

MATHEMATICAL MODELING OF POPULATION GROWTH FOR SINGLE SPECIES

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Abstract

Mathematical models play an important role in studying the change of population qualitatively and quantitatively. It is based on the specific property of population growth. The research results are helpful to predict the developing tendency of role of change of population size. In this article we consider modeling of a single species in cases where spatial variation is not present or is not important. In such case we can simply examine the temporal evolution of the system. The model has been observed to give very well fits to population data in numerous, disparate, scenarios ranging from bacteria and yeast to rats and sheep. The increasing study of realistic and practically useful mathematical models in population biology, whether we are dealing with a human population with or without its age distribution, population of an endangered species, bacterial or viral growth and so on, is a reflection of their use in helping to understand the dynamic processes involved and in making practical predictions. Single species models are of relevance to laboratory studies in particular but in the real world can reflect a telescoping of effects which influence the population dynamic. We start with the simplest exponential model presented by Malthus in 1798 and then the improved model presented by Verhulst (1838, 1845). We also illustrate a particular model "Insect outbreak model: spruce Budworm", which exhibits two positive linearly stable steady state population that for the spruce budworm.

Keywords

Spatial variation; exponential model; logistic growth; carrying capacity; steady state

Introduction

Population biology has involved a long history of mathematicians fascinated by problems associated with the dynamics of population development. Interest was induced by early studies of small mammals and laboratory controlled organisms, since these easily lent themselves to a mathematical formulation. As Maynard Smith (1974) remarks, theory has never played the role in ecology that it has in population genetics, perhaps because there is nothing in ecology comparable to Mendel's law. So when considering the place of mathematics in biology we need to develop models whose design is strongly influenced by considerations of mathematical simplicity. Measuring biological growth has been important in many fields. Many researchers have contributed in developing relevant models : Brody for Brody function, Bertalanffy for Von Bertalanffy function; Richards, France & Thomley for Richard function; Winsor for Gompertz function; Nelder Brown et al Roberton for Logistic function. The growth models have been widely used in many biological growth problems including in animal Sciences and forestry. Mathematical models describing the dynamics of a population can be classified according to whether time considered as a discrete or continuous variable. The growth of a semelparous population reproducing at discrete instants is often most naturally modeled by difference equation. On the other hand if generations overlap and

births are distributed over the year, a continuous model based on differential equations is usually more appropriate. In reality, population dynamics usually involves some continuous processes and some discrete processes. For example, reproduction often occurs in short breeding seasons but competition and death occur continuously. Growth models have been widely studied and applied in many areas specially animals, plant and forestry sciences. A Malthusian growth model sometimes called a simple exponential growth model, is essentially exponential growth based on the idea of the function being proportional to the speed to which the function grows. The model named after Thomas Robert Malthus, who wrote "An Essay on the Principle of population" (1798), one of the earliest and most influential books on population.

Malthusian Population Model

Thomas R. Malthus, in 1798 purposed the mathematical model for the population growth, called Malthusian law of population growth which is widely regarded as the first principle of population dynamics in the field of population ecology. The law is also called the exponential population model.

Let $N(t)$ be the total population of a species at time t . Then

$$N(t+h) = N(t) + \text{births} - \text{deaths} + \text{migration}$$

over the time interval h .

This equation is a conservation equation for the population. In the simplest model we assume that the system is closed so that there is no migration. In any time interval the number of birth/deaths will be (on average) be

No. of birth=(No.of parents) (birth rate) (length of interval)

$$\text{So, } B = N(t) b h$$

$$\text{similarly } D = N(t) d h$$

Where b and d are birth rate and death rate respectively. For closed environment, population migration =0

Then

$$N(t+h)=N(t)+N(t) b h- N(t) d h$$

$$\frac{N(t+h) - N(t)}{h} = (b - d)N(t)$$

Now let $h \rightarrow 0$ we get

$$\frac{dN}{dt} = (b - d)N(t)$$

$$\frac{dN}{dt} = rN(t)$$

Where $r=b-d$ is called growth rate. The above ODE is separable so for $N \neq 0$

$$\int \frac{1}{N} dN = r \int dt$$

$$\log N = rt + C$$

Where C is an arbitrary constant. Using initial condition, $N(0) = N_0$ i.e. the initial population size is N_0

$$\log N_0 = 0 + C$$

$$C = \log N_0$$

$$\text{So, } \log N = r t + \log N_0$$

$$\log \left(\frac{N}{N_0} \right) = r t$$

$$\frac{N}{N_0} = e^{rt}$$

$$N(t) = N_0 e^{rt} \dots\dots\dots(1)$$

This is the Malthus model (1798). This model indicates that the population of any species depends on two parameters; the growth rate r and the initial population size N_0 . The dependence on parameter of the solution of the exponential model is shown in figure 1

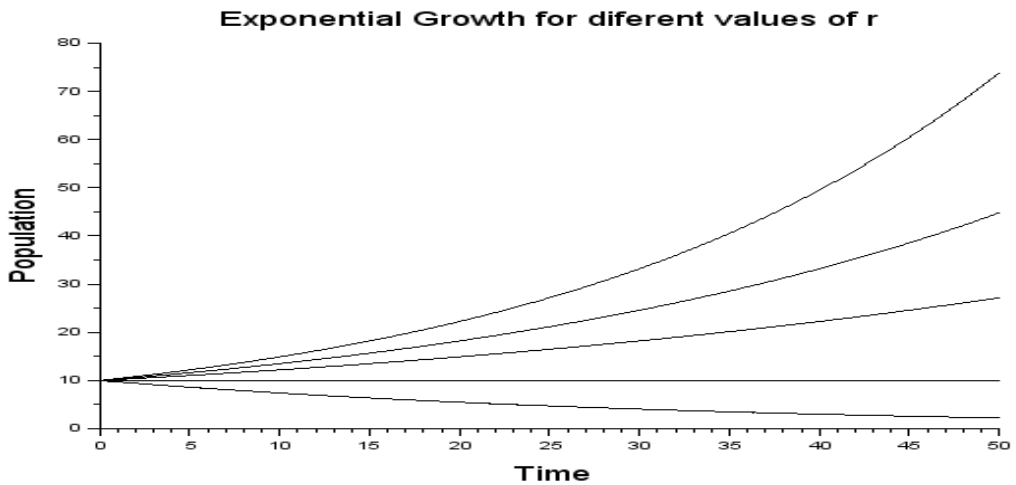


Fig.1 Dependence on parameters of solution of the exponential model

The Malthus model seems to be unrealistic. However, if we consider the past and predicted growth estimates for the total world population from 17th to 21st centuries it is perhaps less unrealistic since 1900 it has grown exponentially. The model says that if $r > 0$ ($b > d$) the population grows exponentially without limit, and if $r < 0$ it decreases to 0. The latter is all too credible nowadays for nonhuman species, but even for humans the former is not. A more plausible model has to put limits on growth.

The Logistic Model

Malthus model is very simple model for population evolution in which the growth rate was independent of the size of the population. One noticeable feature of the exponential model is that when r is positive, the population always grows larger and larger without any finite limit as seen in figure 1. This kind of

grow may be a good model for a new population of bacteria in a beaker, but it does not hold for a long time. It is easy to see the equation would imply a population of bacteria that ultimately outgrew the beaker and even outgrew the planet earth, since the mass of bacteria would ultimately exceed the mass of earth. Such a model is therefore absurd to model a system for a long time. The fundamental difficulty is that the model ignores the fact that there are limits to resources needed for the population to grow. It ignores the need for food, oxygen, and space; and it ignores the accumulation of waste products that inevitably arise.

The Malthus model only has a hope of being successful while the resources available to the population are unlimited. If these resources were finite then there is a maximum population size that can be supported by the environment.

This maximum population is called the carrying capacity. In these circumstances, the growth rate must depend on the size of the population and in particular it must approach zero as the population approaches the carrying capacity. This variation of the growth rate $r(N)$ is illustrated in the figure 2 with maximum population. The logistic model assumes that the growth rate is $r\left(1 - \frac{N}{K}\right)$. The logistic model is developed for population growth as

$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N$$

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \dots\dots\dots(2)$$

Where r the linear growth rate and K , the carrying capacity, are positive constants. This model was first studied by, Belgian Mathematician Pierre Francois Verhulst in the middle of the 19th Century. In this model, like exponential model, population size is dependent on births and death and there is nothing to account for migration into or out of the population.

In this model the per capita birth rate is

$r\left(1 - \frac{N}{K}\right)$ i.e. $\frac{1}{N} \frac{dN}{dt}$ and dependent on N . The carrying capacity K of environment is usually determined by the available sustaining resources.

There are two steady states or equilibrium states for Equation 2, namely $N=0$ and

$$N=K \text{ where } \frac{dN}{dt} = 0.$$

$N=0$ is unstable since linearization

about it yields $\frac{dN}{dt} \approx rN$, and so N grows exponentially from any small initial value. The second equilibrium $N=K$ is stable. Linearization about it gives

$$\frac{d(N-K)}{dt} \approx -r(N-K) \text{ and so } N \rightarrow K \text{ as } t \rightarrow \infty.$$

The carrying capacity K determines the size of the stable steady state population while r is a measure of the rate which it is reached. That is, it is a measure of the dynamics; we could incorporate it in the time by a transformation from r to

rt . Thus $\frac{1}{r}$ is a representative timescale of the response of the model to any change in the population.

The logistic model is a separable first order ODE which may be rewritten as

$$K \frac{dN}{dt} = r(K - N)N$$

The two particular solutions are $N(t)=0$ and $N(t)=K$ for all t corresponding to equilibrium points, and for $N(t) \neq 0, K$ we have

$$\int \frac{K}{(K-N)N} dN = \int r dt$$

$$\Rightarrow \int \frac{(K-N)+N}{(K-N)N} dN = rt + C$$

$$\Rightarrow \int \left[\frac{1}{N} + \frac{1}{(K-N)} \right] dN = rt + C$$

$$\Rightarrow \log|N| - \log|K - N| = rt + C$$

$$\Rightarrow \log \left| \frac{N}{K-N} \right| = rt + C$$

$$\Rightarrow \left| \frac{N}{K-N} \right| = e^{rt+C}$$

$$\Rightarrow \left| \frac{N}{K-N} \right| = e^{rt} \cdot e^C$$

Using initial condition $N(0)=N_0$, we get

$$\left| \frac{N_0}{K-N_0} \right| = e^C$$

$$\text{So, } \left| \frac{N}{K-N} \right| = \left| \frac{N_0}{K-N_0} \right| e^{rt}$$

The orbit of any $N_0 \neq 0$ or K cannot include 0 or K . So, neither N or $K-N$ can change sign

on an orbit and hence the sign of $\frac{N}{K-N}$ is the same for all t . Thus, $\frac{N}{K-N} = \frac{N_0}{K-N_0} e^{rt}$

$$N = \frac{K \frac{N_0}{K-N_0} e^{rt}}{1 + \frac{N_0}{K-N_0} e^{rt}}$$

$$\Rightarrow N = \frac{KN_0 e^{rt}}{K - N_0 + N_0 e^{rt}}$$

Hence, $N(t) = \frac{KN_0}{(K-N_0)e^{-rt} + N_0}$

These solutions depend on two parameters, the initial population N_0 and the linear growth rate r .

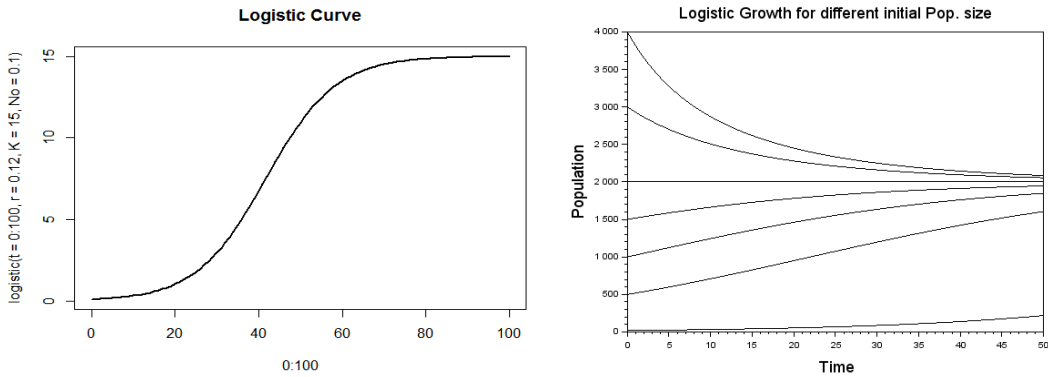


Fig 2. (a) Growth of population in Logistic model. Population cannot grow to infinity but bounded by an upper limit (carrying capacity). (b) Logistic curves, varying the initial population with the fixed $K=2000$ and constant growth rate.

Insect Outbreak Model: Spruce Budworm

The Spruce Budworm is one of the most destructive native insect in the northern spruce and fir forests of the Eastern United States and Canada. Majority of the time, the number of budworms remains at a constant low level. However, every few decades, the population, of budworms increases to huge population, depleting the forest and destroying many trees, before dropping back down to its normal population level. Consider the budworm population dynamics to be modeled by the logistic form equation. If N represents the budworm density, in the absence of predation then

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right)$$

Here r_B is the linear birth rate of the budworm and K_B the carrying capacity

which is assumed to depend upon the amount of foliage (food) available on the tree. The effect of predation is included by subtracting a term $g(N)$. Then the model is modified as

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right) - g(N) \dots (3)$$

The term $g(N)$ represents predation, generally by birds. The qualitative form of the equation is same as in the figure 2 (a). Predation usually saturates for large enough N . There is an approximate threshold value N_c , below which the predation is small while above it predation is close to its saturation value; such a functional form is like a switch with N_c being the critical switch value. For small population densities N , the birds tend to seek food elsewhere and so the predation term $g(N)$ drops, more rapidly, as $N \rightarrow 0$, than a linear rate proportional to N . $g(N)$ should approach

an upper limit β as $N \rightarrow \infty$. This limit β may depend upon the slow variables (i.e., the forest variables), but that possibility is deferred. There is also a decrease in the effectiveness of predation at slow budworm densities. There is a decrease in the effectiveness of predation at low budworm densities. This is a characteristic of a number of predators and arises in birds in part because of the effects of learning. Birds have a variety of alternative foods, and when one of them is scarce, that particular prey item is encountered only incidentally. As the item becomes more common, however, the birds begin to associate reward with that prey and they begin to search selectively for it. Thus, we may assume that $g(N)$ vanishes quadratically as $N \rightarrow 0$. A convenient form of $g(N)$ which has the properties of saturation at a level β and which vanishes like N^2 is

$$g(N) = \beta \frac{N^2}{\alpha^2 + N^2} \dots \dots \dots (4)$$

The parameter α in the equation (4) determines the scale of budworm densities at which saturation begins to take place. The addition of the vertebrate predation to equation (3) thus produces a total equation for the rate of change of N :

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right) - \beta \frac{N^2}{\alpha^2 + N^2}$$

This equation has four parameters, r_B , K_B , β and α , with β and α having the same dimension as N , r_B has dimension $(\text{time})^{-1}$ and β has the dimension of

$N(\text{time})^{-1}$. α is a measure of threshold where the predation is ‘switched on’. If α is small the ‘threshold’ is small, but the effect is just as dramatic.

Discussion

When the population size is very large and birth rate take place continuously then the population growth may be assumed to be continuous function of time. In this study, the commonly used biological growth models Malthus and Logistic model are considered and explicitly show that each is a solution of the rate-state ordinary differential equation $f'(t) = rf(t)$. The model is implemented for the cases of Spruce budworm population growth. It is observed that both the logistic and exponential models of continuous growth share the assumption of absence of migration, genetic variation or age structure in a given population. In addition logistic model assumes constant carrying capacity, limited recourses and density dependent growth. This means that when an individual is added to the population, the per capita growth rate decreases immediately. But this is not the case in general. In many populations, the density dependent response assumes some time lags. Individual does not immediately adjust into their growth and reproduction. Seasonal availability of resources and age structure can also cause time lag in population growth. These delays can affect population dynamics of a given species significantly. There must be more study and research on the effect of such time delays.

Conclusion

Some theoretical mathematical aspects of well known continuous population growth models are studied.

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The idea is implemented for the case that spruce budworm follows Logistic model. The respective predator model is analyzed.