Global Journal of Pure and Applied Mathematics.
ISSN 0973-1768 Volume 17, Number 1 (2021), pp. 79-88

https://dx.doi.org/10.37622/GJPAM/17.1.2021.79-88

Harmless Delay in Mutualist, Prey and Several Predators Systems

Ravinder Kumar[+] and Yogendra Singh[#]

Department of Mathematics,
Dayalbagh Educational Institute (Deemed University),
Dayalbagh, Agra – 282005, U.P., India.

Abstract

We study a model of delay differential equations that involves one mutualist, one prey and several predators. We show that the model is viable. Sufficient conditions are derived for delay to be harmless and preservation of stability/instability of interior equilibrium.

1. INTRODUCTION

We recall that interaction between two species that benefits both is called mutualism. When the interaction is not mandatory for survival, mutualism is called facultative otherwise it is called obligatory. If only one of the species is benefitted in the interaction, it is called commensalism. In this paper we analyze a time delay model of a mutualist, a prey and several predators.

Let E^* be an equilibrium point of a system of autonomous differential equations with retarded time delay(s). The delay(s) is (are) called harmless if for all its non-negative values the stability/ instability of E^* is preserved. Studies involving stabilization, destabilization and harmless delays in predator-prey and related systems have been carried out by various authors. In particular Freedman and Sree Hari Rao [3,4], Erbe et al. [1] and Gopalsamy [5] Gyori [7], Kumar[11,12] and Kumar & Singh [13] study models involving time delays. Hofbauer and So [8] obtain necessary and sufficient conditions for preservation of asymptotic stability of the equilibrium of a system with off-diagonal delays.

In this paper we obtain sufficient conditions for a harmless delay in a model that involves one mutualist, one prey and n-predators.

2. THE MODEL

The delay differential equations model with one constant delay is given by,

$$\left.\begin{aligned} \frac{du}{dt} &= uh(u, x, y_1 \cdots y_n) && (1a) \\ \frac{dx}{dt} &= \alpha x g(u, x) - \sum_{i=1}^{n} p_i(u, x) y_i && (1b) \\ \frac{dy_i}{dt} &= y_i[-s_i(u, y_i) + c_i(u) p_i(u, x(t-\tau))], 1 \le i \le n, && (1c) \end{aligned}\right\} \quad (1)$$

$u(t_0) = u_0 \ge 0, x(t) = \varphi(t) \ge 0, -\tau \le t \le 0, y_i(t_0) = y_{i0} \ge 0, 1 \le i \le n.$

Here the variable $u(t)$ represents the mutualist's density at time t. The functions $x(t)$ and $y_i(t)$ denote the prey and predator densities at time t. The function h represents the specific growth rate of the mutualist and the function $g(u, x)$ that of prey in the absence of any predation. The non-negative constant τ, is the time delay due to gestation, in the prey.

The functions $p_i(u, x), 1 \le i \le n$, denote the predator functional response.

The functions $c_i(u)$, $1 \le i \le n$, are the positive rates of conversion of prey biomass to the predator biomass.

The functions $s_i(u, y_i)$ are the specific death rates of the predator y_i , $1 \le i \le n$, in the absence of predation.

Also $\alpha > 0$ is a parameter.

We also assume that for $u \ge 0$, $x \ge 0$, $y_i \ge 0$, $1 \le i \le n$,

$$(H_1)\ h(0, x, y_1, \cdots y_n) > 0\ , \frac{\partial h}{\partial u} < 0, \qquad (2)$$

The condition (H_1) implies that independent of the $x, y_1, \cdots y_n$ populations, u is capable of growing even when rare. Also the growth rate is assumed to be density dependent and decreases as the mutualist population increases.

We assume that

$$(G_1) \quad g(u, 0) > 0, \qquad \frac{\partial g(u, x)}{\partial x} < 0\ ,$$

(G_2) There exists a unique $K(u)$ such that $g\big(u, K(u)\big) = 0$.

The condition (G_1) implies that the prey population is capable of surviving in the presence or absence of the mutualist and the growth rate in absence of predation is density dependent.

The condition (G_2) implies that $K(u)$ is the carrying capacity of the prey in the absence of predation.

Further, we assume:

$$(P_1)\ p_i(u,0) = 0, \qquad \frac{\partial p_i(u,x)}{\partial x} > 0, \qquad 1 \le i \le n.$$

The above conditions imply that in absence of prey there is no predation. Also, the predator functional response is assumed to be an increasing function of the prey population.

We also assume the death rate is an increasing function of the population, i.e., $\frac{\partial s_i(u,y_i)}{\partial y_i} > 0, 1 \le i \le n.$

Below we give additional hypotheses under which (1) exhibits mutualism:

For facultative mutualism between u and x, we assume:

$$(H_2) \qquad \frac{\partial h}{\partial x} \ge 0, \quad \frac{\partial h}{\partial y_i} \le 0, 1 \le i \le n, \qquad (3)$$

and that there exists a unique function $L(x, y_1, \cdots y_n) > 0$ such that $h(L(x, y_1, \cdots y_n), x, y_1, \cdots y_n) = 0.$

The condition (H_2) implies that $L(x, y_1, \cdots y_n)$ is the mutualist's carrying capacity and in part specifies in what way the predators and prey become part of the mutualist's environment. Further we require,

$$\tilde{\tilde{L}} = \lim_{x\to\infty} L(x, 0, \dots, 0) < \infty.$$

Also let one or more of the following holds:

$$(H_3) \qquad \frac{\partial g(u,x)}{\partial u} \ge 0, \frac{\partial p_j(u,x)}{\partial u} \le 0, \frac{\partial s_j(u,y_j)}{\partial u} \ge 0, c_j'(u) \le 0, j = 1,2, \dots n.$$

For mutualism between u and y_i, we require

$$\frac{\partial h}{\partial x} \le 0, \frac{\partial h}{\partial y_i} \ge 0, \frac{\partial h}{\partial y_j} \le 0, j \ne i$$

There exists a unique function $L(x, y_1, \dots y_n)$ such that $h(L, x, y_1, \dots y_n) = 0$.
$(H_3') \quad \tilde{L} = \lim_{y_i\to\infty} L(0,0, \dots, 0, y_i, 0, \dots 0) < \infty.$

Further we assume that one or more of the following hold:

$$\frac{\partial s_i(u,y)}{\partial u} \le 0, c_i'(u) \ge 0, \frac{\partial p_i(u,x)}{\partial u} \ge 0.$$

3. GENERAL RESULTS

In this section we show that the model is viable, i.e. solutions are positive and bounded.

Theorem 1 If $\left(u_0, \varphi(t_0), y_1(t_0), \dots, y_n(t_0)\right) > (0,0,0,\dots,0)$ then $\left(u(t), x(t), y_1(t), \dots y_n(t)\right) > (0,0,0,\dots,0)$ for $t > 0$.

Proof Integrating $(1a)$ we get $u(t) = u_0 exp\left(\int_{t_0}^{t} h\left(u(s), x(s), y_1(s), \dots, y_n(s)\right)\right) ds$ is positive whenever $u_0 > 0$. Similarly we can prove that $x(t), y_i(t), 1 \le i \le n$ are positive whenever $\varphi(t_0), y_i(t_0), 1 \le i \le n$ are positive.

Next we show that solutions are bounded. The proof extends the idea presented in Theorem 3 of [15]:

Theorem 2 Let

$\widehat{c_l} = \max_{[0,\tilde{L}]} c_l(u) > 0, \widehat{p_l}(x) = \max_{u\epsilon[0,\tilde{L}]} p_l(u,x) < \infty,$

$\widehat{s_l}(y_l) = \min_{[0,\tilde{L}]} s_l(u, y_l) > 0,$

$\widehat{s_l}(0) > 0, \hat{s}_l^{'}(0) > 0, \hat{s}_l^{''}(y_l) \ge 0, l = 1,2, \dots., n.$

Then system (1) has bounded solutions. In fact $0 \le u \le \tilde{L} + \epsilon$, $0 \le x \le \widehat{K} + \epsilon$, $0 \le y_l \le M_l$, for large t,

where, $\widehat{K} = \max_{[0,\tilde{L}]} K(u)$, $M_l = \frac{\widehat{c_l}\widehat{p_l}(\widehat{K})+\epsilon}{\widehat{s_l}(0)}, l = 1,2, \dots \dots n.$

Proof Let $\left(u(t), x(t), y_1(t), \dots \dots, y_n(t)\right)$ be any solution with non-negative initial condition $(u_0, x_0, y_{10}, \dots \dots, y_{n0})$.

Then $u' = uh(u, x, y_1, \dots \dots, y_n)$

$\le uh(u, x, 0 \dots \dots, 0),$

Whenever $u(t) > \widetilde{L},$

$u' \le uh\left(\tilde{L}, x, 0, \dots \dots, 0\right) < 0.$

Thus if $u_0 \le \tilde{L}$, $u(t) \le \tilde{L}\ \forall t \ge 0$. Also $u_0 > \tilde{L} \Rightarrow u(t) \le \tilde{L} + \epsilon$ for large t, any $\epsilon > 0$.

Next, let $g_1(x) = \max_{[0,\tilde{L}]} g(u, x)$.

Then $x' = xg_1(x), x(t_0) = x_0 \ge 0$

satisfies $x(t) \le \widetilde{K}$ and hence $x(t) \le \widetilde{K}\ \forall t \ge 0$, whenever $x_0 \le \widetilde{K}$. If $x_0 > \widetilde{K}$, and $\epsilon > 0$, $x(t) \le \widetilde{K} + \epsilon$, for large t.

Next consider,

$y_l' = y_l\left(-\widehat{s_l}(y_l) + \widehat{c_l}\widehat{p_l}\big(x(t-\tau)\big)\right),$

$y_l' \le y_l\left(-\widehat{s_l}(0) - \widehat{s_l'}(0)y_l + \widehat{c_l}\widehat{p_l}\big(x(t-\tau)\big)\right).$

We claim $y_l(t) \le M_l$ for $t \ge T$, for some $T > 0$. The proof is by contradiction. Let $y_l(t) > M_l$ for large t,

i.e. $y_l > \frac{\widehat{c_l}\widehat{p_l}(\widetilde{K})+\epsilon}{\widehat{s_l'}(0)}, 1 \le l \le n.$

Thus $y_l'(t) < 0$,

$\Rightarrow y_l(t) \to y_{l0} \ge M_l$, as $t \to \infty$.

$\exists\ t_k \to \infty$ such that

$y_l'(t_k) \to 0$ as $k \to \infty$.

$-\widehat{s_l}\big(y_l(t_k)\big) + \widehat{c_l}\widehat{p_l}\big(x(t_k - \tau)\big) \to 0$, as $t \to \infty$.

Also, $\widehat{c_l}\widehat{p_l}\big(x(t_k-\tau)\big) \to p^l = \widehat{s_l}(y_{l0})$

$\le \widehat{c_l}\widehat{p_l}\big(\widehat{K}\big) + \frac{\epsilon}{2}.$

By Mean Value Theorem,

$\widehat{s_l}\big(y_l(t_k)\big) - \widehat{s_l}(0) = y_l(t_k)\widehat{s_l'}(\xi_{lk}),$

where ξ_{lk} lies between $y_l(t_k)$ and zero.

or

$y_l(t_k)\widehat{s_l'}(\xi_{lk}) \to p^l - \widehat{s_l}(0)$

$y_l(t_k)\widehat{s_l'}(0) \le y_l(t_k)\widehat{s_l'}(\xi_{lk}).$

Thus $y_l(t_k) \le \frac{p^l - \widehat{s_l}(0) + \frac{\epsilon}{2}}{\widehat{s_l'(0)}}$, for large k.

$y_l(t_k) < \frac{p^l}{\widehat{s_l'}(0)} < M_l$, for sufficiently small $\epsilon > 0$.

This is a contradiction.

Now let $\exists t_n > 0$ such that $y_l(t_n) < M_l$ and t_l^0 such that $y_l(t_l^0) = M_l$, for some $t_l^0 > t_n$. Let $t_0^l > t_n$ be least such t.

Then $y_l'\big(t_0^l\big) \ge 0$. This gives

$-\widehat{s_l}\left(y_l\big(t_0^l\big)\right) + \widehat{c_l}\widehat{p_l}\left(x\big(t_0^l - \tau\big)\right) \ge 0$

or

$-\widehat{s_l}(0) - y_l\big(t_0^l\big)\widehat{s_l'}(\xi_l) + \widehat{c_l}\widehat{p_l}\left(x\big(t_0^l - \tau\big)\right) \ge 0,$

where ξ_l lies between 0 and $y_l(t_0^l)$.

So

$-y_l(t_0^l)\widehat{s_l'}(0) + \widehat{c_l}\widehat{p_l}(\widehat{K}) > 0$

or

$y_l(t_0^l) < M_l$.

This is a contradiction.

Hence Proof.

4. HARMLESS DELAY

We assume throughout that hypotheses (H_1), (G_1), (G_2) and (P_1) hold. We also assume that mutualism exists between u and x or u and y_i (see section 2) and that an interior equilibrium $E^*(u^*, x_1^*, y_1^*, \dots, y_n^*)$ exists.

Linearizing (1) about E^* we obtain,

$$X' = AX + Be^{-\lambda\tau}, \tag{2}$$

where $A = (a_{ij})_{n+2,n+2}$, $B = (b_{ij})_{n+2,n+2}$,

$a_{11} = uh_u$, $a_{12} = uh_x$, $a_{1j+2} = uh_{y_j}, j = 1, \dots, n.$

$a_{21} = \alpha x g_u - \sum_{i=1}^{n} p_{i_u} y_i$, $a_{22} = \alpha g + \alpha x g_x - \sum_{i=1}^{n} p_{i_x} y_i$, $a_{2j+2} = -p_j$, $j = 1,2, \dots n.$

$a_{i+21} = -y_i s_{i_u} + y_i c_i p_{i_u} + c_i' y_i p_i$, $a_{i+22} = 0, i = 1,2, \dots, n.$

$a_{i+2i+2} = -s_i + c_i p_i - y_i s_{i_{y_i}}, i = 1,2, \dots, n.$

$$a_{i+2j+2} = 0, \quad i,j = 1,2, \dots, n, j \neq i. \tag{3}$$

$b_{ij} = 0, i = 1,2, \quad j = 1,2, \dots, n+2.$

$b_{i+22} = c_i y_i p_{i_x}$, $i = 1, \dots, n,$

and

$b_{i+2j+2} = 0, \quad i,j = 1,2, \dots, n.$

The matrices A and B above are assumed to be evaluated at the interior equilibrium point $E^*(u^*, x^*, y_1^*, \dots, y_n^*)$.

This leads to characteristic quasipolynomial equation,

$$p(\lambda) = det(A + Be^{-\lambda\tau} - \lambda I) = 0, \tag{4}$$

Denote by L the matrix,

$$L(\lambda,\tau) = \left(l_{ij}\right) = A + Be^{-\lambda\tau} - \lambda I = 0, \quad (5)$$

Expanding determinant in (4), we get,

$$F(\lambda,\tau) = P_{n+2}(\lambda) + e^{-\lambda\tau}P_n(\lambda) = 0, \quad (6)$$

where $P_j(\lambda)$ is a polynomial in λ of degree j.

The first result of this section is clear from Theorem 4.1[p.83,10].

Theorem 3 Let

(i) $P_{n+2}(\lambda)$ and $P_n(\lambda)$ have no common imaginary roots.

(ii) $P_{n+2}(0) + P_n(0) \neq 0$

(iii) $Q(y) = |P_{n+2}(iy)|^2 - |P_n(iy)|^2$ for real y has at least a finite number of real zeros.

(iv) Also let $Q(y) = 0$ has no positive roots.

Then the delay is harmless.

Below we assume in (6) λ can be solved as a continuous function $\tau, \tau \geq 0$.

Theorem 4

(i) Let matrix $L(i\mu,\tau)$ be diagonally dominant, for all $\mu \in R$ and $\tau \geq 0$. That is,

$$|a_{ii}|d_i > |b_{i2}|d_2 + \sum_{j\neq i}^{n+2}\left|a_{ij}\right| d_j, i = 1,2,\dots,n+2, \quad (7)$$

for some positive $d_i's$.

Then the non-negative delay in the system (1) is harmless.

(ii) If in addition to (7) at least one eigenvalue of $A + B$ has positive real part or trace of A is positive, then the equilibrium is unstable for all non-negative delays.

(iii) If in addition to (7), $a_{ii} < 0$ for all $i = 1,2,\dots,n+2$. then the equilibrium E^* is asymptotically stable for all non-negative, delays.

Proof: The matrix $\hat{B}$= ($d_i^{-1}l_{ij}\, d_j$) is similar to $L(i\mu,\tau)$ and by conditions (7) is diagonally dominant for all $\mu \in R$. Thus by Gershgorin theorem $detL(i\mu,\tau)$ is non-zero. Therefore all zeros $\lambda(\tau)$ of $detL(\lambda,\tau)$ have non-zero real part and by continuity do not change sign for all non- negative delays. That is (i) holds. In case (ii), both alternatives yield $L(i\mu,0)$ has at least one root with positive real part. This together with (i) implies equilibrium E^* is unstable for any non-negative delay. In case (iii) all eigenvalues of $L(i\mu,0)$ have negative real parts (Takeuchi [16, p. 27]). Hence equilibrium E^* asymptotically stable when τ = 0. Also by case (i) any non-negative delay is harmless. Hence proof.

Remark 1 Using the fact that the matrix A+B is diagonally dominant if and only if $(A+B)^T$ is ([2, p. 144]) we conclude that when $(A+B)^T$ be diagonally dominant then the non-negative delay is harmless.

When $L(i\mu,\tau)$ is a normal matrix, we obtain:

Theorem 5

Let $L(i\mu,\tau)$ be a normal matrix and $(A+A^T)$ be positive definite. Whenever

$$\lambda_{n+2}(A+A^T)-2\sqrt{\sum_{k=3}^{n+2} b_{k2}^2}>0, \tag{8}$$

(Here $\lambda_n(P)$ denotes the least eigenvalue of the n x n matrix P) and E^* is unstable when $\tau=0$ then instability is preserved for all non-negative τ.

Proof By[6] the real parts of the eigenvalues of the normal matrix $L(i\mu,\tau)$ are eigenvalues of the Hermitian matrix

$$\frac{1}{2}(A+A^T)+\frac{1}{2}(B^T+B)\cos\tau\mu+\frac{i}{2}(B^T-B)\sin\tau\mu.$$

Further by [pg.242, 9],

$\lambda_{n+2}(A+A^T+(B^T+B)\cos\tau\mu+i(B^T-B)\sin\tau\mu)$

$\geq\lambda_{n+2}(A+A^T)+\lambda_{n+2}(B^T+B)\cos\tau\mu+\lambda_{n+2}(i(B^T-B)\sin\tau\mu)$

$\geq\lambda_{n+2}(A+A^T)-|\lambda_{n+2}(B^T+B)|-|\lambda_{n+2}(B^T-B)|$

$=\lambda_{n+2}(A+A^T)-2\sqrt{\sum_{k=3}^{n+2} b_{k2}^2}>0.$

Hence by continuity the result follows.

Lastly when all eigenvalues of $A+B$ are real, we give a set of sufficient conditions for preservation of asymptotic stability:

Theorem 6

Let all eigenvalues of matrix $A+B$ be real, and for some positive d_i's,

$$d_i d_j\ a_{ii}a_{jj}>R_i R_j, \text{for i, j} =1,\dots \text{n}+2,\ \text{i}\neq\text{j},$$

where $R_i=\sum_{j\neq i}^{n+2}|a_{ij}+b_{ij}|\,d_j$, for i $=1,\dots,$ n $+2$.
In addition, if $a_{ii}<0, for\ i=1,\dots,n+2$, then the equilibrium E^* is asymptotically stable for all non-negative delays.

Proof Set D = diag$(d_1,\dots,d_{n+2})$. Under the above hypotheses det $(D^{-1}(A+B)$D$)$ is non-zero ([14, p. 149]) and thus $\det(L(i\mu,\tau))$ is non-zero for all real values of μ. By continuity real part of $\lambda(\tau)$ does not change sign and the delay is harmless. Each eigenvalue λ of $A+B$ satisfies [14, p. 149],

$|\lambda - a_{ii}||\lambda - a_{jj}| \leq R_i R_j$, for some i and $j, i \neq j$.

This gives,

$\lambda^2 + a_{ii}a_{jj} - d_i^{-1}d_j^{-1}R_iR_j \leq (a_{ii} + a_{jj})\lambda$.

Under above conditions left-hand side is positive and the result is clear.

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