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PRACTICAL PERSISTENCE FOR DIFFERENTIAL DELAY MODELS OF POPULATION INTERACTIONS

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Abstract. Practical persistence refers to determining specific estimates in terms of model data for the asymptotic distance to the boundary of the feasible region for uniformly persistent population interaction models. In this paper we illustrate practical persistence by computing, using multiple Liapunov functions, such estimates for a few basic examples of competition and predator-prey type which may include time delays in the net per capita growth rates.

1. Introduction

Uniform persistence for the Kolmogorov type models of population interactions

$$\dot{x}_i = x_i f_i(x) \quad (i = 1, \dots, n) \tag{1.1}$$

means that solutions $x = x(t)$ of (1.1) which are initially component-wise positive are asymptotically uniformly component-wise positive: there are positive numbers δ_i such that if $x = x(t) = \{x_i(t)\}$ is any solution of (1.1) with $x_i(0) > 0, i = 1, \dots, n$, then

$$\liminf_{t \to +\infty} x_i(t) > \delta_i. \tag{1.2}$$

In (1.1), $x_i(t)$ represents the population (density) of the i-th species at time t with its (total) net rate of growth given by (1.1). Persistence for (1.1) corresponds to mutual survival for the species represented in the model. Generally one expects populations also to be bounded. More precisely, if also (1.1) is (point) dissipative, i. e., if there are constants $M_i > 0$ such that

$$\limsup_{t \to +\infty} x_i(t) < M_i, \tag{1.3}$$

then (1.1) is said to exhibit permanence. Uniform persistence (or permanence) has emerged as an important stability concept for population dynamics models (see Waltman [15], for example). More generally, permanence indicates that a sustained level of complexity is maintained in (1.1) in that at least the dimension of the system is preserved for arbitrarily large time. The discussion of persistence has been

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extended to differential equations in infinite dimensional spaces including partial differential equations and functional differential equations (Hale and Waltman [11], Hutson and Schmitt [13]). The latter may involve time delays which represent the extent of dependence on the past for solutions. Delays can be discrete type τ_j

$$\dot{x}_i(t) = x_i(t) f_i(x(t), x(t-\tau_1), \ldots, x(t-\tau_m)) \quad (i = 1, \ldots, n) \tag{1.4a}$$

or continuous delays

$$\dot{x}_i(t) = \sum_{j=1}^{m} \int_{-\tau_j}^{0} F_{ij}(x(t), x(t+s), t, t+s)\, k_{ij}(s)\, ds \quad (i = 1, \ldots, n) \tag{1.4b}$$

where the k_{ij} are distributions on the interval $(-\tau, 0], \tau = \max \tau_j$. Also, as (1.4b) suggests, non-autonomous systems can be addressed. For (1.4), initial conditions are functions ϕ defined on the interval $(-\tau, 0]$:

$$x(t) = \phi(t), t \in (-\tau, 0] \tag{1.5}$$

and solutions are naturally considered as mappings on an appropriate function space $Y((-\tau, 0])$

$$x = x_t \in Y : x_t(\theta) = x(t+\theta), t \in (-\tau, 0]. \tag{1.6}$$

To obtain persistence, two techniques have been employed: boundary-flow analysis and construction of Liapunov functions. Here, the Liapunov functions are defined somewhat differently from the classical definition in the equilibrium stability setting. Sometimes referred to as an "average" Liapunov function (see [13] and the references therein) or a "persistence" function ([8]), this type of auxiliary function indicates that the boundary of the (persisting) set repels the flow defined by the differential equation inside the set. Generally such a function is defined (and smooth) in a neighborhood of the boundary, and, in the particular, it is continuous from inside the set at the boundary. For multi-species population interactions models (1.1), the basic choice for the function is

$$V(x) = \prod_{i=1}^{n} x_i^{r_i} \tag{1.7}$$

where $x = (x_1, \ldots, x_n)$, and $r_1, \ldots, r_n$ are positive constants, and the set is the usual positive cone in R^n

$$R_+^n = \{x = (x_1, \ldots, x_n) : x_i > 0, i = 1, \ldots, n\}.$$

In the approach which we take, the single function V is replaced by a number of functions which we call multiple Liapunov or net functions and which satisfy less restrictive conditions than above. The Liapunov function method, especially the variation involving multiple Liapunov or net functions, allows determining practical persistence ([4], [5]). Practical persistence (permanence) refers to obtaining specific estimates for δ_i (and M_i) in terms of the model data

$$\delta_i = \delta_i(f) \quad (\text{and } M_i = M_i(f)) \tag{1.8}$$

such as, for example, in the case of simple food chains, in [7]. Such estimates can give indications whether persistence (and dissipativity) are really meaningful for the model. There seems to be some recent interest in extending the idea of practical persistence to PDE ([1], [2]) and discrete population interaction models ([12]). The main point of this paper is to illustrate practical persistence as simply as possible by calculating the δ's and M's for some elementary 2-species models with explicit self-limitation in each species and with or without a single discrete time delay. We include a specific numerical example - a Lotka-Volterra competition model with time delay τ. The model is globally stable for all $\tau \geq 0$, and so an ideal estimate for practical persistence in this case should involve specifying a small region in the positive quadrant containing the stable equilibrium. The figure summarizing our treatment of this example indicates how well we can achieve this using a pair of simple Liapunov functions.

Generally, in the infinite dimensional case, the Liapunov approach (see Freedman and Ruan[6], Hutson and Schmitt [13] and Lakshmikantham and Matrosov [14]) has amounted to constructing (average) Liapunov functionals on Y, or using the Liapunov-Razumikhin technique ([10]) with Liapunov functions defined on the range space X (the positive cone R^n_+ in R^n) for functions in Y. In this setting, if ∂X denotes the boundary of X, uniform persistence means that there is a $\delta > 0$ such that if $x(t)$ is any solution with $x(0) \in X \backslash \partial X$, then

$$\liminf_{t \to +\infty} d(x(t), \partial X) > \delta \tag{1.9}$$

where d is the distance function in X. Here we construct a set of multiple Liapunov functions

$$\{V_1, \ldots, V_p\}$$

which are defined on possibly only a subset X_0 of X. If a dissipative type property like (1.3) holds, a natural choice for X_0 is generally suggested by the correspondingly bounded elements of X. The main advantage of the multiple Liapunov function approach is that the requirements are parceled out to several functions on different portions of the set X_0, rather than a single Liapunov function (or even a vector Liapunov function) on the whole space X. Another way of looking at this scenario is that a possibly complicated Liapunov function is being assembled piecemeal. Our idea for this approach was originally motivated by the paper of Wendi Wang and Ma Zhien [16]; indeed, our work ([3], [4], [5]) on this problem amounts to a sequence of generalizations and applications of the main result in [16]. This approach amounts to constructing a partition $\{X_1, \ldots, X_{p+1}\}$ of X (or any subset X_0 of X which is the ultimate residence of all solution trajectories) with the property that

$$\text{dist } (X_{p+1}, \partial X) > 0. \tag{1.10}$$

The sets X_k in the partition are determined by the functions V_k and these sets are ordered by increasing time on trajectories: for $k < p + 1$, trajectories in X_k at some time must leave X_k in finite time and cannot move into X_j for any $j < k$ at any future time; consequently, ultimately all trajectories lie in X_{p+1}. In the next section we give a concise summary of our basic results on uniform persistence and practical persistence for differential delay equation models of population interactions. For simplicity and clarity we specialize our results to 2-species interactions here. In section 3 we give a result which determines specific dissipative bounds for 2-species models with explicit self-limitation in each species and with or without a single discrete time delay. We then discuss a numerical example - a Lotka-Volterra competition model - to illustrate our practical persistence result.

2. Persistence via multiple Liapunov functions

We consider two-dimensional Kolmogorov type systems with time delay

$$\begin{aligned}\dot{x}(t) &= x(t)f(x(t), y(t), x(t-\tau), y(t-\tau)) \\ \dot{y}(t) &= y(t)g(x(t), y(t), x(t-\tau), y(t-\tau)).\end{aligned} \tag{2.1}$$

In (2.1), the functions f and g are continuous functions defined on $\overline{R}^4_+$, the usual $4-d$ non-negative cone. The result below is essentially a special case of the main result appearing in [4]. Here we give a self-contained complete proof of the result using two Liapunov functions.

Theorem 2.1. *Suppose that:*

(i) *System (2.1) is dissipative with bounds M_1 and M_2.*

(ii) *There are positive constants α and β such that*

$$f(0, y_0, 0, y_1) - \alpha g(0, y_0, 0, y_1) > 0, \ \ \textit{all } y_0, y_1 \in [0, M_2] \tag{2.2}$$

and either

$$\beta f(x_0, 0, x_1, 0) + g(x_0, 0, x_1, 0) > 0, \ \ \textit{all } x_0, x_1 \in [0, M_1] \tag{2.3}$$

or

$$-\beta f(x_0, 0, x_1, 0) + g(x_0, 0, x_1, 0) > 0, \ \ \textit{all } x_0, x_1 \in [0, M_1] \tag{2.4}$$

provided $\alpha\beta < 1$.

Then (2.1) is uniformly persistent (and hence permanent).

Proof of Theorem 2.1. With M_1 and M_2 as above, we denote

$$X_0 = (0, M_1] \times (0, M_2].$$

We will need the following constants to obtain a more precise version of (ii):

$$\begin{aligned}P_1 &= \min\{f(x_0, y_0, x_1, y_1) : ((x_0, y_0), (x_1, y_1)) \in \overline{X}_0 \times \overline{X}_0\} \\ P_2 &= \min\{g(x_0, y_0, x_1, y_1) : ((x_0, y_0), (x_1, y_1)) \in \overline{X}_0 \times \overline{X}_0\}.\end{aligned} \tag{2.5}$$

P_1 and P_2 are finite by continuity of f and g. The dissipative property means that for any positive solution $(x(t), y(t))$ of (2.1), there is a $t_0 > 0$ such that

$$(x(t), y(t)) \in X_0 \text{ for all } t > t_0. \tag{2.6}$$

If $(x(t),\, y(t))$ is a solution of (2.1) satisfying $(x(t), y(t)) \in X_0$ for all $t \geq t_0^* - 2\tau$ for some $t_0^* > 0$, then for any such t and $0 < \nu < M_1$

$$x(t) \leq \nu \text{ implies } x(t-\tau) \leq \nu e^{-P_1 \tau}. \tag{2.7}$$

This follows because the integrated version of (2.1) on the interval $[t-\tau, t]$ gives

$$x(t) = x(t-\tau) \exp \int_{t-\tau}^{t} f(x(s), y(s), x(s-\tau), y(s-\tau))ds \geq x(t-\tau)e^{P_1\tau}$$

for $t \geq t_0^*$. If $\nu^* = \nu e^{P_1 \tau}$, then (2.7) becomes

$$x(t) \leq \nu^* \Rightarrow x(t-\tau) \leq \nu \tag{2.8}$$

and similarly for $y(t)$. Condition (ii) then implies, for sufficiently small positive numbers ϵ_1 and ϵ_2, there are positive numbers $\nu_1 < M_1$ and $\nu_2 < M_2$ such that

$$\begin{gathered} f(x_0, y_0, x_1, y_1) - \alpha g(x_0, y_0, x_1, y_1) > \epsilon_1 \\ \text{for all } x_0 \in [0, \nu_1^*], x_1 \in [0, \nu_1] \text{ and } y_0, y_1 \in [0, M_2] \\ \text{and} \\ \beta f(x_0, y_0, x_1, y_1) + g(x_0, y_0, x_1, y_1) > \epsilon_2 \\ \text{for all } x_0, x_1 \in [0, M_1] \text{ and } y_0 \in [0, \nu_2^*], y_1 \in [0, \nu_2] \end{gathered} \tag{2.9}$$

where

$$\nu_1^* = \nu_1 e^{P_1 \tau} \text{ and } \nu_2^* = \nu_2 e^{P_2 \tau}. \tag{2.10}$$

The proof of Theorem 2.1 makes use of the two Liapunov functions

$$V_1 = xy^{-\alpha} \quad V_2 = x^{\beta} y. \tag{2.11}$$

One asserts that there are positive constants η_1 and η_2 such that the sets

$$\begin{aligned} X_1 &= \{(x,y) \in X_0 : V_1(x,y) \leq \eta_1\} \\ X_2 &= \{(x,y) \in X_0 : V_2(x,y) \leq \eta_2, V_1(x,y) > \eta_1\} \\ X_3 &= \{(x,y) \in X_0 : V_1(x,y) > \eta_1, V_2(x,y) > \eta_2\} \end{aligned} \tag{2.12}$$

partition X_0 and structure the eventual location of trajectories $(x(t), y(t))$ of positive solutions of (2.1) according to the following scheme. Let t_0 be given by (2.6).

(P1) If $(x(t), y(t)) \in X_j$ for some $t_1 > t_0$ then

$$(x(t), y(t)) \in \bigcup_{i=j}^{3} X_i \text{ for all } t > t_1.$$

(P2) If $(x(t), y(t)) \in X_j$ for some $t_1 > t_0$ and $j < 3$, there is $t_2 > t_1$ such that

$$(x(t_2), y(t_2)) \notin X_j.$$

From (P1) and (P2) it follows that there is a t_3 such that

$$(x(t), y(t)) \in X_3 \text{ for all } t > t_3 \tag{2.13}$$

which gives uniform persistence. The δ's in the definition of uniform persistence are determined from α, β and the η's as follows:

$$(x, y) \in X_3 \Rightarrow V_1 = xy^{-\alpha} > \eta_1 \text{ and } V_2 = x^\beta y > \eta_2 \tag{2.14}$$

from which we obtain

$$y > \eta_2/M_1^\beta = \delta_2 \text{ and } x > \eta_1(\eta_2/M_1^\beta)^\alpha = \delta_1 \tag{2.15}$$

i. e.,

$$X_3 \subseteq (\delta_1, M_1] \times (\delta_2, M_2]. \tag{2.16}$$

It remains to obtain explicit expressions for η_1 and η_2 in terms of f and g such that (P1) and (P2) hold. With ν_1^* and ν_2^* as in (2.10), we choose

$$\eta_1 = \nu_1^*/M_2^\alpha \text{ and } \eta_2 = (\nu_2^*)^{1+\alpha\beta}\eta_1^\beta = (\nu_2^*)^{1+\alpha\beta}(\nu_1^*/M_2^\alpha)^\beta. \tag{2.17}$$

Now the first step toward establishing (P1) is to show

$$X_1 \subseteq \{x \leq \nu_1^*\} \text{ and } X_2 \subseteq \{y \leq \nu_2^*\} \tag{2.18}$$

with η_1 and η_2 given in (2.17). We verify the second containment in (2.18):

$$\begin{gathered} (x, y) \in X_2 \Leftrightarrow (x, y) \in X_0 = (0, M_1] \times (0, M_2] \\ \text{and} \\ V_2(x, y) = x^\beta y \leq \eta_2, V_1(x, y) = xy^{-\alpha} > \eta_1 \end{gathered} \tag{2.19}$$

and from (2.19) it follows that

$$y \leq \eta_2/x^\beta < \eta_2/(y^\alpha\eta_1)^\beta \Leftrightarrow y^{1+\alpha\beta} < \eta_2/\eta_1^\beta.$$

Thus we have

$$y < \left(\eta_2/\eta_1^\beta\right)^{1/(1+\alpha\beta)} = \nu_2^*.$$

From (2.18) and (2.9) we conclude that, for any solution $(x(t), y(t))$ of (2.1) which is in X_1 on the interval $[t - \tau, t]$

$$\begin{aligned} \dot{V}_1(x(t), y(t)) &= \frac{d}{dt}V_1(x(t), y(t)) \\ &= [f(x(t), y(t), x(t-\tau), y(t-\tau)) - \alpha g(x(t), y(t), x(t-\tau), y(t-\tau))]V_1(x(t), y(t)) \\ &\geq \epsilon_1 V_1(x(t), y(t)) \end{aligned} \tag{2.20}$$

and similarly

$$\dot{V}_2(x(t), y(t)) = \frac{d}{dt}V_2(x(t), y(t)) \geq \epsilon_2 V_2(x(t), y(t)) \tag{2.21}$$

if the solution $(x(t), y(t))$ is in X_2 on the interval $[t-\tau, t]$. Now if (P1) fails, there is a $T > 0$, an integer k either 2 or 3, and a positive solution $(x(t),\ y(t))$ of (2.1) satisfying $(x(T), y(T)) \in X_k$ and for which

$$t^* = \inf\{t \geq T : (x(t), y(t)) \notin \bigcup_{i=k}^{3} X_i\} \tag{2.22}$$

is a well-defined finite number. Furthermore, by continuity there is a positive integer $k^* < k$ such that

$$(x(t^*), y(t^*)) \in X_k \text{ and } V_{k^*}((x(t^*), y(t^*)) = \eta_{k^*}. \tag{2.23}$$

Since $(x(T), y(T)) \notin X_{k^*}, t^* > T$. From either (2.20) or (2.21) (depending on whether $k^* = 1$ or 2), $V_{k^*}(x(t), y(t))$ is strictly increasing at $t = t^*$, and so with (2.23) we have

$$V_{k^*}(x(t), y(t)) < \eta_{k^*}, \text{ for } 0 < t^* - t << 1. \tag{2.24}$$

However, by definition of t^* and X_i

$$V_i(x(t), y(t)) > \eta_i, \text{ for all } t \in [T, t^*), i = 1, \ldots, k-1 \tag{2.25}$$

which contradicts (2.24) since k^* is one of these i's. Thus (P1) cannot fail. To verify (P2), we first note that since X_1, X_2, and X_3 partition X_0 and since (2.1) is dissipative, for any positive solution $(x(t), y(t))$ of (2.1) there is a $T > 0$, an integer k either 1, 2 or 3, such that

$$(x(T), y(T)) \in X_k. \tag{2.26}$$

It follows from (P1) that there is a $t_0 \geq T$ and an integer $k_0, k \leq k_0 \leq 3$ such that

$$(x(t), y(t)) \in X_{k_0}, \text{ for all } t \geq t_0. \tag{2.27}$$

If $k_0 \neq 3$, then from (2.18)-(2.21), we have

$$\frac{d}{dt} V_{k_0}(x(t), y(t)) \geq \epsilon_{k_0} V_{k_0}(x(t), y(t)), \text{ for all } t \in [t_0, \infty)$$

which implies

$$V_{k_0}(x(t), y(t)) \to \infty \text{ as } t \to \infty$$

and this contradicts $(x(t), y(t)) \in X_{k_0}$ for all $t \geq t_0$. Thus (P2) is established. □

For practical persistence we will need specific choices for ν_1 and ν_2. Since the magnitudes of ϵ_1 and ϵ_2 are not important, by continuity we can choose ν_1 and ν_2 as large as possible with the property

$$\begin{gathered} f(x_0, y_0, x_1, y_1) - \alpha g(x_0, y_0, x_1, y_1) > 0 \\ \text{for all } x_0 \in [0, \nu_1^*), x_1 \in [0, \nu_1) \text{ and } y_0, y_1 \in [0, M_2] \\ \text{and} \\ \beta f(x_0, y_0, x_1, y_1 + g(x_0, y_0, x_1, y_1) > 0 \\ \text{for all } x_0, x_1 \in [0, M_1] \text{ and } y_0 \in [0, \nu_2^*), y_1 \in [0, \nu_2) \end{gathered} \tag{2.28}$$

with ν_1^* and ν_2^* as in (2.10):

$$\nu_1^* = \nu_1 e^{P_1\tau} \text{ and } \nu_2^* = \nu_2 e^{P_2\tau}. \tag{2.29}$$

Then (2.17) gives

$$\eta_1 = \nu_1^*/M_2^\alpha \text{ and } \eta_2 = (\nu_2^*)^{1+\alpha\beta}(\nu_1^*/M_2^\alpha)^\beta \tag{2.30}$$

which in turn by (2.15) leads to

$$\begin{gathered} \delta_1 = \eta_1(\eta_2/M_1^\beta)^\alpha = \frac{(\nu_1^*\nu_2^{*\alpha})^{1+\alpha\beta}}{M_1^{\alpha\beta}(M_2^\alpha)^{1+\alpha\beta}} \\ \text{and} \\ \delta_2 = \eta_2/M_1^\beta = \frac{\nu_1^{*\beta}(\nu_2^*)^{1+\alpha\beta}}{M_1^\beta M_2^{\alpha\beta}}. \end{gathered} \tag{2.31}$$

If the second case of condition (ii) holds, i. e., (2.4) replaces (2.3), we can use the two Liapunov functions

$$V_1 = xy^{-\alpha} \qquad V_2 = x^{-\beta}y \tag{2.32}$$

In this case

$$(x,y) \in X_3 \Rightarrow V_1 = xy^{-\alpha} > \eta_1 \text{ and } V_2 = x^{-\beta}y > \eta_2$$

implies

$$y > \left(\eta_2\eta_1^\beta\right)^{1/(1-\alpha\beta)} = \delta_2 \text{ and } x > \eta_1\delta_2^\alpha = \delta_1, \tag{2.33}$$

i.e.,

$$X_3 \subseteq (\delta_1, M_1] \times (\delta_2, M_2]. \tag{2.34}$$

Here we require ν_1, ν_2, ν_1^* and ν_2^* such that

$$\nu_1^* = \nu_1 e^{P_1\tau} \text{ and } \nu_2^* = \nu_2 e^{P_2\tau}, \tag{2.35}$$

$$\begin{gathered} f(x_0,y_0,x_1,y_1) - \alpha g(x_0,y_0,x_1,y_1) > 0 \\ \text{for all } x_0 \in [0,\nu_1^*), x_1 \in [0,\nu_1) \text{ and } y_0, y_1 \in [0, M_2] \\ \text{and} \\ -\beta f(x_0,y_0,x_1,y_1) + g(x_0,y_0,x_1,y_1) > 0 \\ \text{for all } x_0, x_1 \in [0, M_1] \text{ and } y_0 \in [0,\nu_2^*), y_1 \in [0,\nu_2). \end{gathered} \tag{2.36}$$

Then with the choices

$$\eta_1 = \nu_1^*/M_2^\alpha \text{ and } \eta_2 = \nu_2^*/M_1^\beta \tag{2.37}$$

we obtain (2.18), and together with (2.33) we have

$$\begin{gathered} \delta_2 = \left(\eta_2\eta_1^\beta\right)^{1/(1-\alpha\beta)} = \left(\frac{\nu_1^{*\beta}\nu_2^*}{M_1^\beta M_2^{\alpha\beta}}\right)^{1/(1-\alpha\beta)} \\ \text{and} \\ \delta_1 = \eta_1\delta_2^\alpha = \nu_1^*/M_2^\alpha\left(\frac{\nu_1^{*\beta}\nu_2^*}{M_1^\beta M_2^{\alpha\beta}}\right)^{\alpha/(1-\alpha\beta)} = \left(\frac{\nu_1^*\nu_2^{*\alpha}}{M_1^{\alpha\beta}M_2^\alpha}\right)^{1/(1-\alpha\beta)}. \end{gathered} \tag{2.38}$$

Estimates of practical persistence for (2.1) are provided by (2.31) and (2.38). We summarize with a more specific version of Theorem 2.1.

Theorem 2.2. *(Practical Persistence) Assume the hypotheses of Theorem 2.1. Let ν_1^* and ν_2^* be determined by (2.28) and (2.29). If $(x(t), y(t))$ is any positive solution of (2.1), there is a $t^* > 0$ such that*

$$(x(t), y(t)) \in [\delta_1, M_1] \times [\delta_2, M_2] \text{ for all } t > t^* \tag{2.39}$$

where δ_1 and δ_2 are given by (2.31). If condition (2.3) in Theorem 2.1 is replaced by (2.4) and if ν_1^* and ν_2^* are given by (2.35) and (2.36), then (2.39) holds with δ_1 and δ_2 are given by (2.38).

3. An example - Identical $L - V$ competitors

We consider the Lotka-Volterra model for a pair of identical competitors with time delay:

$$\begin{aligned} \dot{x}(t) &= x(t)\left[\frac{1}{2} - \frac{2}{3}x(t-\tau) - \frac{1}{3}y(t-\tau)\right] \\ \dot{y}(t) &= y(t)\left[\frac{1}{2} - \frac{1}{3}x(t-\tau) - \frac{2}{3}y(t-\tau)\right]. \end{aligned} \tag{3.1}$$

For any time delay $\tau \geq 0$

$$E = (x^*, y^*) = (.5, .5)$$

is the unique equilibrium for (3.1) in R_+^2, and it is known (e. g., see [9]) that E is a globally (relative to R_+^2) asymptotically stable for all $\tau \geq 0$. We would like our practical persistence (permanence) estimates to be as close as possible to the known attractor E here. First we use the following result from [4] to estimate dissipative constants $M_1 = M_2 = M$. (For completeness, we include its proof in the appendix.)

Proposition 3.1. *Suppose $u(t)$ is a C^1 positive function defined on an interval $[t_0 - \tau, \infty)$ for some $t_0 \geq 0$ which also satisfies the differential delay inequality*

$$\dot{u}(t) \leq u(t)[a - bu(t-\tau)] \tag{3.2}$$

where $a \geq 0$ and $b > 0$ are constants. Then

$$\limsup_{t\to+\infty} u(t) \leq \frac{a}{b}e^{a\tau}. \tag{3.3}$$

Since x and y are non-negative (3.1) immediately gives the uncoupled inequality system with identical components:

$$\begin{aligned} \dot{x}(t) &\leq x(t)\left[\frac{1}{2} - \frac{2}{3}x(t-\tau)\right] \\ \dot{y}(t) &\leq y(t)\left[\frac{1}{2} - \frac{2}{3}y(t-\tau)\right] \end{aligned} \tag{3.4}$$

and hence from Proposition 3.1

$$M = M(\tau) = M_1(\tau) = M_2(\tau) = \frac{1/2}{2/3}e^{(1/2)\tau} = .75e^{.5\tau}. \tag{3.5}$$

Positive solutions of (3.1) must eventually reside in the square

$$X_0 = (0, M] \times (0, M]$$

and, corresponding to $\tau = 0$, .25, and .5, for example, we have

$$M = .75, .85 \text{ and } .97, \tag{3.6}$$

respectively. Also, by symmetry here, we can take $\alpha = \beta$, $\eta_1 = \eta_2$, $\nu_1 = \nu_2 = \nu$, and $P_1 = P_2 = P$. It follows that $\nu_1^* = \nu_2^* = \nu^*$ and $\delta_1 = \delta_2 = \delta$. We make use of the Liapunov functions

$$V_1 = xy^{-.5} \quad V_2 = x^{-.5}y \tag{3.7}$$

to investigate persistence. Our estimate for the attractor is the set

$$\begin{aligned} X_3 &= \{(x,y) \in X_0 : V_1(x,y) > \eta, V_2(x,y) > \eta\} \\ &= \{x \le M, y \le M, V_1(x,y) > \eta, V_2(x,y) > \eta\} \end{aligned} \tag{3.8}$$

where M is given by (3.6) and η is determined below. Toward this end, according to (2.36), we first need ν (as large as possible) with the property

$$f(x,y) - \frac{1}{2}g(x,y) = \frac{1}{4} - \frac{x}{2} > 0$$

for all $x \in [0, \nu)$ and $y \in [0, M]$. Thus $\nu = .5$, and we calculate, from (2.35),

$$\nu^* = \nu e^{P\tau} \tag{3.9}$$

where

$$P = \min\{f(x,y) : (x,y) \in \overline{X}_0\}.$$

Here

$$P = \frac{1}{2} - \frac{2}{3}M - \frac{1}{3}M = \frac{1}{2} - M = -.25, -.35, \text{ and } -.47 \tag{3.10}$$

if $\tau = 0$, .25, and .5, respectively, for example. Thus

$$\nu^* = \nu e^{P\tau} = .5e^{P\tau} = .5, .46, .40$$

for $\tau = 0$, .25, and .5 respectively, and finally we get from (2.37)

$$\eta = \nu^* / \sqrt{M} = .58, .50, .41. \tag{3.11}$$

Finally, from (2.38)

$$\delta = \left(\nu^{1.5}\right)^{1/(.75)} = \eta^2 = .34, .25, .17. \tag{3.12}$$

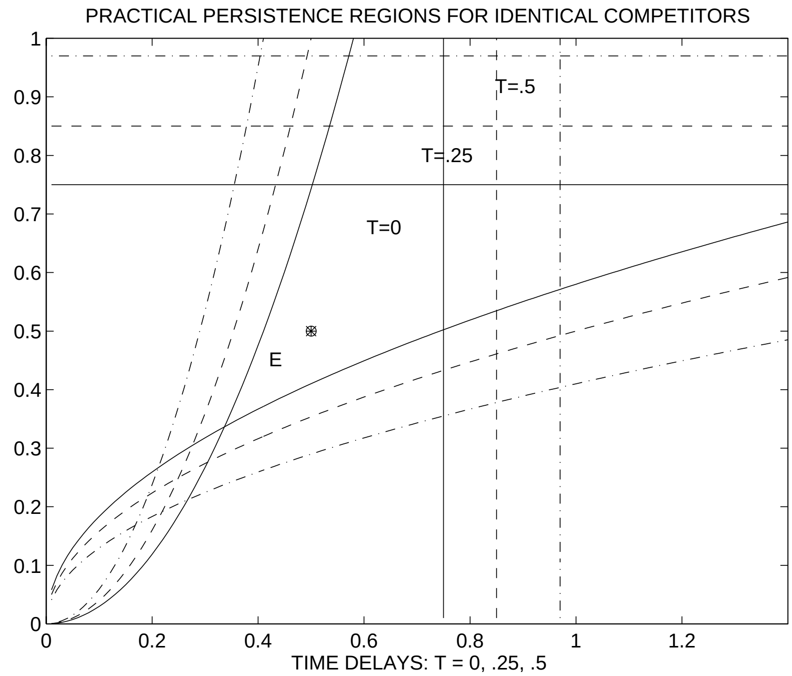

Figure 1.

Actually, for any $0 \le \tau < 1$ we have, from (3.6) and (3.9)-(3.12),

$$\delta = \frac{\nu^2 e^{(1-2M)\tau}}{M} = \frac{(.5)^2 e^{(1-1.5e^{.5\tau})\tau}}{.75e^{.5\tau}} \approx \frac{(1-\tau)}{3}.$$

APPENDIX

Proof of Proposition 3.1. We consider two cases - whether or not $u(t)$ is eventually monotone. In the first case, if $u(t)$ is eventually non-decreasing, say on the interval (t_1, t_2), then $u(t) \le a/b$ for $t > t_1 + \tau$, because $a - bu(t-\tau) \ge 0$ for $t > t_1$ from (3.2). If $u(t)$ is non-increasing on (t_1, ∞), then

$$\lim_{t \to +\infty} u(t) = u_0$$

is finite. If $u_0 > a/b$, then $u(t) > a/b + \epsilon$, some $\epsilon > 0$ and $t >$ some $t_2 > t_1$. Thus for $t > t_2 + \tau, u(t-\tau) > a/b + \epsilon$ and from (3.2)

$$\dot{u}(t) \le u(t)[a - b(a/b + \epsilon)] = -b\,\epsilon\, u(t).$$

But this last inequality implies $u(t) \to 0$, as $t \to \infty$, contradicting that $u_0 > a/b$. We conclude in the monotone case that

$$\limsup_{t \to +\infty} u(t) \le \frac{a}{b}.$$

If $u(t)$ is not eventually monotone, $u(t)$ has a local maximum at each point in a sequence $\{t_n\} \subseteq (t_0+\tau,\infty)$ with $t_n \to \infty$ as $n \to \infty$ and

$$\limsup_{t\to+\infty} u(t) \quad = \lim_{n\to+\infty} u(t_n).$$

Since $\dot{u}(t_n) = 0$, (3.2) yields

$$u(t_n-\tau) \le \frac{a}{b}.$$

Certainly (3.2) gives $\dot{u}(t) \le au(t)$ for all $t > t_0$. Thus integrating (3.2) on each interval $[t_n-\tau, t_n]$ and using the previous two inequalities obtains

$$u(t_n) \le u(t_n-\tau)e^{a\tau} \le \frac{a}{b}e^{a\tau},$$

and then

$$\limsup_{t\to+\infty} u(t) \quad = \lim_{n\to+\infty} u(t_n) \le \frac{a}{b}e^{a\tau}$$

which completes the present proof.

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