

Revisited Hastings and Powell model with omnivory and predator switching



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ABSTRACT

The effect of omnivory in predator-prey system is debatable regarding its stabilizing or destabilizing characteristics. Earlier theoretical studies predict that omnivory is stabilizing or destabilizing depending on the condition of the system. The effect of omnivory in the food chain system is not yet properly understood. In the present paper, we study the effect of omnivory in a tri-trophic food chain system on the famous Hastings and Powell model. Omnivory enhances the chance of predator switching between prey and middle predator. The novelty of this paper is to study the effect of predator switching of the top predator which is omnivorous in nature. Our results suggest that in the absence of switching, an increase of omnivory stabilizes the system from chaotic dynamics, however, if we further increase the strength of omnivory, the system becomes unstable and middle predator goes to extinction. It is also observed that the predator switching enhance the stability and persistence of all populations.

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1. Introduction

The evidence of chaos in the real world is still far reaching. But the literature of chaos and chaos control are vast in different fields such as biological systems, electrical engineering, ecological models, and economics [1–4]. The dynamic relationship between predators and their preys is a dominant theme in both theoretical and mathematical ecology. Without seasonality or structure, chaotic dynamics cannot occur in continuous systems unless at least three species are included. Hastings and Powell [4] suggested that chaos is common in natural systems (interacting tri-trophic food chain). Occurrence of chaos in a simple ecological system produces chaos as a subject of considerable interest among theoretical ecologists [5,4,6,7].

However, there is still lack of experimental evidences of chaos in the real world population dynamics. Chaos detection in natural system is difficult due to the presence of observational noise [8,9]. Becks et al. [10] experimentally showed chaos in the predator-prey interaction between bacterivorous ciliate and two bacterial prey species.

It is to be noted that chaos is rare in the natural populations. One of the main objectives of ecosystems is to study the persistence and stability of these systems [11,12]. Several researchers try to replace this chaotic dynamics by stability and oscillatory behavior because of its rarity in natural systems. Thus, since last two decades chaos control has become a new aspect in ecological modeling. Until now, many researchers proposed how to control the chaos in food chain models by using several reasonable biological phenomena. The biological phenomena like imposition of a population floor [13,14], addition of refugia [15], omnivory [41], intraspecific density dependence [16], toxic inhibition [3], spatial effect [17], disease in the prey [18], migration in the middle predator [19],

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and cascading migration [20] can control the chaos. Among these biological factors, omnivory is one of the most common factors across all types of ecosystems. Though omnivory is widespread and common in natural systems, but little attention has been paid in the study of tri-trophic food chain with omnivory.

Omnivory is a feeding strategy in which a consumer feeds at multiple trophic levels (e.g. in a tri-trophic food chain, top predator predares both prey and middle predator) [21,22]. This may include, but does not require, feeding on both plants and animals. Recently, omnivory has been reported as a common phenomenon in the diverse ecosystems [23–25]. For example, omnivorous birds and lizards can feed on both predatory spiders and the herbivorous insects that the spiders prey upon [26]. Black and grizzly bears feed on wild berries in terrestrial habitat and fish in aquatic habitat without competing with either prey type [27]. Review of published food webs recently showed that the proportion of omnivorous species was highest in marine planktonic systems, lowest in streams, and intermediate in the lake and terrestrial ecosystems [28,29]. Furthermore, experimental studies [30,31,26] and casual observations suggest that omnivory is an important biological phenomena in nature.

Though omnivory is common in various ecosystems, the effect of omnivory in population stability is yet not properly understood. Whether the omnivory act as a stabilizing or destabilizing factor has become a longstanding debatable issue in ecology. Earlier theoretical literature suggests that omnivory is destabilizing in the context of food webs [21,32,33]. Omnivory increases the connectance or complexity of a food web, which is predicted to decrease the stability of randomly assembled communities [34]. Long et al. experimentally showed that the increasing prevalence of omnivory among the top predators decline the stability of herbivore abundance and microalgae [35]. Holt and Polis theoretically explored that intraguild predation could destabilize a three species Lotka-Volterra model with linear functional responses [36] and Holt also verified that the Lotka-Volterra model of intraguild predation could exhibit a limit cycle [37]. Recently, Tanabe and Namba [38] have reinvestigated Holt and Polis's model and numerically showed that omnivory creates chaos in a simple three species Lotka-Volterra model with linear functional response. In contrast, France (2012) suggested that omnivory shorten the vertical structure of food webs under the condition of low productivity, which may enhance community stability [39]. Pillai et al. (2011) also suggested that in a landscape of connected patches, omnivory is not only possible, but also necessary for the stability of the metacommunity [40]. McCann and Hastings [41] theoretically explored that the addition of omnivory in a simple food chain model stabilizes the food web from chaos to order [41]. Fagan experimentally showed that omnivory has the stabilizing effect in a food web [42]. Therefore, Omnivory may be either stabilizing or destabilizing, depending on the conditions of the system [41,43,44]. While strong omnivory is always destabilizing, weak to intermediate omnivorous interaction strengths confer substantial stability to food webs in most cases [45].

Recently, Kratina et al. (2012) suggested that inducible prey defenses, prey switching and external interactions

with the rest of the food web can promote the persistence of food webs with omnivory [46]. In a tri-trophic food chain, the top predator becomes an omnivore if it also consumes the basal resource (prey). Interestingly, in tri-trophic food chain with omnivory, predator switching might occur between prey and middle predator as the top predators have prey and middle predator to predate upon.

Predator switching occurs in multi-species food chain/web while predator has more than one prey species to graze. In preferential predation, the number of preferred prey reduced due to heavy predation; this would force the predator to change its attention temporarily towards another prey. This preferential change of attack on prey type by the predator is well-known as predator switching. Predator switching mechanism [47] is a biological phenomenon where the predator population prefers to eat most abundant prey when other prey population is rare [48]. For example, the intertidal snail *Nucella lapillus* prefers either barnacles or mussels depending on their availability [49]. In laboratory experiments, switching has also been observed in *Notonecta* and *Ischnura* [50].

It is well documented that predator switching is more relevant than proportion-based predation because this enhance the stability of food webs and promote biodiversity [51]. If the predator switch between multiple preys then individuals of rare species are with lower risk of being predated upon than individuals of abundant species which enhance the persistence of larger and more complex communities [52]. Recently, Vallina et al. (2014) have also explored that phytoplankton diversity increases significantly when active switching is combined with maximal feeding through predator-mediated coexistence [53]. Abrams and Matsuda suggested that predator switching is the most important factor for persistence and community stability with diverse prey species [54]. Predator switching is a very resemble biological phenomena to omnivory and likely to occur with it [55]. In tri-trophic food chain with omnivory, predator have both prey and middle predator to predate upon, which clearly indicates that there might be a chance of predator switching between prey and middle predator. Therefore, tri-trophic food chain would be more interesting and complex in the presence of predator switching along with omnivory. Holt and Polis suggested that if adaptive foraging by the omnivore predator leads to switching between the prey and the middle predator, the system will be stabilized [36]. Recently, Kritina et al. also suggested that the prey defence mechanism and predator switching might modify the stability of omnivory systems [46]. However, the effect of predator switching in omnivory system is yet not studied explicitly.

In the present paper, we are going to present four mathematical models; Hastings-Powell model (HP), HP model with omnivory in top predator and the models with predator switching (preferential switching and density dependent switching). Our results suggest that omnivory in tri-trophic food chain stabilizes the system from chaos to order, but if the resource (prey) grazing rate of top predator increases, then the system may lose the stability and the extinction of middle predator is almost certain. However, the system becomes stable if we incorporate predator

switching between prey and middle predator. The paper is organized as follows. In Section 2, we consider the HP model and investigate the analytical and numerical results. We modify the HP model step by step by incorporating omnivory and predator switching in top predator in Section 3 and 4 respectively and the corresponding model analysis has been done. Finally, the paper ends with a conclusion.

2. The mathematical model

Our basic aim is to observe the dynamics of a tri-trophic food chain system in the presence of omnivory and predator switching. To start with, there is no other better choice other than HP model. To make our presentation self sufficient, we first briefly state the main results of the model proposed by Hastings and Powell [4].

$$\begin{aligned} \frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - \frac{C_1 A_1 XY}{B_1 + X}, \\ \frac{dY}{dT} &= \frac{A_1 XY}{B_1 + X} - \frac{A_2 YZ}{B_2 + Y} - D_1 Y, \\ \frac{dZ}{dT} &= \frac{C_2 A_2 YZ}{B_2 + Y} - D_2 Z. \end{aligned} \quad (2.1)$$

where X , Y and Z be the densities of prey, middle predator and top predator population respectively. In the absence of predation, the prey population grows logically with intrinsic growth rate R_0 and carrying capacity K_0 . A_1 and A_2 are the maximum predation rates of middle predator on prey and top predator on middle predator respectively. B_1 and B_2 are the half saturation constants of middle predator and top predator respectively. C_1^{-1} , C_2 represent the conversion efficiencies of middle predator and top predator respectively. D_1 and D_2 are the natural mortality rates of middle predator and top predator respectively.

Now, introducing dimensionless variables $x = X/K_0$, $y = C_1 Y/K_0$, $z = C_1 Z/C_2 K_0$, and $t = R_0 T$ we obtain the following dimensionless system

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x) - \frac{a_1 xy}{1 + b_1 x}, \\ \frac{dy}{dt} &= \frac{a_1 xy}{1 + b_1 x} - \frac{a_2 yz}{1 + b_2 y} - d_1 y, \\ \frac{dz}{dt} &= \frac{a_2 yz}{1 + b_2 y} - d_2 z. \end{aligned} \quad (2.2)$$

The system has to be analyzed with the initial conditions $x(0) > 0$, $y(0) > 0$, $z(0) > 0$, where, the dimensionless parameters are $a_1 = \frac{A_1 K_0}{R_0 B_1}$, $b_1 = \frac{K_0}{B_1}$, $a_2 = \frac{A_2 K_0 C_2}{R_0 B_2 C_1}$, $b_2 = \frac{K_0}{B_2 C_1}$, $d_1 = \frac{D_1}{R_0}$, $d_2 = \frac{D_2}{R_0}$.

2.1. Equilibria and stability analysis

The above model (2.2) has at most four non-negative equilibria.

- (i) The trivial equilibrium $\tilde{E}_0(0, 0, 0)$.
- (ii) The middle predator and top predator free axial equilibrium $\tilde{E}_1(1, 0, 0)$.

- (iii) The top predator free equilibrium $\tilde{E}_2(\tilde{x}_2, \tilde{y}_2, 0)$, where $\tilde{x}_2 = \frac{d_1}{a_1 - b_1 d_1}$, and $\tilde{y}_2 = \frac{(1-\tilde{x}_2)(1+b_1\tilde{x}_2)}{a_1}$.
- (iv) The positive interior equilibrium $\tilde{E}^*(\tilde{x}^*, \tilde{y}^*, \tilde{z}^*)$, where $\tilde{y}^* = \frac{d_2}{a_2 - b_2 d_2}$, $\tilde{x}^* = \frac{(b_1 - 1) + \sqrt{(b_1 - 1)^2 - 4b_1(a_1\tilde{y}^* - 1)}}{2b_1}$, $\tilde{z}^* = \frac{1 + b_2\tilde{y}^*}{a_2} \left(\frac{a_1\tilde{x}^*}{1 + b_1\tilde{x}^*} - d_1 \right)$, provided that $a_1\tilde{y}^* < 1$.

It is to be noted that the trivial equilibrium $\tilde{E}_0(0, 0, 0)$ and the axial equilibrium $\tilde{E}_1(1, 0, 0)$ always exist. However, the top predator free equilibrium $\tilde{E}_2(\tilde{x}_2, \tilde{y}_2, 0)$ exists if $\frac{a_1}{d_1} > 1 + b_1$ i.e. if the ratio of the predation rate and mortality rate of the middle predator is greater than a threshold value determined by the sum of the half saturation constant of middle predator and unity. The interior equilibrium $\tilde{E}^*(\tilde{x}^*, \tilde{y}^*, \tilde{z}^*)$ exists if the per capita growth rate of middle predator is greater than the per capita death rate and the predation rate of top predator is greater than a threshold value determined by the product of the half saturation constant of top predator for consumption of middle predator and mortality rate of top predator.

Theorem 2.1. *The trivial equilibrium point $\tilde{E}_0(0, 0, 0)$ is always unstable.*

The axial equilibrium point $\tilde{E}_1(1, 0, 0)$ is locally stable if $\frac{a_1}{d_1(1+b_1)} < 1$.

The top predator free equilibrium point $\tilde{E}_2(\tilde{x}_2, \tilde{y}_2, 0)$ is locally stable if $\frac{a_1 b_1 \tilde{y}_2}{(1+b_1\tilde{x}_2)^2} < 1$ and $\frac{1}{d_2} \left(\frac{a_2 \tilde{y}_2}{(1+b_2\tilde{y}_2)} \right) < 1$.

Proof. For proof see Appendix A.1 \square

Here, $\frac{a_1}{d_1(1+b_1)} < 1$ implies that the conversion of prey into middle predator during the life span of middle predator is less than unity. If the above condition holds, then the energy/biomass flow from prey to higher trophic level will stop, and as a result both the middle predator and top predator will be extinct from the system. We have also observed that the top predator will go to extinction from the system if $\frac{1}{d_2} \left(\frac{a_2 \tilde{y}_2}{(1+b_2\tilde{y}_2)} \right) < 1$ i.e. the conversion of middle predator into top predator during the life span of top predator is less than unity provided that $\frac{a_1 b_1 \tilde{y}_2}{(1+b_1\tilde{x}_2)^2} < 1$.

Theorem 2.2. *The interior equilibrium point $\tilde{E}^*(\tilde{x}^*, \tilde{y}^*, \tilde{z}^*)$ is locally stable if $\tilde{\sigma}_1 > 0$, $\tilde{\sigma}_3 > 0$ and $\tilde{\sigma}_1 \tilde{\sigma}_2 > \tilde{\sigma}_3$, where $\tilde{\sigma}_1$, $\tilde{\sigma}_2$, $\tilde{\sigma}_3$ are defined in Appendix A.2.*

Proof. For proof see Appendix A.2 \square

It is to be noted here that the stability conditions of the interior equilibrium point are very complicated. Therefore, it is difficult to explain the biological meanings of such mathematical expressions. Using the numerical computations we have verified and illustrated the existence and stability of all three species.

Hastings and Powell [4] studied the model (2.2) extensively through numerical simulations only. They observed the switching of the dynamics of the system between stable focus, limit cycle oscillations and chaos for changing the half saturation constant (b_1). We also observe the changes in the dynamical behavior of the system

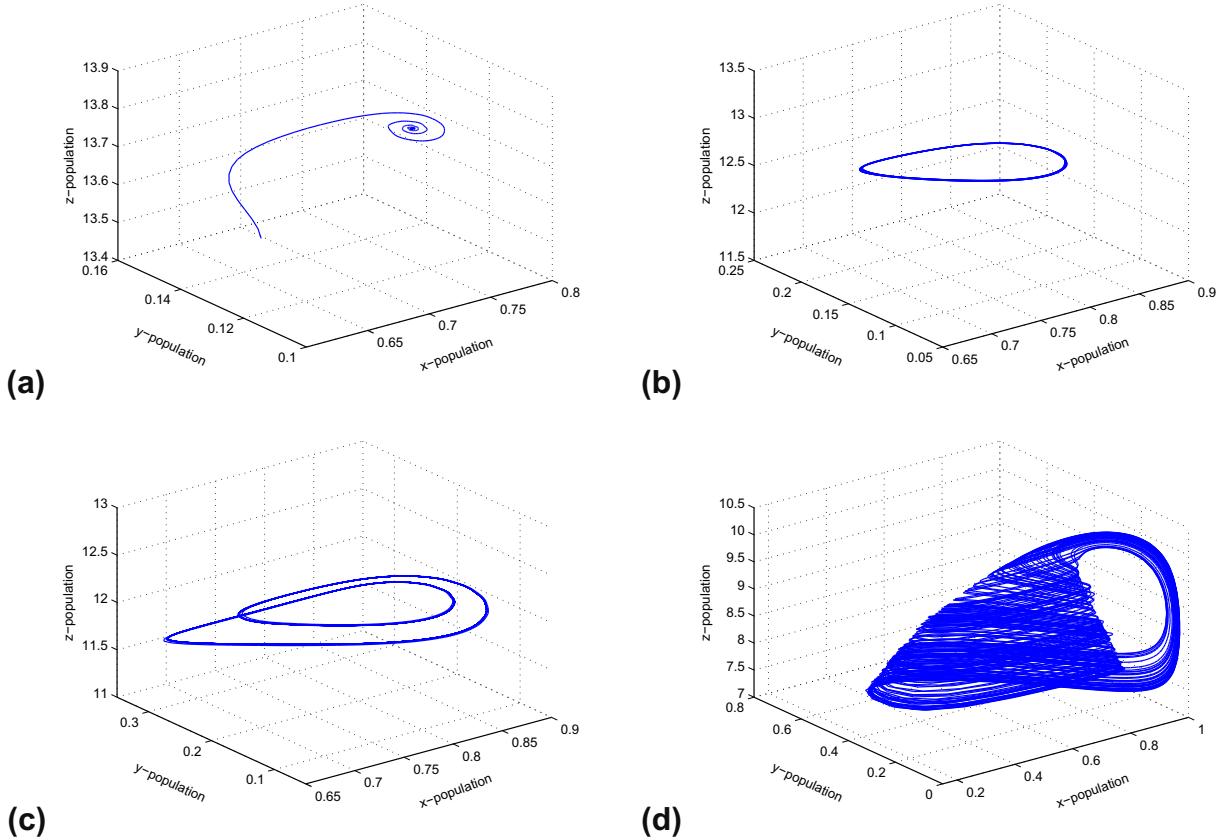


Fig. 1. (a) Phase portrait of the system (2.2) with $a_1 = 5.0$, $a_2 = .1$, $b_2 = 2.0$, $d_1 = .4$, $d_2 = .01$, and $b_1 = 2$ (b) phase portrait of the system (2.2) with $b_1 = 2.3$. Finally, (c) phase portrait of the system (2.2) for $b_1 = 3.0$. (d) phase portrait of the system (2.2) for $b_1 = 3$.

(stability-limit cycle-period doubling- chaos) keeping the parameter values same as [4]. The parameter values are $a_1 = 5$, $a_2 = 0.1$, $b_1 = 3$, $b_2 = 2$, $d_1 = 0.4$, $d_2 = 0.01$.

It is observed that for $0 < b_1 < 2.1$ the system is stable around the positive steady state. For $b_1 = 2$ we obtain a unique positive interior equilibrium $\tilde{E}^*(0.75, 0.125, 13.75)$ and we also obtain $\tilde{\sigma}_1 = 0.38$, $\tilde{\sigma}_3 = 0.0268$, $\tilde{\sigma}_1\tilde{\sigma}_2 - \tilde{\sigma}_3 = 0.0049$ which satisfy the Routh-Hurwitz stability criterion of order 3 and ensure the local stability of the system (2.2) around the positive interior equilibrium (see Fig. 1(a)). Further, for $2.1 < b_1 < 2.3$ it shows limit cycle oscillations (Fig. 1(b)). The period doubling is observed at $b_1 = 2.3$ (Fig. 1(c)). Finally, chaotic dynamics is observed for $b_1 > 2.38$ (Fig. 1(d)).

Although, Hastings and Powell [4] predicted that chaos is common in natural systems, there are lack of evidences (field and/or experimental) of chaos in nature. Early theoretical studies suggest that self-regulating factors (like, prey refuge, intraspecific density dependence, omnivory, toxic inhibition, disease, migratory behavior) stabilize the chaotic behavior of a simple tri-trophic food chain system. Though omnivory is common in natural food chains (both terrestrial and aquatic systems), it has been addressed rarely in tri-trophic food chain systems. In the next section,

we study the effect of omnivory in the model proposed by Hastings and Powell.

3. Tri-trophic food chain with omnivory

Early theoretical studies suggest omnivory to be rare because of its destabilizing effect on food web [21]. Empirical food web data also initially supported the prediction that omnivory is rare in nature [56]. In the last three decades, it has become more clear that omnivory is widespread, occurring in a wide range of taxa and variety of ecosystems [57–59], which motivate us to study the effect of omnivory in a tri-trophic food chain. If the top predator predate middle predator and prey also then the HP model becomes

$$\begin{aligned} \frac{dX}{dT} &= R_0 X \left(1 - \frac{X}{K_0}\right) - \frac{C_1 A_1 XY}{B_1 + X} - \frac{A_3 XZ}{B_3 + X}, \\ \frac{dY}{dT} &= \frac{A_1 XY}{B_1 + X} - \frac{A_2 YZ}{B_2 + Y} - D_1 Y, \\ \frac{dZ}{dT} &= \frac{C_2 A_2 YZ}{B_2 + Y} + \frac{C_3 A_3 XZ}{B_3 + X} - D_2 Z. \end{aligned} \quad (3.1)$$

The corresponding dimensionless model is

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_1xy}{1+b_1x} - \frac{a_3xz}{1+b_3x}, \\ \frac{dy}{dt} &= \frac{a_1xy}{1+b_1x} - \frac{a_2yz}{1+b_2y} - d_1y, \\ \frac{dz}{dt} &= \frac{a_2yz}{1+b_2y} + \frac{a_3\bar{c}xz}{1+b_3x} - d_2z, \end{aligned} \quad (3.2)$$

where, $a_3 = \frac{a_3C_2K_0}{B_3C_1R_0}$, $b_3 = \frac{K_0}{B_3}$ and $\bar{c} = \frac{C_1C_3}{C_2}$.

The system has been analyzed with the initial conditions $x(0) > 0$, $y(0) > 0$, $z(0) > 0$.

3.1. Equilibria and stability analysis

The above model (3.2) has at most five non-negative equilibria.

- (i) The trivial equilibrium $\bar{E}_0(0, 0, 0)$.
- (ii) The middle predator and top predator free axial equilibrium $\bar{E}_1(1, 0, 0)$.
- (iii) The middle predator free planer equilibrium $\bar{E}_2(\bar{x}_2, 0, \bar{z}_2)$, where $\bar{x}_2 = \frac{d_2}{ca_3 - b_3d_2}$ and $\bar{z}_2 = \frac{(1-\bar{x}_2)(1+b_3\bar{x}_2)}{a_3}$.
- (iv) The top predator free equilibrium $\bar{E}_3(\bar{x}_3, \bar{y}_3, 0)$, where $\bar{x}_3 = \frac{d_1}{a_1 - b_1d_1}$, and $\bar{y}_3 = \frac{(1-\bar{x}_3)(1+b_1\bar{x}_3)}{a_1}$.
- (v) The positive interior equilibrium $\bar{E}^*(\bar{x}^*, \bar{y}^*, \bar{z}^*)$, where $(\bar{x}^*, \bar{y}^*, \bar{z}^*)$ is a positive root of the system of equation

$$\begin{aligned} 1-x - \frac{a_1y}{1+b_1x} - \frac{a_3z}{1+b_3x} &= 0, \\ \frac{a_1x}{1+b_1x} - \frac{a_2z}{1+b_2y} - d_1 &= 0, \\ \frac{a_2y}{1+b_2y} + \frac{a_3\bar{c}x}{1+b_3x} - d_2 &= 0. \end{aligned} \quad (3.3)$$

We have observed that the trivial equilibrium $\bar{E}_0(0, 0, 0)$ and the axial equilibrium $\bar{E}_1(1, 0, 0)$ always exist. The middle predator free equilibrium $\bar{E}_2(\bar{x}_2, 0, \bar{z}_2)$ exists if $\frac{ca_3}{d_2} > 1 + b_3$ i.e. if the ratio of the conversion rate and the mortality rate of top predator is greater than a threshold value determined by the sum of the half saturation constant of top predator for prey uptake and unity. However, the top predator free equilibrium $\bar{E}_3(\bar{x}_3, \bar{y}_3, 0)$ exists if $\frac{a_1}{d_1} > 1 + b_1$ i.e. if the ratio of the predation rate and mortality rate of the middle predator is above a threshold value determined by the sum of the half saturation constant of middle predator and unity.

Theorem 3.1. The trivial equilibrium point $\bar{E}_0(0, 0, 0)$ is always unstable.

The axial equilibrium point $\bar{E}_1(1, 0, 0)$ is locally stable if $\frac{a_1}{d_1(1+b_1)} < 1$ and $\frac{ca_3}{d_2(1+b_3)} < 1$.

The middle predator free equilibrium point $\bar{E}_2(\bar{x}_2, 0, \bar{z}_2)$ is locally stable if $\frac{a_3b_3\bar{z}_2}{(1+b_3\bar{x}_2)^2} < 1$ and $\frac{a_1\bar{x}_2}{(1+b_1\bar{x}_2)} < d_1 + a_2\bar{z}_2$.

The top predator free equilibrium point $\bar{E}_3(\bar{x}_3, \bar{y}_3, 0)$ is locally stable if $\frac{a_1b_1\bar{y}_3}{(1+b_1\bar{x}_3)^2} < 1$ and $\frac{1}{d_2} \left(\frac{a_2\bar{y}_3}{(1+b_2\bar{y}_3)} + \frac{ca_3\bar{x}_3}{(1+b_3\bar{x}_3)} \right) < 1$.

Proof. For proof see Appendix B.1. \square

Here, $\frac{a_1}{d_1(1+b_1)} < 1$ implies that the conversion of prey into middle predator during the life span of middle predator is less than unity and $\frac{ca_3}{d_2(1+b_3)} < 1$ implies that the conversion of middle predator into top predator during the life span of top predator is less than unity. If the above conditions hold, then the energy/biomass flow from prey to middle predator and from middle predator to top predator will stop. Consequently, both the middle predator and the top predator will extinct from the system. The relation $\frac{a_1\bar{x}_2}{(1+b_1\bar{x}_2)} < d_1 + a_2\bar{z}_2$ implies that the per capita growth rate of middle predator is less than the per capita removal rate due to natural mortality and consumption of top predators. If this condition holds, then the middle predator will extinct from the system provided that $\frac{a_3b_3\bar{z}_2}{(1+b_3\bar{x}_2)^2} < 1$. We have also observed that the top predator will go to extinction from the system if $\frac{1}{d_2} \left(\frac{a_2\bar{y}_3}{(1+b_2\bar{y}_3)} + \frac{ca_3\bar{x}_3}{(1+b_3\bar{x}_3)} \right) < 1$ i.e. the conversion of prey and middle predator into top predator through omnivory predation is less than unity during the life span of top predator provided $\frac{a_1b_1\bar{y}_3}{(1+b_1\bar{x}_3)^2} < 1$ relation holds.

Theorem 3.2. The interior equilibrium point $\bar{E}^*(\bar{x}^*, \bar{y}^*, \bar{z}^*)$ is locally stable if $\bar{\sigma}_1 > 0$, $\bar{\sigma}_3 > 0$ and $\bar{\sigma}_1\bar{\sigma}_2 > \bar{\sigma}_3$, where $\bar{\sigma}_1$, $\bar{\sigma}_2$, $\bar{\sigma}_3$ are defined in Appendix B.2.

Proof. For proof see Appendix B.2. \square

The stability conditions of the interior equilibrium imply that all populations coexist in a stable manner. However, it is difficult to explain the explicit biological meanings of the existence and stability conditions of the interior equilibrium. Using the numerical computations we have shown the existence and stability of all three species.

Observations: We fixed the parameter values in such a way that the HP model shows chaotic oscillations. We also chose the new parameters $b_3 = 2$, $C_1 = 1.2$, $C_2 = 0.85$, $C_3 = 0.2$, and gradually increase the predation rate (a_3) of prey by top predator. We observe that increase in omnivory (in terms of prey grazing rate) makes the system regular from chaos. To make it clearer, we draw a bifurcation diagram of the system (3.2) with respect to a_3 (see Fig. 2). The bifurcation diagram for the biologically plausible parameter set corresponds to the following dynamical outcomes arise in the system (3.2) – chaos, limit cycles, stable solutions and species extinction.

Chaos: We observe that for $0 < a_3 < 0.03$ the system (3.2) shows chaotic and higher periodic oscillations (Fig. 2). Increasing the strength of omnivory (e.g. consumption of prey by top predator) invokes a period-halving bifurcation and omnivory control the chaos for $a_3 > 0.03$.

Limit cycle: If we increase a_3 further then the system (3.2) shows limit cycle oscillations for $0.03 < a_3 < 0.089$.

Stable: For $0.089 < a_3 < 0.129$ the system shows the stable coexistence of all three species. Hence the presence of omnivory makes the system (3.2) stable.

Extinction of middle predator: Further, if we increase a_3 then we observe that for $a_3 > 0.129$ the middle predator goes to extinction. Naturally the system becomes a simple

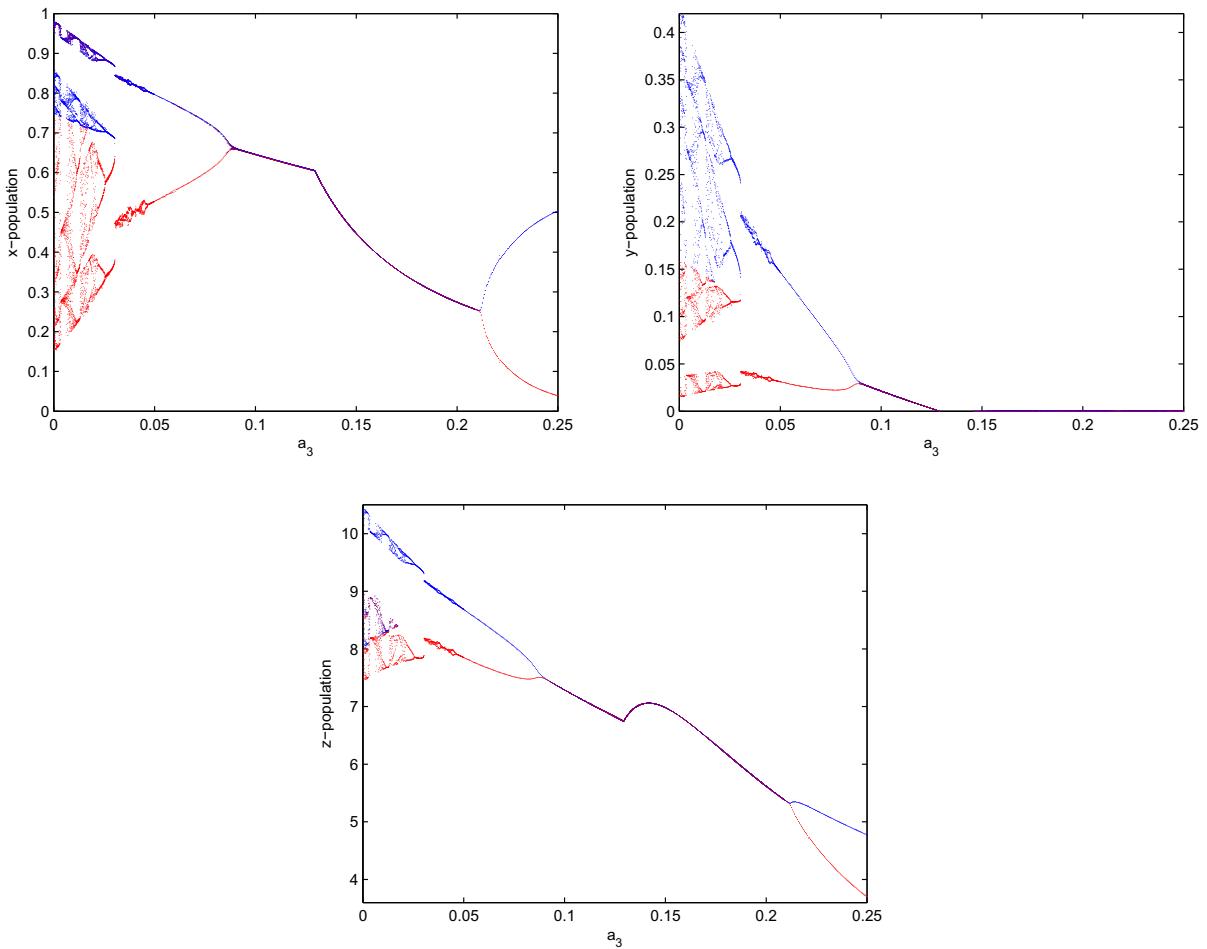


Fig. 2. The bifurcation diagram of the system (3.2) corresponding to the bifurcating parameter a_3 . Other parameter values are kept same as in Fig. 1(d).

two dimensional prey-predator system with prey and top predator populations. We also observe that in the absence of middle predator, the prey and top predator follow stable coexistence, but show boom-bust oscillation for above a critical value of $a_3(a_3 = 0.212)$. The extinction of middle predator can be interpreted as a result of lack of prey availability due to over predation of prey population by the top predator as well as the predation pressure from top predator.

The classical results from food chain models, suggest that omnivory stabilize food chain and enhance persistence, but very strong omnivory is detrimental (destabilize and species extinction). In contrast, recent conceptual syntheses and experimental result suggest that omnivory should be a stabilizing factor in food webs. Recently, Fagan experimentally showed that increases in the degree of omnivory stabilize the community dynamics contrasting the outcome of the previous omnivory model i.e. the species extinction due to strong omnivory [42]. Thus, it is our task to comment on such observation. Apart from omnivory there is (are) some other biological factor(s) associated with the system. Such biologically realistic factor(s) that may promote stability in food chain model with omnivory is adaptive foraging [36]. The omnivore may

modify its diet based on the profitability and abundance of its two types of preys, either by switching prey or by adjusting the proportion of each in a mixed diet. This particular observation motivates us to study the dynamics under the influence of predator switching also.

4. Tri-trophic food chain with omnivory and predator switching

In nature, it has been observed that if the predator population has more than one species to predate, the predator has a tendency to switch towards the most abundant or more profitable prey. In case of tri-trophic food chain with omnivory, the top predator might show predator switching between prey and middle predator. A potential outcome is that if either of the prey or the middle predator becomes temporarily depleted, it will suffer reduced exploitation by the omnivore, allowing it to recover and stabilize the system. Theoretical studies predict that optimal foraging allow the coexistence of omnivore and consumer over a wider range of degrees of omnivory [43] than without prey switching [60]. Top predator usually switch between middle predator and prey populations. Such switching in

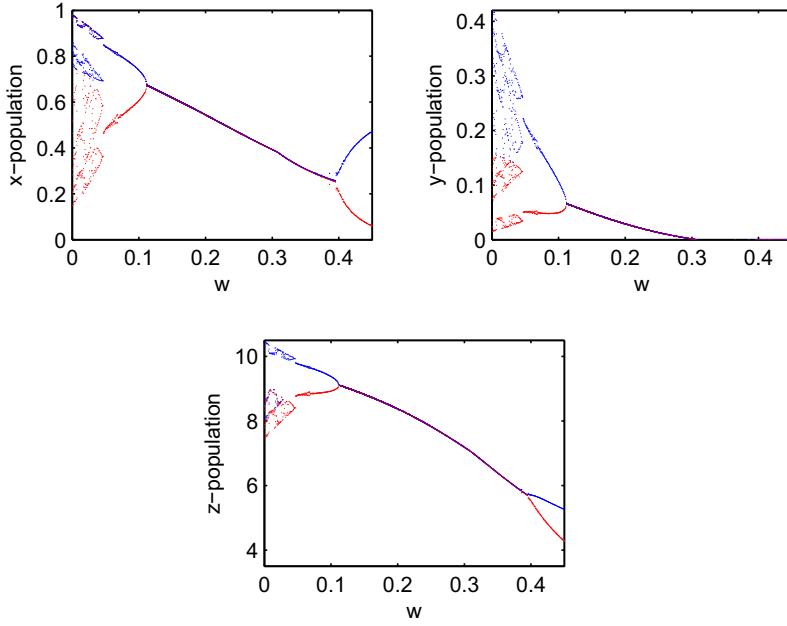


Fig. 3. The bifurcation diagram of the system (4.1) corresponding to the bifurcating parameter w . Other parameter values are kept same as in Fig. 1(d).

omnivory predator is very common in aquatic food webs [28,29]. Predator switching depends on the availability of multiple prey, the preference of most profitable prey, abundance of prey and prey size [61,62,48].

In this section, we assume that predator switching is occurring mainly in two ways: (i) depending on the preference of any particular prey species and (ii) depending on the relative abundance of the available prey species.

System with preferential switching

If there is a preference on prey species, then introducing preference parameter (w) into the previous omnivory system (3.2) we obtain the omnivory model with switching. The dimensionless model is given below

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_1xy}{1+b_1x} - \frac{wa_3xz}{1+b_3x}, \\ \frac{dy}{dt} &= \frac{a_1xy}{1+b_1x} - \frac{(1-w)a_2yz}{1+b_2y} - d_1y, \\ \frac{dz}{dt} &= \frac{(1-w)a_2yz}{1+b_2y} + \frac{wa_3\bar{c}xz}{1+b_3x} - d_2z, \end{aligned} \quad (4.1)$$

where, $w \in [0, 1]$. For $w = 0$, the system represents a simple tri-trophic food chain and for $w = 1$ the system becomes one prey two predator system. However, for intermediate values of w ($0 < w < 1$) the system becomes omnivory. We study the system numerically and compare the results with the omnivory system without such preferential predation.

Observations: To study the effect of such preferential switching towards prey population rather than middle predator we draw a bifurcation diagram of the system (4.1) with respect to switching parameter w . We set $a_3 = 0.5$ and the other parameter values are kept same as in Fig. 2. We observe different interesting dynamical behavior of the system for the variation of switching

parameter. The system (4.1) shows chaotic and higher periodic oscillations for $0 < w < 0.048$, 2-point limit cycle oscillations for $0.048 < w < 0.115$ and stable coexistence of all three species for $0.115 < w < 0.3$ (Fig. 3). Further, we observe for $w > 0.3$ the middle predator goes to extinction. The prey and top predator population coexist with stable pattern for $0.3 < w < 0.4$ whereas they coexist in an oscillatory pattern for $w > 0.4$.

System with density dependent switching

If the top predator switches between middle predator and prey population depending on their availability, then the system (3.1) becomes

$$\begin{aligned} \frac{dX}{dT} &= R_0X\left(1 - \frac{X}{K_0}\right) - \frac{C_1A_1XY}{B_1+X} - \frac{A_3}{1+C_X^Y} \frac{XZ}{B_3+X}, \\ \frac{dY}{dT} &= \frac{A_1XY}{B_1+X} - \frac{A_2}{1+C_Y^X} \frac{YZ}{B_2+Y} - D_1Y, \\ \frac{dZ}{dT} &= \frac{C_2A_2}{1+C_Y^X} \frac{YZ}{B_2+Y} + \frac{C_3A_3}{1+C_X^Y} \frac{XZ}{B_3+X} - D_2Z. \end{aligned} \quad (4.2)$$

Here we assume that top predator and middle predator graze their preys following Holling type II functional response. The functions $\frac{A_2}{1+C_Y^X}$ and $\frac{A_3}{1+C_X^Y}$ have the characteristic property of a switching mechanism governed by the relative abundance of prey and middle predator [48] and C is the switching intensity.

The corresponding dimensionless model is

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_1xy}{1+b_1x} - \frac{a_3}{1+\frac{C}{C_1}y} \frac{xz}{1+b_3x}, \\ \frac{dy}{dt} &= \frac{a_1xy}{1+b_1x} - \frac{a_2}{1+CC_1\frac{x}{y}} \frac{yz}{1+b_2y} - d_1y, \\ \frac{dz}{dt} &= \frac{a_2}{1+CC_1\frac{x}{y}} \frac{yz}{1+b_2y} + \frac{\bar{c}a_3}{1+\frac{C}{C_1}y} \frac{xz}{1+b_3x} - d_2z, \end{aligned} \quad (4.3)$$

where, $\bar{c} = \frac{c_1 c_3}{c_2^2}$ and the system has to be analyzed with the initial conditions $x(0) > 0$, $y(0) > 0$, $z(0) > 0$.

Before we perform the equilibrium analysis and stability analysis of the model (4.3), we observe some preliminary results, boundedness and permanence of the system.

4.1. Boundedness

Let us define the function

$$P = x + y + z. \quad (4.4)$$

The time derivative of the Eq. (4.4) along with the solutions of (4.3) is

$$\begin{aligned} \frac{dP}{dt} &= \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt} \\ &= x(1-x) - d_1y - d_2z + (\bar{c}-1) \frac{a_3}{1+\frac{c}{c_1}x} \cdot \frac{xz}{1+b_3x} \\ &\Rightarrow \frac{dP}{dt} + \mu P = x(1-x+\mu) - (d_1-\mu)y - (d_2-\mu)z \\ &\leq \frac{(1+\mu)^2}{4} = Q(\text{say}), \end{aligned}$$

where $\mu \leq \min\{d_1, d_2\}$ and $\bar{c} \leq 1$.

Applying the theorem of differential inequality [63] we obtain $0 \leq P(x, y, z) \leq \frac{Q}{\mu}(1 - e^{-\mu t}) + P(x_0, y_0, z_0)e^{-\mu t}$, which implies that $0 \leq P \leq Q/\mu$ as $t \rightarrow \infty$. Hence, all the solutions of (4.3), that initiate in $R_+^3 - \{0\}$, are confined in the region $B = \{(x, y, z) \in R_+^3 : P \leq Q/\mu + \epsilon\}$.

4.2. Permanence

Persistence is often a better measure of the type of stability, which is a point of interest of most ecologists, and can be applied under both equilibrium and non-equilibrium conditions. Persistence means that the minimal densities of all species in the focal food web are bounded away from zero, and that they can therefore coexist for a long period of time [64].

Dissipativeness:

Using the standard inequality theorem we shall show that the solution of the system (4.3) always exists and stays positive. From the system (4.3), we can obtain

$$\begin{aligned} \frac{dx}{dt} &\leq x - \frac{a_3}{1+\frac{c}{c_1}x} \frac{xz}{1+b_3x}, \\ \frac{dy}{dt} &\leq a_1xy - d_1y, \\ \frac{dz}{dt} &\leq a_2yz + a_3\bar{c}xz - d_2z. \end{aligned} \quad (4.5)$$

Using the standard comparison theorem [65], we observe that the above inequality implies

$$\limsup_{t \rightarrow \infty} x(t) \leq r_1, \quad \limsup_{t \rightarrow \infty} y(t) \leq r_2, \quad \limsup_{t \rightarrow \infty} z(t) \leq r_3,$$

where, (r_1, r_2, r_3) is the positive root of the system of equations

$$\begin{aligned} 1 - \frac{a_3}{1+\frac{c}{c_1}x} \frac{z}{1+b_3x} &= 0, \\ a_1x - d_1 &= 0, \\ a_2y + a_3\bar{c}x - d_2 &= 0 \\ \text{and } r_1 = \frac{d_1}{a_1}, \quad r_2 = \frac{a_1d_2 - a_3\bar{c}d_1}{a_1a_2}, \quad \text{and } r_3 = \frac{(r_1 + \frac{c}{c_1}r_2)(1+b_3r_1)}{a_3r_1}. \end{aligned} \quad (4.6)$$

Lemma 1. If $a_1d_2 > a_3\bar{c}d_1$, then the system (4.3) is dissipative.

Permanence:

From biological point of view, permanence of a system means the survival of all populations in future time.

From the system of Eqs. (4.3), we have

$$\begin{aligned} \frac{dx}{dt} &\geq x(1-x) - a_1xy - a_3xz, \\ \frac{dy}{dt} &\geq \frac{a_1xy}{1+b_1x} - a_2yz - d_1y, \\ \frac{dz}{dt} &\geq \frac{\bar{c}a_3}{1+\frac{c}{c_1}x} \frac{xz}{1+b_3x} - d_2z. \end{aligned} \quad (4.7)$$

Let (u_1, u_2, u_3) is the positive root of the system of equations

$$\begin{aligned} 1 - x - a_1y - a_3z &= 0, \\ \frac{a_1x}{1+b_1x} - a_2z - d_1 &= 0, \\ \frac{\bar{c}a_3}{1+\frac{c}{c_1}x} \frac{x}{1+b_3x} - d_2 &= 0. \end{aligned} \quad (4.8)$$

Using the standard comparison theorem [65], we observe that the above inequality implies

$$\liminf_{t \rightarrow \infty} x(t) \geq u_1, \quad \liminf_{t \rightarrow \infty} y(t) \geq u_2, \quad \liminf_{t \rightarrow \infty} z(t) \geq u_3,$$

where u_1 is a root of the equation

$$Px^3 + Qx^2 + Rx + S = 0$$

where $P = a_1a_2c_1b_1(a_3\bar{c} - b_3d_2) + ca_2b_1b_3d_2$, $Q = a_1a_2c_1(a_3\bar{c} - b_3d_2 - b_1d_2) + ca_2b_1d_2 - cb_3d_2(a_2b_1 + a_3b_1d_1 - a_2 - a_1a_3)$, $R = -a_1a_2c_1d_2 - cd_2(a_2b_1 + a_3b_1d_1 - a_2 - a_1a_3) - cb_3d_2(a_2 + a_3d_1)$, $S = -cd_2(a_2 + a_3d_1)$.

Note that u_1, u_2, u_3 are positive if $a_3\bar{c} > b_3d_2$, $a_3\bar{c}u_1 > d_2(1 + b_3u_1)$ and $(\frac{a_1u_1}{1+b_1u_1}) > d_1$. Therefore, combining these along with the Lemma 1 yields the following conclusion.

Theorem 4.1. The system (4.3) is permanent if $a_3\bar{c} > b_3d_2$, $a_3\bar{c}u_1 > d_2(1 + b_3u_1)$ and $(\frac{a_1u_1}{1+b_1u_1}) > d_1$.

4.3. Equilibrium analysis

The above model (4.3) has at most five non-negative equilibria.

- (i) The trivial equilibrium $E_0(0, 0, 0)$.
- (ii) The middle predator and top predator free axial equilibrium $E_1(1, 0, 0)$.
- (iii) The middle predator free planer equilibrium $E_2(x_2, 0, z_2)$, where $x_2 = \frac{d_2}{ca_3 - b_3d_2}$ and $z_2 = \frac{(1-x_2)(1+b_3x_2)}{a_3}$.

- (iv) The top predator free equilibrium $E_3(x_3, y_3, 0)$, where $x_3 = \frac{d_1}{a_1 - b_1 d_1}$, and $y_3 = \frac{(1-x_3)(1+b_1 x_3)}{a_1}$.
(v) The positive interior equilibrium $E^*(x^*, y^*, z^*)$, where (x^*, y^*, z^*) is a positive root of the system of equation

$$\begin{aligned} 1 - x - \frac{a_1 y}{1 + b_1 x} - \frac{a_3}{1 + \frac{C}{C_1} \frac{y}{x}} \frac{z}{1 + b_3 x} &= 0, \\ \frac{a_1 x}{1 + b_1 x} - \frac{a_2}{1 + CC_1 \frac{x}{y}} \frac{z}{1 + b_2 y} - d_1 &= 0, \\ \frac{a_2}{1 + CC_1 \frac{x}{y}} \frac{y}{1 + b_2 y} + \frac{\bar{c}a_3}{1 + \frac{C}{C_1} \frac{y}{x}} \frac{x}{1 + b_3 x} - d_2 &= 0. \end{aligned} \quad (4.9)$$

It is to be noted that the trivial equilibrium $E_0(0, 0, 0)$ and the middle predator as well as top predator free equilibrium $E_1(1, 0, 0)$ always exist. The middle predator free equilibrium $E_2(x_2, 0, z_2)$ exists if $\frac{ca_3}{d_2} > 1 + b_3$ i.e if the ratio of the conversion rate of prey into top predator due to omnivory predation and the mortality rate of top predator is above a threshold value determined by the sum of the half saturation constant of top predator for prey uptake and unity. However, the top predator free equilibrium $E_2(x_2, y_2, 0)$ exists if $\frac{a_1}{d_1} > 1 + b_1$ i.e. if the ratio of the consumption rate of prey by middle predator and the mortality rate of middle predator is higher than a threshold value determined by the sum of the half saturation constant of middle predator and unity.

4.4. Stability analysis

The system (4.3) is not well defined at the trivial equilibrium point $E_0(0, 0, 0)$ and difficult to study the behavior of the system at that point. To overcome such situation, we modify the model (4.3) as

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{a_1 xy}{1+b_1 x} - \frac{a_3}{1+\frac{C}{C_1} \frac{y}{x}} \frac{xz}{1+b_3 x}, \\ \frac{dy}{dt} &= \frac{a_1 xy}{1+b_1 x} - \frac{a_2}{1+CC_1 \frac{x}{y}} \frac{yz}{1+b_2 y} - d_1 y, \\ \frac{dz}{dt} &= \frac{a_2}{1+CC_1 \frac{x}{y}} \frac{yz}{1+b_2 y} + \frac{\bar{c}a_3}{1+\frac{C}{C_1} \frac{y}{x}} \frac{xz}{1+b_3 x} - d_2 z \end{aligned} \quad (4.10)$$

when $(x, y, z) \neq (0, 0, 0)$ and $\frac{dx}{dt} = \frac{dy}{dt} = \frac{dz}{dt} = 0$ at $E_0(0, 0, 0)$. To analyze the behavior of the system at trivial equilibrium, we follow the method developed by Arino et al. [66]. We rewrite the model as

$$\frac{dV}{dt} = H(V(t)) + Q(V(t)) \quad (4.11)$$

where $H(\cdot)$ is a continuous and homogeneous function of degree one; $V = (x, y, z)$; Q is a C^1 function with $Q(V) = o(V)$. For the present problem, $H = (x, -d_1 y, -d_2 z)$. Let $V(t)$ be a solution of (4.11) such that $\liminf_{t \rightarrow \infty} \|V(t)\| = 0$ and $V(t_n, \cdot)$ be the corresponding sequence which tends to zero as $t_n \rightarrow \infty$.

Define $y_n = (V(t_n + s)/\|V(t_n + s)\|)$. Then y_n is a sequence such that $\|y_n\| = 1$. Now, by Ascoli-Arzela theorem, there should exist a subsequence of y_n that converges to a function $y(t)$ satisfying the equation

$$\frac{dy}{dt} = H(y(t)) - (y(t), H(y(t)))y(t). \quad (4.12)$$

The steady state of (4.12) will be given by the vector $v(t) = (v_1, v_2, v_3)$ where $H(v) = (v, H)v$ are the solutions of the eigenvalue problem

$$\begin{aligned} H(v) &= \lambda v \\ \lambda &= (v, H(v)). \end{aligned} \quad (4.13)$$

From (4.13) we have $(1 - \lambda)v_1 = 0$; $(d_1 + \lambda)v_2 = 0$; $(d_2 + \lambda)v_3 = 0$.

We now study the following cases:

Case I: $v_1 \neq 0$, $v_2 = v_3 = 0$.

In this case, the system cannot reach the trivial equilibrium (origin) along the x -axis with $\lambda = 1$.

Case II: $v_1 = v_3 = 0$, $v_2 \neq 0$.

The system will reach the origin along the y -axis with $\lambda = -d_1$.

Case III: $v_1 = v_2 = 0$, $v_3 \neq 0$.

The system will reach the origin along the z -axis with $\lambda = -d_2$.

The stability conditions for the boundary equilibria and the positive interior equilibrium of the system (4.3) are stated in the theorem given below.

Theorem 4.2. *The axial equilibrium point $E_1(1, 0, 0)$ is locally stable if $\frac{a_1}{d_1(1+b_1)} < 1$ and $\frac{\bar{c}a_3}{d_2(1+b_3)} < 1$.*

The middle predator free equilibrium point $E_2(x_2, 0, z_2)$ is locally stable if $\frac{a_1 x_2}{d_1(1+b_1 x_2)} < 1$ and $\frac{a_3 b_3 z_2}{(1+b_3 x_2)^2} < 1$.

The top predator free equilibrium point $E_3(x_3, y_3, 0)$ is locally stable if $\frac{a_1 b_1 y_3}{(1+b_1 x_3)^2} < 1$ and

$$\frac{1}{d_2} \left(\frac{a_2 y_3^2}{(y_3 + CC_1 x_3)(1+b_2 y_3)} + \frac{\bar{c}a_3 x_3^2}{(x_3 + \frac{C}{C_1} y_3)(1+b_3 x_3)} \right) < 1.$$

Proof. For proof see Appendix C.1 \square

It is worthy to mention that the trivial equilibrium is always unstable i.e. all species cannot extinct simultaneously. The relation $\frac{a_1}{d_1(1+b_1)} < 1$ implies that the conversion of prey into middle predator during the life span of middle predator is less than unity and $\frac{\bar{c}a_3}{d_2(1+b_3)} < 1$ implies that the conversion of middle predator into top predator during the life span of top predator is less than unity. Therefore, if the above conditions hold, then the energy/biomass flow from prey to middle predator and from middle predator to top predator will stop and both the middle predator and top predator will extinct from the system. Moreover, $\frac{a_1 x_2}{d_1(1+b_1 x_2)} < 1$ implies that the conversion rate of prey into middle predator is less than unity during the average life span of middle predator. If the above condition holds, then the middle predator will extinct from the system provided that $\frac{a_3 b_3 z_2}{(1+b_3 x_2)^2} < 1$. If the effectual conversion of prey and middle predator into top predator through omnivory

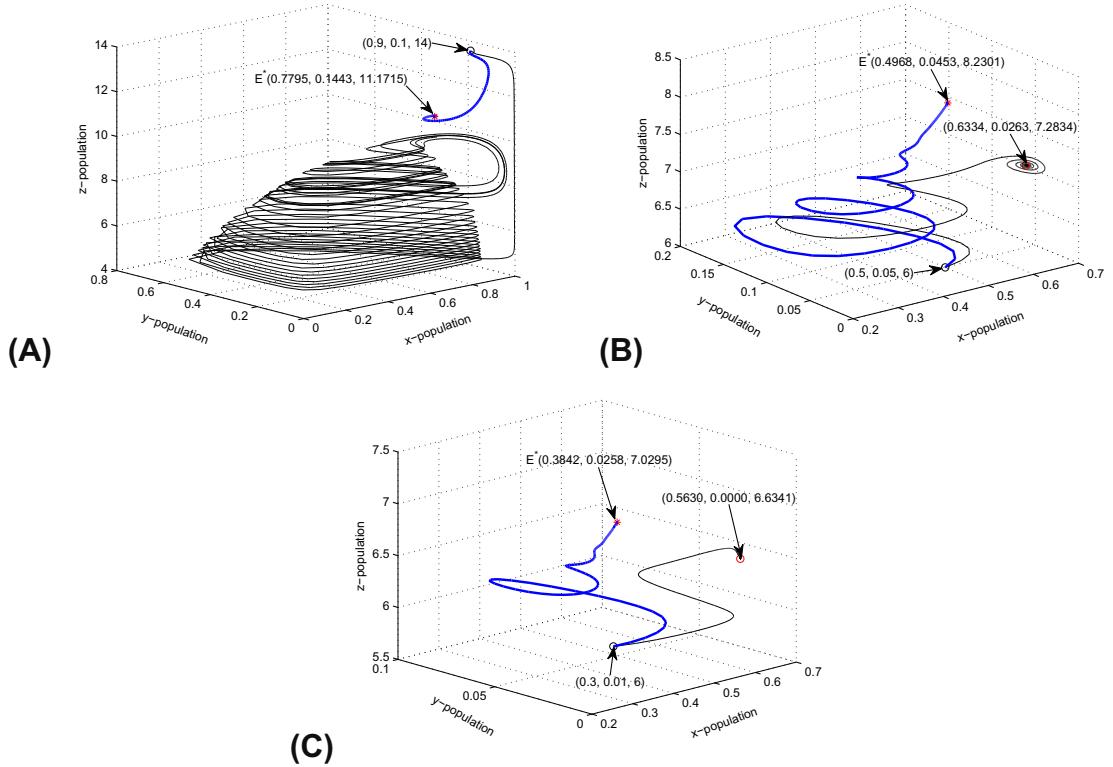


Fig. 4. Figure predict that the system with predator switching (4.3) is more stable than that of the system with omnivory only (3.2). In Fig. 4(A–C), corresponding to $a_3 = 0.001, 0.1, 0.14$, bold lines denote the trajectories of the solutions of the system (4.3) and the thinner lines denote the solutions of the system (3.2).

predation is less than unity during the life span of top predator $\left(\frac{1}{d_2} \left[\frac{a_2 y_3^2}{(y_3 + CC_1 x_3)(1+b_2 y_3)} + \frac{c a_3 x_3^2}{(x_3 + \frac{c}{C_1} y_3)(1+b_3 x_3)} \right] < 1 \right)$, then the top predator extinct from the system provided $\frac{a_1 b_1 y_3}{(1+b_1 x_3)^2} < 1$ relation holds.

Theorem 4.3. The interior equilibrium point $E^*(x^*, y^*, z^*)$ is locally stable if $\sigma_1 > 0$, $\sigma_3 > 0$ and $\sigma_1 \sigma_2 > \sigma_3$, where σ_1 , σ_2 , σ_3 are defined in Appendix C.2.

Proof. For proof see Appendix C.2.

Furthermore, a Hopf-bifurcation of the system (4.3) may occurred if the following condition holds

$$\sigma_1 \sigma_2 - \sigma_3 = 0. \quad \square$$

Theorem 4.4. When the switching intensity (C) of the top predator crosses a critical value, the system (4.3) undergoes a Hopf-bifurcation around the positive equilibrium point. The necessary and sufficient conditions for the occurrence of Hopf-bifurcation at $C = C^*$ are

$$(a) \sigma_1(C^*) > 0, \sigma_3(C^*) > 0 \quad \text{and} \\ H(C^*) = \sigma_1(C^*) \sigma_2(C^*) - \sigma_3(C^*) = 0,$$

(b) $\frac{d}{dC}(\operatorname{Re}(\lambda(C)))|_{C=C^*} \neq 0$ where λ is the root of the characteristic equation corresponding to the interior equilibrium point and σ_1 , σ_2 , σ_3 are defined in Appendix C.2.

Proof. For $C = C^*$, the characteristic equation become

$$\lambda^3 + \sigma_1 \lambda^2 + \sigma_2 \lambda + \sigma_3 = 0 \text{ or}$$

$(\lambda^2 + \sigma_2)(\lambda + \sigma_1) = 0$, which has three roots $\lambda_1 = i\sqrt{\sigma_2}$, $\lambda_2 = -i\sqrt{\sigma_2}$ and $\lambda_3 = -\sigma_1$.

For all C , the roots are in general of the form.

$$\lambda_1(C) = \phi_1(C) + i\phi_2(C),$$

$$\lambda_2(C) = \phi_1(C) - i\phi_2(C),$$

$$\lambda_3(C) = -\sigma_1.$$

Now, we shall verify the transversality condition.

$$\frac{d}{dC}(\operatorname{Re}(\lambda(C)))|_{C=C^*} \neq 0, \quad j = 1, 2.$$

Substituting $\lambda_1(C) = \phi_1(C) + i\phi_2(C)$ into the characteristic equation and calculating the derivative, we have.

$$P(C)\phi'_1(C) - Q(C)\phi'_2(C) + U(C) = 0,$$

$$Q(C)\phi'_1(C) + P(C)\phi'_2(C) + V(C) = 0, \text{ where,}$$

$$P(C) = 3\phi_1^2(C) + 2\sigma_1(C)\phi_1(C) + \sigma_2(C) - 3\phi_2^2(C),$$

$$Q(C) = 6\phi_1(C)\phi_2(C) + 2\sigma_1(C)\phi_2(C),$$

$$U(C) = \phi_1^2(C)\sigma'_1(C) + \sigma'_2(C)\phi_1(C) + \sigma'_3(C) - \sigma'_1(C)\phi_2^2(C),$$

$$V(C) = 2\phi_1(C)\phi_2(C)\sigma'_1(C) + \sigma'_2(C)\phi_2(C).$$

Noticing that $\phi_1(C^*) = 0$, $\phi_2(C^*) = \sqrt{\sigma_2(C^*)}$, we have.

$$P(C^*) = -2\sigma_2(C^*), \quad Q(C^*) = 2\sigma_1(C^*)\sqrt{\sigma_2(C^*)}, \quad U(C^*) = \sigma'_3(C^*) - \sigma'_1(C^*)\sigma_2(C^*) \text{ and } V(C^*) = \sigma'_2(C^*)\sqrt{\sigma_2(C^*)}.$$

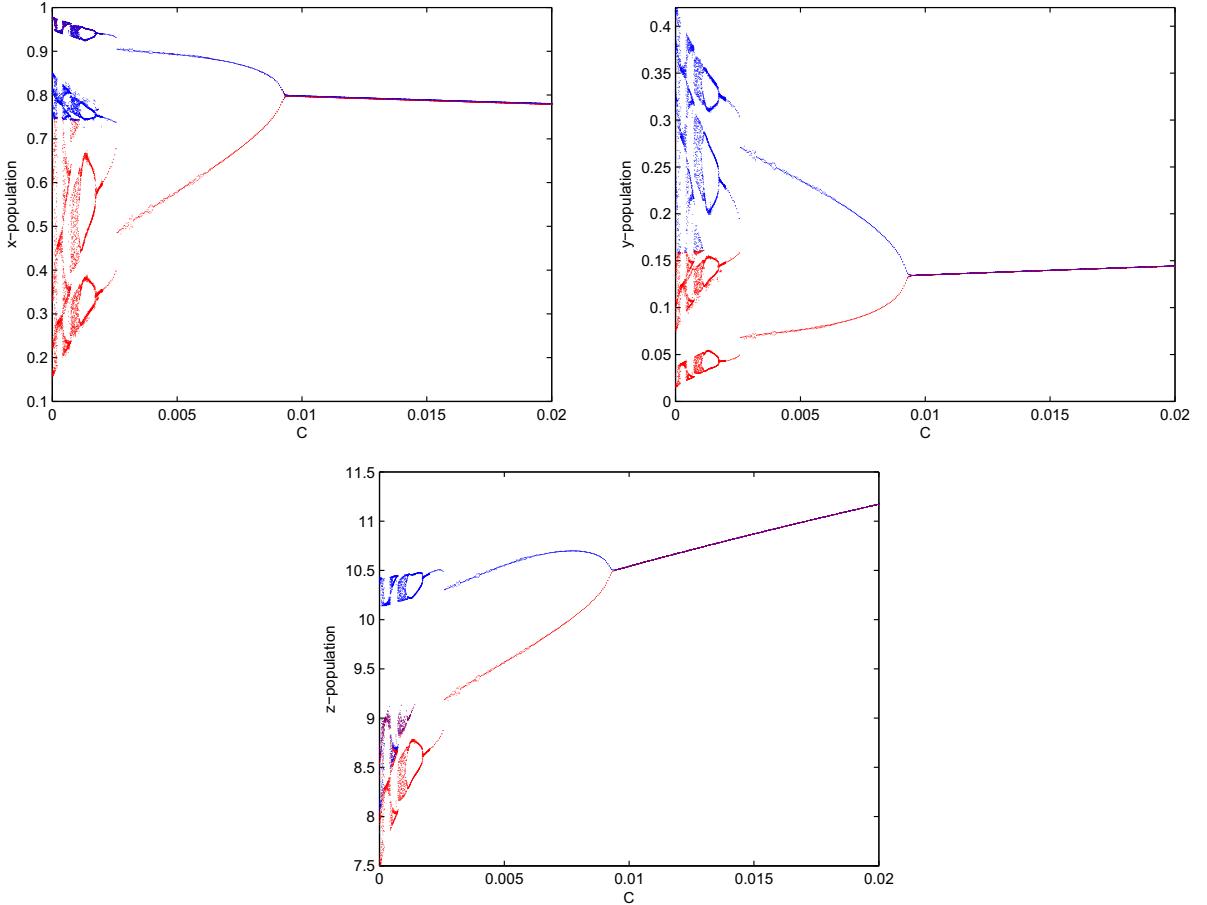


Fig. 5. The bifurcation diagram of the system (4.3) corresponding to the bifurcating parameter C . Other parameter values are kept same as in Fig. 4 and $a_3 = .001$.

Now,

$$\begin{aligned} \frac{d}{dC}(Re(\lambda(C)))|_{C=C^*} &= -\frac{Q(C^*)V(C^*)+P(C^*)U(C^*)}{P(C^*)^2+Q(C^*)^2} \\ &= -\frac{2\sigma_1(C^*)\sqrt{\sigma_2(C^*)}\times\sigma'_2(C^*)\sqrt{\sigma_2(C^*)}+(-2\sigma_2(C^*))(\sigma'_3(C^*)-\sigma'_1(C^*)\sigma_2(C^*))}{(-2\sigma_2(C^*))^2+(2\sigma_1(C^*)\sqrt{\sigma_2(C^*)})^2} \\ &= -\frac{\sigma_1(C^*)\sigma'_2(C^*)-\sigma'_3(C^*)+\sigma'_1(C^*)\sigma_2(C^*)}{2(\sigma_2(C^*)+(\sigma_1(C^*))^2)} \neq 0, \\ \text{if } &\sigma_1(C^*)\sigma'_2(C^*) \\ &-\sigma'_3(C^*)+\sigma'_1(C^*)\sigma_2(C^*) \neq 0, \end{aligned}$$

and $\lambda_3(C^*) = -\sigma_1(C^*) \neq 0$.

Therefore, the transversality conditions hold and the Hopf bifurcation occurs at $C = C^*$. Hence the theorem. \square

Observations: Here we observe the effect of predator switching depending on the availability of prey and middle predator on the omnivory system (3.2) through numerical simulation. Firstly, we chose three different values of a_3 ($a_3 = 0.001$, $a_3 = 0.1$, $a_3 = .14$) where the tri-trophic system (3.2) with omnivory behave chaotic, stable focus and unstable with extinction of middle predator respectively while other parameter values are same as in Fig. 2. For the omnivory rate $a_3 = 0.001$ where the system (3.2) shows chaotic oscillations, we introduce predator switching with switching intensity $C = 0.02$ and observe that the system with omnivory as well as predator switching

(4.3) has a unique positive interior equilibrium $E^*(0.7795, 0.1443, 11.1715)$. For the same set of parameter values we have $\sigma_1 = 0.5398$, $\sigma_2 = 0.0417$, $\sigma_3 = 0.0046$, $\sigma_1\sigma_2 - \sigma_3 = 0.0179$, which satisfy the Routh-Hurwitz stability criterion of order 3. Hence the system (4.3) is locally asymptotically stable around the positive interior equilibrium E^* (see Fig. 4(A)). We also observe that for $a_3 = 0.1$ (stable coexistence of all populations) and $a_3 = 0.14$ (extinction of middle predator) the system (4.3) becomes stable (see Fig. 4(B)–(C)). Therefore, predator switching depending on the relative prey density stabilizes the system (4.3) and makes the system more regular.

We have also drawn the bifurcation diagram of the system (4.3) with respect to switching intensity for $a_3 = 0.001$. We observe that for $0 < C < 0.0018$ the system shows chaotic and higher periodic oscillations (Fig. 5), for $0.0018 < C < 0.0029$ it shows 4-point limit cycle, for $0.0029 < C < 0.0093$, it shows 2-point limit cycle oscillations and for $C > 0.0093$ the system shows the stable coexistence of all three species.

If the predator population has more than one prey species (prey and middle predator) to prey upon, the predator population predares heavily upon the most abundant species [47]. When a particular prey species decline in numbers, partly owing to the predation, the predator switchs its

Table 1

The table shows the dynamic behavior of four systems, (2.2), (3.2), (4.1) and (4.3). The other parameter values are $a_1 = 5$, $a_2 = 0.1$, $b_2 = 2$, $d_1 = 0.4$, $d_2 = 0.01$, $b_3 = 2$, $C_1 = 1.2$, $C_2 = 0.85$, $C_3 = 0.2$.

Model	b_1	a_3	C	Remarks
HP	$0 < b_1 < 2.1$			Stable
	$2.1 < b_1 < 2.3$	0	0	Limit cycle oscillations
	$b_1 > 2.38$			Chaos
HP with omnivory	3	$0 < a_3 < .03$		Chaos
		$.03 < a_3 < .089$	0	Limit cycle
		$.089 < a_3 < 0.129$		Stable
HP with omnivory and preferential switching	3	$a_3 > .129$		Middle predator extinct
			$0 < w < 0.048$	Chaos
			$0.048 < w < 0.115$	Limit cycle oscillations
HP with omnivory and switching depending on availability	3	0.5	$0.115 < w < 0.3$	Stable
			$w > 0.3$	Middle predator extinct
		0.001	$0 < C < 0.0018$	Chaos
			$0.0018 < C < 0.0093$	Limit cycle oscillations
			$C > 0.0093$	Stable

attack to another prey which has become more abundant. In this way, no prey population is drastically reduced nor any prey species are allowed to become very abundant. Such mechanism mediates the prey predator interaction and enhances the stability and persistence of the system (4.3). We also summarize the numerical results of four models in (Table 1).

It is to be noted that omnivory has stabilizing or destabilizing effect on a tri-trophic food chain depending on the previous conditions. In the present investigation, we observe that the introduction of omnivory into a three species chaotic (HP) system makes the system stable. We have considered the predation rate of basal prey by top predator as the measure of omnivory. We have observed that if the measure of omnivory increases, the system becomes stable from chaotic situation. However, further increment in the strength of omnivory results loss of stability and extinction of middle predator. Now, if we incorporate the preferential switching of top predator towards basal prey, then the stability results are very similar to the HP model with omnivory only. In omnivory system, the top predator predares middle predator at a constant rate, which is not influenced by the strength of omnivory. However, in omnivory system with preferential switching, whenever the preference of top predator towards basal prey increases simultaneously the consumption rate of middle predator reduces. We observe that the stability range of the omnivory system with preferential switching increases in terms of the strength of omnivory. Furthermore, density dependence switching can also stabilize an otherwise unstable omnivory system. Though these two types of predator switching are seemed to be similar and have stabilizing effect on omnivory system, the density dependence switching is biologically more plausible. If the predator consumes a specific preferred prey and reduce its abundance, the predator cannot wait until that prey species regain its abundance adequately rather it will consume another prey which is more available in the same or another habitat. In density dependence switching, no prey reduces drastically nor any prey become very abundant. Density dependence predator switching between prey and middle predator balances their abundance and prevents species exclusion, enhances community stability and persistence.

5. Conclusions

It is well documented that omnivory and predator switching are common and very resemble biological phenomena in terrestrial and aquatic ecosystems [24,47,55]. In a tri-trophic food chain with omnivory, top predator has two types of food sources, namely, basal prey and middle predator, which enhance the chance of predator switching between prey and middle predator. However, as far our knowledge goes, the three species food chain model [4] with omnivory and predator switching simultaneously was not considered previously.

We modify the famous HP model step by step by considering omnivory and predator switching into the system. Incorporating omnivory (additional predation of prey by top predator) into the chaotic HP model we observe that for increase in omnivory the system changes its stability from chaotic to stable but for a strong omnivory it becomes unstable and causes species extinction. In the modified HP model with omnivory, we consider the consumption rate of top predators on prey population as the measure of omnivory. When the top predator does not predate prey population and its growth is determined by consumption of middle predator only then the system reduces to the original Hastings-Powell system. Further, we observe that for higher values of consumption rate of prey by top predator results middle predator extinction. It may be explained by the top down and bottom up process. If the predation rate of top predators on prey population is high enough, then the prey density reduces meanwhile the top predator predate middle predator also. Therefore, the middle predator population suffers due to predation pressure as well as the lack of prey availability to carry on their metabolic costs which may cause the extinction of middle predator. Therefore, omnivory can be either stabilizing or destabilizing, depending on the previous conditions and the strength of omnivory.

Furthermore, we incorporate predator switching into the omnivory system in two ways; the preferential switching and the switching depending on the prey availability. Preferential switching is such a switching phenomenon where the predator population shows its preference towards a particular prey population independent of prey

density. However, in density dependent switching [47,48], the effectual predation on prey populations by a predator is determined by their relative abundance. Such predator switching is biologically more relevant. If there is any preference towards a specific prey, the predator population initially prefers to predate that prey, but whenever the density reduces, the predator can't wait till they regain their abundance sufficiently, rather the predator like to switch to another prey in the same or another habitat for their livelihood. The preferential switching towards a prey population makes the system stable up to a threshold value, but above that the system becomes unstable. The dynamic behavior of the model with preferential switching is very similar to the dynamics of the model with omnivory only. However, preferential switching enlarges the range of upper threshold of the degree of omnivory for the system stability. Moreover, if the predator switch between middle predator and prey depending on their abundance, then we observe that all types of dynamic situation (unstable and/or stable in omnivory model) becomes stable for an adequate switching intensity. In the presence of predator switching, all species coexist. Though the rate of predation by top predator to prey is high, it switches to middle predator whenever the abundance of prey population becomes low. This phenomenon helps the system to balance the population abundance and enhance stability and persistence of the system.

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Appendix A

A.1

Proof of Theorem 2.1. The trivial equilibrium is $\tilde{E}_0(0, 0, 0)$.

Now

$$J(\tilde{E}_0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -d_1 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}$$

The eigenvalues are $1, -d_1$ and $-d_2$. So the system around the equilibrium point $\tilde{E}_0(0, 0, 0)$ is always unstable.

The eigenvalues of the Jacobian matrix around the equilibrium point $\tilde{E}_1(1, 0, 0)$ are $-1, \frac{a_1}{1+b_1} - d_1$ and $-d_2$. Hence the equilibrium point $\tilde{E}_1(1, 0, 0)$ is locally asymptotically stable (LAS) if $\frac{a_1}{d_1(1+b_1)} < 1$. Where the Jacobian matrix at \tilde{E}_1 is

$$J(\tilde{E}_1) = \begin{pmatrix} -1 & -\frac{a_1}{1+b_1} & 0 \\ 0 & \frac{a_1}{1+b_1} - d_1 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}.$$

The Jacobian matrix around the equilibrium point $\tilde{E}_2(\tilde{x}_2, \tilde{y}_2, 0)$ is

$$J(\tilde{E}_2) = \begin{pmatrix} P_1 & -P_2 & 0 \\ P_3 & 0 & -P_4 \\ 0 & 0 & P_5 \end{pmatrix}$$

and the corresponding characteristic equation is

$$(P_5 - \lambda)(\lambda^2 - P_1\lambda + P_2P_3) = 0,$$

where $P_1 = \frac{a_1 b_1 \tilde{x}_2 \tilde{y}_2}{(1+b_1 \tilde{x}_2)^2} - \tilde{x}_2$, $P_2 = \frac{a_1 \tilde{x}_2}{1+b_1 \tilde{x}_2}$, $P_3 = \frac{a_1 \tilde{y}_2}{(1+b_1 \tilde{x}_2)^2}$, $P_4 = \frac{a_2 \tilde{y}_2}{(1+b_2 \tilde{y}_2)}$, $P_5 = \frac{a_2 \tilde{y}_2}{(1+b_2 \tilde{y}_2)} - d_2$.

All the eigenvalues of the characteristic equation are negative or having negative real part if $P_1 < 0$ and $P_5 < 0$.

Therefore, the equilibrium point \tilde{E}_3 is LAS if $\frac{a_1 b_1 \tilde{y}_2}{(1+b_1 \tilde{x}_2)^2} < 1$ and $\frac{a_2 \tilde{y}_2}{d_2(1+b_2 \tilde{y}_2)} < 1$.

A.2

Proof of Theorem 2.2. The Jacobian matrix around the equilibrium point $\tilde{E}^*(\tilde{x}^*, \tilde{y}^*, \tilde{z}^*)$ is

$$J(\tilde{E}^*) = \begin{pmatrix} \tilde{V}_1 & -\tilde{V}_2 & 0 \\ \tilde{V}_3 & \tilde{V}_4 & -\tilde{V}_5 \\ 0 & \tilde{V}_6 & 0 \end{pmatrix}$$

and the corresponding characteristic equation is

$$\lambda^3 + \tilde{\sigma}_1 \lambda^2 + \tilde{\sigma}_2 \lambda + \tilde{\sigma}_3 = 0,$$

where $\tilde{\sigma}_1 = -(\tilde{V}_1 + \tilde{V}_4)$, $\tilde{\sigma}_2 = (\tilde{V}_1 \tilde{V}_4 + \tilde{V}_2 \tilde{V}_3 + \tilde{V}_5 \tilde{V}_6)$, $\tilde{\sigma}_3 = -\tilde{V}_1 \tilde{V}_5 \tilde{V}_6$ and $\tilde{V}_1 = -\tilde{x}^* + \frac{a_1 b_1 \tilde{x}^* \tilde{y}^*}{(1+b_1 \tilde{x}^*)^2}$, $\tilde{V}_2 = \frac{a_1 \tilde{x}^*}{1+b_1 \tilde{x}^*}$, $\tilde{V}_3 = \frac{a_1 \tilde{y}^*}{(1+b_1 \tilde{x}^*)^2}$, $\tilde{V}_4 = \frac{a_2 b_2 \tilde{y}^* \tilde{z}^*}{(1+b_2 \tilde{y}^*)^2}$, $\tilde{V}_5 = \frac{a_2 \tilde{y}^*}{1+b_2 \tilde{y}^*}$, $\tilde{V}_6 = \frac{a_2 \tilde{z}^*}{(1+b_2 \tilde{y}^*)^2}$.

Therefore the system will be stable if $\tilde{\sigma}_1 > 0$, $\tilde{\sigma}_3 > 0$ and $\tilde{\sigma}_1 \tilde{\sigma}_2 > \tilde{\sigma}_3$.

Appendix B

B.1

Proof of Theorem 3.1. The trivial equilibrium is $\bar{E}_0(0, 0, 0)$.

Now

$$J(\bar{E}_0) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -d_1 & 0 \\ 0 & 0 & -d_2 \end{pmatrix}$$

The eigenvalues are $1, -d_1$ and $-d_2$. So the system around the equilibrium point $\bar{E}_0(0, 0, 0)$ is always unstable.

The eigenvalues of the Jacobian matrix around the equilibrium point $\bar{E}_1(1, 0, 0)$ are $-1, \frac{a_1}{1+b_1} - d_1$ and $\frac{\bar{c}a_3}{1+b_3} - d_2$. Hence the equilibrium point $\bar{E}_1(1, 0, 0)$ is LAS if $\frac{a_1}{d_1(1+b_1)} < 1$ and $\frac{\bar{c}a_3}{d_2(1+b_3)} < 1$. Where the Jacobian matrix at \bar{E}_1 is

$$J(\bar{E}_1) = \begin{pmatrix} -1 & -\frac{a_1}{1+b_1} & -\frac{a_3}{1+b_3} \\ 0 & \frac{a_1}{1+b_1} - d_1 & 0 \\ 0 & 0 & \frac{\bar{c}a_3}{1+b_3} - d_2 \end{pmatrix}.$$

The Jacobian matrix around the equilibrium point $\bar{E}_2(\bar{x}_2, 0, \bar{z}_2)$ is

$$J(\bar{E}_2) = \begin{pmatrix} M_1 & -M_2 & -M_3 \\ 0 & M_4 & 0 \\ M_5 & M_6 & 0 \end{pmatrix}$$

and the characteristic equation is

$$(M_4 - \lambda)(\lambda^2 - M_1\lambda + M_3M_5) = 0,$$

$$\text{where, } M_1 = \frac{a_1b_2x_2\bar{z}_2}{(1+b_1x_2)^2} - \bar{x}_2, \quad M_2 = \frac{a_1x_2}{(1+b_1x_2)}, \quad M_3 = \frac{a_3x_2}{1+b_3x_2},$$

$$M_4 = \frac{a_1x_2}{1+b_1x_2} - a_2\bar{z}_2 - d_1, \quad M_5 = \frac{a_3\bar{c}z_2}{(1+b_3x_2)^2}, \quad M_6 = a_2\bar{z}_2.$$

All the eigenvalues of the characteristic equation are negative or having negative real part if $M_1 < 0$ and $M_4 < 0$.

Therefore, the equilibrium point \bar{E}_2 is LAS if $\frac{a_1b_2x_2\bar{z}_2}{(1+b_1x_2)^2} < 1$ and $\frac{1}{d_1}\left(\frac{a_1x_2}{(1+b_1x_2)} - a_2\bar{z}_2\right) < 1$.

The Jacobian matrix around the equilibrium point $\bar{E}_3(\bar{x}_3, \bar{y}_3, 0)$ is

$$J(\bar{E}_3) = \begin{pmatrix} N_1 & -N_2 & -N_3 \\ N_4 & 0 & -N_5 \\ 0 & 0 & N_6 \end{pmatrix}$$

and the corresponding characteristic equation is

$$(N_6 - \lambda)(\lambda^2 - N_1\lambda + N_2N_4) = 0,$$

$$\text{where } N_1 = \frac{a_1b_1x_3y_3}{(1+b_1x_3)^2} - \bar{x}_3, \quad N_2 = \frac{a_1x_3}{1+b_1x_3}, \quad N_3 = \frac{a_3x_3}{(1+b_3x_3)},$$

$$N_4 = \frac{a_1\bar{y}_3}{(1+b_1x_3)^2}, \quad N_5 = \frac{a_2\bar{y}_3}{(1+b_2y_3)}, \quad N_6 = \frac{a_2y_3}{(1+b_2y_3)} + \frac{a_3\bar{c}x_3}{(1+b_3x_3)} - d_2.$$

All the eigenvalues of the characteristic equation are negative or having negative real part if $N_1 < 0$ and $N_6 < 0$.

Therefore, the equilibrium point \bar{E}_3 is LAS if $\frac{a_1b_1\bar{y}_3}{(1+b_1x_3)^2} < 1$ and $\frac{1}{d_2}\left(\frac{a_2\bar{y}_3}{(1+b_2y_3)} + \frac{\bar{c}a_3x_3}{(1+b_3x_3)}\right) < 1$.

B.2

Proof of Theorem 3.2. The Jacobian matrix around the equilibrium point $\bar{E}^*(\bar{x}^*, \bar{y}^*, \bar{z}^*)$ is

$$J(\bar{E}^*) = \begin{pmatrix} \bar{V}_1 & -\bar{V}_2 & -\bar{V}_3 \\ \bar{V}_4 & \bar{V}_5 & -\bar{V}_6 \\ \bar{V}_7 & \bar{V}_8 & 0 \end{pmatrix}$$

and the corresponding characteristic equation is

$$\lambda^3 + \bar{\sigma}_1\lambda^2 + \bar{\sigma}_2\lambda + \bar{\sigma}_3 = 0,$$

$$\text{where } \bar{\sigma}_1 = -(\bar{V}_1 + \bar{V}_5), \quad \bar{\sigma}_2 = (\bar{V}_1\bar{V}_5 + \bar{V}_2\bar{V}_4 + \bar{V}_3\bar{V}_7 + \bar{V}_6\bar{V}_8), \quad \bar{\sigma}_3 = (\bar{V}_3\bar{V}_4\bar{V}_8 - \bar{V}_1\bar{V}_6\bar{V}_8 - \bar{V}_2\bar{V}_6\bar{V}_7 - \bar{V}_3\bar{V}_5\bar{V}_7) \text{ and}$$

$$\bar{V}_1 = -\bar{x}^* + \frac{a_1b_1x^*\bar{y}^*}{(1+b_1x^*)^2} + \frac{a_3b_3x^*\bar{z}^*}{(1+b_3x^*)^2}, \quad \bar{V}_2 = \frac{a_1x^*}{1+b_1x^*}, \quad \bar{V}_3 = \frac{a_3x^*}{1+b_3x^*},$$

$$\bar{V}_4 = \frac{a_1\bar{y}^*}{(1+b_1x^*)^2}, \quad \bar{V}_5 = \frac{a_2b_2y^*\bar{z}^*}{(1+b_2y^*)^2}, \quad \bar{V}_6 = \frac{a_2y^*}{1+b_2y^*}, \quad \bar{V}_7 = \frac{a_3\bar{c}z^*}{(1+b_3x^*)^2},$$

$$\bar{V}_8 = \frac{a_2z^*}{(1+b_2y^*)^2}.$$

Therefore the system will be stable if $\bar{\sigma}_1 > 0$, $\bar{\sigma}_3 > 0$ and $\bar{\sigma}_1\bar{\sigma}_2 > \bar{\sigma}_3$.

Appendix C

C.1

Proof of Theorem 4.2. Here, we calculate the Jacobian matrix of the system (4.3)

$$J = \begin{pmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{pmatrix}, \text{with } J_{11} = 1 - 2x - \frac{a_1y}{(1+b_1x)} +$$

$$\frac{a_1b_1xy}{(1+b_1x)^2} - \frac{2a_3xz}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)} + \frac{a_3x^2z}{\left(x+\frac{c}{C_1}y\right)^2(1+b_3x)} + \frac{a_3b_3x^2z}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)^2},$$

$$J_{12} = -\frac{a_1x}{1+b_1x} + \frac{a_3Cx^2z}{C_1\left(x+\frac{c}{C_1}y\right)^2(1+b_3x)}, \quad J_{13} = -\frac{a_3x^2}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)}, \quad J_{21} =$$

$$\frac{a_1y}{(1+b_1x)^2} + \frac{a_2CC_1y^2z}{(y+CC_1x)^2(1+b_2y)}, \quad J_{22} = \frac{a_1x}{(1+b_1x)} - \frac{2a_2yz}{(y+CC_1x)(1+b_2y)} +$$

$$\frac{a_2y^2z}{(y+CC_1x)^2(1+b_2y)} + \frac{a_2b_2y^2z}{(y+CC_1x)(1+b_2y)^2} - d_1, \quad J_{23} = -\frac{a_2y^2}{(y+CC_1x)(1+b_2y)},$$

$$J_{31} = -\frac{a_2CC_1y^2z}{(y+CC_1x)^2(1+b_2y)} + \frac{2ca_3xz}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)} - \frac{ca_3x^2z}{\left(x+\frac{c}{C_1}y\right)^2(1+b_3x)} -$$

$$\frac{ca_3b_3x^2z}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)^2}, \quad J_{32} = \frac{2a_2yz}{(y+CC_1x)(1+b_2y)} - \frac{a_2y^2z}{(y+CC_1x)^2(1+b_2y)} -$$

$$\frac{a_2b_2y^2z}{(y+CC_1x)(1+b_2y)^2} - \frac{ca_3x^2z}{C_1\left(x+\frac{c}{C_1}y\right)^2(1+b_3x)}, \quad J_{33} = \frac{a_2y^2}{(y+CC_1x)(1+b_2y)} +$$

$$\frac{ca_3x^2}{\left(x+\frac{c}{C_1}y\right)(1+b_3x)} - d_2.$$

Calculating the Jacobian matrix at each equilibrium point, we conclude about the local stability of the equilibrium points.

The eigenvalues of the Jacobian matrix around the equilibrium point $E_1(1, 0, 0)$ are $-1, \frac{a_1}{1+b_1} - d_1$ and $\frac{ca_3}{1+b_3} - d_2$. Hence the equilibrium point $E_1(1, 0, 0)$ is locally asymptotically stable if $\frac{a_1}{d_1(1+b_1)} < 1$ and $\frac{ca_3}{d_2(1+b_3)} < 1$. Where the Jacobian matrix at E_1 is

$$J(E_1) = \begin{pmatrix} -1 & -\frac{a_1}{1+b_1} & -\frac{a_3}{1+b_3} \\ 0 & \frac{a_1}{1+b_1} - d_1 & 0 \\ 0 & 0 & \frac{ca_3}{1+b_3} - d_2 \end{pmatrix}.$$

The Jacobian matrix around the equilibrium point $E_2(x_2, 0, z_2)$ is

$$J(E_2) = \begin{pmatrix} A_1 & A_2 & -A_3 \\ 0 & A_4 & 0 \\ A_5 & -A_6 & 0 \end{pmatrix}$$

and the characteristic equation is

$$(\lambda^2 - A_1\lambda + A_3A_5)(A_4 - \lambda) = 0,$$

$$\text{where, } A_1 = \frac{a_3b_3x_2z_2}{(1+b_3x_2)^2} - x_2, \quad A_2 = -\frac{a_1x_2}{(1+b_1x_2)} + \frac{a_3z_2c}{C_1(1+b_3x_2)}, \quad A_3 =$$

$$\frac{a_3x_2}{1+b_3x_2}, \quad A_4 = \frac{a_1x_2}{1+b_1x_2} - d_1, \quad A_5 = \frac{ca_3z_2}{(1+b_3x_2)^2}, \quad A_6 = \frac{ca_3z_2c}{C_1(1+b_3x_2)}.$$

All the eigenvalues of the characteristic equation are negative or having negative real part if $\frac{a_1x_2}{d_1(1+b_1x_2)} < 1$ and $\frac{a_3b_3z_2}{(1+b_3x_2)^2} < 1$. Therefore, the equilibrium point E_2 is LAS if $\frac{a_1x_2}{d_1(1+b_1x_2)} < 1$ and $\frac{a_3b_3z_2}{(1+b_3x_2)^2} < 1$.

The Jacobian matrix around the equilibrium point $E_3(x_3, y_3, 0)$ is

$$J(E_3) = \begin{pmatrix} B_1 & -B_2 & -B_3 \\ B_4 & 0 & -B_5 \\ 0 & 0 & B_6 \end{pmatrix}$$

and the characteristic equation is

$$(\lambda^2 - B_1\lambda + B_2B_4)(B_6 - \lambda) = 0,$$

where, $B_1 = \frac{a_1b_1x_3y_3}{(1+b_1x_3)^2} - x_3$, $B_2 = \frac{a_1x_3}{1+b_1x_3}$, $B_3 = \frac{a_3x_3^2}{\left(x_3 + \frac{c_1}{c_1}y_3\right)(1+b_3x_3)}$

$$B_4 = \frac{a_1y_3}{(1+b_1x_3)^2}, \quad B_5 = \frac{a_2y_3^2}{(y_3+CC_1x_3)(1+b_2y_3)}, \quad B_6 = \frac{a_2y_3^2}{(y_3+CC_1x_3)(1+b_2y_3)} + \frac{a_3Cx_3^2}{\left(x_3 + \frac{c_1}{c_1}y_3\right)(1+b_3x_3)} - d_2.$$

All the eigenvalues of the characteristic equation are negative or having negative real part if $B_1 < 0$ and $B_6 < 0$.

Therefore, the equilibrium point E_3 is LAS if $\frac{a_1b_1y_3}{(1+b_1x_3)^2} < 1$ and.

$$\frac{1}{d_2} \left(\frac{a_2y_3^2}{(y_3+CC_1x_3)(1+b_2y_3)} + \frac{a_3x_3^2}{\left(x_3 + \frac{c_1}{c_1}y_3\right)(1+b_3x_3)} \right) < 1.$$

C.2

Proof of Theorem 4.3. The Jacobian matrix around the equilibrium point $E^*(x^*, y^*, z^*)$ is

$$J(E^*) = \begin{pmatrix} V_1 & -V_2 & -V_3 \\ V_4 & V_5 & -V_6 \\ V_7 & V_8 & 0 \end{pmatrix}$$

and the corresponding characteristic equation is

$$\lambda^3 - (V_1 + V_5)\lambda^2 + (V_1V_5 + V_2V_4 + V_3V_7 + V_6V_8)\lambda + (V_3V_4V_8 - V_1V_6V_8 - V_2V_6V_7 - V_3V_5V_7) = 0,$$

i.e.

$$\lambda^3 + \sigma_1\lambda^2 + \sigma_2\lambda + \sigma_3 = 0,$$

where $\sigma_1 = -(V_1 + V_5)$, $\sigma_2 = (V_1V_5 + V_2V_4 + V_3V_7 + V_6V_8)$, $\sigma_3 = (V_3V_4V_8 - V_1V_6V_8 - V_2V_6V_7 - V_3V_5V_7)$ and

$$V_1 = 1 - 2x^* - \frac{a_1y^*}{(1+b_1x^*)} + \frac{a_1b_1x^*y^*}{(1+b_1x^*)^2} - \frac{2a_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)(1+b_3x^*)} + \frac{a_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)^2(1+b_3x^*)} + \frac{a_3b_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)(1+b_3x^*)^2},$$

$$V_2 = \frac{a_1x^*}{1+b_1x^*} - \frac{a_3Cx^*z^*}{c_1\left(x^* + \frac{c_1}{c_1}y^*\right)^2(1+b_3x^*)}, \quad V_3 = \frac{a_3x^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)(1+b_3x^*)},$$

$$V_4 = \frac{a_1y^*}{(1+b_1x^*)^2} + \frac{a_2CC_1y^*z^*}{(y^*+CC_1x^*)^2(1+b_2y^*)}, \quad V_5 = \frac{a_1x^*}{(1+b_1x^*)} - \frac{2a_2y^*z^*}{(y^*+CC_1x^*)(1+b_2y^*)} + \frac{a_2y^*z^*}{(y^*+CC_1x^*)^2(1+b_2y^*)} + \frac{a_2b_2y^*z^*}{(y^*+CC_1x^*)(1+b_2y^*)^2} - d_1, \quad V_6 = \frac{a_2y^*}{(y^*+CC_1x^*)(1+b_2y^*)},$$

$$V_7 = -\frac{a_2CC_1y^*z^*}{(y^*+CC_1x^*)^2(1+b_2y^*)} + \frac{2ca_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)(1+b_3x^*)} - \frac{ca_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)^2(1+b_3x^*)} - \frac{\bar{c}a_3b_3x^*z^*}{\left(x^* + \frac{c_1}{c_1}y^*\right)(1+b_3x^*)^2},$$

$$V_8 = \frac{2a_2y^*z^*}{(y^*+CC_1x^*)(1+b_2y^*)} - \frac{a_2y^*z^*}{(y^*+CC_1x^*)^2(1+b_2y^*)} - \frac{a_2b_2y^*z^*}{(y^*+CC_1x^*)(1+b_2y^*)^2} - \frac{\bar{c}Ca_3x^*z^*}{c_1\left(x^* + \frac{c_1}{c_1}y^*\right)^2(1+b_3x^*)}.$$

Therefore, the system will be stable if $\sigma_1 > 0$, $\sigma_3 > 0$ and $\sigma_1\sigma_2 > \sigma_3$.

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