



Stability analysis of a tritrophic model with stage structure in the prey population



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Abstract

We analyze the role of the age structure of a prey in the dynamics of a tritrophic model. We study the effect of predation on a non-reproductive prey class, when the reproductive class of the prey has a defense mechanism. We consider two cases accordingly to the interaction between predator and reproductive class of the prey. In the first case, the functional response is Holling type II and it is possible to show up to two positive equilibria. When we consider a defense mechanism the functional response is Holling type IV. In both cases, we show sufficient parameter conditions to have a stable limit cycle obtained by a supercritical Hopf bifurcation. Some numerical simulations are carried out.

Keywords: Hopf's Bifurcation, tritrophic model, coexistence of species, prey age structure.

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1. Introduction

The mathematical modelling has become a very useful tool in ecology because it can be used to answer general or specific questions about an ecosystem. One of the interactions between species that has been most studied is the predator-prey type. Its study began with the Lotka-Volterra model, from which other models have been obtained considering more variables and more parameters in order to be closer to reality, [13]. For example, it has been included the carrying capacity, the handling time, the interference among predators and defense mechanism, among others. Since the age specific fecundity or fertility rate of a population is one of the most fundamental parameter in both the theory and practice of populations dynamics, [3], the study of age structured models is a topic of ecological interest.

The analysis of prey-predator interaction with age structure has been approached with different models. At first, the structure of ages was considered in the predator population, such is the case of Beddington et al. work, who studied a difference equations system dividing the predator population into the

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young and adult class and assuming that each one has a different attack rate. They showed that stable coexistence is possible, [1]. Hasting et al. analyzed a differential equations system with age structure in the predator. They proved the existence of stable equilibria and determined the effect of age structure, [6]. Cushing et al. studied an integro differential equations system derived from the McKendrick model. They considered an age structure in the predator and proved the parameter conditions to have the coexistence, [3]. Toth analyzed the effects of age structure on the predator prey resource chemostat model, he proved the coexistence equilibrium and the parameter condition to have a Hopf bifurcation, [19]. Xi et al. analyzed a delayed tritrophic food chain model with stage structure in predator and superpredator populations. They determined sufficient conditions to have positivity and permanence in the solution of the system, [20].

On the other hand, in nature it has also been found predators that eat only adults, or immature prey, it is the cicada case, which is preyed only in adult stage, or some species of perch which feed on immature prey, [9–11]. Hence, it is important to study the model with age structure in the prey population. Zhang et al. considered a predator prey model with two stage structure in the prey (immature and mature). They supposed that predator feeds only on the immature class with Lotka-Volterra functional response and they obtained necessary and sufficient conditions for the coexistence or extinction. Falconi, analyzed a predator prey model, dividing the prey population in the reproductive and non reproductive class. He considered three different functional responses to predation on the nonreproductive class and he showed the conditions to have the coexistence, [5]. More recently, it has been considered the analysis of predator prey systems with age structure in the population prey or in the population predator. Tang et al. analyzed a predator prey model with age structure in the predator population. They showed the existence and uniqueness of positive equilibrium and exhibit a Hopf bifurcation, [18]. Promrak et al. considered a predator prey model with age structure in the prey population. They showed the stability solutions and the bifurcation diagrams of the system, [15].

In this paper we analyze a tritrophic model focusing on two classes (reproductive and nonreproductive) in the prey population. Reproductive population will be denoted as w , the non-reproductive by x , the predator and superpredator populations by y and z , respectively. We will assume that the predator population attacks in a different way to the two classes in the prey. The non-reproductive class contains the oldest organisms and its interaction with the predator is of a Lotka-Volterra type. The interaction between the reproductive population and predator is modeled by a functional response Holling type II or IV, this last functional response considers a defense mechanism in the reproductive class. Explicitly, we have the following differential equations system

$$\begin{aligned} \frac{dw}{dt} &= w\rho \left(1 - \frac{w+x}{R}\right) - f_1(w,x)y - \nu w, & \frac{dx}{dt} &= \nu w - d_1x - a_3xy, \\ \frac{dy}{dt} &= c_1yf_1(w,x) + c_2a_3xy - d_2y - \frac{a_2y}{y+b_2}z, & \frac{dz}{dt} &= c_3\frac{a_2y}{y+b_2}z - d_3z. \end{aligned} \quad (1.1)$$

We consider two cases, which are obtained by considering that the functional response $f_1(w,x) = \frac{a_1w}{w+x+b_1}$ or $f_1(w,x) = \frac{a_1w}{w^2+x+b_1}$. Even though these functional responses are not precisely of the classical Holling type (see for instance [4, 17]), through this paper we will call them of Holling type II and IV, respectively. We assume that the birth rate of the non reproductive population is proportional to the reproductive one with proportionality constant ν , hence the non reproductive population does not extinguish unless the reproductive class does.

For ecological reasons, all the parameters are positive and we restrict our analysis to the positive set $\Gamma := \{(w,x,y,z) \in \mathbb{R}^4 : w > 0, x > 0, y > 0, z > 0\}$.

2. Criteria for stability and Hopf bifurcation

In next lemma we characterize under some hypothesis the Routh-Hurwitz test, [16], and the necessary condition to have a Hopf bifurcation.

Let $\text{pol}(\lambda) = \lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4$ be the characteristic polynomial for the linear approximation of the system (1.1) at some equilibrium point P. Set

$$\mathbf{EQ} := A_1^2A_4 - A_1A_2A_3 + A_3^2. \tag{2.1}$$

On the other hand, to have a Hopf bifurcation of the differential system (1.1) at P it is needed that the characteristic polynomial $\text{pol}(\lambda)$ at P factorizes as

$$(\lambda - \lambda_3)(\lambda - \lambda_4)(\lambda^2 + \omega^2), \quad \omega > 0. \tag{2.2}$$

In this notation we state the following criteria which will be used later.

Lemma 2.1. *If $A_i > 0, i = 1, \dots, 4$, the following statements hold.*

- (i) *The equilibrium point P is locally asymptotically stable if and only if $\mathbf{EQ} < 0$.*
- (ii) *Assume that $\text{pol}(\lambda)$ factorizes as in (2.2). Then, its roots are*

$$\omega = \pm i\sqrt{\frac{A_3}{A_1}} \quad \text{and} \quad \lambda_{3,4} = \frac{-A_1 \pm \sqrt{A_1^2 - 4A_2 + 4\omega^2}}{2}$$

if and only if $\mathbf{EQ} = 0$.

Proof. We prove (i). Under the hypothesis, the claim follows directly observing that the Hurwitz determinants for $\text{pol}(\lambda)$ are given by

$$\det_1 = A_1, \quad \det_2 = A_1A_2 - A_3, \quad \det_3 = -A_3^2 + A_1^2(-A_4) + A_1A_2A_3, \quad \det_4 = -A_4(-A_1A_2A_3 + A_3^2 + A_1^2A_4)$$

and all are positive if and only if $A_2 > \frac{A_1^2A_4 + A_3^2}{A_1A_3}$. We now prove (ii). Assume that $\text{pol}(\lambda)$ is as in the hypothesis. Then it factorizes as

$$P(\lambda) = (\lambda - \alpha_1)(\lambda - \alpha_2)(\lambda^2 + \omega^2),$$

where $\omega > 0$ if and only if

$$A_1 = -(\alpha_1 + \alpha_2), \quad A_2 = (\omega^2 + \alpha_1\alpha_2), \quad A_3 = -(\alpha_1 + \alpha_2)\omega^2, \quad A_4 = \alpha_1\alpha_2\omega^2.$$

Equivalently,

$$A_2 = (\omega^2 + \alpha_1\alpha_2), \quad A_3 = A_1\omega^2, \quad A_4 = \alpha_1\alpha_2\omega^2.$$

That is,

$$\alpha_1\alpha_2 = A_2 - \omega^2, \quad A_3 = A_1\omega^2, \quad A_4 = \alpha_1\alpha_2\omega^2.$$

Equivalently,

$$(-A_1 - \alpha_2)\alpha_2 = A_2 - \frac{A_3}{A_1} \quad \text{and} \quad A_4 = \left(A_2 - \frac{A_3}{A_1}\right) \frac{A_3}{A_1},$$

that is,

$$\alpha_2^2 + A_1\alpha_2 + \frac{A_2A_1 - A_3}{A_1} = 0 \quad \text{and} \quad A_1^2A_4 - A_1A_2A_3 + A_3^2 = 0.$$

This completes the proof. □

Along this paper, the transversality condition to have a Hopf bifurcation will be computed by means of the following result that appeared as an exercise in [7, p. 189].

Proposition 2.2. *Let $M(\tau)$ be a parameter-dependent real $(n \times n)$ -matrix which has a simple pair of complex eigenvalues $\xi(\tau) \pm i\omega(\tau)$ such that $\xi(\tau_0) = 0$ and $\omega(\tau_0) := \omega_0 > 0$. Then, the derivative of the real part of the complex eigenvalues is given by*

$$\frac{d\xi}{d\tau}(\tau_0) = \text{Re} \left(\bar{\mathbf{p}}^{\text{tr}} \cdot \left(\frac{dM}{d\tau}(\tau_0) \cdot \mathbf{q} \right) \right),$$

where $\mathbf{p}, \mathbf{q} \in \mathbb{C}^n$ are eigenvectors satisfying the normalization conditions

$$M(\tau_0)\mathbf{q} = i\omega_0\mathbf{q}, \quad M^{\text{tr}}(\tau_0)\mathbf{p} = -i\omega_0\mathbf{p}, \quad \text{and} \quad \bar{\mathbf{p}}^{\text{tr}} \cdot \mathbf{q} = 1.$$

3. Case $f_1(w, x)$ Holling II

Lemma 3.1. *The differential system (1.1) has:*

(i) *A unique equilibrium point in Γ if*

$$a_2 = \frac{d_3 + k_1}{c_3}, \quad d_2 = \frac{a_1 c_1 k_1 k_2 (a_3 b_2 d_3 + d_1 k_1)}{(a_3 b_2 d_3 + k_1 (d_1 + \nu))(a_1 b_2 d_3 + k_1 (b_1 \nu + k_2))}, \quad \rho = \frac{a_1 b_2 d_3}{b_1 k_1} + \nu, \quad R = \frac{b_1 (a_1 b_2 d_3 + k_1 (b_1 \nu + k_2))}{a_1 b_2 d_3},$$

where k_1 and k_2 are positive real numbers. The equilibrium is given by

$$P_0 = \left(\frac{b_1 k_1 k_2 (a_3 b_2 d_3 + d_1 k_1)}{(a_1 b_2 d_3 + b_1 k_1 \nu)(a_3 b_2 d_3 + k_1 (d_1 + \nu))}, \frac{b_1 k_1^2 k_2 \nu}{(a_1 b_2 d_3 + b_1 k_1 \nu)(a_3 b_2 d_3 + k_1 (d_1 + \nu))}, \frac{b_2 d_3}{k_1}, \frac{a_3 b_1 b_2 c_2 c_3 k_1 k_2 \nu}{(a_1 b_2 d_3 + b_1 k_1 \nu)(a_3 b_2 d_3 + k_1 (d_1 + \nu))} \right).$$

(ii) *Two equilibrium points in Γ if*

$$a_1 = k_2 \left(\frac{k_2 (w_0 + x_0)}{4w_0 y_0 (2d_1 x_0 + 2k_1 + k_2)} + \frac{w_0 + x_0}{2w_0 y_0} \right), \quad a_2 = \frac{d_3 (b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{k_1}{x_0 y_0},$$

$$b_1 = \frac{k_2 (w_0 + x_0)}{2(2d_1 x_0 + 2k_1 + k_2)}, \quad c_1 = \frac{2(2c_2 c_3 k_1 (4d_1 x_0 + 4k_1 + k_2) + k_8)}{c_3 k_2 (4d_1 x_0 + 4k_1 + 3k_2)}, \quad d_2 = \frac{c_2 k_1}{y_0},$$

$$R = 2(w_0 + x_0) \quad \text{and} \quad \rho = \frac{2d_1 x_0 + 2k_1 + k_2}{w_0},$$

where k_1, k_2, k_8, w_0, y_0 and x_0 are positive real numbers. The equilibrium points are given by

$$P_0 = \left(w_0, x_0, y_0, \frac{2c_2 c_3 k_1 (4d_1 x_0 + 4k_1 + k_2) + k_8}{d_3 (4d_1 x_0 + 4k_1 + 3k_2)} \right),$$

$$P_1 = \left(\frac{k_2 w_0}{4d_1 x_0 + 4k_1 + 2k_2}, \frac{k_2 x_0}{4d_1 x_0 + 4k_1 + 2k_2}, y_0, \frac{k_8}{8d_1 d_3 x_0 + 8d_3 k_1 + 4d_3 k_2} \right).$$

Proof. In any case, since all the parameters are positive and the points of interest are in Γ , the equilibrium points for the differential system (1.1) must satisfy the system

$$\begin{aligned} a_1 R y + (b_1 + w + x)(R(\nu - \rho) + \rho(w + x)) &= 0, \\ \nu w - x(a_3 y + d_1) &= 0, \\ (b_2 + y)((b_1 + w + x)(d_2 - a_3 c_2 x) - a_1 c_1 w) + a_2 z(b_1 + w + x) &= 0, \\ -a_2 c_3 y + b_2 d_3 + d_3 y &= 0. \end{aligned} \tag{3.1}$$

Assume that $P_0 = (w_0, x_0, y_0, z_0) \in \Gamma$ is an equilibrium point satisfying system (3.1). From fourth equation we have that $y_0 = \frac{b_2 d_3}{k_1}$ where $k_1 = a_2 c_3 - d_3 > 0$, that is, $a_2 = \frac{k_1 + d_3}{c_2}$. Substituting y_0 in the other equations, the system (3.1) at P_0 simplifies to

$$\begin{aligned} a_1 b_2 d_3 R + k_1 (b_1 + w_0 + x_0)(R(\nu - \rho) + \rho(w_0 + x_0)) &= 0, \\ \nu k_1 w_0 - x_0 (a_3 b_2 d_3 + d_1 k_1) &= 0, \\ c_3 b_2 ((b_1 + w_0 + x_0)(d_2 - a_3 c_2 x_0) - a_1 c_1 w_0) + k_1 z_0 (b_1 + w_0 + x_0) &= 0. \end{aligned}$$

Solving second equation for w_0 , we have $w_0 = \frac{x_0 (a_3 b_2 d_3 + d_1 k_1)}{k_1 \nu}$. Substituting w_0 in the other equations, the system (3.1) at P_0 becomes

$$\begin{aligned} \nu^2 a_1 b_2 d_3 k_1 R + (a_3 b_2 d_3 x_0 + k_1 \nu (b_1 + x_0) + d_1 k_1 x_0)(a_3 b_2 d_3 \rho x_0 + k_1 (\rho x_0 (d_1 + \nu) + \nu R(\nu - \rho))) &= 0, \\ ((a_3 b_2 d_3 x_0 + k_1 \nu (b_1 + x_0) + d_1 k_1 x_0)(b_2 c_3 (d_2 - a_3 c_2 x_0) + k_1 z_0) - a_1 b_2 c_1 c_3 x_0 (a_3 b_2 d_3 + d_1 k_1)) &= 0. \end{aligned} \tag{3.2}$$

Solving second equation in (3.2) for z_0 we have

$$z_0 = \frac{b_2 c_3}{k_1} \left(\frac{a_1 c_1 x_0 (a_3 b_2 d_3 + d_1 k_1)}{a_3 b_2 d_3 x_0 + k_1 \nu (b_1 + x_0) + d_1 k_1 x_0} + a_3 c_2 x_0 - d_2 \right). \tag{3.3}$$

Substituting z_0 in first equation in (3.2) we have that the system (3.1) simplifies to

$$R \left(\frac{a_1 b_2 d_3}{k_1} + b_1(\nu - \rho) \right) + \frac{x_0(b_1 \rho + R(\nu - \rho))(a_3 b_2 d_3 + k_1(d_1 + \nu))}{k_1 \nu} + \frac{\rho x_0^2(a_3 b_2 d_3 + k_1(d_1 + \nu))^2}{k_1^2 \nu^2} = 0.$$

Now, assume that $R(\nu - \rho) + b_1 \rho < 0$. Then there is a positive real number k_2 such that $R(\nu - \rho) + b_1 \rho = -k_2$. Set $\rho = k_3 + \nu$ for some $k_3 > 0$ and $k_3 = \frac{a_1 b_2 d_3}{b_1 k_1}$. Then, $R = \frac{b_1(a_1 b_2 d_3 + k_1(b_1 \nu + k_2))}{a_1 b_2 d_3}$. Substituting R and ρ in the above quadratic equation with respect to x_0 it has a positive root x_0 given by

$$x_0 = \frac{b_1 k_1^2 k_2 \nu}{(a_1 b_2 d_3 + b_1 k_1 \nu)(a_3 b_2 d_3 + k_1(d_1 + \nu))}.$$

Finally, from (3.3) we have that $z_0 > 0$ if we take $d_2 = \frac{a_1 c_1 x_0(a_3 b_2 d_3 + d_1 k_1)}{a_3 b_2 d_3 x_0 + k_1 \nu(b_1 + x_0) + d_1 k_1 x_0}$. Hence we have proved the claim (i).

We now prove claim (ii). We suppose that $P_0 = (w_0, x_0, y_0, z_0) \in \Gamma$ satisfies (3.1). Solving first, second, third, and fourth equation in the variables a_1, a_2, a_3 , and c_1 , respectively, one gets

$$a_1 = -\frac{(b_1 + w_0 + x_0)(R(\nu - \rho) + \rho(w_0 + x_0))}{R y_0}, \quad a_2 = \frac{d_3(b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{\nu w_0 - d_1 x_0}{x_0 y_0}, \quad \text{and}$$

$$c_1 = -\frac{R(c_2 c_3(d_1 x_0 - \nu w_0) + c_3 d_2 y_0 + d_3 z_0)}{c_3 w_0(\nu R + \rho(-R + w_0 + x_0))}.$$

Taking $\nu = \frac{d_1 x_0 + k_1}{w_0}$, $d_2 = \frac{c_2 k_1}{y_0}$, $R = 2(w_0 + x_0)$, and $\rho = \frac{2d_1 x_0 + 2k_1 + k_2}{w_0}$, where $k_1, k_2 > 0$ we have that

$$a_1 = \frac{k_2(b_1 + w_0 + x_0)}{2w_0 y_0}, \quad a_2 = \frac{d_3(b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{k_1}{x_0 y_0}, \quad c_1 = \frac{2d_3 z_0}{c_3 k_2}$$

and $P_0 \in \Gamma$ is an equilibrium point for the differential system (1.1). Hence under these conditions for the parameters a_1, a_2, a_3 , and c_1 the system (3.1) takes the form

$$\begin{aligned} y_0(b_1 + w + x) (2d_1 x_0(w - w_0 + x - x_0) + 2k_1(w - w_0 + x - x_0) + k_2(w - 2w_0 + x - 2x_0)) \\ + k_2 y(w_0 + x_0)(b_1 + w_0 + x_0) = 0, \\ x_0 y_0 w(d_1 x_0 + k_1) - w_0 x(x_0 y_0 d_1 + k_1 y) = 0, \\ \frac{(b_1 + w + x)(d_3 x_0 z(b_2 + y_0) - c_2 c_3 k_1(b_2 + y)(x - x_0))}{x_0} - \frac{d_3 w z_0(b_2 + y)(b_1 + w_0 + x_0)}{w_0} = 0, \\ b_2 d_3(y_0 - y) = 0. \end{aligned} \tag{3.4}$$

Assume that $P_1 = (w_1, x_1, y_1, z_1) \in \Gamma \setminus \{P_0\}$ satisfies (3.4). We will give conditions to find expressions for P_1 . Since all the parameters are positive, from fourth equation we have $y_1 = y_0$ and substituting y_1 in the other equations we have that system (3.4) simplifies to

$$\begin{aligned} (w_1 - w_0 + x_1 - x_0)(2k_1(w_1 + x_1) + k_2(w_1 - w_0 + x_1)) \\ + (-k_2 + 2d_1(w_1 + x_1))x_0 + b_1(2k_1 + k_2 + 2d_1 x_0) = 0, \\ w_1 x_0 - w_1 x_1 = 0, \\ -w_0(b_1 + w_1 + x_1)(c_2 c_3 k_1(x_1 - x_0) - d_3 x_0 z_1) - d_3 w_1 x_0 z_0(b_1 + w_0 + x_0) = 0. \end{aligned}$$

Therefore, from second equation $w_1 = \frac{w_0 x_1}{x_0}$. Substituting w_1 in first equation and solving the resulting equation for x_1 , we have $x_1 = \frac{x_0(k_2(w_0 + x_0) - b_1(2d_1 x_0 + 2k_1 + k_2))}{(w_0 + x_0)(2d_1 x_0 + 2k_1 + k_2)}$. Since x_1 must be positive, we have $k_2(w_0 + x_0) - b_1(2d_1 x_0 + 2k_1 + k_2) = k_9$ for some $k_9 > 0$. Take $k_9 = \frac{1}{2}k_2(w_0 + x_0)$. Then, substituting w_1 and x_1 in third equation we have $z_1 = \frac{d_3 z_0(4d_1 x_0 + 4k_1 + 3k_2) - 2c_2 c_3 k_1(4d_1 x_0 + 4k_1 + k_2)}{4d_3(2d_1 x_0 + 2k_1 + k_2)}$. Since z_1 must be positive, we take $k_8 > 0$ such that $-2c_2 c_3 k_1(4k_1 + k_2 + 4d_1 x_0) + d_3(4k_1 + 3k_2 + 4d_1 x_0)z_0 = k_8$. These conditions guarantee that P_1 and P_0 are as claim (ii) states. \square

3.1. Dynamics of one equilibrium point

Lemma 3.2. *If the hypothesis of Lemma 3.1 (i) are satisfied and*

$$k_1 = d_3, \quad a_1 = \frac{b_1\nu}{b_2}, \quad a_2 = \frac{2d_3}{c_3}, \quad a_3 = \frac{3\nu}{b_2}, \quad d_1 = 2\nu, \quad k_2 = 35b_1\nu, \quad c_1 = \frac{2738c_2}{395},$$

$$d_2 = \frac{1295b_1c_2\nu}{237b_2}, \quad b_{20} := b_1c_2 \left(\frac{27983097891d_3}{16779436846\nu} + \frac{28749}{37756} \right), \quad \text{and } \nu \neq \frac{30421101094081d_3}{16443848109080},$$

then the eigenvalues of the linear approximation $M_0(b_{20})$ of system (1.1) at P_0 are

$$\lambda_{1,2} = \pm i \frac{\sqrt{\frac{41948592115}{237}\nu}}{8214},$$

$$\lambda_{3,4} = -\frac{10961510700d_3\nu}{7038482959d_3 \pm \sqrt{745681}\sqrt{d_3(30421101094081d_3 - 16443848109080\nu)}}.$$

Proof. Assume that the hypothesis in Lemma 3.1 (i) are valid. To simplify the analysis we set $k_1 = d_3$, $a_1 = \frac{b_1\nu}{b_2}$ and $a_3 = \frac{d_1+\nu}{b_2}$. Then the characteristic polynomial for the linear approximation $M(P_0)$ of system (1.1) at P_0 is $\text{pol}_0(\lambda, b_2) = \lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4$, where

$$A_1 = \frac{4b_2(2d_1 + \nu) E_0 - c_2k_2(d_1 + \nu)(2b_1\nu + k_2)^2}{8b_2(d_1 + \nu)(2b_1\nu + k_2)^2},$$

$$A_2 = \frac{k_2(4\nu(2d_1 + \nu) E_1 + c_2(d_1 + \nu)(2b_1\nu + k_2) E_2)}{16b_2(d_1 + \nu)^2(2b_1\nu + k_2)^3},$$

$$A_3 = \frac{k_2(2d_1 + \nu)(4b_1c_1\nu^3(8b_1^2\nu(2d_1 + \nu) - k_2^2) + c_2(2b_1\nu + k_2) E_3)}{16b_2(d_1 + \nu)(2b_1\nu + k_2)^3},$$

$$A_4 = \frac{c_2d_3k_2^3\nu(2d_1 + \nu)}{8b_2(2b_1\nu + k_2)^2},$$

$$E_0 = \nu(8b_1^2\nu^2 + 8b_1k_2\nu + 3k_2^2) + 2d_1(2b_1\nu + k_2)^2,$$

$$E_1 = b_1c_1\nu(8b_1^2\nu^3 - d_1(k_2 - 2b_1\nu)(4b_1\nu + k_2) - k_2^2\nu) + 4b_2k_2(d_1 + \nu)^2(2b_1\nu + k_2),$$

$$E_2 = \nu(\nu(8b_1^2\nu^2 + 8b_1k_2\nu + k_2^2) + 2d_3(2b_1\nu + k_2)^2) + 2d_1(d_3(2b_1\nu + k_2)^2 + 4b_1\nu^2(b_1\nu + k_2)),$$

$$E_3 = \nu(16b_1^2\nu^3 + 8b_1\nu^2(b_1d_3 + k_2) + 8b_1d_3k_2\nu + 3d_3k_2^2) + 2d_1(2b_1\nu + k_2)(2b_1d_3\nu + 4b_1\nu^2 + d_3k_2).$$

Therefore, setting $d_1 = 2\nu$ expression (2.1) becomes the function, in the variable b_2 ,

$$\text{EQ}(b_2) = \frac{5k_2^2 \left(360b_2(2b_1\nu + k_2)^2 (G_0)^2 - \frac{(G_1)(G_2)(G_3)}{\nu} + 36c_2d_3k_2\nu^2(2b_1\nu + k_2)^2 (G_4)^2 \right)}{165888b_2^3(2b_1\nu + k_2)^8},$$

where

$$G_0 = 4b_1c_1\nu^3(40b_1^2\nu^2 - k_2^2) + c_2\nu(2b_1\nu + k_2)(48b_1^2\nu^3 + 24b_1\nu^2(b_1d_3 + k_2) + 24b_1d_3k_2\nu + 7d_3k_2^2),$$

$$G_1 = 20b_2\nu(24b_1^2\nu^2 + 24b_1k_2\nu + 7k_2^2) - 3c_2k_2(2b_1\nu + k_2)^2,$$

$$G_2 = 4b_1c_1\nu^3(40b_1^2\nu^2 - k_2^2) + c_2\nu(2b_1\nu + k_2)(48b_1^2\nu^3 + 24b_1\nu^2(b_1d_3 + k_2) + 24b_1d_3k_2\nu + 7d_3k_2^2),$$

$$G_3 = 20\nu^3(b_1c_1(24b_1^2\nu^2 - 4b_1k_2\nu - 3k_2^2) + 36b_2k_2(2b_1\nu + k_2) + 3c_2\nu(2b_1\nu + k_2)(\nu(24b_1^2\nu^2 + 24b_1k_2\nu + k_2^2) + 6d_3(2b_1\nu + k_2)^2)),$$

$$G_4 = 3c_2k_2(2b_1\nu + k_2)^2 - 20b_2\nu(24b_1^2\nu^2 + 24b_1k_2\nu + 7k_2^2).$$

Now, if $k_2 = 35b_1\nu$, then

$$EQ(b_2) = \frac{30625b_1v^4 (12v^2(2738c_2 - 395c_1) G_5 + 9154363015180278b_1^2c_2^3d_3^2 + G_6)}{582678191652046848b_2^3},$$

where

$$G_5 = -28749b_1^2c_2(75820c_1 - 231879c_2) + 4b_1b_2(598861900c_1 + 5322323571c_2) - 35203694400b_2^2,$$

$$G_6 = 37b_1c_2d_3v(37756b_2(598861900c_1 - 8080460229c_2) - 28749b_1c_2(832468060c_1 - 9699735333c_2)).$$

Taking $c_1 = \frac{2738c_2}{395}$, we have

$$A_1 = \frac{105577244385d_3v}{18375071202d_3 + 8389718423v},$$

$$A_2 = \frac{5v^2(417079125059936669046d_3 + 70387375217225606929v)}{15990341652(18375071202d_3 + 8389718423v)},$$

$$A_3 = \frac{18686990554143624575d_3v^3}{67469796(18375071202d_3 + 8389718423v)},$$

$$A_4 = \frac{214375d_3v^3}{10952 \left(\frac{27983097891d_3}{16779436846v} + \frac{28749}{37756} \right)}.$$

Hence, (2.1) simplifies to

$$EQ(b_2) = \frac{30625b_1^2c_2^2d_3v^4(8389718423v(28749b_1c_2 - 37756b_2) + 528264921986298b_1c_2d_3)}{33624234580359168b_2^3}$$

and $EQ(b_{20}) = 0$, where $b_{20} = b_1c_2 \left(\frac{27983097891d_3}{16779436846v} + \frac{28749}{37756} \right)$. The proof follows from Lemma 2.1 (ii). □

Lemma 3.3. *If the hypothesis of Lemma 3.2 are valid and $d_3 = 10$, $c_2 = \frac{1}{10}$, $c_3 = \frac{1}{2}$, $b_1 = 1$, then there exist ν_0, ν_1 positive real numbers such that the first Lyapunov coefficient for the system (1.1) at P_0 is positive if either $0 < \nu < \nu_0$ or $\nu > \nu_1$, and it is negative if $\nu_0 < \nu < \nu_1$. Moreover, the transversality condition holds: $\frac{dRe(\lambda_{1,2})}{db_2}(b_{20}) \neq 0$.*

Proof. If the hypothesis are valid, using Proposition 2.2 for the transversality condition and the Kuznetsov formulae (see [2, 7, 8]) for the first Lyapunov coefficient, the Mathematica software allows to get by a direct calculation:

$$\frac{dRe(\lambda_{1,2})}{db_2}(b_{20}) = -\frac{22070466729033979537997184429118254339826180728050v^3}{s_1(\nu)} \neq 0,$$

where

$$s_1(\nu) = 118072143(4954382589970505556215207055672412811041v^2 - 153100675464069678846765525147766678141320v + 31089982892973169931537646413835378802713600).$$

And that $\ell_1(P_0, b_{20}) = -\frac{N_0}{N_1}$, where

$$N_0 = 351936876086128034645\sqrt{\frac{3313938777085}{3}}v$$

$$\times \left(66100655705229180407012562120741326878526172401290087447529295055585272751069329615626823335v^5 - 5976171976577332106606135926837595167406791205883486650756176985676594548604919209508115326404v^4 - 76596224628557684030051225997470099342353475309263857165708452193625218362629656244443950086020v^3 \right)$$

$$\begin{aligned}
 & - 6170102643931266987022838519078935939108816686869336913207841796659032566131751047615550510714400v^2 \\
 & - 5653648766502639134187836199614462873235179102144729125824880862755619868039896864986829728800000v \\
 & + 1 \quad 574303131909464229944026194947529078952694682667394044189255748718719649104366999659556460800000 \Big); \\
 N_1 = & 6573938 \left(876241431697782963899717150349773v^2 + 75662348547641698853038918874340v \right. \\
 & \left. + 828574316667181373417609314915800 \right) \left(4954382589970505556215207055672412811041v^2 \right. \\
 & \left. - 153100675464069678846765525147766678141320v + 31089982892973169931537646413835378802713600 \right) \\
 & \times \left(4954382589970505556215207055672412811041v^2 + 124490364366450894812917026926295506809680v \right. \\
 & \left. + 8258827593974963520933437147080834871447100 \right).
 \end{aligned}$$

A numeric calculation shows that the positive roots of $\ell_1(P_0, b_{20})$ are $\nu_0 \approx 0.223694$ and $\nu_1 \approx 108.971$ which satisfy the desired properties (see Fig. 1).

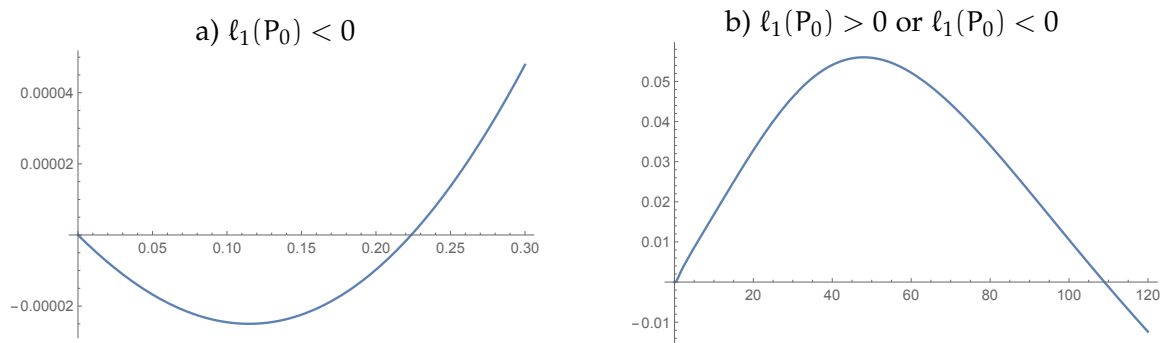


Figure 1: First Lyapunov coefficient.

□

Theorem 3.4 (f_1 Holling II, one equilibrium point). Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 3.3. Then, the system exhibits a Hopf bifurcation at P_0 with respect to the parameter b_2 and its bifurcation value is b_{20} . This bifurcation is supercritical if $0 < \nu < \nu_0$ or $\nu > \nu_1$, and it is subcritical if $\nu_0 < \nu < \nu_1$.

Proof. It follows from Lemma 3.2 and the Andronov-Hopf Theorem [8, 12, 14].

□

3.2. Dynamics of two equilibria

Lemma 3.5. If the hypothesis of Lemma 3.1 (ii) are satisfied and

$$\begin{aligned}
 c_2 = & \frac{365y_0}{44w_0}, \quad d_1 = \frac{2920d_3}{87}, \quad k_1 = \frac{365d_3w_0}{87}, \quad k_2 = \frac{2920d_3w_0}{87}, \\
 k_8 = & \frac{97254250b_2c_3d_3^2w_0}{7569}, \quad \text{and } b_{20} := \frac{2361971095625y_0}{131632971184},
 \end{aligned}$$

then the eigenvalues of the linear approximation $M_0(b_{20})$ of system (1.1) at P_0 are

$$\lambda_{1,2} = \pm i 365 \sqrt{\frac{2525226}{1668424897}} d_3, \quad \lambda_{3,4} = -\frac{73 \left(1056 \pm i \sqrt{677949239} \right) d_3}{22968}.$$

Proof. The proof is similar to the given for Lemma 3.1 (i). Assume that the hypothesis in Lemma 3.1 (ii) hold. In order to simplify the calculations set $x_0 = w_0$,

$$k_8 = \frac{b_2 c_3 (24d_1^2 w_0^2 + 18d_1 k_2 w_0 + 24k_1^2 + 18k_1 k_2 + k_2^2)}{4w_0} \quad \text{and} \quad c_2 = \frac{y_0 (24d_1^2 w_0^2 + 18d_1 k_2 w_0 + 24k_1^2 + 18k_1 k_2 + k_2^2)}{8k_1 w_0 (4d_1 w_0 + 4k_1 + k_2)}.$$

Now making $k_1 = \frac{k_2}{8}$ and $k_2 = d_1 w_0$ we have that the linear approximation at P_0 for the system (1.1) has characteristic polynomial

$$\text{pol}_0(\lambda, b_2) = \lambda^4 + A_{10}\lambda^3 + A_{20}\lambda^2 + A_{30}\lambda + A_{40},$$

where

$$A_{10} = \frac{d_1}{5}, \quad A_{20} = \frac{d_1(803b_2(11d_1 + 48d_3) - 20233d_1 y_0)}{25344y_0},$$

$$A_{30} = \frac{73d_1^2(22b_2(d_1 + 3304d_3) - 38261d_1 y_0)}{2027520y_0}, \quad \text{and} \quad A_{40} = \frac{10439b_2 d_1^3 d_3}{5120y_0}.$$

In this case, expression (2.1) is $\mathbf{EQ} = \frac{73d_1^4 T_1}{20554186752000y_0^2}$, where

$$T_1 = -176660b_2^2(d_1 + 3304d_3)(87d_1 - 2920d_3) + 572b_2 d_1 y_0 (46255055d_1 - 3097232904d_3) + 472394219125d_1^2 y_0^2.$$

Taking $d_1 = \frac{2920d_3}{87}$, we have that all the coefficients of $\text{pol}_0(\lambda, b_2)$ are positive and $\mathbf{EQ}(b_{20}) = 0$, where

$$b_{20} = \frac{2361971095625y_0}{131632971184}.$$

The proof concludes using Lemma 2.1 (ii). □

Lemma 3.6. *Under the hypothesis of Lemma 3.5 the first Lyapunov coefficient for the system (1.1) at P_0 is negative. Moreover, the transversality condition holds: $\frac{d\text{Re}(\lambda_{1,2})}{db_2}(b_{20}) \neq 0$.*

Proof. Similarly to the proof of Lemma 3.3, a calculation proves that

$$\frac{d\text{Re}(\lambda_{1,2})}{db_2}(b_{20}) = -\frac{9287262564940698723330882878656d_3}{41362560595546268863797036236319y_0} \neq 0$$

and that the first Lyapunov coefficient is $\ell_1(P_0) = -\frac{N_0}{N_1}$, where

$$N_0 = 8507365617004380447171374616484388706047917265654519261322268539426856405245286959597$$

$$329625166819212900509434773841920 \sqrt{\frac{110116043202}{38261}};$$

$$N_1 = 9430175494429761358556394005879301699402603777598726258708502056302804492108705495457$$

$$\times (48807341380019929 (777031385380692461328125c_3^2 + 186770227571152422912) y_0^2$$

$$+ 3353725607660164343881855230232467456w_0^2).$$

□

Under the hypothesis of Lemma 3.1 (ii), a direct calculation shows that the characteristic polynomial for the linear approximation of system (1.1) at P_1 has constant term

$$A_{41} = -\frac{b_2 d_3 k_8 (d_1 x_0 + k_1) (4d_1 x_0 + 4k_1 + k_2)}{32c_3 w_0 x_0 y_0 (b_2 + y_0) (2d_1 x_0 + 2k_1 + k_2)},$$

which is negative since all the parameters are positive. Hence from the Routh-Hurwitz test we have that the equilibrium point P_1 is locally unstable. In summary, we have proved next result, which follows from Lemma 3.6 and the Andronov-Hopf Theorem.

Theorem 3.7 (f_1 Holling II, two equilibrium points). *Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 3.5. Then, P_1 is locally unstable and the system (1.1) exhibits a supercritical Hopf bifurcation at P_0 with respect to the parameter b_2 and its bifurcation value is b_{20} .*

4. Case $f_1(w, x)$ Holling IV

Lemma 4.1. *The differential system (1.1) has:*

i) *An equilibrium point in Γ if*

$$a_2 = \frac{d_3 + k_1}{c_3}, \quad b_1 = \frac{k_1^2 v^2 + k_4}{(a_3 b_2 d_3 + d_1 k_1)^2}, \quad d_2 = \frac{a_1 c_1 k_1 k_4 v (a_3 b_2 d_3 + d_1 k_1)}{(k_1^2 v^2 + k_4)^2}, \quad \rho = \frac{a_1 b_2 d_3 (a_3 b_2 d_3 + d_1 k_1)^2}{k_1 (k_1^2 v^2 + k_4)} + v \text{ and}$$

$$R = \frac{(k_1^2 v^2 + k_4) (a_3 b_2 d_3 + k_1 (d_1 + v)) (a_1 b_2 d_3 (a_3 b_2 d_3 + d_1 k_1)^2 + k_1^3 v^3 + k_1 k_4 v)}{a_1 b_2 d_3 k_1 v (a_3 b_2 d_3 + d_1 k_1)^4},$$

where k_1, k_4 are positive real numbers. The equilibrium is given by

$$P_0 = \left(\frac{k_4}{a_3 b_2 d_3 k_1 v + d_1 k_1^2 v}, \frac{k_4}{(a_3 b_2 d_3 + d_1 k_1)^2}, \frac{b_2 d_3}{k_1}, \frac{a_3 b_2 c_2 c_3 k_4}{k_1 (a_3 b_2 d_3 + d_1 k_1)^2} \right).$$

ii) *Two equilibrium points in Γ if*

$$a_1 = \frac{(d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (6d_1 w_0^4 + 12k_1 w_0^2 + 7k_3)^2}{32w_0 y_0 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)^2}, \quad a_2 = \frac{d_3 (b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{2k_1}{w_0^2 y_0},$$

$$b_1 = \frac{1}{16} w_0^2 \left(\frac{k_3 (12d_1 w_0^4 + 24k_1 w_0^2 + 13k_3)}{(d_1 w_0^4 + 2k_1 w_0^2 + k_3)^2} + 12 \right), \quad d_2 = \frac{c_2 k_1}{y_0}, \quad R = w_0 (w_0 + 2),$$

$$c_1 = \frac{w_0^2 (2c_2 c_3 k_1 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (4d_1 w_0^4 + 8k_1 w_0^2 + 3k_3) + k_5)}{c_3 k_3 \left(\frac{d_1 w_0^4}{2} + k_1 w_0^2 + k_3 \right) (6d_1 w_0^4 + 12k_1 w_0^2 + 7k_3)} \text{ and } \rho = \frac{2 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}{w_0^3},$$

where w_0, y_0, k_1, k_3 and k_5 are positive real numbers. The equilibrium points are given by

$$P_0 = \left(w_0, \frac{w_0^2}{2}, y_0, \frac{2c_2 c_3 k_1 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (4d_1 w_0^4 + 8k_1 w_0^2 + 3k_3) + k_5}{d_3 k_3 (6d_1 w_0^4 + 12k_1 w_0^2 + 7k_3)} \right),$$

$$P_1 = \left(\frac{k_3 w_0}{4d_1 w_0^4 + 8k_1 w_0^2 + 4k_3}, \frac{k_3 w_0^2}{8 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}, y_0, \frac{k_5}{8d_3 (d_1 w_0^4 + 2k_1 w_0^2 + k_3) (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3)} \right).$$

iii) *Three equilibrium points in Γ if*

$$a_1 = \frac{3 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (4d_1 w_0^4 + 8k_1 w_0^2 + 5k_3) (12d_1 w_0^4 + 24k_1 w_0^2 + 13k_3)}{128w_0 y_0 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)^2},$$

$$a_2 = \frac{d_3 (b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{2k_1}{w_0^2 y_0}, \quad b_1 = \frac{3}{64} w_0^2 \left(\frac{k_3 (16d_1 w_0^4 + 32k_1 w_0^2 + 17k_3)}{(d_1 w_0^4 + 2k_1 w_0^2 + k_3)^2} + 16 \right),$$

$$c_1 = \frac{w_0^2 (4c_2 c_3 k_1 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (8d_1 w_0^4 + 16k_1 w_0^2 + 7k_3) + k_6)}{3c_3 k_3 \left(\frac{d_1 w_0^4}{2} + k_1 w_0^2 + k_3 \right) (4d_1 w_0^4 + 8k_1 w_0^2 + 5k_3)}, \quad c_2 = \frac{c_2 k_1}{y_0},$$

$$R = w_0 (w_0 + 2), \text{ and } \rho = \frac{2 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}{w_0^3},$$

where w_0, y_0, k_1, k_3 , and k_5 are positive real numbers. The equilibrium points are

$$P_0 = \left(w_0, \frac{w_0^2}{2}, y_0, \frac{4c_2 c_3 k_1 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3) (8d_1 w_0^4 + 16k_1 w_0^2 + 7k_3) + k_6}{3d_3 k_3 (4d_1 w_0^4 + 8k_1 w_0^2 + 5k_3)} \right),$$

$$P_1 = \left(\frac{k_3 w_0}{8 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}, \frac{k_3 w_0^2}{16 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}, y_0, \frac{k_6}{32d_3 (d_1 w_0^4 + 2k_1 w_0^2 + k_3) (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3)} \right),$$

$$P_2 = \left(\frac{3k_3 w_0}{8 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}, \frac{3k_3 w_0^2}{16 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)}, y_0, z_2 \right),$$

where

$$z_2 = \frac{3(8c_2 c_3 k_1 k_3^2 + k_6)}{k_3 (d_1 w_0^4 + 2k_1 w_0^2 + k_3)} + \frac{32(k_6 - 9c_2 c_3 k_1 k_3^2)}{k_3 (4d_1 w_0^4 + 8k_1 w_0^2 + 5k_3)} + 192c_2 c_3 k_1 - \frac{11k_6}{k_3 (d_1 w_0^4 + 2k_1 w_0^2 + 2k_3)} > 0.$$

Proof. The proof of i) and ii) is analogous to the given for Lemma 3.1. We only will prove claim iii). In the present case, since all the parameters are positive and the points of interest are in Γ , the equilibrium points for the differential system (1.1) must satisfy the system

$$\begin{aligned} a_1 R y + (b_1 + w^2 + x)(R(v - \rho) + (w + x)\rho) &= 0, \\ -x(d_1 + a_3 y) + w v &= 0, \\ (-a_1 c_1 w + (b_1 + w^2 + x)(d_2 - a_3 c_2 x))(b_2 + y) + a_2 (b_1 + w^2 + x) z &= 0, \\ -a_2 c_3 y + d_3 (b_2 + y) &= 0. \end{aligned} \tag{4.1}$$

Assume that $P_0 = (w_0, x_0, y_0, z_0) \in \Gamma$ is an equilibrium point satisfying system (4.1). Solving first, second, third, and fourth equation in the variables $a_1, a_2, a_3,$ and $c_1,$ respectively, one gets

$$\begin{aligned} a_1 &= -\frac{(b_1 + w_0^2 + x_0)(R(v - \rho) + \rho(w_0 + x_0))}{R y_0}, \quad a_2 = \frac{d_3 (b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{v w_0 - d_1 x_0}{x_0 y_0}, \\ c_1 &= -\frac{R(c_2 c_3 (d_1 x_0 - v w_0) + c_3 d_2 y_0 + d_3 z_0)}{c_3 w_0 (v R + \rho(-R + w_0 + x_0))}. \end{aligned}$$

Taking $v = \frac{d_1 x_0 + k_1}{w_0}, d_2 = \frac{c_2 k_1}{y_0}, R = 2(w_0 + x_0)$ and $\rho = \frac{2d_1 x_0 + 2k_1 + k_2}{w_0},$ where $k_1, k_2 > 0$ we have that

$$a_1 = \frac{k_2 (b_1 + w_0^2 + x_0)}{2w_0 y_0}, \quad a_2 = \frac{d_3 (b_2 + y_0)}{c_3 y_0}, \quad a_3 = \frac{k_1}{x_0 y_0}, \quad c_1 = \frac{2d_3 z_0}{c_3 k_2},$$

and $P_0 \in \Gamma$ is an equilibrium point for the differential system (1.1). Hence under these conditions for the parameters $a_1, a_2, a_3,$ and c_1 the system (4.1) takes the form

$$\begin{aligned} (b_1 + w^2 + x)(k_2(w - 2w_0 + x - 2x_0) + 2k_1(w - w_0 + x - x_0) + 2d_1(w - w_0 + x - x_0)x_0) \\ + (1/y_0)k_2(w_0 + x_0)(b_1 + w_0^2 + x_0)y = 0, \\ -k_1 w_0 x y + x_0(k_1 w - d_1 w_0 x + d_1 w x_0)y_0 = 0, \\ (1/x_0)(b_1 + w^2 + x)(-c_2 c_3 k_1(x - x_0)(b_2 + y) + d_3 x_0(b_2 + y_0)z) - (1/w_0)d_3 w(b_1 + w_0^2 + x_0)(b_2 + y)z_0 = 0, \\ b_2 d_3(-y + y_0) = 0. \end{aligned} \tag{4.2}$$

Assume that $P_1 = (w_1, x_1, y_1, z_1) \in \Gamma \setminus \{P_0\}$ satisfies (4.2). We will give conditions to find expressions for P_1 . Since all the parameters are positive, from fourth equation we have $y_1 = y_0$ and substituting y_1 in the other equations we have that system (4.2) simplifies to

$$\begin{aligned} k_2(w_0 + x_0)(b_1 + w_0^2 + x_0) + (b_1 + w_1^2 + x_1)(k_2(w_1 - 2w_0 + x_1 - 2x_0) \\ + 2k_1(w_1 - w_0 + x_1 - x_0) + 2d_1(w_1 - w_0 + x_1 - x_0)x_0) = 0, \\ w_1 x_0 - w_0 x_1 = 0, \\ -w_0(b_1 + w_1^2 + x_1)(c_2 c_3 k_1(x_1 - x_0) - d_3 x_0 z_1) - d_3 w x_0(b_1 + w_0^2 + x_0)z_0 = 0. \end{aligned} \tag{4.3}$$

From the third equation in (4.3) and solving for z_1 we have an expression in terms of x_1

$$z_1 = \frac{w_1 z_0 (b_1 + w_0^2 + x_0)}{w_0 (b_1 + w_1^2 + x_1)} + \frac{c_2 c_3 k_1 (x_1 - x_0)}{d_3 x_0}. \tag{4.4}$$

Now, from second equation $w_1 = \frac{w_0 x_1}{x_0}$. Substituting w_1 in first equation we have the equation

$$\frac{1}{w_0 x_0^3} (x_1 - x_0)(w_0 + x_0) S_0 = 0, \tag{4.5}$$

where S_0 is a quadratic polynomial in the variable x_1 :

$$S_0 = w_0^2(2k_1 + k_2 + 2d_1 x_0)x_1^2 + x_0(k_2(-w_0^2 + x_0) + 2x_0(k_1 + d_1 x_0))x_1$$

$$+ x_0^2(-k_2(w_0^2 + x_0) + b_1(2k_1 + k_2 + 2d_1x_0)).$$

Suppose that $x_1 \neq x_0$ and let $k_3 > 0$ such that $k_2(-w_0^2 + x_0) + 2x_0(k_1 + d_1x_0) = -k_3$ and $x_0 = \frac{w_0^2}{2}$. Then, $k_2 = 2k_1 + (2k_3)/w_0^2 + d_1w_0^2$ and S_0 simplifies to

$$S_0 = (1/8)(4b_1w_0^2(k_3 + 2k_1w_0^2 + d_1w_0^4) - 3(2k_3w_0^4 + 2k_1w_0^6 + d_1w_0^8)) \\ - (1/2)k_3w_0^2x_1 + 2(k_3 + 2k_1w_0^2 + d_1w_0^4)x_1^2.$$

Let $k_4 > 0$ such that $4b_1w_0^2(k_3 + 2k_1w_0^2 + d_1w_0^4) - 3(2k_3w_0^4 + 2k_1w_0^6 + d_1w_0^8) = k_4$, that is,

$$b_1 = \frac{3d_1w_0^8 + 6k_1w_0^6 + 6k_3w_0^4 + k_4}{4d_1w_0^6 + 8k_1w_0^4 + 4k_3w_0^2}$$

and equation (4.5) becomes the condition

$$S_0 = (k_4/8) - (1/2)k_3w_0^2x_1 + 2(k_3 + 2k_1w_0^2 + d_1w_0^4)x_1^2 = 0.$$

Solving $S_0 = 0$ for x_1 we have two roots which without loss of generality will be labeled as

$$x_{1,2} = \frac{k_4}{2k_3w_0^2 \pm 2\sqrt{w_0^4(k_3^2 - 4d_1k_4) - 8k_1k_4w_0^2 - 4k_3k_4}}.$$

Let $k_5 > 0$ such that $w_0^4(k_3^2 - 4d_1k_4) - 8k_1k_4w_0^2 - 4k_3k_4 = k_5^2$. Taking $k_5 = k_3w_0^2/2$ we have $k_4 = \frac{3k_3^2w_0^4}{16(d_1w_0^4 + 2k_1w_0^2 + k_3)}$ and

$$x_1 = \frac{k_3w_0^2}{16(d_1w_0^4 + 2k_1w_0^2 + k_3)}, \quad x_2 = \frac{3k_3w_0^2}{16(d_1w_0^4 + 2k_1w_0^2 + k_3)}.$$

Since $w_1 = \frac{w_0x_1}{x_0}$, we have that w_1 takes two values at $x_{1,2}$ given by $w_1 = \frac{k_3w_0}{8(d_1w_0^4 + 2k_1w_0^2 + k_3)}$ and $w_2 = \frac{3k_3w_0}{8(d_1w_0^4 + 2k_1w_0^2 + k_3)}$.

On the other hand, from (4.4) we have two values for z_1 given by

$$z_1 = \frac{3d_3k_3z_0(4d_1w_0^4 + 8k_1w_0^2 + 5k_3) - 4c_2c_3k_1(d_1w_0^4 + 2k_1w_0^2 + 2k_3)(8d_1w_0^4 + 16k_1w_0^2 + 7k_3)}{32d_3(d_1w_0^4 + 2k_1w_0^2 + k_3)(d_1w_0^4 + 2k_1w_0^2 + 2k_3)}, \\ z_2 = \frac{3d_3k_3z_0(12d_1w_0^4 + 24k_1w_0^2 + 13k_3) - 4c_2c_3k_1(d_1w_0^4 + 2k_1w_0^2 + 2k_3)(8d_1w_0^4 + 16k_1w_0^2 + 5k_3)}{32d_3(d_1w_0^4 + 2k_1w_0^2 + k_3)(d_1w_0^4 + 2k_1w_0^2 + 2k_3)}.$$

Since z_1 must be positive, let $k_6 > 0$ such that

$$3d_3k_3z_0(4d_1w_0^4 + 8k_1w_0^2 + 5k_3) - 4c_2c_3k_1(d_1w_0^4 + 2k_1w_0^2 + 2k_3)(8d_1w_0^4 + 16k_1w_0^2 + 7k_3) = k_6$$

and hence solving this equation for z_0 we have

$$z_0 = \frac{4c_2c_3k_1(d_1w_0^4 + 2k_1w_0^2 + 2k_3)(8d_1w_0^4 + 16k_1w_0^2 + 7k_3) + k_6}{3d_3k_3(4d_1w_0^4 + 8k_1w_0^2 + 5k_3)}.$$

Since $y_1 = y_0$ we have obtained two points $P_1, P_2 \in \Gamma \setminus \{P_0\}$ that are equilibrium points for system (1.1) and hence P_0, P_1 and P_2 satisfy the conditions as in claim iii) which completes the proof. \square

4.1. Dynamics of one equilibrium point

In this case we will consider that the hypothesis in Lemma 4.1 i) are valid. And that the linear approximation of the differential system (1.1) at P_0 is a one parameter matrix with respect to d_3 , which we denote as $M_0(d_3)$. We will guarantee that a Hopf bifurcation takes place.

Lemma 4.2. *If the hypothesis of Lemma 4.1 i) are satisfied and*

$$\begin{aligned} a_1 &= \frac{(m+7)v}{4b_2}, \quad a_2 = \frac{2d_3}{c_3}, \quad a_3 = \frac{v}{2b_2}, \quad b_1 = 2, \quad c_1 = b_2, \quad c_2 = \frac{b_2}{2}, \\ d_1 &= \frac{v}{2}, \quad d_2 = \frac{1}{16}(m+7)v, \quad R = \frac{32}{m+7} + 4, \quad \rho = \frac{m+15}{8}, \quad \text{and} \\ d_{31} &= \frac{(m+7) \left(29m + 7 \left(\sqrt{m(25m-354) + 4489} - 67 \right) \right) v}{1024}, \end{aligned}$$

where $m > 0$, then the eigenvalues of the linear approximation $M_0(d_{31})$ of system (1.1) at P_0 are

$$\lambda_{1,2} = \pm i\sqrt{\mathcal{R}_0}v \quad \text{and} \quad \lambda_{3,4} = -\frac{1}{128} \left(\pm\sqrt{2}\sqrt{\mathcal{R}_1} + 56 \right) v,$$

where

$$\begin{aligned} \mathcal{R}_0 &= \frac{(m+7) \left(5m + \sqrt{m(25m-354) + 4489} - 45 \right)}{1024} > 0, \\ \mathcal{R}_1 &= 7 \left(\sqrt{m(25m-354) + 4489} + 157 \right) + m \left(-5m + \sqrt{m(25m-354) + 4489} - 102 \right). \end{aligned}$$

We have that

$$\mathcal{R}_1 > 0 \text{ if } m < m_0 := 14.7403; \quad \mathcal{R}_1 = 0 \text{ if } m = m_0; \quad \text{and} \quad \mathcal{R}_1 < 0 \text{ if } m > m_0.$$

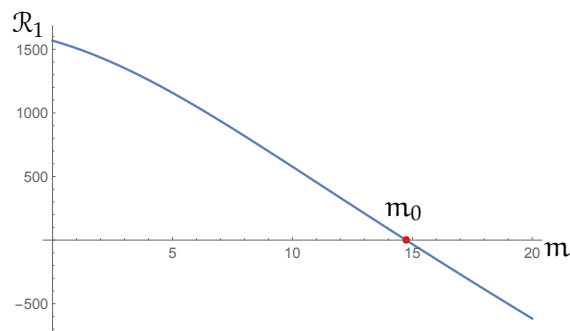


Figure 2: Graphic of $\mathcal{R}_1(m)$.

Proof. We assume the hypothesis as in Lemma 4.1 i) are valid. In this occasion we set $a_3 = \frac{d_1 k_1}{b_2 d_3}$, $k_4 = k_1^2 v^2$, $d_1 = \frac{v}{2}$ and $k_1 = d_3$. Then we have that the linear approximation $M_0(d_3)$ has characteristic polynomial

$$\text{pol}_0(\lambda, d_3) = \lambda^4 + A_{10}\lambda^3 + A_{20}\lambda^2 + A_{30}\lambda + A_{40},$$

where

$$\begin{aligned} A_{10} &= v - \frac{c_2 v}{4b_2}, \quad A_{20} = \frac{a_1^2 b_2^2 c_1 + a_1 b_2 v(2b_2 - c_1) + 8c_2 d_3 v}{32b_2}, \\ A_{30} &= \frac{v(3a_1^2 b_2^2 c_1 + 28a_1 b_2 c_2 v + 64c_2 d_3 v)}{256b_2} \quad \text{and} \quad A_{40} = \frac{1}{64} a_1 c_2 d_3 v^2. \end{aligned}$$

In this case, we have that (2.1) is $\mathbf{EQ} = \frac{v^2 F_0}{65536b_2^3}$, where

$$\begin{aligned} F_0 &= b_2(3a_1^2 b_2^2 c_1 + 28a_1 b_2 c_2 v + 64c_2 d_3 v)^2 - 2(4b_2 - c_2) \times (a_1^2 b_2^2 c_1 + a_1 b_2 v(2b_2 - c_1) + 8c_2 d_3 v) \\ &\quad \times (3a_1^2 b_2^2 c_1 + 28a_1 b_2 c_2 v + 64c_2 d_3 v) + 64a_1 b_2 c_2 d_3 v^2 (c_2 - 4b_2)^2. \end{aligned}$$

Make $c_2 = \frac{b_2}{2}$, $c_1 = b_2$, $a_1 = \frac{k_5+7\nu}{4b_2}$, and $k_5 = m\nu$, where m is a positive real number. Then, we have that $\text{EQ}(d_{31}) = 0$, where

$$d_{31} = \frac{(m + 7) \left(29m + 7 \left(\sqrt{m(25m - 354) + 4489} - 67 \right) \right) \nu}{1024} > 0$$

and all the coefficients of $\text{pol}_0(\lambda, d_{31})$ are positive. The roots of the characteristic polynomial are obtained from Lemma 2.1 (ii) and a direct calculation shows that \mathcal{R}_1 satisfies the claimed properties (see Fig. 2). \square

Lemma 4.3. *If the hypothesis of Lemma 4.2 are satisfied and $m = \frac{354}{25}$, then the first Lyapunov coefficient for the system (1.1) at P_0 is negative. Moreover, the transversality condition holds: $\frac{\partial \text{Re}(\lambda_{1,2})}{\partial d_3}(d_{31}) \neq 0$.*

Proof. Under the hypothesis of Lemma 4.2 if $m = \frac{354}{25}$, we have that

$$\frac{\partial \text{Re}(\lambda_{1,2})}{\partial d_3}(d_{31}) = \frac{10720000}{2218824689} \neq 0$$

and that the first Lyapunov coefficient is $\ell_1(P_0) = -\frac{N_0}{N_1} < 0$, where

$$N_0 = 18789363664718319688470457812986851 \sqrt{\frac{29}{5}},$$

$$N_1 = 9534260680917181346060000(18351686591 + 766720b_2^2(15341 + 125c_3^2)).$$

\square

Next theorem follows from Lemma 4.3 and the Andronov-Hopf Theorem.

Theorem 4.4 (f_1 Holling IV, one equilibrium point). *Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 4.3. Then, the system exhibits a supercritical Hopf bifurcation at P_0 with respect to the parameter d_3 and its bifurcation value is d_{31} .*

4.2. Dynamics of two equilibrium points

If the hypothesis of Lemma 4.1 ii) hold and $k_1 = d_1w_0^2$ and $k_3 = d_1w_0^4$, then a direct calculation shows that the linear approximation for the system (1.1) at P_1 has a characteristic polynomial with constant term equals to zero. Hence, from the Routh-Hurwitz test we have that in these conditions P_1 is locally unstable.

Now, we will consider the linear approximation of system (1.1) at P_0 as a one parameter matrix with respect to b_2 , which we denote as $M_0(b_2)$.

Lemma 4.5. *If the hypothesis of Lemma 4.1 ii) are satisfied and*

$$\begin{aligned} a_1 &= \frac{92015625d_3}{246208y_0}, & a_2 &= \frac{d_3(b_2 + y_0)}{c_3y_0}, & a_3 &= \frac{58890d_3}{3847y_0}, & b_1 &= \frac{241}{64}, \\ c_1 &= \frac{351(b_2 + y_0)}{2500}, & c_2 &= \frac{351(b_2 + y_0)}{6040}, & d_1 &= \frac{29445d_3}{3847}, & d_2 &= \frac{13689d_3(b_2 + y_0)}{7694y_0}, \\ R &= 8, & \rho &= \frac{471120d_3}{3847}, & b_{20} &= \frac{95480385736y_0}{16391886457}, \end{aligned}$$

then the eigenvalues of the linear approximation $M_0(b_{20})$ of system (1.1) at P_0 are

$$\lambda_{1,2} = \pm i 353340 \sqrt{\frac{21305}{63059587200079}} d_3 \text{ and } \lambda_{3,4} = -\frac{117 \left(94375 \mp i \sqrt{194109621935} \right) d_3}{1923500}.$$

Proof. Suppose that the parameters of the system (1.1) satisfy the hypothesis as in Lemma 4.1 ii). As was made in the other cases, setting $k_1 = d_1w_0^2$ and $k_3 = d_1w_0^4$, the linear approximation $M_0(b_2)$ has

characteristic polynomial $\text{pol}_0(\lambda, b_2) = \lambda^4 + B_1\lambda^3 + B_2\lambda^2 + B_3\lambda + B_4$, such that

$$B_1 = \frac{1}{125}d_1 \left(-\frac{755c_2w_0^2}{b_2 + y_0} - 256w_0 + \frac{125(11w_0 + 6)}{w_0 + 2} \right), \quad B_2 = \frac{d_1w_0(\mathcal{K}_0)}{31250(w_0 + 2)y_0(b_2 + y_0)},$$

$$B_3 = -\frac{c_2d_1^2w_0^2(\mathcal{K}_1)}{15625(w_0 + 2)y_0(b_2 + y_0)}, \quad B_4 = \frac{16308b_2c_2d_1^3d_3w_0^3}{625y_0(b_2 + y_0)},$$

where

$$\mathcal{K}_0 = b_2(w_0 + 2)(c_2w_0(85315d_1w_0 - 14812d_1 + 188750d_3) + 135000d_1y_0) + d_1y_0(c_2w_0(w_0(471875w_0 - 1147312) - 1162124) + 135000(w_0 + 2)y_0),$$

$$\mathcal{K}_1 = b_2(16d_1w_0(229w_0 - 12902) + 755d_3(w_0(256w_0 - 863) - 750)) + 4d_1w_0(102841w_0 + 152242)y_0.$$

Setting $w_0 = 2$, $c_2 = \frac{351(b_2 + y_0)}{6040}$ and $d_1 = \frac{29445d_3}{3847}$, we have that (2.1) is

$$\mathbf{EQ} = \frac{1092211792881596337270411d_3^6(95480385736y_0 - 16391886457b_2)}{2532346607490523417913281250y_0}.$$

Moreover, all the coefficients of $\text{pol}_0(\lambda, b_{20})$ are positive and $\mathbf{EQ}(b_{20}) = 0$, where $b_{20} = \frac{95480385736y_0}{16391886457}$. Therefore, the proof is concluded using Lemma 2.1 ii). □

Lemma 4.6. *If the hypothesis of Lemma 4.5 are satisfied, then the first Lyapunov coefficient $\ell_1(P_0, b_{20})$ for the system (1.1) at P_0 is negative. Moreover, the transversality condition holds: $\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{20}) \neq 0$.*

Proof. Under the hypothesis of Lemma 4.5 we have that

$$\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{20}) = -\frac{11801569339356166931213599722872813535d_3}{19478350806921655804860578959172649472y_0} \neq 0$$

and that the first Lyapunov coefficient is $\ell_1(P_0, b_{20}) = -\frac{\mathcal{M}_0}{\mathcal{M}_1} < 0$, where

$$\mathcal{M}_0 = 217676423201567543587668555270113809421753406988141195772466$$

$$9764374472301079117588144055366058034338623801083047117711125\sqrt{\frac{315297936000395}{4261}},$$

$$\mathcal{M}_1 = 607150697028745575459137144567343632577578601721847016911101682580953931726107867136$$

$$\times (2409398303445653547654 (457623738857453785461c_3^2 + 4926530250006171875) y_0^2$$

$$+ 222238726372030874554317307928114420046875).$$

□

Next theorem follows from Lemma 4.6 and the Andronov-Hopf Theorem.

Theorem 4.7 (f_1 Holling IV, two equilibrium points). *Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 4.6. Then, the system exhibits a supercritical Hopf bifurcation at P_0 with respect to the parameter b_2 and its bifurcation value is b_{20} .*

4.3. Dynamics of three equilibrium points

If the hypothesis of Lemma 4.1 iii) hold and $k_1 = d_1w_0^2$ and $k_3 = d_1w_0^4$, then a direct calculation shows that the linear approximation for the system (1.1) at P_2 has a characteristic polynomial with a negative constant term. Hence, from Routh-Hurwitz test we have that under these conditions the equilibrium point P_2 is locally unstable.

This time we will consider the linear approximations of system (1.1) at P_0 and P_1 as one parameter matrices with respect to b_2 , which we denote as $M_0(b_2)$ and $M_1(b_2)$, respectively.

Lemma 4.8. Assume that the hypothesis of Lemma 4.1 iii) are satisfied.

a) If

$$\begin{aligned} a_1 &= \frac{819909405d_3}{45928192y_0}, \quad a_2 = \frac{d_3(b_2 + y_0)}{c_3y_0}, \quad a_3 = \frac{65619d_3}{717628y_0}, \quad b_1 = \frac{963}{64}, \quad c_1 = \frac{317(b_2 + y_0)}{333200}, \\ c_2 &= \frac{317(b_2 + y_0)}{1622880}, \quad d_1 = \frac{65619d_3}{1435256}, \quad d_2 = \frac{100489d_3(b_2 + y_0)}{703275440y_0}, \quad R = 24, \quad \rho = \frac{262476d_3}{179407}, \text{ and} \\ b_{20} &= \frac{13416348622408722y_0}{582645121928723}, \end{aligned}$$

then P_1 is locally stable and the eigenvalues of the linear approximation $M_0(b_{20})$ of system (1.1) at P_0 are

$$\lambda_{1,2} = \pm i 393714 \sqrt{\frac{19316813}{104530613389866407261}} d_3 \text{ and } \lambda_{3,4} = -\frac{951 \left(57477 \mp i \sqrt{31910155004111} \right) d_3}{23911364960}.$$

b) If

$$\begin{aligned} a_1 &= \frac{326483386887d_3}{29814521554138240y_0}, \quad a_2 = \frac{d_3(b_2 + y_0)}{c_3y_0}, \quad a_3 = \frac{7617820000d_3}{46585189928341y_0}, \quad b_1 = \frac{47187}{640000}, \\ c_1 &= \frac{5441300(b_2 + y_0)}{332367}, \quad c_2 = \frac{13603250(b_2 + y_0)}{4047057}, \quad d_1 = \frac{3808910000d_3}{46585189928341}, \quad d_2 = \frac{11843098276000d_3(b_2 + y_0)}{549658655964495459y_0}, \\ R &= \frac{399}{625}, \quad \rho = \frac{8531958400d_3}{46585189928341}, \text{ and } b_{21} = \frac{1283288513820972429108420117140000y_0}{1003762066972593392736885855153}, \end{aligned}$$

then P_0 is locally unstable and the eigenvalues of the linear approximation $M_1(b_{21})$ of system (1.1) at P_1 are

$$\begin{aligned} \lambda_{1,2} &= \pm i 761782000 \sqrt{\frac{1473121548605}{18186082630409313413515160609495761}} d_3, \\ \lambda_{3,4} &= -\frac{272065 \left(+210492409575823459 \mp \sqrt{44189378141813568890621430192477481} \right) d_3}{462833171939453734903948632}. \end{aligned}$$

Proof. Suppose that the parameters of the system (1.1) satisfy the hypothesis as in Lemma 4.1 iii). To simplify the calculations set $k_1 = d_1 w_0^2$ and $k_3 = d_1 w_0^4$.

We prove claim a).

The linear approximation $M_0(b_2)$ has characteristic polynomial $\text{pol}_0(\lambda, b_2) = \lambda^4 + B_{01}\lambda^3 + B_{02}\lambda^2 + B_{03}\lambda + B_{04}$, such that

$$\begin{aligned} B_{01} &= d_1 \left(-\frac{5120w_0}{2499} - \frac{16}{w_0 + 2} + 11 \right) - \frac{620c_2c_3d_1^3w_0^{10} + k_6}{51c_3d_1^2w_0^8(b_2 + y_0)}, \quad B_{02} = \frac{S_0}{254898c_3d_1^2w_0^8(w_0 + 2)y_0(b_2 + y_0)}, \\ B_{03} &= \frac{S_1}{254898c_3d_1w_0^8(w_0 + 2)y_0(b_2 + y_0)}, \quad B_{04} = \frac{3596b_2d_3(620c_2c_3d_1^3w_0^{10} + k_6)}{42483c_3w_0^7y_0(b_2 + y_0)}, \end{aligned}$$

where

$$\begin{aligned} S_0 &= b_2(w_0 + 2) \left(4c_3d_1^4w_0^9(c_2w_0(349525w_0 - 189991) + 275094y_0) + 3098760c_2c_3d_1^3d_3w_0^{10} + d_1k_6(2255w_0 - 2048) + 4998d_3k_6 \right) \\ &\quad + d_1y_0 \left(4c_3d_1^3w_0^9(c_2w_0(w_0(1936725w_0 - 4838131) - 5028122) + 275094(w_0 + 2)y_0) + k_6(w_0(12495w_0 - 32036) - 34084) \right), \\ S_1 &= b_2 \left(-2d_3(w_0(5120w_0 - 17249) - 14994) \left(620c_2c_3d_1^3w_0^{10} + k_6 \right) \right. \\ &\quad \left. - d_1w_0 \left(c_2c_3d_1^3(999565w_0 - 868998)w_0^{10} + k_6(3011w_0 + 7974) \right) \right) \\ &\quad - d_1w_0y_0 \left(c_2c_3d_1^3(14376685w_0 + 25885242)w_0^{10} + k_6(24587w_0 + 51126) \right). \end{aligned}$$

Setting $k_6 = c_2c_3d_1^3w_0^{10}$, $w_0 = 4$, $k_7 = \frac{1}{10}$, $c_2 = \frac{317(b_2+y_0)}{1622880}$, and $d_1 = \frac{65619d_3}{1435256}$, it follows that (2.1) for P_0 becomes

$$EQ_{P_0} = \frac{590603773376433329361449973d_3^6(13416348622408722y_0 - 582645121928723b_2)}{526097508598209708322692022112329253539418243072000y_0}.$$

Moreover, all the coefficients of $\text{pol}_0(\lambda, b_{20})$ are positive and $\mathbf{EQ}_{P_0}(b_{20}) = 0$, where $b_{20} = \frac{13416348622408722y_0}{582645121928723}$. Therefore, the proof of the claim for P_0 is concluded using Lemma 2.1 (ii). Now, we prove the claim for P_1 . Under these assignments as above a calculation shows that the characteristic polynomial $\text{pol}_1(\lambda)$ of $M_1(b_2)$ has positive coefficients and that (2.1) for P_1 is

$$\mathbf{EQ}_{P_1} = -\frac{22195448555703486537d_3^6 J_0}{36987799937559506249199370394982860028164827198259200000000y_0^2} < 0,$$

where

$$J_0 = 17776155316167905958812163517b_2^2 + 1095685583423619310437058086372b_2y_0 + 1077907578968001990869491705056y_0^2.$$

Hence, from Lemma 2.1 (i) P_1 is locally asymptotically stable.

We now prove claim b).

The linear approximation $M_1(b_2)$ has characteristic polynomial $\text{pol}_1(\lambda, b_2) = \lambda^4 + B_{11}\lambda^3 + B_{12}\lambda^2 + B_{13}\lambda + B_{14}$, such that

$$B_{11} = d_1 \left(-\frac{51w_0}{3920} - \frac{1}{2(w_0 + 2)} + \frac{13}{4} \right) - \frac{k_6}{640c_3d_1^2w_0^8(b_2 + y_0)}, \quad B_{12} = \frac{D_0}{2508800c_3d_1^2w_0^8(w_0 + 2)y_0(b_2 + y_0)},$$

$$B_{13} = \frac{D_1}{2508800c_3d_1w_0^8(w_0 + 2)y_0(b_2 + y_0)}, \quad \text{and} \quad B_{14} = \frac{93b_2d_3k_6}{2508800c_3w_0^7y_0(b_2 + y_0)},$$

where

$$D_0 = b_2(w_0 + 2)(20c_3d_1^4w_0^9(c_2w_0(773109w_0 + 3872) + 2976y_0) + d_1k_6(24939w_0 - 128) + 3920d_3k_6) + 2d_1y_0(10c_3d_1^3(w_0 + 2)w_0^9(c_2w_0(773109w_0 + 3872) + 2976y_0) + k_6(w_0(12495w_0 + 18556) - 11888)),$$

$$D_1 = b_2(d_1w_0(20c_2c_3d_1^3(2351229w_0 + 4764062)w_0^{10} + k_6(73431w_0 + 148786)) + d_3k_6(w_0(12638 - 51w_0) + 23520)) + 2d_1w_0y_0(10c_2c_3d_1^3(2351229w_0 + 4764062)w_0^{10} + k_6(36669w_0 + 74300)).$$

Setting $k_6 = c_2c_3d_1^3w_0^{10}$, $w_0 = \frac{28}{100}$, $k_7 = \frac{2}{10}$, $c_2 = \frac{13603250(b_2 + y_0)}{4047057}$ and $d_1 = \frac{3808910000d_3}{46585189928341}$, we have that equation (2.1) is

$$\mathbf{EQ}_{P_1} = \frac{D_1}{91868984290256955917703199862023417243228416635468310974676089991421968882194679209837255865548448y_0},$$

$$D_1 = 551669191500464941759890880349889453125d_3^6(1003762066972593392736885855153b_2 - 1283288513820972429108420117140000y_0).$$

Moreover, all the coefficients of $\text{pol}_1(\lambda, b_{21})$ are positive and $\mathbf{EQ}_{P_1}(b_{21}) = 0$, where

$$b_{21} = \frac{1283288513820972429108420117140000y_0}{1003762066972593392736885855153}.$$

Therefore, the proof is concluded by using Lemma 2.1 ii). Finally, under these parameter conditions a calculation shows that the characteristic polynomial $\text{pol}_0(\lambda, b_{21})$ has positive coefficients and $\mathbf{EQ}_{P_0}(b_{21}) > 0$. Hence claim for P_0 follows from Lemma 2.1 i). □

Lemma 4.9.

- i) If the hypothesis of Lemma 4.8 a) are satisfied, then the first Lyapunov coefficient $\ell_1(P_0, b_{20})$ for the system (1.1) at P_0 is negative. Moreover, the transversality condition holds: $\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{20}) \neq 0$.
- ii) If the hypothesis of Lemma 4.8 b) are satisfied, then the first Lyapunov coefficient $\ell_1(P_1, b_{21})$ for the system (1.1) at P_1 is negative. Moreover, the transversality condition holds: $\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{21}) \neq 0$.

Proof. Proof of claim i): Under the hypothesis of Lemma 4.8 a) we have that

$$\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{20}) = -\frac{83966322790024614390702183754882228526848866556509d_3}{560365662081392491481014219333781446381362348589949294y_0} \neq 0$$

and that the first Lyapunov coefficient is $\ell_1(P_0, b_{20}) = -\frac{\mathcal{H}_0}{\mathcal{H}_1} < 0$, where

$$\begin{aligned} \mathcal{H}_0 &= 65108103224918914363893060962780\sqrt{(58833390947229894479548164019310703020583084463339583499808327} \\ &\quad 7521455881344535933813014375028123233745774466401515794984655051823072} \\ &\quad 9424619846403866903862305677316411299296215210484026129430957410007553} \\ &\quad 2702430128458655852906518055999193476399240810745150112683711440889205} \\ &\quad 645543737105859057067802577242101/19316813), \\ \mathcal{H}_1 &= 135750239588722107527224073922273432429534300327621012960131383507859631752974912752548439494} \\ &\quad 1032826238376353233980675799(149014220778833149749810123716943909346072211821852591354202912} \\ &\quad + 70372176667364736659077623(417323813582325947581870707654400 + 23383467340027183581879286644543c_3^2)y_0^2). \end{aligned}$$

Proof of claim ii): Under the hypothesis of Lemma 4.8 b) we have that $\frac{\partial \text{Re}(\lambda_{1,2})}{\partial b_2}(b_{21}) = \frac{\mathcal{J}_0}{\mathcal{J}_1} \neq 0$, where

$$\begin{aligned} \mathcal{J}_0 &= 47671642942992449797220740874336686735021383216432164461984587938993170270841661065492697 d_3, \\ \mathcal{J}_1 &= 8660650070812536285392147610785201852358859609440080367793759296208919851350789498468218223447310664565380 y_0, \end{aligned}$$

and that the first Lyapunov coefficient is $\ell_1(P_1, b_{21}) = -\frac{\mathcal{L}_0}{\mathcal{L}_1} < 0$, where

$$\begin{aligned} \mathcal{L}_0 &= 6503722355183270578986766038515916230112374732311207160516265784528904} \\ &\quad 3153320886782792177614429546205729992837090314159291751234486162303263} \\ &\quad 4656439013516076244599512292579159910216834713481092680382200019744055} \\ &\quad 7432486287623580845946403420610582397043771383526920963463168628907547} \\ &\quad 106947691435788481666011312625306834124000000} \\ &\quad \times \sqrt{(636512892064325969473030621332351635/42089187103)}, \\ \mathcal{L}_1 &= 1238643346392328912044675932710950343631164158700044380545912113846936} \\ &\quad 0791269184611969358195576410247489562144022760515809253707052505638169} \\ &\quad 7947297683537158372905436825837200512339727096499853148746706661906624} \\ &\quad 7656923(4345553384671872346235422851807062198737763810095857262301925} \\ &\quad 1110349971499132513730659984821588845514436143324311469} \\ &\quad + 84144203552867157412129081289671638443958865502261810000000} \\ &\quad \times (14528750538623337057293427186537423079390182027665096772538931652} \\ &\quad + 572583807522980563175352059472333142429712816870609580978125 c_3^2)y_0^2). \end{aligned}$$

□

Next theorem follows from Lemma 4.9 and the Andronov-Hopf Theorem.

Theorem 4.10 (f_1 Holling IV, three equilibrium points).

- i) Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 4.8 a). Then, P_1 is locally stable and the system exhibits a supercritical Hopf bifurcation at P_0 with respect to the parameter b_2 and its bifurcation value is b_{20} .
- ii) Assume that the parameters of system (1.1) satisfy the hypothesis of Lemma 4.8 b). Then, P_0 is locally unstable and the system exhibits a supercritical Hopf bifurcation at P_1 with respect to the parameter b_2 and its bifurcation value is b_{21} .

5. Numerical examples

In all cases, the coexistence of the three species takes place due to the existence of a supercritical Hopf bifurcation with respect to the corresponding parameters. A direct calculation shows that the hypothesis of the proved theorems for the differential system (1.1) are valid for parameters values with ecological sense, we show this in the following numerical examples.

5.1. f_1 Holling II

In the following two examples the functional response f_1 in the system (1.1) is Holling type II.

Example 5.1. From the hypothesis in Theorem 3.4 the differential system (1.1) takes the form

$$\begin{aligned} \dot{w} &= \frac{1}{37}vw \left(-\frac{37y}{b_2(w+x+1)} - 2w - 2x + 37 \right), & \dot{x} &= v \left(x \left(-\frac{3y}{b_2} - 2 \right) + w \right), \\ \dot{y} &= y \left(\frac{v \left(\frac{8214w}{w+x+1} + 3555x - 6475 \right)}{11850b_2} - \frac{40z}{b_2+y} \right), & \dot{z} &= \frac{10z(y-b_2)}{b_2+y}. \end{aligned}$$

Therefore, the equilibrium point is $P_0 = \left(\frac{175}{12}, \frac{35}{12}, b_2, \frac{7v}{160} \right)$ and $b_{20} = \frac{1}{10} \left(\frac{28749}{37756} + \frac{139915489455}{8389718423v} \right)$. Taking $v = 110$ we have that $b_{20} \approx 0.0913051$ and P_0 is $(14.5833, 2.91667, b_2, 4.8125)$. The first Lyapunov coefficient is $\ell_1(P_0, b_{20}) \approx -0.00118615$. Hence the system exhibits a supercritical Hopf bifurcation at P_0 with respect to b_2 . Setting $b_2 = b_{20} - 10^{-3} \approx 0.0903051$, we have in Figure 3 a projection to the (x, y, z) space of an orbit with initial condition $Q_0 = (14.5933, 2.92667, 0.100305, 4.8225)$ which tends to the stable limit cycle. Figure 4 shows the corresponding time series.

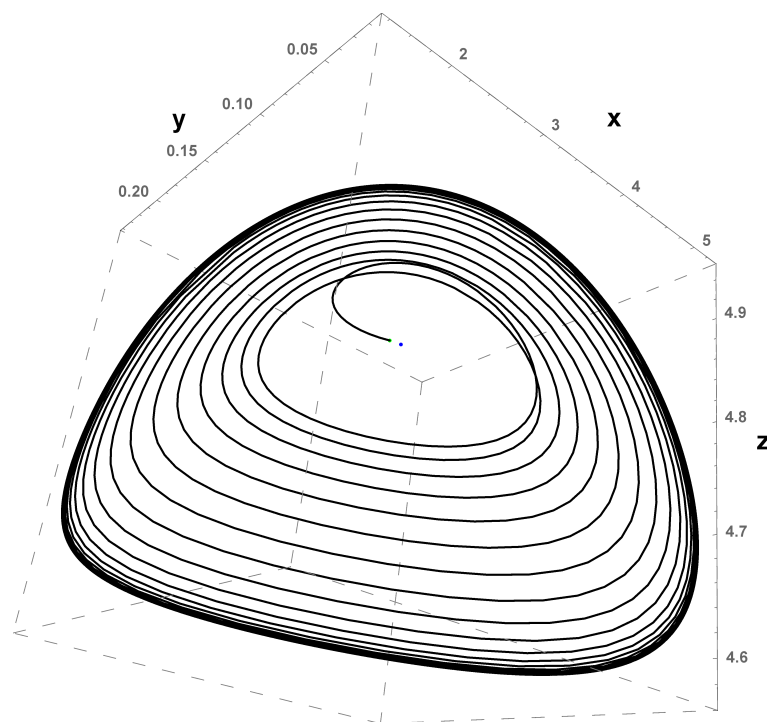


Figure 3: Projection of limit cycle (one equilibrium, f_1 Holling II).

Remark 5.2. The bifurcation parameter value b_{20} depends directly on v and is bounded below. Near the bifurcation value, the third coordinate of P_0 (predator density) is approximately b_{20} . The fourth coordinate of P_0 (superpredator density) is directly proportional to v .

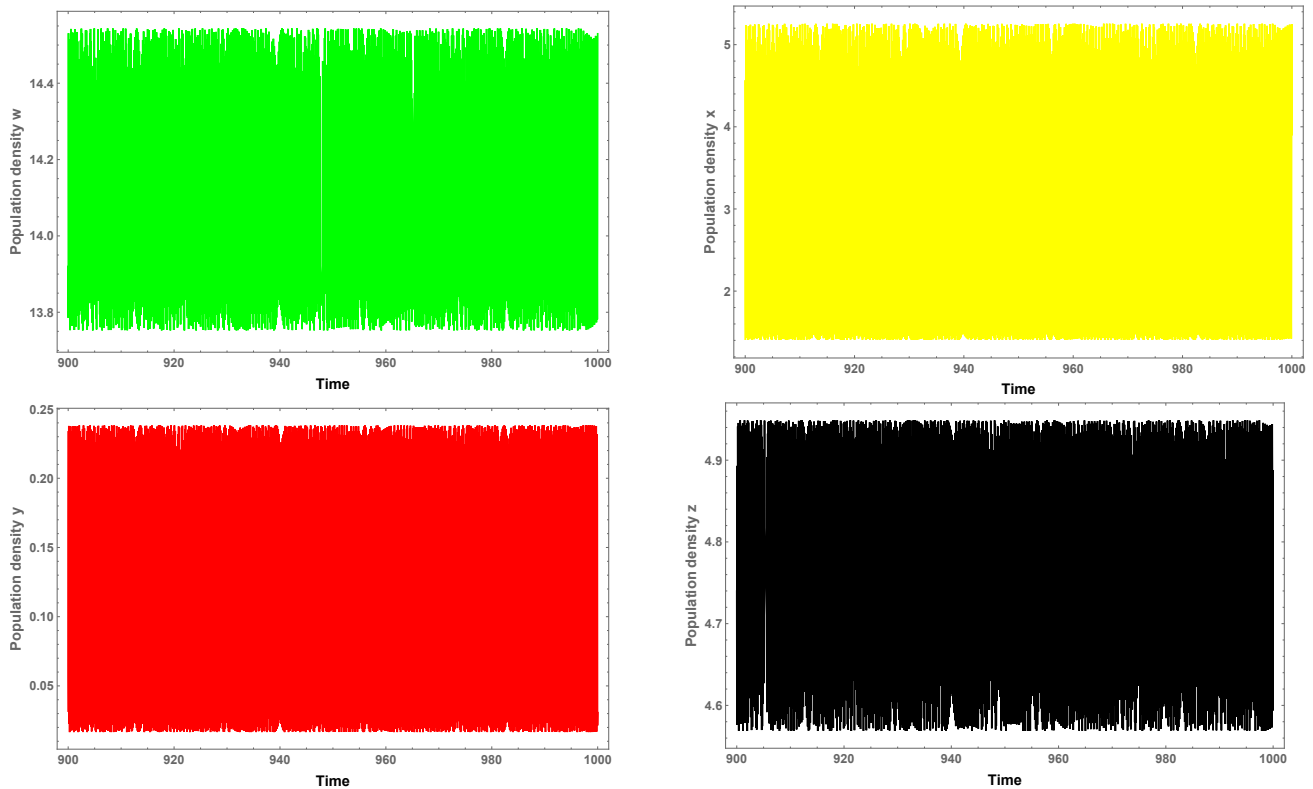


Figure 4: Time series (One equilibrium, f_1 Holling II).

Example 5.3. From the hypothesis in Theorem 3.7 the differential system (1.1) takes the form

$$\begin{aligned} \dot{w} &= \frac{365d_3w}{1131} \left(-\frac{1560w_0y}{13wy_0 + 4w_0y_0 + 13xy_0} - \frac{169(w+x)}{2w_0} + 221 \right), \\ \dot{x} &= \frac{365d_3(9wy_0 - x(y + 8y_0))}{87y_0}, \\ \dot{y} &= \frac{d_3y}{3828} \left(\frac{133225(44b_2w + y_0(31w - 4w_0 - 13x))}{(13w + 4w_0 + 13x)y_0} - \frac{3828z(b_2 + y_0)}{y_0c_3(b_2 + y)} + \frac{133225x}{w_0} \right), \\ \dot{z} &= \frac{b_2d_3z(y - y_0)}{y_0(b_2 + y)}. \end{aligned}$$

Therefore, $b_{20} = \frac{2361971095625y_0}{131632971184}$,

$$P_0 = \left(w_0, w_0, y_0, \frac{26645}{522}c_3(b_2 + y_0) \right) \text{ and } P_1 = \left(\frac{2w_0}{13}, \frac{2w_0}{13}, y_0, \frac{133225b_2c_3}{4524} \right).$$

Taking $c_3 = \frac{1}{2}$, $d_3 = 1$, $w_0 = 58$ and $y_0 = 1$ we have that $b_{20} \approx 17.9436$ and the first Lyapunov coefficient at P_0 is $\ell_1(P_0, b_{20}) \approx -0.0000736782$. Hence the system exhibits a supercritical Hopf bifurcation at P_0 with respect to b_2 . Setting $b_2 = b_{20} - 10^{-1} \approx 17.8436$, we have in Figure 5 a projection to the (x, y, z) space of an orbit with initial condition $Q_0 = (58.01, 58.01, 1.01, 480.937)$ which tends to the stable limit cycle. Figure 6 shows the corresponding time series.

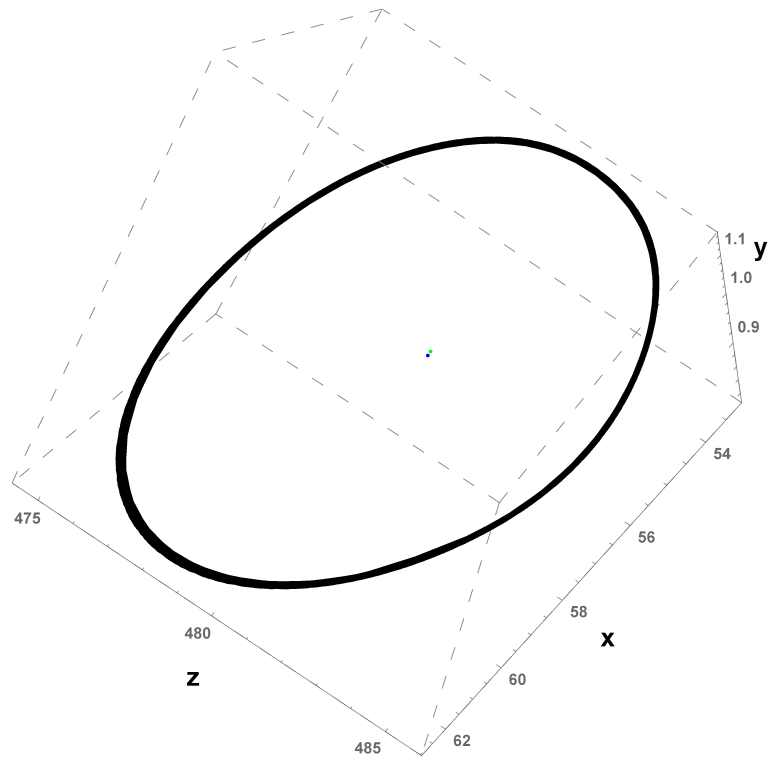


Figure 5: Projection of limit cycle with respect to P_0 (two equilibria, f_1 Holling II).

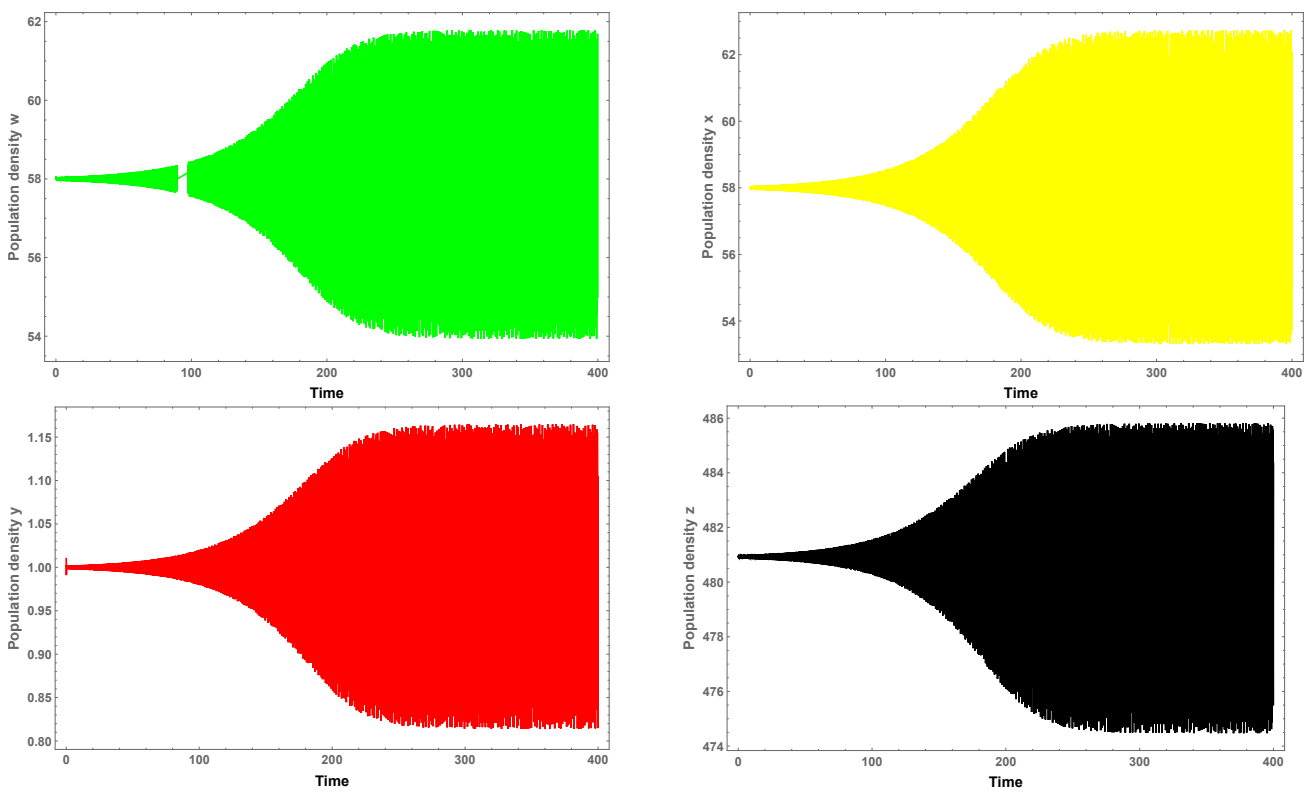


Figure 6: Time series with respect to P_0 (two equilibria, f_1 Holling II).

Remark 5.4. When the system (1.1) has two equilibrium points and the parameter b_2 is near to the bifurcation value b_{20} , the third and fourth coordinates of P_0 are directly proportional to y_0 .

5.2. f_1 Holling IV

In the following three examples the functional response f_1 in the system (1.1) is Holling type IV.

Example 5.5. From the hypothesis in Theorem 4.4 the differential system (1.1) takes the form

$$\begin{aligned} \dot{w} &= \frac{529}{800}vw \left(-\frac{8y}{b_2(w^2 + x + 2)} - w - x + 4 \right), & \dot{x} &= \frac{1}{2}v \left(2w - \frac{x(b_2 + y)}{b_2} \right), \\ \dot{y} &= \frac{1}{400}y \left(v \left(529 \left(\frac{4w}{w^2 + x + 2} - 1 \right) + 100x \right) - \frac{800d_3z}{c_3(b_2 + y)} \right), & \dot{z} &= \frac{d_3z(y - b_2)}{b_2 + y}. \end{aligned}$$

Therefore, if $v = 110$, $b_2 = \frac{1}{2}$, $c_3 = \frac{1}{2}$, then $d_{31} = \frac{29868927}{32000} \approx 933.404$ and the positive equilibrium point is $P_0 = \left(1, 1, \frac{1}{2}, \frac{55}{8d_3} \right)$.

The first Lyapunov coefficient is $\ell_1(P_0, d_{31}) \approx -0.222841$. Hence the system exhibits a supercritical Hopf bifurcation at P_0 with respect to d_3 . Setting $d_3 = b_{31} + 10^{-1} \approx 933.504$, we have in Figure 7 a projection to the (x, y, z) space of an orbit with initial condition $Q_0 = (1.00001, 1.00001, 0.50001, 0.00737472)$ which tends to the stable limit cycle. Figure 8 shows the corresponding time series.

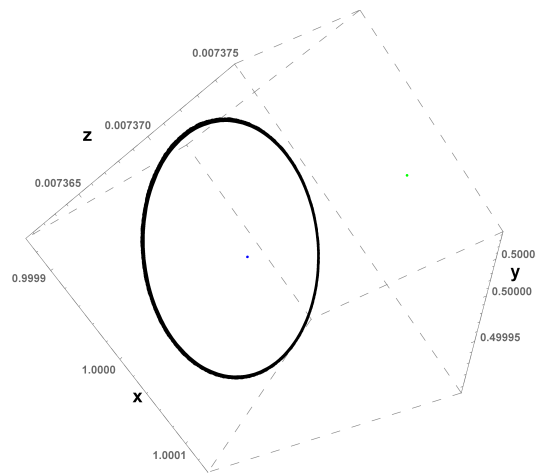


Figure 7: Projection of limit cycle with respect to P_0 (one equilibrium, f_1 Holling IV).

Example 5.6. From the hypothesis in Theorem 4.7 the differential system (1.1) takes the form

$$\begin{aligned} \dot{w} &= \frac{29445d_3w}{246208} \left(-\frac{3125y}{y_0(w^2 + x + \frac{241}{64})} - 128w - 128x + 832 \right), & \dot{x} &= \frac{29445d_3(3wy_0 - x(2y + y_0))}{3847y_0}, \\ \dot{y} &= \frac{d_3y(b_2 + y_0)}{984832y_0} \left(-\frac{984832z}{c_3(b_2 + y)} + \frac{51675975w}{w^2 + x + \frac{241}{64}} + 876096x - 1752192 \right), & \dot{z} &= \frac{b_2d_3z(y - y_0)}{y_0(b_2 + y)}. \end{aligned}$$

Therefore, $b_{20} = \frac{95480385736y_0}{16391886457}$ and

$$P_0 = \left(2, 2, y_0, \frac{2067039c_3(b_2 + y_0)}{192350} \right), \quad P_1 = \left(\frac{1}{8}, \frac{1}{8}, y_0, \frac{13689c_3(b_2 + y_0)}{1231040} \right).$$

Taking $y_0 = 1$, $d_3 = 1$, $c_3 = \frac{1}{2}$, we have that $b_{20} \approx 5.82486$ and the first Lyapunov coefficient is $\ell_1(P_0, b_{20}) \approx -1.91318$. Hence the system exhibits a supercritical Hopf bifurcation at P_0 with respect to b_2 . Setting $b_2 = b_{20} - 10^{-1} \approx 5.72486$, we have in Figure 9 a projection to the (x, y, z) space of an orbit with initial condition $Q_0 = (2.01, 2.01, 1.01, 36.1435)$ which tends to the stable limit cycle. Figure 10 shows the corresponding time series.

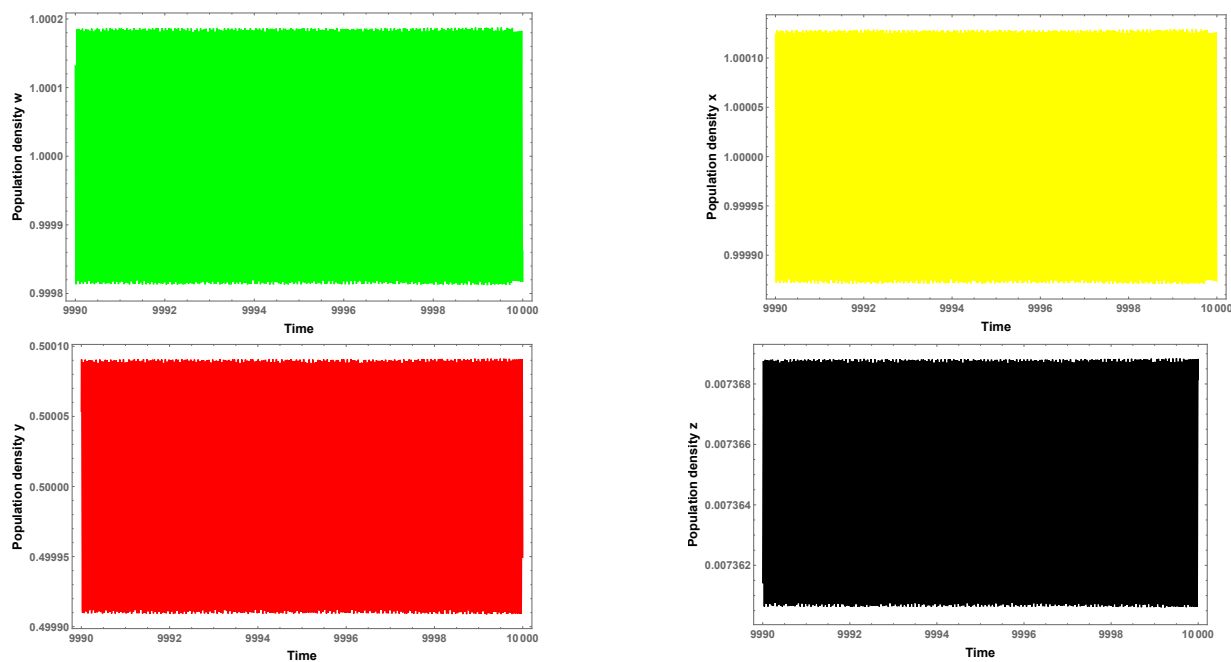


Figure 8: Time series with respect to P_0 (one equilibrium, f_1 Holling IV).

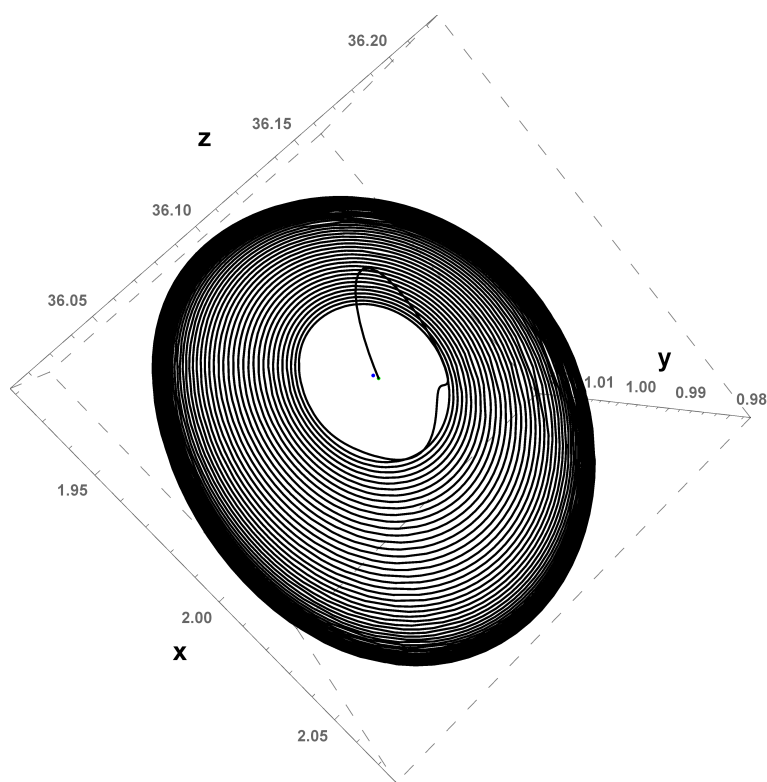


Figure 9: Projection of limit cycle with respect to P_0 (two equilibria, f_1 Holling IV).

Remark 5.7. When the system (1.1) has two equilibrium points and the parameter b_2 is near to the bifurcation value b_{20} , the third and fourth coordinates of P_0 are directly proportional to y_0 .

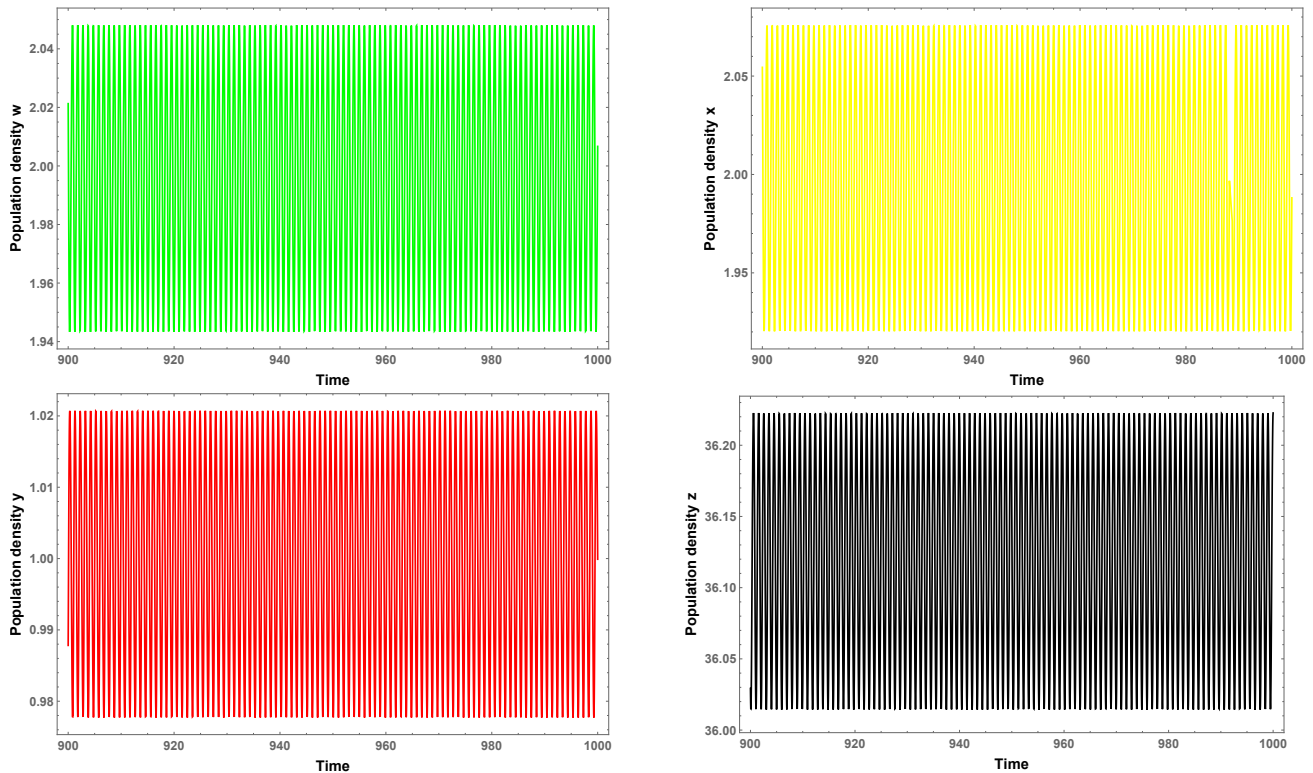


Figure 10: Time series with respect to P_0 (two equilibria, f_1 Holling IV).

Example 5.8. From the hypothesis in Theorem 4.10 i) the differential system (1.1) takes the form

$$\begin{aligned} \dot{w} &= \frac{21873d_3w}{45928192} \left(-\frac{37485y}{y_0(w^2 + x + \frac{963}{64})} - 128w - 128x + 2496 \right), \\ \dot{x} &= \frac{65619d_3(6wy_0 - x(2y + y_0))}{1435256y_0}, \\ \dot{y} &= \frac{d_3y(b_2 + y_0)}{180038512640y_0} \left(256 \left(-\frac{703275440z}{c_3(b_2 + y)} - 100489 \right) + \frac{3057779781w}{w^2 + x + \frac{963}{64}} + 3215648x \right), \\ \dot{z} &= \frac{b_2d_3z(y - y_0)}{y_0(b_2 + y)}. \end{aligned}$$

We have that $b_{20} = \frac{13416348622408722y_0}{582645121928723}$ and the positive equilibrium points are

$$P_0 = \left(4, 8, y_0, \frac{20801223(b_2 + y_0)}{23911364960} \right), \quad P_1 = \left(\frac{1}{8}, \frac{1}{4}, y_0, \frac{100489(b_2 + y_0)}{900192563200} \right), \quad P_2 = \left(\frac{3}{8}, \frac{3}{4}, y_0, \frac{2066958241(b_2 + y_0)}{15303273574400} \right).$$

Taking $d_3 = 1$, $c_3 = \frac{1}{2}$ and $y_0 = 40$, the first Lyapunov coefficient is $\ell_1(P_0, b_{20}) \approx -0.0134592$. Hence the system exhibits a supercritical Hopf bifurcation at P_0 with respect to b_2 and P_1 is locally asymptotically stable. Setting $b_2 = b_{20} - 10^{-2} \approx 921.055$, we have in Figure 11 a projection to the (x, y, z) space of an orbit with initial condition $Q_0 = (4.01, 8.01, 40.01, 0.846051)$ which tends to the stable limit cycle. Figure 12 shows the corresponding time series.

Remark 5.9. When the system (1.1) has three equilibrium points and the parameter b_2 is near to the bifurcation value b_{20} , the third and fourth coordinates of P_0 are directly proportional to y_0 .

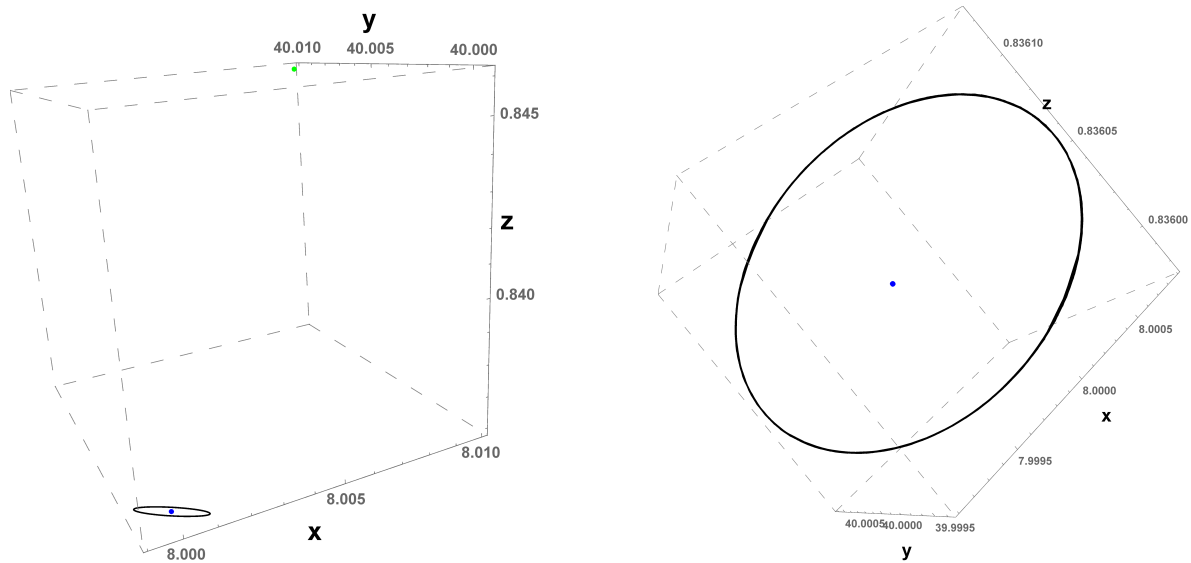


Figure 11: Projection of limit cycle with respect to P_0 (three equilibria, f_1 Holling IV).

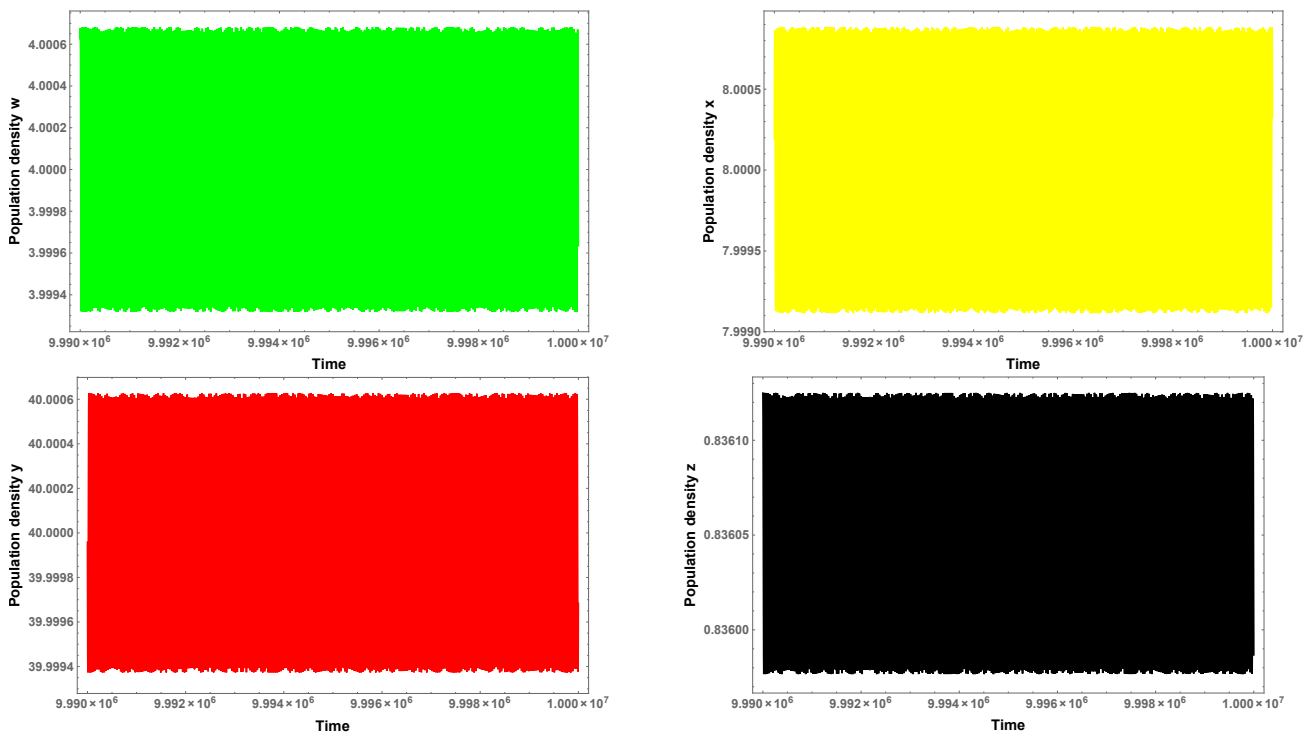


Figure 12: Time series with respect to P_0 (three equilibria, f_1 Holling IV).

6. Conclusions

The dynamics of the tritrophic chain model with age structure in the prey given by the differential system (1.1) is determined under sufficient conditions on the parameter space. We considered two different types of interaction between predator and reproductive population prey: through a Holling type II or IV functional response f_1 .

If f_1 is Holling type II it is possible to have one or two positive equilibria P_0 and P_1 . There are parameters conditions such that the differential system (1.1) has a Hopf bifurcation at P_0 with respect to the parameter b_2 representing the handling time. If there is only one equilibrium point, the bifurcation could be sub- or super-critical, whereas if there are two equilibria, it is only supercritical and the the other

equilibrium point is locally unstable.

When f_1 is Holling type IV, there are sufficient conditions to have one, two or three positive equilibrium points, P_0, P_1, P_2 . In all cases the differential system (1.1) exhibits a supercritical Hopf bifurcation at P_0 . In the first case, the bifurcation is with respect to d_3 which represents the mortality superpredator rate growth. In the second case, the bifurcation is with respect to b_2 and P_1 is locally unstable. In the third case, there is a non simultaneous Hopf bifurcation at P_0 and P_1 with respect to b_2 , and P_2 is locally unstable. From Theorems 3.4, 3.7, 4.7, and 4.10 we have that given a predator density there are parameters values that guarantee the coexistence coming from a supercritical Hopf bifurcation whose bifurcation value is approximately the predator density. Finally, we emphasize that the differential system (1.1) may presents bistability (see Theorem 4.10 i)) when there is defense in the prey.

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