

ASYMPTOTIC STABILITY OF LINEAR AND NONLINEAR MODEL SYSTEMS REPRESENTING AGE-STRUCTURED PREDATOR-PREY INTERACTIONS*

M. SALEEM

*Department of Applied Mathematics, Zakir Hussain College of Engineering & Technology,
A.M.U., Aligarh (UP), India*

AND

A. K. TRIPATHI

Govt. M.L.B. Girls Higher Secondary School, Datia (MP), India

(Received 3 October 1997; after revision 7 June 1999; accepted 21 September 1999)

We consider a predator-prey model system assuming predator population to be age-structured. This assumption works two folds (i) it facilitates consideration of predators' active involvement in predation to be predator age-dependent (ii) it helps incorporate delay effects into the system. Our model formulation yields a nonlinear system of integro-differential equations of which Sih model¹⁵ becomes a special case when all predators are assumed to be equally active in predation.

We analyse both linear and nonlinear systems under fairly general conditions on functions and give sufficient conditions for asymptotic stability of the positive equilibrium solution of our model system. It is found that the advanced age-group predators' active involvement in predation promotes co-existence of species. This result seems to be against the usual rule of thumb that a large delay destabilizes the system. Finally, we emphasize that the stability results of this paper can be used in the study of prey-refuge effects on age-structured predator-prey interactions.

Key Words : Predator-Prey; Age-structure; Time-delay; Asymptotic stability

1. INTRODUCTION

Mathematical modelling on predator-prey interactions is quite a familiar phenomenon now. Many generalizations to the classical Lotka-Volterra model have been studied¹⁻⁶ and a large body of stability results exists.¹⁻¹⁴

*This work was initiated when the first author was employed with Bundelkhand Institute of Engineering & Technology, Jhansi (U.P.)

In many situations, predators and prey appear to co-exist at relatively stable population levels. In other cases, instability has been observed either in terms of prey driven extinct or prey population showing large explosions. Different authors have explained these phenomenon addressing different factors⁷ & ¹¹. One observes from the literature that a large part of the theory developed for the explanation of stability and instability patterns of predator and prey populations deals with predator responses to prey (e.g. functional, switching etc.). In contrast to this, very little empirical or theoretical work is found in the literature which deals with prey responses to predator. Sih¹⁵ studies (as one of the simplest examples of prey responses to predator) prey refuges and its effects on the stability of a predator-prey model. More references on prey refuge may be seen in^{11,12,16 & 17}.

The purpose of the present paper is to generalize the model of Sih¹⁵ to make it applicable to age-structured predator-prey interactions. We assume only predator population to be age-structured. This assumption works two folds. On the one hand, it allows consideration of predators' active involvement in predation to be predator age-dependent. On the other hand, it helps incorporate delay effects into the system. To be more specific, we assume that predators' active participation in predation depends on their age and is represented by a general weight function of age of predator. Time delays in the growth dynamics of a population or of several interacting species have been considered by many researchers,^{2, 13, 14 & 20} We introduce delays into our model system through age-structure of predators. Thus the main model system (3) of this paper (of which Sih model¹⁵ becomes a special case when all predators are assumed to be equally active in predation) can also be considered to be representing predator-prey interactions with unbounded delay. More specifically, it may represent a situation where growth and removal rates of species depend on the size of the predator in the present and in the past. Not to mention, the study of delays is important as at times they produce contrasting results.

We analyse both linear and nonlinear systems. The main tools in our analysis are the Miller's method, construction of Liapunov functionals and the Krasovskii's method. We give sufficient conditions for asymptotic stability of the positive equilibrium solution of the model system (3) and emphasize that likewise¹⁵ the stability results of this paper can be used in the study of prey refuge effects on age-structured predator-prey interactions. Such a study will be a part of a future paper by the authors.

In section 2, we formulate the main model system Section 3. Deals with stability results for linear system. Stability analysis for nonlinear system is discussed in section 4. Main conclusions are given in section 5.

2. MODEL SYSTEM

Denoting by $\rho(a, t)$ the predator population density with individuals of age a at time t , we assume the evolution of this population to be governed by (see^{3,4} for details)

$$\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = -c\rho$$

and

$$\rho(0, t) = bF(P, N) \int_0^{\infty} \beta(a) \rho(a, t) da. \quad \dots (1)$$

Various terms in (1) have the following meaning:

$c > 0$ is the death rate of the predator population and $1 > b > 0$ denotes the rate of conversion of food (in terms of prey eaten) to individuals of predators of age zero.

$P = P(t) = \int_0^{\infty} \rho(a, t) da$ represents the total predator population at time t .

$N = N(t)$ represents the total prey population at time t .

$F(P, N)$ denotes the number of prey eaten by an active individual predator. $\beta \eta(a)$ is a weight function of age of predator representing the weighted effect of active predators.

Under the natural assumption $\rho(+\infty, t) = 0$ for all t and following^{3, 4} eq. (1) can be written as

$$\frac{dP}{dt} = -cP + bF(P, N) \left[\delta P + \int_{-\infty}^t K(t-s) P(s) ds \right], \quad \dots (2)$$

where

$$\delta = \beta(0) \text{ and } K(u) = \beta(u) e^{-cu} \text{ with } ' = d/da.$$

We augment eq. (2) with a similar equation for the dynamics of prey and obtain the main model system of this paper as follows :

$$\frac{dP}{dt} = -cP + bF(P, N) \left[\delta P + \int_{-\infty}^t K(t-s) P(s) ds \right]$$

and

$$\frac{dN}{dt} = rN - F(P, N) \left[\delta P + \int_{-\infty}^t K(t-s) P(s) ds \right]. \quad \dots (3)$$

Here $r > 0$ denotes the intrinsic growth rate of prey in the absence of predators. The negative term on the right hand side of (3b) represents the removal of prey due to predation.

We shall need the following assumptions in our subsequent analysis.

(A0) For any positive continuous and bounded initial function $(\xi, \gamma) = (\xi(t), \gamma(t))$ on $(-\infty < t < 0)$, there exists a unique positive solution¹⁸ $(P(t), N(t)) \equiv (P(t, \xi), N(t, \eta))$ of the model system (3) for all $t \in [0, \infty)$ such that

$$P(t), N(t) = (\xi(t), \gamma(t)) \text{ for all } t \in (-\infty, 0].$$

(A1) The function F is continuously differentiable in the set

$$S = \{(P, N) \in R^2 : 0 < P < \infty, 0 < N < \infty\}$$

(A2) $\beta(a)$ is a non-negative continuously differentiable function satisfying

$$\beta(a) \geq 0 \text{ and } 0 < \int_0^{\infty} e^{-za} \beta(a) da = \beta^*(z) < \infty.$$

We shall be using the following specific forms for weight function $b\eta(a)$ for illustration of our stability results in the following sections:

$$(i) \beta(a) = \frac{1}{\alpha} e^{-a/\alpha},$$

$$\text{and } (ii) \beta(a) = \frac{1}{\alpha^2} a e^{-a/\alpha} \quad \alpha > 0, a \geq 0 \quad \dots (4)$$

Here the first form for $\beta(a)$ emphasizes that small age group predators are more active in predation, the second form represents a situation where predators of age $a = \alpha$ are more active.

Considering further appropriate conditions (in addition to A1) on the function F , it can be assumed that the system (3) has a unique positive equilibrium solution (P^*, N^*) satisfying

$$b\beta^*(c) F(P, N) - 1 = 0$$

and

$$cP - brN = 0.$$

Remark : Considering $\beta(a) \equiv 1$ (or assuming predators' active involvement in predation to be independent of age of predator) reduces the model system (3) to

$$\frac{dP}{dt} = -cP + bF(P, N)P$$

and

$$\frac{dN}{dt} = rN - F(P, N)P,$$

which is the model of Sih¹⁵.

3. LINEAR SYSTEM

Invoking the transformations $P(t) = P^* + p(t)$ and $N(t) = N^* + n(t)$, the vector-matrix form of the linearized system corresponding to model system (3) turns out to be

$$\frac{dX}{dt} = AX + \int_{-\infty}^t K(t-s) MX(s) ds, \quad \dots (5)$$

where

$$X = X(t) = \begin{bmatrix} p(t) \\ n(t) \end{bmatrix}, \quad M = \begin{bmatrix} bF & 0 \\ -F & 0 \end{bmatrix},$$

and

$$A(a_{ij}), \quad i, j = 1, 2,$$

with

$$a_{11} = b\delta F - c + Pcb \beta^*(c) \frac{\partial F}{\partial P}, \quad a_{12} = Pcb \beta^*(c) \frac{\partial F}{\partial N},$$

$$a_{21} = -\delta F - Pc \beta^*(c) \frac{\partial F}{\partial P}, \quad a_{22} = r - Pc \beta^*(c) \frac{\partial F}{\partial N}$$

$$P = P^*, \quad N = N^*, \quad F = F(P^*, N^*),$$

$$\frac{\partial F}{\partial P} = \frac{\partial F}{\partial P} \Bigg|_{P=P^*, N=N^*} \quad \text{and} \quad \frac{\partial F}{\partial N} = \frac{\partial F}{\partial N} \Bigg|_{P=P^*, N=N^*}$$

We analyse the system (5) using the Miller's method and the construction of Liapunov functionals and investigate the asymptotic stability of its zero solution.

Miller's Method :

According to Miller¹⁹ (also see^{2,3}), the zero solution of (5) is asymptotically stable if the characteristic equation associated with it i.e.

$$(z-r)(z+c) \left[1 - \frac{\beta^*(z+c)}{\beta^*(c)} \right] - (z-r)bPc \beta^*(c) \frac{\partial F}{\partial P} + (z=c)Pc \beta^*(c) \frac{\partial F}{\partial N} = 0 \quad \dots (6)$$

has no roots such that $Re z \geq 0$.

Construction of Liapunov Functionals :

Relegating the necessary details to Appendix A, the zero solution of (5) is asymptotically stable if

$$\frac{\partial F}{\partial N} > \frac{1}{1-b} \frac{F}{N}$$

and

$$\frac{1}{\beta^8(c)} > \left[\frac{(b-1)Pc \frac{\partial F}{\partial P}}{c + (1-b)\delta F} \right] \quad \dots (7)$$

In order to gain a better understanding of conditions (6) and (7) and with a view to interpret them in biological terms, we consider a few specialised situations and study the following cases :

Case I — When predators do not interfere with each other $\left(\text{or } \frac{\partial F}{\partial P} = 0 \right)$

Under this assumption, conditions (6) and (7) change to following conditions (8) and (9) respectively. Necessary details may be seen in *Appendix B*.

$$\frac{\partial F}{\partial N} > 2 \frac{F}{N} \quad \dots (8)$$

and

$$\frac{\partial F}{\partial N} > \frac{1}{1-b} \frac{F}{N} \quad \dots (9)$$

Both these conditions likewise¹⁵ suggest that predators cause density dependent mortality of prey for co-existence of species. A close comparison of conditions (8) and (9) with the one reported in¹⁵ i.e.

$$\frac{\partial F}{\partial N} > \frac{F}{N}$$

gives the following three types of stability regions denoted Regions I, II and III.

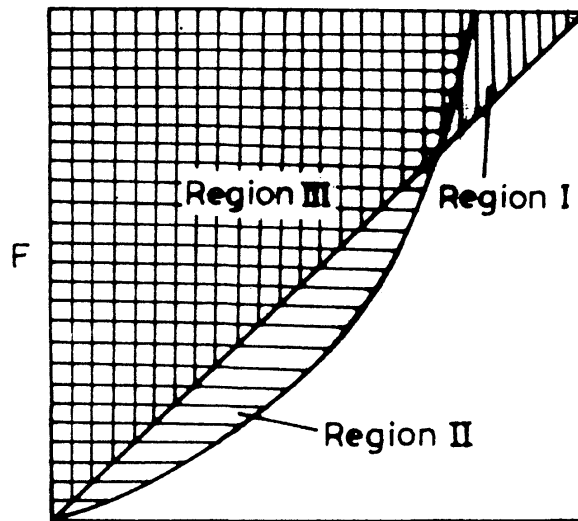


FIG. 1. Stability regions due to density dependent mortality of prey.

Region I denoted by vertical lines corresponds exclusively to Sih model¹⁵. Region II denoted by horizontal lines corresponds exclusively to our model. Region III shown by squares represents the common region of stability suggested by both models. It is clear from this figure that age structure may be beneficial for co-existence of species if predators cause density dependent mortality of prey for low densities of prey (see Region II). On the other hand, age-structure may be harmful if the predators cause density dependent mortality of prey for large densities of prey (see Region I). Noting that $0 < b < 1$, a further comparison of conditions (8) and (9) yields that the construction of Liapunov functional method provides a better condition for stability than Miller's. Indeed (8) is a special case of (9) for $b = 1/2$.

Case II — When predators interfere with one another $\left(\text{or } \frac{\partial F}{\partial P} < 0 \right)$.

In this case, stability conditions (7) due to construction of Liapunov functionals remain the same. One special but interesting case satisfying equation (6) may be reported as follows. One may refer to Appendix C for necessary details.

$$F + \frac{P}{4} \frac{\partial F}{\partial P} < 0,$$

$$-\frac{P}{2N} \frac{\partial F}{\partial P} > \frac{\partial F}{\partial N} > 2 \frac{F}{N} .$$

and

$$\frac{1}{\beta^*(c)} > v \left(\frac{PF}{N} \right),$$

where

$$v = \frac{N \frac{\partial F}{\partial N}}{N \frac{\partial F}{\partial N} + P \frac{\partial F}{\partial P}} > 1. \quad \dots (10)$$

As such the stability conditions (7) and (10) do not seem to be simple regard to their biological interpretation. With a view to illustrate them to some understandable limits, we further refer to some special situations. First, we discuss (10). Let us assume

$$N \frac{\partial F}{\partial N} + P \frac{\partial F}{\partial P} > 0$$

for otherwise the characteristic equation (6) has at least one real positive root and the zero solution of (5) is unstable. Let us further assume

$$PF > \frac{1}{v} N. \quad \dots (11)$$

This means that the total prey eaten is greater than a definite fraction $\left(\frac{1}{v} < 1 \right)$ of the prey.

To be more specific, $v=2$ requires that the total prey eaten is greater than half of the prey. Finally, assuming the specific form (4b) for the weight function $\beta(a)$, stability conditions (10) reduce to

$$F + \frac{P}{4} \frac{\partial F}{\partial P} < 0,$$

$$-\frac{P}{2N} \frac{\partial F}{\partial P} > \frac{\partial F}{\partial N} > 2 \frac{F}{N}$$

and
$$\alpha > \frac{1}{c} \left[\sqrt{\frac{vPF}{N}} - 1 \right]. \quad \dots (12)$$

We now turn to conditions (7). Assuming

$$(b-1)P \frac{\partial F}{\partial P} > 1, \quad \dots (13)$$

(which may hold true if the interference among the predators is high) and the specific form (4b) for $b\eta(a)$, conditions (7) reduce to

$$\frac{\partial F}{\partial N} > \frac{1}{1-b} \frac{F}{N}$$

and

$$\alpha > \frac{1}{c} \left[\sqrt{\left\{ (b-1)P \frac{\partial F}{\partial P} \right\}} - 1 \right]. \quad \dots (14)$$

Both conditions (12) and (14) hint at a possibility of co-existence of species even if the interference among the predators is too strong (see (12a) and (13)). It may be noted that such a possibility does not exist in non-age-structured model¹⁵. Furthermore, both conditions (12) and (14) suggest that the advanced age-group predators' involvement in predation may promote co-existence of species. This result seems to be against the usual rule of thumb that large delays cause instability.

4. NONLINEAR SYSTEM

In this section, we use Krasovskii's method to investigate sufficient conditions for asymptotic stability of the positive equilibrium solution (P^*, N^*) of the nonlinear system (3).

In addition to assumptions (A0) - (A2) (see section 2), we assume as in^{2, 22} the following:

(A3) All the positive solutions $(P(t), N(t))$ of the model system (3) exist and are bounded for all $t \in (0, \infty)$ and are such that

$$K_1 \leq P(t) \leq K_2$$

and

$$L_1 \leq N(t) \leq L_2, \quad \dots (15)$$

where K_i and L_i are positive real numbers.

Introducing the transformations

$$p_1 = \log \frac{P}{P^*} \text{ and } n_1 = \log \frac{N}{N^*}, \quad \dots (16)$$

we reduce the model system (3) to the following vector form.

$$\frac{dX}{dt} = \bar{f}(X, t)$$

where

$$X = \begin{bmatrix} p_1 \\ n_1 \end{bmatrix} \text{ and } \bar{f}(X, t) = \begin{bmatrix} h_1(p_1, n_1, t) \\ h_2(p_2, n_2, t) \end{bmatrix},$$

with

$$h_1(p_1, n_1, t) = -c + be^{-p_1} F(P^* e^{p_1}, N^* e^{n_1}) \left[\delta e^{p_1} + \int_{-\infty}^t k(t-s) e^{p_1(s)} ds \right]$$

and

$$h_2(p_2, n_2, t) = r - \frac{P^*}{N^*} e^{-n_1} F(P^* e^{p_1}, N^* e^{n_1}) \left[\delta e^{p_1} + \int_{-\infty}^t k(t-s) e^{p_1(s)} ds \right].$$

It is obvious that $\bar{f}(0, t) = 0$ for all $t \in (-\infty, \infty)$.

Following analysis steps of Rao and Pal²² yields that the positive equilibrium solution of (3) is asymptotically stable if

$$\frac{\partial h_1}{\partial p_1} < 0$$

and

$$\frac{\partial h_1}{\partial p_1} \cdot \frac{\partial h_2}{\partial n_1} > \frac{1}{4} \left[\frac{\partial h_1}{\partial n_1} + \frac{\partial h_2}{\partial p_1} \right]^2. \quad \dots (17)$$

Using (15) and (16), inequality (17b) takes the form

$$b \frac{\partial F}{\partial P} \left[\frac{F}{L_1} - \frac{\partial F}{\partial N} \right] > \frac{1}{4} \left[\frac{bL_2}{K_1} \frac{\partial F}{\partial N} - \left(F + K_2 \frac{\partial F}{\partial P} \right) \frac{1}{L_1} \right]^2. \quad \dots (18)$$

It seems that the large conversion rate of food eaten by predators into new predator individuals and greater predator interference may help satisfy condition (18).

In view of (16), condition (17a) requires that

$$\frac{\partial F}{\partial P} \left[\delta P(t) + \int_{-\infty}^t K(t-s) P(s) ds \right] < 0,$$

which holds true if

$$\frac{\partial F}{\partial P} < 0$$

and

$$\delta P(t) + \int_{-\infty}^t K(t-s) P(s) ds > 0. \quad \dots (19)$$

Again with a view to give some biological meaning to conditions (18) and (19), we consider the following cases :

Case I — Predators' predation capacity decreases with age (or $\beta(a) < 0$ for all $a \geq 0$)

In this case, making use of (15), condition (19b) is satisfied if

$$\frac{1}{\beta^*(c)} < \frac{cK_2}{\delta(K_2 - K_1)}$$

which takes the form

$$\frac{1}{\alpha} < \frac{cK_2}{(K_2 - K_1)} \quad \dots (20)$$

for specific form (4a) of the weight function $\beta(a)$. Condition (20) suggests that less and less smaller age-group predators should be involved in predation to ensure co-existence of species.

Case II — Predators' predation capacity is distributed about a particular age (or $\beta(a) > 0$ for $a \leq A$ and $-\beta'(a) < 0$ for $a > A$).

Under this assumption, condition (19b) is satisfied if

$$\delta K_1 + K_1 \int_0^A \beta'(a) e^{-ca} da + K_2 \int_A^\infty \beta'(a) e^{-ca} da > 0$$

which takes the form

$$\alpha e^{\alpha c} > \frac{(K_2 - K_1)}{K_1 c e} \quad \dots (21)$$

for specific form (4b) of weight function $\beta(a)$. Condition (21) once again confirms that the advanced age-group predators' active participation in predation may promote co-existence of species.

5. CONCLUSIONS

We consider a generalised predator-prey interaction model assuming age-structure in predator population. Firstly, this assumption facilitates consideration of predators' active participation in predation to be predator age-dependent. Secondly, it helps introduce delay effects into the system. To be more specific, we assume that different predators have different predation capabilities as per their age according to which they take part in predation. The weighted effect of a predator individual of age a to predation is assumed to be represented by a nonnegative continuous general weight function $\beta(a)$.

The introduction of age-structure into predator population leads to a nonlinear system of integro-differential eqs. (3) that may also be considered as a model system representing predator-prey interactions with unbounded delay. More specifically, it may be said that the model system (3) represents a situation where growth and removal rates of populations depend on the size of the predator population in the present and in the past.

We analyse both linear and nonlinear systems. The main tools in our analysis are the Miller's method and construction of Liapunov functionals for linear system (5) and the Krasovskii's method for nonlinear system (3). We give sufficient conditions for asymptotic stability of the positive equilibrium solution of the model system (3).

Some important observations that can be made from the stability results of this paper are :

Under the assumption that predators do not interfere with each other in predation, our model system guarantees co-existence of species if predators cause density dependent mortality of prey. This is clear from conditions (8) and (9) which are of the type $\frac{\partial F}{\partial N} > \xi \frac{F}{N}$ where $\xi > 1$ and F denotes the number of prey eaten by an active predator. Note that $\xi = 1$ in model¹⁵. Thus it may be concluded from the results of section 3. that age-structure may be beneficial (in comparison to non-age-structured model¹⁵) for co-existence of species if predators cause density dependent mortality of prey for low densities of prey. On the other hand, it may be harmful if predators cause density dependent mortality of prey for large densities of prey. (see figure in section 3)

Under the assumptions (i) predators interfere with each other (ii) the total prey eaten is greater than a definite fraction of the prey (see condition (11)), it is observed that the advanced age-group predators' active involvement in predation promotes co-existence of species. This result seems to be against the usual rule of thumb that a large delay causes instability.

Even more interestingly the same unusual result (suggesting advanced age-group predators' active participation for co-existence of species) follows for nonlinear system (3). It is also seen that small age-group predators' involvement in predation should be lesser and lesser to ensure co-existence of species.

Unlike non-age-structured model¹⁵, it is seen that a greater interference among predators may help co-existence of species.

Finally, it is important to mention that the stability results of this paper can be used in the study of prey refuge effects on age-structured predator-prey interactions. Such a study will be a part of a future paper by the authors.

Appendix A

Following^{20, 21} we construct the Liapunov functional L as

$$L(p(\cdot), n(\cdot)) = |p(t) + |n(t)|. \quad \dots (A_1)$$

Obviously, L is positive definite on R^2 . Computing the time derivative of (A_1) along a solution $((P, n) \neq (0, 0))$ of (5), we see that $\frac{dL}{dt} < 0$ under conditions (7).

Appendix B

Condition (9) is trivially obtained from conditions (7). Under the assumption $\frac{dF}{dP} = 0$, the characteristic equation (6) can be written as

$$\frac{\beta^*(z+c)}{\beta^*(c)} = \frac{z+k}{z-r}, \quad \dots (A_2)$$

where

$$k = Pc\beta^*(c) \frac{\partial F}{\partial N} - r.$$

One can see that the left hand side of (A2) maps $Re z \geq 0$ into a unit circle whereas its right hand side maps $Re z \geq 0$ outside the unit circle under the condition (8) because if $w = \frac{z+k}{z-r}$ then $|w|^2 - 1 \geq 0$ under (8).

Appendix C

We write the characteristic eq. (6) as

$$\frac{\beta^*(z+c)}{\beta^*(c)} = 1 + \frac{k_1(z+c) + k_2(z-r)}{(z-r)(z+c)}, \quad \dots (A_3)$$

where

$$k_1 = Pc\beta^*(x) \frac{\partial F}{\partial N} > 0$$

and

$$k_2 = -bPc\beta^8(c) \frac{\partial F}{\partial P} > 0.$$

Writing $w = 1 + \frac{k_1(z+c) + k_2(z-r)}{(z-r)(z+c)},$

and following the argument of *Appendix B* again, one can see that while the left hand side of (A3) maps $Re z \geq 0$ into the unit circle, its right hand side maps $Re z \geq 0$ outside the unit circle under conditions (10).

ACKNOWLEDGEMENT

We wish to thank anonymous referees whose valuable suggestions have improved this paper considerably.

REFERENCES

1. F. M. Scudo and J. R. Zeigler, *L N Biomath*, **22**, Springer-Verlag, 1978.
2. J. M. Cushing, *L. N. Biomath* **20**, Springer-Verlag, 1977.
3. J. M. Cushing, *CBMS - NSF Reg. Conf. Ser. Appl. Math.* SIAM, Philadelphia (1998).
4. J. M. Cushing and M. Saleem, *J. math. Biol.* **14** (1982) 231-50.
5. H. I. Freedman and R. M. Mathsen, *Bull. math. Biol.* **55** (1993) 817-27.
6. M. E. Gurtin and D. S. Levine, *SIAM J. appl. Math* **42** (1) (1982) 94-108.
7. M. P. Hassell, *The Dynamics of Anthropol Predator Prey System*, Princeton Univ Press, Princeton, N.J., 1978.

8. Hsu, Sze-B1 and T. W. Huang, *SIAM J. appl. Math.* **553(3)** (1995) 763-83.
9. A. Hastings, *Theor. Pop. Biol.* **23** (1983) 347-62.
10. T. Lindstrom, *J. math. Biol.* **31** (1993) 341-61.
11. W. W. Murdoch and A. Oaten, *Adv. ecol. Res.* **9** (1975) 1-31.
12. R. M. May, *Stability and Complexity in Model Ecosystems*, Princeton Univ Press, Princeton, N.Y (1975).
13. R. M. May, *Ecology* **54** (1973) 315-325.
14. G. Stepan, *Nonlinear Anal. Theory Method Appl.* **10** (1986) 913-29.
15. A. Sih, *Theor. Pop. Biol.* **31** (1987) 1-12.
16. R. H. Smith and R. Mead, *Theor. Pop. Biol.* **6** (1974) 308-22.
17. P. G. Crowley, *Amer. nat.* **118** (1981) 673-701.
18. M. R. M. Rao and S. Sivasundaram, *J. math. Anal. Appl.* **131** (1988) 97-105.
19. R. K. Miller, *Delay and Functional Differential Equations and Their Applications* (Ed: K. Schmitt) Acad Press, N. Y., 1972.
20. T. A. Burton, *Volterra Integral and Differential Equations* Acad. Press, N.Y., 1983.
21. C. Corduneanu and V. Lakshmikantham, *Nonlin. anal. Theory Method Appl.* **4** (1980) 831-77.
22. M. R. M. Rao and V. N. Pal, *J. math. Anal. Appl.* **163** (1) (1992) 60-72.