

Population dynamics with and without selection

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A model describing population dynamics is presented. We study the effect of selection pressure and inbreeding on the time evolution of the population and the chances of survival. We find that the selection is in general beneficial, enabling survival of a population whose size is declining. Inbreeding reduces the survival chances since it leads to clustering of individuals. We have also found, in agreement with biological data, that there is a threshold value of the initial size of the population, as well as of the habitat, below which the population will almost certainly become extinct. We present analytical and computer simulation approaches.

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I. INTRODUCTION

There are many models describing evolution of biological populations. Some of them came from theoretical physicists and are based on the concept of self-organized criticality [1–3], the Penna model [4,5], or adapting populations [6,7,9]. In [1–3] the stress is on showing that closed systems subject to well defined and simple rules can exhibit complex behavior, interpreted sometimes as the mass extinction of the species. The Penna model tries to explain how genetic diseases coded in the genotype manifest themselves during the individual's growth, how they are transmitted to the offspring, and how they influence the population dynamics. In the third series of papers the general goal was to see how the genetic composition of a population influenced the fate of the population when for some reason the conditions of living changed. In all these papers the basic entity was an individual. It is still debated whether the fundamental blocks of evolution are individuals or rather populations [10]. In [8] we considered a metapopulation, where the basic unit is a population (a deme). We investigated how the interactions among populations influence the evolution of the metapopulation.

There are of course numerous models of population dynamics constructed by biologists and mathematicians. For reviews, see, e.g., [11–13]. Of the many questions asked by biologists regarding population dynamics some have not yet been answered in a satisfactory way. In general, the biologists' models are based on differential equations for global variables; hence they belong to the class of mean-field-like approaches. Some exceptions are [14,15], where microscopic models are solved via computer simulations. Although the analytic solutions are important, they often neglect the fine details, which may sometimes be crucial. It is therefore good policy to start from a microscopic model and establish which details are essential to understanding macroscopic regularities [13].

The questions frequently discussed by biologists using the mean-field approach include the following. (1) Is there a critical concentration of a population, below which the population has a low chance of survival [16–18]? (2) Is there a direct relation between survival probability for a population and the size of the habitat [20]? (3) What is the role of natural selection? In particular, can it “save” a doomed

population [18]? (4) What is the role of inbreeding [14]?

In the present paper we shall address the above questions using mostly a microscopic model solved by computer simulations. In some cases we shall present analytical results also.

The paper is organized as follows. In Sec. II we present the model. Section III contains analytical results; data from simulations are given in Sec. IV and Sec. V contains final conclusions.

II. MODEL

We consider a square $L \times L$ lattice with hard boundary conditions. No more than one individual may occupy a lattice site. Although there are no sexes in our model the breeding requires two parents. We shall call the first one a *father* and the second one a *mother*. In order to procreate an individual (father) must move to an adjacent empty site and find a partner (mother) in the nearest neighborhood of the new site. The moves and search follow the “blind ant” rule, i.e., the choice of direction is made only once. If the attempt is unsuccessful there is not a second one. Once the partner is found, the pair produces three offspring and the parents die. This is a dynamics with nonoverlapping generations.

Each i th individual is characterized by its genotype G_i , which in our model is represented as a double string (two gametes) of L_G sites (loci). At each locus there might be either a zero or a 1. Zero corresponds to a recessive and 1 to a dominant allele. Similar representations of a multilocus genotypes have already been introduced in, e.g., [7,9,15]. We assume total domination of an allele denoted by 1; thus the phenotype $F_i = \{F_i^1, F_i^2, \dots, F_i^{L_G}\}$ of the i th individual is constructed from the genotype in the following way. If at a certain locus there are two zeros (recessive homozygote at this locus) then we put zero at the corresponding locus of the phenotype. Otherwise (dominant homozygote or heterozygote) we put a 1. Hence the phenotype of each individual is a string, also of L_G loci, of zeros and 1s [7]. For example ($L_G = 10$),

$$G_i = \left\{ \begin{array}{c} 1110001100 \\ \hline 0010011110 \end{array} \right\},$$

$$F_i = 1110011110.$$

The offspring's genotype is constructed in the following way. Two strings of the mother's genotype are broken at the same random position. The pieces are joined across to form two female gametes. The same process occurs with the father's genotype. Finally, one of the female and one of the male gametes are randomly chosen to form the genotype of the baby. From the genotype the phenotype is constructed along the steps explained above. This procedure is repeated independently for all three offspring.

At the beginning of our simulations the individuals are randomly distributed over the lattice and their genotypes are random sequences of zeros and 1s. All external factors are modeled here by the optimal phenotype $O_F = \{O_F^1, O_F^2, \dots, O_F^{L_G}\}$ [7,9,18], which we take as a set of all 1s. Hence, a 1 in an individual phenotype could be called a *good gene*, and a zero a *bad gene*. The optimal phenotype remains constant in time, which corresponds to constant environmental and climate conditions. The choice of all 1s as the optimal phenotype is, to some extent, arbitrary. However a zero in the phenotype is more restrictive than a 1, since the former is realized by just one combination of the alleles, and the latter by three combinations. Therefore an optimal phenotype containing, e.g., as many zeros as 1s would lead to more frequent extinction of the populations [19].

We shall consider here two cases—when the population is subject to natural selection and when selection does not work. The selection pressure is realized in the following way. After an individual at site i is selected and before it is permitted to move, its survival probability is checked. The probability of survival p_i (one may also call it the *fitness*) is defined as follows:

$$p_i = \frac{1}{L_G} \sum_{j=1}^{L_G} O_F^i \bullet F_i^j, \quad (1)$$

where we have introduced the operation \bullet :

$$a \bullet b = \begin{cases} 1 & \text{if } a=b \\ 0 & \text{otherwise.} \end{cases} \quad (2)$$

Such a survival probability is the rate of agreement of the individual phenotype with the optimal one. An individual having the same phenotype as the optimal one has $p_i = 1$.

When we consider dynamics without selection pressure, each individual has the same chance of surviving. Hence, instead of calculating p_i for every member of the population we take a constant survival probability (p).

In the following we shall also discuss the role of inbreeding. It is realized by putting two offspring on the dead parents' sites and the third one in the site occupied by the father before he moved. Clearly the three sites are nearest neighbors and there is a significant chance that in the future the offspring will mate and the progeny will receive genes coming from two genetically closely related parents. Hence the genetic diversity of the population will be reduced. Another effect of the inbreeding in this model is to diminish the number of empty sites in the neighborhood. This reduces the

effective number of newborn babies. When inbreeding is absent, the sites for the babies are chosen randomly in the whole lattice.

III. ANALYTICAL RESULTS

Let us start with no selection pressure and no inbreeding. We assume here periodic boundary conditions. The concentration of individuals at time t is $c(t)$. We want to find out whether the population will survive starting from an arbitrary low initial concentration, or whether, as we suspect, there is a threshold value. We want also to determine the lowest survival probability below which the population will die out. In the model we have two processes that can change the population size. In the mean-field approximation they have the following values: death of an individual with probability $1-p$; and birth of three offspring and death of their parents if (1) an individual will survive with probability p , (2) will then move with probability $1-c(t)$, and (3) will then find a partner to mate with probability $\frac{3}{4}c(t)$ (for a square lattice).

The conditions for mating and producing offspring can therefore be written as the following dynamic rule for the concentration $c(t+1)$ at time $t+1$:

$$c(t+1) = c(t) + c(t) \left[-\frac{3}{4}pc^2(t) + \frac{3}{4}pc(t) - (1-p) \right]. \quad (3)$$

Since all offspring are located randomly in the lattice (no inbreeding) and the parents die, the mean-field approximation should give nearly the exact result. The fixed points c^* are given by the set of equations

$$c^* = 0, \quad (4)$$

$$\frac{3}{4}pc^*(1-c^*) - (1-p) = 0. \quad (5)$$

The solution $c^* = 0$ is valid for every value of the survival probability p , but of course this solution is not interesting. For $p < \frac{16}{19} \approx 0.84$ this is the only solution; hence below the threshold value $p^* = \frac{16}{19}$ the population has no chance of survival. For $p > \frac{16}{19}$ there are two additional fixed points

$$c_{1,2}^* = \frac{1}{2}p \mp \frac{2}{3p} \sqrt{\Delta}, \quad (6)$$

where

$$\Delta = 3p \left(\frac{19}{16}p - 1 \right). \quad (7)$$

The resulting phase diagram is shown in Fig. 1. Apart from the line of stable fixed points $c^* = 0$, there are two lines of fixed points c^* . The lower is an unstable one (the so-called MVP—*minimum viable population*), below which the population dies and above which it tends to the upper (stable) branch of fixed points (known in biology as the *car-*

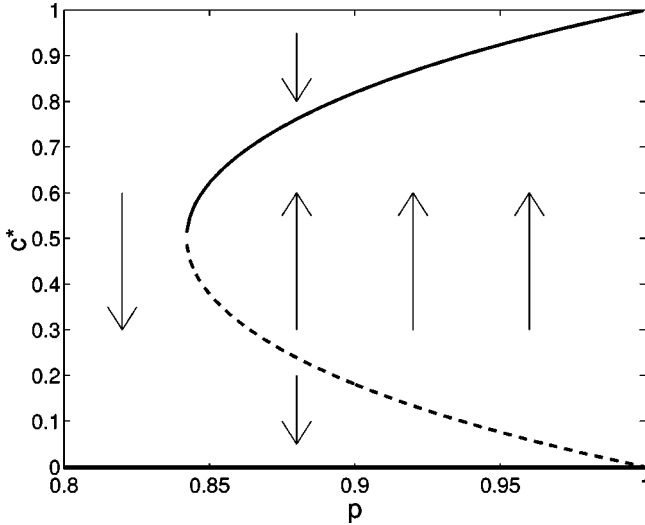


FIG. 1. Phase diagram (analytical) without selection or inbreeding.

rying capacity). The existence of three steady states (two stable and one unstable) in population dynamics has been suggested by biologists [21].

We have not found oscillating solutions here. They were present and discussed in a similar model in [22].

From Eq. (2) we can also get the time evolution for the populations starting from several initial concentrations $c(0)$, as shown in Fig. 2. Clearly there are two asymptotic states [e.g., for $p=0.85$, $c(\infty)=0$ and $c(\infty)\approx 0.62$]. The threshold initial concentration separating the two states is (for the value $p=0.85$ assumed here) about 0.38. All the curves are clearly monotonic, i.e., a population with declining concentration is doomed. This is indeed what has been observed by biologists [18,16].

We investigate the role of selection by using a mean-field-like approach. Its basic effect is an improvement of the adaptation (or fitness). Hence the survival probability is, on

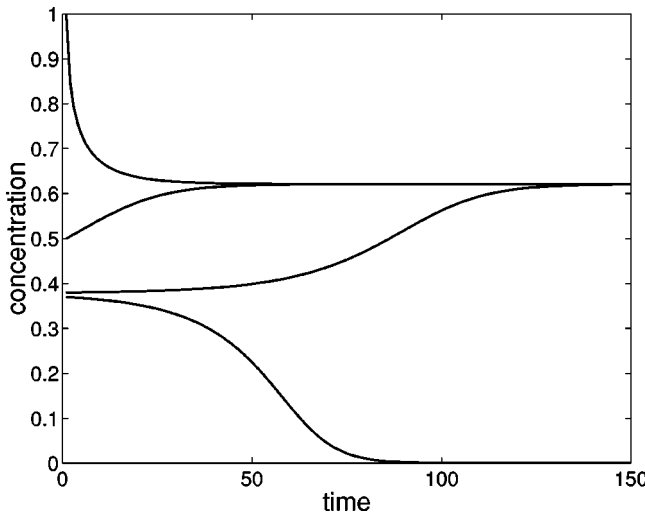


FIG. 2. Time evolution of population without selection or inbreeding taken from Eq. (3) for several initial values of $c(0)$; $p=0.85$.

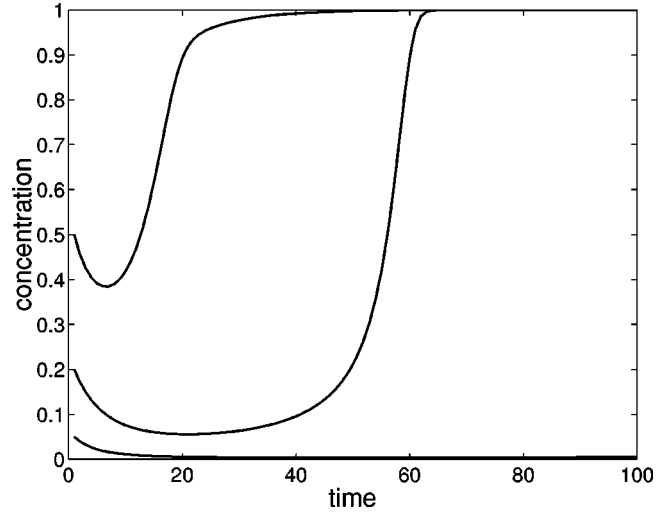


FIG. 3. Time evolution of population with selection and without inbreeding taken from Eq. (8) for several initial values of $c(0)$; $p(0)=0.75$.

average, growing with time. We assume therefore that p is not constant but is growing with time as a logistic function with the rate r . Then [denoting $c(t+1)$ by c' , $p(t+1)$ by p' , $c(t)$ by c , and $p(t)$ by p], instead of Eq. (2) we get the set of iteration equations

$$c' = c + c \left[\frac{3}{4} p c (1 - c) - (1 - p) \right],$$

$$p' = p + r p (1 - p),$$
(8)

which can be solved numerically; the time evolution of the population concentration is shown in Fig. 3. The pattern is now quite different. The curves are nonmonotonic, i.e., selection can save a doomed population (a fact noticed also in [18]), final concentrations are much higher, and even a population with a very low initial concentration has a chance to survive.

In the approach presented above all individual features of the members of the population are missing. We have been mimicking the selection rather than modeling it along the lines presented in Sec. II.

One should note that adaptation, which may also be called fitness, depends on the phenotype only, since the selection in our model acts via the phenotype. As the exact relation between a genotype and a phenotype is yet unknown, we took the simplest, biologically reasonable one. Genotype driven selection, via, e.g., diseases, is considered in [23] or in the Penna model (see [5]).

IV. COMPUTER SIMULATIONS

To account for the detailed features of the individuals, and, in particular, to determine the time dependence of the survival probability, we have to turn to computer simulations. In this approach we shall consider four cases: with and without selection and with and without inbreeding. In the simulations we use “hard” boundary conditions, i.e., if an

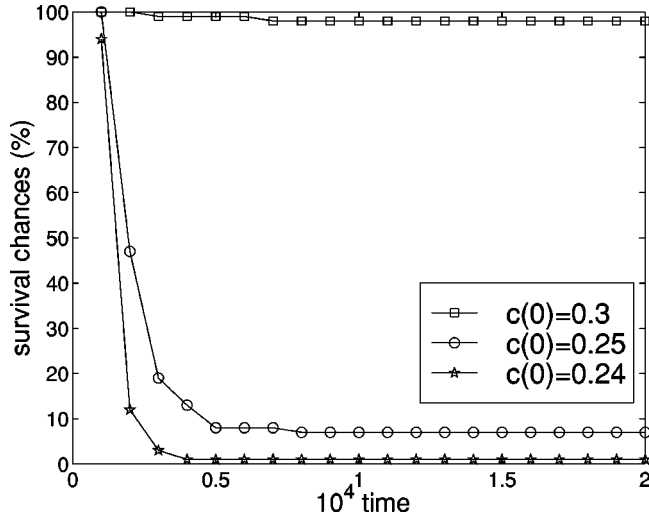


FIG. 4. Percentage of populations that survived for the model without selection or inbreeding and $p=0.84$.

individual is at the edge of the lattice and chooses the direction that would take it outside the lattice, the move is not realized.

A. No selection and no inbreeding

There are the following parameters of the model: size of the habitat (lattice) L , initial concentration $c(0)$, and survival probability p . Individuals are selected, moved, paired, and produce progeny according to the rules given in Sec. II.

According to our simulations there is a critical value of $p^* \approx 0.82$ below which no population has a chance to survive. For $p > p^*$ there is a threshold value for the initial concentration (minimum viable population in biological terms) below which a population will become extinct. Above the threshold value, as in the analytic results, the concentration grows to a steady state K (carrying capacity of the habitat). The value of K does not depend on L . If we defined p^* as that probability at which the population has at least 90% chance of survival (as did Shaffer [16]) we would get $p^* = 0.84$, which is exactly what we got from analytical calculations. Such a very good agreement follows from taking, after Shaffer, $p^* = 90\%$. For other definitions of p^* we can expect good agreement also. The survival probability, however, depends crucially on the initial size (concentration) of the population. For $c(0) = 0.23$ and p

TABLE I. Model without selection and inbreeding, $p=0.87$, $c(0)=0.175$.

L	K (carrying capacity)	Survival chance
10	0.717	0.04
20	0.737	0.11
30	0.723	0.12
50	0.730	0.10
100	0.738	0.09

TABLE II. Model without selection, with inbreeding, $p=0.87$, $c(0)=0.15$.

L	K (carrying capacity)	Survival chance
25	0.717	0.02
30	0.737	0.11
40	0.723	0.43
50	0.730	0.71
70	0.738	0.94

$=0.84$, $L=50$, the chances for survival are less than 2%. As shown in Fig. 4, with increasing $c(0)$ the chances grow very fast.

We have found therefore a feature observed in nature [21]—that populations inhabiting a larger territory have a greater chance of survival. However, this is true only when the survival probability is slightly above the threshold value. If the survival probability is much larger than p^* the dependence of the extinction rate on the size of the habitat disappears (see an example in Table I). Although populations living in a small territory have a weaker chance to survive, those that do reach the carrying capacity of the habitat much faster. Generally, processes occurring in small populations are much more violent.

B. No selection, with inbreeding

Here also we have found that there is a threshold value p^* of the survival probability, which also depends on the size of the habitat. We have again the island population effect, i.e., that the survival chances of the population increase with the size of the habitat (see Table II).

As before, the chances of survival depend on the initial concentration of the population (see Fig. 5), and they clearly grow fast with increasing $c(0)$. However, we did not observe stabilization of the survival. Even populations that after 30 Monte Carlo steps (MCS) showed over 90% chances of survival were declining in size. Placing progeny on the

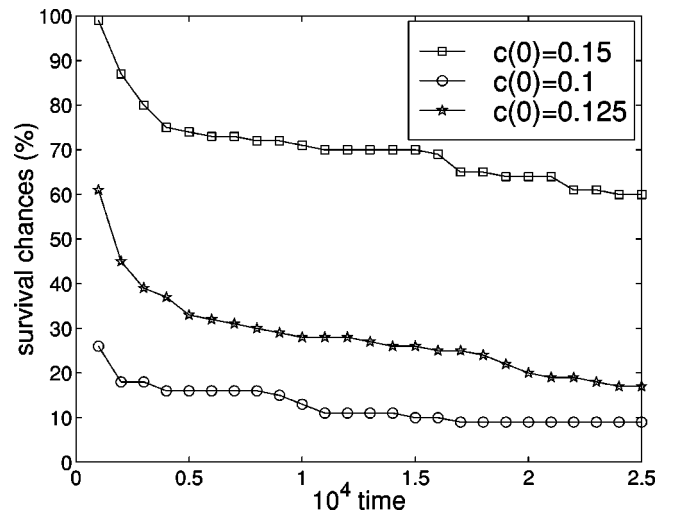


FIG. 5. Percentage of populations that survived for the model without selection, with inbreeding, and $p=0.87$.

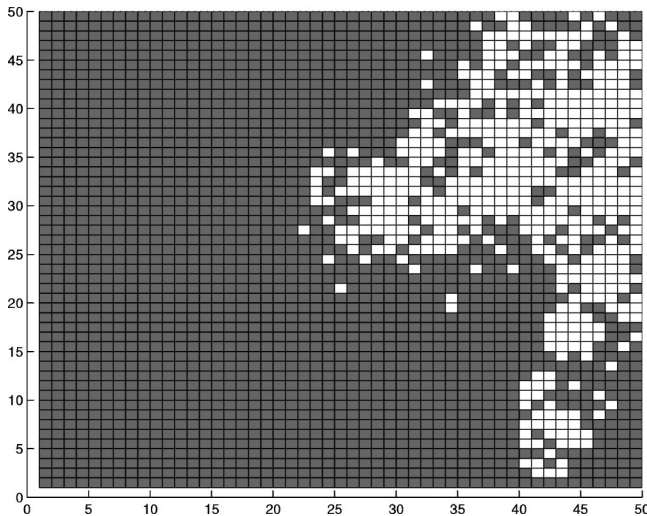


FIG. 6. Spatial distribution of individuals (bright) for the model without selection but with inbreeding.

neighboring sites led to clustering of individuals close to the habitat border, due to lack of symmetry there (see Fig. 6). In the case of no inbreeding the spatial distribution of a population showed no clustering. Because of the clustering effect caused by inbreeding, the situation is different for a population that started from a low concentration, e.g., $c(0)=0.1$, and after some time reached the value of 0.2, and a population that started from $c(0)=0.2$. The former is clustered, and individuals have not much room for reproduction; hence the population may finally disappear. On the other hand the latter is more or less homogeneous, with enough sites around the occupied ones. Hence the population may survive. This shows that in this model the history of the population plays a role.

C. Selection, no inbreeding

Now the individuals forming a population may adapt to the environment. Since we start from a random population and the optimal phenotype is always taken as the sequence of 1s, the initial mean survival probability is always the same (≈ 0.66). We observe, as in the case without selection, the existence of a minimum initial concentration below which the population has essentially no chance of evolving. This concentration, of course, depends on the size of the lattice. For $L=50$ the results are plotted in Fig. 7. On small territories the dynamics of the evolution is, as in the case without selection, more rapid (Fig. 8). However, when the time t is scaled by a factor of L^{-2} ($\tau=1000t/L^2$), the three curves nearly overlap, showing a minimum a little below $\tau=1$ and reaching a maximum at about $\tau=4$.

However, on very small lattices ($L=10$) even a large initial concentration does not guarantee survival—a population with $c(0)=0.35$ has a 1% chance of surviving up to 10 kmCS. There is always a chance, although a slim one, that one population will reach a very high level of adaptation very soon (generally after just 1 kmCS), and then it will survive “forever,” since in our model there are no mutations or environmental changes. In general, for a given initial con-

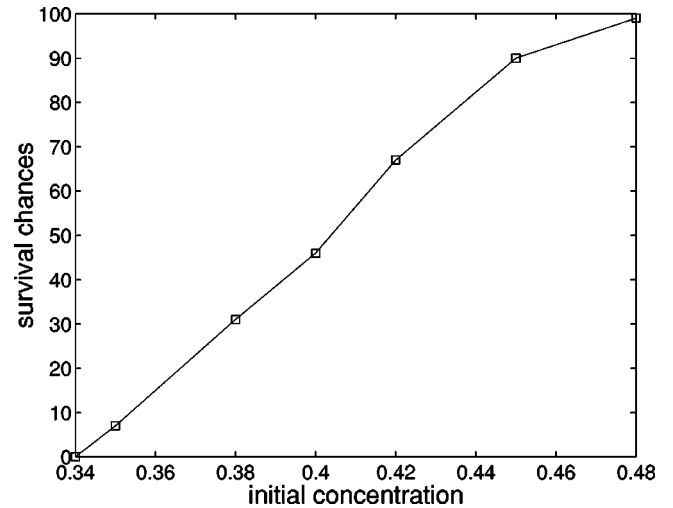


FIG. 7. Percentage of populations that survived for the case without selection with inbreeding.

centration, the chances of survival grow with the size of the habitat. We have found that the dependence of the survival on the lattice size follows a power law:

$$\text{survival} \sim L^\alpha, \tag{9}$$

with $\alpha=1.66$.

A feature not found in the dynamics without selection is the nonmonotonic character of the time dependence of concentration (Fig. 9). Such a pattern has been observed earlier by biologists [18] and is interpreted as the ability of selection to save a population that without it would be extinct. We observed an analogous phenomenon in Sec. III of this paper, where we presented a mean-field-like approach to our model with survival probability increasing with time. The evolution of mean fitness indeed shows a logistic growth (like the one considered in Sec. III).

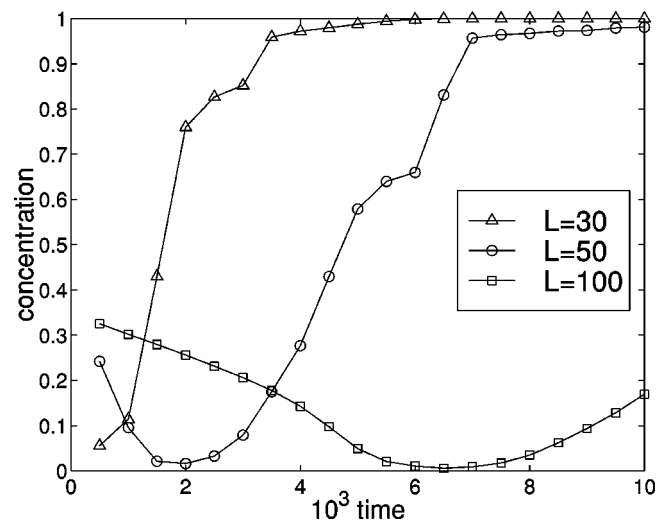


FIG. 8. Concentration as a function of time for the case with selection and without inbreeding for several habitat sizes.

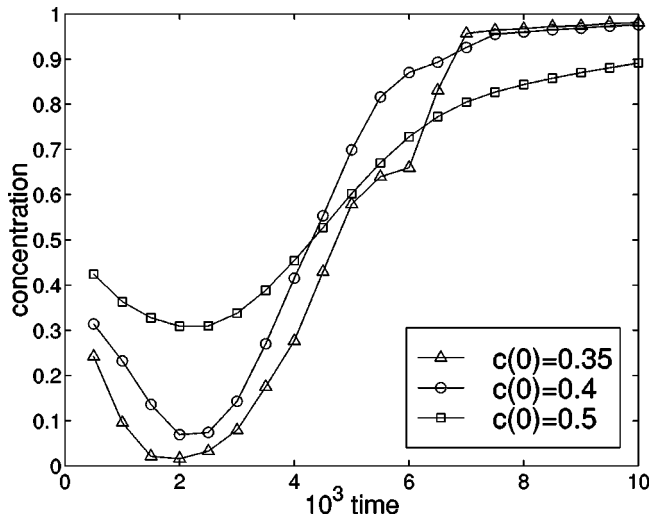


FIG. 9. Concentration as a function of time for the case with selection and with inbreeding for lattice size $L=50$.

D. Selection and inbreeding

Here also we have a minimum in the concentration versus time dependence characteristic for inbreeding, like that we have reported in Sec. III. Now, however, the minimum is more pronounced. Before reaching the minimum the population is more or less randomly dispersed but after passing the minimum clustering occurs. We observe, as in the previous cases, an increase of the survival chance with increasing initial concentration. The growth, however, is much slower, as shown in Fig. 10.

V. CONCLUDING REMARKS

We have presented a model describing population dynamics with and without selection pressure. The population was reproducing in a quasisexual way, i.e., without differentiating the sexes but with the recombination of two parents. Wherever it was possible we derived analytical results which agreed very well with those obtained from our computer simulations. In the latter, individual features of the individuals were accounted for. In order to breed an individual must first move and then find a partner in its nearest neighborhood. The number of progeny that a pair can effectively produce depends on the chance of finding an empty place on the lattice for them. These two procedures permitted us to avoid invoking the Verhulst factor, which must be used in continuous (with no lattice) models [4,5] to account for the limited resources of the habitat. Our approach is clearly an improvement since the Verhulst factor is a very crude approximation (of the mean-field character) of the biological reality.

On the basis of the results presented above we may answer now the questions posed in the Introduction. In all four cases considered here—selection with inbreeding and with-

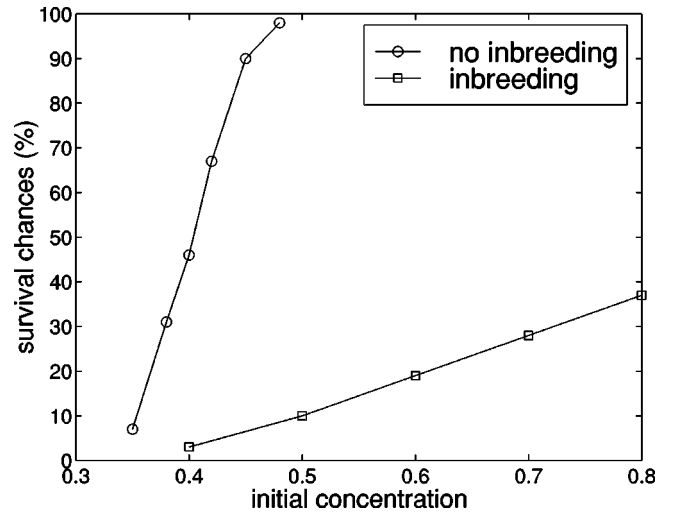


FIG. 10. Dependence of the percentage of populations that survived on the initial concentration for the selection model with and without inbreeding.

out it and no selection with inbreeding and without it—we have found a critical value of the initial concentration (MVP) below which the population has a very small chance of survival. The same kind of behavior has been found in real biological systems [16–18].

The survival probability in our model depends also on the size of the habitat. For quite small sizes no population can survive, irrespective of its initial concentration. In general the chances for survival grow with increasing size of the habitat. This phenomenon is well known in biology and was described by MacArthur and Wilson as long ago as 1967 [20].

The role of selection pressure is indeed crucial. Without selection, a population whose size is initially declining will surely die, because the concentration monotonically changes with time in that case. In contrast, when a population evolves under selection pressure, after an initial decrease of the concentration, it is possible, although not guaranteed, that the population size will grow. This is caused by an increase of the mean fitness, as was shown in Sec. III. Thus we can say that selection can “save” the population, a fact also suggested by biologists [18].

Inbreeding reduces the population’s chance for surviving. It leads to clustering of individuals, which in our model makes breeding more difficult. This again is a very well-known biological fact [14]. Since we did not introduce any environmental changes, which can be easily done by changing the optimal phenotype O_F [7], we did not observe in the case of inbreeding extinction caused by decrease of the genetic diversity as, e.g., in [24–26].

ACKNOWLEDGMENT

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