

Instabilities in population dynamics

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Received 15 February 2000

Abstract. Biologists have long known that the smaller the population, the more susceptible it is to extinction from various causes. Biologists define *minimum viable population size* (MVP), which is the critical population size, below which the population has a very small chance to survive. There are several theoretical models for predicting the probability that a small population will become extinct. But these models either embody unrealistic assumptions or lead to currently unresolved mathematical problems. In other popular models of population dynamics, like the logistic model, MVP does not exist. In this paper we find the existence of such a critical concentration in a simple model of evolution. We solve this model by a mean field theory and show, in one and two dimensions, the existence of the critical adaptation and concentration below which a population dies out. We also show that, like in the logistic model, above the critical value a population reaches its carrying capacity. Moreover, in the two-dimensional case we find – the so common in biological models – periodic solutions and their bifurcations.

PACS. 87.23.-n Ecology and evolution – 87.10.+e General theory and mathematical aspects – 05.45.-a Nonlinear dynamics and nonlinear dynamical systems

1 Introduction

Paraphrasing James Murray [1] – Physical biology is a fast growing, well recognized, albeit not clearly defined subject. It is also one of the most exciting modern applications of statistical physics. For this reason, biological evolution as a conducting biological theory has been under a special interest of physicists for the last couple of years (*e.g.* [2–9]).

Population dynamics lies at the core of ecological and evolutionary theory. It shapes the structure of communities and generates evolutionary processes [10]. One of the most important questions both in ecology and evolution is the question about extinction of populations. Extinction, even extinction of whole species is a quite common event [11–15]. In an important article [16] Shaffer suggested that there are only (in general) four sources of uncertainty which cause extinction:

- *demographic stochasticity*, which arises from chance events in the survival and reproductive success of a finite number of individuals;
- *environmental stochasticity*, *i.e.* variation of habitat parameters, competition between populations, predators, parasites, diseases, etc.;
- *natural catastrophes*, such as floods, fires, etc.;
- *genetic stochasticity* resulting from changes in gene frequencies.

Little is known about the role of any of these factors in any specific case of extinction. However, biologists discovered

that until the population size decays to a certain critical value (called *minimum viable population size* (MVP)) the population has big chance to survive. Shaffer [16] gave the following definition of MVP: *A minimum viable population for any given species in any given habitat is the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.* This definition has, how noticed by Shaffer, a tentative nature. The critical level for survival probabilities might be set at 95% or 100%, or any different level. Similarly the time frame of 1000 years might be changed.

What is interesting there, is still no better definition of MVP [17–22]. So, the first question immediately appears [22] – does the critical population size really exist or is it just a heuristic device? If MVP really exists, can we find its precise definition? In reality it is very difficult to answer these questions. Natural populations always live in a given habitat, which is never constant. Besides, we can never find a completely isolated population, so there is always some environmental stochasticity (competition, predators, etc.). Moreover, even in laboratory we can not check the existence of MVP, because there is always some genetic stochasticity. But as physicists we have a powerful tool in our hands – the ability to build a model.

In the model of evolution proposed by Mróz *et al.* [23] (MPSW model) Monte Carlo simulations have shown that a population dies out rather fast if the initial density is below a certain value. However, it was not checked whether

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the critical density really exists. In this paper we adapt the MPSW model to investigate the existence of MVP. We will call the new model (adapted MPSW model) – the K model. We will solve it analytically and show the existence of the critical density and adaptation, below which a population has to die out.

2 The K model

In the K model, the habitat for the investigated population is represented by a lattice with fixed boundary conditions. The population consists of $N(t)$ individuals. No more than one individual can occupy a lattice site. Each individual is characterized by a certain survival probability p_i . Because we want to investigate the existence of MVP, we have to assume that there is no natural selection, so the average survival probability:

$$p = (N(t))^{-1} \sum_{j=1}^{N(t)} p_i,$$

remains constant. This is the necessary change we have to make in the MPSW model to study MVP. To produce an offspring two parents are needed. After producing an offspring the parents die. An individual can become a parent provided it moves to a new location (see below).

The simulation algorithm of the MPSW model consisted of initially putting M individuals on a lattice. According to the myopic ant rules the individual was moved to one of its nearest neighboring sites. The neighbor for mating was chosen at random. The condition that only the individual which moved could mate represented all acts necessary to breed in real life. This activity was required from one partner only; such situation is often observed in nature, *i.e.* activity belongs to the father. The parents produced three (*i.e.* the smallest number needed to survive) offsprings, which were located randomly on the lattice and then died.

The MPSW model was studied on a two-dimensional square lattice and the simulations showed that for an average adaptation of $p = 0.666$ a population died out if its initial concentration was below ≈ 0.2 . It was also shown that in order to grow, the population must have an adaptation larger than a certain critical value. In what follows we show that these and even more interesting results can be obtained from the K model analytically.

3 One-dimensional lattice

For simplicity let us start with a one-dimensional lattice. This case was not studied in [23], however, it seems interesting to check if there is any criticality in the K model in one dimension. Let $N(t)$ be the population size at time t , then the rate of change

$$N(t+1) - N(t) = \text{births} - \text{deaths}, \quad (1)$$

is a *conservation equation* [1] for the population. Observe that in the model we have the following processes that can change the population size:

- death of an individual with probability $1 - p$;
- birth of three offsprings and death of their parents if:
 - 1) an individual will survive with probability p ,
 - 2) then will move with probability R_1 ,
 - 3) and then will find a partner to mate with probability R_2 .

Hence, the evolution equation for the investigated model is given by:

$$N(t+1) = N(t) + N(t) [pR_1R_2 - (1 - p)], \quad (2)$$

where:

- R_1 denotes the probability of movement, *i.e.* the probability that at least one of the neighboring sites is empty;
- R_2 denotes the probability of mating, *i.e.* the probability that after the move at least one of the neighboring sites is occupied.

Since all offsprings are located in the lattice randomly and parents die, we can make mean field approximation assuming that the probability that a lattice site is occupied is given by the concentration:

$$c(t) = \frac{N(t)}{K}, \quad (3)$$

where K is the total number of lattice sites. Thus for the one-dimensional lattice we have:

$$\begin{aligned} R_1(t) &= (1 - c(t))^2 + 2c(t)(1 - c(t)) = 1 - c^2(t) \\ R_2(t) &= c(t). \end{aligned}$$

Dividing equation (2) by K we obtain the following evolution equation:

$$c(t+1) = c(t) + c(t) (-pc(t)^3 + pc(t) + p - 1). \quad (4)$$

A numerical solution of the evolution equation (4) is shown in Figure 1. We can see that below a certain value of concentration the population dies out and that concentration is critical. In other words, the equation (4) has an unstable steady state (eq. for $p = 0.8c \approx 0.28$) and a stable steady state $c = 0$. It is also obvious that if the concentration is “large enough” the population reaches a certain concentration $c < 1$ (eq. for $p = 0.8c \approx 0.83$), which is called by biologists the *carrying capacity*. We thus expect a third (stable) steady state.

It is very easy to show that there are exactly three steady states. All we have to do is plot $c(t+1) - c(t)$ against $c(t)$ and look when it is equal to zero. This is done in Figure 2, where for $p = 0.8$ (dashed line) we can see all three steady states – the trivial $c_1^* = 0$, which is a solution of equation (4) for all p , and two other c_2^* , c_3^* – solutions of the following equation:

$$-pc^3 + pc + p - 1 = 0.$$

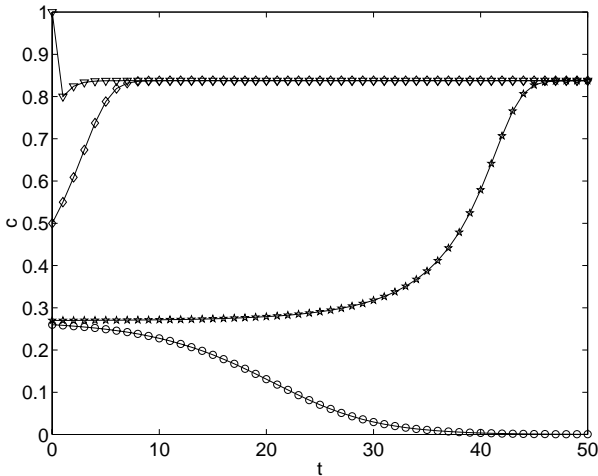


Fig. 1. Numerical solution of equation (4). Survival probability $p = 0.8$.

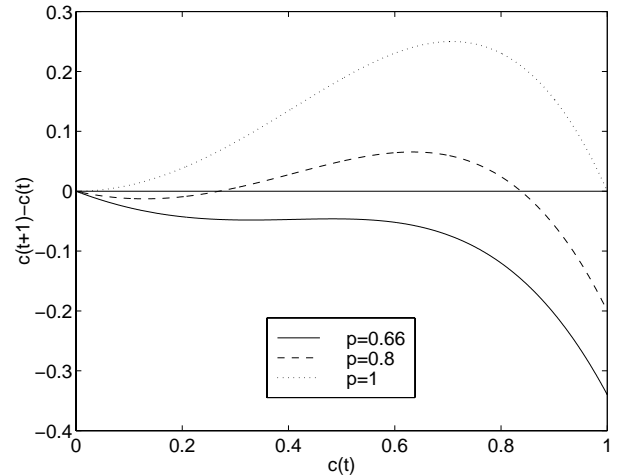


Fig. 2. Graphical representation of steady states. For $p < p^*$ the only steady state is $c_1^* = 0$.

Observe that the above equation has non-imaginary solutions only for

$$p \geq p^* = \frac{27 - 6\sqrt{3}}{23} \sim 0.72.$$

Thus we can conclude that (see Fig. 3)

- for $p < p^*$ only one $c_1^* = 0$ steady state exists;
- for $p \geq p^*$ three: $c_1^* = 0$, c_2^* and c_3^* steady states exist, however, for $p = p^*$, $c_2^* = c_3^*$.

We can easily check that see that:

$$\left| \frac{dc(t+1)}{dc(t)} \right|_{c=c_1^*, c_3^*} < 1,$$

which means that $c_1^* = 0$ and $c_3^* (> c_2^*)$ are stable steady states [24]. Analogously we can check that c_2^* is unstable:

$$\left| \frac{dc(t+1)}{dc(t)} \right|_{c=c_2^*} > 1.$$

The stability of critical points can be also checked using a graphical procedure [1], as is shown in Figure 4.

What is very interesting for us, the results of the one-dimensional system are in agreement with the following biological observations:

- In order to grow a population must have an adaptation larger then the critical value p^* . Below that value the population becomes extinct.
- For $p > p^*$ there is a certain critical density below which the population becomes extinct.
- When adaptation and initial density are above critical values, the population reaches its p -dependent carrying capacity.

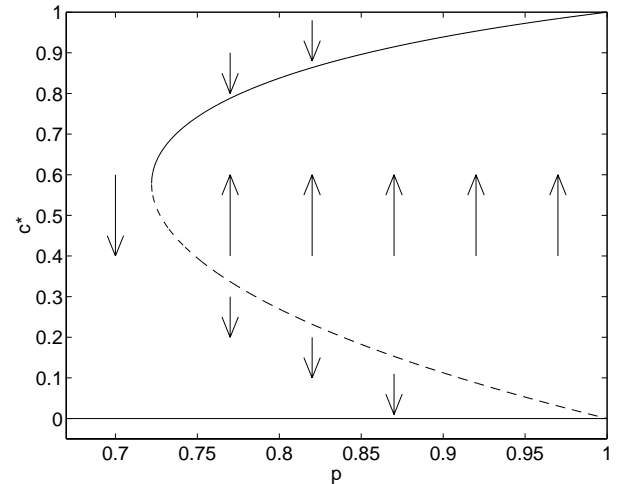


Fig. 3. Flow diagram for a one-dimensional system.

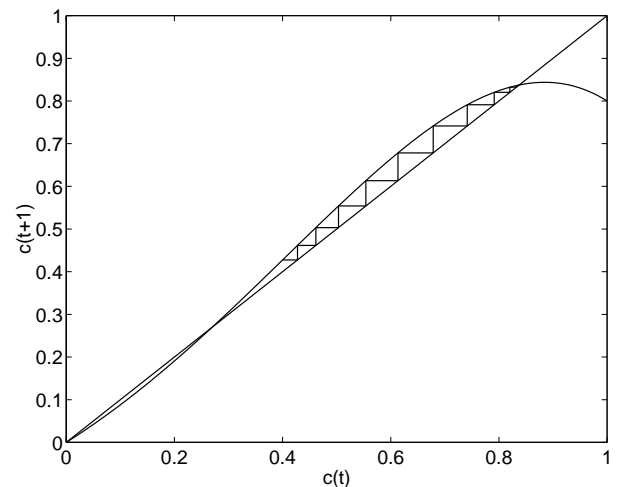


Fig. 4. Graphical determination of a steady state and demonstration of how $c(t)$ approaches it.

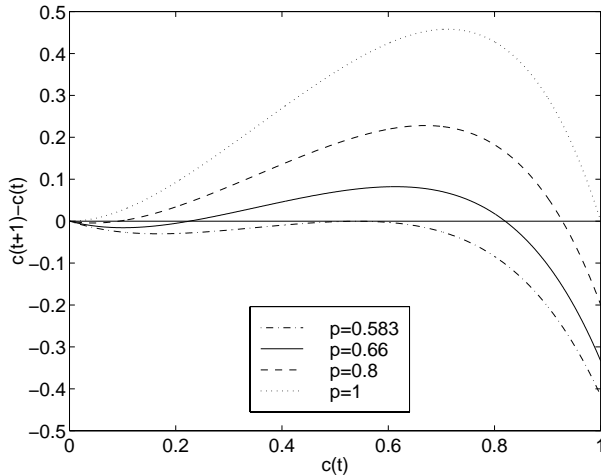


Fig. 5. Graphical representation of steady states for the two-dimensional lattice.

4 Two-dimensional lattice

For a two-dimensional square lattice (studied by Monte Carlo simulations in [23]) the probabilities of movement and of mating are given by:

$$R_1(t) = (1 - c(t))^4 + 4c(t)(1 - c(t))^3 + 4c^2(t)(1 - c(t))^2 + 4c^3(t)(1 - c(t)),$$

$$R_2(t) = c^3(t) + 3c^2(t)(1 - c(t))^2 + 3c(t)(1 - c(t))^3.$$

Hence, from equation (2) we have

$$c(t+1) = c(t) + c(t)(-3pc^7(t) + 13pc^6(t) - 23pc^5(t) + 18pc^4(t) - 5pc^3(t) - 3pc^2(t) + 3pc(t) + p - 1). \quad (5)$$

Like in the one-dimensional system, a certain critical value of survival probability is needed in order for the population to grow. The analytically obtained value of $p^* = 0.583$ agrees quite well with Monte Carlo results presented in [23], where p^* was estimated to lie between 0.55 and 0.62. For $p > p^*$ there are again three steady states (see Fig. 5). Notice that for $p = 0.66$ the critical value below which a population dies out is equal to 0.22. This is also in agreement with the simulation results [23].

One can ask if there is any qualitative difference between the one- and two-dimensional case. The answer can be seen in Figure 6, where we present a graphical solution of the two-dimensional system for $p = 0.8$. We can see that the population concentration does not reach the third steady state (like in the one-dimensional case), but a certain limit cycle. Indeed, the flow diagram for the two-dimensional case shows not only steady points, but bifurcations to the steady limit cycles, see Figure 7. Such a phenomenon can be observed in real biological systems [1]. Moreover, Dennis *et al.* [19] presented a very interesting experiment with the flour beetle *Tribolium* in which a transition from the logistic growth to periodic solutions was

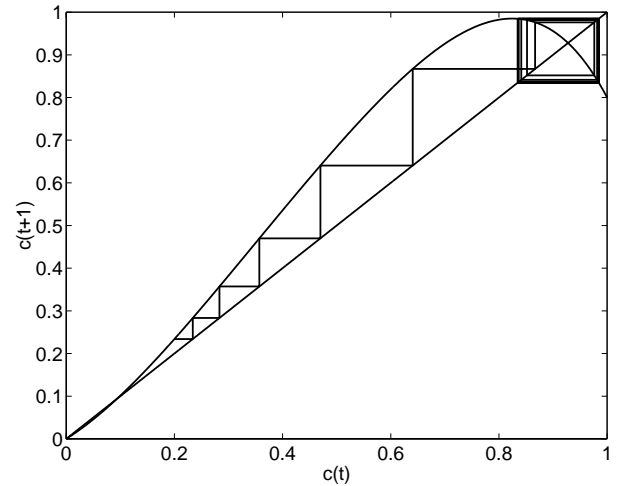


Fig. 6. Graphical determination of the solution – in this case we have a stable periodic solution of period 2.

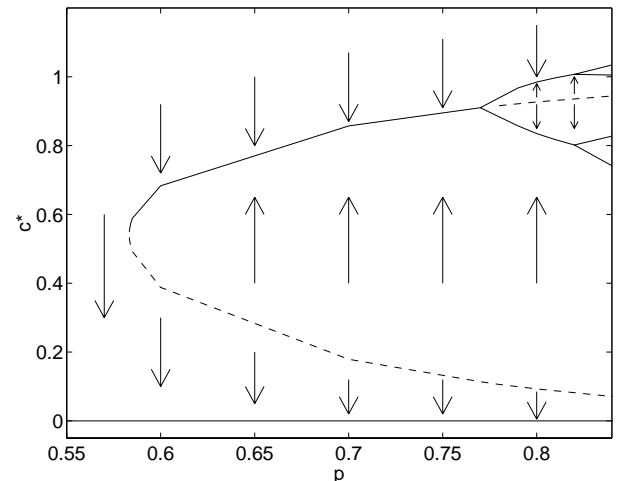


Fig. 7. Flow diagram for the two-dimensional system. Stable steady states are represented by solid lines and unstable steady states by dashed lines.

observed. The behavior of the population depended, like in our model, on the mortality rate.

5 Final remarks

We have presented the K model and its analytical solutions in one and two dimensions. On the basis of the microscopic K model, with realistic biological assumptions, we have constructed the evolution equation (4).

The evolution equation of the K model has features observed in real biological systems, which many other models (including the logistic model) lack. These features include: existence of a critical concentration below which a population dies out, dependence of the adaptation on carrying capacity and minimal critical concentration, existence of

a critical minimal adaptation below which a population cannot survive, and periodic behavior.

It should be noticed, that the critical concentration is not a critical point as in statistical phase transitions. It is just a steady point-stable (carrying capacity) or unstable (MVP) of evolution equation (4). Thus in the K model, we can precisely define both, the carrying capacity and MVP.

Moreover, we have found in the K model the critical value of adaptation (survival probability), below which a population has no chance to survive. Both steady states (carrying capacity and MVP) depend on the value of adaptation.

However, the most unexpected result of the K model is the existence of limit cycles in two dimensions. Such periodic behaviour of population was often suggested in biological literature, not only for predator-prey systems.

Due to our mean field approximation we cannot observe here the accidental extinction of small populations ($K \rightarrow \infty$ at constant $c = N/K$) seen for time $\rightarrow \infty$ [11].

This research was supported by University of Wrocław, grant no. 2318/W/IFT/99.

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