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MATRIX METHODS OF APPROXIMATING CLASSICAL PREDATOR–PREY PROBLEMS

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1. INTRODUCTION

In many cases, the modeling of a physical problem leads to a system of differential equations. A system of first-order, linear, homogeneous differential equations may be written concisely in matrix notation and may be solved using the methods presented here. The particular problem to which these techniques will be applied involves the determination of the population levels of two species, one of which preys upon the other for instance, foxes and rabbits.

2. DEVELOPMENT OF THE PROBLEM

2.1. Formulation of the model

In an ecological system involving a killer population and a victim population, we assume that the rate of growth of the victim population is proportional to the number of current members of the species and is negatively related to the number of meetings of killer and victim. The number of meetings should be proportional to the product of the killer and victim populations. The growth rate of the killer population, on the other hand should be positively related to the number of meetings. Finally, a large number of killers would increase competition for the victims, which are limited in supply. Thus, growth of the killer population is negatively related to the number of killers. Letting $V(t)$ represent the population of victims at time t and $K(t)$ the number of killers at time t, we have the following system of differential equations:

$$\begin{aligned} V'(t) &= \alpha_1 V(t) - \beta_1 V(t)K(t) \\ K'(t) &= -\alpha_2 K(t) + \beta_2 V(t)K(t) \end{aligned} \tag{1}$$

where α_1, α_2, β_1 and β_2 are positive constants to be determined empirically.

2.2. Linearization

Equations (1) represent a nonlinear system of differential equations since there are terms involving the product of V and K. In a linear system, V and K may appear individually only. In order to ease the mathematical treatment of this system of equations we will make an approximation which reduces the system to a linear form in the vicinity of certain equilibrium populations.

The first step is the determination of the equilibrium population levels—those population levels for which the rates of change with respect to time are zero. Setting $V'(t)$ and $K(t)$ to 0 in equations (1) and denoting the equilibrium values of $V(t)$ and $K(t)$ by V^* and K^* yields

$$\begin{aligned} V^*(\alpha_1 - \beta_1 K^*) &= 0 \\ K^*(-\alpha_2 + \beta_2 V^*) &= 0. \end{aligned} \tag{2}$$

Since the products in equations (2) are zero, either $V^* = K^* = 0$ or

$$\begin{aligned} V^* &= \alpha_2/\beta_2 \\ K^* &= \alpha_1/\beta_1. \end{aligned} \tag{3}$$

The case of both population levels being equal to zero is of no physical interest, so we use the equilibrium populations given by equations (3).

Now introduce the new variables

$$v(t) = V(t) - V^* = V(t) - \alpha_2/\beta_2$$

and

$$k(t) = K(t) - K^* = K(t) - \alpha_1/\beta_1,$$

which represent deviations from the equilibrium populations. This gives

$$V(t) = v(t) + \alpha_2/\beta_2, \qquad V'(t) = v'(t)$$

and

$$K(t) = k(t) + \alpha_1/\beta_1, \qquad K'(t) = k'(t). \tag{4}$$

Substituting expressions (4) into equations (1) and combining terms leads to

$$\begin{aligned} v'(t) &= -k(t)\alpha_2\beta_1/\beta_2 - \beta_1 v(t)k(t) \\ k'(t) &= v(t)\alpha_1\beta_2/\beta_1 + \beta_2 v(t)k(t). \end{aligned} \tag{5}$$

It is now important to notice that V, K, v and k may be thought of as either absolute populations or as population densities. It is prudent here to use population densities in units such that the equilibrium values of $V(t)$ and $K(t)$ are approximately 1. In this case $v(t)$ and $k(t)$ are much less than one for small deviations from equilibrium and the terms involving $v(t)k(t)$ are likely to be much smaller than the other terms in equations (5). Thus, as an approximation, we can drop the last terms in each equation and get

$$\begin{aligned} v'(t) &= -k(t)\alpha_2\beta_1/\beta_2 \\ k'(t) &= v(t)\alpha_1\beta_2/\beta_1. \end{aligned} \tag{6}$$

Equations (6) are now a linear differential system because $v(t)$ and $k(t)$ only appear individually.

2.3. The matrix form of the problem

If we let

$$\mathbf{x}(t) = \begin{bmatrix} v(t) \\ k(t) \end{bmatrix} \quad \text{and} \quad \mathbb{A} = \begin{bmatrix} 0 & -\alpha_2\beta_1/\beta_2 \\ \alpha_1\beta_2/\beta_1 & 0 \end{bmatrix},$$

equations (6) can be written in the form

$$\frac{\mathrm{d}}{\mathrm{d}t}\mathbf{x}(t) = \mathbb{A}\mathbf{x}(t). \tag{7}$$

This follows from the ordinary definition of multiplication of a matrix and a vector. The derivative of a matrix (or a vector) is defined as the differentiation of each individual element of the matrix. Since equation (7) is a differential system, we also need to specify an initial condition, $\mathbf{x}(0) = \mathbf{x}_0$. This form may apply to a similar system of n equations for arbitrary n. The matrix $\mathbb{A}$ would be $n \times n$, and $\mathbf{x}$ would be a column vector of n components.

We might expect the solution of equation (7) to be analogous to the solution of the similar equation involving scalars. Indeed, this is the case, with the solution being

$$\mathbf{x}(t) = \mathrm{e}^{\mathbb{A}t}\mathbf{x}_0. \tag{8}$$

This solution involves raising e to a matrix power. To make sense of this concept we resort to the Taylor's series expansion of e^x and define

$$\mathrm{e}^{\mathbb{A}t} = \mathbb{I} + \mathbb{A}t + (\mathbb{A}t)^2/2! + (\mathbb{A}t)^3/3! + (\mathbb{A}t)^4/4! + \dots \tag{9}$$

It can be shown that for any given $\mathbb{A}$, this series converges $\forall\, t$ [1]. Now let us see if $x(t)$ as given by equation (8) actually satisfies equation (7). Since the series representation of $\mathrm{e}^{\mathbb{A}t}$ converges for any given $\mathbb{A}$ $\forall\, t$, we can differentiate equation (9) term by term to get

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\mathrm{e}^{\mathbb{A}t} &= \mathbb{A} + \mathbb{A}^2 t + \frac{\mathbb{A}^3 t^2}{2!} + \cdots \\ &= \mathbb{A}(\mathrm{e}^{\mathbb{A}t}).\end{aligned} \tag{10}$$

Thus equation (8) really is the solution of the linear differential system (7). The following section is devoted to explaining a practical method for calculating $\mathrm{e}^{\mathbb{A}t}$.

3. CALCULATING THE EXPONENTIAL OF A MATRIX

3.1. Eigenvalues and the characteristic polynomial

The first step in finding $\mathrm{e}^{\mathbb{A}t}$ involves determining the fundamental values or eigenvalues of the matrix $\mathbb{A}$. The eigenvalues are the roots of the equation $\det(\mathbb{A} - \lambda\mathbb{I}) = 0$, where $\mathbb{I}$ represents the identity matrix of the same order as $\mathbb{A}$. This is called the characteristic equation for the matrix $\mathbb{A}$. If $\det(\mathbb{A} - \lambda\mathbb{I})$ is written in the form of a polynomial, it is called the characteristic polynomial.

As a numerical example, consider the system

$$\begin{aligned} x_1'(t) &= 4x_1 - 5x_2, \qquad x_1(0) = 8 \\ x_2'(t) &= 2x_1 - 3x_2, \qquad x_2(0) = 5. \end{aligned} \tag{11}$$

Here $\mathbf{x}(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}$, $\mathbb{A} = \begin{bmatrix} 4 & -5 \\ 2 & -3 \end{bmatrix}$ and $\mathbf{x}_0 = \begin{bmatrix} 8 \\ 5 \end{bmatrix}$. The characteristic equation is given by

$$\det\begin{vmatrix} 4-\lambda & -5 \\ 2 & -3-\lambda \end{vmatrix} = (4-\lambda)(-3-\lambda) + 10 = 0. \tag{12}$$

The characteristic polynomial is thus

$$\lambda^2 - \lambda - 2.$$

The roots of equation (12) give us the eigenvalues $\lambda_1 = -1$ and $\lambda_2 = 2$.

3.2. The Cayley–Hamilton theorem

The Cayley–Hamilton theorem states that every matrix is a root of its characteristic polynomial. A proof may be found in Ref. [2].

The importance of the Cayley–Hamilton theorem in this application results from the following fact (see Ref. [2] for a proof): given polynomials $f(\lambda)$ and $c(\lambda)$, we can always find polynomials $q(\lambda)$ and $r(\lambda)$ such that

$$f(\lambda) = c(\lambda)q(\lambda) + r(\lambda) \tag{13}$$

with the degree of $r(\lambda)$ less than the degree of $c(\lambda)$. If we choose $c(\lambda)$ to be the characteristic polynomial for the matrix $\mathbb{A}$, then the Cayley–Hamilton theorem implies

$$f(\mathbb{A}) = r(\mathbb{A}) \tag{14}$$

since $c(\mathbb{A}) = 0$.

This approach is valid even if $f(\lambda)$ is an infinite polynomial such as $e^{\lambda t}$. We simply need to find the remainder polynomial r and evaluate $r(\mathbb{A})$.

3.3. Finding the remainder polynomial

The degree of the characteristic polynomial of a nonsingular $n \times n$ matrix is always n. Thus, the remainder polynomial is of the form

$$a_0 + a_1\lambda + a_2\lambda^2 + \cdots + a_{n-1}\lambda^{n-1}.$$

If λ_j is an eigenvalue of the matrix $\mathbb{A}$, $c(\lambda_j) = 0$, so it follows from equation (13) that

$$f(\lambda_j) = r(\lambda_j) = a_0 + a_1\lambda_j + a_2\lambda_j^2 + \cdots + a_{n-1}\lambda_j^{n-1}. \tag{15}$$

If we have n distinct eigenvalues we substitute λ_1 through λ_n into equation (15) to obtain a system of n equations in the n unknowns a_0 through a_{n-1}. Solving for the a's by Gaussian elimination gives us the remainder polynomial r.

In the numerical example of Section 3.1, $n = 2$. For $f(\lambda) = e^{\lambda t}$, equation (15) with $\lambda_1 = -1$ and $\lambda_2 = 2$ gives us

$$\begin{aligned} e^{-t} &= a_0 - a_1 \\ e^{2t} &= a_0 + 2a_1. \end{aligned} \tag{16}$$

This linear system of equations can be solved for a_0 and a_1 by Gaussian elimination to yield

$$\begin{aligned} a_0 &= \tfrac{2}{3}e^{-t} + \tfrac{1}{3}e^{2t} \\ a_1 &= -\tfrac{1}{3}e^{-t} + \tfrac{1}{3}e^{2t}. \end{aligned}$$

Now, we will calculate $e^{\mathbb{A}t}$ for the matrix in our example:

$$r(\mathbb{A}) = a_0\mathbb{I} + a_1\mathbb{A} = \begin{bmatrix} a_0 + 4a_1 & -5a_1 \\ 2a_1 & a_0 - 3a_1 \end{bmatrix} = \begin{bmatrix} -\frac{2}{3}e^{-t} + \frac{5}{3}e^{2t} & \frac{5}{3}e^{-t} - \frac{5}{3}e^{2t} \\ -\frac{2}{3}e^{-t} + \frac{2}{3}e^{2t} & \frac{5}{3}e^{-t} - \frac{2}{3}e^{2t} \end{bmatrix} \tag{17}$$

Thus, the solution of system (11) is

$$\mathbf{x}(t) = e^{\mathbb{A}t}\mathbf{x}_0 = \begin{bmatrix} 3e^{-t} + 5e^{2t} \\ 3e^{-t} + 2e^{2t} \end{bmatrix}$$

or

$$\begin{aligned} x_1(t) &= 3e^{-t} + 5e^{2t} \\ x_2(t) &= 3e^{-t} + 2e^{2t}. \end{aligned} \tag{18}$$

3.4. Repeated eigenvalues

Suppose we have to find $e^{\mathbb{B}t}$ for the matrix

$$\mathbb{B} = \begin{bmatrix} 2 & 3 \\ 0 & 2 \end{bmatrix}. \tag{19}$$

This matrix has a double eigenvalue, $\lambda_1 = \lambda_2 = 2$. Because of the repeated root of the characteristic polynomial, it is not possible to obtain two distinct equations from equation (15) and solve for the coefficients. A slight modification will cure the problem.

If an eigenvalue λ_i is repeated k times (occurs $k + 1$ times altogether), then, not only is $f(\lambda_i) = r(\lambda_i)$, but also

$$\left.\begin{aligned} f'(\lambda_j) &= r'(\lambda_j) = a_1 + a_2\lambda_j + a_3\lambda_j^2 + \cdots a_{n-2}\lambda_j^{n-1} \\ f''(\lambda_j) &= r''(\lambda_j) = a_2 + a_3\lambda_j + a_4\lambda_j^2 + \cdots + a_{n-3}\lambda_j^{n-2} \\ f^{[k]}(\lambda_j) &= r^{[k]}(\lambda_j) = a_k + a_{k+1}\lambda_j + a_{k+2}\lambda_j^2 + \cdots + a_{n-k-1}\lambda_j^{n-k}. \end{aligned}\right\} \tag{20}$$

This enables us to fill out the necessary set of n equations in the n unknowns a_0 through a_{n-1}.

4. SOLUTION OF THE LINEARIZED MODEL

We return to the problem in which

$$\mathbb{A} = \begin{bmatrix} 0 & -\alpha_2\beta_1/\beta_2 \\ \alpha_1\beta_2/\beta_1 & 0 \end{bmatrix}.$$

The eigenvalues of $\mathbb{A}$ are given by $\lambda^2 + \alpha_1\alpha_2 = 0$. Since $\alpha_1 > 0$ and $\alpha_2 > 0$ the roots of this equation are $\lambda_1 = i\sqrt{\alpha_1\alpha_2}$ and $\lambda_2 = -i\sqrt{\alpha_1\alpha_2}$, where $i = \sqrt{-1}$. Note that the techniques of the preceding sections apply equally well to complex eigenvalues as to real ones. If we are to apply equation (15) and the methods of the preceding section, we must evaluate $f(\lambda) = e^{\lambda t}$ at the complex eigenvalues $i\sqrt{\alpha_1\alpha_2}$ and $-i\sqrt{\alpha_1\alpha_2}$. To do this we will make use of the Euler formula

$$e^{i\theta} = \cos\theta + i\sin\theta \tag{21}$$

as well as trigonometric identities $\cos(-\theta) = \cos\theta$ and $\sin(-\theta) = -\sin\theta$. Thus equation (15) becomes

$$\begin{aligned}\cos\sqrt{\alpha_1\alpha_2}t + i\sin\sqrt{\alpha_1\alpha_2}t &= a_0 + a_1 i\sqrt{\alpha_1\alpha_2}t \\ \cos\sqrt{\alpha_1\alpha_2}t - i\sin\sqrt{\alpha_1\alpha_2}t &= a_0 - a_1 i\sqrt{\alpha_1\alpha_2}t\end{aligned} \tag{22}$$

with the solution

$$\begin{aligned}a_0 &= \cos\sqrt{\alpha_1\alpha_2}t \\ a_1 &= \sqrt{1/\alpha_1\alpha_2}\sin\sqrt{\alpha_1\alpha_2}t\end{aligned}$$

obtained by Gaussian elimination. For $e^{\mathbb{A}t}$, we get

$$a_0\mathbb{I} + a_1\mathbb{A} = \begin{bmatrix}\cos\sqrt{\alpha_1\alpha_2}t & -(\alpha_2\beta_1/\beta_2\sqrt{\alpha_1\alpha_2})\sin\sqrt{\alpha_1\alpha_2}t \\ (\alpha_1\beta_2/\beta_1\sqrt{\alpha_1\alpha_2})\sin\sqrt{\alpha_1\alpha_2}t & \cos\sqrt{\alpha_1\alpha_2}t\end{bmatrix}. \tag{23}$$

Since the initial conditions of the populations are $v(0) = v_0$ and $k(0) = k_0$, we can now write an approximate expression for the populations of victims and killers:

$$\begin{bmatrix}v(t)\\k(t)\end{bmatrix} = \begin{bmatrix}v_0\cos\sqrt{\alpha_1\alpha_2}t - k_0(\sqrt{\alpha_2}\beta_1/\beta_2\sqrt{\alpha_1})\sin\sqrt{\alpha_1\alpha_2}t \\ v_0(\sqrt{\alpha_1}\beta_2/\beta_1\sqrt{\alpha_2})\sin\sqrt{\alpha_1\alpha_2}t + k_0\cos\sqrt{\alpha_1\alpha_2}t\end{bmatrix}.$$

Applying basic trigonometric identities, this can be simplified to

$$\begin{bmatrix}v(t)\\k(t)\end{bmatrix} = \begin{bmatrix}C(\beta_1\sqrt{\alpha_2}/\beta_2\sqrt{\alpha_1})\cos(\sqrt{\alpha_1\alpha_2}t + \theta) \\ C\sin(\sqrt{\alpha_1\alpha_2}t + \theta)\end{bmatrix}, \tag{24}$$

where C and θ are constants which may be determined from the initial conditions. This shows that v and k vary sinusoidally with the same period, with the oscillation of the killer population lagging one-quarter period behind that of the victim population.

We may also wish to find the direct relationship between v and k. To eliminate t from equation (24) note that

$$\frac{v^2}{(\beta_1\sqrt{\alpha_2}/\beta_2\sqrt{\alpha_1})^2} + k^2 = C^2. \tag{25}$$

This represents an elliptical orbit about the origin of the v–k plane. Since v and k are deviations from the equilibrium population levels, we have, in the plane of the original V and K (called the phase plane), an elliptical orbit around the point corresponding to the equilibrium values of V and K.

5. ADDITIONAL OBSERVATIONS

In this problem it is also possible to proceed from the original system directly to the phase plane. This is easy because the system (1) is autonomous, meaning that t does not appear explicitly in the equations. Writing dV/dt for V' and dK/dt for K', and formally dividing the first equation by the second, yields the single differential equation

$$dV/dK = V(\alpha_1 - \beta_1 K)/K(-\alpha_2 + \beta_2 V) \tag{26}$$

or, rearranging,

$$(-\alpha_2/V + \beta_2)\mathrm{d}V = (\alpha_1/K - \beta_1)\mathrm{d}K. \tag{27}$$

Integrating and exponentiating both sides yields

$$\frac{\mathrm{e}^{\beta_2 V}}{V^{\alpha_2}} \cdot \frac{\mathrm{e}^{\beta_1 K}}{K^{\alpha_1}} = \mathrm{c} \tag{28}$$

where c is a constant determined by the initial conditions. Though we cannot solve explicitly for V or K, this equation leads to closed orbits about the equilibrium point. When the perturbations from equilibrium are small, the orbits may be approximated by the ellipses of equation (25).

The approximation which has been presented for the model under consideration has proven quite reasonable, but one must, in general, be very careful in attempting to simplify such systems. Other more simplistic modifications may at first appear reasonable but can lead to poor results.

6. REFERENCES

1. R. Bellman, *Introduction to Matrix Analysis*. McGraw-Hill, New York (1970).
2. K. Hoffman and R. Kunze, *Linear Algebra*. Prentice-Hall, Englewood Cliffs. N.J. (1971).
3. N. S. Goel, S. C. Maitra and E. W. Montroll, *Nonlinear Models of Interacting Populations*. Academic Press, New York. (1971).

7. EXERCISES

1. Why is the number of killer–victim meetings assumed to be proportional to the product of their populations? How reasonable do other assumptions embodied in the model seem to be? What other factors might be included in the model to make it more realistic?
2. Find the characteristic polynomial and the eigenvalues for the matrix $\begin{pmatrix} 8 & 1 \\ -1 & 6 \end{pmatrix}$.
3. Verify the Cayley–Hamilton theorem for the matrix in Exercise 2.
4. Verify the correctness of solution (18) by substituting it into system (11).
5. Find $\mathrm{e}^{\mathbb{B}t}$ for the matrix $\mathbb{B}$ given in equation (19).
6. Choose several different sets of values of α_1, α_2, β_1, β_2 and c. Then, for each set, sketch the graph of V vs K according to equation (28) and note its shape. Find the corresponding values of C in equation (25) and see how these ellipses compare to the other graphs.

8. ANSWERS

1. Think of the meetings as being one–one so that meetings occur during contacts between pairs of individuals from the two groups. The number of pairs at time t is given by $V(t)K(t)$.
2. Characteristic polynomial $= \lambda^2 - 14\lambda + 49$. $\lambda_1 = \lambda_2 = 7$.
3. $\mathbb{A}^2 - 14\mathbb{A} + 49\mathbb{I} = \begin{pmatrix} 8 & 1 \\ -1 & 6 \end{pmatrix}^2 - 14\begin{pmatrix} 8 & 1 \\ -1 & 6 \end{pmatrix} + 49\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$

5. $\left.\begin{matrix} \mathrm{e}^{2t} = a_0 + 2a_1 \\ t\mathrm{e}^{2t} = a_1 \end{matrix}\right\} \Rightarrow \begin{cases} a_0 = \mathrm{e}^{2t} - 2t\mathrm{e}^{2t} \\ a_1 = t\mathrm{e}^{2t} \end{cases}$

$$\mathrm{e}^{\mathbb{B}t} = a_0\mathbb{I} + a_1\mathbb{B} = \begin{pmatrix} \mathrm{e}^{2t} & 3t\mathrm{e}^{2t} \\ 0 & \mathrm{e}^{2t} \end{pmatrix}$$