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An Investigation of the Logistic Model of Population Growth

Graham K. Winley

Department of Information Technology, Faculty of Science and Technology, Assumption University, Bangkok, 10240, Thailand.
e-mail: gkwinley@scitech.au.edu

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Abstract

This article examines the popular logistic model of growth from three perspectives: its sensitivity to initial conditions; its relationship to analogous difference equation models; and the formulation of stochastic models of population growth where the mean population size satisfies the logistic relationship. The results indicate that the appealing sigmoid logistic curve is sensitive to initial conditions and care must be exercised in developing difference equation models which display the same appealing long term behavior as the logistic growth curve. It is shown that although the logistic model is appealing in terms of its simplicity its realism is questionable in terms of the degree to which it reflects demographically accepted assumptions about the probabilities of individual births and deaths in the growth of a population. In particular this lack of realism has serious implications for the computer simulation of stochastic birth and death processes where the mean population size satisfies the logistic.

Keywords: difference equations, logistic growth, stochastic models.

1. Introduction

It is common in many fields of study to use a deterministic model of the values of a variable of interest $N(t)$ using an autonomous differential equation of the form,

$$\frac{dN(t)}{dt} = F(N(t)), \quad (1)$$

where $N(t)$ is a continuous real-valued function of time t . In the cases where realistically $N(t)$ is an integer-valued function of t (1) is considered to be a model of the mean value of the integer-valued process. Assuming that the coefficient of variation of that process is small, the continuous model in (1) is used to represent $N(t)$. If $\frac{1}{N(t)} \frac{dN(t)}{dt}$ is constant, then the growth in $N(t)$ is said to be density independent and otherwise it is density dependent.

In many situations, experimental values of $N(t)$ exhibit an S-shaped graphical representation and although many possible functions $F(N(t))$ may be used in (1) to produce models with sigmoid growth curves, the Verhulst [1] logistic model represented by the logistics differential equation in (2) is certainly one of the most popular [2],

$$\frac{dN(t)}{dt} = \lambda [K - N(t)] N(t), \quad (2)$$

where normally $N(0) = N_0 < K$, $\lambda > 0$, K is the carrying capacity which is an upper bound on the value of $N(t)$ and it reflects environmental conditions that may limit the population size (e.g. the food supply), and the product λK is referred to as the intrinsic rate of increase. The model in (2) has been studied and used extensively over a long period of time by researchers in demography, the biological sciences, ecology, genetics, applied statistics (logistic regression), software metrics, and many other fields of study [3- 11].

However, the popularity of the logistic model is probably based more on its simplicity than its realism. Some of its features and its relationship to analogous models using difference equations and stochastic growth models are often not well understood by researchers who use the model simply on the basis of its appealing sigmoid growth curve. In particular, as early as 1940 Feller [3] warned against blind faith in the use of the logistic. He considered S-shaped data from an experiment and then selected several S-shaped functions at random. Applying the usual criteria for best fit, he ranked the various functions. The results showed that the logistic fitted the data worse than any of the other selected functions and he concluded that the recorded agreement between the logistic and actually observed phenomena of growth does not produce any significant new evidence in support of the logistic beyond the plausibility of its deduction.

The purpose of this article is to: (a) examine the sensitivity of the solution to the logistic differential equation in (2) under various initial conditions (section 2); (b) examine the formulation and features of models using difference equations which are considered to be analogous to the solution to the logistic differential equation (2) (section 3); and (c) investigate stochastic birth and death processes which have mean behavior represented by the logistic differential equation in (2) (section 4). Throughout the article, an attempt has been made to select references which direct the reader to primary sources and consequently provide the interested reader with an historical perspective on the topic.

2. The Graphical Representation of the Logistic Model

The solution to the differential equation (2) if $N(0) = N_0$ and $\lambda > 0$ is:

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0) \exp(-\lambda K t)}, \quad (3)$$

and the graphical representation of $N(t)$ for $K > N_0 > 0$ is the usual S-shaped curve as shown in Figure 1.

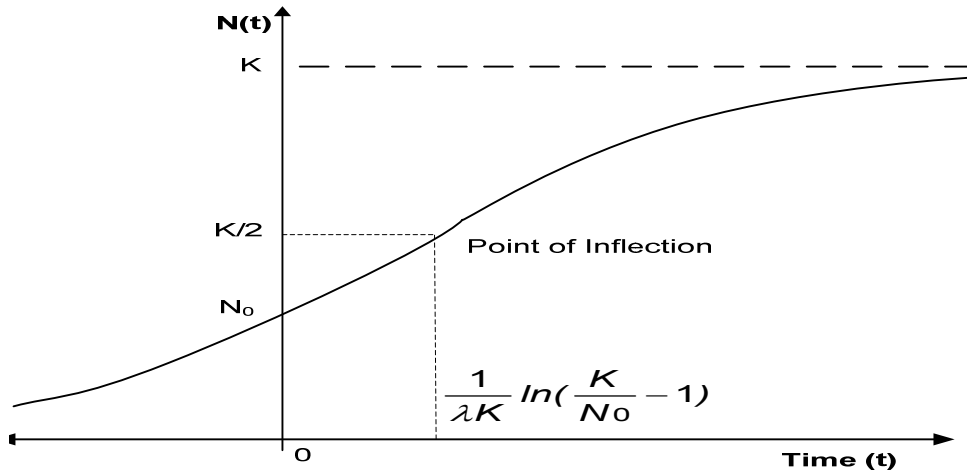


Figure 1. The S-shaped logistic curve.

In Figure.1, the point of inflection is in the first quadrant if $K > 2N_0$, the second quadrant if $N_0 < K < 2N_0$, and at $(0, N_0)$ if $K = 2N_0$. The slope of the tangent at the point of inflection is $\lambda K^2/4$. The curve approaches the t -axis asymptotically as $t \rightarrow -\infty$ and it approaches $N(t) = K$ asymptotically as $t \rightarrow \infty$. The curve is approximately exponential for values of $t < \frac{1}{\lambda K} \ln\left(\frac{K}{N_0} - 1\right)$ when the growth is in a transient stage.

However, if the initial conditions are $N(0) = N_0 > K > 0$ and $\lambda > 0$, then, the logistic function has a less well known form as shown in Figure 2 where the solution curve is no longer S-shaped.

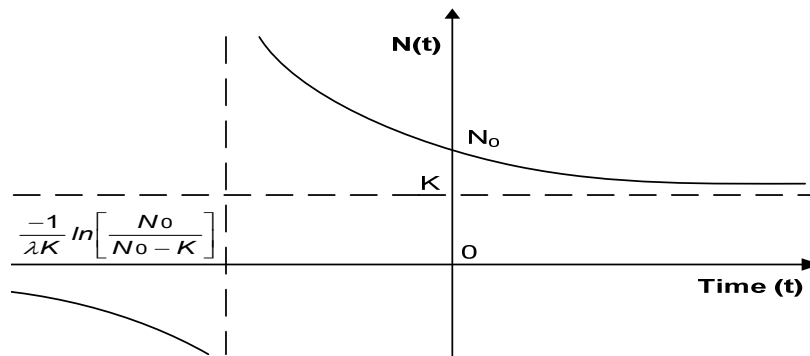


Figure 2. Non S-shaped logistic curve.

3. Difference Equations and the Logistic

Difference equations are relations between the values of an unknown function at a discrete pattern of values of the argument, such as $t - \tau$, $t - 2\tau$, $t - 3\tau$, ... where τ is a fixed known number and the argument t varies continuously. Recurrence relations, on the other hand, while defined in the same way, do not allow t to vary continuously and in fact t will take on only equally spaced discrete values which are multiples of τ . However, in accordance with common usage, the terms difference equation and recurrence relation are used interchangeably.

There is a considerable literature on the relationship between differential equations and difference equations [12 - 14]. Two fundamental questions arise: (a) *Starting with a differential equation how can one find the difference equation with the "same" solutions as the differential equation?* and (b) *In what sense are the solutions the same?* In what follows, these questions are examined using two different methods that are commonly used to develop a difference equation analogous to the solution in (3) for the logistic differential equation (2).

Method 1

For the logistic differential equation (2) a difference equation can be formulated where solutions at each time t have the same values as those obtained from the solution

in (3). Thus from (3) with $t = t + \tau$, $N(t + \tau) = \frac{N_0 K}{N_0 + (K - N_0) \exp[-\lambda K(t + \tau)]}$ and since

$\exp(-\lambda K t) = \frac{N_0(K - N(t))}{N(t)(K - N_0)}$ the required difference equation

is $N(t + \tau) = \frac{KN(t) \exp(\lambda \tau K)}{K + [\exp(\lambda \tau K) - 1]N(t)}$, which has the solution,

$$N(n\tau) = \frac{N_0 K \exp(n\lambda \tau K)}{K + [\exp(n\lambda \tau K) - 1]N_0}, \text{ for } n = 1, 2, 3, \dots \quad (4)$$

It is noted that making the substitution $n = t / \tau$ in (4) and taking the limit of $N(n\tau)$ as $\tau \rightarrow 0$ reproduces the solution in (3).

Method 2

A different approach to the development of a difference equation analogous to the logistic is proposed by May [12] and uses $\frac{dN(t)}{dt} = \lim_{\tau \rightarrow 0} \left[\frac{N(t + \tau) - N(t)}{\tau} \right]$, which when applied to (2) gives the difference equation,

$$N(t + \tau) = [1 + \tau \lambda K - \tau \lambda N(t)]N(t). \quad (5)$$

Analysis of the behavior of $N(t + \tau)$ in (5) produces the following three sets of results (*R1*, *R2*, and *R3*) which are then used to compare the behavior of the difference equation (5) with the solution in (3) to the logistic differential equation.

R1. If $\lambda K \tau < 1$ then: **(a)** $N(t) < N(t + \tau) < K$ for $t \geq 0$ when $0 < N(t) < K < 1/(\lambda \tau)$; **(b)** $N(t) > N(t + \tau) > K$ for $t \geq 0$ when $0 < K < N(t) < 1/(\lambda \tau)$; and **(c)** $N(t) > K > N(t + \tau)$ for $t \geq 0$ when $0 < K < 1/(\lambda \tau) < N(t)$.

R2. If $\lambda \tau K > 1$ then: **(a)** $N(t + \tau) > K > N(t)$ for $t \geq 0$ when $0 < 1/(\lambda \tau) < N(t) < K$; **(b)** $N(t + \tau) < K < N(t)$ for $t \geq 0$ when $0 < 1/(\lambda \tau) < K < N(t)$; and **(c)** $N(t) < (\lambda \tau K)N(t) < N(t + \tau) < K$ for $t \geq 0$ when $0 < N(t) < 1/(\lambda \tau) < K$.

R3. From *R2(c)* it is seen that if $0 < N(t + \tau) < 1/(\lambda \tau) < K$ then $K > N(t + 2\tau) > (\lambda \tau K)N(t + \tau) > (\lambda \tau K)^2 N(t)$ and if this pattern continues then $N(t + n\tau) > (\lambda \tau K)^n N(t) > N(t)$ and $(\lambda \tau K)^n N(t) > 1/(\lambda \tau)$ for an integer $n > \frac{-\ln(\lambda \tau N(t))}{\ln(\lambda \tau K)}$. Under these conditions $K > N(t + n\tau) > 1/(\lambda \tau)$ and the subsequent behavior of $N(t)$ is described by *R2(a)* and *R2(b)*.

The proof of *R1(a)* is provided in order to illustrate the manner in which the reader may construct proofs for the other results.

Proof for R1(a): If $0 < N(t) < K < 1/(\lambda \tau)$ then $0 < \lambda \tau N(t) < \lambda \tau K < 1 = \frac{[K - N(t)]}{[K - N(t)]}$, and

so $0 < \lambda \tau N(t)[K - N(t)] < K - N(t)$ and adding $N(t)$ throughout gives $N(t) < N(t + \tau) < K$ as stated. ■

From R1(a) and R1(c) it is seen that $N(\tau) < N(2\tau) < N(3\tau) < \dots < K$, which resembles the behavior of $N(t)$ in (3). However, under the conditions in R1(b) one can see that $N_0 > N(\tau) > N(2\tau) > N(3\tau) > \dots > K$, and from R2(a), R2(b), R2(c) and R3 it is seen that regardless of the positive value of N_0 the values of $N(t)$ eventually oscillate asymptotically around the value of K . Consequently, the difference equation (5) exhibits very different behavior to the difference equation (4) which exhibits exact agreement with the solution in (3). In fact, there is no differential equation of the form in (1) which has a solution that exhibits exact agreement with the difference equation (5). This follows from the result that $N(t + \tau)$ in (5) does not satisfy the group property which requires that, for $t_2 > t_1 > 0$, $[1 + t_2\lambda K - t_2\lambda N_0]N_0 = [1 + (t_2 - t_1)\lambda K - (t_2 - t_1)\lambda N(t_1)]N(t_1)$ where $N(t_1) = [1 + t_1\lambda K - t_1\lambda N_0]N_0$ ([14]).

4. Stochastic Models of Population Growth and the Logistic

May [12] refers to stochastic features arising from the fact that the population size is fundamentally discrete as demographic stochasticity and these features are incorporated into a model by considering the probabilities that an individual will give birth or die in the next time interval Δt . By analyzing the birth and death process it is possible to either make a probability statement about the population size at time t , which is represented by the random variable $N(t)$, or at least determine the mean population size $M(t) = E[N(t)]$ and the variance at that time. In a different approach Levins [15] introduces stochasticity into the model parameters in order to incorporate stochastic elements which reflect a fluctuating environment. With this approach the analysis of the probability distribution of population size normally uses the Fokker-Planck diffusion equation where it is assumed that the variability in the environmental parameter is white noise [12].

Here the concern is only with demographic stochasticity which involves a system of differential equations describing the transition probabilities associated with changes in the value of the random variable $N(t)$. Suppose that: $P_k(t) = P[N(t) = k \mid N(0) = N_0]$ is the probability at time t that the population size is k given that the initial size of the population is N_0 ; $B_k\Delta t + o(\Delta t)$ is the probability at time t that in a population of size k there will be a single birth in the next time interval Δt ; $D_k\Delta t + o(\Delta t)$ is the probability at time t that in a population of size k there will be a single death in the next time interval Δt ;

and $o(y)$ is any function such that $o(y)/y \rightarrow 0$ as $y \rightarrow 0$. B_k and D_k are referred to as the infinitesimal birth and death rates, respectively, and if they are functions of t then they are said to be time inhomogeneous and otherwise they are time homogeneous. It follows that $P_k(t + \Delta t) = B_{k-1}P_{k-1}(t)\Delta t + D_{k+1}P_{k+1}(t)\Delta t + (1 - (B_k + D_k)\Delta t)P_k(t) + o(\Delta t)$ and subtracting $P_k(t)$ from both sides, dividing through by Δt , and then taking the limit as Δt approaches 0 gives,

$$\frac{dP_k(t)}{dt} = \begin{cases} D_1P_1(t), & k = 0, \\ B_{k-1}P_{k-1}(t) + D_{k+1}P_{k+1}(t) - (B_k + D_k)P_k(t), & k = 1, 2, 3, \dots \end{cases} \quad (6)$$

The following assumptions are made concerning a single individual in the population: $b(t)\Delta t + o(\Delta t)$ is the probability of a single individual producing a single birth in the time interval $(t, t + \Delta t)$; $d(t)\Delta t + o(\Delta t)$ is the probability of a single individual dying in the time interval $(t, t + \Delta t)$; and births and deaths of individuals are independent. This means that in (6) $B_k = kb(t)$ and $D_k = kd(t)$ and so (6) becomes,

$$\frac{dP_k(t)}{dt} = \begin{cases} d(t)P_1(t), & k = 0, \\ (k-1)b(t)P_{k-1}(t) + (k+1)d(t)P_{k+1}(t) - k(b(t) + d(t))P_k(t), & k = 1, 2, 3, \dots \end{cases} \quad (7)$$

Multiplying both sides of (7) by k and summing over the values of k gives,

$$\frac{dM(t)}{dt} = \sum_{k=0}^{\infty} k \frac{dP_k(t)}{dt} = [b(t) - d(t)]M(t), \quad (8)$$

where, $M(t) = \sum_{k=0}^{\infty} kP_k(t) = E[N(t)]$. Also, if K is the saturation level for this birth and

death process then it is assumed that $b(t)$ and $d(t)$ decrease and increase, respectively, to the same limiting value.

Now we investigate choices for $b(t)$ and $d(t)$ which may result in $M(t)$ satisfying the logistic differential equation (2).

Choice 1

Suppose that,

$$\begin{aligned} b(t) &= b - \gamma_1 \lambda M(t), \\ d(t) &= d + \gamma_2 \lambda M(t), \end{aligned} \quad (9)$$

where $b - d = \lambda K$.

If $\gamma_1 + \gamma_2 = 1$ then substituting (9) in (8) gives $\frac{dM(t)}{dt} = [b(t) - d(t)]M(t) =$

$\lambda[K - M(t)]M(t)$ and as hoped $M(t)$ satisfies the logistic differential equation (2).

Also, provided $1 \geq \gamma_1 \geq 0$, then $b(t)$ and $d(t)$ have the desired behavior of decreasing and increasing, respectively, to the same limiting value $b(1 - \gamma_1) + \gamma_1 d$.

It is noted that the $b(t)$ and $d(t)$ in (9) are not the only choices that result in $M(t)$ having logistic behavior but in all such cases $b(t)$ and $d(t)$ will depend on $M(t)$ and this illustrates a problem which is discussed following the consideration of a different choice for $b(t)$ and $d(t)$.

Choice 2

The stochastic model that is usually regarded as the analogue of the logistic is described by Pielou [8] and uses,

$$\begin{aligned} b(t) &= b - \gamma_1 \lambda k, \\ d(t) &= d + (1 - \gamma_1) \lambda k, \end{aligned} \quad (10)$$

where, as in (9), $b - d = \lambda K$ and if $1 \geq \gamma_1 \geq 0$ then $b(t)$ and $d(t)$ have same desired behavior.

This means that the probabilities of a birth and death for a single individual in the time interval t to $t + \Delta t$, in a population of size k at time t , depend on the actual population size k rather than the mean population size $M(t)$ as is the case in (9). This is a demographically plausible assumption. However, substituting (10) in (7), multiplying by k , and summing over k gives,

$$\frac{dM(t)}{dt} = \lambda \left[K - \frac{S(t)}{M(t)} \right] M(t), \quad (11)$$

where the second moment $S(t) = E[N^2(t)] > \{E[N(t)]\}^2 = M^2(t)$. Consequently, from (11)

under the demographically plausible assumptions in (10) $\frac{dM(t)}{dt} < \lambda[K - M(t)]M(t)$ and

$M(t)$ does not satisfy the logistic differential equation (2). Furthermore, it is not possible to choose any $b(t)$ and $d(t)$ which depend on the actual size of the population k at time t and have the mean population size $M(t)$ satisfy the logistic differential equation (2).

If it is assumed that $S(t) = M^2(t)$ then the differential equation (11) for $M(t)$ is the logistic differential equation (2). However, this assumption means that the variance is zero and so the process is no longer stochastic but is deterministic. This correspondence is the reason why the stochastic birth and death process using (10) is regarded as the stochastic analogue of the deterministic logistic but it is clear that the analogy is not based on exact agreement between the mean of the stochastic process and the solution to the logistic differential equation (2). Although the assumption in (10) that $b(t)$ and $d(t)$ are dependent on the actual population size k at time t rather than the mean population size $M(t)$ is demographically plausible it does not result in the mean of the stochastic process having exact logistic behavior. Consequently, the logistic model of population growth is not supported by an underlying stochastic birth and death process which is

based on demographically plausible assumptions about the probabilities of a birth or death in the population.

Conclusions Regarding Stochastic Models with Mean Logistic Behavior

Stochastic models have been described in (9) that have mean behavior corresponding to the logistic and these appear to be reasonable models since they require that the individual birth rate is initially greater than the death rate and that the birth rate decreases while the death rate increases over time to the same limiting value. These models assume that the density dependent effect is based on the mean population size $M(t)$ rather than the actual population size k at time t . Any attempt to take account of the actual population size k in determining the transition probabilities results in the introduction of the second moment $S(t)$ in the differential equation for $M(t)$ and consequently the loss of the logistic relationship. This means that the logistic growth process cannot be simulated on a computer relying only on information contained in the simulated population level. Instead, in order to determine the probability of a birth or death in the population in the next time interval the mean size of the population must be calculated. This is not demographically plausible since it implies that for the stochastic process to have mean logistic behavior regardless of the actual size of the population at time t the probability of an individual dying is the same for every member of the population and the same implication applies to births. It is well accepted by demographers that the probabilities of births and deaths are proportional to the actual population size k at time t and not the mean value of the size of the population $M(t)$. Consequently, in order for the stochastic birth and death process to have a mean population size which satisfies the logistic equation requires individual behavior that is not demographically acceptable.

5. Conclusion

This article has investigated three aspects concerning the popular logistic model of growth: (a) the features of the solution to the logistic differential equation for various initial conditions; (b) methods for the formulation of difference equations which are considered to be analogous to the logistic model; and (c) the development of stochastic models which have mean logistic behavior.

It is shown that the appealing S-shaped graphical features of the logistic model are sensitive to initial conditions. In particular, the S-shaped graphical representation of the logistic is lost if the initial population size exceeds the carrying capacity.

Two different methods for constructing difference equations analogous to the logistic were considered. The first method produced a difference equation model which agreed exactly with the solution to the logistic differential equation. However, the second method, despite the plausibility of its formulation, produced a difference equation which under certain conditions has very different long term behavior to the solution of the logistic differential equation. Consequently, a clear warning is sounded for those interested in formulating difference equations with logistic behavior since although such models may realistically compute discrete integer values for the population size they may exhibit long term behavior that is not commensurate with the appealing long term behavior of the logistic.

It is shown that it is possible to construct stochastic models with mean logistic behavior and this was done in the context of stochastic models of birth and death processes. It was demonstrated that in order to construct stochastic models with mean logistic behavior it is necessary to have the birth and death rates for individuals in the population dependent on the mean size of the population and that this requirement is demographically unacceptable and in particular poses problems for computer simulations of the process. On the other hand, if these rates are dependent on the actual population size, which is more realistic, then the mean size of the population does not satisfy the logistic equation. Thus stochastic birth and death processes which incorporate demographically acceptable assumptions about the probabilities of individual births and deaths do not have mean logistic behavior.

The results indicate that although, subject to appropriate initial conditions, the logistic model is simple and intuitively appealing its appeal is based more on its simplicity than its plausibility as it does not reflect demographically accepted assumptions about the probabilities of individual births and deaths in a population. In addition, care must be taken in constructing difference equations which are expected to have logistic behavior. It is hoped that these results will guide researchers to a deeper understanding of the commonly used logistic model of growth.

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