



Dynamics and Bifurcation Analysis of a Predator-Prey System with Monod-Haldane Functional Response

Tau Keong Ang^{1,3,*}, Chai Jian Tay², Hamizah M. Safuan³, Lee Chang Kerk⁴

¹ Department of Mathematical Sciences, Faculty of Science, Universiti Teknologi Malaysia, 81310 Johor Bahru, Johor, Malaysia

² Centre for Mathematical Sciences, Universiti Malaysia Pahang, 26300 Gambang, Pahang, Malaysia

³ Centre for Computational Applied Mathematics, Faculty of Applied Sciences and Technology, Universiti Tun Hussein Onn Malaysia, Pagoh, 86400 Muar, Johor, Malaysia

⁴ Mathematical Sciences Studies, College of Computing, Informatics and Mathematics, Universiti Teknologi MARA (UiTM), Segamat Campus, 85000 Segamat, Johor, Malaysia

ABSTRACT

This paper studies the bifurcation analysis of a prey-predator model with Monod-Haldane functional response with respect to the prey harvesting parameter. Both the prey and predator species are harvested using the conventional Catch-Per-Unit-Effort (CPUE) harvesting strategy. We study and supplement the proposed model by studying the bifurcation analyses of the system with respect to the harvesting parameter. We study the local stability criteria of the system via Routh-Hurwitz criterion. From the numerical simulations, the system undergoes Transcritical bifurcation, Hopf bifurcation and Bistability behaviour at different values of the prey harvesting parameter. The results imply that prey harvesting parameter is crucial to influence the persistence and extinction properties in the proposed system.

Keywords:

Predator-prey; Monod-Haldane functional response; Harvesting; Bifurcation; Bistability

1. Introduction

In ecology, studying the relationship between the predator and prey species remains the primary concern among researchers. Mathematical researchers are interested in examining the stability properties of ecological models by investigating the persistence of both predator and prey species via mathematical approaches [1-3].

To understand the inherent relationship between the predator and prey species, the research on functional response is essential in mathematical ecology. A functional response of predator species can be defined as the per capita feeding rate of predator species on prey abundance [4]. A series of work has been done to investigate the stability and bifurcation results of prey-predator models with several Holling type functional responses. Mukherjee and Maji [5] found that a predator-prey model with Holling type II functional response and prey refuge exhibited rich dynamics such as Transcritical, saddle-node, Hopf as well as Bogdanov-Takens bifurcations around the interior equilibrium. The

* Corresponding author.

E-mail address: taukeong@utm.my

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research of Shaikh *et al.*, [6] and Baisad and Moonchai [7] focused on the stability analysis of predator-prey models with Holling type III functional response.

However, it is proven in some experiments that the inhibitory effect in predator-prey interaction may be obvious when the nutrient concentration increases [8]. Therefore, Holling type IV functional response or Monod-Haldane function is proposed to model such inhibitory effect in predator-prey models. Few literatures incorporated Monod-Haldane functional response into predator-prey models to investigate the dynamical behaviours with respect to the direct measure and inhibitory effect [9-13].

Apart from the studies of functional responses, many research studied the impacts of harvesting in predator-prey models to consider a farming effect on the harvested species. A series of work has been done to study harvested predator-prey models by considering the traditional Catch-Per-Unit-Effort (CPUE) or constant proportion harvesting strategy [14-17]. Moreover, there are some researchers have been accomplished to study the dynamics of predator-prey models by incorporating nonlinear harvesting strategy [18-22]. In their research, the sustainability and extinction of the prey and predator populations in system is greatly influenced by the harvesting activity.

The present paper aims to analyse the qualitative dynamical fluctuations of a predator-prey model subjected to Monod-Haldane type response function with respect to the harvesting parameter.

2. Predator-Prey Model

Referring to the work of Liu [23], a classical predator-prey model by incorporating the Monod-Haldane functional response has been studied in a detailed way. In this paper, our main emphasis is to study and supplement the previous work done by Liu [23] using bifurcation analysis to observe the impacts of harvesting on the changes of qualitative dynamical behaviours. Therefore, we consider the following predator-prey model:

$$\begin{aligned} \frac{dX}{dt} &= r_1 X \left(1 - \frac{X}{K}\right) - \frac{XY}{a+bX+X^2} - cE_1 X, \\ \frac{dY}{dt} &= -r_2 Y + \frac{uXY}{a+bX+X^2} - dE_2 Y. \end{aligned} \quad (1)$$

In the above model Eq. (1), r_1 stands for the growth rate of prey population. K depicts the carrying capacity. The death rate of the predator species is r_2 in the absence of the prey species. In the concept of Monod-Haldane functional response, parameter a represents the half saturation constant while parameter b represents the handling time. Parameter u is the maximum growth rate of predator species without inhibitory effect. Both prey and predator species are harvested using independent harvesting strategy with c and d representing the catchability coefficients while E_1 and E_2 represent the harvesting efforts applied on prey and predator species, respectively.

3. Equilibria and Stability Analysis

Model Eq. (1) can be simplified by reducing the number of representative parameters through a rescaling process. By adopting the variables of $x = \frac{X}{K}$, $y = \frac{Y}{r_1}$ and $\tau = r_1 t$, the non-dimensional predator-prey model is acquired as follows:

$$\begin{aligned} \frac{dx}{d\tau} &= x(1-x) - \frac{xy}{a+\alpha x+\beta x^2} - \delta x, \\ \frac{dy}{d\tau} &= -\sigma y + \frac{\rho xy}{a+\alpha x+\beta x^2} - \varepsilon y, \end{aligned} \tag{2}$$

where $\alpha = bK, \beta = K^2, \delta = \frac{cE_1}{r_1}, \sigma = \frac{r_2}{r_1}, \rho = \frac{uK}{r_1}$ and $\varepsilon = \frac{dE_2}{r_1}$. All the parameters are assumed to be strictly positive. It is found that system Eq. (2) possesses three equilibria of P_i in the form of (x^*, y^*) where $i = 1, 2, 3$:

1. $P_1 = (0, 0)$,
2. $P_2 = (-\delta + 1, 0)$,
3. $P_3 = \left(\hat{x}, \frac{\rho}{\beta(\varepsilon + \sigma)} \{(\varepsilon + \sigma)[\beta \hat{x}(1 - \delta) + a + \alpha \hat{x}] - \rho \hat{x}\} \right)$, where \hat{x} is a root by solving $\beta(\varepsilon + \sigma)\hat{x}^2 + [\alpha(\varepsilon + \sigma) - \rho]\hat{x} + a(\varepsilon + \sigma) = 0$.

3.1 Stability of Extinction Equilibrium P_1

The corresponding Jacobian matrix for extinction equilibrium P_1 is given by $J_{P_1} = \begin{pmatrix} -\delta + 1 & 0 \\ 0 & -(\sigma + \varepsilon) \end{pmatrix}$.

Theorem 1. Equilibrium P_1 is locally stable if the condition $\delta > 1$ holds.

Proof: The corresponding characteristic equation for equilibrium P_1 is

$$\lambda^2 + (\delta - 1 + \varepsilon + \sigma)\lambda + (\delta - 1)(\varepsilon + \sigma) = 0. \tag{3}$$

It can be seen that $\varepsilon + \sigma$ is always greater than 0. Therefore, if the condition of $\delta > 1$ holds, both $(\delta - 1 + \varepsilon + \sigma)$ and $(\delta - 1)(\varepsilon + \sigma)$ are greater than 0, therefore, Routh-Hurwitz condition can prove the equilibrium P_1 is locally stable.

3.2 Stability of Predator Free Equilibrium P_2

The corresponding Jacobian matrix for equilibrium P_2 is given by $J_{P_2} = \begin{pmatrix} \delta - 1 & \frac{\delta - 1}{\beta(1-\delta)^2 + \alpha(1-\delta) + a} \\ 0 & \frac{\rho(1-\delta)}{\beta(1-\delta)^2 + \alpha(1-\delta) + a} - \sigma - \varepsilon \end{pmatrix}$.

Theorem 2. Equilibrium P_2 is locally stable if both the conditions $1 > \delta$ and $(\varepsilon + \sigma)[\beta(1 - \delta)^2 + \alpha(1 - \delta) + a] + \rho(\delta - 1) > 0$ hold.

Proof: The associated characteristic equation for equilibrium P_2 is given by

$$\begin{aligned} \lambda^2 + \left\{ \frac{(1-\delta+\varepsilon+\sigma)[\beta(1-\delta)^2 + \alpha(1-\delta) + a] + \rho(\delta-1)}{\beta(1-\delta)^2 + \alpha(1-\delta) + a} \right\} \lambda \\ + \frac{(1-\delta)\{(\varepsilon+\sigma)[\beta(1-\delta)^2 + \alpha(1-\delta) + a] + \rho(\delta-1)\}}{\beta(1-\delta)^2 + \alpha(1-\delta) + a} = 0. \end{aligned} \tag{4}$$

From the above equation, we know that $\delta - 1$ is one of the eigenvalues of equilibrium P_2 and therefore $\delta < 1$ must be strictly held. It is obvious that if the condition $(\varepsilon + \sigma)[\beta(1 - \delta)^2 + \alpha(1 - \delta) + a] + \rho(\delta - 1) > 0$ holds together, both the coefficients of the characteristic equation

(4) are positive, thus by referring to Routh-Hurwitz criterion, we can ensure the local stability of equilibrium P_2 .

From Theorems 1 and 2, we can notice that the local stability of equilibrium P_1 implies that equilibrium P_2 is unstable and vice versa. The reason is the local stability criterion of $\delta > 1$ for equilibrium P_1 is a contradiction to the local stability criterion of $\delta < 1$ for equilibrium P_2 .

3.3 Stability of Coexistence Equilibrium P_3

The characteristic equation of interior equilibrium P_3 is relatively complex and cumbersome to solve, therefore we study the stability and the dynamical behaviours of equilibrium P_3 via numerical simulations in the next section.

4. Numerical Simulation and Discussion

4.1 Bifurcation Diagrams

To identify the effects of prey harvesting parameter on dynamical behaviours, bifurcation analyses are performed by using XPPAUT and MatCont, respectively [24,25]. By taking the non-dimensional parameter values $a = 0.2, \alpha = 0.9, \beta = 0.9, \delta = 0.05, \sigma = 0.4, \rho = 0.9$ and $\varepsilon = 0.08$, first, we perform bifurcation analysis of prey, x against δ and the result is illustrated in Figure 1. In this case, both transcritical (T1, T2 and T3) and Hopf (H1) bifurcations exist. In the bifurcation diagrams, Equilibria E1 and E4 correspond to the predator-free equilibrium P_2 ; equilibrium E3 corresponds to the coexistence equilibrium P_3 while equilibrium E5 corresponds to the extinction equilibrium P_1 in Section 3. Three types of equilibria are obtained as δ varies:

- i. predator-free
- ii. coexistence of prey and predator
- iii. extinctions of both prey and predator equilibria.

A stable predator-free equilibrium exists along E1 when $\delta < 0.1915$. At $\delta = 0.1915$, the stable predator-free equilibrium loses its stability and becomes unstable. Another stable equilibrium E2 exists when $\delta > 0.1915$. However, the equilibrium along E2 shows a negative value of predator. Hence, it is not biologically meaningful and it is not considered in our discussion. Coexistence of prey and predator occurs in the range $0.3556 < \delta < 0.7251$ (stable equilibrium E3). Further increase in δ would lead to stable predator-free equilibrium E4 ($0.7251 < \delta < 1$). By referring to Theorem 1, equilibrium $P_1 = (0,0)$ is locally stable if the condition $\delta > 1$ holds. This can be verified in Figure 1 where the extinction of both prey and predator populations occurs when $\delta > 1$ (stable equilibrium E5).

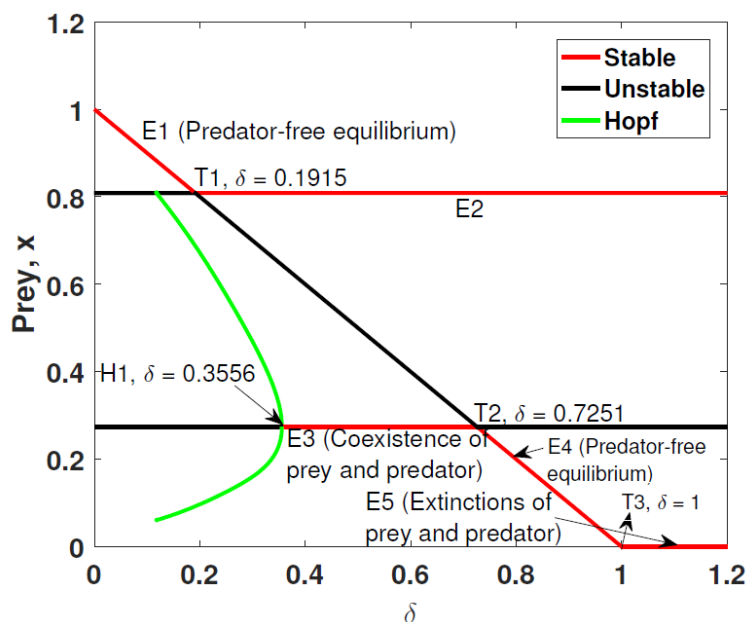


Fig. 1. Bifurcation diagram of prey, x against δ

At $\delta = 0.3556$, Hopf bifurcation occurs and the solution behaviour changes from stable equilibrium to oscillatory solution when $0.1179 < \delta < 0.3556$. Bistable behaviour of the system can be detected in the small range of $0.1179 < \delta < 0.1915$, where the solution can either converge to the predator-free equilibrium E1 or a limit cycle of coexistence equilibrium E3, depending on the initial conditions. For example, at initial condition $x_0 = 0.2$ and at parameter $\delta = 0.2$, oscillatory solutions of prey and predator are obtained. At the same value of $\delta = 0.2$, the oscillatory solution changes to predator-free equilibrium if we are considering the initial condition of $x_0 = 0.9$.

4.2 Time Series Diagrams

To verify the three types of equilibria obtained in Figure 1, we plot several time series diagrams. First, we illustrate the bistable behaviour of the system. By considering $x_0 = 0.9, y_0 = 0.9$ and $\delta = 0.18$, the system possesses predator-free equilibrium as shown in Figure 2(a). From Figure 2(a), initially, both prey and predator populations decrease sharply as time increases. When the extinction of predator population occurs ($y = 0$), the prey population starts to increase steeply until a stable equilibrium is attained. When we change the initial conditions to $x_0 = 0.2, y_0 = 0.2$ at $\delta = 0.18$, the solutions exhibit oscillatory behaviour as illustrated in Figure 2(b). From Figure 2(b), it can be observed that both prey and predator populations oscillate between high and low values. It is observed that the prey population reaches its peak value before that of predator population. At high prey population, the predator population starts to increase and consume the prey population, thereby reducing the prey population. Since the food resource (prey population) available for predator consumption decreases, the predator population also decreases and reaches a low value. At low predator population, the prey population then increases. This process repeats and hence induces the oscillatory behaviour of the system.

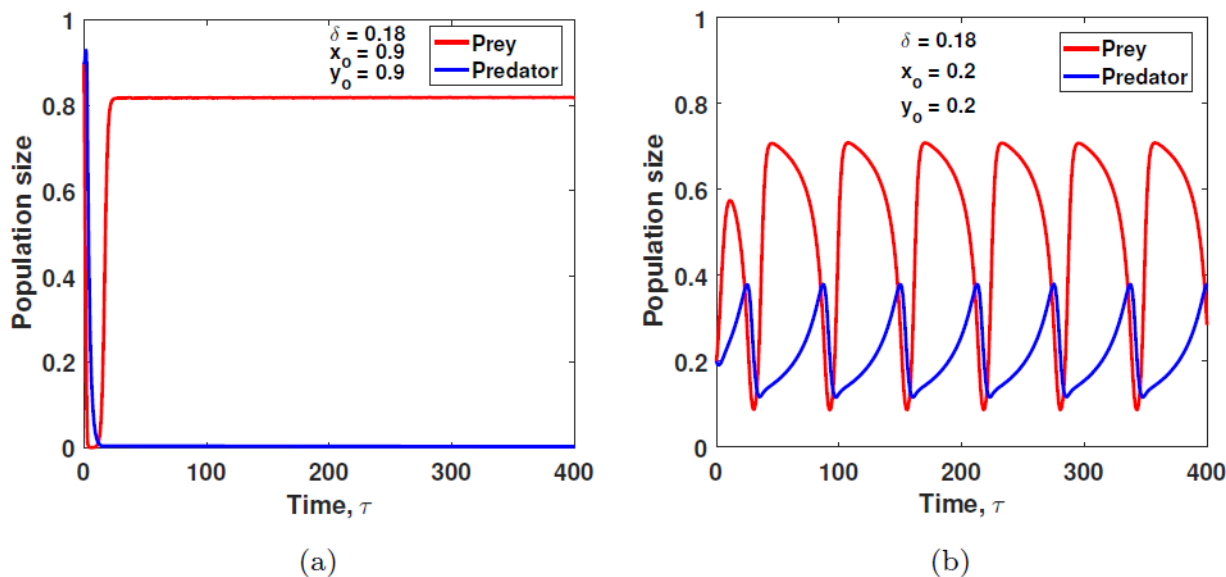


Fig. 2. Bistable behaviours of the system where the solutions converge to (a) a predator-free equilibrium at $x_0 = 0.9$ and $y_0 = 0.9$, and (b) to a limit cycle of coexistence equilibrium at $x_0 = 0.2$ and $y_0 = 0.2$

Next, when we increase the value of δ from $\delta = 0.18$ to $\delta = 0.6$, coexistence of prey and predator is obtained in Figure 3(a). From Figure 3(a), initially, both prey and predator populations decrease. At low predator population, the prey population starts to increase. The predator population then increases gradually. Finally, both prey and predator populations reach a stable equilibrium.

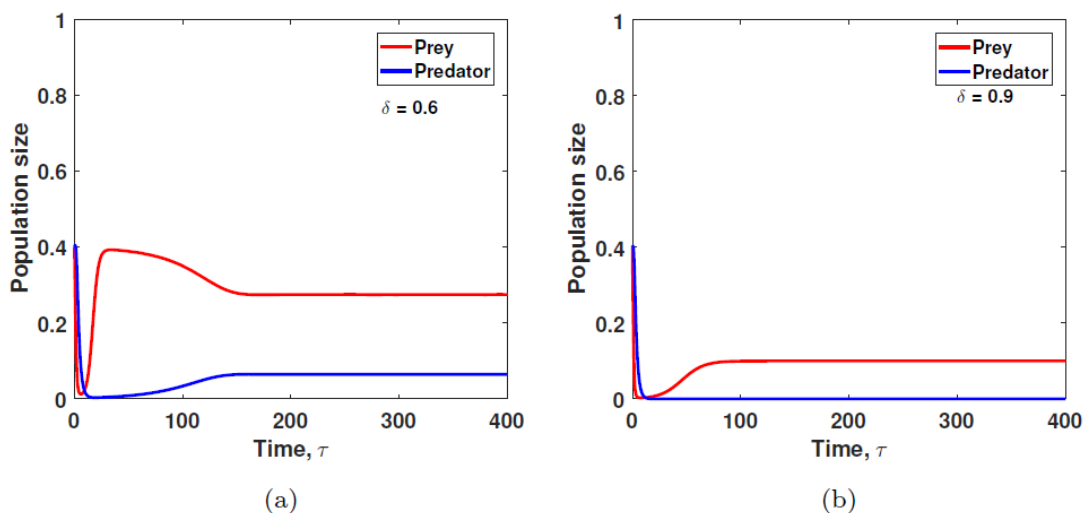


Fig. 3. (a) Coexistence of prey and predator at $\delta = 0.6$. (b) The solutions approach to a predator-free equilibrium at $\delta = 0.9$

At higher prey harvesting $\delta = 0.9$, the prey population decreases more sharply compared to that of predator population at the beginning of time as shown in Figure 3(b). It then approaches to a very low value. The predator population continues to decrease and finally converges to zero, i.e., the predator population extinct. With no predator population, the prey population begins to increase and reach a stable equilibrium. A predator-free equilibrium is obtained at high value of δ . At extremely high level of prey harvesting, i.e, $\delta = 1.2$, the prey population decreases more steeply

compared to that of predator population (Figure 4). Both the population sizes drop to zero and the extinction of the entire ecosystem occurs.

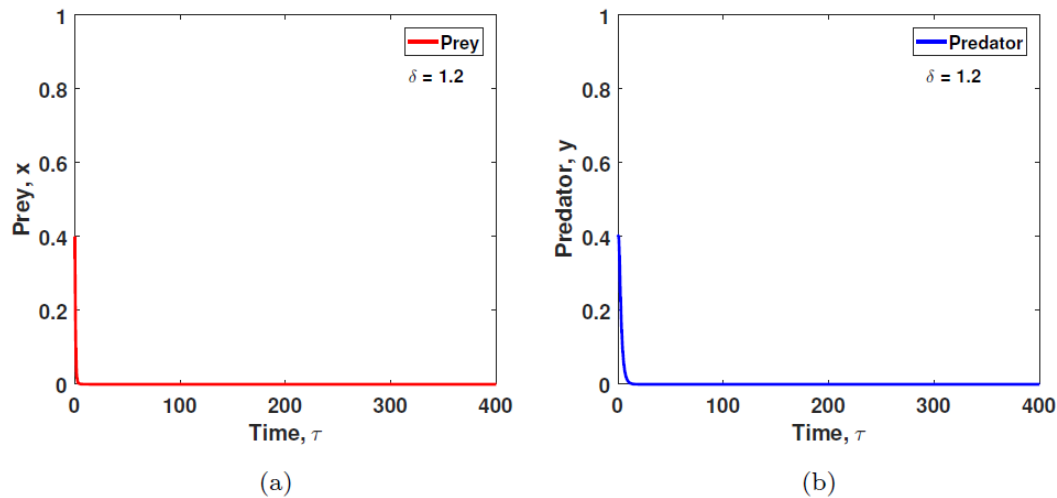


Fig. 4. Extinctions of (a) prey and (b) predator at $\delta = 1.2$

4. Conclusions

Mathematical modelling is one of the primary concerns to solve real-life problems [26]. In this study, the qualitative dynamical changes of a harvested predator-prey model incorporating Monod-Haldane type response function has been studied in regards to the prey harvesting parameter. The trivial equilibrium together with non-trivial equilibrium are studied based on the local and global stability criteria. Bifurcation results showed that the prey harvesting parameter has a higher impact to influence the population dynamics by inducing transcritical and Hopf bifurcations as well as bistability phenomenon. It can be concluded that at low prey harvesting level, the system exhibited a bistable behaviour. This bistable behaviour occurs where the prey-predator system can possess both predator-free equilibrium or a limit cycle of coexistence equilibrium, based on the different initial conditions. At the intermediate level of prey harvesting, the bistability behaviour diminished and the coexistence equilibrium becomes stable in terms of the global asymptotic perspective. The global asymptotically stable predator-free equilibrium implies the extinction of the predator species at relatively high level of prey harvesting. Finally, the extinction equilibrium is stable at extremely high level of prey harvesting. Overall, prey harvesting parameter is impactful in governing the dynamical behaviours in the proposed system.

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Name of Author	Email
Tau Keong Ang	taukeong@utm.my
Chai Jian Tay	taycj@ump.edu.my
Hamizah M. Safuan	hamizahs@uthm.edu.my
Lee Chang Kerk	kerkleechang@uitm.edu.my