CLASSIFICATION OF MODELS

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Contents

Summary

We give the description and motivations of some mathematical models arising in biology, in discrete and continuous time.

1. Discrete-time Models

We will consider in this section models describing a phenomenon varying with time: the time will be discrete, but the variables of the model will be continuous (real numbers). We will give some examples, mainly taken from biological models. The basic methods for studying these models will be given in the next section.

1.1. A Model for Cell Division

The simplest model for this category is maybe the model of the division of a cell into a daughter cells, at each generation. Let us suppose that the number of cell is $x(k)$ at the kth generation (the index in the initial generation is taken as 0). Then, the number of cells at the next generation will be:

$$x(k+1) = ax(k).$$

The number of cells will be successively

$$x(0), ax(0), a^2 x(0), \ldots, a^n x(0).$$

These numbers follow a geometrical law. If a is greater than one, the population will grow over successive generations, and become unbounded.

This situation is not very realistic, because from a biological point of view the population will be subject to limitations of the resources. Some models describe the limitations to be proportional to the square x^2 of the population, because of the competition between individuals. The model becomes:

$$x(k+1) = ax(k) - bx^2(k),$$

where b is a positive parameter describing the strength of the competition. It is called the logistic equation, and has become one of the most famous simple nonlinear models; it has a wide spectrum of behavior, from stability to chaos (see *Complexity, pattern recognition and neural models*). There are many other discrete models for a single population (see *Mathematical Models of Biology and Ecology*).

1.2. Matrix and Leslie Models

Often biologists wish to model the life cycle of a population in a more structured way. The Leslie matrices describe the transitions between the categories, or stages, determining the life cycle. The simplest model describes the transition between age classes, with the hypothesis that all the individuals in an age class either die or go to the next class. Let us take the example of three age classes; the life cycle can be represented in an intuitive way on a graph with nodes (the age classes) and arrows (the possible transitions). In Figure 1, the transitions are possible from age 2 and 3 towards the first age class; that means that the ages 2 and 3 are fertile.

The set of equations describing the growth for the time k is:

$$
\begin{aligned}
x_1(k+1) &= F_2 x_2(k) + F_3 x_3(k) \\
x_2(k+1) &= P_1 x_1(k) \\
x_3(k+1) &= P_2 x_2(k)
\end{aligned}
$$

or in matrix form

$$x(k+1) = Ax(k)$$

with

$$A = \begin{pmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}.$$

The parameters F_i are the fertility coefficients, and P_i are the probabilities of survival. This kind of matrix is called a Leslie matrix, and has particular mathematical properties linked with Perron-Frobenius theorem (see next section). The model itself is a linear matrix model, with constant coefficients. The mathematical study shows that the solutions of this model have a dominant behavior, that can be characterized by a dominant growth rate (called dominant eigenvalue) playing a role quite similar to the growth rate of our geometrical law in one dimension. If this dominant eigenvalue λ_1 is greater than one, then the numbers of individuals in every age class grow and become unbounded. If λ_1 is smaller that one (λ_1 is nonnegative), then the population goes extinct. Cyclic behavior is possible, as can be seen by taking $F_2 = 0$ (case when the second age class is not fertile), and the other parameters equal to one; if the population starts with some number in the first age class and nothing in the second and third age classes, then this number simply jumps from one age class to the next, without alteration (see *Basic Methods of the Development and Analysis of Mathematical Models*).
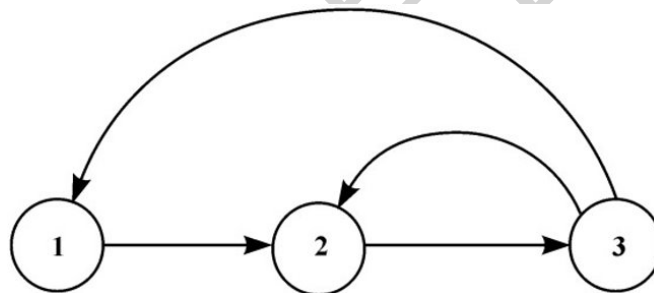

Figure 1. A life cycle

The Leslie models, or, more generally, the life cycle models are very appealing to represent complex transitions in the life of organisms; but they cannot incorporate nonlinear effects that appear frequently in the biological processes.

1.3. Nonlinear Discrete Models

Let us consider the equation giving the number of the first age class:

$$x_1(k+1) = F_2 x_2(k) + F_3 x_3(k).$$

The linear relation between the older age classes and the first one is not very realistic; a more refined model could be to suppose (and to justify with experimental data) that the relation is nonlinear, and that the number of young decreases when the total number $s(k) = x_1(k) + x_2(k) + x_3(k)$ increases. A possible model is:

$$x_1(k+1) = F_2 x_2(k)e^{-bs(k)} + F_3 x_3(k)e^{-bs(k)},$$

where the function $e^{(-bs)}$ is introduce to represent the decreasing of fertility when the density increases. We obtain a density-dependent nonlinear model; the behavior (and the mathematical study...) can be complicated.

One can also build nonlinear models with no matrix structure; let us cite, among many others, the Nicholson-Bailey model which describes the interaction between hosts and parasitoids. This is a simplified description for the complex and interlaced life cycles of the two species. The parasitoid deposits its eggs in an host (this host being at some stage of its life, often larval or pupal), that becomes a parasited host; the eggs develop at the expense of the host, eventually killing the host. Let x_1 the density of host and x_2 the density of parasitoids, then the model is:

$$
\begin{aligned}
x_1(k+1) &= \lambda x_1(k) f(x_1(k), x_2(k)) \\
x_2(k+1) &= c x_1(k)(1 - f(x_1(k), x_2(k))).
\end{aligned}
\tag{1}
$$

The parameter λ is the host reproductive rate, c is the average number of eggs laid by the parasitoid in the host. The function $f(x_1(k), x_2(k))$ is the fraction of non-parasited hosts, and is chosen to be $e^{-ax_2(k)}$, given the hypotheses that the encounters are random, and choosing a Poisson probability distribution to describe the first encounter. This leads to the model:

$$
\begin{aligned}
x_1(k+1) &= \lambda x_1(k) e^{-ax_2(k)}) \\
x_2(k+1) &= c x_1(k)(1 - e^{-ax_2(k)}).
\end{aligned}
$$

It can be shown (see *Basic Methods of the Development and Analysis of Mathematical Models*) that this model has an equilibrium, and that this equilibrium is unstable: an initial condition near the equilibrium results in diverging oscillations.

2. Continuous-time Models

We consider in this section the continuous models which describe a phenomenon varying in time. The time will vary continuously. Assume that we have selected the state variables $x(t)$ at time t. It remains to write the equations giving the state variables at time $t + \Delta t$ where Δt is a very short interval of time. Let us denote by $f(t, x(t))\Delta t$ the variation of $x(t)$ during time Δt:

$$x(t + \Delta t) - x(t) = f(t, x(t))\Delta t.$$

This equation can be rewritten as

$$\frac{x(t + \Delta t) - x(t)}{\Delta t} = f(t, x(t)).$$

Let us postulate the existence of a time derivative

$$\frac{dx}{dt}(t) = \lim_{\Delta t \to 0} \frac{x(t + \Delta t) - x(t)}{\Delta t},$$

which we shall usually denote by $\dot{x}(t)$. Thus, if we go to the limit when Δt goes to 0 we can write

$$\dot{x}(t) = f(t, x(t)).\tag{2}$$

In general $x(t)$ is a vector of n real variables $x(t) = (x_1(t), \cdots, x_n(t))$, so that, the above equation is a set of differential equations or a differential system

$$
\begin{aligned}
\dot{x}_1(t) &= f_1(t, x_1(t), \cdots, x_n(t)) \\
&\qquad \cdots \\
\dot{x}_n(t) &= f_n(t, x_1(t), \cdots, x_n(t)).
\end{aligned}
\tag{3}
$$

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Biographical Sketches

Jean-Luc Gouzé is a Senior Research Scientist at INRIA (National French Institute for Computer Science and Control), and the head of the research team COMORE (Control and Modeling of Renewable Resources, see http://www.inria.fr/comore). After graduating from the engineering school Ecole Centrale de Paris (Applied Mathematics Department) in 1980, he completed his doctorate from the Paris XI University in 1983, working on mathematical models in neurobiology. He joined INRIA as a research scientist in 1984. His main scientific interests are in the mathematical models in biology, biomathematics, the qualitative studies of dynamical systems, the study of positive biological systems, and the estimation and control for biological systems.

Tewfik Sari was born in Casablanca (Morocco) in 1955. After graduating from Oran University (Algeria) in 1976, he received the PhD degree in mathematics from Strasbourg University (France) in 1983. Since 1994 he is Professor of Mathematics at UHA (Université de Haute Alsace, Mulhouse, France). From 1983 to 1993 he taught mathematics in the universities of Sidi Bel Abbes (Algeria), Groningen (Netherlands), Nice and La Rochelle (France). From 2000 to 2002 he was affiliated, as an associated researcher, with INRIA (National French Institute for Computer Science and Control). His current research interests include dynamical systems, perturbation theory, and mathematical models in biology.