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INVERSE PROBLEMS IN ECOLOGY

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PREFACE

This Memorandum is a part of a continuing mathematical study of biological systems sponsored by the National Institutes of Health and The RAND Corporation. It describes a computational technique for the determination of growth and interaction parameters from observations of interacting populations. This Memorandum is of interest to researchers in the fields of biological and chemical kinetics.

SUMMARY

The question of describing interactions of populations is studied. From observations of population growths, parameters in models may be estimated. This concept is illustrated by an example of two interacting species. The sensitivity of the parameters to the accuracy of the observations is computationally investigated, using the technique of quasilinearization.

INVERSE PROBLEMS IN ECOLOGY

INTRODUCTION

Stimulated by his friend's questions concerning an explanation of the fluctuation of the yearly catch of certain types of fish, Volterra (1931, 1938) began a systematic study of the interactions of populations. If there are k interacting species, under certain simplified assumptions a reasonable description of the process over time can be obtained by a study of a system of ordinary differential equations

$$\frac{dN_i}{dt} = g_i(N_1, N_2, \ldots, N_k), \tag{1}$$

$N_i(0) = c_i$, $i = 1,2,\ldots,k$. For more precise descriptions, it is necessary to employ differential-difference equations and generally equations with hereditary effects.

Here, we propose to study the question of determining how accurate an explanation of observed phenomena can be obtained using a system of the type appearing in (1). The technique we shall employ is that of quasilinearization (Bellman and Kalaba, 1965), aided by a digital computer. It is only with the aid of these devices that we can hope to tackle these questions in a unified and sophisticated fashion.

To illustrate the approach, we shall consider the simple case of two species interacting, prey and predator. An interesting feature is a series of experiments determining the sensitivity of the parameters in the model to the accuracy of the observations of the population sizes at various times.

AN INVERSE PROBLEM

Let us consider the Lotka-Volterra equations

$$\frac{dN_1}{dt} = (c_3 - c_5 N_2)N_1, \qquad N_1(0) = c_1,$$
$$\frac{dN_2}{dt} = -(c_4 - c_6 N_1)N_2, \qquad N_2(0) = c_2, \tag{2}$$

where $c_1, c_2, c_3, c_4, c_5, c_6$ are positive constants. The parameters c_3, c_4 correspond to growth constants, while c_5, c_6 represent interaction coefficients; N_1, N_2 denote, respectively, the prey and predator populations.

We consider the case in which the constants are

$$\begin{aligned} c_1 &= 1.2, \\ c_2 &= 1.1, \\ c_3 &= 1.0, \\ c_4 &= 1.0, \\ c_5 &= 1.0, \\ c_6 &= 1.0. \end{aligned} \tag{3}$$

We produce the population curves as functions of time by integrating equations (2), using the constants given by (3), with a step length of $\Delta t = 0.01$. These curves, on the interval $0 \le t \le 10$, are shown in Fig. 1.

Now we pose the following inverse problem: Given the observations of N_1, $\{a_i\}$, and the observations of

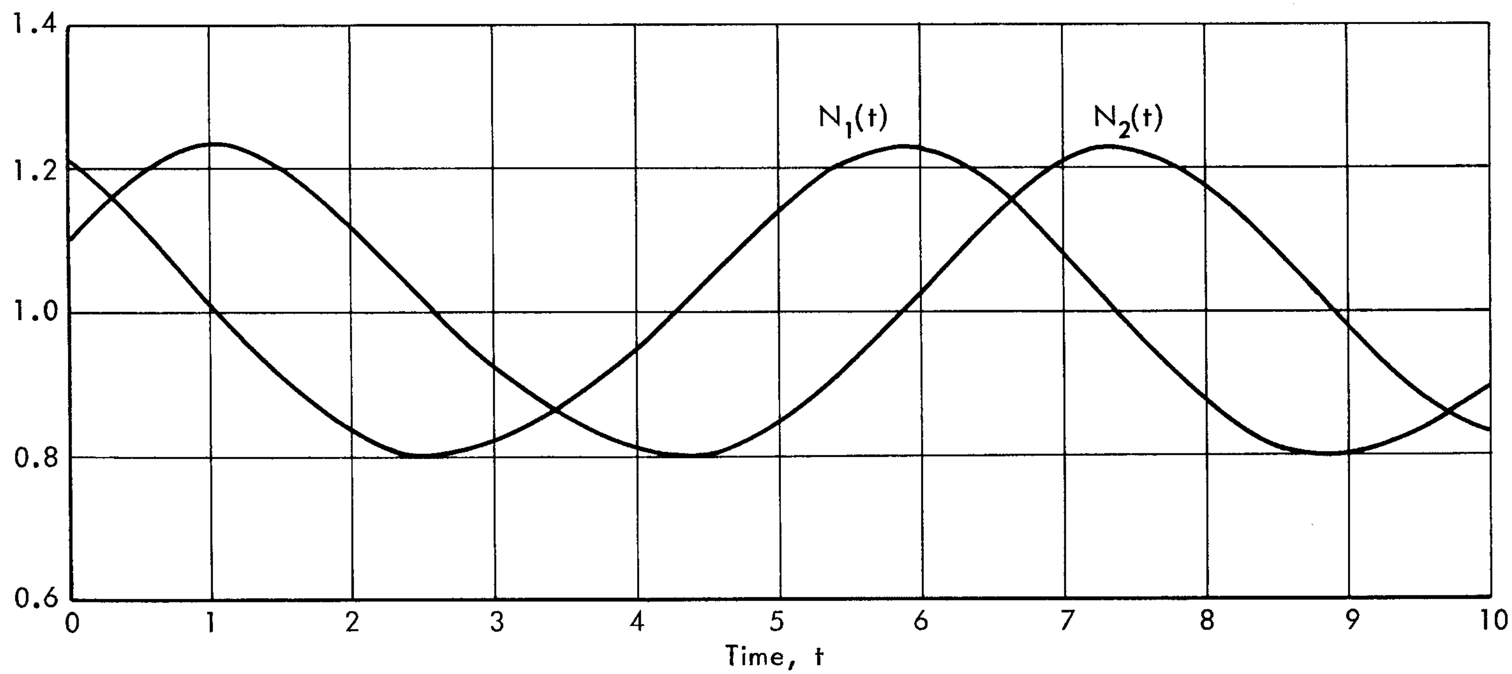

Fig. 1—Curves of population growth of two interacting species

N_2, $\{b_i\}$, at discrete times t_i, $i = 1,2,\ldots,M$, determine the values of the six constants $c_1,c_2,\ldots,c_6$ that would produce solutions of (2) in best agreement with the observations, in a least squares sense. We wish to minimize the expression

$$\sum_{i=1}^{M} \{[N_1(t_i) - a_i]^2 + [N_2(t_i) - b_i]^2\} \tag{4}$$

by a proper choice of $c_1,c_2,\ldots,c_6$.

This is a nonlinear multipoint boundary-value problem that can be solved via the successive approximation method of quasilinearization (Bellman and Kalaba, 1965). Suppose that there is a current approximation of the solution. Improved approximations are produced by solving a sequence of related linear multipoint boundary-value problems. The sequence of such approximations is quadratically convergent, when convergent at all. Details of the method may be found in the above reference.

For the ecology problem at hand, we begin with an estimate of each of the six constants $c_1,c_2,\ldots,c_6$, and the two population functions $N_1(t)$ and $N_2(t)$. In order to obtain the next set of approximations, we numerically integrate fourteen linearized equations, we invert a 6×6 matrix for improved values of the six constants, and we use these constants to produce improved approximations of $N_1(t)$ and $N_2(t)$. We repeat these steps several times, and we find that we rapidly converge to a solution of the inverse problem.

COMPUTATIONAL RESULTS

We performed a series of numerical experiments for the determination of the six constants. In some trials, we truncated the correct values $N_1(t_k)$, $N_2(t_k)$ after two decimal places, in other trials after one decimal place to simulate noisy observations. The total number of observations is 2M, where M is the number of instants at which the populations are observed. The results are given in Table 1. The true values of the constants are given at the bottom of the table. The estimated values for each trial are the result of three to five iterations.

The computations are carried out on an IBM 7044 machine using FORTRAN IV. Each trial consumes about two minutes of computer time.

Several trends may be noted. First, it is obvious that increasing the accuracy of the data yields superior estimates of parameters. Second, if the accuracy is fixed, increasing the number of observations tends to produce more accurate estimates. Next, looking at the results of trials 5 and 6, we note that six observations (the minimum number required) correct to two decimal places gives very good results, and that 202 observations gives only slightly improved estimates. Then, comparing the constants of trial 4 against those of trial 5, we see that the minimum number of observations correct to

Table 1

Computational Results for the Estimation of Parameters and Initial Conditions of the Population Equations

Trial	Observations		$c_1=N_1(0)$	$c_2=N_2(0)$	c_3	c_4	c_5	c_6
	2M	No. of decimal places						
1	6	1	1.200	1.000	1.552	0.648	1.669	0.688
2	10	1	1.197	1.014	1.103	0.942	1.146	0.983
3	22	1	1.186	1.019	1.080	0.993	1.119	1.035
4	202	1	1.152	1.058	0.982	1.019	1.026	1.063
5	6	2	1.200	1.090	0.998	1.008	0.999	1.011
6	202	2	1.196	1.096	0.998	1.003	1.002	1.008
True values of constants			1.2	1.1	1.0	1.0	1.0	1.0

two decimals is of greater value in the determination of constants than is a large quantity of data of lower accuracy.

It is clear that such information, gained through numerical experiments, is of value in planning and interpreting ecological field studies.

BIBLIOGRAPHY

Bellman, R. & Kalaba, R. (1965). "Quasilinearization and Nonlinear Boundary-value Problems." New York: American Elsevier.

Volterra, V. (1931). "Lecons sur la Theorie Mathematique de la Lutte Pour La Via." Paris: Cahiers Scientifiques.

Volterra, V. (1938). Human Biology, **10**, 1.