

Non-autonomous Logistic Equations as Models of Populations in a Deteriorating Environment

T. G. HALLAM AND C. E. CLARK

Department of Mathematics and Program in Ecology, University of Tennessee, Knoxville, Tennessee 37916, U.S.A.

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The non-autonomous logistic equation

$$\frac{dx(t)}{dt} = r(t)x(t) \left[1 - \frac{x(t)}{K(t)} \right]$$

is studied under conditions that include an environment which is completely deteriorating. In this setting, when the population's growth rate, r , is large on the average, solutions track the environment with a consequent extinction of the population. However, when both r and rK^{-1} are small in the sense that they are in $L^1[0, \infty)$ then an asymptotic equivalence, where all solutions tend to positive limits as t approaches infinity, results and the population is persistent, independent of initial density. The asymptotic equivalence produces an unreasonable overshoot of carrying capacity which leads to concern about employing the logistic equation in the above form as a population model when growth rates are close to zero.

A re-interpretation of the parameters of the logistic equation leads to the alternative logistic formulation

$$\frac{dx(t)}{dt} = x(t) \left[r(t) - \frac{c}{B(t)}x(t) \right], \quad (c > 0).$$

A biological interpretation of the parameters is presented and this equation is compared with the classical logistic model in the case where the parameters are constant. If the alternative logistic model is applied in a situation with time-varying parameters, then a deteriorating environment always leads to extinction of the population regardless of the behavior of r . Similarly, a growth rate which is small on the average results in extinction regardless of the behavior of B . Furthermore, if r and B have limiting values as t approaches infinity then so does x and the terminal value of x is equal to the terminal value of the carrying capacity of the population. In general, the alternative formulation seems to be the more reasonable model in situations where perturbations lead to severe decreases in environmental quality and growth rates.

1. Introduction

When the logistic equation is employed as a model for population growth, it is most often written in the form

$$\frac{dx(t)}{dt} = rx(t) \left[1 - \frac{x(t)}{K} \right]. \quad (1)$$

The intrinsic growth parameter r reflects biological characteristics specific to the population while the carrying capacity K represents the totality of all environmental attributes that affect individuals of the population.

Allowing r and/or K to be time dependent is, theoretically, a way of modeling environmental fluctuations, changes in growth rates, and in general, effects of perturbation of the system. All populations are affected to some extent by perturbation. Depending upon one's perspective, perturbations can be regarded as endogenous or exogenous inputs to the system. Often these stresses are a regulating factor for many natural populations (Wellington, 1952; Vogl, 1974; Cooper, 1961; Kozlowski & Ahlgren, 1974).

Examples of perturbations that can result in a deteriorating environment and decreased growth rates occur when environmental toxicants are introduced into a system. The stress effects of toxicants take many forms including changes in fecundity, growth, mortality (Sick & Windom, 1975; Sorenson, 1976; Reeve, Gambel & Walter, 1977; Koeller & Wallace, 1977) as well as morphological, physiological and behavioral characteristics of the population (Tompkins & Blinn, 1976; Bachenheimer & Bennett, 1961; Kania & O'Hara, 1974). The traditional approach to the application of the logistic growth model to situations with changing levels of environmental support and changes in the intrinsic growth rate has been merely to modify equation (1) to allow the parameters r and K to vary with time. Decreased levels of environmental support are reflected in equation (1) by a decrease in K and changes in the intrinsic fecundity and mortality by changes in r , (e.g. Coleman, 1979; Coleman, Hsieh & Knowles, 1979; Keister & Barakat, 1974; May, 1976). In such situations, equation (1) is replaced by

$$\frac{dx(t)}{dt} = r(t)x(t) \left[1 - \frac{x(t)}{K(t)} \right]. \quad (2)$$

This article examines the biological consequences of the application of equation (2) in the context of a theoretical population in a completely deteriorating environment (section 2). The paradoxical nature of these results (from a biological point of view) forces a re-evaluation of the validity of equation (2) as a model for population dynamics with time-varying

parameters. In section 3, an alternative approach is suggested which, although still a logistic model, leads to results which are biologically tenable.

2. The Logistic Equation With Time-varying Parameters

In this section equation (2) is used to model the survival of a theoretical population in an environment that is allowed to completely deteriorate. This setting might arise as a consequence of natural phenomena such as a climate shift resulting in a severe change in environment or through artificial means such as the effects of toxicants as mentioned above. A deteriorating environment is assumed here to be modeled by functions K with the properties that K is positive on $[0, \infty)$ and

$$\lim_{t \rightarrow \infty} K(t) = 0. \quad (3)$$

The parameter r in equation (2) will also be allowed to vary with time to permit the comparison of the survival of systems with different growth rates and for the remainder of this section, r will be required to be positive (this restriction is removed later).

Equation (2) is a Bernoulli equation and is solvable in an explicit form if r and K are piecewise continuous on $[0, \infty)$. The solution of equation (2) which passes through the point (t_0, x_0) can be written as

$$x(t, t_0, x_0) = \frac{x_0 \exp \left[\int_{t_0}^t r(\tau) d\tau \right]}{1 + x_0 \int_{t_0}^t \exp \left[\int_{\tau}^t r(\xi) d\xi \right] \frac{r(\tau)}{K(\tau)} d\tau}. \quad (4)$$

A condition that is often useful in determining the asymptotic behavior of differential equations is integrability, in the L^p sense, of the coefficients (Lakshmikantham & Leela, 1969). An L^1 criterion is used here to classify solution behavior of equation (1). If the function r is in $L^1[0, \infty)$, that is if

$$\int_0^\infty r(t) dt < \infty, \quad (5)$$

we say that r is *small on the average*. The function r is *large on the average* if

$$\int_0^\infty r(t) dt = \infty. \quad (6)$$

First assume that r is large on the average and K satisfies condition (3). It follows from equation (4), by employing L'Hospital's rule, that all

solutions have the property

$$\lim_{t \rightarrow \infty} x(t, t_0, x_0) = 0.$$

Thus a large growth rate coupled with a deteriorating environment causes the population to track its environment to extinction. This is a completely plausible and, in fact, the expected result. No population is expected to persist in an environment which progressively loses its ability to provide the requirements for existence. However, the situation with growth rates which are small on the average provides quite different results.

Assume now that r is small on the average (satisfies hypothesis (5)). In the analysis which follows, the deteriorating environment condition (3) is not a necessary requirement although the results obtained here will be interpreted for this situation. If hypothesis (5) is satisfied and if K and r are related so that

$$\int_0^\infty r(t) K^{-1}(t) dt < \infty, \quad (7)$$

then each solution, $x(t, t_0, x_0)$, of equation (2) with $t_0 \geq 0$, $x_0 \geq 0$, satisfies

$$\lim_{t \rightarrow \infty} x(t, t_0, x_0) = x_\infty, \quad (8)$$

where

$$x_\infty = \frac{x_0 \exp \left[\int_{t_0}^\infty r(\tau) d\tau \right]}{1 + x_0 \int_{t_0}^\infty \exp \left[\int_0^\tau r(\xi) d\xi \right] r(\tau) K^{-1}(\tau) d\tau}. \quad (9)$$

The integrals in formula (9) exist by virtue of the hypotheses (5) and (7).

For a fixed t_0 , there is a one-to-one correspondence between positive initial values x_0 and allowable terminal values x_∞ for solutions of equation (2). The range of terminal values of solutions of equation (2) consists of all positive numbers x_∞ such that

$$x_\infty < M(t_0, r, K) \equiv \frac{\exp \left[\int_{t_0}^\infty r(\tau) d\tau \right]}{\int_{t_0}^\infty \exp \left[\int_{t_0}^\tau r(\xi) d\xi \right] r(\tau) K^{-1}(\tau) d\tau}. \quad (10)$$

To any $x_\infty < M(t_0, r, K)$, there corresponds an initial position x_0 , related to x_∞ by

$$x_0 = \frac{x_\infty}{\exp \left[\int_{t_0}^\infty r(\tau) d\tau \right] - x_\infty \int_{t_0}^\infty \exp \left[\int_{t_0}^\tau r(\xi) d\xi \right] r(\tau) K^{-1}(\tau) d\tau}$$

such that hypothesis (8) holds. The one-to-one correspondence between initial and terminal values with an asymptotic behavior as in hypothesis

(8) is similar to what is called an asymptotic equivalence in the differential equation literature (Lakshmikantham & Leela, 1969).

When K satisfies the inequalities

$$0 < K_{\inf} \leq K(t) \leq K_{\sup}, \quad (11)$$

for constants K_{\inf} and K_{\sup} , a straightforward manipulation of inequalities leads to

$$\begin{aligned} K_{\inf} \left\{ 1 - \exp \left[- \int_{t_0}^{\infty} r(\tau) d\tau \right] \right\}^{-1} &\leq M(t_0, r, K) \\ &\leq K_{\sup} \left\{ 1 - \exp \left[- \int_{t_0}^{\infty} r(\tau) d\tau \right] \right\}^{-1}. \end{aligned} \quad (12)$$

For a prescribed environment, K is assumed known, and it is possible to select a growth rate r that allows $M(t_0, r, K)$ to be arbitrarily large. For example, if K is constant on $[0, \infty)$, the value of $M = M(t_0, r, K)$ is

$$M = K \left\{ 1 - \exp \left[- \int_{t_0}^{\infty} r(\tau) d\tau \right] \right\}^{-1}.$$

Hence, there always exist solutions of equation (2) whose terminal values exceed the system carrying capacity. If $\int_{t_0}^{\infty} r(\tau) d\tau$ is sufficiently small, M can be arbitrarily large, and the carrying capacity of the system is exceeded by any solution that is initially above K .

Hypotheses (6) and (7) can be satisfied by functions r and K that approach zero as t approaches infinity. In a deteriorating environment where equation (3) holds r must, therefore, approach zero faster than K . Since $r(t) > 0$ for $t \geq t_0$, then, from formula (10)

$$M(t_0, r, K) > \frac{\exp \left[\int_{t_0}^{\infty} r(\tau) d\tau \right]}{\int_{t_0}^{\infty} \exp \left[\int_{t_0}^{\infty} r(\xi) d\xi \right] r(\tau) K^{-1}(\tau) d\tau} = \left[\int_{t_0}^{\infty} r(\tau) K^{-1}(\tau) d\tau \right]^{-1}.$$

Again, M , and hence x_{∞} , can be made arbitrarily large by choosing r sufficiently small relative to K . In any case, since, from formula (9), all solutions have positive limits, every population terminal density exceeds the terminal value of the carrying capacity.

If one attempts a biological interpretation of the results of this section, the following conclusions are apparent. A growth rate that is large on the average can lead to extinction while a small average growth rate can result in persistence independent of initial population and, in fact, can result in arbitrarily large terminal values which exceed the terminal values of the carrying capacity. The parameter r is often interpreted as the growth rate of the population in the absence of environmental stress. Thus we are

confronted with a situation where a population which (because of a very small intrinsic growth rate) is barely able to persist under the best of conditions is able to do as well or better in an intolerable environment. These conclusions point out rather vividly the inadequacy of equation (2) as a model of logistic growth in the situation described above. In the next section an alternative approach is investigated.

3. A Non-autonomous Modified Logistic Equation

Modelling deficiencies of the classical logistic equation (1) are promulgated by the role of both model parameters r and K . The model defects in the previous section are consequences of the domination of the intrinsic growth rate r in the equation. An equation, of modified logistic type, which does not allow solution behavior to be subjugated by r is

$$\frac{dx(t)}{dt} = x(t) \left(r - \frac{c}{K} x(t) \right). \quad (13)$$

In equation (13), the intrinsic growth rate, r , is expressed in units $(\text{time})^{-1}$ as is the positive parameter c . This new independent parameter c is a measure of the population response to environmental stress as represented by the ratio x/K .

A problem with the parameter K in the classical logistic equation is that it can be ambiguously interpreted as either a population carrying capacity or a steady state of the population. Since these interpretations need not be equivalent, it is convenient to reformulate the model as

$$\frac{dx(t)}{dt} = x(t) \left[r(t) - c \frac{x(t)}{B(t)} \right] \quad (14)$$

where B denotes the maximum population which the environment can support; that is, the environment can provide all necessary requirements for the maintenance of B individuals but it will not support $B + 1$ individuals. When r and B are constants, equation (14) has a stable equilibrium at $x = rB/c$. This motivates the definition of the (ultimate) population level parameter K as

$$K = \begin{cases} rB/c & \text{if } r > 0 \\ 0 & \text{if } r \leq 0. \end{cases} \quad (15)$$

It must be the case that $r \leq c$ in equation (14). For species that have evolved in a manner which allows the population to exploit the full potential of the environment, one would expect to have $K = B$ and $r = c$; that is, the traditional logistic equation is applicable.

Equation (14) can be shown to palliate some of the modelling difficulties associated with equation (1) as it yields plausible results in many instances where equation (1) does not. For example, a completely bizarre behavior occurs for solutions of equation (1) when $r < 0$. Any solution that is initially above K has a finite escape time; that is, the solution approaches infinity at a finite time. On the other hand, when $r < 0$, solutions of the autonomous equation (14) behave as expected since all solutions exist for all time and approach zero as t approaches infinity.

In the case that model (14) is non-autonomous, it can be demonstrated that the undesirable attributes of equation (2) as indicated in section 2 are eliminated. For example, two results for equation (14) that contrast sharply with the behavior of equation (2) are the following.

- (i) Either a deteriorating growth rate or a deteriorating environment assures extinction of the population.
- (ii) Or more generally, when $r(t)$ and $B(t)$ have terminal values r_∞ and B_∞ respectively, every solution of equation (14) has a terminal value x_∞ and, if $x_0 \neq 0$, then $x_\infty = K_\infty$ where K_∞ is the terminal value of the population level as given by equation (15).

A brief indication of the arguments used to verify (i) and (ii) is now presented under the hypotheses that r and B are piecewise continuous functions with $0 < B(t) \leq B_M$ on $[0, \infty)$ where B_M is a constant.

From a representation similar to equation (4), of the solutions of equation (14), it follows that when $\int_{t_0}^{\infty} r(t) dt = \infty$, then $x_\infty = K_\infty$ and when $\int_{t_0}^{\infty} r(t) dt = -\infty$, then $x_\infty = 0 = K_\infty$.

If $\int_{t_0}^{\infty} r(\tau) d\tau \neq \pm\infty$, then $r_\infty = 0$, and for any $\varepsilon > 0$ there exists t^* such that $|r(t)| < \varepsilon$ for $t \geq t^*$. Then, for $t \geq t^*$,

$$\begin{aligned} x(t, t^*, x(t^*, t_0, x_0)) \\ = \frac{x_0}{\exp[-\int_{t^*}^t r(\tau) d\tau] + x_0 c \int_{t^*}^t \exp[-\int_{\tau}^t r(\xi) d\xi] B^{-1}(\tau) d\tau} \\ < \frac{x_0}{e^{-\varepsilon(t-t^*)} + (x_0 c / B_M) \int_{t^*}^t e^{-\varepsilon(t-\tau)} d\tau} \\ = \frac{\varepsilon x_0 B_M}{(\varepsilon B_M - x_0 c) e^{-\varepsilon(t-t^*)} + x_0 c}. \end{aligned}$$

Since the solution $x(\cdot, t_0, x_0)$ is unique,

$$\lim_{t \rightarrow \infty} x(t, t_0, x_0) = \lim_{t \rightarrow \infty} x(t, t^*, x(t^*, t_0, x_0)) \leq \frac{\varepsilon B_M}{c}$$

for every positive ε . It follows that $x_\infty = 0 = K_\infty$.

To establish (i), two observations are in order. First, the arguments used above to show that $x_\infty = 0$ whenever $r_\infty \leq 0$ do not depend on the existence of a terminal value for B . Hence, a growth rate deteriorating to a non-positive value assures extinction regardless of the nature of fluctuations in environmental quality. Second, if the environment is deteriorating, $B_\infty = 0$, then an argument similar to that used above establishes that $x_\infty = 0$. Hence, a deteriorating environment assures extinction regardless of the limiting behavior of r .

4. Discussion

Non-autonomous logistic models employing equation (2) were investigated by Coleman (1979); Coleman *et al.* (1979); and May (1976). Coleman avoided the paradoxical biological conclusions of section 2 by requiring that r be positive and bounded away from zero. In fact, assuming that both r and K are bounded away from zero, Coleman shows that there is a special canonical solution $x^* = x^*(t)$ that is approached in the limit of large t by each solution with positive initial position. He also points out the interesting fact that x^* , and hence all solutions of equation (2) asymptotically depend upon the complete past history of the population's biological and environmental influences as reflected by r and K . Coleman *et al.* assume that the carrying capacity is specified, then they search for an intrinsic growth rate that will minimize probability of extinction by making the minimum of the canonical solution large. They found that the preferred choices involved smaller rather than larger growth rates. Their conclusion is a consequence of the model (2) they utilized; it would not be valid for the modified logistic model proposed here.

May writes the time-dependent logistic equation in the form equation (2) but in the example presented, r is taken to be a positive constant. In this case, the behaviors of equations (2) and (14) are similar. May also gives the canonical solution of equation (2) in the case that r is constant.

Under certain conditions, equation (14) also has a canonical solution. If $\int_0^\infty r(t) dt = \infty$, the canonical solution x^* is given by

$$x^*(t) = \left[c \int_0^t \exp \left[- \int_\tau^t r(\xi) d\xi \right] B^{-1}(\tau) d\tau \right]^{-1}.$$

If $\int_0^\infty |r(t)| dt < \infty$, the canonical solution is $x^* = 0$.

There has been criticism of the logistic equation for its many deficiencies (e.g. Gray, 1929; Kavanagh & Richards, 1934; Andrewartha & Birch, 1945; Pielou, 1977; Murray, 1979), and nearly every textbook treatment of the equation is accompanied by disclaimers pointing out the restrictive

and sometimes conflicting assumptions required for its application. May (1976) was perhaps most to the point with his statement that the logistic equation "is not to be taken seriously". However, despite the criticisms and obvious deficiencies, the equation continues to be the most frequently used continuous deterministic model of single species population growth in a limited environment, its advantages being its analytical simplicity, the elementary interpretation of its biological parameters, and the fact that it often fits to data, especially in laboratory population studies.

Our study indicates that a re-parametrization of the logistic equation might prove beneficial for modelling populations with small growth rates or where the environment is changing in an unfavorable manner.

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