

Mathematical Modeling in Population Dynamics: The Case of Single Species Population

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Abstract

The growth and decline of population in nature and the struggle of species to predominate over one another has been a subject of interest dating back through the ages. Applications of simple mathematical concepts to such phenomena were noted centuries ago. This paper discusses mathematical models in biology, their formulation, analysis and interpretation. Much emphasis is placed on how appropriate assumptions simplify the problem, how important variables are identified and how differential equations are tailored to describing the essential features of a continuous process. The thrust of this paper is the application of mathematical models in helping to unravel the underlying mechanisms involved in biological and ecological processes.

Introduction

In contemporary society, almost all domains of human knowledge have to apply mathematical and computational methods. Mathematics is thus “sine quo non” in the area of science and technology. Biology is a natural science that deals with the study of living things and their interactions with their environment. In their study biologists make use of mathematical models containing differential equations which enable them come out with laws regarding the behavior of living things in relation to their environment. The increasing study of realistic mathematical models in ecology (basically the study of the relation between species and their environment) is a reflection of their use in helping to understand the dynamic processes involved in such areas as predator-prey and competition reactions, multi-species societies and ecological control of pests.

The increasing use of mathematics in biology is inevitable as biology becomes more quantitative. Mathematical biology research, which has direct impact on agriculture development, is useful and functional as an academic activity to pursue. From mathematical point of view, the art of good modeling relies on:

First: A sound understanding and appreciation of the biological problem;

Second: A realistic mathematical representation of the important biological phenomena. That is the variables involve must be carefully defined and the governing laws identified. The mathematical model is the some equations representing an idealization of the physical laws, taking into account some simplifying assumptions in order to make the model tractable.

Third: Finding useful solutions. When permitted, exact solutions are usually desired, but in many cases, one must rely on appropriate solutions, using numerical techniques.

Fourth: A biological interpretation of the mathematical results in terms of insights and predictions is then given. That is the solutions obtained should be consistent with physical intuition and evidence.

The Biological Problem

Human activities have brought about drastic changes in the global environment. One grave consequence of this is the increased incidences of biological invasions and growth. In nature, all organisms reproduce, migrate or disperse and go to extinction. These processes can take a diversity of forms as in walking, swimming, flying or being transported by wind or flowing water. Dispersive movements become noticeably active when an offspring leaves its natal sites, or when an organism's habitat deteriorates from overcrowding. Seen from a geological time scale, the geographical distribution of species on the earth's surface has changed each time a large-scale climatic or geomorphological change has taken place (Cox and Moore, 1993). These changes have resulted in geographical separations in a species' range, at times causing further speciation.

Mathematical Formulation

The spatial spread of an invading species can basically be seen as a process in which individuals disperse while multiplying their numbers. One model in which dispersal is formulated as a random diffusion process is the Fisher's equation. Assume that a few individuals invade the center of a two-dimensional homogenous space. If $n(x,t)$ denotes the population density at time t and spatial coordinate $x = (x,y)$, the Fisher's equation in two-dimensional space is expressed as

$$\frac{\partial n}{\partial t} = D \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + (\varepsilon - \mu n)n. \quad (1)$$

The left-hand side of this equation indicates the change in the population density with time, which is caused by random diffusion and local population growth, expressed respectively by the first and second terms on the right-hand-side. D is the diffusion coefficient, which is a measure of how quickly the organisms disperse. The population growth is

formulated by the logistic growth function, where ε is the intrinsic rate of increase and $\mu(\geq 0)$ represents the effect of intraspecific competition on the reproduction rate. Fisher (1937) first proposed this equation as a model in population genetics to describe the process of spatial spread when mutant individuals with higher adaptivity appear in a population.

The Diffusion Model

If a range expands solely by diffusion without population growth, the Fisher equation (1) becomes the so-called diffusion equation in two-dimensional space:

$$\frac{\partial n}{\partial t} = D \left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right). \quad (2)$$

In this model, let the number of individuals that invade the origin at time $t = 0$ be n_0 . Then the initial distribution is given by $n(x,0) = n_0 \delta(x)$.

Here, $\delta(x)$ is the delta function, which indicates that the probability of finding an individual is concentrated in the immediate vicinity of the origin. Under this initial condition, the diffusion equation (2) has a solution:

$$n(x,t) = \frac{n_0}{4\pi Dt} \exp\left(-\frac{x^2 + y^2}{4Dt}\right), \quad (3)$$

which is the two-dimensional Gaussian (or normal) distribution.

Let $r = \sqrt{x^2 + y^2}$, the radial distance from the origin to a point (x,y) , then equation (3) is rewritten as a function of r and t :

$$n(r,t) = \frac{n_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right). \quad (4)$$

Here, $n(r,t)$ expresses the population density of an arbitrary point on a circle of radius r .

Logistic Model

The model above describes the spread of population by diffusion alone. If conversely the population changes by growth (i.e. reproduction), alone without diffusion, equation (1) becomes the so-called logistic equation. Thus we shall have:

$$\frac{dn}{dt} = (\varepsilon - \mu n)n, \quad (5)$$

where $n(r,t)$ is the population density at time t for some fixed location. The expression $(\varepsilon - \mu n)$ represents the per capita growth rate, which declines linearly with the density. The intrinsic rate of increase ε is the growth rate (i.e., difference between the birth rate and death rate) when

density is low, while μn represents the density effect on the reproductive rate. As the density grows, competition for food or space increases, either directly through interactions between individuals or directly by exploitation of resources, resulting in the decline of the rate of reproduction.

Let $k = \frac{\varepsilon}{\mu}$, then equation (5) becomes

$$\frac{dn}{dt} = \varepsilon \left(1 - \frac{n}{k} \right) n, \quad (6)$$

where k is the *carrying capacity* of the environment, which is usually determined by the available sustaining sources. If there is no competition within the species (i.e. $\mu = 0$), the logistic equation becomes the so-called Malthusian equation

$$\frac{dn}{dt} = \varepsilon n, \quad (7)$$

whose solution is given by

$$n(t) = n_0 e^{\varepsilon t}, \quad (8)$$

where n_0 denotes the initial density. When $\varepsilon > 0$, the population increases exponentially without limit. On the other hand when competition exists within the species (i.e., $\mu > 0$), the solution for equation (5) is given as:

$$n(t) = \frac{n_0 k e^{\varepsilon t}}{k + n_0 (e^{\varepsilon t} - 1)}. \quad (9)$$

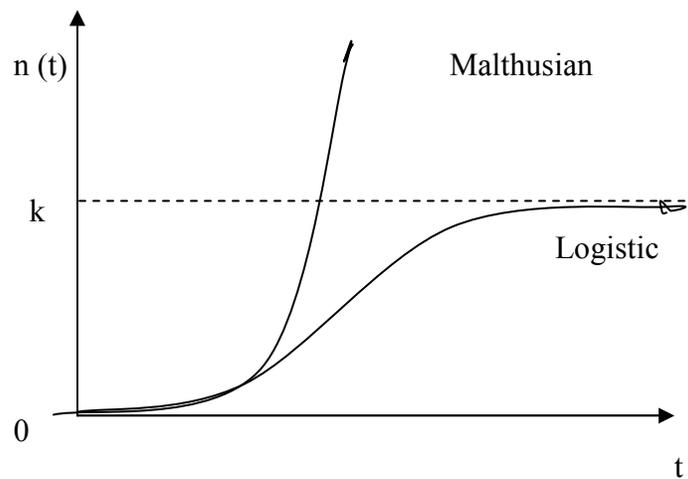


Fig. 1 Solution of Malthusian equation and logistic equation.

Figure 1 shows the change in density over time as given by equations (8) and (9). Initially when the density is low, the curves for both equations increase exponentially. With increasing density, the effect of compition becomes apparent in the logistic equation, with the growth rate slowing down after the density reaches half the carrying capacity, and eventually the density asymptotically approaches the carrying capacity k .

There are two steady states or equilibrium states for equation (6) namely $n = 0$ and $n = k$ where $\frac{dn}{dt} = 0$. The steady state $n = 0$ is unstable since

linearization about it gives $\frac{dn}{dt} \approx \varepsilon n$ and so n grows exponentially from any initial value. The other steady state $n = k$ is stable.

Linearization about it gives

$$\frac{d(n-k)}{dt} \approx -\varepsilon(n-k) \text{ and so } n \rightarrow k \text{ as } t \rightarrow \infty.$$

From equation (6), if $n_0 < k$, $n(t)$ simply increases monotonically to k . In this case there is a qualitative difference depending on whether $n_0 > \frac{k}{2}$ or $n_0 < \frac{k}{2}$.

With $n_0 < \frac{k}{2}$, the form has a typical sigmoid character. If $n_0 > \frac{k}{2}$, $n(t)$ decreases monotonically to k . (See Fig. 2). This implies that the per capita rate is negative. The carrying capacity k determines the size of the stable steady state population while ε is a measure of the rate at which it is reached.

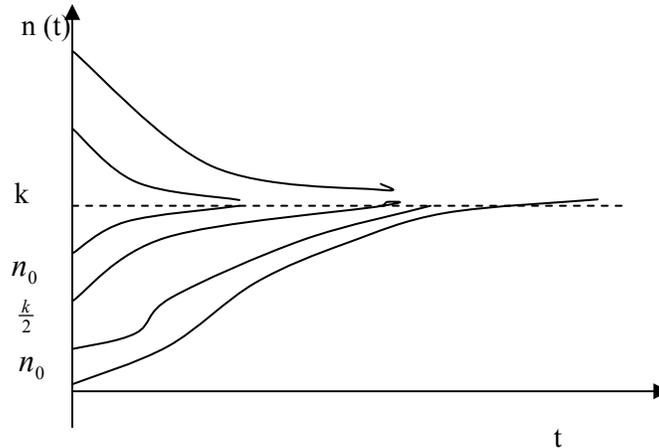


Fig. 2 Logistic population growth.

Generalization

To place both of the above into a somewhat broader context, we proceed from a more general assumption, that for an isolated population (no migration) the rate of growth depend on the population density. Therefore we write that

$$\frac{dn}{dt} = f(n). \quad (10)$$

In this model, we consider the function f as an infinite power (Taylor) series as sufficiently smooth:

$$f(n) = \sum_{i=0}^{\infty} a_i n^i = a_0 + a_1 n + a_2 n^2 + a_3 n^3 + \dots$$

Thus any growth function may be written as a (possibly infinite) polynomial (Lamberson and Biles, 1981). In equation (10) we require that $f(0) = 0$ to dismiss the probability of spontaneous generation, the production of living organisms from inanimate matter (Hutchinson, 1978). In any growth law this is equivalent to

$$\left. \frac{dn}{dt} \right|_{n=0} = f(0) = 0.$$

In this case assume that

$$a_0 = 0$$

$$\begin{aligned} \frac{dn}{dt} &= a_1 n + a_2 n^2 + a_3 n^3 + \dots \\ &= n(a_1 + a_2 n + a_3 n^2 + \dots) = ng(n). \end{aligned}$$

The polynomial $g(n)$ is the intrinsic growth rate of the population. The function $f(n)$ in equation (10) is nonlinear so the steady state solutions \bar{n} are solutions of $f(n) = 0$.

There may be several steady state solutions depending on the form of $f(n)$. The gradient $f'(\bar{n})$ at each steady state then determines its linear stability. These steady states solutions are linearly stable to small perturbations if $f'(\bar{n}) < 0$ and unstable if $f'(\bar{n}) > 0$.

Because of its simple structure and explicitly solution, the logistic equation has been widely employed in theoretical work and in empirical studied to describe the growth of populations both in the field and under laboratory conditions (Brown and Rottry, 1993).

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