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The dynamics in an intraguild prey-predator model with Holling type III functional response

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Abstract

In prey-predator models, nonlinear interaction between prey and predator populations results in oscillatory behavior that shows the dynamic growth of the populations. In the growth process, very often both prey and predator share the same resource in their habitat. This is an intraguild predation model. This study focuses on an intraguild prey-predator model generalized by introducing Holling type III functional response. The existence of biologically meaningful equilibria has been investigated. The stability analysis of the equilibria has been determined. Finally, bifurcation and numerical analyses have been presented to illustrate the dynamic behavior of the system. Taking the biotic resource enrichment as the bifurcation parameter, a Hopf bifurcation takes place, where solutions with limit cycle behavior appear. Varying further the parameter, a fold bifurcation of the limit cycle takes place, where the unstable limit appeared due to Hopf bifurcation reverses its growing direction and changes its stability. Taking the predation rate as the bifurcation parameter, saddle-node bifurcations take place. The existence of stable interior equilibria and stable periodic solutions, of which all prey and predator populations and the resource co-exist, guarantee the boundedness of the size of the populations and the resource. This is good from the conservation of an ecosystem point of view.

Keywords: Intraguild, prey, predator, stability, bifurcation.

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1. Introduction

In mathematical ecology, the prey-predator dynamic is vastly used to study the phenomenon of interacting populations in the environment. Since introduced by Lotka (1925) and Volterra (1926) at the same time but in a different context, Lotka-Volterra of prey-predator model has been utilized by many researchers to study the behavior of any species in an ecosystem while they interact with other species or its ecosystem (see [8, 19] and references therein for the model).

The analysis of the simple Lotka-Volterra model is not as simple as it is, because when the model is related to real-world situations it could produce a multiparameter system that leads to a delicate analysis approach. Relating the model to real-world situations simply incorporates the model with broadly relevant biological features, such as carrying capacity which is related to the available sustaining resources,

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functional response; the rate at which predators remove prey, and the predator population dynamics including intra- and interspecific interaction between predators and external factors. See May [16] for a more thorough discussion of the model and see Wangersky [28] for a nice review of the model.

One of the biological features that is of greatest concern to many researchers is carrying capacity. Firstly introduced in 1838 by a Belgian mathematician, Verhulst [27] and elaborated by a biologist, Pearl [20], the Verhulst-Pearl logistic equation given by

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}), \tag{1.1}$$

where $N(t)$ is the density of a population at time t, and r and K are positive constants. The quantity $r(1 - N/K)$ is the per capita birth rate of the population and K is the carrying capacity of the environment. In more recent literature, the assumption of the carrying capacity as a constant is not realistic any more. The continuous growth of the earth's population results in not only the need for more food but also immense improvement in average well-being, environmental quality, and cultural values due to the development of knowledge and technology [9, 11, 17]. Therefore, instead of taking a constant value, the carrying capacity in (1.1) is a function of time t as follows:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K(t)}),$$

where $K(t)$ can be any function. In his book, Banks [6] described models where $K(t)$ varies linearly, sinusoidal, or logistically.

The use of variable carrying capacity in the studies on prey-predator models has been done by many researchers recently, particularly the ones that consider the populations of prey and predator share the resources. In this case, the resources being shared belong to the habitat, where the prey and predators live. In such a prey-predator model, a phenomenon called intraguild predation takes place ([15, 21]). Studies on prey-predator model with intraguild predation have been done by many researchers. A few to be mentioned are the works by Safuan [5, 23–25], Holt and Polis [15], Polis [21], Cohen [9], Basener and Ross [7], and Ganguli et al. [13]. More recent works were done by Al-Moqbali et al. [2] and Al-Salti et al. [3], where they considered Holling type I and II functional responses with delay in the resource's growth. Meanwhile, Ang and Safuan [4, 5] considered an intraguild fishery model with Holling type I and Michaelis-Menten functional responses and harvesting factor(s) to prey and/or predator.

In their study, Safuan et al. [24] implemented Holling type I functional response and interpreted the variable carrying capacity as biotic resource enrichment. They considered the following system:

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{pz}) - axy, \quad \frac{dy}{dt} = r_2 y(1 - \frac{y}{qz}) + bxy, \quad \frac{dz}{dt} = z(c - dx - ey), \tag{1.2}$$

where prey population (x) and predator population (y) both grow logistically with growth rates r_1 and r_2, respectively and are limited proportionally by the availability of biotic resource (z) with the proportion pz and qz, respectively. Assuming $p + q = 1$, then $pz + qz$ is the total carrying capacity. The constant a is the maximal predator consumption rate and b is the biomass conversion rate of the predator. The biotic resource grows linearly with the rate of c, whereas d and e are the intake rate of the resource by x and y, respectively. The results show that by varying the value of the biotic enrichment parameter c, the model can predict co-existence, extinction, and limit cycle behaviors of the solutions. Quite recently, similar results were also shown by Putra et al. [22] when they studied a similar system to equation (1.2) by applying Holling type II functional response.

This study was based on the works by Safuan et al. [24] and Putra et al. [22] mentioned before. This study considered a prey-predator system with intraguild predation generalized by implementing Holling type III functional response and assuming variable carrying capacity to represent biotic resource enrichment of the environment. The solutions of the system being constructed were analyzed, including their stability and bifurcations, both analytically and numerically.

2. Model formulation

The proposed model in this study uses the assumptions used in [22, 24] and implements Holling type III functional response by substituting $f(x) = \frac{x^2}{m+x^2}$ for $f(x) = x$ in equation (1.2) or for Holling functional response II in [22] to obtain

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{pz}) - \frac{ax^2 y}{m + x^2}, \quad \frac{dy}{dt} = r_2 y(1 - \frac{y}{qz}) + \frac{bx^2 y}{m + x^2}, \quad \frac{dz}{dt} = z(c - dx - ey). \tag{2.1}$$

The definitions of variables and parameters follow similar lines with those in equation (1.2), while m in Holling type III functional response is related to the learning behavior of predator due to low densities of prey [10]. Transforming equation (2.1) by using the transformations $\tau = r_1 t$, $\hat{x} = \frac{b}{r_1}x$, $\hat{y} = \frac{a}{r_1}y$, $\hat{z} = \frac{bp}{r_1}z$, we obtain the corresponding non-dimensionless system (after dropping the hats)

$$\frac{dx}{d\tau} = x(1 - \frac{x}{z}) - \frac{\alpha x^2 y}{\mu + x^2}, \quad \frac{dy}{d\tau} = \sigma y(1 - \frac{\eta y}{z}) + \frac{\beta x^2 y}{\mu + x^2}, \quad \frac{dz}{d\tau} = z(\rho - \delta x - \varepsilon y), \tag{2.2}$$

with $\alpha = \frac{b}{r_1}$, $\beta = \frac{b}{a}$, $\mu = \frac{mb^2}{r_1^2}$, $\sigma = \frac{r_2}{r_1}$, $\eta = \frac{bp}{aq}$, $\rho = \frac{r_1 c}{bp}$, $\delta = \frac{dr_1}{b}$, $\varepsilon = \frac{er_1}{a}$.

3. Results and discussion

3.1. Existence of equilibria

The equilibria of system (2.2) are obtained by taking $\frac{dx}{d\tau} = \frac{dy}{d\tau} = \frac{dz}{d\tau} = 0$ or

$$x(1 - \frac{x}{z}) - \frac{\alpha x^2 y}{\mu + x^2} = 0, \quad \sigma y(1 - \frac{\eta y}{z} + \frac{\beta x^2 y}{\mu + x^2} = 0, \quad z(\rho - \delta x - \varepsilon y) = 0.$$

From this system of equations, by avoiding trivial solution $E_0(0, 0, 0)$, biologically meaningful equilibria can be obtained as follow.

1. Boundary equilibria.
   - Free from prey equilibrium, $E_1(0, \frac{\rho}{\varepsilon}, \frac{\eta\rho}{\varepsilon})$
     Condition when predator survive in the absence of prey.
   - Free from predator equilibrium, $E_2(\frac{\rho}{\delta}, 0, \frac{\rho}{\delta})$
     Condition when prey survive in the absence of predator.
2. Interior equilibria $E_3(\bar{x}, \bar{y}, \bar{z})$, where

$$\begin{aligned}
\bar{y} &= -\frac{1}{\varepsilon}(\delta\bar{x} - \rho), \\
\bar{z} &= \frac{1}{\mathcal{K}}(\alpha^2\beta\delta^2\eta\rho\sigma + \alpha\beta\delta\eta\rho\sigma\varepsilon + \alpha\beta^2\rho\varepsilon^2 + \alpha\beta\rho\sigma\varepsilon^2)\bar{x}^2 \\
&\quad + (\alpha^2\delta^3\eta\mu\sigma^2 - 2\alpha^2\beta\delta\eta\rho^2\sigma - \alpha^2\delta\eta\rho^2\sigma^2 + \alpha\beta\delta^2\eta\mu\sigma\varepsilon - \alpha\beta\delta\mu\sigma\varepsilon^2 - \alpha\beta\eta\rho^2\sigma\varepsilon + \beta^2\mu\varepsilon^3)\bar{x} \\
&\quad + \alpha^2\delta^2\eta\mu\rho\sigma^2 + \alpha^2\beta\eta\rho^3\sigma + \alpha^2\eta\rho^3\sigma^2 - \alpha\beta\delta\eta\mu\rho\sigma\varepsilon,
\end{aligned}$$

   with

$$\mathcal{K} = (\alpha^2\delta^2\mu\sigma^2 + \alpha^2\beta\rho^2\sigma + \alpha^2\rho^2\sigma^2 - 2\alpha\beta\delta\mu\sigma\varepsilon + \beta^2\mu\varepsilon^2)\varepsilon.$$

   $\bar{x}$ is real positive roots of the following cubic equation

$$C_3\bar{x}^3 + C_2\bar{x}^2 + C_1\bar{x} + C_0 = 0, \tag{3.1}$$

with $C_0 = \eta\mu\rho\sigma\varepsilon$, $C_1 = \alpha\eta\rho^2\sigma + \delta\eta\mu\sigma\varepsilon$, $C_2 = -2\alpha\delta\eta\rho\sigma - \eta\rho\sigma\varepsilon$, and $C_3 = \alpha\delta^2\eta\sigma + \delta\eta\sigma\varepsilon + \beta\varepsilon^2\sigma\varepsilon^2$. The existence of positive roots of equation (3.1) can be determined by using del Ferro-Tartaglia-Cardano formula [26] by first reducing equation (3.1) into $\bar{x}^3 + \kappa_2\bar{x}^2 + \kappa_1\bar{x} + \kappa_0 = 0$, with $\kappa_2 = C_2/C_3$, $\kappa_1 = C_1/C_3$, $\kappa_0 = C_0/C_3$. Using the transformation $\bar{x} = \zeta - 1/3\kappa_2$, the polynomial is again reduced into

$$\zeta^3 + u\zeta + v = 0 \tag{3.2}$$

with $u = \kappa_1 - \frac{\kappa_2^2}{3}$ and $v = \frac{2\kappa_2^3}{27} - \frac{\kappa_1\kappa_2}{3} + \kappa_0$. The discriminant of equation (3.2) can be derived as

$$\Delta^2 = \frac{v^2}{4} + \frac{u^3}{27},$$

from which the existence of positive root(s) of equation (3.2) can be determined as the following criteria:

(i) $\Delta^2 \geqslant 0$, there exists one positive root of the polynomial;
(ii) $\Delta^2 < 0$, there exist three distinct positive roots of the polynomial.

Therefore, criterion (i) guarantees that there exists one value of $\bar{x}$ of the interior equilibria of system (2.2), and hence there exists one interior equilibrium of the system. Criterion (ii) guarantees that there exist three values of $\bar{x}$ of the interior equilibria of system (2.2), and hence the system has three distinct interior equilibria. Due to the complexity of the coefficients of the polynomial, the explicit expression of the positive roots obtained following the criteria above, and hence the value of $\bar{x}$ of the interior equilibria of system (2.2), cannot be presented here. It will be confirmed later from the numerical simulations. The existence of the interior equilibrium E_3 is also determined by the condition derived from the positivity conditions of $\bar{y}$ and $\bar{z}$.

3.2. *The stability of the equilibria*

The stability analysis of the boundary equilibria of system (2.2) can be easily done by using linearization to obtain the Jacobian matrix of the system as follows:

$$J(x,y,z) = \begin{pmatrix} 1 - \frac{2x}{z} - \frac{2\alpha xy}{x^2+\mu} + \frac{2\alpha x^3 y}{(x^2+\mu)^2} & -\frac{\alpha x^2}{x^2+\mu} & \frac{x^2}{z^2} \\ \frac{2\beta xy}{x^2+\mu} - \frac{2\beta x^3 y}{(x^2+\mu)^2} & \sigma - \frac{2\eta\sigma y}{z} + \frac{\beta x^2}{x^2+\mu} & \frac{\eta\sigma y^2}{z^2} \\ -z\delta & -z\varepsilon & -\delta x - \varepsilon y\rho \end{pmatrix}.$$

Substituting $E_1(0, \frac{\rho}{\varepsilon}, \frac{\eta\rho}{\varepsilon})$ into the Jacobian to find the following characteristics equation

$$(\lambda - 1)(\lambda^2 + \lambda\sigma + \rho\sigma) = 0,$$

from which the corresponding eigenvalues are: $\lambda_1 = 1$, $\lambda_{2,3} = -\frac{\sigma}{2} \pm \frac{\sqrt{\sigma^2 - 4\sigma\rho}}{2}$. Since one of the eigenvalues is positive ($\lambda_1 = 1$), then $E_1(0, \frac{\rho}{\varepsilon}, \frac{\eta\rho}{\varepsilon})$ is linearly unstable. Substituting $E_2(\frac{\rho}{\delta}, 0, \frac{\rho}{\delta})$ into the Jacobian to find the following characteristics equation

$$(-\delta^2\lambda\mu + \delta^2\mu\sigma + \beta\rho^2 - \lambda\rho^2 + \rho^2\sigma)(\lambda^2 + \lambda + \rho) = 0,$$

from which the corresponding eigenvalues are: $\lambda_1 = \frac{\delta^2\mu\sigma + \beta\rho^2 + \rho^2\sigma}{(\delta^2\mu + \rho^2)}$, $\lambda_{2,3} = -\frac{1}{2} \pm \frac{\sqrt{1-4\rho}}{2}$. Since all the parameters are positive, then $\lambda_1 > 0$ and hence $E_2(\frac{\rho}{\delta}, 0, \frac{\rho}{\delta})$ is linearly unstable. The above local stability analyses are summarized in the following theorem.

Theorem 3.1. *The boundary equilibria* $E_1(0, \frac{\rho}{\varepsilon}, \frac{\eta\rho}{\varepsilon})$ *and* $E_2(\frac{\rho}{\delta}, 0, \frac{\rho}{\delta})$ *are linearly unstable.*

The stability of the interior equilibrium of $E_3(\bar{x}, \bar{y}, \bar{z})$ of system (2.2) is cumbersome if applying linear (local) analysis as those of the boundary equilibria. Therefore, following the idea of Ganguli [13] and Ang and Safuan [4, 5], a stability analysis for the interior equilibrium is performed by constructing an appropriate Lyapunov function. Hence, the stability of the interior equilibrium is concluded by proving the following theorem.

Theorem 3.2. *The interior equilibrium $E_3(\bar{x}, \bar{y}, \bar{z})$ is asymptotically stable in the domain of attraction that is restricted by:*

(1) $\frac{1}{\bar{z}} + \frac{\alpha y(\mu - x\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)} > 0$;

(2) $4\left[\frac{1}{\bar{z}} + \frac{\alpha y(\mu - x\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)}\right]\left[\frac{\varepsilon\sigma}{\delta}\frac{x}{y\bar{z}}\right] > \left[\alpha\bar{x}(\mu+x^2) - \frac{\varepsilon\beta\mu}{\delta\eta}\frac{x}{y}(x+\bar{x})\right]^2$.

Proof. Let the Lyapunov function for system (2.2) be

$$V(x,y,z) = \left[(x-\bar{x}) - \bar{x}\ln\frac{x}{\bar{x}}\right] + \mathcal{G}\left[(y-\bar{y}) - \bar{y}\ln\frac{y}{\bar{y}}\right] + \mathcal{H}\left[(z-\bar{z}) - \bar{z}\ln\frac{z}{\bar{z}}\right],$$

where functions $\mathcal{G}$ and $\mathcal{H}$ will be determined. Obviously, $V(\bar{x}, \bar{y}, \bar{z}) = 0$ and $V(x, y, z) > 0$ for all positive values of x, y, and z. Next, the derivative of the Lyapunov function is

$$\begin{aligned}
\frac{dV}{d\tau} &= \left(\frac{x-\bar{x}}{x}\right)\frac{dx}{d\tau} + \mathcal{G}\left(\frac{y-\bar{y}}{y}\right)\frac{dy}{d\tau} + \mathcal{H}\left(\frac{z-\bar{z}}{z}\right)\frac{dz}{d\tau} \\
&= (x-\bar{x})\left[\frac{\bar{x}}{\bar{z}} - \frac{z}{x} + \alpha\left(\frac{\bar{x}\bar{y}}{\mu+\bar{x}^2} - \frac{xy}{\mu+x^2}\right)\right] + \mathcal{G}(y-\bar{y})\left[\sigma\eta\left(\frac{\bar{y}}{\bar{z}} - \frac{y}{z}\right) + \beta\left(\frac{x^2}{\mu+x^2} - \frac{\bar{x}^2}{\mu+\bar{x}^2}\right)\right] \\
&\quad + \mathcal{H}(z-\bar{z})\left[\delta(\bar{x}-x) - \varepsilon(\bar{y}-y)\right] \\
&= (x-\bar{x})\left[\frac{\bar{x}-x}{z} + \frac{x(z-\bar{z})}{z\bar{z}} + \alpha\left(\frac{(\mu\bar{x}+x^2\bar{x})(\bar{y}-y) + (\mu y + x^2 y - (x+\bar{x})xy)(x-\bar{x}))}{(\mu+x^2)(\mu+\bar{x}^2)}\right)\right] \\
&\quad + \mathcal{G}(y-\bar{y})\left[\sigma\eta\frac{\bar{y}-y}{\bar{z}} + \sigma\eta\frac{y(z-\bar{z})}{z\bar{z}} + \beta\mu\frac{(x-\bar{x})(x+\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)}\right] + \mathcal{H}(z-\bar{z})[\delta(\bar{x}-x) + \varepsilon(\bar{y}-y)] \\
&= -\left\{(x-\bar{x})^2\left[\frac{1}{\bar{z}} + \alpha\frac{\mu\bar{x} + x^2 y - (x+\bar{x})xy}{(\mu+x^2)(\mu+\bar{x}^2)}\right] + (x-\bar{x})(y-\bar{y})\left[\frac{\alpha(\mu\bar{x}+x^2\bar{x}) - \mathcal{G}\beta\mu(x+\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)}\right]\right. \\
&\quad \left. + \mathcal{G}(y-\bar{y})^2\left[\frac{\sigma\eta}{\bar{z}}\right] + (x-\bar{x})(z-\bar{z})[\delta\mathcal{H} - \frac{x}{z\bar{z}}] + (y-\bar{y})(z-\bar{z})\left[\varepsilon\mathcal{H} - \mathcal{G}\eta\frac{y}{z\bar{z}}\right]\right\}.
\end{aligned}$$

Now, choosing $\mathcal{G} = \frac{\varepsilon x}{\delta\eta y}$ and $\mathcal{H} = \frac{x}{\delta z\bar{z}}$, we obtain

$$\begin{aligned}
\frac{dV}{d\tau} = -&\left\{(x-\bar{x})^2\left[\frac{1}{\bar{z}} + \frac{\alpha y(\mu - x\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)}\right]\right. \\
&\left. + (x-\bar{x})(y-\bar{y})\left[\frac{\alpha y(\mu + x\bar{x}) - \frac{\varepsilon\beta\mu}{\delta\eta}\frac{x}{y}(x+\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)}\right] + (y-\bar{y})^2\left[\frac{\varepsilon\sigma}{\delta}\frac{x}{y\bar{z}}\right]\right\}.
\end{aligned} \tag{3.3}$$

The right-hand side of (3.3) can be expressed into a quadratic form matrix

$$-\left\{\begin{pmatrix}(x-\bar{x}) & (y-\bar{y})\end{pmatrix} A \begin{pmatrix}(x-\bar{x}) \\ (y-\bar{y})\end{pmatrix}\right\},$$

where

$$A = \begin{pmatrix} \frac{1}{\bar{z}}\frac{\alpha y(\mu - x\bar{x})}{(\mu+x^2)(\mu+\bar{x}^2)} & \frac{1}{2}\left(\alpha\bar{x}(\mu+x^2) - \frac{\varepsilon\beta\mu}{\delta\eta}\frac{x}{y}(x+\bar{x})\right) \\ \frac{1}{2}\left(\alpha\bar{x}(\mu+x^2) - \frac{\varepsilon\beta\mu}{\delta\eta}\frac{x}{y}(x+\bar{x})\right) & \frac{\varepsilon\sigma}{\delta}\frac{x}{y\bar{z}} \end{pmatrix}.$$

Since matrix A satisfies conditions (1) and (2) of Theorem 3.2, then the matrix is positive definite, and hence $\frac{dV}{d\tau} < 0$. Therefore, this implies that the interior equilibrium $E_3(\bar{x}, \bar{y}, \bar{z})$ is asymptotically stable in the restricted domain. The proof is concluded. □

3.3. *Numerical simulation, bifurcations, and its interpretation*

This section is devoted to simulating the behavior of the equilibria of system (2.2) whose stability are determined in the previous section. This section also equips the analytical stability analysis, particularly the stability of the interior equilibria of the system. The simulations were done by using MatCont, an open-source numerical continuation package that is used to integrate the system numerically to find the solution of the system and its stability [12]. MatCont also can be used to locate possible bifurcation of the solution of the system (see [18] for a more updated package and documentation). The simulation utilizes two sets of parameters considering the existence criteria of interior equilibria (criteria (i) and (ii) above) as in Table 1.

Table 1: Sets of parameter values.

dimensionless parameters	rescale of	Set I	Set II
α	b/r_1	0.003	0.07 (varied)
β	b/a	0.3	1.16
δ	dr_1/b	2	0.289
η	bp/aq	0.5	1.169
μ	mb^2/r_1^2	0.5	0.0095
ρ	r_1c/bp	0.5 (varied)	2.226
σ	r_2/r_1	0.003	0.818
ε	er_1/a	2.5	0.169

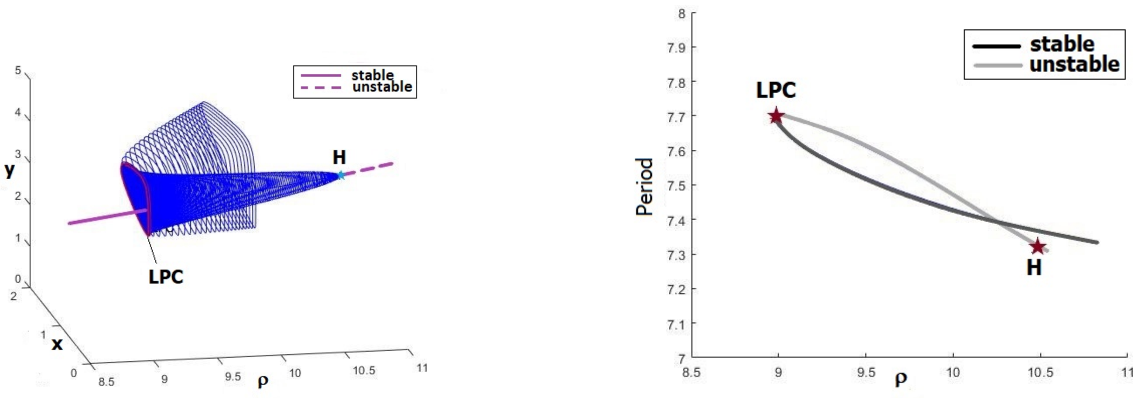
Parameter set I corresponding to criterion (i) of the existence of interior equilibria gives one interior equilibrium. Thus, with these initial values, the system has three equilibria, i.e., $E_1(0, 0.2, 0.1)$, $E_2(0.25, 0, 0.25)$, and $E_3(0.5174, 0.158, 0.5174)$. The boundary equilibria E_1 and E_2 are known already from Theorem 3.1 that they are unstable. While E_3, from Theorem 3.2, can be determined as an asymptotically stable equilibrium. Varying the value of ρ, the interior equilibrium bifurcates and changes its stability when $\rho = 10.513472$; a subcritical Hopf bifurcation takes place, where unstable limit cycles or periodic solutions emanate in the direction of the stable interior equilibrium. This bifurcation is indicated in MatCont by showing the label H, and the coordinate of the interior equilibrium when $\rho = 10.513472$. Since the first Lyapunov coefficient is positive, there must be an unstable limit cycle that emerges from the equilibrium.

```
label = H, x = (0.213917 4.034255 0.214937 10.513472)
      First Lyapunov coefficient = 2.936629e-01
```

Varying further the value of ρ, the limit cycles grow and end up to a critical limit cycle (LPC) at $\rho = 8.974815$. As indicated by MatCont, the critical limit point has approximately double multipliers equal to 1 and the normal form coefficient is nonzero.

```
Limit point cycle (period = 7.692959, parameter = 8.974815)
         Normal form coefficient = 2.012404
```

The limit cycles run into fold bifurcation; the limit cycle branches, after the LPC cycle, into larger stable limit cycles, as indicated that the nontrivial multipliers are positive but less than 1. The stable limit cycles continue to exist as the value of ρ is increasing. This description is well illustrated in Figure 1 below. Figure 1 (a) illustrates the appearance of the unstable limit cycles that come out of the subcritical Hopf bifurcation and then the limit cycles grow and bifurcate through the LPC cycle to become stable limit cycles. Meanwhile, Figure 1 (b) indicates the presence of two limit cycles (one stable and one unstable) with different periods for $\rho > 8.974815$ and later both limit cycles will have the same period when $\rho \approx 10.2$.



(a) (b)

Figure 1: Bifurcation diagram of the interior equilibrium E_3 when ρ varies; (a) in $\rho - x - y$ space; (b) in ρ-period (of the limit cycles).

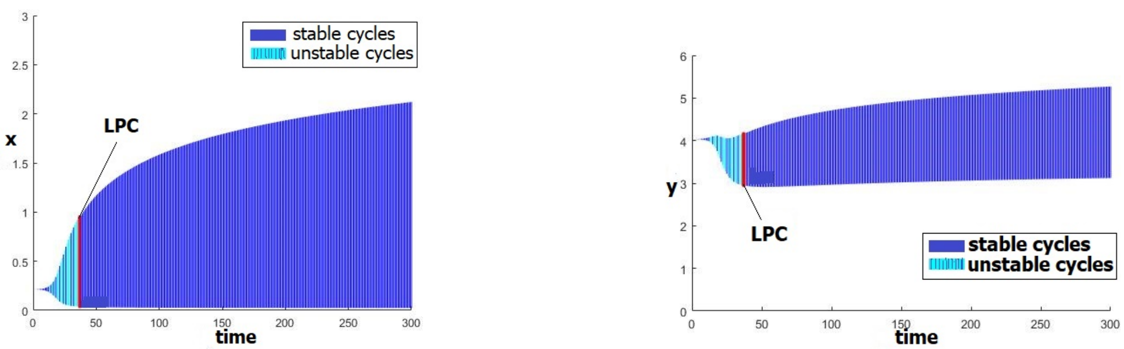
Therefore, despite the two unstable boundary equilibria, the system still manages its stability for all values of ρ, as it can be divided into the following subintervals.

1) In the subinterval $0 < \rho \leqslant 10.513472$, the interior equilibrium is stable.
2) In the subinterval $8.974815 \leqslant \rho < \infty$, the (outer) stable limit cycle appears due to fold bifurcation.

Hence, in the subinterval $8.974815 \leqslant \rho \leqslant 10.513472$, there exists a bi-stability, i.e., the interior equilibrium and the (outer) stable limit cycle due to fold bifurcation.

The stability of interior equilibrium, in which all prey and predator populations and the resource co-exist, is important for the conservation of not only the populations of prey and predator but also the environment where both populations live. On the other hand, the presence of the stable limit cycle or periodic solution, represents a cyclic growth of the interacting prey and predator populations. As a consequence, the resource evolutes also in a cyclic manner. In addition, the presence of a stable limit cycle or periodic solution guarantees the boundedness of the populations and the availability of the resource. In the case of the existence of bi-stability in the subinterval $8.974815 \leqslant \rho \leqslant 10.513472$, the populations tend either to the stable interior equilibrium or to the stable limit cycle, depending on the initial size of the populations.

The behavior of both stable and unstable limit cycles (when the value of ρ varies) can be better observed when it is plotted in a time series. Figures 2 (a) and (b) correspond to the dynamics of x and y populations, respectively, for $0 \leqslant t \leqslant 300$.



(a) (b)

Figure 2: The dynamics of stable and unstable limit cycles when ρ varies; (a) time with respect to x population; (b) time with respect to y population.

From those figures it can be seen that the stable limit cycles (after LPC) lead to a bounded limit cycle. These suggest that the periodic behavior of the growth dynamics of co-existing of prey and predator will persist for a long time. This co-existing situation can be described as the availability of the resource can guarantee the conservation of both prey and predator populations for a long time.

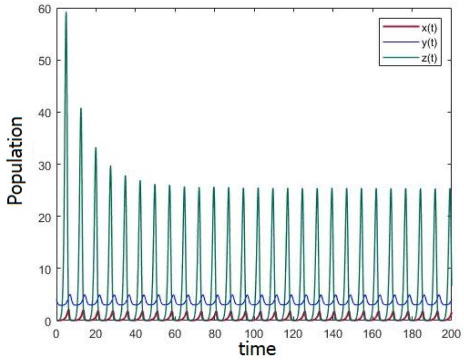


Figure 3: The time plots of a stable limit cycle when $\rho = 9.8$ with respect to x, y, z populations.

Figure 3 illustrates the periodically stable behavior of prey and predator population density when the biotic enrichment parameter $\rho > 8.974815$; after the occurrence of fold bifurcation. Among the populations, the oscillation of the resource density $z(t)$ is the largest, which is expected as the resource is usually available in large numbers.

Parameter set II of Table 1 corresponding to criterion (ii) of the existence of interior equilibria gives three interior equilibria. With these initial values, the system has five equilibria, i.e., two boundary equilibria: $E_1(0, 13.15789, 15.384615)$, $E_2(7.692307, 0, 7.692307)$, and three interior equilibria: $E_3(3.11631, 7.827363, 3, 769888)$, $E_4(0.950066, 11.532781, 5.585712)$, and $E_5(0.010633, 13.139706, 15.110597)$. As before, the boundary equilibria E_1 and E_2 are known already previously that they are unstable. The stability analyses of E_3, E_4, and E_5 were done numerically by using MatCont. The simulation using parameter set II does not give an interesting result when varying the value of ρ as in the previous case. Therefore, in this case, by varying the value of parameter α, corresponding to the predation rate of the predator, the following bifurcation diagram is obtained.

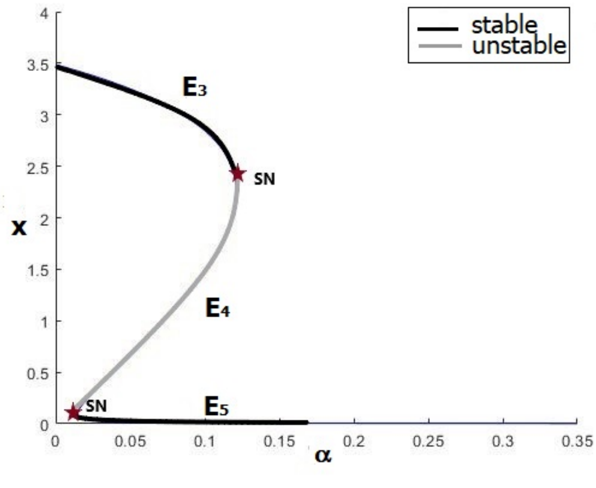


Figure 4: The bifurcation diagram of interior equilibria E_3, E_4 and E_5 when varying α.

From Figure 4 it can be noticed that by varying the value of α, there are two saddle node bifurcations taking place, i.e., at $\alpha = 0.014825$ and at $\alpha = 0.121219$. Therefore, in the interval $0.014825 \leqslant \alpha \leqslant 0.121219$

there exist three equilibria, i.e., E_3 which is stable, E_4 which is unstable, and E_5 which is stable. This is in line with criterion (ii) above.

In this case, the system can manage its stability for all positive values of α. In the subinterval $0 < \alpha \leqslant 0.014825$ only E_3 is stable, while in the subinterval $\alpha \geqslant 0.121219$ only E_5 is stable. Meanwhile, in the subinterval $0.014825 \leqslant \alpha \leqslant 0.121219$ there exists a bi-stability, i.e., both E_3 and E_5 are stable. Hence, the existence of interior equilibria of the system guarantees the conservation of the population of prey and predator and the availability of the resource.

4. Conclusions

The results of the study of a system that consists of intraguild predation involving Holling type III functional response are quite interesting both biological and mathematically. The results in this study are complementary to similar results done by Safuan et al. [24] and Putra et al. [22], where by applying Holling type III functional response, the results lead to more complete information, particularly the criteria of the existence of positive interior equilibrium and its stability, which is comparably consistent with those done by Ang and Safuan [4, 5].

The existence of limit cycles is typical in prey-predator systems. Nevertheless, the appearance of fold bifurcation of the limit cycle still needs to be studied further, particularly such that it is biologically meaningful. In addition, the fold bifurcation can be studied further mathematically.

The existence of stable interior equilibria and stable periodic solutions due to Hopf and fold bifurcations guarantee the conservation of both populations of prey and predator in the availability of the resource. So is the existence of three interior equilibria due to multiple saddle node bifurcations.

In terms of conservation, the results in this study can be compared with those by Ghosh et al. [14]. While in their work they considered a (constant) parameter related to marine protected areas, this study implements variable carrying capacity and has observed that how the parameter related to the biotic resource growth affects the solution of the system. In addition, the appearance of bistability due to multiple saddle node bifurcations may lead to the possibility of the appearance of hydra effects, especially when an external factor, such as harvesting, is implemented (see [1] for the study on hydra effects and bifurcations on Bazykin's model).

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