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On density and extinction in continuous population models

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Abstract. Survival analyses, investigations of extinction and persistence, are executed for populations represented by a nonautonomous differential equation model. The population is assumed governed by density dependent and time varying density independent demographic parameters. While traditional approaches to extinction postulate extinction on an infinite time horizon and at zero abundance level, survival analysis is developed not only for this traditional setting but also on a finite time horizon and at a nonzero threshold level. A main conclusion is that extinction of a temporally stressed population is determined by a totality of density independent and density dependent factors.

Key words: Density dependence — Persistence — Extinction — Population — Finite time horizon

1. Introduction

Since antiquity in theoretical population biology (Malthus (1798); Verhulst (1838), (1847)) density dependence, a euphorism for environmental limitations expressed through size differentiated levels of mortality or natality, has been postulated as a regulator of growth. While much effort has been directed toward assessment of density dependent relationships at saturation level, low density levels and their relationships to population dynamics have been virtually ignored. Problems of biotechnology and ecotoxicology such as the invasion capability of introduced species or the survival of toxicant stressed populations have sparked renewed interest in relationships between extinction and population abundance. The purpose of this article is to demonstrate that relationships between density dependent and time-varying density independent population demographics are fundamental to population survival. This is a complement of the results of some recent analyses of classical population models which establish that density independent demographic parameters are solely responsible for extinction or persistence of a stressed population (Hallam et al. (1983); Hallam and de Luna (1984)).

A primary reason for this anomaly lies in the traditional definition of extinction at zero population level where density dependent effects are often regarded as negligible. Another perceived deficiency arises because standard model representations result in extinction only on an infinite time horizon. This article explains the role of density dependence in extinction, discusses finite-time extinction as well as survival on an infinite time horizon, and views extinction at levels other than just zero-density populations.

The model

The generic differential equation

$$dx/dt = g(x)[r(t) - f(x)x], \qquad t \in \mathbb{R}_+ = [0, \infty), \; x \in \mathbb{R}_+, \tag{1}$$

is assumed to represent the model population at abundance measure x. The functions g and f represent density dependent formulations (units: size and $(\text{time})^{-1}(\text{size})^{-1}$ respectively) and are generally assumed to be in $C^1[\mathbb{R}_+, \mathbb{R}_+]$ with $g(0) = 0$, $xg(x) > 0$ for $x > 0$, and $xf(x) > 0$ for $x > 0$. The function r is the time dependent intrinsic growth rate (units: $(\text{time})^{-1}$) and is assumed to be in $C[\mathbb{R}_+, I]$ where $I = [a, b]$ with $b - a < \infty$. Population stress, including that caused by density independent mortality, is effected through the growth rate r.

When population size is small, the function g is important in governing population dynamics as it reflects attributes such as density dependent natality. It has been traditional to take $g(x) = x$ so that the *per capita* growth rate is employed in the model formulation. A percursory review of the literature reveals that g should be a function of the specific population. Classical experiments by Gause (1934) on growth of *Paramecium aurelia* are quoted as an illustration of logistic growth (Roughgarden (1977), p. 307) but they reveal that at small densities, there are strong oscillations in the *per capita* growth rate when viewed as a function of density. Data of Smith (1963) for *Daphnia magna* in expanding culture experiments also indicate that g is nonlinear; in fact, he proposed and utilized $g(x) = x/(k_1 + k_2x)$ in a model representation for growth of *D. magna*.

The function f is involved in density dependent mortality representation and is more important at density levels other than small ones. There are many candidates for representations of f in the literature (e.g. Wiegert (1975); Clark (1976); May (1976); Hallam (1986)) some of which appear sufficiently often to be put into classifications such as types I, II, and III, compensatory or depensatory.

Extinction

A realistic theory must be grounded in viable concepts, sound definitions, testable hypotheses and demonstrable conclusions. Traditional approaches to extinction have deficiencies in several of these areas. Investigation of population survival requires adequate representation of growth at low levels of population size. This representation, as well as the threshold level for survival, depends upon the particular abundance measure (numbers, biomass, density) of population employed. Extinction requires dynamic assessment of small population sizes and for this purpose, discrete models are probably more appropriate than continuous ones. However, the complexity of discrete models, even rudimentary autonomous difference equations are difficult to analyze due to a behavior spectrum ranging from simple extinction to persistence regimes that include chaos (May (1976)), makes a continuous model yielding appropriate phenomenological predictions a viable option.

Traditionally in model analysis, extinction has been considered equivalent to model trajectories approaching zero (Freedman and Waltman (1977), (1984), (1985), Gard and Hallam (1979), Gard (1984)). In addition, for Kolmogorov models, where $g(x)=x$, extinction can only occur on an infinite time horizon. The conditions that allow finite time extinction at zero population level are now discussed.

Although the past studies of zero level extinction (0-extinction) are reasonable compromises between mathematical techniques and biological realism, some difficulties arise. The fact that a population size cannot be infinitesimally small, makes it impossible to determine the low density dependent natality representation, g, for x very small. For modelling purposes, one way of defining g is to use the extrapolation to zero from low density data. Information about the structure of g is needed because, as seen below, the mathematical requirements for developments in 0-extinction are stringent.

It is natural to impose the condition $g(0)=0$ so that the function $x(t)\equiv 0$ is a solution of (1). It is also reasonable to expect that a low density population should go to extinction in a finite time if the population is under extreme stress. However, if solutions to zero initial value problems are unique, there is no possibility of an extinction on a finite time horizon. One approach leading to finite-time extinction and, by necessity, violating the uniqueness of solutions to initial value problems, is to assume that the integral $\int_0 dx/g(x)$ converges. Indeed, if $\int_0 dx/g(x)$ converges and r is not identically zero on $\mathbb{R}_+$, then there is a nontrivial solution of equation (1) through each point $(0, t_0)$, $t_0 \in \mathbb{R}_+$. This may be demonstrated by first observing that the function u defined on $[0, x_0]$ as

$$u(x)=\begin{cases} \displaystyle\int_0^x ds/g(s), & x\neq 0: \\ 0, & x=0, \end{cases}$$

is continuous on $[0, x_0]$. Since $du/dx=[g(x)]^{-1}$ is positive on $(0, x_0)$, u is increasing on $[0, x_0]$. Thus, the inverse of $u(x)$, $x=\varphi(u)$ is well defined, is differentiable on $(0, u(x_0))$, and, from (1), satisfies

$$du/dt=r(t)-\varphi(u)f(\varphi(u)), \tag{1u}$$

The initial value problem consisting of (1u) and the point $(t_0, 0)$ has a nontrivial solution if and only if r is not identically zero. In particular, from (1u) it follows that when $r(t_0)$ is positive then $u(t)$ is positive for t in an interval to the right of t_0. Analogously, if $r(t_0)$ is negative, $u(t)$ is positive for t in an interval to the left of t_0.

Hence, with the hypothesis that the integral $\int_0 dx/g(x)$ converges, there exist nontrivial solutions to the problems, $x(t_0)=0$, and extinction in a finite time occurs on intervals where $r(t)$ is negative. However, on intervals where $r(t)$ is positive, the nonuniqueness manifests itself in an undesirable manner—nontrivial populations emerge from the initial population size $x(t_0)=0$.

Coupled with the biological rationale, the mathematical complexities required for 0-extinction in finite time—additional hypotheses such as convergence of the integral $\int_0 dx/g(x)$, multiple solutions to initial value problems generating "creationist" trajectories provide motivation for development of a more reasonable concept, the concept of β-extinction, that is, extinction at a nonzero threshold level β.

A population, $x=x(t)$, of (1) is said to *go to extinction at population level* β, $0\leq\beta$, at time T, $0<T\leq\infty$, provided $x(t)>\beta$ for $t\in[0, T)$ and $\lim_{t\to T^-} x(t)=\beta$; for brevity this phenomenon will be called *β-extinction.* The classical definition of extinction is the case $\beta=0$; in the current literature only $T=\infty$ has been considered. A population is *β-persistent* on $[0, T]$ if it does not go to β-extinction for any time in $[0, T]$.

Motivation to develop the concepts of β-extinction and β-persistence arises from biological, economical, as well as mathematical directions. If the population variable is measured in biomass, then for the population to be viable, x must always exceed the neonatal biomass at which an individual has a positive probability of survival. This threshold level provides an example of a biologically motivated choice of β. Another similar example when a sexually reproducing population is measured in density, might be with β chosen as the threshold density below which the number of reproductive encounters is too infrequent to maintain the population. There might be other reasons such as economic viability of a population where a β-level of extinction is applicable.

The concepts of β-persistence and β-extinction presented here are, as far as we know, new; however, the mathematical and ecological stability literature is replete with related formulations (Lakshmikantham and Leela (1969); Levin (1975)). For example, the work of Weiss and Infante (1965) introduces finite-time stability, a definition akin to our idea of β-persistence. Some analogous control theoretic based stability notions that are set in ecological contexts include Goh's (1976) nonvulnerability and Wu's (1975) total stability.

Many stability results exist for autonomous models and are often grounded in Liapunov theory. Our developments are primarily founded upon intrinsic time variation in models.

2. Finite-time survival analysis at level β, $\beta>0$

The determination of survival or extinction of a population at level β, $\beta>0$, depends upon characteristics of the growth rate expression, $G(t, x)\equiv r(t)-xf(x)$, in Eq. (1). The function G reflects the interaction between the density independent demographic parameters and density dependent mortality. Conditions for finite time survival and finite time extinction are presented in the next result.

Theorem 1. (i) *If, for given $\beta>0$ and for all t in $[0, T]$, $T<\infty$, the function $G(t,\beta)=r(t)-\beta f(\beta)$ is positive then any population with $x(0)>\beta$ is β-persistent on* $[0, T]$.

(ii) *If there exists a t_0 in $(0, T]$ where $G(t_0,\beta)$ is negative then there is a threshold function, $\mathcal{T}=\mathcal{T}(t)$, related to certain trajectories associated with* (1) *which* *separates those populations that go to β-extinction at some time in the interval* $[0, T]$ *from those that do not.*

Indications of the proof of this and subsequent results are in the final section of this article. There are several types of threshold functions as described in (ii) that can occur. In each situation the threshold depends upon g, f, and r as well as β; that is, both density dependent and density independent factors play a role in β-extinction. The construction of the threshold involves knowledge of special trajectories of (1). Of interest is the vector field along $x=\beta$. To determine this vector field, it is convenient to locate the zeros of $G(t, \beta)=r(t)-\beta f(\beta)$ as follows. Let the interval $[0, T]=S\cup[\gamma, T]$ where $S=\bigcup_{i=1}^{N}(I_i\cup I_i^a)$ with $I_i=[\tau_i, \sigma_i]$ consecutive intervals with $G(\tau_i, \beta)=G(\sigma_i, \beta)=0$ and $G(t, \beta)<0$ for $t\in[\tau_i, \sigma_i]$, except for isolated points where $G(t, \beta)=0$; $I_i^a=(\sigma_{i-1}, \tau_i)$ are the complementary adjacent intervals with $\sigma_0=0$ and where $G(t, \beta)>0$ for $t\in I_i^a$ except for isolated t-values where $G(t, \beta)=0$, $i=1, 2, \ldots, N$, $N<\infty$, and $[\gamma, T]$ is the remainder of the interval $([0, T]-S)$.

From the sign of $G(t, \beta)$, the vector field is determined only on the line $x=\beta$ (Fig. 1). To construct the threshold, the intersection of certain trajectories, $x=x(t)$, with the curve $x=G(t, \beta)$ is important. Unfortunately, as the threshold is composed of portions of trajectories, a threshold for a particular Eq. (1) will, in general, have to be computed numerically. It is, however, possible to describe the procedure employed to construct the threshold. Suppose that $\sigma_N\leq T$; consider the solution, $x=x(t;\, \sigma_N, \beta)$, to the terminal value problem: (1) and (σ_N, β). We have assumed that this problem has a unique solution. If $x(t;\, \sigma_N, \beta)>\beta$ for all $t\in(0, \sigma_N)$, then $x(t;\, T, \beta)$ is the threshold function which separates solutions that go to β-extinction on $[0, T]$ from those that are β-persistent in $[0, T]$. If $x(t_0, \sigma_N, \beta)=\beta$ for some t_0 in $(0, \sigma_N)$ then the threshold might be composed of several segments. When $dx(t_0;\, \sigma_N, \beta)/dt=0$ so that $t_0=\sigma_i$ for some i then the threshold will still consist of $x(t;\, T, \beta)$ to the left of t_0. If $dx(t_0;\, \sigma_N, \beta)/dt>0$ then define the threshold, $\mathcal{T}(t)$, on $[\sigma_i, t_0]$, where $\sigma_i\leq t_0$ is the zero of $G(t, \beta)$ to the immediate left of t_0, by $\mathcal{T}(t)=\beta$. The process is now repeated by considering the solution, $x(t;\, \sigma_i, \beta)$, of (1) through (σ_i, β). If $x(t;\, \sigma_i, \beta)>\beta$ for all $t\in(0, \sigma_i)$ then $\mathcal{T}(t)=x(t;\, \sigma_i, \beta)$ on $[0, \sigma_i]$; if $x(t_1, \sigma_i, \beta)=\beta$ for some $t_1\leq\sigma_i$ then $\mathcal{T}(t)=\beta$ on $[\sigma_k, t_1]$, where $\sigma_k\leq t_1$ is the root of $G(t, \beta)=0$ to the immediate left of t_1. If $\sigma_k>0$, the process continues. If τ_N is the last zero of $G(t, \beta)$ before T then $dG(\tau_N, \beta)/dt<0$. In this situation, the solution $x(t;\, T, \beta)$ is the final portion of $\mathcal{T}(t)$. The rest of the threshold is constructed as indicated above.

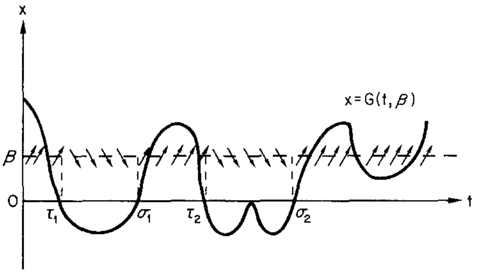

Fig. 1. The vector field along $x=\beta$ as determined by the function $x=G(t, \beta)$

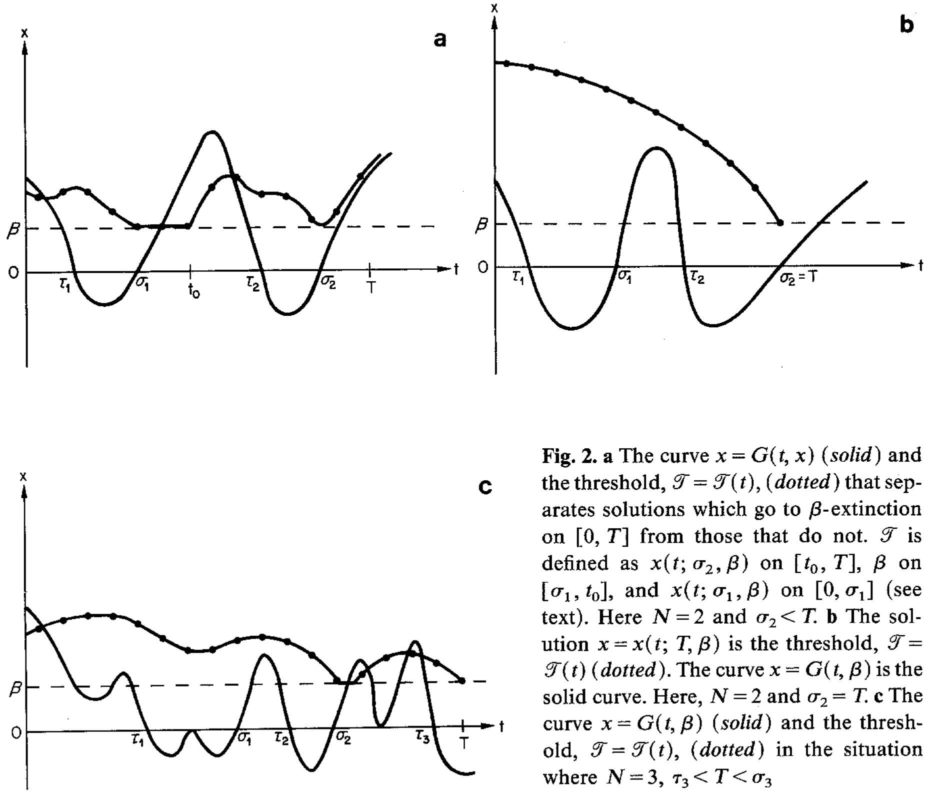

Fig. 2. a The curve $x = G(t, x)$ (*solid*) and the threshold, $\mathcal{T} = \mathcal{T}(t)$, (*dotted*) that separates solutions which go to β-extinction on $[0, T]$ from those that do not. $\mathcal{T}$ is defined as $x(t; \sigma_2, \beta)$ on $[t_0, T]$, β on $[\sigma_1, t_0]$, and $x(t; \sigma_1, \beta)$ on $[0, \sigma_1]$ (see text). Here $N = 2$ and $\sigma_2 < T$. **b** The solution $x = x(t; T, \beta)$ is the threshold, $\mathcal{T} = \mathcal{T}(t)$ (*dotted*). The curve $x = G(t, \beta)$ is the solid curve. Here, $N = 2$ and $\sigma_2 = T$. **c** The curve $x = G(t, \beta)$ (*solid*) and the threshold, $\mathcal{T} = \mathcal{T}(t)$, (*dotted*) in the situation where $N = 3$, $\tau_3 < T < \sigma_3$

Illustrations of thresholds are given in Fig. 2. Figure 2a sketches $\mathcal{T}(t)$ when $\sigma_N \leq T$ and $dG(\sigma_N, \beta)/dt = dr(\sigma_N)/dt > 0$; here, there is a single interval where $\mathcal{T}(t) = \beta$. Figure 2b has $\sigma_N = T$ and $\mathcal{T}(t) = x(t; T, \beta)$ for $t \in [0, T]$. Figure 2c assumes that the largest zero of $G(t, \beta)$ in $[0, T]$ is τ_N; hence, $\tau_N \leq T$ and $dG(\tau_N, \beta) < 0$.

3. Survival analysis on $\mathbb{R}_+$

The behavior of (1) on the infinite interval R_+ has similar characteristics to that delineated in Theorem 1 for the finite time horizon. Again, the behavior is governed by $G(t, \beta) = r(t) - \beta f(\beta)$ however, as the behavior is asymptotic, it will be described in more refined detail than that used for finite time horizons.

The case where $G(t, \beta)$ is of constant sign provides a basis for the analysis. If $G(t, \beta) > 0$ on $\mathbb{R}_+$ then Theorem 1 implies that all populations with $x(0) > \beta$ are β-persistent on finite intervals; hence, β-extinction is only possible asymptotically; hence, this hypothesis, $G(t, \beta) > 0$ for $t \in \mathbb{R}_+$, guarantees that all populations, x, with $x(0) > \beta$ are defined for all large t. When $G(t_0, \beta)$ is negative for some t_0 then Theorem 1 indicates there are always solutions that go to β-extinction in finite time. The analysis of the asymptotic behavior of (1) is summarized below.

The notation $\langle p\rangle(t)$ designates the mean of

$$p\colon \frac{1}{t}\int_0^t p(s)\,ds.$$

Theorem 2. *Each population,* $x=x(t)$, *of* (1) *with* $x(0)>\beta$ *has the asymptotic behavior indicated below.*

(i) *If* $\limsup_{t\to\infty} G(t,\beta)<0$ *and* $f(x)\geq f(\beta)$ *for* $x\geq\beta$, *then all solutions go to* β*-extinction at a finite time.*

(ii) *If* $\liminf_{t\to\infty} G(t,\beta)>0$ *and* $G(t,\beta)>0$ *for all* $t\in\mathbb{R}_+$, *then any population,* x, *satisfies* $x(t)>\beta$ *for* $t\in\mathbb{R}_+$ and $\liminf_{t\to\infty} x(t)>\beta$.

(iii) *If* $\liminf_{t\to\infty} G(t,\beta)>0$ *and there exists a* t_0 *where* $G(t_0,\beta)<0$ *then there is a threshold which separates populations that are* β*-persistent on* $\mathbb{R}_+$ *from those that go to extinction at a finite time.*

(iv) *If* $\liminf_{t\to\infty} G(t,\beta)=0$, $f(x)\geq f(\beta)$ *for* $x\geq\beta$, *and* $G(t,\beta)>0$ *for all* $t\in\mathbb{R}_+$ *then any population* $x(t)$ *with* $x(0)>\beta$ *satisfies* $x(t)>\beta$ *for* $t\in\mathbb{R}_+$, *and* $\liminf_{t\to\infty} x(t)=\beta$.

(v) *If* $\limsup_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)>0$ *and* $G(t,\beta)>0$ *for all* $t\in\mathbb{R}_+$ *then any population* $x(t)$ *with* $x(0)>\beta$ *satisfies* $x(t)>\beta$ *for* $t\in\mathbb{R}_+$ *and is weakly* β*-persistent in that* $\limsup_{t\to\infty}x(t)>\beta$. *If, in addition, there is a function* $H\in C[\mathbb{R}_+,\mathbb{R}_+]$ *with* $H(\beta)=\beta f(\beta)$ *and* $\langle xf(x)\rangle\leq H(\langle x\rangle)$ *for all functions* $x\in C[\mathbb{R}_+,I]$, $I=(\beta,\gamma]$, $\beta<\gamma<+\infty$, *then* $\liminf_{t\to\infty}\langle x\rangle(t)>\beta$.

(vi) *If* $\liminf_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)=0$, $G(t,\beta)>0$ *for* $t\in\mathbb{R}_+$ *and* $f(x)>f(\beta)$ *when* $x>\beta$ *then any population* $x=x(t)$ *satisfies* $x(t)>\beta$ *for* $t\in\mathbb{R}_+$ *and* $x(t)$ *goes to* β*-extinction in the mean, that is,* $\lim_{t\to\infty}\langle x\rangle(t)=\beta$.

Results that are somewhat similar to these on $\mathbb{R}_+$ for zero-survival analyses may be found in Hallam and Ma (1986).

4. Discussion

The survival analysis presented here is novel from several perspectives. First, the approach requires that extinction in continuous models be formulated by employing nonzero thresholds. While threshold concepts are replete in the literature (e.g. Wiegert (1975); Woodwell (1975); Steele (1976)), the concept of β-extinction and its connection with population density dependent and density independent parameters are explored here from a new perspective.

Developments of finite-time extinction are presented to placate an antipodal attribute of smooth Kolmogorov models where extinction can result only on an infinite time horizon. Mathematical hypotheses necessary to obtain finite-time 0-extinction lead to ill-posed problems; this, coupled with cumbersome methods needed for finite-time 0-extinction provide additional motivation to develop β-extinction concepts where no grandiloquent hypotheses or methods are needed. Previous studies of 0-extinction in traditional population models have shown that 0-extinction is solely governed by demographic parameters and is density independent. According to the developments here, both density dependent and density independent mortality can influence survival in certain situations. In these instances, there is a survival threshold that separates β-extinction trajectories from those that are β-persistent. The concept of β-extinction can lead to a spectrum of behavior, comparable to the behavioral spectrum for stochastically perturbed population models (Roughgarden (1979)), including finite and infinite-time horizons for β-extinction as well as β-persistence in the same model.

The initial theoretical developments presented here indicate that the survival of a population is governed by a totality of density independent and density dependent factors. An implementible scheme to assess risk of extinction to stressed populations appears feasible in view of these developments.

5. Indications of the proofs

Proof of Theorem 1. (i) the hypotheses guarantee that the vector field determined by (1) at $x=\beta$ is positive; hence, any population with $x(0)>\beta$ cannot go to extinction.

(ii) The construction of the threshold is indicated in the discussion following Theorem 1. In order to have trajectories with $x(t)>\beta$ that go to β-extinction, at $t=T$, there must exist a time when x decreases. This is assured by the hypothesis $G(t_0, \beta)<0$. The definition of the threshold necessitates separation of extinction and persistence trajectories. Uniqueness of solutions to initial value problems guarantees that the threshold construction is unique (we note that if initial value problems do not have unique solutions, it is possible to construct a threshold by utilizing the maximal solution to the terminal value problem).

Proof of Theorem 2. (i) From the hypothesis, there exists a $\delta>0$ and a time $T>0$ such that $r(t)-\beta f(\beta)<-\delta<0$ for $t\geqslant T$. The solution, $x=x(t)$, with $x(0)>\beta$, must intersect the line $t=T$ if it is β-persistent on [0, T]. Since $g(x)\geqslant\eta>0$ for $x\geqslant\beta$,

$$dx/dt = g(x)[r(t)-xf(x)] \leqslant g(x)G(t,\beta) < -\delta g(x) < -\delta\eta = -\delta_1.$$

Hence, $x(t)\leqslant x(T)-\delta_1(t-T)$, and it follows there is a t_1 where $x(t_1)=\beta$.

(ii) The assumptions imply that for any solution $x=x(t)$ with initial value $x(0)=\beta_1>\beta$ there exists a β_2, $\beta<\beta_2<\beta_1$, such that $r(t)>\beta_2 f(\beta_2)$ for all $t\in\mathbb{R}_+$ and $\liminf_{t\to\infty} G(t,\beta_2)>0$. From the remarks preceding Theorem 2 it follows that $x(t)>\beta_2$ for $t\in\mathbb{R}_+$. Thus, $\liminf_{t\to\infty} x(t)\geqslant\beta_2>\beta$.

(iii) The method of construction of an extinction threshold has been indicated in the text.

(iv) The proof is by contradiction; suppose $x=x(t)$ is a solution of (1) that satisfies $\liminf_{t\to\infty} x(t)>\beta$. From Eq. (1) it follows that

$$f(\beta)\langle x\rangle(t) = \langle r\rangle(t) - t^{-1}\int_0^t z(x(\tau))\,d\tau - t^{-1}\int_{x(0)}^{x(t)} du/g(u) \tag{2}$$

where $z(x)=x[f(x)-f(\beta)]$. From this it follows that

$$\beta < \liminf_{t\to\infty} x(t) \leqslant \liminf_{t\to\infty} \langle x\rangle(t)$$

$$\leqslant \frac{1}{f(\beta)}\left\{\liminf_{t\to\infty}(\langle r\rangle(t)) - \liminf_{t\to\infty} t^{-1}\int_0^t z[x(\tau)]\,d\tau\right.$$

$$+t^{-1}\int_{x_0}^{x(t)}[g(u)]^{-1}\,du\Big\}$$

$$\leqslant\frac{1}{f(\beta)}\left[\beta f(\beta)-\liminf_{t\to\infty}\frac{1}{t}\int_0^t z[x(\tau)]\,d\tau\right.$$

$$\left.-\liminf_{t\to\infty}\frac{1}{t}\int_{x(0)}^{x(t)}\frac{1}{g(u)}\,du\right]\leqslant\beta.$$

This contradiction shows that $\liminf_{t\to\infty}x(t)=\beta$.

(v) First, we observe that if a function q satisfies $q(t)\geqslant\gamma$ for $t\geqslant t_0>0$ and $\liminf_{t\to\infty}\langle q\rangle(t)=\gamma$ then $\lim_{t\to\infty}\langle q\rangle(t)=\gamma$. It is an immediate consequence of L'Hôpital's rule that $\liminf_{t\to\infty}q(t)=\gamma$. Since $\liminf_{t\to\infty}\langle q\rangle(t)=\liminf_{t\to\infty}q(t)=\gamma$, Lemma 2 of Hallam and Ma (1986) establishes that $\limsup_{t\to\infty}\langle q\rangle(t)=\gamma$; hence, $\lim_{t\to\infty}\langle q\rangle(t)=\gamma$.

Turning now to the first proposition in (v), we employ the above observation to determine that $\liminf_{t\to\infty}\langle G(t,\beta)\rangle>0$. This follows because if $\liminf_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)=0$, it also follows that $\limsup_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)=0$. From (2) and $\liminf_{t\to\infty}\langle G(t,\beta)\rangle>0$ the inequality

$$\frac{1}{t}\int_{x_0}^{x}\frac{du}{g(u)}+f(\beta)\langle x\rangle(t)+\frac{1}{t}\int_0^t z(x(\tau))\,d\tau>\beta f(\beta)+\delta,\qquad t\geqslant t_0,\tag{3}$$

may be obtained for some $t_0>0$ and some $\delta>0$.

Assume, for purpose of contradiction, that $\limsup_{t\to\infty}x(t)=\beta$ and, consequently, $\lim_{t\to\infty}x(t)=\beta$. Choose t_1, $t_1>t_0$, such that for $t\geqslant t_1$,

$$t^{-1}\int_0^t z(x(\tau))\,d\tau<\delta/3\quad\text{and}\quad t^{-1}\int_{x_0}^{x(t)}du/g(u)<\delta/3.$$

From (3) it follows that

$$\beta f(\beta)+\delta<\frac{\delta}{3}+f(\beta)\langle x\rangle(t)+\frac{\delta}{3},\qquad t\geqslant t_1$$

or, $\langle x\rangle(t)>\beta+\delta/(3f(\beta))$. This is a contradiction, since $\lim_{t\to\infty}\langle x\rangle(t)=\beta$, which establishes $\limsup_{t\to\infty}x(t)>\beta$.

To show that $\liminf_{t\to\infty}\langle x\rangle(t)>\beta$, we utilize (2) to obtain the equality

$$\langle xf(x)\rangle(t)=\langle r\rangle(t)-t^{-1}\int_{x_0}^{x(t)}[g(u)]^{-1}\,du.$$

The assumption $\limsup_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)>0$ implies that $\liminf_{t\to\infty}\langle G(\cdot,\beta)\rangle(t)>0$; that is, $\liminf_{t\to\infty}\langle r\rangle(t)>\beta f(\beta)$ (Hallam and Ma (1986)). Because $\langle xf(x)\rangle(t)\leqslant H(\langle x\rangle(t))$,

$$\liminf_{t\to\infty}H(\langle x\rangle(t))\geqslant\liminf_{t\to\infty}[\langle r\rangle(t)-t^{-1}\int_{x_0}^{x(t)}[g(u)]^{-1}\,du$$

$$\geqslant\liminf_{t\to\infty}\langle r\rangle(t)-\limsup_{t\to\infty}\int_{x_0}^{x(t)}[g(u)]^{-1}\,du$$

$$>\beta f(\beta).$$

This implies that $\limsup_{t\to\infty}\langle x\rangle(t) > \beta$. The observation in the proof of (v), paragraph one, above shows that $\liminf_{t\to\infty}\langle x\rangle(t) > \beta$.

(vi) It has been remarked that $x(t) > \beta$ for all $t \geqslant 0$ provided $x(0) > \beta$; hence $\langle x\rangle(t) > \beta$. From (2) it follows that

$$\liminf_{t\to\infty}\langle x\rangle(t) \leqslant \beta$$

which implies that $\liminf_{t\to\infty}\langle x\rangle(t) = \beta$. Using the observation in (v) shows that $\lim_{t\to\infty}\langle x\rangle(t) = \beta$.

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