Dynamics of Two Preys – One Predator System with Competition between Preys

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Abstract. We study the dynamics of two preys – one predator interaction with competition between prey populations. The proposed model is developed from the Lotka-Volterra predator-prey model. We first discuss some fundamental issues such as equilibrium points and the stability of each equilibrium point. The analysis shows that there are seven equilibrium points and some of them are conditionally locally asymptotically stable. The dynamical behavior of the proposed model is then verified numerically. We also observe numerically the occurrence of bistability, as well as a Hopf bifurcation which is driven by the conversion rate of predation into the predator growth rate.

1. Introduction

Predator-prey interactions are one of the main topics in theoretical ecology. The first mathematical model to describe this interaction is the Lotka-Volterra equation. So far, there has been a lot of work to improve the Lotka-Volterra model based on a more realistic biological situation, see e.g. [1-3]. Some studies often focus on the patterns of predation and behavior when the growth of one population is influenced by other populations. In the case of one prey – one predator interaction, functional response which measures the predation rate is one of important factors that influence the growth rate of both prey and predator. In this respect, Holling [4] has introduced the consumption rate of the predator which varies with the prey density alone. Holling categorized the prey-dependent responses into three types, namely Holling types I, II, and III. When the number of species includes in the food web interaction is bigger, the complex dynamics may be achieved. For example some researchers have introduced mathematical models for a two preys – one predator and addressed the stability of coexistence, extinction, stable limit-cycle (periodic solution), as well as predator switching between prey population, see e.g. [5-9]. In those cases, the authors applied the bilinear functional response (Holling type I). Jana [10] analyzed a predator-two prey system with functional responses Holling type I for weak prey and Holling type II functional response for strong prey. They described conditions for local and derived the Lyapunov function for global dynamics.
Recently, Raymond et al. [11] proposed a model of two preys – one predator with Holling type II functional response, competition between preys and harvesting for all populations. Their discussion focuses on the harvesting policy to produce maximum economic benefit and simultaneously to maintain the sustainable populations. In this paper we revisit the work of Raymond et al. [11] but without considering the harvesting effects. Here we discuss more about the dynamics of the three species rather than harvesting policies. In particular, we study numerically the effects of the conversion rate of predation into predator growth rate, the occurrence of bistability and the possibility of Hopf bifurcation.

2. Model Mathematics

The mathematical model to study the dynamics of two prey – one predator interaction is described as follows. Here $x$, $y$ and $z$ denote the population of prey-1, prey-2 and predator, respectively. The term that represents the logistic growth of the prey species in the absence of the predator is included in the both prey equations. The intrinsic growth rate $r$ for the prey-1 population and the intrinsic growth rate prey-2 population $s$ cause an increase in population. We assume that the coefficients of environmental protection or carrying capacity $k_1$ for prey-1 and $k_2$ for the prey-2 population. This model describes the same predation pattern of predators feed on both preys. Both of prey are easy to capture and predator takes less time in searching and handling it, and therefore the predation behavior is modeled by the Holling type II functional response, which are given by $h(x,y) = \frac{fxy}{1+ax}$ for the prey-1 and $g(x,y) = \frac{gxy}{1+by}$ for the prey-2. In this case, $f$ and $g$ are the predation rate of prey-1 and prey-2, while $a$ and $b$ are the coefficient of environmental protection for the prey-1, the prey-2, respectively. The competition between the two preys is assumed to be bilinear. Under these assumption, we obtain the following mathematical model for the interaction of two prey – one predator:

$$\begin{align*}
\frac{dx}{dt} &= rx \left(1 - \frac{x}{k_1}\right) - \frac{fxy}{1+ax} - axy \\
\frac{dy}{dt} &= sy \left(1 - \frac{y}{k_2}\right) - \frac{gxy}{1+by} - byy \\
\frac{dz}{dt} &= \frac{pxy}{1+ax} + \frac{nyz}{1+by} - \mu z.
\end{align*}$$

Parameter $\alpha$ in system (1) is the maximum value of per capita competition of $x$ due to $y$, and $\beta$ is the maximum value of per capita competition of $y$ due to $x$. Parameter $\rho$ is the conversion rate of predation into predator growth rate. Parameter $\mu$ is the per capita the natural death rate of a predator in the absence both of prey. All parameters in the model are positive real numbers.

3. Equilibrium Points

Equilibrium point of the system (1) is solutions of the following system

$$\begin{align*}
rx \left(1 - \frac{x}{k_1}\right) - \frac{fxy}{1+ax} - axy &= 0 \\
sy \left(1 - \frac{y}{k_2}\right) - \frac{gxy}{1+by} - byy &= 0 \\
\frac{pxy}{1+ax} + \frac{nyz}{1+by} - \mu z &= 0.
\end{align*}$$
It is found that the system (1) has seven feasible equilibrium points. Among them are three trivial equilibrium points, namely $E_1 = (0, 0, 0)$, $E_2 = (0, k_2, 0)$, $E_3 = (k_1, 0, 0)$, which always exist. Other equilibrium points and their existence conditions are shown in Table 1.

The interior equilibrium point $E_7 = (x^*, y^*, z^*)$ is positive solution of the following system (2). To get an explicit form of this equilibrium point, it is necessary to solve a cubic equation. Since the coefficients of the cubic equation are very complicated, the cubic equation is not shown here. The existence of positive solutions to this problem can be analyzed by the Cardan’s method.

4. **The Local Stability**

The Jacobian matrix of the system (1) at a point $(x, y, z)$ is

$$
J(x, y, z) = \begin{bmatrix}
    -s - 2r_1 & f_2 & f_3 x a + a y \\
    -\beta y & s - 2r_2 & f_2 y a + a y \\
    -\beta y & s - 2r_3 & f_2 y a + a y \\
\end{bmatrix}
$$

The stability properties of an equilibrium point $(\hat{x}, \hat{y}, \hat{z})$ is determined by the roots of the characteristic equation of $J(\hat{x}, \hat{y}, \hat{z})$. In the following theorems we present the stability properties of all possible equilibrium points of system (1).

**Theorem 1.** The trivial equilibrium point $E_1 = (0, 0, 0)$ is a saddle point.

*Proof.*

The characteristic equation of the matrix $J(E_1)$ is $(\lambda + \mu)(\lambda - s)(\lambda - r) = 0$. It is obvious that one of eigenvalue $\lambda_1 = -\mu$ is negative, while two other eigenvalues are always positive $\lambda_2 = s > 0$ and $\lambda_3 = r > 0$. Hence, $E_1$ is a saddle-point. □

**Theorem 2.** The extinction of prey-1 and predator point $E_2 = (0, k_2, 0)$ is asymptotically stable if $ak_2 > r$ and $b\mu > \eta$.

*Proof.*

The Jacobian matrix at $E_2$ has eigenvalues: $\lambda_1 = -ak_2 + r$, $\lambda_2 = -s < 0$, and $\lambda_3 = -\frac{bk_2\mu - \eta k_2 + \mu}{bk_2 + 1} = \frac{k_2(b\mu - \eta) + \mu}{bk_2 + 1}$. We see that $\lambda_1$ and $\lambda_3$ are negative if $ak_2 > r$ and $b\mu > \eta$, and this completes the proof. □

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**Table 1.** Conditions for the existence of equilibrium point

| The equilibrium point | Type equilibrium | Condition of the existence |
|-----------------------|-----------------|---------------------------|
| $E_4$ | The prey-1 extinction | $\eta > b\mu, k_2(\eta - b\mu) > \mu$ |
| $E_5$ | The prey-2 extinction | $\rho > a\mu, k_1(\rho - a\mu) > \mu$ |
| $E_6$ | The predator extinction | $r < ak_2, s < k_1, a\beta k_1 k_2 > rs$ |
| $E_7$ | The interior equilibrium | See comments in text |
Theorem 3. The extinction of prey-2 and predator point $E_3 = (k_1, 0, \beta)$ is locally asymptotically stable if $s < \beta k_1$ and $a \mu > \rho$.

Proof. The eigenvalue of $f(E_3)$ is $\lambda_1 = -r < 0$, $\lambda_2 = -\beta k_1 + s$, and $\lambda_3 = -\frac{ak_1-\mu k_1+\mu}{a k_1+1} = -\frac{k_1 a \mu - \rho k_1 + \mu}{a k_1+1}$. $\lambda_2$ and $\lambda_3$ are negative if $s < \beta k_1$ and $a \mu > \rho$. □

Theorem 4. The equilibrium point $E_4 = \left(0, \frac{\mu}{\eta-b \mu}, \frac{\eta k_2 (\eta-b \mu) (\eta-a \mu) - \mu}{g k_2 (\eta-b \mu)^2}\right)$ and $E_5 = \left(\frac{\mu}{\rho-a \mu}, 0, \frac{r \rho (k_1 (\rho-a \mu) - \mu)}{f k_1 (\rho-a \mu)^2}\right)$ are conditionally asymptotically stable.

Proof. The Jacobian matrix at $E_4 = \left(0, \frac{\mu}{\eta-b \mu}, \frac{\eta k_2 (\eta-b \mu) (\eta-a \mu) - \mu}{g k_2 (\eta-b \mu)^2}\right)$ is

$$J(E_4) = \begin{bmatrix}
A_1 & 0 & 0 \\
\frac{\rho \eta}{\eta-b \mu} & A_2 & A_3 \\
-\frac{\rho s \eta k_2 (\eta-b \mu) (\eta-a \mu) - \mu}{g k_2 (\eta-b \mu)^2} & A_4 & A_5
\end{bmatrix},$$

where $A_1 = r + \frac{f s \eta (b \mu - \eta) k_2 + \mu}{(b \mu - \eta)^2 g k_2}$, $A_2 = s + \frac{2 s \mu}{(b \mu - \eta) k_2}$, $A_3 = \frac{g \mu}{(b \mu - \eta)}$, $A_4 = -\frac{\eta^2 s (b \mu - \eta) k_2 + \mu}{(b \mu - \eta) k_2}$, and $A_5 = \left(\frac{\eta}{(b \mu - \eta)} \left(-\frac{\mu r}{b \mu - \eta} + 1\right)\right)$. Clearly that $\lambda_1 = A_1$ is one of the eigenvalues of $f(E_4)$ and two other eigenvalues are determined by $\lambda^2 - T \lambda + D = 0$, where $T = A_2 + A_5$ and $D = A_2 A_5 - A_3 A_4$. Therefore $E_4$ is stable if $A_1 < 0, T < 0$ and $D > 0$.

Similarly, the Jacobian matrix at $E_5$ is

$$J(E_5) = \begin{bmatrix}
B_1 & \frac{\mu}{\eta-b \mu} & B_2 \\
0 & B_3 & 0 \\
B_4 & -\frac{\rho s \eta k_2 (\eta-b \mu) (\eta-a \mu) - \mu}{g k_2 (\eta-b \mu)^2} & B_5
\end{bmatrix},$$

where $B_1 = r + \frac{2 r \mu + r (k_1 (a \mu - \rho) + \mu)}{(a \mu - \rho) k_1}$, $B_2 = \frac{\mu \rho (a \mu - \rho) k_1 + \mu}{(a \mu - \rho) k_1}$, $B_3 = s + \frac{g r (a \mu - \rho) k_1 + \mu}{(a \mu - \rho) k_1}$, $B_4 = -\frac{\rho \eta (a \mu - \rho) k_1 + \mu}{(a \mu - \rho) k_1}$, and $B_5 = -\frac{\rho \eta}{(a \mu - \rho) \left(-\frac{a \mu}{\eta} + 1\right)}$. Using the same previous argument, we can show that $E_5$ is asymptotically stable if $B_3 < 0, T_1 = B_1 + B_5 < 0$ and $D_2 = B_2 B_5 - B_2 B_4 > 0$. The Jacobian matrix evaluated at $E_6$ is

$$J(E_6) = \begin{bmatrix}
C_1 & C_2 \\
C_3 & C_4 \\
0 & C_5
\end{bmatrix},$$

where $C_1 = \frac{f k_1 k_2 - r (a k_1 k_2 - r s)}{(a \beta k_1 k_2 - r s) (a \beta k_1 k_2 - r s + 1)}$, $C_2 = \frac{f k_1 k_2 - r (a k_1 k_2 - r s)}{(a \beta k_1 k_2 - r s) (a \beta k_1 k_2 - r s + 1)}$, $C_3 = \frac{f k_1 k_2 - r (a k_1 k_2 - r s)}{(a \beta k_1 k_2 - r s) (a \beta k_1 k_2 - r s + 1)}$, $C_4 = \frac{f k_1 k_2 - r (a k_1 k_2 - r s)}{(a \beta k_1 k_2 - r s) (a \beta k_1 k_2 - r s + 1)}$, and $C_5 = \frac{f k_1 k_2 - r (a k_1 k_2 - r s)}{(a \beta k_1 k_2 - r s) (a \beta k_1 k_2 - r s + 1)}$. 


where \( C_4 = r \left( 1 - \frac{s(\alpha k_2-r)}{\alpha \beta k_1 k_2-r s} \right) - \frac{\beta k_2 r (\beta k_1-s)}{\alpha \beta k_1 k_2-r s} \),
\( C_4 = s \left( 1 - \frac{r s(\alpha k_2-r)}{\alpha \beta k_1 k_2-r s} \right) - \frac{\beta k_2 r (\beta k_1-s)}{\alpha \beta k_1 k_2-r s} \),
\( C_2 = -\frac{a k_1 s(\alpha k_2-r)}{\alpha \beta k_1 k_2-r s} \),
\( C_3 = -\frac{a k_2 r (\beta k_1-s)}{\alpha \beta k_1 k_2-r s} \),
\( C_5 = \frac{(a k_1 s(\alpha k_2-r)+\alpha \beta k_1 k_2-r s)}{(k_2 r (\beta k_1-s)+\alpha \beta k_1 k_2-r s)} - \mu \). Hence, \( E_6 \) is asymptotically stable if \( C_5 < 0, T_2 = C_1 + C_4 < 0 \) and \( D_2 = C_1 C_4 - C_2 C_3 > 0 \). This completes the proof. □

**Theorem 5.** The equilibrium point \( E_7 = (x^*, y^*, z^*) \) is conditionally asymptotically stable.

**Proof.**
Suppose that the Jacobian matrix evaluated at the equilibrium point \( E_7 = (x^*, y^*, z^*) \) is written as

\[
J(E_7) = \begin{bmatrix}
a_{11} & a_{12} & a_{13} \\
a_{21} & a_{22} & a_{23} \\
a_{31} & a_{32} & a_{33} 
\end{bmatrix}.
\]

The characteristic equation of \( J(E_7) \) is given by

\[
\lambda^3 + P_1 \lambda^2 + P_2 \lambda + P_3 = 0,
\]

where \( P_1 = -(a_{11} + a_{22} + a_{33}) \), \( P_2 = a_{22} a_{33} + a_{11} a_{23} + a_{12} a_{21} + a_{13} a_{21} - a_{23} a_{32} - a_{31} a_{33} \), and \( P_3 = a_{11} a_{23} a_{32} - a_{11} a_{22} a_{33} + a_{13} a_{21} a_{32} \). According to the Routh-Hurwitz criterion, the equilibrium point \( E_7 = (x^*, y^*, z^*) \) is asymptotically stable if \( P_1 > 0, P_3 > 0, \) and \( P_1 P_2 - P_3 > 0 \). The proof is complete. □

5. **Numerical Simulation**
Some numerical simulations are presented to illustrate the analytical stability properties given in the previous section. The simulations are performed by solving the system (1) using the fourth-order Runge-Kutta method which is implemented in Phyton. To get better view on the dynamics of system (1) we take some different parameter values as in Table 2 and Table 3. The chosen parameter values are not based on field data, and they are only hypothetical parameters to illustrate the dynamics of system (1).

5.1 **Transcritical Bifurcation**
First we study the behavior of the system (1) due to the variety of the conversion rate of predation into predator growth rate. For this aim, we apply numerical continuation package MatCont to trace the equilibrium points of the system (1) using parameters in Table 2. As the result, we show in Figure 1 the density of prey as the conversion rate (\( \rho \)) is varied. A similar graph could be obtained for the predator density. Figure 1 shows the existence of transcritical bifurcation where the bifurcation point is marked by BP, i.e. at \( \rho^*_1 = 0.35323808 \). For \( \rho < \rho^*_1 \), there are two equilibrium points, i.e. the unstable extinction of prey-2 (\( E_5 \)) and the stable interior point (\( E_7 \)). However, if \( \rho > \rho^*_1 \) then \( E_5 \) becomes stable while \( E_7 \) is now unstable.

| Table 2. Parameter value for numerical simulation |
|--------------------------------------------------|
| \( r \) | \( s \) | \( k_1 \) | \( k_1 \) | \( a \) | \( b \) | \( f \) | \( g \) | \( \alpha \) | \( \beta \) | \( \rho \) | \( \eta \) | \( \mu \) |
| Simulation 1 | 0.6 | 0.5 | 1 | 1 | 0.2 | 0.2 | 0.4 | 0.4 | 0.4 | 0.4 | 0.351 | 0.3 | 0.2 |
| Simulation 2 | 0.6 | 0.5 | 1 | 1 | 0.2 | 0.2 | 0.4 | 0.4 | 0.4 | 0.4 | 0.35324 | 0.3 | 0.2 |
FIGURE 1. The density of prey for the system (1) with parameters as given in Table 2 and varying the value of \( \nu \), which shows the transcritical bifurcation driven by the conversion rate (\( \rho \)). The bifurcation point is shown by BP, i.e. at \( \nu^* = 0.35323808 \).

FIGURE 2. The phase portraits of system (1) which shows the stability of the interior equilibrium point \( E_T \).

To give more view on the transcritical bifurcation, we show in Figure 2 and Figure 3 the phase-portrait of the system (1) using parameter values as in Table 2. For \( \rho = 0.351 < \rho^*_1 \), it is seen in Figure 2 that solutions of the system (1) using three different initial values \( (N_1(0.7, 1.2, 4.4), N_2(2.3, 2.4, 1.8) \) and \( N_3(3.3, 0.5, 1.3) \) are convergent to the interior equilibrium point \( E_T = (0.6385, 0.422 \times 10^{-5}, 0.6132) \); showing that \( E_T \) is stable. If we take \( \rho = 0.35324 > \rho^*_1 \), then \( E_T \) becomes unstable. Instead,
all solutions of the system (1) converges to the extinction of prey-2 point $E_5 = (0.643087, 0.604227)$, see Figure 3. This shows that $E_5 = (0.6385, 0.6115)$ is an asymptotically stable. These dynamical behaviors are consistent with the results of the previous analysis.

5.2. Bistability and Hopf Bifurcation

A more rich dynamics in the model (1) may be observed by varying some parameter values. To see these dynamics, we again implement numerical continuation package MatCont using parameter values as in Table 3, and vary the conversion rate parameter ($\rho$). As shown in Figure 4, only equilibrium point $E_2 = (0.20, 0)$ exists and is stable for $\rho < \rho_2^* = 0.885$. When the conversion rate passes the Branch Point (BP), i.e. at $\rho_2^* = 0.885$ then there also appears a stable equilibrium point $E_5 = (10, 0.13492)$ while $E_2 = (0.20, 0)$ remains stable. In this case, the equilibrium point $E_5$ becomes unstable when the conversion rate parameter crosses the critical point $\rho_5^* = 0.975306113536747$ (see point Hopf in Figure 4) and a stable limit cycle appears around $E_5$. Hence, there occurs a Hopf bifurcation which is driven by $\rho$. The bifurcation point in this case is at $\rho_5^*$. These bistability behavior and Hopf bifurcation have not been observed by Raymond et al. [11]. To see the bistability behavior in more detail, we plot in Figure 5 the numerical solutions using parameter as in Table 3 where $\rho = 0.97530612$. From Figure 5, it is seen that when we take initial values $(N_1(0.7, 1.01, 2.9),$ and $N_2(10.3, 8.4, 1.8))$ then the solutions are asymptotically convergent to the extinction of prey-1 and predator point ($E_2$). However, if we take $N_3(3.3, 0.5, 1.3)$ as the initial value, then the numerical solution converges to the extinction of prey-2 point ($E_5$). Such bistability behavior is consistent with the previous analytical results (see Theorem 2 and Theorem 4). Furthermore, if we take a larger value of $\rho$ such that $\rho > \rho_3^*$ then the extinction of prey-2 point is unstable while the extinction of prey-1 and predator point remains stable. Such typical behavior can be observed from numerical solutions of the system (1) as shown in Figure 6, where $\rho = 1.3 > \rho_3^*$. In this figure we see that solution with initial value $N_3(3.3, 0.5, 1.3)$ is convergent to a limit cycle around $E_5$; while solutions with initial values $N_3(10.3, 8.4, 1.8)$ are convergent to the equilibrium $E_2$. This confirms the occurrence of Hopf bifurcation around $E_5$ which is driven by $\rho$. 

FIGURE 3. The phase portraits of system (1) which shows the stability of the extinction of prey-2 point ($E_5$).
Table 3. Parameter value for numerical simulation

|          | r  | s  | k₁ | k₂ | a  | b  | f  | g  | α  | β  | ρ  | η   | μ  |
|----------|----|----|----|----|----|----|----|----|----|----|----|-----|----|
| Simulation 3 | 1.7| 1.9| 12 | 20 | 0.9| 1.6| 2.1| 2.8| 2.1| 2.1| 0.97530612 | 1.3 | 0.9 |
| Simulation 4 | 1.7| 1.9| 12 | 20 | 0.9| 1.6| 2.1| 2.8| 2.1| 2.1| 1.3 | 1.3 | 0.9 |

FIGURE 4. The density of prey for the system (1) with parameters as given in Table 3 and varying the value of ρ, which shows the occurrence of bistability and Hopf bifurcation driven by the conversion rate (ρ).

FIGURE 5. The phase portrait of system (1) which shows bistability phenomenon (both equilibrium point E₂ and equilibrium point E₅ are locally asymptotically stable).
FIGURE 5. The phase portrait of system (1) which shows the stability of equilibrium points $E_2$ and at the same time there exists a stable limit cycle around equilibrium point $E_5$.

6. Conclusion
We have investigated the dynamics of two preys – one predator interaction with competition between prey populations. To study this dynamics, we proposed a model of two preys – one predator interaction, which is based on the Lotka-Volterra predator-prey model. The proposed model has seven equilibrium points. By observing the eigenvalues of the Jacobian matrix or using the Routh-Hurwitz criterion, we have shown that the extinction point of all population ($E_1$) is always unstable; while other equilibrium points ($E_2, E_3, E_4, E_5, E_6, \text{and } E_7$) are conditionally asymptotically stable. These stability properties have been verified by our numerical simulations. We have noticed the existence of transcritical bifurcation in the proposed model. We have also observed numerically the appearance of bistable phenomenon around the extinction point of prey-1 and predator point and the extinction of prey-2 point. The bistable phenomenon shows that the long-time behavior is very sensitive to the initial value. Furthermore, our numerical simulations have also shown the phenomenon where an equilibrium point is locally stable and simultaneously there appears a stable limit cycle. The appearance of limit cycle indicates the occurrence of a Hopf bifurcation which is driven by the conversion rate of predation into predator growth rate $\rho$. Further investigation on the existence of a Hopf bifurcation or other type of bifurcations is a challenge for future research.

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