

Stability and optimal harvesting in a stage structure predator-prey switching model

Q. J. A. Khan and Lakdere Benkherouf
Department of Mathematics and Statistics,
College of Science, Sultan Qaboos University,
P.O. Box 36, P. C. 123, Al-Khod , Muscat,
Sultanate of Oman

Abstract

This paper is concerned with a stage structure predator-prey interaction where the prey is a stage structure with two life stages immature and mature. The predator consumes both the young and adult of the prey and the prey population is more prone to predator at higher densities. Local and global stabilities of the equilibrium sets are discussed. With harvesting for the mature population we obtain conditions for a threshold of the harvesting for sustainable yield.

Keywords: Stage structure, Local stability, Global stability, Optimal harvesting, Switching

1 Introduction

It is now recognized that the predator prefers to eat the prey species according to age, size, weight, numbers, etc. Several models have been put forward where a predator prefers to catch the prey species that is most abundant one at that time (Stephens and Krebs 1986). When a prey species is of small size, with little or insignificant defence capability with respect to predator then a predator catches a member of given species proportional to their abundances. The predator feeds preferentially on the most numerous species, which is thus over-represented in the predators diet. However, it is likely that in many cases a predator will consume more individuals of other species when one of its prey becomes relatively less abundant. This behaviour is termed predator switching. Many examples may be cited where a predator prefers to prey on species that are most abundant at any time, see Fisher - Pitte [1], Lawton,

et al. [2] and Murdoch [3]. They also established that switching is a normal feature of predator behaviour. Mathematical models involving one predator and two prey species have been generally studied, in which the predator feeds more intensively on the more abundant species (e.g. Holling [4], Takahashi [5], May [6,7], Murdoch and Oaten [8], Rougharden and Feldman [9], Tanksky [10], Prajneshu and Holgate [11], Khan et al. [12,13].

In the natural world, almost all animals have the age structure of immature and mature. In particular, mammalian populations and some amphibious animals exhibit these two stages. There are two types of stage dependent predation in predator-prey models. In the first of these the predators eat only adults. These are cases where insects are preyed upon only in the adult stage (e.g. Lloyd and Dybas [14]. On the other hand, there are well documented cases where predators consume only immature prey. Le Caven et al. [15] and Nielsen [16] have described such cases.

Several models have been proposed to account for the stage structure of immature and mature of the species. One can refer to Freedman et al. [17], Gurney et al. [18] Xinyu Song and Lansun Chen [19], Khan et al. [20], Zhang et al. [21] investigated a mathematical model of two species with stage structure of immature and mature of the prey species. They assumed that predators interact only with immature population of prey species. In this paper we consider the case where a second specie is a predator of both mature and immature prey species. The predator can feed on either stage of prey but instead of choosing individuals at random predator would catch a member of the immature or adult prey populations which is proportional to their abundance, that is the predator feeds preferentially on the most numerous stage species. This implies a kind of switching from immature to mature alternately. This is the normal feature of predator behaviour. Similar to Zhang [21] model we also considered harvesting of mature prey population, which is more appropriate to the economic and biological views of renewable resources management. Economic and biological aspects of renewable resource management have been considered by Clark [23], Leng [24], Bhattacharya et al. [25] and John [26]. We obtain conditions for local and global stabilities of the equilibrium sets and a threshold of the harvesting for sustainable yield.

Tansky [10] investigated a mathematical model of two prey and one predator system which has the switching property of predation of the following

form

$$\begin{aligned}\frac{dx}{dt} &= \left\{ \gamma_1 - \frac{az}{1 + (y/x)^n} \right\} x, \\ \frac{dy}{dt} &= \left\{ \gamma_2 - \frac{bz}{1 + (x/y)^n} \right\} y, \\ \frac{dz}{dt} &= -\delta + \frac{a_1xz}{1 + (y/x)^n} + \frac{a_2yz}{1 + (x/y)^n}, \quad n = 1, 2, 3\end{aligned}$$

where x, y and z denote abundance of two kinds of the prey species and a predator species, respectively. γ_1 and γ_2 are the specific growth rates of the prey species in the absence of predation and δ is the per capita death rate of the predator. The functions $\frac{a}{1 + (y/x)^n}$ and $\frac{b}{1 + (x/y)^n}$ have a characteristic property of switching mechanism. The predatory rate that an individual of the prey species is attacked by a predator decreases when the population of that species becomes rare compared with the population of another prey species. This property is much amplified for large value of n . This paper is organized as follows - The model for the species is presented in the section 2. Section 3 is concerned with equilibrium and stability analysis. Section 4 deals with Global Stability. Optimal harvesting is discussed in Section 5. Final discussion and results are summarized in Section 6.

2 The model

The prey-predator model with simple multiplicative effect where prey species is stage structure of immature and mature is of the form:

$$\begin{aligned}\frac{dx_1}{dt} &= \alpha x_2 - \kappa x_1 - \beta x_1 - \eta_1 x_1^2 - \frac{bx_1^2 y}{x_1 + x_2}, \\ \frac{dx_2}{dt} &= \beta x_1 - \kappa x_2 - \frac{bx_2^2 y}{x_1 + x_2} - h, \\ \frac{dy}{dt} &= \left(\frac{bx_1^2}{x_1 + x_2} + \frac{bx_2^2}{x_1 + x_2} - d \right) y,\end{aligned}\tag{2.1}$$

with $x_i(0) > 0$, $i = 1, 2$, $y(0) > 0$.

- x_i : the population of the immature and mature prey species of stage i
- y : population of predator species
- α : per capita birth rate of matured prey species
- β : maturation rate from immature stage to mature stage
- κ : per capita death rate of both stages of prey species
- η : proportionality of self interaction of immature population
- d : per capita death rate of predator

where $h = qEx_2$ is the harvesting yield, q is the catchability coefficient and E is the harvesting effort. We are considering optimal harvesting of the mature population. In order to reduce the number of parameters, we consider

$$bt = \tau, \frac{\alpha}{b} = \alpha_1, \frac{\eta}{b} = \eta_1, \frac{\kappa}{b} = \kappa_1, \frac{h}{b} = H, \frac{\beta}{b} = \beta_1, \frac{d}{b} = d_1$$

Then (2.1) turned into

$$\begin{aligned} \frac{dx_1}{d\tau} &= \alpha_1 x_2 - k_1 x_1 - \beta_1 x_1 - \eta_1 x_1^2 - \frac{x_1^2 y}{x_1 + x_2} \\ \frac{dx_2}{d\tau} &= \beta_1 x_1 - k_1 x_2 - \frac{x_2^2 y}{x_1 + x_2} - H \\ \frac{dy}{d\tau} &= \left(\frac{x_1^2}{x_1 + x_2} + \frac{x_2^2}{x_1 + x_2} - d_1 \right) y \end{aligned} \quad (2.2)$$

3 Steady States and Stability Analysis

We find the steady states of equations (2.2) by equating the derivatives on the left hand sides to zero and solving the resulting algebraic equations. This gives two possible steady states

(i) $\bar{E}_1 = (\bar{x}_1, \bar{x}_2, 0)$

where \bar{x}_1 is the positive root of the equation

$$\eta_1 \bar{x}_1^2 + \bar{x}_1 \left(\kappa_1 + \beta_1 - \frac{\alpha_1 \beta_1}{\kappa_1} \right) + \frac{\alpha H}{\kappa_1} = 0, \quad (3.1)$$

and

$$\bar{x}_2 = \frac{\beta_1 \bar{x}_1 - H}{\kappa_1}. \quad (3.2)$$

This will exist if $\frac{\alpha_1 \beta_1}{\kappa_1} > (\kappa_1 + \beta_1)$ and $\beta_1 \bar{x}_1 > H$.

(ii) $\bar{E}_2 = (\hat{x}_1, \hat{x}_2, \hat{y}) = \left(\frac{d_1(\bar{x} + 1)\bar{x}}{C(1 + \bar{x}^2)}, \frac{d_1(1 + \bar{x})}{C(1 + \bar{x}^2)}, \frac{(1 + \bar{x})}{\bar{x}} \left(\frac{\alpha_1}{\bar{x}} - \kappa_1 - \beta_1 - \eta_1 x_1 \right) \right)$,

or equivalently

$$= \left(\frac{d_1(\bar{x} + 1)\bar{x}}{C(1 + \bar{x}^2)}, \frac{d_1(1 + \bar{x})}{C(1 + \bar{x}^2)}, (1 + \bar{x})(\beta_1 \bar{x} - H_1 - qE_1) \right). \quad (3.3)$$

Here $\bar{x} = \frac{\hat{x}_1}{\hat{x}_2}$ is a real positive root of the equation,

$$\beta_1 C \bar{x}^5 + \bar{x}^4 (-C(\kappa_1 + qE_1)) + \bar{x}^3 ((\kappa_1 + \beta_1)C + \beta_1 C + \eta_1 d_1) + \bar{x}^2 (-C\kappa_1 + qE_1 C + \eta_1 d_1 - \alpha_1 C) + \bar{x} ((\kappa_1 + \beta_1)C) - \alpha_1 C = 0. \quad (3.4)$$

For equilibrium values $(\hat{x}_1, \hat{x}_2, \hat{y})$ to be positive, a positive real root of (3.4) must be bounded as

$$\frac{\kappa_1 + qE_1}{\beta_1} < \bar{x} < \frac{\alpha_1}{\kappa_1 + \beta_1 + \eta_1 \bar{x}_1}. \quad (3.5)$$

Stability Analysis

We proceed in the usual manner by considering small disturbances from the steady state and linearising the resulting equations.

It is easy to show that the equilibrium $\bar{E}_1 = (\bar{x}_1, \bar{x}_2)$ is locally unstable so proof is omitted.

Stability analysis of equilibrium (ii).

The stability matrix of the equilibrium, $\bar{E}_2 = (\hat{x}_1, \hat{x}_2, \hat{y})$ is

$$\begin{bmatrix} L - \lambda & B & \frac{-\hat{x}_1 \bar{x}}{1 + \bar{x}} \\ A & -A\bar{x} - \lambda & \frac{-\hat{x}_2}{1 + \bar{x}} \\ C + D\hat{x}_1 & C + D\hat{x}_2 & -\lambda \end{bmatrix}, \quad (3.6)$$

where

$$\begin{aligned} B &= \alpha_1 + \frac{\hat{x}_1^2 \bar{y}}{(\hat{x}_1 + \hat{x}_2)^2}, \\ L &= -\frac{B}{\bar{x}} - \eta_1 \hat{x}_1, \\ A &= \beta_1 + \frac{\hat{x}_2^2 \bar{y}}{(\hat{x}_1 + \hat{x}_2)^2}, \\ C &= \frac{-\bar{y}(\hat{x}_1^2 + \hat{x}_2^2)}{(\hat{x}_1 + \hat{x}_2)^2}, \quad D = \frac{2\hat{y}}{\hat{x}_1 + \hat{x}_2}. \end{aligned} \quad (3.7)$$

The characteristic equation associated with the positive equilibrium $\bar{E}_2 (\hat{x}_1, \hat{x}_2, \hat{y})$

of this model is

$$\begin{aligned} \lambda^3 + \lambda^2 (A\bar{x} - L) - \lambda \left(LA\bar{x} - \frac{\hat{x}_2}{1 + \bar{x}} (C + D\hat{x}_2) + AB - \frac{\hat{x}_1\bar{x}}{1 + \bar{x}} (C + D\hat{x}_1) \right) \\ + \left[-\frac{L\hat{x}_2}{(1 + \bar{x})} (C + D\hat{x}_2) + \frac{B\hat{x}_2}{1 + \bar{x}} (C + D\hat{x}_1) + \frac{AC\hat{x}_1\bar{x}}{1 + x} + \frac{AC\hat{x}_1\bar{x}^2}{1 + \bar{x}} \right] \\ + \frac{AD\hat{x}_1\bar{x}}{1 + \bar{x}} (\hat{x}_2 + \hat{x}_1\bar{x}) = 0 \end{aligned} \quad (3.8)$$

Equation (3.8) can be written in the form

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \quad (3.9)$$

where

$$\begin{aligned} a_1 &= A\bar{x} - L \\ a_2 &= \frac{\hat{x}_2}{1 + \bar{x}} (C + D\hat{x}_2) + \frac{\hat{x}_1\bar{x}}{1 + \bar{x}} (C + D\hat{x}_1) - LA\bar{x} - AB \\ a_3 &= \frac{B\hat{x}_2}{1 + \bar{x}} (C + D\hat{x}_1) + \frac{AD\hat{x}_1\bar{x}}{1 + \bar{x}} (\hat{x}_2 + \hat{x}_1\bar{x}) + AC\hat{x}_1\bar{x} \\ &\quad - \frac{L\hat{x}_2}{(1 + \bar{x})} (C + D\hat{x}_2). \end{aligned} \quad (3.10)$$

The Routh-Hurwitz stability criteria for the third order system is

- (a) $a_1 > 0, a_3 > 0$
- (b) $a_1a_2 > a_3$.

Hence, the equilibrium (ii) will be locally stable to small perturbations provided $\bar{x} > 1$. The details of the analysis is given in Appendix.

We summarized the results by the following theorem.

Theorem 1 *If $\bar{x} > 1$ then \bar{E}_2 is asymptotically stable.*

4 Global Stability of Interior Equilibrium

Theorem 2 *Existence of positive interior equilibrium of system equation (2.1) implies its global asymptotic stability around the positive interior equilibrium provided the ratio of the young and adult prey species at any time has nearly same value as at the equilibrium.*

We make use of the general Lyapunov function

$$v(x_1, x_2, y) = \sum_{i=1}^2 \left[(x_i - \hat{x}_i) - \bar{x}_i \ln \left(\frac{x_i}{\hat{x}_i} \right) \right] + (y - \hat{y}) - \bar{y} \ln \left(\frac{y}{\hat{y}} \right). \quad (4.1)$$

Now calculating time derivative of equation (4.1) along the solutions of equation (2.1), we have

$$\begin{aligned} \frac{dv}{dt} &= (x_1 - \hat{x}_1) \left[\alpha_1 \frac{x_2}{x_1} - \beta_1 - \kappa_1 - \eta_1 x_1 - \frac{x_1 y}{x_1 + x_2} \right] \\ &\quad + (x_2 - \hat{x}_2) \left[\beta_1 \frac{x_1}{x_2} - \kappa_1 - \frac{x_2 y}{x_1 + x_2} - q_1 E \right] \\ &\quad + (y - \hat{y}) \left[\frac{x_1^2}{x_1 + x_2} + \frac{x_2^2}{x_1 + x_2} - \frac{\hat{x}_1^2}{\hat{x}_1 + \hat{x}_2} - \frac{\hat{x}_2^2}{\hat{x}_1 + \hat{x}_2} \right]. \end{aligned}$$

At equilibrium

$$\begin{aligned} \kappa_1 + \beta_1 &= \frac{\alpha_1 \hat{x}_2}{\hat{x}_1} - \eta_1 \hat{x}_1 - \frac{\hat{x}_1 \hat{y}}{\hat{x}_1 + \hat{x}_2} \\ q_1 E \hat{x}_2 &= \beta_1 \hat{x}_1 - \kappa_1 \hat{x}_2 - \frac{\hat{x}_2^2 \hat{y}}{\hat{x}_1 + \hat{x}_2}. \end{aligned}$$

So

$$\begin{aligned} \frac{dv}{dt} &= -\eta_1 (x_1 - \hat{x}_1)^2 + \frac{(\hat{x}_1 x_2 - x_1 \hat{x}_2)}{(x_1 + x_2)(\hat{x}_1 + \hat{x}_2)} [\hat{y} (x_1 - x_2) - y (\hat{x}_1 - \hat{x}_2)] \\ &\quad + \alpha (x_1 - \hat{x}_1) \left(\frac{(\hat{x}_1 x_2 - x_1 \hat{x}_2)}{x_1 \hat{x}_1} \right) - \beta_1 (x_2 - \hat{x}_2) \left(\frac{(\hat{x}_1 x_2 - x_1 \hat{x}_2)}{x_1 x_2} \right). \end{aligned}$$

If $\frac{\hat{x}_1}{\hat{x}_2} = \frac{x_1}{x_2}$ (i.e. the ratio of young and adult prey species is nearly same as at equilibrium value) then

$$\frac{dv}{dt} = -\eta (x_1 - \hat{x}_1)^2 < 0$$

Hence, $\bar{E}_2(\hat{x}_1, \hat{x}_2, \hat{y})$ is globally asymptotically stable for $\frac{\hat{x}_1}{\hat{x}_2} \simeq \frac{x_1}{x_2}$ for all $t \geq 0$.

5 Optimal Harvesting

From the economic and biological point of view of renewable resources management it is more appropriate the exploitation of mature population. It

is desirable to have a unique positive equilibrium which is globally asymptotically stable. If the ratio of mature and immature population is nearly the same as their respective population at equilibrium point then the unique positive equilibrium of system (2.2) is globally asymptotically stable. In this section, we are considering the harvesting with a mature population and studying the maximum sustainable yield of the system (2.2)

System (2.2) has a positive equilibrium \hat{E}_2 if and only if

$$E_1 < \frac{\beta_1 \bar{x} - \kappa_1}{q}. \quad (5.1)$$

Hence, the maximum value of the harvesting effort is given by equation (5.2)

$$E_1 = E_1^* = \frac{\beta_1 \bar{x} - \kappa_1}{q}, \quad (5.2)$$

i.e.

$$E_1 \in [0, E_1^*].$$

Let $x_2 = \hat{x}_2$, the harvesting of the system (2.2) is

$$H(E_1) = qE_1 \hat{x}_2 = \frac{d_1 q}{C} \left[\frac{E_1 (1 + \bar{x})}{(\bar{x}^2 + 1)} \right]. \quad (5.3)$$

Finding the derivative of $H(E_1)$, we get

$$\begin{aligned} \frac{dH}{dE_1} &= \frac{d_1 q}{C} \left[\frac{\left\{ (1 + \bar{x}) + \frac{d\bar{x}}{dE_1} E_1 \right\} (\bar{x}^2 + 1) - 2\bar{x} (\bar{x} + 1) E_1 \frac{d\bar{x}}{dE_1}}{(\bar{x}^2 + 1)} \right] \\ \frac{dH}{dE_1} &> 0 \text{ if } E_1 < \frac{(1 + \bar{x}) (\bar{x}^2 + 1)}{\frac{d\bar{x}}{dE_1} (\bar{x}^2 + 2\bar{x} - 1)}. \end{aligned} \quad (5.4)$$

(i) If $E_1 \in [0, E_1^*]$ and inequality given in (5.4) is satisfied then the maximum sustainable yield is

$$\text{Max}H(E_1) = qE_1^* \hat{x}_2 = \frac{d_1 (\beta_1 \bar{x} - \kappa) (1 + \bar{x})}{C (\bar{x}^2 + 1)} \quad (5.5)$$

(ii) The solution of $\frac{dH}{dE_1} = 0$ is $E_1 = \bar{E}_1 = \frac{(1 + \bar{x}) (\bar{x}^2 + 1)}{\frac{d\bar{x}}{dE_1} (\bar{x}^2 + 2\bar{x} - 1)}$.

The maximum yield depends on the value of \bar{E}_1 and E^* . The corresponding results are given as follows:

- (a) $\bar{E}_1 > E_1^*$, then the maximum yield is given by equation (5.5)
- (b) $\bar{E}_1 \in [0, E_1^*]$ and inequality (5.4) is not satisfied then the corresponding maximum yield is

$$MaxH = H(\bar{E}_1) = \frac{qd_1(1 + \bar{x})^2}{C \frac{d\bar{x}}{dE_1}(\bar{x}^2 + 2\bar{x} - 1)}$$

Theorem 3 (i) If $E_1 < \frac{(1 + \bar{x})(\bar{x}^2 + 1)}{\frac{d\bar{x}}{dE_1}(\bar{x}^2 + 2\bar{x} - 1)}$, and either $E_1 \in [0, E_1^*]$ or $\bar{E}_1 > E_1^*$, then, the maximum sustainable yield in system (2.2) is

$$MaxH = \frac{d_1(\beta_1\bar{x} - \kappa)(1 + \bar{x})}{C(\bar{x}^2 + 1)}.$$

$$(ii) \text{ If } E_1 \geq \frac{(1 + \bar{x})(\bar{x}^2 + 1)}{\frac{d\bar{x}}{dE_1}(\bar{x}^2 + 2\bar{x} - 1)},$$

and $\bar{E}_1 \in [0, E_1^*]$, then the maximum sustainable yield in system (2.2) is

$$MaxH = \frac{qd_1(1 + \bar{x})^2}{C \frac{d\bar{x}}{dE_1}(\bar{x}^2 + 2\bar{x} - 1)}.$$

6 Discussion

The mathematical model which we have proposed consists of three non-linear ordinary differential equations, namely, an immature population, mature population and their predator. The predator can feed on either stage of prey but instead of choosing individuals at random would catch a member of the immature or mature prey population which is proportional to their abundance. The predator feeds preferentially on the most numerous stage species. This behaviour is termed predator switching. We have given conditions for the stability of the equilibria. The dynamical behaviour of the system shows that the system around positive interior equilibrium is locally stable in some region of parametric space and unstable in some other region of parametric space. It has been also observed that the system around

the positive equilibrium is globally asymptotically stable if the ratio of the young and adult prey species at any time has nearly the same value as at the equilibrium point. We studied the maximum sustainable yield of the system. For economic and biological views of renewable resources management we studied exploitation of mature population. From the point of view of ecological management, it is desirable to have a unique positive equilibrium which is globally asymptotically stable, in order to plan harvesting strategies and keep sustainable development of ecosystem. We obtain conditions for threshold of harvesting for the mature population. The optimal harvesting for the mature population is also considered.

References

- [1] C. R. Fisher-Piatt, *Soc. Biolgeogr*, 92, 47-48 (1934).
- [2] J. H. Lawton, J. R. Beddington and R. Bonser, Switching in invertebrate predators. *Ecological studies*, 9, 144-158 (1974).
- [3] W. W. Murdoch and A. Oaten, Predation and population stability. *Adv. Ecol. Res.*, 9, 1-131 (1975).
- [4] C. S. Holling, Principles of insect predation. *Ann. Rev. Entomol.* 6, 163-182 (1961).
- [5] F. Takahashi, Reproduction curve with two equilibrium points: a consideration of the fluctuation of insect population. *Res. Pop. Ecol.* 47, 733-745 (1964).
- [6] R. M. May, *Stability and Complexity in model ecosystems*. Princeton, NJ: Princeton Univesity Press (1973).
- [7] R. M. May, some mathematical problems in biology, Providence, RI. *Am. math. Soc.*, 4, 11-29 (1974).
- [8] W. W. Murdoch and A. Oaten, Predation and population stability *Adv. Ecol. Res.*, 9, 1-131 (1975).
- [9] J. Roughgarden and M. Feldman, Species packing and predation pressure, *Ecology*, 56, 489-492 (1975).
- [10] M. Tansky, Switching effects in prey-predator system, *J. Theor. Biol.* 70, 263-271 (1978).

- [11] Prajneshu and P. Holgate, A prey-predator model with switching effect. *J. theor. Biol.* 125, 61-61-66 (1987).
- [12] Q. J. A. Khan, B. S. Bhatt and R. P. Jaju, Stability of a switching model with two habitats and a predator, *J. Phys. Soc. Jpn.*, 63, 1995-2001 (1994).
- [13] Q. J. A. Khan, B. S. Bhatt and R. P. jaju, Hopf Bifurcation analysis of a predator-prey system involving switching, *J. Phys. Soc. Jpn.*, 65, 3, 864-867 (1996).
- [14] M. Lloyd and H. S. Dybas, The periodical cicada problem, *Evolution* 20, 133-149, 466-505 (1966).
- [15] E. D. LeCaven, C. Kipling, J. C. McCormack, A study of the numbers, biomass and year-class strengths of perch (*perca fluviatillis* L) in winteremiere, *J. Anim., Ecol.* 46, 281-306 (1977).
- [16] L. Nielsen, Effect of Walleye (*Stizostedion Vitreum*), Predation on Juvenile mortality and recruitment of yellow perch (*perca flavereens*) in Oneida lake, New York. *Can. J. Fish. Aquat. Sci.* 37, 11-19 (1980).
- [17] H. I. Freedman, Joseph W.-H. So and Jianhong Wu, A model for the growth of a population exhibiting stage structure: Cannibalism and cooperation, *J. Comp. and App. Math.*, 52, 177-198 (1994).
- [18] W. S. C. Gurney, R. M. Nisbet and J. H. Lawton, The systematic formulation of tractable single-species population models incorporating age structure, *J. Animal Ecol.* 52, 479-495 (1983).
- [19] Xinyu Song and Lansun Chen, Optimal harvesting and stability for a two-species competitive system with stage structure, *Math. Biosci.*, 170, 173-186 (2001).
- [20] Q. J. A. Khan, E. V. Krishnan and M. A. Al-Lawatia, A stage structure model for the growth of a population involving switching and cooperation, *Z. Angew. Math. Mech.*, 82, 125-135 (2002).
- [21] Xin-an Zhang, L. Chen and A. U. Neumann, The stage structured predator-prey model and optimal harvesting policy, *Math. Biosci.*, 168, 201-210 (2000).
- [22] W. Wang and L. Chen, A predator-prey system with stage structure for predator, *Comput. Math. Appl.* 33, 207 (1997).

- [23] C. W. Clark, *Mathematical Bioeconomics: The Optimal management of renewable resources*, 2nd Ed., Wiley, New York (1990).
- [24] A. W. Leng, Optimal harvesting-coefficient control of steady-state prey-predator diffusive Volterra-Lotka systems, *Appl. Math. Optim*, 31, 219 (1995).
- [25] D. K. Bhattacharya and S. Begun, Bioeconomic equilibrium of two-species systems I, *math. Biosci.*, 135, 111 (1996).
- [26] T. L. John, *Variational Calculus and Optimal control*, Springer, New York (1996).

Appendix

To show that the non-zero equilibrium is locally stable to small perturbations, we need to show the Routh-Hurwitz conditions are satisfied

$$(a) \ a_1 > 0, a_3 > 0; \quad (b) \ a_1 a_2 > a_3.$$

Clearly

$$a_1 = A\bar{x} - L = \beta_1\bar{x} + \frac{\hat{x}_2^2\hat{y}}{(\hat{x}_1 + \hat{x}_2)^2} + \frac{\alpha_1}{\bar{x}} + \frac{\hat{x}_1^2\hat{y}}{\bar{x}(\hat{x}_1 + \hat{x}_2)^2} + \eta_1\hat{x}_1 > 0. \quad (A.1)$$

To show $a_3 > 0$.

Write

$$P = \frac{C\hat{x}_2}{\bar{x}} + \frac{D\hat{x}_2^2}{\bar{x}} + C\hat{x}_2 + D\hat{x}_1\hat{x}_2,$$

$$Q = C\hat{x}_1\bar{x} + D\hat{x}_1\hat{x}_2\bar{x} + C\hat{x}_1\bar{x}^2 + D\hat{x}_1\bar{x}^2, \quad (A.2)$$

$$S = C\hat{x}_1\hat{x}_2 + D\hat{x}_1\hat{x}_2\bar{x} + C\hat{x}_1\bar{x}^2 + D\hat{x}_1\bar{x}^2,$$

so that

$$a_3 = \frac{1}{(1+x)} [BP + AQ + \eta s], \quad (A.3)$$

where

$$P = \frac{-\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\hat{x}_2^2}{(\widehat{\bar{x}}_1 + \widehat{\bar{x}}_2)^2 \widehat{\bar{x}}_1} + \frac{2\hat{y}\hat{x}_2^3}{(\widehat{\bar{x}}_1 + \widehat{\bar{x}}_2)\widehat{\bar{x}}_1} - \frac{\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\hat{x}_2}{(\widehat{\bar{x}}_1 + \widehat{\bar{x}}_2)^2} + \frac{2\hat{y}\hat{x}_1\hat{x}_2}{\hat{x}_1 + \hat{x}_2} = \frac{\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\hat{x}_2}{\hat{x}_1(\hat{x}_1 + \hat{x}_2)} > 0, \quad (\text{A.4})$$

$$Q = C\hat{x}_1\bar{x} + D\hat{x}_1\hat{x}_2\bar{x} + C\hat{x}_1\bar{x}^2 + D\hat{x}_1^2\bar{x}^2 = \frac{-\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\widehat{\bar{x}}_1\bar{x}}{(\hat{x}_1 + \hat{x}_2)^2} + \frac{2\hat{y}\hat{x}_1\hat{x}_2\bar{x}}{(\hat{x}_1 + \hat{x}_2)} - \frac{\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\hat{x}_1\bar{x}^2}{(\hat{x}_1 + \hat{x}_2)^2} + \frac{2\hat{y}\hat{x}_1^2\bar{x}^2}{(\hat{x}_1 + \hat{x}_2)} = \frac{\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)\hat{x}_1^2}{\hat{x}_2^2(\hat{x}_1 + \hat{x}_2)} > 0, \quad (\text{A.5})$$

$$S = C\hat{x}_1\hat{x}_2 + D\hat{x}_1\hat{x}_2^2 = \frac{\hat{y}\hat{x}_1\hat{x}_2(\hat{x}_2^2 + 2\hat{x}_1\hat{x}_2 - \hat{x}_1^2)}{(\hat{x}_1 + \hat{x}_2)^2}, \quad (\text{A.6})$$

Now, from (A.3), (A.4), (A.5) and (A.6),

$$a_3 = \frac{\hat{y}\widehat{\bar{x}}_2}{(\widehat{\bar{x}}_1 + \widehat{\bar{x}}_2)^2} \left[\begin{array}{l} \frac{\alpha_1\widehat{\bar{x}}_2(\hat{x}_1^2 + \hat{x}_2^2)}{\hat{x}_1} + \frac{\hat{x}_1\hat{x}_2\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)}{(\hat{x}_1 + \hat{x}_2)^2} \\ + \frac{\beta_1\hat{x}_1^2(\hat{x}_1^2 + \hat{x}_2^2)}{\hat{x}_2^2} + \frac{\hat{x}_1^2\hat{y}(\hat{x}_1^2 + \hat{x}_2^2)}{(\hat{x}_1 + \hat{x}_2)^2} \\ + \frac{\eta_1\hat{x}_1\widehat{\bar{x}}_2}{(\hat{x}_1 + \hat{x}_2)}(\hat{x}_2^2 + 2\hat{x}_1\hat{x}_2 - \hat{x}_1^2) \end{array} \right]. \quad (\text{A.7})$$

Recall that

$$\hat{y} = \left[\frac{1 + \bar{x}}{\bar{x}} \left(\frac{\alpha_1}{\bar{x}} - \kappa_1 - \beta_1 - \eta_1\bar{x}_1 \right) \right] > 0,$$

So

$$\alpha_1\hat{x}_2 - \eta_1\hat{x}_1^2 > 0. \quad (\text{A.8})$$

Thus, $a_3 > 0$.

This completes the proof of (a).

(b) We must show that $a_1a_2 > a_3$.

From (3.10),

$$\begin{aligned}
a_1 a_2 > a_3 &\Rightarrow (A\bar{x} - L) \left[-LA\bar{x} + \frac{\hat{x}_2}{(1 + \bar{x})} (C + D\hat{x}_2) - AB + \frac{\hat{x}_1 \bar{x} C}{1 + \bar{x}} + \frac{D\bar{x} \hat{x}_1^2}{1 + \bar{x}} \right] \\
&> -\frac{L\hat{x}_2 C}{1 + \bar{x}} - \frac{LDx_2^2}{1 + \bar{x}} + \frac{B\hat{x}_2}{1 + x} (C + D\hat{x}_1) + \frac{AC\hat{x}_1 \bar{x}}{1 + \bar{x}} + \frac{AD\hat{x}_1 \hat{x}_2 \bar{x}}{1 + \bar{x}} \\
&\quad + \frac{AC\hat{x}_1 \bar{x}^2}{1 + \bar{x}} + \frac{AD\hat{x}_1^2 \hat{x}^2}{1 + \bar{x}}.
\end{aligned} \tag{A.9}$$

After some simplifications (A.9) can be expressed as

$$\begin{aligned}
&\frac{-AC\bar{x}(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} + \frac{BC(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} - \frac{AD\hat{x}_2 \bar{x}}{1 + \bar{x}} (\hat{x}_1 - \hat{x}_2) \\
&+ \frac{BD\hat{x}_1}{1 + \bar{x}} (\hat{x}_1 - \hat{x}_2) + \eta_1 \left[A_1^2 \hat{x} \bar{x}^2 + \eta_1 \hat{x}_1^2 A\bar{x} + \frac{C\hat{x}_1^2 \bar{x}}{1 + \bar{x}} + \frac{D\bar{x}_1 \bar{x}_1^3}{1 + \bar{x}} + AB\hat{x}_1 \right] > 0.
\end{aligned} \tag{A.10}$$

All terms inside square bracket of inequality (A.10) are positive except $\frac{C\hat{x}_1^2 \bar{x}}{1 + \bar{x}}$

Where

$$\begin{aligned}
\frac{C\hat{x}_1^2 \bar{x}}{1 + \bar{x}} + \frac{D\bar{x} \hat{x}_1^3}{1 + \bar{x}} &= \frac{\hat{x}_1^2 \bar{x}}{1 + \bar{x}} (C + D\hat{x}_1) = \frac{\hat{x}_1^2 \bar{x} \bar{y}}{(1 + \bar{x})(\hat{x}_1 + \hat{x}_2)^2}, \\
&[(\hat{x}_1 - \hat{x}_2)(\hat{x}_1 + \hat{x}_2) + 2\hat{x}_1 \hat{x}_2] > 0
\end{aligned} \tag{A.11}$$

if $\hat{x}_1 > \hat{x}_2$

Now

$$\begin{aligned}
&\frac{AC\bar{x}(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} + \frac{BC(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} - \frac{AD\hat{x}_2 \bar{x}(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} + \frac{BD\hat{x}_1(\hat{x}_1 - \hat{x}_2)}{1 + \bar{x}} \\
&= \frac{(\hat{x}_1 \hat{x}_2)}{(\hat{x}_1 + \hat{x}_2)} [C(\alpha_1 \hat{x}_2 - \beta_1 \hat{x}_1) + D\hat{x}_1 \hat{x}_2 (\alpha_1 - \beta_1)] \\
&\quad + \frac{\hat{x}_1 - \hat{x}_2 (\hat{x}_1 - \hat{x}_2)}{(\hat{x}_1 + \hat{x}_2)^3} [C + D(\hat{x}_1 + \hat{x}_2)].
\end{aligned} \tag{A.12}$$

Let

$$\begin{aligned}
U &= C(\alpha_1 \hat{x}_2 - \beta_1 \hat{x}_1) + D\hat{x}_1 \hat{x}_2 (\alpha_1 - \beta_1), \\
V &= C + D(\hat{x}_1 + \hat{x}_2),
\end{aligned} \tag{A.13}$$

$V > 0$ since $C + D\hat{x}_1 > 0$ from (A.11)

To show that $U > 0$ where

$\alpha_1\hat{x}_2 - \beta_1\hat{x}_1 < \alpha_1\hat{x}_2 - \beta_1\hat{x}_2$ since we are assuming $\hat{x}_1 > \hat{x}_2$ and $D\hat{x}_1 > C$ from (A.11)

So

$$U > 0.$$

Hence, $a_1a_2 > a_3$ if $\bar{x} > 1$. This completes the proof.