advantageous mutation in one of these will sweep through the whole system deterministically. Furthermore, if this advantageous mutation is accompanied to

some degree by assortative. mating, where the new homozygote is strongly advantageous, then the image we shall have is that shown in Fig. 3, where the particular neutral mutations
characteristic of the locality where the advantageous type originates are "fixed" throughout the system.

Thus the "fixation" of a "neutral" drift is entirely in agreement with the results of our analysis, and the evolutionary trees characteristic of molecular evolution can be understood on this basis. Thus the "character" of any particular population can therefore only be "explained" in terms of both advantageous and quasi-neutral mutations that have occurred during its history, and a view that concentrates entirely on either of these is incomplete.

Another result that follows from this analysis concerns the probable evolution of the relative values of the birth and death
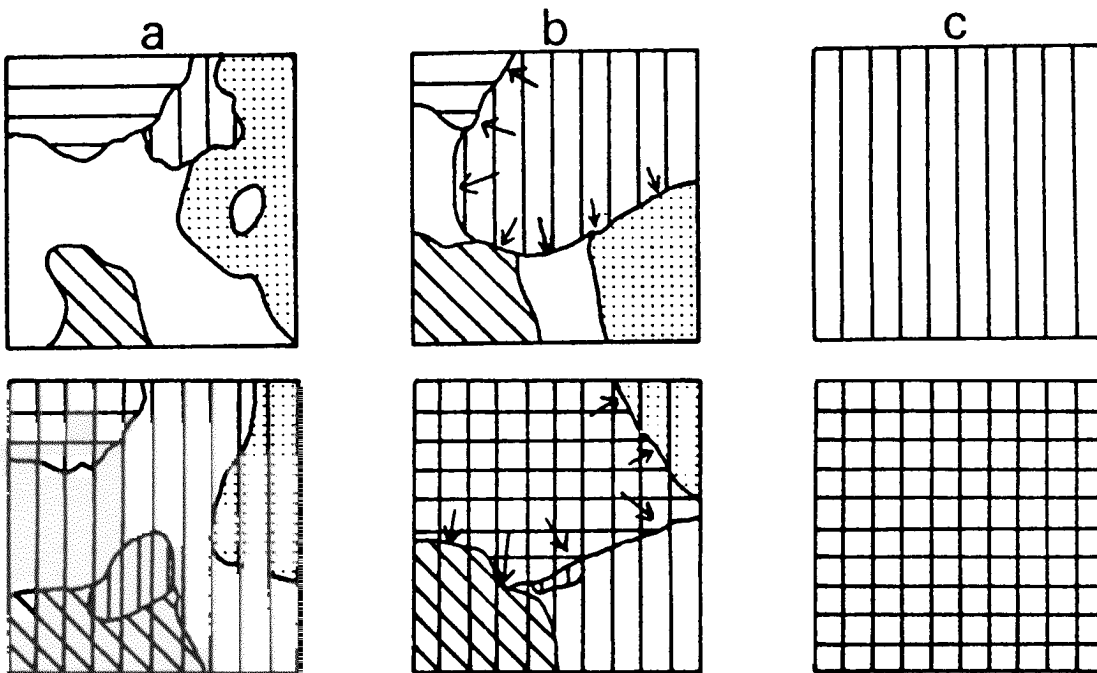

Fig. 3. A sequence of events which fixes two successive neutral mutations. (a) An evolutionary drift occurs in different localities. (b) After some time, a strongly advantageous mutation occurs in and spreads throughout the system. (c) 7he neutral mutation is fixed in the population. (d) Local drift occurs again. (e) An advantageous gene occurs in and spreads throughout the system. (f) A second neutral mutation is thus

rates. To see this let us return to our simple example involving the evolutionary state of a prey species in the space a and s.

We will find that there is a certain spread of population types present. But because of the selective elimination this spread is mainly along a line of slope a/s, roughly of width σ, which as we have seen correspond to quasi-neutral mutations that can remain in the system for many generations. If we suppose that the rate of mutation is proportional to the "total" birth rate of a type i,

$$M(\delta) = \text{rate of appearance of mutant } \delta$$

$$a_i \left(\frac{2\pi}{\sigma}\right) e^{-\delta^2/2\sigma^2} \tag{17}$$

since the "total" birth rate must equal the integral of this function over δ. Now let us consider the relative probabilities of the appearance and survival for some long time of mutants coming from different types among the spread shown in Fig. 4. For example, consider mutations coming from the zones 1 and 2, characterised by birth rates a_1, and a_2 respectively, where

$$a_1/a_2 = a \quad \text{and} \quad a > 1 \tag{18}$$

Clearly, a mutation of efficiency δ will arise α times more frequently from 1 than from 2, but if it is to survive the same length of time as the mutant arising from 2, it must
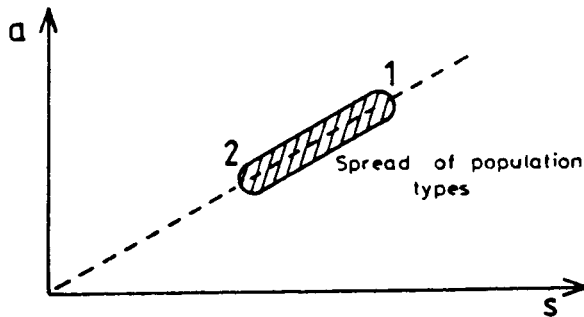

Fig. 4. Showing the spread of population types in the parameter space a and s.

survive αn generations, instead of simply n. However, it can be shown that for $\delta > 0$,

$$\alpha P(\delta, \alpha n) > P(\delta, n)$$

which means that evolutionary steps come more frequently from the 'high birth rate, high death rate" end of the population spectrum, than from the "low birth rate, low death rate" end. We may speculate that this small effect will tend to penalize, in the long run, an evolution towards species having extremely long lifetimes for the individuals making them up. Perhaps this remark is important for the understanding of evolutionary processes in their relation to aging, and in particular to the idea of Conrad that "adaptability" is part of the evolutionary heritage (Conrad, 1979).

4. The influence of spatial dispersion effects on the survival of mutants

Clearly the mechanism by which a mutant population invades the area surrounding its immediate locality is that of a diffusion-like process. In fact the thoughts provoked by the writing of this section have opened a vast field of research concerning the balance that could perhaps exist between diffusion and mixing in a population, and possible non-linear relationships between genotypes. Here we shall only indicate some preliminary results and leave the full exploration of this domain to a later paper. Let us first consider the effect of spatial dispersion on our result for the probability of extinction of a mutant population.

This result was based on the analysis of the linearized master equation around the previous stationary state. It takes into account only the "first order" effects of the spread of a new gene, being entirely dependent on the properties of the heterozygote x_{ab}, for a genetic problem concerning mutant b. The result of the calculation of the probability of survival of $n.2$ mutants in a single sub-volume V, was

$$P_{ext}(0,t) = \left\{ \frac{\frac{e^{(A-D)t} - 1}{A}}{\frac{A}{D} e^{(A-D)t} - 1} \right\}^{n_2} \qquad (20)$$

n_2 at $t = 0$

Clearly, if we compare this to the probability of extinction of the mutant population when a single mutant is placed in n_2 different boxes, then this should give us the effect of spatial dispersion on the process. In fact, this probability is, the multiple of the proba-
bility of extinction in each box,

$$P_{ext}(0,t) = \left\{ \frac{\frac{e^{(A-D)t} - 1}{A}}{\frac{A}{D} e^{(A-D)t} - 1} \right\}$$

$$\times \left\{ \frac{\frac{e^{(A-D)t} - 1}{A}}{\frac{A}{D} e^{(A-D)t} - 1} \right\} \quad \cdots \cdot n_2 \text{ times}$$

in n_2 boxes

which clearly is identical to (Eqn. 20) and we conclude that for the linear approximation diffusion, or mixing has no effect on the evolutionary process.

However, in the more 'general case of an arbitrary non-linear growth rate g(x2), although we cannot solve the stochastic equation for such a problem we can perform the following deterministic analysis. Let us suppose that the rate of change of the mutant population at the point r, is given by an
equation of the type,

$$\frac{\partial x_2}{\partial t} (r,t) = g(x_2(r,t)) + D \frac{\partial^2 x_2}{\partial r^2} (r,t) \qquad (21)$$

where $x_2(r,t)$ is the local density at the co-ordinate r, and D is the diffusion coefficient.

Assuming that the diffusion fluxes are zero at the boundary, we have by integration over the whole volume,

$$\frac{dx_2}{dt} = 1/V \int g(x_2(r,t)) dr \qquad (22)$$

In order to ascertain the effect of spatial dispersion and mixing on the growth rate of the mutant, we can make the comparison between this growth rate (Eqn. 22) and that which would appertain if the mutants were distributed uniformly in space:

$$\left[\frac{dx_2}{dt} \right]_{uniform} = g(x_2(t)) \qquad (23)$$

Now let us suppose that the rate law is convex in the region of small x_2,

$$g(x) = Ax_2 + Bx_2^2 \qquad (24)$$

then, using the inequality,

$$1/V \int dr\, g(x_2(r,t)) \geqslant g\left(1/V \int dr\, x_2(r,t) \right)$$

we find that necessarily,

$$\frac{dx_2(t)}{dt} \geqslant g(x_2(t)) = \left[\frac{dx_2(t)}{dt} \right]_{uniform} \qquad (25)$$

Therefore we may conclude that the mutant growth in a non-uniform system is always larger than in the corresponding uniform system. Spatial concentration of the new population in a narrow region is advantageous to growth. Diffusion, which has, of course, the tendency to smooth out inhomogeneities is therefore a disadvantage for a mutant with a convex growth law.
The opposite is true if the mutant has a concave growth law, $g = Cx_2 - Dx_2^2$ then using the inequality,

$$1/V \int dr\, g(x_2(r,t)) \leqslant g\left(1/V \int dr\, x_2(r,t) \right)$$

we find that,

$$\frac{dx_2}{dt} \leqslant g(x_2) = \left[\frac{dx_2}{dt} \right]_{uniform} \qquad (26)$$

Therefore, in this case, the mutant growth in the non-uniform system is always smaller

than in the corresponding uniform system. Diffusion is of advantage to these kinds of mutant. The case of linear growth, the only terms retained in our stochastic analysis, lies between the convex and concave cases and is therefore indifferent with respect to diffusion.

In fact the study of the effects of initially neutral (that is for the linear terms) mutations with however, non-linear effects operating between members of the population at higher order and the complex dependence of the outcome on the spatial dispersion or the mixing of the species concerned opens up a whole new and fascinating series of questions about evolutionary processes. The ideas that have emerged from the study of dissipative structures can surely help here to understand the occurrence of spatial instabilities in the evolutionary process. Let us briefly illustrate this with a simple example of a mutant gene characterized by a particular "convex" growth term. This corresponds to the case of the invasion of the system by an "altruistic" gene.

Let us suppose that initially we have a homogeneous population of homozygotes, $x_~$ obeying a simple logistic equation.

$$\frac{dx_{AA}}{dt} = ax_{AA}(1 - x_{AA}/N) \quad mx_{AA} \quad (27)$$

where a is the birth rate, m is the death rate and N gives the resource limitation of the system. Now let us write down equations which would correspond to the population dynamics of a recessive "altruist", x_{BB}. First, we write (see reference) equations of the form:

$$\frac{dx_{AA}}{dt} = a\left(\frac{x_{AA}^2 + x_{AA}x_{AB} + \frac{1}{4}x_{AB}^2}{X}\right)$$

$$\times \left(1 - \frac{x}{N}\right) \quad (d - \alpha(1)x_{BB})x_{AA}$$

at

$$= a\left(\frac{x_{AA}x_{AB} + x_{BB}x_{AB} + 2x_{AA}x_{BB} + \frac{1}{2}x_{AB}^2}{X}\right)$$

$$\times \left(1 - \frac{x}{N}\right) - (d - \alpha(2)x_{BB})x_{AB} \quad (28)$$

$$\frac{dx_{BB}}{dt} = a\left(\frac{x_{BB}^2 + x_{BB}x_{AB} + \frac{1}{4}x_{AB}^2}{X}\right)$$

$$\times \left(1 - \frac{x}{N}\right) - (d - \alpha(3)x_{BB})x_{BB}$$

$$- Rx_{BB}$$

where $x = x_{AA} + x_{AB} + x_{BB}$

$$\alpha(1) \sim e^{-d_{x_{BB}x_{AA}}} \quad \alpha(2) \sim e^{-d_{x_{BB}x_{AB}}}$$

$$\alpha(3) \sim e^{-d_{x_{BB}x_{BB}}}$$

$d_{x_{AA}x_{BB}}$ = average distance separating x_{BB} and x_{AA}, etc. where apart from the usual birth terms involving x_{AA}, x_{AB} and x_{BB}, we have supposed that the "altruist", x_{BB}, when present locally, reduces the death rate of other members of the local population, to a certain extent. The exact extent depends in fact on the average distance separating x_{BB} from x_{AA}, x_{AB} and other x_{BB}. The difference between these average distances depends on the relative strengths of two opposing tendencies. First that of the inhomogeneous distribution of x_{BB} and x_{AB} due to the spatial pattern of its production, initiating in some small sub-volume of the system. Second the "smoothing" and "mixing" that is occurring all the time depending on the strength of the diffusion terms. Since x_{BB}, is only produced from parents x_{AB} and x_{BB}, then if diffusion is below some critical value of effectiveness, then the mean separations of x_{BB} from x_{AA} and x_{AB} will be sufficiently different, and the "altruistic" benefits of x_{BB}, will be mainly felt by the x_{AB}. Also, of course, in our equation we have added the term Rx_{BB} to take into account the extra losses incurred by the altruist.
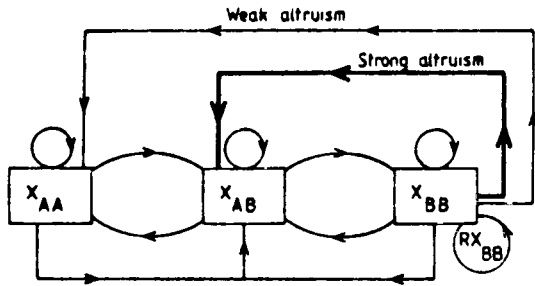
Fig. 5. The interaction diagram for the genotypes *XAA, XAB* and *XBB* where apart from the usual genetic reproduction coefficients based on a local random mating approximation, we also have a differential altruistic interaction resulting from the spatial structure of the system. The average separation of *XBB* from X*AA* is greater than that from *XAB.*

In the schematic diagram of Fig. 5, we show the basic feedbacks operating in such a system. As this indicates, it is indeed possible for the extra risk run by the "altruist" to be more than compensated by the positive feedback on its own production coming from the heterozygote, $_{XAB.}$ The equations (28) have been run on a computer, and in Fig. 6 we show that for an altruist who reduces the death rate of the local population by 10%, at an added risk to himself of 20%, an initially

small concentration of B will grow and establish itself in the system.

In fact we see that the usual manner in which "inclusive fitness" is stated is perhaps a little misleading, where one speaks of an "altruist" saving his brothers or "cousins" at his own expense. The important point is perhaps that altruism is an example where the "inclusive fitness" of a gene is buried partly in the spatial correlations of the system. Our treatment generalizes, we believe, the rather particular arguments of Maynard-Smith, in agreement with the work of D.S. Wilson that has appeared since this paper was first written. What is being uncovered here is the "mechanism" by which evolution may change its "unit of selection" to some extent by evolving towards mutually dependent, spatially grouped organisms among whom complex inter-relationships can develop. One of the results of the above discussion was to show that for a convex growth law, as is the case here, it will be advantageous to reduce "diffusion". In other words successive mutants which reduce "mixing" in the population will be retained once "altruism" is present, and we can thus
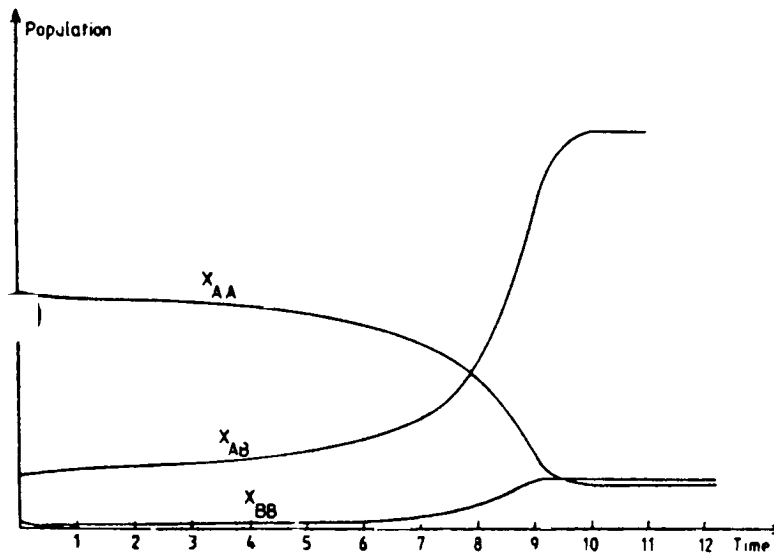

Fig. 6. A computer simulation of equations (28) showing establishment of the altruist in the population. This results from the spatial structure of the population distributions, and corresponds to the idea that part of the "fitness" of any one of the genotypes is "buried" in the spatial interactions.

establish the existence of one possible branch of evolution, starting from a situation of sufficiently weak diffusion, which leads to the formation of strongly interdependent groups of individuals, with perhaps dominance relations, a division of labour etc. Of course, another branch of evolution also exists and is that characterized by the solitary individual, out-competing rivals.

An important point of this analysis is that our stochastic equations show us how easy it is for initially quasi-neutral mutations to invade a small sub-volume, and it is because of this that the instability due to second order effects can nevertheless appear and grow quite naturally in the system.

5.Conclusions

In summary, we see that the stochastic analysis presented above gives several new insights into the evolutionary process. Firstly, we learn something about two contradictory perspectives of the role of "selection" in evolutionary theory: either as giving rise to species which are of "optimal" form, marvellously, and precisely adapted to their complex environment, or alternatively as merely setting a "lower limit" of viability, by weeding out those individuals which are totally unfit. Our analysis shows that, although selection does have an effect, it is only of limited power. Quasi-neutral, and even quite negative mutations can survive a long time in a locality, long enough anyway for new evolutionary paths to be explored, while frequently even quite advantageous mutations may be lost in the "noise" surrounding their birth. We find therefore an intermediate result from which we may deduce that much of the character of evolution will depend on the form of probability distribution for the occurrence of mutations.

We find that depending on the particular form of the probability distribution for mutations (in δ) we have different sized "most probable events", and we may either

have a smooth progression or perhaps, in each locality, long periods of stagnation separated by sudden advances resulting from the occurrence of a particularly favourable mutation. Indeed, if we supposed a skew-negative distribution for the occurrence of mutations, evolution may even drift backwards more that it jumps forward. Such thoughts lead to the idea that the form of this distribution will itself be a result of evolution, since the "negative evolution" which could occur in such a case in a particular area will eventually be replaced by a species from outside capable of a less negative evolution; i.e. having a more favourable distribution. This idea is in agreement with the views expressed in recent papers by Conrad, as indeed is the result we have already obtained in Eqn. (19) showing that evolution towards species with extremely long individual lifetimes is penalized to some extent by tending to reduce the size of the mutation probability per unit time. Such questions, however, can probably best be explored using computer simulations of a stochastic dynamics, and this is an area of future research which we hope to explore.

In the second part of our paper we take a first step towards the proper treatment of spatial effects on the evolutionary process. We find that by taking into account the effect of diffusion on an initially localized mutant population, then for the linear terms nothing is changed. However, for the terms of higher order, the non-linear terms, then we find the fascinating possibility of the genesis of more complex behaviour involving spatial inhomogeneities. This seems to mark the transition to a sort of kin or group selection from individual selection, where, although we may still discuss the invasion of the system by new genes, part of the "fitness" of the genes is buried in the spatial interactions with other individuals in the system. Let us further underline that the above discussion merely shows how it is perfectly possible for complex inter-relationships to arise on the basis we have described, concerning the non-linear interaction of different genotypes.

However, it must be made absolutely clear that once groups of organisms exist, then their interaction through communication of different types, together with the evolution of a brain brings into play a whole new range of complex phenomena which then become of dominant importance for evolution. The spread of new behaviour, possibly a division of labour, or of dominance roles, etc. can then take place through the processes of random initiatives and imitation or learning, and this is a far more rapid, and adaptable mechanism than that associated with genetic change. The main point here is simply that we wish to show that using what we consider a more correct formulation of the idea underlying "the selfish gene", a deeper understanding of evolution and the effects of stochasticity and space can be attained than when only the simple intuitive ideas of ESS are used. In other words, in order to understand evolution, we must study the dynamic interaction of the various population types in a system, using a basic stochastic process, which under suitable circumstances can be approximated by deterministic equations, and including the complex effects of space. In such a system, we must then see which genes and new behaviours can invade the system and then try to decide what is the probability that any particular gene or new behaviour will in fact occur.

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This paper showed that evolution is much "fuzzier" than traditionally it is painted. So, it means that selection makes only a weak distinction between individuals that are within say, 10% of average performance. So, instead of seeing mutation as either being "lethal" or being "successful", instead we see that there is a great tolerance of diversity – even diversity that actually affects performance. This is very important because it means that individuals can "drift" and explore different behaviours, even when they are slightly worse, and can therefore "cross valleys" in their fitness landscapes. This is a vital issue because it enables radically new forms to be discovered, and underlies what is called – discontinuous innovation. This stochastic model provides a basis for understanding the dynamics of "new ideas" and shows that even an idea that is potentially 10% better than existing ones, only has about a 1 in 10 chance of reaching fruition. This work establishes the basis for a much softer view of evolution that allows and indeed encourages diversity. Clearly, since each individual is only "tested" against the others present, then if these others are of varying effectiveness it reduces the sharpness of the selection process acting on any individual. Indeed it focuses attention on the fact that evolution results both from selection, which we have shown to be weaker than expected, and from the distribution of new types being created in the system. If too large a proportion of these are worse than existing types, then it is entirely possible that selection cannot counter this, and the system could actually "degenerate". Of course, this would really build a extremely diverse population, and perhaps produce a successful response to the environment.