

DYNAMICAL MODELS IN BIOLOGY

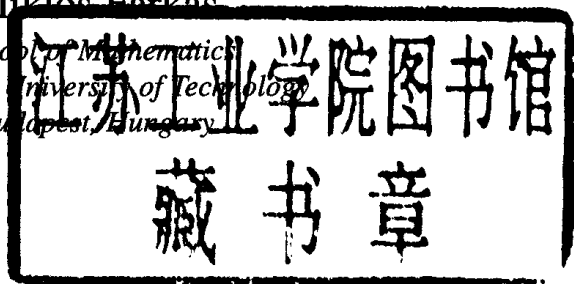


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Dynamical Models in Biology

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Preface

“But you, as a man of science, will have seen
A host of curious things—recall that worm
Which lives only inside a cat or kestrel,
But nonetheless must spend the earliest phase
Of its life-cycle inside a common mouse.
No particular mouse is singled out
To feel the cat’s claw, or the kestrel’s talon,
One that is careful could avoid them both
And die at home, at a venerable age.
But there’s an iron law which so requires,
That there be mice enough to go around
That even the defenceless worm survives
And prospers after many thousand years.”

Madách: The Tragedy of Man
G. Szirtes’ translation

Twelve years ago as a visiting professor I taught a course on Mathematical Population Dynamics at the Universidad Central de Venezuela in Caracas. For the past 10 years I have been teaching a broader spectrum Biomathematics graduate course at the Budapest University of Technology. This book is a result of these two courses. It is aimed at mathematicians interested in applications as well as biologists, medical doctors, and agricultural engineers who have a somewhat higher than average mathematical background. I do not want to teach biology here; I try to present and treat those *mathematical methods* that are used to describe dynamical phenomena in biology. As much biological explanation of the problems is given as seems to be absolutely necessary for a nonbiologist to understand the situation, and the mathematical formulae are explained intuitively to aid both nonmathematicians and beginning ones. At the same time, I do not want to avoid the really difficult topics. The main mathematical tools applied here are dynamical systems, ordinary and partial differential equations, and bifurcation theory. Rigorous background material is often found in the Appendices. It is assumed that the reader has a knowledge of advanced calculus and linear algebra. Everything else needed is contained in a concise form in the Appendices. I attempt to cover the most important branches of biomathematics that are treated by deterministic models, with the emphasis placed on supraindividual biology. Some branches were deliberately

excluded, the most important of which, perhaps, deal with the functioning of the living body (models of the heart, neural networks, etc.). I believe that the modeling of these systems is very similar to the modeling of complex systems of technology and, as a consequence, the same ideas apply for the most part.

The first two Chapters deal with population dynamics. The first one shows models in which time is passing in discrete steps; these are applied, for example, to modeling the dynamics of insect populations. In this Chapter I also treat a model of a single population with age structure. In the Chapter 2 time is a continuous variable, and different relations of species interaction, predator-prey, competition, cooperation etc. are examined. In addition, models are shown that take into consideration the delay in biological systems, age structure, and spatial distribution. Chapter 3 explores the spread of epidemics using the simplest Susceptibles-Infectives-Removed model, a model for sexually transmitted diseases, and one for pair formation. The spread of epidemics in a spatial domain is also presented. Chapter 4 on evolution explores the fundamental principles of population genetics, and the problems of evolution leading to the appearance of living creatures and immunology. Chapter 5 gives an overview of René Thom's elementary catastrophe theory whose aim was to model the evolution of the embryo and treats models of pattern formation that explain animal coat markings in Nature. In Appendix 1 the tools from linear algebra, difference equations, and stochastic processes that are needed are presented and some treatment of chaotic dynamics is included. Appendix 2 deals with ordinary differential equations the emphasis is on stability and bifurcations. Appendix 3 treats partial differential equations with an emphasis on reaction-diffusion equations and Turing instability. Appendix 4 contains a light introduction into local Riemannian geometry, with the purpose of explaining the metric in the phase space of genotype frequencies where the equations of selection govern the dynamics.

Some of the figures were prepared with MAPLE-V and some with PHASER (Kocak [1989]); this is noted in the figure captions.

I hope that this book (having been kept so slender with considerable effort) may serve as a good introduction into this fascinating subject and will invoke interest which then may lead to more in-depth studies and research. I believe also that it may be used as a textbook for an introductory graduate course.

In the preparation of this volume Tamás Czárán's comments were extremely useful. I have learned much on immunology in Gábor Tusnády's seminar. Gábor Salfer helped to solve the problems that arose in my struggle with computers. Flora Géczy did an excellent job in preparing the final latex copy and producing some of the figures. I thank them all. I also thank my wife Kati for her patience and understanding because the larger part of the time spent writing was robbed from her.

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Medellín, February 2001

Miklós Farkas

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Chapter 1

DISCRETE POPULATION MODELS

Population dynamics looks at the problem of how the number, the quantity of a well-defined group of living creatures, a species or a system of species, that is, those that share a common habitat, varies in time. Living creatures are born, reproduce, and die at a certain rate that depends on circumstances, including their specific genetically determined properties, the quantity of food available, their own density etc., and in case of a shared habitat, on the properties of those species with whom they live together. In this chapter we deal first with species of *nonoverlapping generations*. This means that the parent generation has disappeared by the time the next generation is born. One may imagine some insects that lay their eggs in the soil in the autumn and then die while the next generation is born the next spring. Next we consider a single species with discrete age groups.

1.1 Nonoverlapping Generations and Discrete Time Models

In this Section a single isolated population will be considered first. Its number or abundance at time t is denoted by N_t . Time is measured in discrete units (seconds, hours, years etc.) and it is assumed that the number of the generation of the moment (year etc.) t determines the number of the next generation, that is, the number N_{t+1} . In other words, this means that the previous generations influence the abundance of the generation at time $t + 1$ only through the generation at time t . It is also assumed that the circumstances that may have an effect on reproduction, food, temperature etc. remain the same, for example, each year is like the previous one. Consider the difference between the numbers of the $(t + 1)$ st and the t th generation. If we divide this difference by the quantity of the t th generation we obtain the *per capita growth rate at time*

t . It is usually given in percentages. Population dynamics depends on how this per capita growth rate at time t depends on the actual size of the population. The simplest assumption is that this rate is constant. If this constant is negative then this means that there are fewer in each successive generation. If this negative rate is constant, the obvious consequence is a population that dies out rapidly. If this constant is positive then the equation that governs the dynamics is

$$(N_{t+1} - N_t) / N_t = r ,$$

where the constant $r > 0$ is now the per capita growth rate of the population. This equation can be written in the form

$$N_{t+1} = (1 + r) N_t . \quad (1.1.1)$$

If we express the number at time $t+2$ by the number at time $t+1$, and then the number at time $t+3$ by the number at time $t+2$ and so on, then the number of the generation at time $t+n$ will be

$$N_{t+n} = (1 + r)^n N_t .$$

As $r > 0$, this clearly means that the numbers go to infinity as time increases indefinitely. If the per capita growth rate is, for example, 2%, then the hundredth generation numbers $1.02^{100} = 7.24$ times as much as the original one. In Nature such *exponential growth* cannot go on indefinitely because some limiting factor of the environment, lack of food, oxygen, space etc. or simply the adverse effects of overcrowding, slows down growth sooner or later. We arrive at a more realistic model if we assume that the per capita growth rate is a decreasing function of the abundance of the population, which equals zero when the size of the population reaches the maximum that can be maintained by the environment. The simplest way to do this is to set the per capita growth rate as a linear function of the quantity with negative slope. In a graph of this function, the point where this line intersects the horizontal axis of the quantity is the maximum amount the environment can maintain. This value is called the *carrying capacity* and is denoted by $K > 0$. Accordingly, Eq. (1.1.1) is modified to

$$\begin{aligned} [N_{t+1} - N_t] / N_t &= r(1 - N_t/K) \quad \text{or} \\ N_{t+1} &= N_t(1 + r - rN_t/K) . \end{aligned} \quad (1.1.2)$$

Here $r > 0$ is called the *intrinsic growth* rate of the population. It prevails if N_t is small; then the per capita growth rate is approximately equal to r . If we look at Eq. (1.1.2) we see that in case N_t is less than the carrying capacity K then N_{t+1} will be larger than N_t , while if N_t is larger than K then N_{t+1} will be smaller than N_t . If N_t is equal to K then N_{t+1} will be the same. The variation of the size of the population according to Eq. (1.1.2) is called *logistic dynamics*. Besides $N = 0$ (when there is no population present), $N = K$ is its *equilibrium point*. For certain values of the intrinsic growth rate this point is stable in the

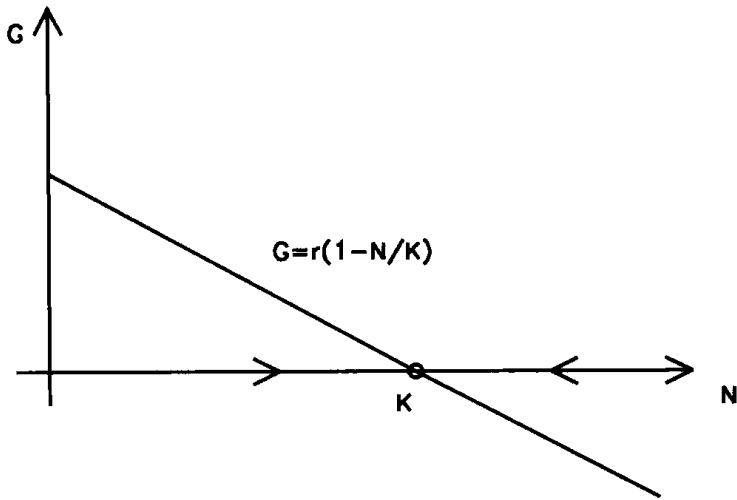


Figure 1.1.1: The growth rate of the logistic dynamics.

sense that if the population is higher or lower than this value its size goes to K (see Fig. 1.1.1).

Logistic dynamics has the great advantage that it does not let a population grow indefinitely, and if the population follows this rule then it settles down in the long run at a constant value, its carrying capacity. However, Eq. (1.1.2) has the disadvantage that if a very large value is substituted for N_t then N_{t+1} may be negative, which is meaningless. This difficulty can be overcome by the application of *exponential dynamics*:

$$(N_{t+1} - N_t) / N_t = e^{r(1-N_t/K)} - 1, \quad \text{or} \quad N_{t+1} = N_t e^{r(1-N_t/K)}, \quad r, K > 0. \tag{1.1.3}$$

Here again, if the size of the population is $< K$ then the next generation will be larger than the previous one and if the size is larger than the carrying capacity then the next generation will be smaller, and the population may finally settle down at K . One may substitute any positive number for N_t and the size N_{t+1} of the next generation will always be positive.

In the three cases discussed in the preceding, the set up is as follows. A function $F(N) = N \cdot f(N)$ is given such that if we divide it by N then we obtain the ratio of the size of the next generation to the actual one: $F(N)/N = f(N)$. In the first case the latter is constant, in the second it is a linearly decreasing function, and in the third it is exponentially decreasing. The dynamics starts at a certain time t , which will be taken as 0 in what follows and an initial size of the population N_0 is given. Then the size of the next generation is given by $N_1 = F(N_0) = N_0 f(N_0)$. The process continues like this. We have arrived at the concept of the *one-dimensional discrete forward dynamical system* or

semiflow that is given by

$$N_{k+1} = F(N_k), \quad (k = 0, 1, 2, 3, \dots) . \quad (1.1.4)$$

If we substitute successively the obtained values of N into Eq. (1.1.4) we get a sequence $N_0, N_1, N_2, \dots, N_k, \dots$, which is called the path of N_0 . It is also the path of any term N_k in it provided that we start the count of time at $t = k$. It may happen that a number E is such that the value of F at E is E , that is, $E = F(E)$. In this case E is an *equilibrium* (or *fixed*) *point* of the dynamical system, its path is E, E, E, \dots . We say that the equilibrium point is *stable in the Lyapunov sense* if for any N_0 that is sufficiently close to E the path of N_0 stays near to E in the whole future. We say that E is *asymptotically stable* if it is stable in the Lyapunov sense and for any N_0 that is sufficiently close to E the path of N_0 tends to E as time tends to infinity. In Fig. 1.1.2 we show the graph of a function F , actually the one on the right-hand side of Eq. (1.1.3), the iteration process (1.1.4) and an asymptotically stable equilibrium.

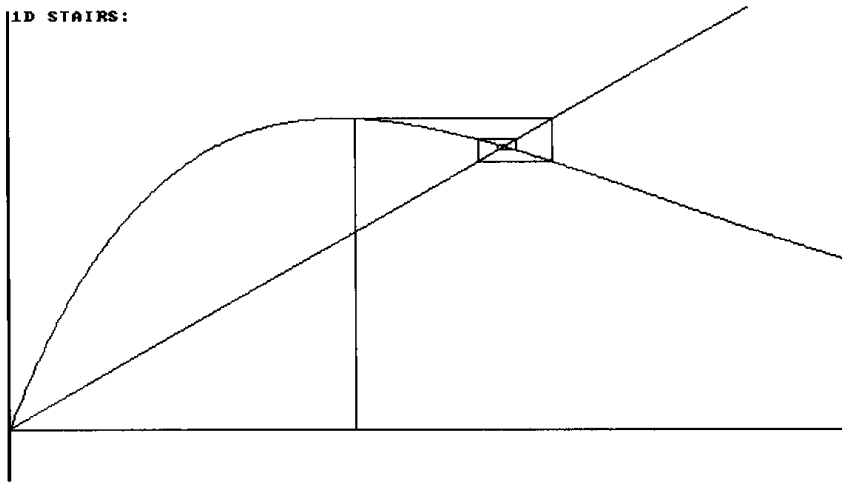


Figure 1.1.2: The dynamical system (1.1.3) with $r = 1.5$ and with $K = 1 = E$ an asymptotically stable equilibrium (PHASER).

It may happen that a point P is not an *equilibrium* but after n iterates of F one arrives back at P (and n is the least integer for which this happens); this means that

$$P = F(F(\dots F(P))) = F \circ F \circ \dots \circ F(P) = F^n(P) . \quad (1.1.5)$$

If this is the case we say that P is a *periodic point of period n* , and its path is then a periodic or closed path that closes in after n steps. Naturally, each point $P_k = F^k(P)$, ($k = 1, 2, 3, \dots, n; P = P_0 = P_n$) of the path is also a periodic point of period n . An equilibrium point is a periodic point of period 1. We say that the *periodic path is stable in the Lyapunov sense, respectively, asymptotically stable* if P is a Lyapunov stable, respectively, asymptotically

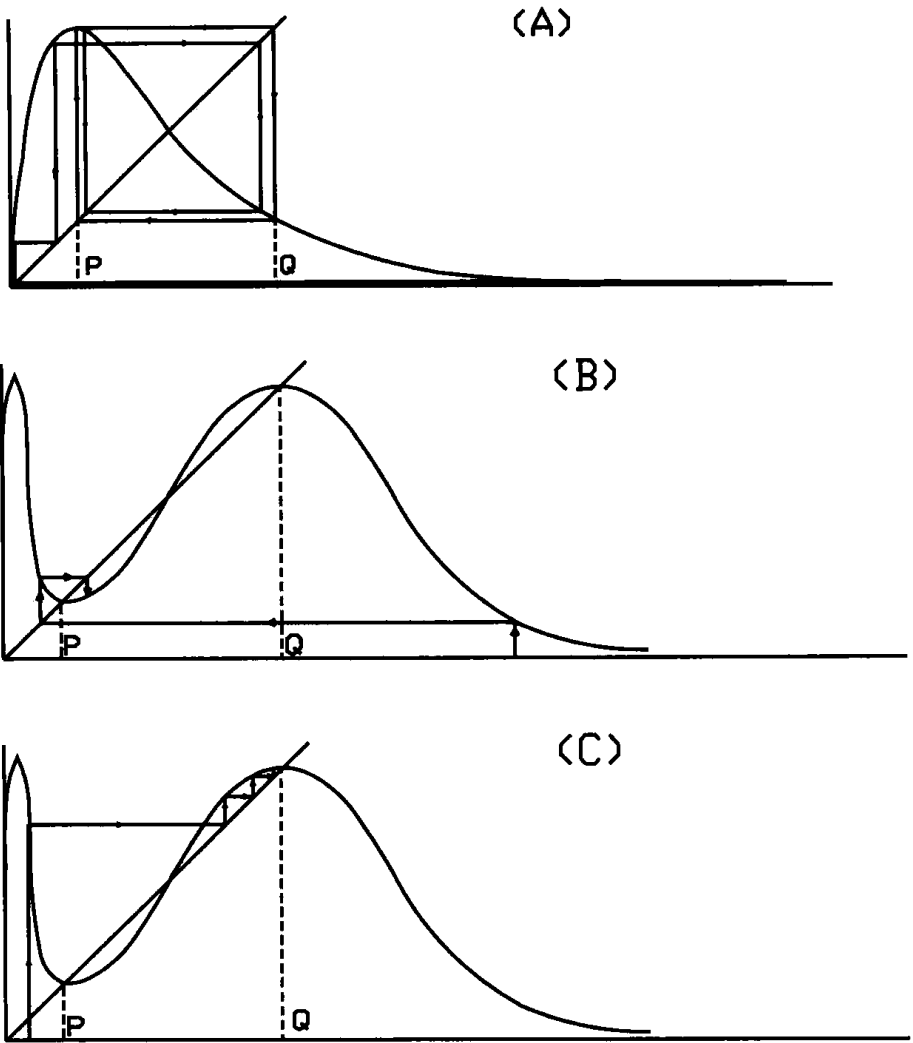


Figure 1.1.3: (A): The graph of $F(N) = Ne^{r(1-N/K)}$ with $r = 2.3$, $K = 1$, an asymptotically stable 2-periodic path P, Q . (B),(C): The graph of F^2 with asymptotically stable equilibria P and Q (PHASER).

stable equilibrium point of the dynamics defined by function F^n . That it is an equilibrium of F^n is clear from Eq. (1.1.5). If the period is 2, say, then this means that F maps P into a point Q and Q into P . Then $F(Q) = F(F(P)) = P$, and also $F(P) = F(F(Q)) = Q$. When the closed path P, Q is asymptotically stable then each path starting near to it tends to it, and each path of the dynamics determined by F^2 and starting near to P or Q , respectively, tends to P or Q , respectively. Figure 1.1.3 A shows the graph of the right-hand side of Eq. (1.1.3) with $K = 1$ and $r = 2.3$. In this case the dynamics has an asymptotically stable periodic path of period 2. Figure 1.1.3 B show the graph of the second iterate of

this function with its two asymptotically stable equilibrium points, which form the graph of the 2-periodic path on (A).

When one observes that an insect population is larger every second year and smaller every first one then it may seem to be reasonable to model its dynamics by a one-dimensional (1D) discrete semiflow with an asymptotically stable 2-periodic path.

In Appendix 1.2 the 1D discrete forward dynamical systems are treated in some detail mainly because, besides their stable equilibria and periodic paths, they may present *chaotic dynamics* that, in such systems, can be studied relatively easily. Chaotic dynamics is briefly described in the appendix and how it may arise by an infinite sequence of *period doubling bifurcations* is discussed. Chaotic dynamics is now the focus in many branches of science. For example, if we have an insect population (whose subsequent generations appear yearly) that achieves a maximum population size every fourth year then we may try to describe its dynamics by a forward dynamical system that has a stable period-4 trajectory. If in case of an insect population one observes that the numbers (quantities) of subsequent populations vary chaotically, then one may draw the conclusion that the dynamics of the population may be modeled by a semiflow in the domain of the parameter where its dynamics is chaotic. Figure 1.1.4 shows the stable 4-periodic path of system (1.1.3) when $r = 2.65$ and $K = 1$; Fig. 1.1.5 shows the stable 8-periodic path when $r = 2.67$ and $K = 1$; and Fig. 1.1.6 shows the chaotic stage when $r = 3.3$ and $K = 1$.

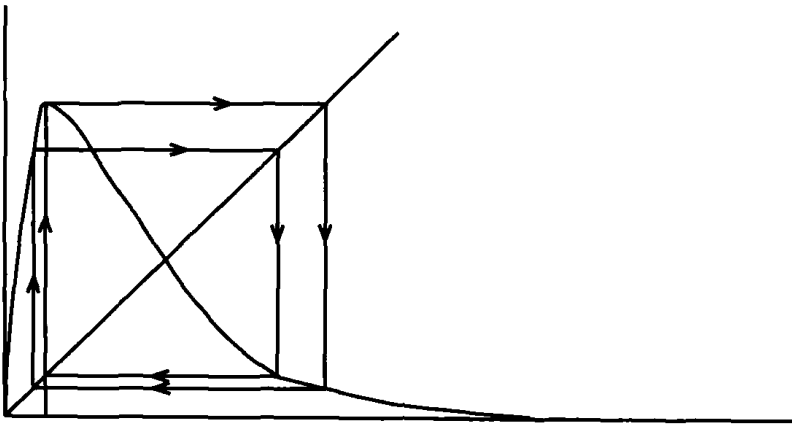


Figure 1.1.4: The stable 4-periodic path of system (1.1.3) at $r = 2.65$ and $K = 1$ (PHASER).

Discrete forward dynamical systems also can be applied in describing the dynamics of an ecological community consisting of interacting populations with nonoverlapping generations. In such a situation we speak of higher dimensional discrete semiflows. Here we are to treat a two-dimensional (2D) predator-prey system denoting the quantity of prey and predator at time $t = k$ ($k = 0, 1, 2, 3, \dots$) by N_k and P_k , respectively. In what follows we shall speak about the *relative growth* N_{k+1}/N_k or P_{k+1}/P_k of the respective species instead

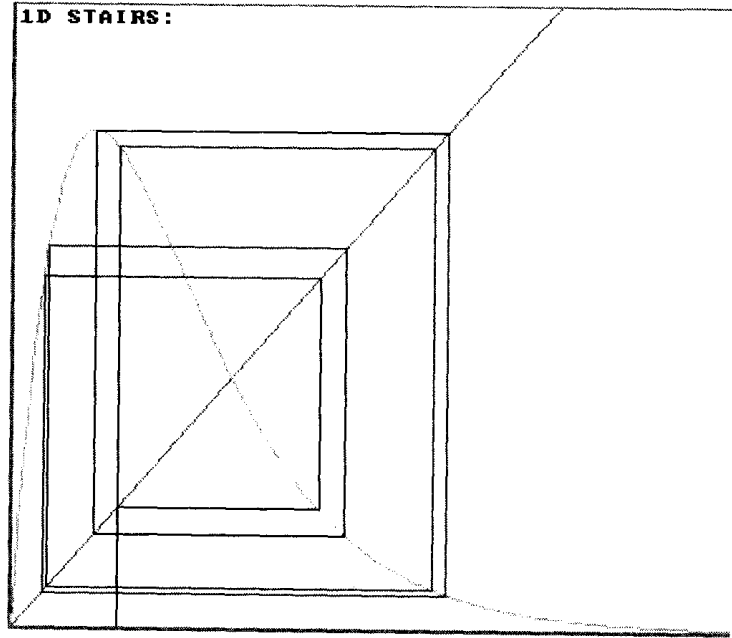


Figure 1.1.5: The stable 8-periodic path of system (1.1.3) at $r = 2.67$ and $K = 1$ (PHASER).

of the per capita growth rate. We want to have a model describing the interaction of the two species with the property that if there is no predation, $P = 0$, the system should reduce to the exponential dynamics of system (1.1.3) with respect to the prey and if there are predators present then they should reduce the relative growth of prey by a factor e^{-aP} where a is a positive number, so that $e^{-aP} < 1$. Further, in case of the predator we suppose that its relative growth is proportional to the quantity of prey (food) available but the factor of proportionality is decreasing with the quantity of predator due to the, so called *intraspecific competition* in the predator population. An often studied model with these basic properties is

$$N_{k+1} = N_k e^{r(1 - N_k/K - P_k a/r)}, \quad P_{k+1} = N_k (1 - e^{-aP_k}), \quad (1.1.6)$$

where $a > 0$ has already been described: e^{-a} is a kind of *predation rate*, where one unit of predator decreases the relative growth of prey by this factor; $K > 0$ is the carrying capacity as in the preceding: if there is no predation, prey can grow in numbers up to this value in the long run (if there are predators present then, clearly, the exponential factor in the prey equation, that is, the relative growth of prey becomes < 1 before N can reach the value of the carrying capacity, in other words, prey begins to decrease earlier); $r > 0$ is again the intrinsic growth rate of prey: if the quantities of prey and predator are small (and also r is small), then the exponential factor is $\approx 1 + r$, which may be called the intrinsic relative growth because, in this case $N_{k+1}/N_k \approx e^r \approx 1 + r$. If we look now

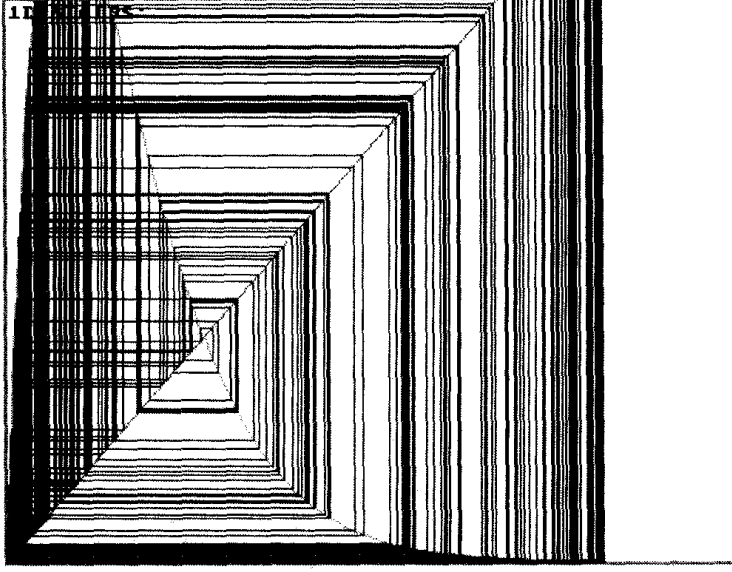


Figure 1.1.6: The chaos of system (1.1.3) at $r = 3.3$ and $K = 1$ (PHASER).

at the predator equation and divide both sides by P_k we see that the relative growth of the predator is given by the function

$$g(N, P) = N(1 - e^{-aP})/P. \quad (1.1.7)$$

Thus, the relative growth is proportional to the quantity of prey but the factor of proportionality $(1 - e^{-aP})/P$ is a decreasing positive function of the predator quantity, its limit at $P = 0$ is a , and its limit, as P tends to infinity, is zero. The dynamics of the predator-prey system (1.1.6) is generated by the pair of functions

$$(F(N, P), G(N, P)) = (Nf(N, P), Pg(N, P)),$$

where $f(N, P) = e^{r(1-N/K-Pa/r)}$ and the function g is given by Eq. (1.1.7). We discuss now the dynamics of this 2D semiflow studied by Beddington et al. (1975); background material is contained in Appendix 1.2. Here we mention only that *equilibria*, *periodic trajectories*, and *stability* can be defined in complete analogy to how this was done in the case of 1D semiflows. First it is to be noted, that system (1.1.6) inherited the property of the 1D exponential dynamics that if starting from a positive (N, P) the trajectories stay positive, therefore, in what follows the nonnegativity of N and P will always be tacitly assumed. If there are no predators, that is, we start from a point $(N, 0)$, then the trajectory stays on the N axis. If there is no food, that is, we start from a point $(0, P)$, then the next and all subsequent generations of the predator will be extinct and the predator dies out.

The equilibria of the system will be determined next. It is easy to see that $(0, 0)$ and $(K, 0)$ are fixed points. In order to find any equilibria in the interior

of the positive quadrant of the plane N, P we divide the first equation of (1.1.6) by N_k , the second one by P_k and make the right-hand sides equal to one (the requirement is that $N_{k+1}/N_k = P_{k+1}/P_k = 1$). The system of equations that is to be satisfied by the coordinates is then

$$e^{r(1-N/K-Pa/r)} = 1, \quad N(1 - e^{-aP})/P = 1,$$

or

$$N/K + Pa/r = 1, \quad N = P/(1 - e^{-aP}). \tag{1.1.8}$$

The straight line determined by the first equation and the graph of the second equation can be easily drawn; see Fig. 1.1.7. The figure shows that there is an intersection in the positive quadrant only if $1/a < K$, that is,

$$aK > 1. \tag{1.1.9}$$

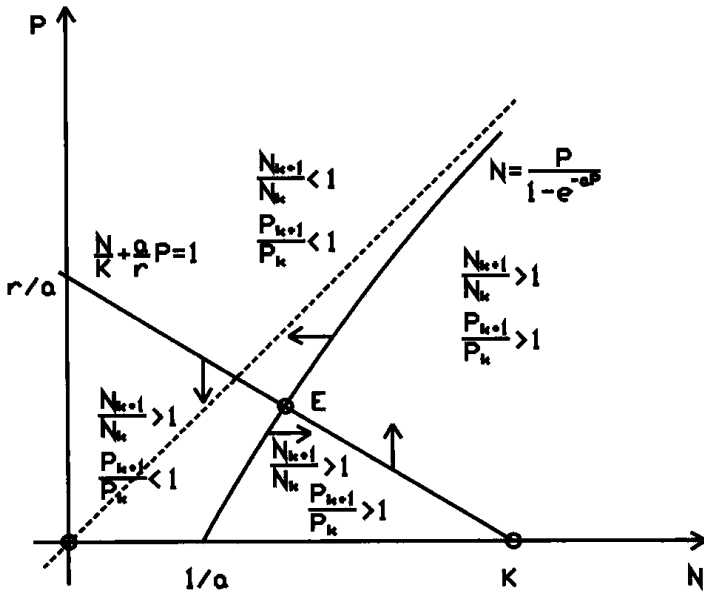


Figure 1.1.7: The phase portrait of system of equations (1.1.6) with the zero growth rate “isoclines” of prey and predator. The arrows show the direction in which the respective point moves.

This will be assumed in the sequel. It is also clear that if this condition holds then there is just one fixed point in the positive quadrant. The straight line and the other graph are important not only for finding the equilibrium point graphically, but they are the curves on which the relative growth of prey, respectively, predator is one. Above the straight line the relative growth of prey is < 1 , that is, the prey is decreasing; below the line the relative growth is > 1 , that is, the number of prey is increasing. This is intuitively reasonable; above the line there are too many predators or too many prey, resulting in a saturating effect in view of the intraspecific competition within the prey species. Above (and to the

left of) the other graph the relative growth of predators is < 1 , with predators decreasing because there are too many of them for the available food. To the right of (and below) this graph there is an abundance of food and relatively little competition within the predator species, resulting in a relative growth > 1 . The stability analysis of the fixed points is carried out in Appendix 1.3. One has to linearize the system at the respective fixed point, that is, generate the Jacobi matrix of functions F and G and check the location of the eigenvalues. If the moduli of the eigenvalues are < 1 , then the fixed point is asymptotically stable. It turns out that for any feasible choice of the parameters of the system the equilibria $(0, 0)$ and $(K, 0)$ are unstable. The equilibrium point inside the positive quadrant (denoted by E in Fig. 1.1.7) is asymptotically stable for relatively small values of the intrinsic growth rate r of the prey but as r is increased it loses its stability and at certain values of the parameters a and K the system may have periodic trajectories of high periods and behave chaotically in a bounded domain of the phase plane N, P . Figure 1.1.8 shows four different ways this system may behave at various choices of the parameters: (A) it has an asymptotically stable equilibrium point; (B) there is a closed invariant curve that attracts the trajectories but the motion on the curve itself seems to be irregular, that is, “chaotic”; (C) it has an asymptotically stable periodic trajectory of period 20; and (D) there is a bounded region of sharp contour in the phase plane inside which the dynamics seems to be chaotic.

