THE EFFECT OF THE PREY AGE STRUCTURE ON A PREDATOR-PREY SYSTEM

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Abstract. In this paper, we are concerned with the role of the age structure of a prey in the dynamic of a predator prey model. Specifically, we study the effect of predation on a non-reproductive class of the prey, when the reproductive class of the prey presents a group defense mechanism. Three different scenarios are analyzed: (1) Constant predation rate on the nonreproductive class, no defense mechanism; (2) Predation of Type II of Holling on the non-reproductive class, no defense mechanism; and (3) Predation of Type II of Holling on the non-reproductive class, defense mechanism.

1 Introduction Predator–prey is one of the most important interspecific interaction and it has received extensive attention from many points of view. Recently some models have been built to study the dynamical properties of a system where predation is age–dependent. The study of age structured models is a topic of ecological interest. In nature we find predators that eat only adults, or immature prey, or sometimes they prefer the most conspicuous class. An example is the cicada which is preyed only in adult stage [8], or some species of perch which feed on immature prey [4]. In [13] they have considered a predator–prey model with a two age class prey. Under the assumption that predator feeds only on the immature class and the predation rate is constant they obtain necessary and sufficient conditions for coexistence and extinction. However, their hypothesis of constant predation rate is unrealistic, due to the mutual interference between the predators which increases with the predator density. Interference between predators see [1]. The phenomenon of predation on the more abundant prey known as switching has been considered in many papers, see for example [6], [9], [10], [11]. In [7] a system is analyzed containing a predator species and a structured prey species with fixed maturity time. This model presents a kind of switching from one age class to the other. It is found that the introduction of a time delay is a destabilizing process in the sense that increasing the time delay could cause population's fluctuations. Another important aspect that could be present in a predator-prey relationship is the ability of the prey to better defend themselves when their number is large. Pairs of musk-oxen can be successfully attacked by wolves but groups often are not attacked [12]. Examples of this kind of group defense can be found in [5], [3].

In this paper, we are concerned with the role of the age structure of a prey in the dynamic of a predator prey model. Specifically, we study the effect of predation on a non-reproductive class of the prey, when the reproductive class of the prey presents a group defense mechanism. Three different scenarios are analyzed: (1) Constant predation rate on the non-reproductive class, no defense mechanism; (2) Predation of Type II of Holling on the non-reproductive class, no defense mechanism; and (3)Predation of Type II of Holling on the non-reproductive class, defense mechanism. We assume that the class of the youngest organisms reproduces logistically and the maturation rate is constant. The second class

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contains the oldest organisms and it is assumed that they are not reproductive. A grouping defense mechanism of the first class is simulated by taking a predation rate which is a decreasing function of the size's class. To know the dynamical consequences of each one of the considered aspects -selective predation and defense mechanism- we start with a basic predation–prey model which is progressively modified by incorporating at each step, one of the mechanisms. In this way, when a new dynamical property arises, we know what it is the mechanism that produces it.

2 The model There exist a lot of examples of predator species which preferentially feed on the most conspicuous age class of their prey. On the other hand, when the prey species is numerous it may develop defense mechanisms and consequently a lower predation rate is observed. These two aspects –selective predation and defense mechanism– are considered in the following model.

$$\begin{aligned} \dot{x} &= x(\gamma(1-\frac{(x+y)}{K}) - f(x,y)z - \nu) = xF_1(x,y,z), \\ \dot{y} &= \nu x - \tau y - g(y)z = G_1(x,y,z), \\ \dot{z} &= z(\mu x f(x,y) + \beta g(y) - D) = zH_1(x,y,z). \end{aligned} \tag{1}$$

The term $x+y$ stands for the population of the prey, x is the reproductive class and y represents the eldest and non-reproductive class. The defense of the prey based on its size is simulated assuming that $(\frac{\partial f(x,y))}{\partial x})$ and $(g(y)/y)'$ are negative. Also, we assume that $(\frac{\partial f(x,y))}{\partial y}) < 0$ to introduce a kind of switching effect.
In this paper f and g are given by

$$\begin{aligned} f(x,y) &= \frac{1}{1+x^2+y}, \\ g(y) &= \frac{\delta y}{1+y}. \end{aligned}$$

When the non–reproductive class is not considered, the Model (1) becomes

$$\begin{aligned} \dot{x} &= x(\gamma(1-\frac{x}{K}) - \frac{z}{a+x^2}), \\ \dot{z} &= z(\frac{\mu z}{a+x} - D), \end{aligned} \tag{2}$$

whose dynamical behavior has been analyzed in [2].
First, we study the system

$$\begin{aligned} \dot{x} &= x(\gamma(1-\frac{(x+y)}{K}) - \frac{z}{1+x+y} - \nu) = xF_2(x,y,z), \\ \dot{y} &= \nu x - \tau y - yz = G_2(x,y,z), \\ \dot{z} &= z(\frac{\mu x}{1+x+y} + \beta y - D) = zH_2(x,y,z), \end{aligned} \tag{3}$$

where predation rate on y is size independent.
Then, we consider the system

$$\begin{aligned} \dot{x} &= x(\gamma(1-\frac{(x+y)}{K}) - \frac{z}{1+x+y} - \nu) = xF_3(x,y,z), \\ \dot{y} &= \nu x - \tau y - \frac{yz}{1+y} = G_3(x,y,z), \\ \dot{z} &= z(\frac{\mu x}{1+x+y} + \frac{\beta yz}{1+y} - D) = zH_3(x,y,z), \end{aligned} \tag{4}$$

where we have a density dependent predation rate on y, of the type II of Holling. Finally, model (1) is analyzed.

3 The analysis of the models As usual, we are interested in the dynamics on the feasible region R defined by R $=\{x \geq 0, y \geq 0, z \geq 0\}$. Notice that $(0,0,0)$ is a global attractor of the systems

$$
\begin{aligned}
\dot{x} &= xF_i(x,y,z), \\
\dot{y} &= G_i(x,y,z), \\
\dot{z} &= zH_i(x,y,z),
\end{aligned}
\tag{5}
$$

for $i = 1,2,3$, when $\gamma < \nu$. This is due to $F_i(x,y,z) < 0$ for each $(x,y,z) \in R$. Hence, we will assume that $\gamma > \nu$. An equilibrium point is called a *coexistence equilibrium point* (*ce*-point) if all its coordinates are no null. In any of the above considered cases, the equilibrium points of the system with at least one null coordinate are $O = (0,0,0)$ and $N = (\overline{x}, \overline{y}, 0)$, where $\overline{x} = \frac{K(\gamma-\nu)}{\gamma}\frac{\tau}{\tau+\nu}$ and $\overline{y} = \frac{\nu}{\tau}\overline{x}$. Although, the points O and N are non hyperbolic points, it is not hard to prove the following proposition.

Proposition 1 *(a) The point O is an unstable equilibrium point of the system (5), for $i = 1,2,3$.*

(b) The point N is a stable (an unstable) equilibrium point of the system (5), if $H_i(N) < 0$ ($H_i(N) > 0$) for $i = 1,2,3$.

Proof. (a) Since $F_i(0,0,0) = \gamma - \nu > 0$, there exists a neighborhood V of O, such that $F_i(x,y,z) > \frac{\gamma-\nu}{2}$, for each $(x,y,z) \in V$. This implies that $x(t)$ increases as long as the trajectory $(x(t), y(t), z(t))$ remains in V. Thus, the point O is unstable. (b) Now, we prove that N is stable. Since $H_i(N) < 0$, there exists a neighborhood V_1 of N such that $H_i(x,y,z) < 0$ for each $(x,y,z) \in V_1$). Notice that N is a stable equilibrium point of the planar restricted flow; then, there exists a planar neighborhood V_2 of N such that the solution $(x(t), y(t))$ of the system

$$
\begin{aligned}
\dot{x} &= x((\gamma-\nu) - \frac{\gamma}{K}(x+y)), \quad x(0) = x_0, \\
\dot{y} &= \nu x - \tau y, \quad y(0) = y_0,
\end{aligned}
$$

tends to N when $t \to \infty$, for $(x_0, y_0) \in V_2$. We take α and β such that

$$
\begin{gathered}
\alpha < x((\gamma-\nu) - \tfrac{\gamma}{K}(x+y)) < \beta, \\
\alpha < \nu x - \tau y < \beta,
\end{gathered}
$$

for each $(x,y) \in V_2$. Let V_3 denote an open planar set contained in V_2, and let ρ be a positive number such that

$$
\begin{gathered}
\alpha < xF_i(x,y,z) < \beta, \\
\alpha < G_i(x,y,z)\beta,
\end{gathered}
$$

for all $(x,y,z) \in V_3 \times [0,\rho]$. Hence, the component $(x(t), y(t))$a of any solution starting in $V_3 \times [0,\rho]$ remain in V_2 and the component $z(t) \to 0$. Analogously, it is proved that N is unstable when $H_i > 0$. $\square$

Proposition 2 *All the solutions of the system (5) are bounded, for $i = 1,2,3$.*

Proof. To be explicit, we consider the case $i = 1$. Notice that $\dot{x} < 0$ while $x + y > K$. Therefore, given a solution $(x(t), y(t), z(t))$ there exist $X > 0$ and $t_0 > 0$, such that $x(t) \leq X$ for $t \geq t_0$. Since $\dot{y} \leq \nu X - \tau y$ for $t \geq t_0$, we see that $y(t) \leq \frac{\nu X}{\tau} + 1$ if $t \geq t_1$, for a $t_1 > 0$. So, $x(t)$ and $y(t)$ are bounded functions of t; let C a bound of $x(t)$ and $y(t)$. Before to prove that $z(t)$ is bounded we show that it does not converge monotonically to infinity. If $z(t)$ tends to infinity monotonically, then (1) $\dot{z}(t) > 0$ and also (2) we have a $\Lambda > 0$ such that $z(t) > \Lambda$ for t large enough and both $F_1(x(t), y(t), \Lambda)$ and $G_1(x(t), y(t), \Lambda)$ are negative. Item (2) implies that $(x(t), y(t)) \to (0, 0)$, consequently $H_1(x, y) < 0$. This a contradiction since item (1) holds. Also, it is worth noting that $z(t)$ is an increasing function on an interval $I = (t_0, t_1)$ if $z(I) = (n_1\Lambda, n_2\Lambda)$, with $n_1 < n_2$ and $n_1, n_2 \in \mathbb{N}$. Otherwise, there is $\overline{t} \in (t_0, t_1)$ such that $z(\overline{t}) > z(t)$ for some $t > \overline{t}$. This implies that $H_1(x(t), y(t)) < 0$. On the other hand, $\dot{x}$ and $\dot{y}$ are lesser than zero, since $z(t) > \Lambda$. Therefore, $H_1(x(t), y(t))$ will remain lesser than zero, while $z(t)$ takes values greater than Λ. Hence, $z(I) \neq (n_1\Lambda, n_2\Lambda)$. This contradiction proves that $z(t)$ increases monotonically.
We have the inequalities

$$\dot{x} < x((\gamma - \nu) - \frac{z}{1 + 2C}), \tag{6}$$

$$\dot{y} < \nu y, \tag{7}$$

If $z(t)$ is not bounded, then given $n_1, n_2 \in \mathbb{N}$ there exists an interval (t_0, t_1) such that $z(I) = (n_1\Lambda, n_2\Lambda)$. The equality $\gamma - \nu = k\Lambda$ holds for some $k > 0$. We have $(\gamma - \nu) - \frac{z(t)}{2C} < (k - \frac{n_1}{2C})\Lambda$. We choose n_1 such that $\alpha < 0$, where α stands for the term $k - \frac{n_1}{2C}$. In this way, we have that $\dot{x} < \alpha x$, when $z(t)$ belongs to $(n_1\Lambda, n_2\Lambda)$. This shows that $x(t)$ decreases exponentially fast and together with the inequality 7 imply that after $z(t)$ surpasses n_1, the time that $z(t)$ remains increasing is bounded. As a consequence, we can get arbitrarily large growth rate of $z(t)$, by choosing conveniently n_2. This is not possible, since $\frac{\dot{z}}{z}$ is bounded by $\max H_1(x, y)$. $\square$
The *ce*-points are the positive roots of the system of equations given by

$$F_i = 0, \quad G_i = 0, \quad H_i = 0, \tag{8}$$

for $i = 1, 2, 3$.
The equation $F_i = 0$ defines a bounded surface which cuts the $x - y$ plane along the line $L_x : x + y = K(\frac{\gamma - \nu}{\gamma})$. This surface is positive (that is, the coordinate z is greater or equal than zero) in the triangle defined by the lines $(x = 0, z = 0)$, $(y = 0, z = 0)$ and L_x. The surface $G_i = 0$ is positive for (x, y) in the planar region below the line $L_y : \nu x - \tau y = 0$ and tends asymptotically to the plane $y = 0$. Notice that L_y is the intersection of $G_i = 0$ with the $x - y$ plane. The equation H_i defines a cylindrical surface orthogonal to the plane $x - y$. Indeed, $H_i = 0$ is a hyperbolic cylinder for $i = 2, 3$. Let L_z denotes the intersection of $H_i = 0$ with the plane $x - y$ (see Figure (1).
Because our purpose is to relate the dynamical changes with the interaction mechanisms, we only show those cases which present some new dynamical feature concerning the *ce*-points. On the other hand, the general description of the coexistence equilibrium points is almost an impossible task due to the great number of parameters involved.

3.1 Equilibrium points of the system (5): $i = 2$. First of all, we analyze the geometry of the nullclines. The shape of the cylindrical surface $H_1 = 0$ is determined by the hyperbola given by

$$\beta y^2 + \beta xy + (\beta - D)y + (\mu - D)x - D = 0. \tag{9}$$

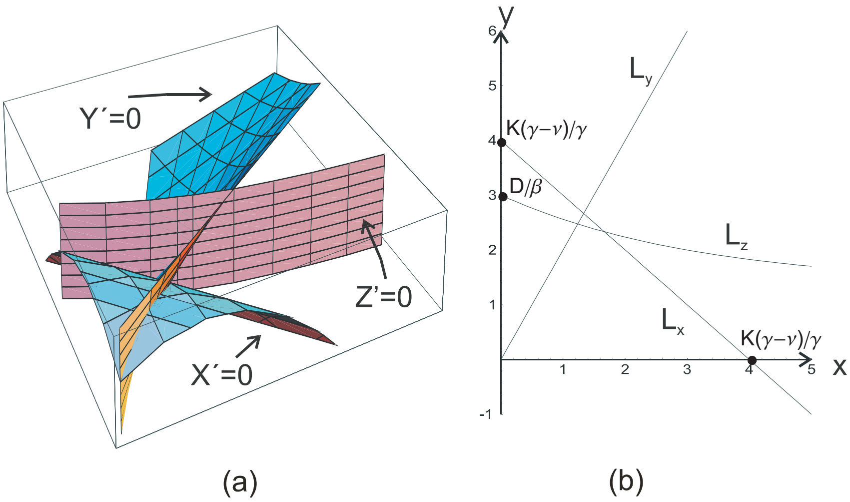

Figure 1: (a) The nullclines for i=2. (b) L_x, L_y, L_z for i=2.

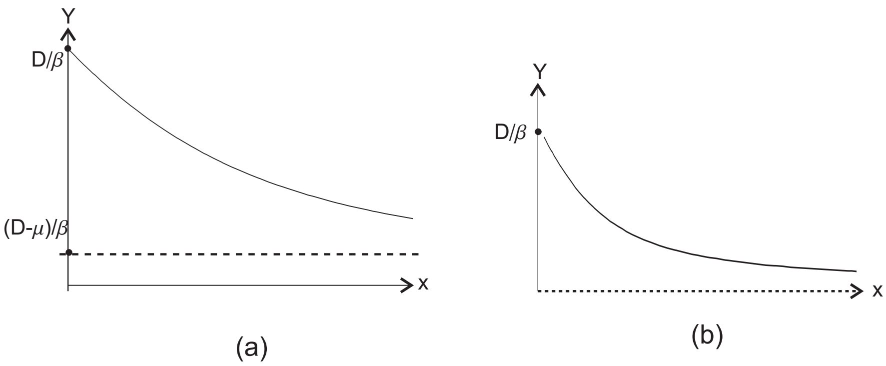

Figure 2: (a) $\mu < D$. (b) $\mu = D$. The asymptote is the discontinuous line

Remark 1 *This hyperbola intersects the x axis in $x^* = D/(\mu - D)$. If $\mu = D$, it does not intersect the x axis. The intersections with the y axis are $y = -1$ and $y = d/\beta$. The asymptotes are given by the equations $y = \frac{D-\mu}{\beta}$ and $y = -x + \frac{\mu-\beta}{\beta}$.*

We are only interested in the branch of the hyperbola contained in R, that we denote by P. In Figures (2) and (3), we show P according to the sign of $D - \mu$.

Proposition 3 *Assume that $\mu < D$ and $i = 2$. There exists an interval $J = (0, \tau^*)$ such that the system (5) has a ce-point for each $\tau \in J$ if and only if $K\frac{\gamma-\nu}{\gamma} > \frac{D}{\beta}$. The ce-point is unique for each τ.*

Proof. A *ce*-point is a point in the intersection of the surfaces given by 8. The surface $F_2 = 0$ is foliated by the lines $l_a : \{y = -x + a,\ z = ((\gamma - \nu) - \frac{\gamma}{K}a)(1 + a)\}$. We take $a \in [0, K(\frac{\gamma-\nu}{\gamma}))$, since we are interested in the portion of the surface contained in the region R. The hyperbolic cylinder $H_2 = 0$ is projected onto the convex curve P, whose slope (the tangent line slope) is greater or equal than $\frac{-\mu}{\beta+D} > -1$. it follows that if $K(\frac{\gamma-\nu}{\gamma}) < \frac{D}{\beta}$,

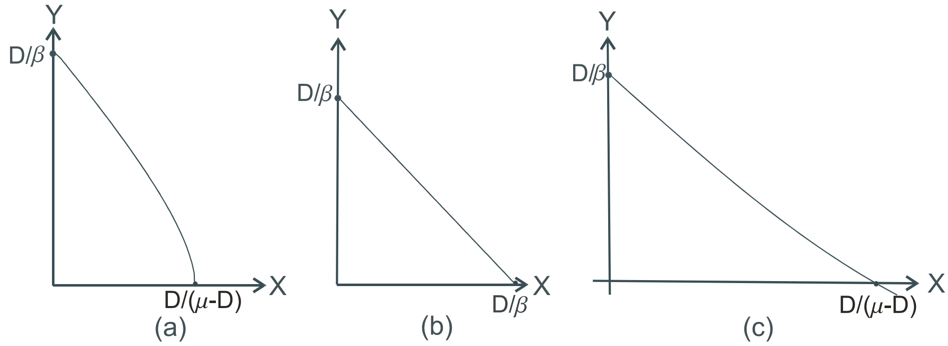

Figure 3: μD. (a) $D+\beta<\mu$. (b) $D+\beta=\mu$, P becomes a line segment. (c) $D+\beta\mu$.

there does not exist a *ce*-point since the line l_a does not cut the surface $H_2=0$, for each $a\in[0,K(\frac{\gamma-\nu}{\gamma})$. Now, we consider $K(\frac{\gamma-\nu}{\gamma})>\frac{D}{\beta}$. Notice that l_a cuts the surface $H_2=0$ if and only if $a\in[D/\beta,K(\frac{\gamma-\nu}{\gamma})]$. The intersections of the lines l_a with $H_1=0$ define a continuous curve which we denote by L. The z coordinate of L is positive, except the corresponding to $a=K(\frac{\gamma-\nu}{\gamma})$ which is null. The surface $G_2=0$ is foliated by the lines $h_m:\{y=mx, z=\frac{\nu}{m}-\tau\}$. Hence, the intersection of F_2 with G_2 denoted by M is a curve that its z coordinate grows from zero to infinity when m goes from $\frac{\nu}{\tau}$ to 0. The *ce*-points are the intersection points of L with M. Notice that M does not cut the curve L if $\frac{\nu}{\tau}$ is lesser or equal than $\frac{\overline{y}}{\overline{x}}$, where $(\overline{x},\overline{y},0)$ is the point in L corresponding to $a=K(\frac{\gamma-\nu}{\gamma})$. In that case, it does not exist any *ce*-point. If $\nu/\tau\geq\overline{y}/\overline{x}$, L intersects M in exactly one point. The interval $J=(0,\frac{\nu\overline{x}}{\overline{y}})$. □

Proposition 4 *Let $\mu>D$ and $i=2$. The following statements holds.*

(a) If $D+\beta<\mu$, then there exists an interval $J=(\tau^*,\infty)$ such that the system (5) has a ce-point for each $\tau\in J$ if and only if $K(\frac{\gamma-\nu}{\gamma})>\frac{D}{\mu-D}$. The ce-point is unique for each τ. We can take $\tau^*=0$, if $K(\frac{\gamma-\nu}{\gamma})>\frac{D}{\beta}$.

(b) If $D+\beta\geq\mu$, then the system (5) has a ce- point for each $\tau\in J=(0,\infty)$ if and only if $K(\frac{\gamma-\nu}{\gamma})\geq\frac{D}{\beta}$. The ce-point is unique for each τ.

Proof. The notation is as in the proof of Proposition (3). In this case $(\mu>D)$, the curve P cuts the x axis. Indeed, the intersection point is $(D/(\mu-D),0,0)$. (a) P is a concave curve with slope lesser than -1, when $D+\beta<\mu$ (see Figure 3.(a)), then a line l_a intersects the surface $H_2=0$ if and only if $a>\frac{D}{\mu-D}$. So, there is not any *ce*-point when $K(\frac{\gamma-\nu}{\gamma})\leq\frac{D}{\mu-D}$. Now, we consider $\frac{D}{\mu-D}<K(\frac{\gamma-\nu}{\gamma})\leq D/\beta$. The intersection point of $l_K(\gamma-\nu)/\gamma)$ with P is a point $(\overline{x},\overline{y},0)$, where $0<\overline{x}<D/\mu-D$ and $0<\overline{y}<D/\beta$. Clearly, the curve L intersects the curve M if $\nu/\tau\leq\overline{y}/\overline{x}$. Therefore, there exists a *ce*-point. We claim that $L\bigcap M=\emptyset$ if τ is small enough. Straightforward but cumbersome calculations show that the z coordinate of M grows faster than the corresponding one of L. On the other hand, if $\nu/\tau>\overline{y}/\overline{x}$, then $\overline{z}$ is greater than 0, where $(\overline{x},\overline{y},\overline{x})$ belongs to M. The claim holds and the proof of (a) follows. We omit the proof of (b) because it is similar to the previous one. □

We remark that some numerical calculations and the local analysis of certain cases make plausible that the *ce*-points are always asymptotically stable.

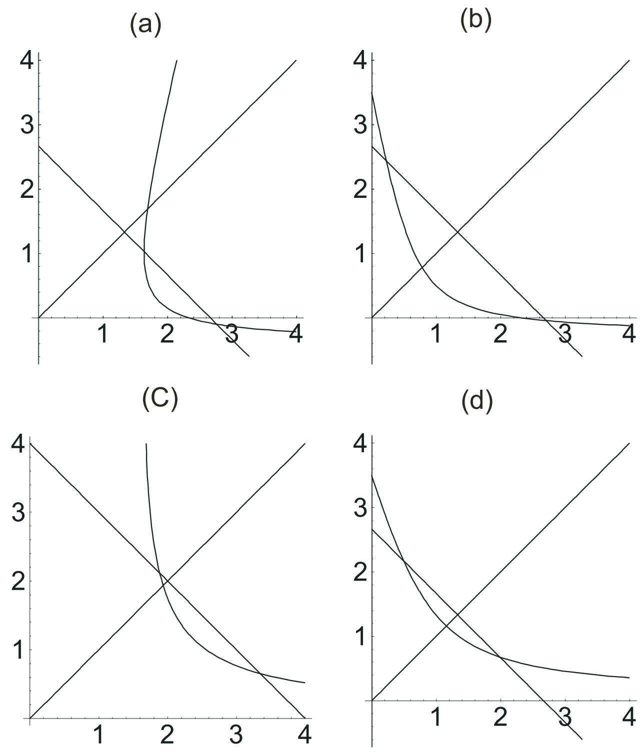

Figure 4: (a) $\mu \geq D$, $\beta < D$. (b) $\mu \geq D$, $\beta \geq D$. (c) $\mu < D$, $\beta \leq D$. (d) $\mu < D, \beta > D$.

3.2 Equilibrium points of the system (5): $i = 1, 3$. We will do a numerical exploration to discover the new dynamical features which arise when we introduce: first, a predation of type II of Holling on the oldest class; then, a defense mechanism of the youngest class.

3.2.1 Case i=3. In Figure 4, we see the intersections of the surfaces $F_3 = 0$, $G_3 = 0$, $H_3 = 0$ with the plane $z = 0$. As in the case $i = 2$, the surface $H_3 = 0$ is a hyperbolic cylinder. Now, in the following remark we point out some of the main dynamical features of this case. We suppose that $K > D/\beta$.

Remark 2 *1. We consider the case $\mu \geq D$, $\beta < D$. There exist τ_1, τ^* satisfying $\tau_1 < \tau^*$, such that the system has a ce-point if and only if $\tau > \tau_1$. There exist two ce-points if τ belongs to (τ_1, τ^*). One of them is a stable point, and the other one is a saddle. the 2-dimensional unstable manifold of the saddle point defines a separatrix of the flow in such a way that any solution starting below the separatrix tends to N. As τ tends to τ^*, these equilibrium points collide and a new point arises which is stable for $\tau > \tau^*$.*

2. We assume that $\mu \geq D$, $\beta \geq D$. A unique ce-point exists for all $\tau > 0$. This point which is unstable for small values of τ, becomes a stable point as τ increases beyond a certain value τ_2. There exists a stable limit cycle for $\tau < \tau_2$

3. Let $\mu < D$, $\beta \leq D$. A unique and stable ce-point exists if and only if $\tau_3 < \tau < \tau_4$, for some positive numbers $\tau_3 < \tau_4$. If $\mu < D$, $\beta > D$, a stable ce-point exists if and only

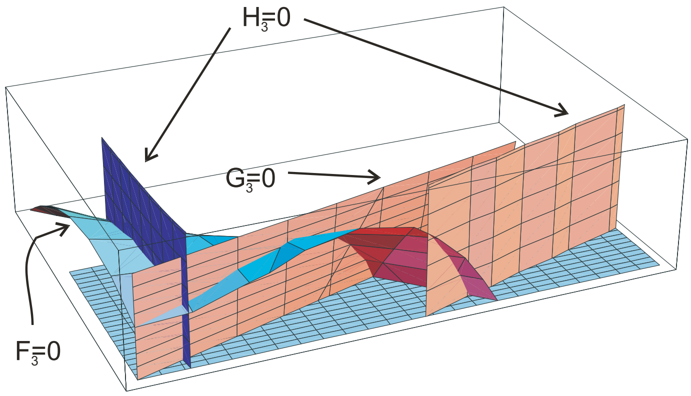

Figure 5: Nullclines of the system for $i = 1$

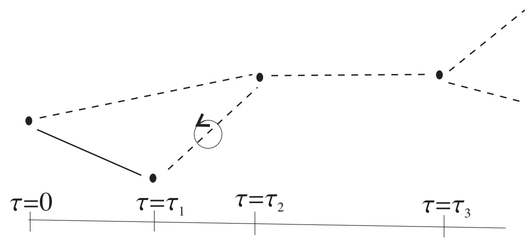

Figure 6: Bifurcation diagram. $i = 1$.

if $\tau < \tau_5$, for some $\tau_5 > 0$.

3.2.2 Case i=1. Although, we do not make an exhaustive numerical exploration for this case, we have found that the system can show a bifurcation diagram as the following.

Remark 3 *There exist $0 < \tau_1 < \tau_2 < \tau_3$ such that for $\tau < \tau_1$, the system has two equilibrium points which we denote by Q_1 and Q_2. One of them is a stable point, say Q_1. Two of the eigenvalues of Q_1 are complex numbers. We have a Hopf bifurcation when $\tau = \tau_1$. For $\tau \in (\tau_1, \tau_2)$, Q_2 and Q_1 are unstable and there exists a stable limit cycle. These two points collide when $\tau = \tau_2$ in such a way that the system has a unstable point Q_3, for $\tau \in (\tau_2, \tau_3)$. The point Q_3 bifurcates in two unstable points at $\tau = \tau_3$.*

In Figure (5) and Figure (6) are shown the null surfaces of the system and the bifurcation diagram, respectively.

By comparing Propositions 3 and 4 with Remark 2, we realize that a II Holling predation instead of a constant predation rate makes possible the arising of an extinction threshold for z (the separatrix manifold) and the existence of limit cycles. The new dynamical feature that arises when we introduce the group defense is that a high mortality rate of y leads to the extinction of z (see Remark 3). Indeed, large value of τ implies small level of y and consequently, higher values of x. Thus due to the group defense, the class x is protected against attacks of a small predator population.

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