

Université de Yaoundé I
Centre de Recherche et de Formation
Doctorale en Science, Technologies et
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Unité de Recherche et de Formation
Doctorale en Mathématiques,
Informatique, Bioinformatiques et
Applications



University of Yaoundé I
Postgraduate School of
Science, Technology and
Geosciences
Research and Training Unit
for Doctorate in Mathematics,
Computer Sciences, Bioinformatics and
Applications

DEPARTMENT OF MATHEMATICS
DÉPARTEMENT DE MATHÉMATIQUES
Laboratory of Applied Mathematics
Laboratoire de Mathématiques Appliquées

Hopf Bifurcation Analysis And Optimal Harvest In Delayed Leslie-Gower Predator-Prey Models With Preys Refuge And Supply Of Additional Food To Predators

DISSERTATION

Submitted to the graduate school in partial fulfillment of the requirements for the
degree of Doctor of Philosophy/PhD in Mathematics

Option : Mathematical Modelling and Dynamical Systems

Option: Modélisation Mathématiques et Systèmes Dynamiques

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DOCTORAT/PhD

Nous soussignés, Pr. ANDJIGA Nicolas Gabriel , Pr. TEWA Jean Jules,
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DEDICATION

This thesis is dedicated to my late father **Télesphore ÉBODÉ NDJANA** and my late grand-mother **Adèle ALIMA** for all they have done for me particularly ensuring my education, always taking care of me, helping me in acquiring very important personal qualities as humility and hard working. Dad, you asked me to allow you to be proud of having a PhD Holder in your family, It will be possible without you. I miss you everyday. May the will of The Almighty God be done. May your souls rest in perfect peace.

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ABSTRACT

Since the formulation of the Lotka-Volterra model, which is nowadays considered as the first and the basic model for interactions between two species, with one species (predators) eating the other species (preys), many others models have been proposed by several researchers. The Leslie-Gower's models are among those models obtained by modifying some assumptions of the basic Lotka-Volterra predator-prey models. In the literature, some modified Leslie-Gower predator-prey models incorporating different functional responses, additional fixed food, harvesting of species and optimal harvesting, discrete time delay(s), have been formulated and studied. In our thesis, two Leslie-Gower predator-prey models are formulated and studied. The first model is formulated with the incorporation of a discrete time delay in the dynamic of the predators, the refuge for the preys species and continuous threshold harvesting (with two thresholds) of the preys species. The aim of our work is to study the combined effects of continuous harvesting and time delay on the dynamics of the modified newly formulated Leslie-Gower predator-prey model. We completely determine the existence and local stability of equilibria of the system with or without the discrete time delay. Considering the discrete time delay as the bifurcation parameter, we investigate the effect of delay on stability of the coexisting equilibrium. It is observed that there are stability switches and a Hopf bifurcation occurs when the delay crosses some critical values. By applying the normal form theory and the center manifold theorem, the direction of the Hopf bifurcation and the stability of the bifurcated periodic solution are determined. The optimal harvesting of the prey is also investigated. Theoretical analysis are supported by some numerical simulations. The second model is also a modified Leslie-Gower predator-prey model. It incorporates additional fixed food for predators, refuge for preys, harvesting of preys through a continuous threshold policy, a discrete time delay in the dynamic of the predator dynamic to take into account the maturity time. The aim is to study the impact of the prey refuge, additional fixed food, harvesting and discrete time delay. A qualitative analysis of the model without the discrete time-delay is carried out. The stability of equilibria of the non-delayed model is studied. The impact of additional food, prey refuge and harvesting is studied using some constructed bifurcation diagrams. Once more, considering the discrete time-delay as bifurcation parameter, we analyze the stability of the coexistence equilibria and prove the system can undergo a Hopf bifurcation. The direction of that Hopf bifurcation and the stability of the bifurcated periodic solution are determined by applying the normal form theory and the center manifold theorem. Numerical simulations are presented to illustrate our theoretical results.

Keywords : Predator-prey - Functional response - Harvesting - Hopf bifurcation - Retarded optimal control - Stability analysis - Center manifold - Normal form - Continuous threshold policy - Additional food.

RESUMÉ

Depuis la formulation du modèle de Lotka-Volterra, considéré de nos jours comme le premier et modèle de base traduisant les interactions entre deux espèces, dont l'une (prédateur) se nourrit de l'autre (proie), plusieurs autres modèles ont été proposés par plusieurs chercheurs. Les modèles proies-prédateurs de Leslie-Gower font partie de ces modèles. Dans la littérature, plusieurs modèles modifiés de Leslie-Gower avec refuges pour les proies, différentes fonctions réponses, source additive fixe de nourriture pour le prédateur, récolte de l'une ou des deux espèces, retard(s) discret(s) ont été formulés et étudiés. Dans cette thèse, deux modèles proies-prédateurs de Leslie-Gower sont formulés et étudiés. La formulation du premier modèle est faite avec les hypothèses suivantes : l'introduction d'un retard discret dans la dynamique des prédateurs, la prise en compte d'un refuge pour les proies, la récolte des proies à l'aide d'une fonction réponse définie avec deux seuils de récolte. Le but de ce modèle est d'étudier l'impact du retard et de la récolte sur la dynamique du modèle de Leslie-Gower. Une analyse de stabilité complète du modèle avec et sans retard est faite avec la détermination des conditions d'existence des points d'équilibre et l'étude de leur stabilité locale. Considérant le retard discret comme paramètre de bifurcation, nous étudions l'impact de ce retard sur la stabilité de l'équilibre de coexistence. Nous observons la possibilité d'un changement de stabilité et l'existence de valeurs critiques (de bifurcation) pour lesquelles il y'a apparition d'une bifurcation de Hopf. En appliquant la théorie de la forme normale et le théorème de la variété centrale, nous déterminons la direction de la bifurcation de Hopf et la stabilité de la solution périodique. Le problème de la récolte optimale des proies est étudié à en appliquant la théorie du contrôle optimal dans le cas particulier des modèles avec retard. Des simulations numériques sont faites pour une illustration graphique des résultats obtenus par calculs. Le deuxième modèle quant à lui, est aussi formulé à partir du modèle de Leslie-Gower. Il prend en compte les hypothèses suivantes : la présence d'une quantité fixe de nourriture additive pour le prédateur, un retard discret prenant en compte le temps de maturité pour la dynamique des prédateurs, la possibilité de refuge des proies, une récolte des proies par une fonction récolte continue définie à l'aide d'un seul seuil. Une analyse qualitative du modèle sans retard est faite. La stabilité des équilibres du modèle sans retard est étudiée. L'impact de la nourriture additive, du refuge et de la récolte est étudié en exploitant des diagrammes de bifurcation construits à cet effet. Comme dans le cas du premier modèle, l'étude de l'impact du retard discret est faite en considérant le retard comme paramètre de bifurcation. La stabilité de l'équilibre de coexistence est étudiée. La possibilité d'avoir une bifurcation de Hopf pour des valeurs critiques du retard est prouvée. Une fois

de plus, la direction de la bifurcation de Hopf et la stabilité de la solution périodique sont déterminées en appliquant la théorie des formes normales et le théorème de la variété centrale. L'illustration des résultats théoriques obtenus par calculs est faite par des simulations numériques.

Mots Clés : Proie-prédateur - Fonction réponse - Récolte - Bifurcation de Hopf - Contrôle optimal avec retard - Analyse de stabilité - Variété centrale - Forme normale - Nourriture additive.

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GENERAL INTRODUCTION

In natural communities, we always have many different species. No species lives without interacting with other species. Organisms interact when individuals enter into the live of others. Concerning interactions among and between individuals of different species and according to M. Begon et al. (2006)([14]), we distinguish five main categories which are competition, predation, parasitism, mutualism and detritivory. In our thesis, we are interested in two of the five above categories of interactions, competition and very particularly predation. According to M. Begon et al. (2006)([14]), competition is an interaction in which one organism consumes a resource that would have been available to, and might have been consumed by, another. One organism deprives another, and, as a consequence, the other organism grows more slowly, leaves fewer progeny or is greater risk of death. The act of deprivation can occur between two members of the same species and the competition is named intraspecific competition or, between individuals of different species and the competition is called interspecific competition. Predation between species can be defined as an interaction in which one organism (predator) consumes another organism (prey) and in which the prey is alive when the predator first attacks it. This excludes detritivory, the consumption of dead organic matter. The following situation are considered as predation. The situation in which one organism kills and eats another organism (such as a cat preying on a mouse). The situation in which the consumer takes only part of its prey, which may then regrow to provide another bite another day (grazing). Herbivores (animals eating plants) and carnivores (animals eating animals) can also be included.

In order to describe, to understand the dynamics of the interacting species, to provide useful predictions and guidance so that better strategy for control and prevention can be established, mathematical models have been and are still formulated. For the formulation of models concerning interactions between predator and their preys, many assumptions are taken into account. The first of them is the growth rate function which describes the growth of each single species. The first growth rate function named the exponential or malthusian growth function has been introduced by Malthus (2012)([26]). The second one named the logistic growth function, more realistic has been proposed by Verhulst (2012)([26]). This logistic growth function has been generalized by Richards (1959)([145]). The second assumption for the formulation of a model is the functional response of the predator, which is defined as the number of preys consumed by the predator per unit of time. In the literature, there is two different categories of functional responses. The first one is those depending only on the preys density called density-dependent functional responses (Holling type I, II, III, IV, Ivlev, . . .). The second

one is those depending on predators and preys densities named ratio-dependent functional responses (Beddington-DeAngelis, Crowley-Martin, . . .). The first predator-prey model is the Lotka-Volterra model which has been proposed by Lotka (1925)([123]) and Volterra (1926)([176]). Models incorporating those different functional responses have been formulated and studied by several authors ([8], [97], [86], [85], [138], [148], [150], [186], [180], [193], [201]). The Lotka-Volterra model and some other models of Lotka-Volterra type are formulated with the principle of conversion of biomass for example. Leslie and Gower ([113], [114], [115]) have formulated predator-prey models without taking into account the principle of the biomass conservation and, with logistic growth of predator in which the carrying capacity is proportional to the preys density.

When it is possible and in order to avoid predation, the prey species often use refuge known as areas where they are safe from their predators. In order to study effects of preys refuge on the dynamics of interactions of predators and their preys, several authors ([87], [91], [98], [105], [124], [131], [140], [171]) have formulated models by taking into account the hypothesis of prey refuge. Their studies have revealed that preys refuge can have effects as reducing the prey mortality, stabilizing or destabilizing the system and avoiding the extinction of the prey species.

Practical considerations such as harvesting for food and commercial purposes when it is possible for the interacting species, have been incorporated in predator-preys models. Different harvesting functions (constant, linear, non linear, continuous threshold policy) have been used for different predator-prey models. But for the conservation of biodiversity, the balance between harvesting and conservation remain a key problem in bioeconomic management of species in an ecological environment. Optimal control theory is applied in predator-prey models incorporating harvesting, in order to ensure the optimal harvest of the species being harvested while ensuring conservation of the non-harvested one. ([23], [49], [56], [102], [111], [112], [132], [169], [173])

While taking into account the principle of causality, that is to say, the future state of the system is determined by the current state only, while the past has no impact on the future with the present of the current state, interactions between species are governed by ordinary differential equations. But due to the fact that, for example, when a predator consumes a prey, the benefit is not immediate, it is necessary and more realistic to take into account the maturation time by using a discrete or variable time delay. Models incorporating discrete time delay(s) are then formulated with so-called retarded differential equations, which are different to ordinary differential equations. Many predator-prey models have been formulated and studied by several authors ([5], [7], [11], [17], [25], [61], [106], [125], [194], [193]) with discussion on the impact the discrete time delay. Models incorporating harvesting and discrete time delay have been formulated and for some of them, optimal control theory especially for models with delay has been applied ([169], [173]).

Because a predator can be provided with another source of food different to its preys, it is important to take into account the assumption of providing additional food to the predator for the formulation of a predator-prey model, in order to study the consequences of providing additional food and the effect on the dynamic of the system. The assumption of providing additional food to the predator can be motivated by conservation of species or control of the pest population. In literature, several articles

on predator-prey models incorporating additional food for predator are proposed ([9], [73], [81], [82], [83], [152], [163], [164], [165]).

In literature, we have not yet found a Leslie-Gower predator-prey model incorporating discrete time delay for the predator, preys refuge and harvesting of preys by a continuous threshold policy harvesting function, and for which the problem of optimal harvesting has been solved. We have not yet found a Leslie-Gower predator-prey model incorporating additional fixed food for predator, preys refuge, discrete time delay for predators. Due to the fact that it is important and necessary to take into account all those assumptions simultaneously, in order to formulate models which are close to the reality, we have formulated and studied intensively two modified Leslie-Gower predator-prey models.

Outline of the thesis

The organization of this thesis is as follows :

The first chapter deals with some mathematical tools on existence and uniqueness of solution of an ordinary differential equation, the normal form theory and the centre manifold method, stability analysis, Some types of bifurcations and optimal control theory. Notes on single species models, how to proceed for formulation of models of interacting species, some functional responses very necessary for formulation of models are given in this chapter. Models formulated in this thesis, their analysis and discussion on results must be easily readable and understandable. That is the aim of this chapter. The second chapter is devoted to predator-prey models due to the fact that our thesis is done on predator-prey interactions. Some predator-prey models are presented in order to recall what can be effects of preys refuge, functional responses, additional food, harvesting and discrete time delay on the dynamic of predator-prey model.

The third chapter is devoted to the optimal harvesting and the stability analysis of the newly formulated Leslie-Gower predator-prey model. A brief literature review on Leslie-Gower predator-prey models is presented. After some notes on the basic Leslie-Gower predator-prey models and their historical, some modified Leslie-Gower predator-prey models are given in order to recall and illustrate effects of preys refuge, different functional responses, harvesting and discrete time delay on the dynamic of a Leslie-Gower predator-prey model. A modified Leslie-Gower predator-prey model is formulated by assuming that there is a preys refuge, preys are harvested through a continuous threshold harvesting function with two thresholds and there is a discrete time delay for the predator dynamic. The aim of this chapter is to study effects of discrete time delay and harvesting, and to solve if possible the problem of optimal harvesting. We show that the model is biologically meaningful because all the solutions of the system are positive and uniformly bounded. The stability and bifurcation analysis are done. We also solved the problem of optimal harvesting of preys while maintaining the coexistence of the two species. Numerical simulations using Matlab are done in order to illustrate our theoretical results.

The fourth and last chapter deals with Hopf bifurcation analysis in a delayed Leslie-Gower predator-prey model incorporating preys refuge, harvesting of preys through a harvesting function defined with one threshold and additional fixed food for predators. Some modified Leslie-Gower predator-

prey models incorporating additional fixed food for predators are presented in order to recall effects of that additional fixed food on the dynamic of a Leslie-Gower predator-prey model. Leslie-Gower predator-prey models can be used to solve practical ecological problems concerning the predator-prey interactions. That is why some applications of Leslie-Gower predator-preys models are presented. The aim of this chapter is to study effects of additional fixed food, discrete time delay, refuge and harvesting of preys. We prove the biological meaningfulness of our model. We carry out the stability and the bifurcation analysis. With some bifurcation diagrams, we study effects of the strength of refuge, the harvest limit value and preference rate for additional fixed food. Our theoretical results are illustrated by some numerical simulations using Matlab.

MATHEMATICAL NOTES AND PREDATOR-PREY MODELLING

Abstract

In this chapter, some mathematical notes on existence and uniqueness of solution, the stability analysis of an ordinary differential equation, center manifold method, some types of bifurcations and optimal control theory for time delayed models are given. The aim of this chapter is to provide some mathematical tools and notes on predator-prey modelling in order to improve the readability, the comprehension of the models recalled and formulated in this thesis as well as their analysis and results. The contents of this chapter is presented as follows : the first section is a brief summary of some theoretical mathematical elements which are usually used for the qualitative and quantitative analysis of a mathematical model such as stability analysis (local and global), some types of bifurcations, optimal control theory particularly especially for time delayed predator-prey models and for predator-prey models with harvesting are recalled, in the second section, some notes on predator-preys modelling are presented and finally, the third section is a non-exhaustive review of some functional responses.

1.1 Some mathematical notes

After the model formulation, one always has to analyze the model qualitatively and quantitatively, one can study the impact of a particular parameter on the dynamic of the model. In the following subsections, we recall some mathematical notes on existence and uniqueness of solutions of an ordinary differential equation, stability analysis, some types of bifurcations, center manifold method and optimal control theory.

1.1.1 Existence and uniqueness theorems

Let D be an open set in \mathbb{R}^{n+1} and $f : D \rightarrow \mathbb{R}^n$ be continuous.

Consider an ordinary differential equation

$$\dot{x} = f(t, x), \quad x \in \mathbb{R}^n. \quad (1.1)$$

1.1. Some mathematical notes

Definition 1.1. (Solution)([68])

x is a solution of (1.1) on an interval $I \subseteq \mathbb{R}$ if x is a continuously differentiable function defined on I such that for all t in I , $(t, x(t)) \in D$ and x satisfies (1.1) on I .

Definition 1.2. (Extended Solution)([45])

Let x_1 and x_2 be two solutions of (1.1) on interval I_1 and I_2 respectively. The solution x_2 extends the solution x_1 if $I_1 \subset I_2$ and for all $t \in I_1$, $x_1(t) = x_2(t)$.

Definition 1.3. (Maximal Solution)([45])

A maximal solution of (1.1) defined on an interval I is a solution of (1.1) which does not admit an extension on an interval J with $I \subset J$.

Theorem 1.1. (Peano-Existence)([68]).

If f is continuous in D , then for any $(t_0, x_0) \in D$, there is at least one solution of (1.1) passing through (t_0, x_0) .

Theorem 1.2. (Existence and uniqueness)([68]).

If $f(t, x)$ is continuous in D and locally lipschitzian with respect to x in D , then for any $(t_0, x_0) \in D$, there exists a unique solution $x(t, t_0, x_0)$, $x(t_0, t_0, x_0) = x_0$, of (1.1) passing through (t_0, x_0) . Furthermore, the domain E in \mathbb{R}^{n+2} of definition of the function $x(t, t_0, x_0)$ is open and $x(t, t_0, x_0)$ is continuous in E .

1.1.2 Stability analysis

Consider a general autonomous vector field

$$\dot{x} = f(x), \quad x \in \mathbb{R}^n. \quad (1.2)$$

Definition 1.4. (Equilibrium solution)([178])

An equilibrium solution of (1.2) is a point \bar{x} such that $f(\bar{x}) = 0$, i.e., a solution of (1.2) which does not change in time.

Other terms often substituted for the term "equilibrium solution" are fixed point, stationary point, rest point, singularity, critical point or steady state.

Definition 1.5. (Hyperbolic Fixed Point)([178])

Let $x = \bar{x}$ be an equilibrium solution of (1.2). Then \bar{x} is called a hyperbolic equilibrium solution if none of the eigenvalues of $Df(\bar{x})$ have zero real part, where Df denotes the derivative of f .

Definition 1.6. (Lyapounov stability)([178])

A solution $\bar{x}(t)$ of (1.2) is said to be Lyapounov stable or stable if given $\epsilon > 0$, it exists a $\delta = \delta(\epsilon) > 0$ such that for any other solution $y(t)$ of (1.2) satisfying $|\bar{x}(t_0) - y(t_0)| < \delta$ then $|\bar{x}(t) - y(t)| < \epsilon$ for $t > t_0$, $t_0 \in \mathbb{R}$.

A solution which is not stable is said to be unstable.

1.1. Some mathematical notes

It means that $\bar{x}(t)$ is said to be stable if solutions of (1.2) starting "close" to $\bar{x}(t)$ at a given time remain close to $\bar{x}(t)$ for all later times.

Definition 1.7. (Asymptotic stability)([178])

A solution $\bar{x}(t)$ is said to be asymptotically stable if it is Liapunov stable and for any other solution, $y(t)$ of (1.2), there exists a constant $\delta > 0$ such that, if $|\bar{x}(t_0) - y(t_0)| < \delta$ then $\lim_{x \rightarrow \infty} |\bar{x}(t) - y(t)| = 0$.

It means that $\bar{x}(t)$ is asymptotically stable if nearby solutions not only stay close, but also converge to $\bar{x}(t)$ as $t \rightarrow +\infty$.

Definition 1.8. (Dynamical system)([107])

A dynamical system is a triple $\{X, T, \phi^t\}$, where T is a time set, X is a state space, and $\phi^t : X \rightarrow X$ is a family of evolution operators parametrized by $t \in T$ and satisfying the following properties :

(i) $\phi^0 = id$

where id is the identity map on X .

The property means that the system does not change its state "spontaneously".

(ii) $\phi^{t+s} = \phi^t \circ \phi^s$ for all $t, s \in T$

The property states that the result of the evolution of the system in the course of $t + s$ units of time, starting at a point $x \in X$ is the same as if the system were first allowed to change from the state x over only s units of time, and then evolved over the next time t units of time from the resulting state $\phi^s x$.

In the continuous-time case, the family $\{\phi^t\}_{t \in T}$ of evolution operators is called a flow. It is such that for the pair $(x, t) \in X \times T$, $\phi^t x$ when it is defined, is the solution of (1.2) at the time t with initial value x (at $t = 0$).

Definition 1.9. (Topological equivalence)([18])

Two dynamical systems $\{X, T, \phi^t\}$ and $\{X, T, \psi^t\}$ are topological equivalent if there is a homeomorphism h that maps the orbits of the first system onto orbits of the second one, preserving the direction of time.

Definition 1.10. (Topological Conjugation)([18])

Two flows $\phi(x, t)$ and $\psi(h(x), t)$ that correspond, respectively, to ordinary differential equations $\dot{x} = f(x)$ and $\dot{y} = g(y)$ are said to be topologically conjugate if there exists a homeomorphism h such that :

$$\phi(x, t) = h^{-1}(\psi(h(x), t)).$$

Theorem 1.3. (Hartman-Grobman)([18]).

The dynamics close to a hyperbolic equilibrium point are topologically equivalent to that of the system linearized about that point.

1.1. Some mathematical notes

Theorem 1.4. (Stability of an equilibrium)([178])

Suppose all of the eigenvalues of $Df(\bar{x})$ have negative real parts. Then the equilibrium solution \bar{x} of the nonlinear vector field (1.2) is asymptotically stable.

Theorem 1.5. (Lyapounov First Stability Theorem)([178])

Let \bar{x} be an equilibrium solution of (1.2) and $V : U \rightarrow \mathbb{R}$ a C^1 function defined on some neighborhood U of \bar{x} such that :

(i) $V(\bar{x}) = 0$ and $V(x) > 0$ if $x \neq \bar{x}$.

(ii) $\dot{V}(x) \leq 0$ in $U \setminus \{\bar{x}\}$.

Then \bar{x} is stable. Moreover, if

(iii) $\dot{V}(x) < 0$ in $U \setminus \{\bar{x}\}$

then \bar{x} is asymptotically stable.

Definition 1.11. (Lyapounov function)([178])

The function V defined in the above Lyapounov first stability theorem satisfying the properties (i) and (ii) is called a Lyapounov function.

1.1.3 Centre manifold method

The center manifold theory is important for the reduction of equations to ones of lower dimension.

Suppose that the origin is an equilibrium point of (1.2). If the linearization of f at the origin has no pure imaginary eigenvalues, then the Hartman's theorem states that the number of eigenvalues with positive or negative real parts determine the topological equivalence of the flow near the origin. If there are eigenvalues with zero real parts, then the flow near the origin can be quite complicated. In general, the center manifold method isolated the complicated asymptotic behavior by locating an invariant manifold tangent to the subspace spanned by the (generalized) eigenspace of eigenvalues on the imaginary axis.

Theorem 1.6. (Center manifold theorem for flows)([62]).

Let f be a C^r vector field on \mathbb{R}^n vanishing at the origin ($f(0) = 0$) and let $A = Df(0)$. Divide the spectrum of A into three parts $\sigma_s, \sigma_c, \sigma_u$ with

$$\operatorname{Re}\lambda \begin{cases} < 0 & \text{if } \lambda \in \sigma_s, \\ = 0 & \text{if } \lambda \in \sigma_c, \\ > 0 & \text{if } \lambda \in \sigma_u. \end{cases}$$

Let the (generalized) eigenspaces of $\sigma_s, \sigma_c, \sigma_u$ be E^s, E^c and E^u respectively.

Then there exists C^r stable and instable invariant manifolds W^u and W^s tangent to E^u and E^s at the origin, and a C^{r-1} center manifold W^c tangent to E^c at the origin. The manifold W^u, W^s and W^c are all invariant for the flow of f . The stable and unstable manifolds are unique, but the center manifold W^c need not be.

1.1. Some mathematical notes

For simplicity, and because it is the most interesting case physically, we assume that the unstable manifold is empty and that the linear part of the bifurcating system is in the block diagonal form

$$\begin{cases} \dot{x} &= Bx + f(x, y), \\ \dot{y} &= Cy + g(x, y). \end{cases} \quad (1.3)$$

where $(x, y) \in \mathbb{R}^n \times \mathbb{R}^m$, B and C are $n \times n$ and $m \times m$ matrices whose eigenvalues have, respectively, zero real parts and, negative real parts. f and g vanish along with the first derivatives, at the origin. Since the center manifold W^c is tangent to E^c , we can represent it as a (local) graph

$$W^c = \{(x, y) \in \mathbb{R}^n \times \mathbb{R}^m, y = h(x), h(0) = Dh(0) = 0\}$$

where $h : U \rightarrow \mathbb{R}^m$ is defined on some neighborhood $U \subset \mathbb{R}^n$ of the origin.

Considering the projection of the vector field on $y = h(x)$ onto E^c , we have :

$$\dot{x} = Bx + f(x, h(x)) \quad (1.4)$$

Theorem 1.7. (Stability)([62]).

If the origin of (1.4) is stable (asymptotically stable) (unstable) then the origin of (1.3) is also stable (asymptotically stable) (unstable).

1.1.4 Some types of bifurcations

According to P. Glendinning (1994)([58]), the bifurcation theory describes the way that topological features of a flow (properties such as the number of stationary points and periodic orbits) vary as one or more parameters are varied.

Definition 1.12. (Bifurcation) ([107])

A bifurcation is a change of the topological type of a system depending on parameters as its parameters pass through a (critical) value called bifurcation parameter.

There exist two types of bifurcations which are local and global bifurcations. Local bifurcations are those detectable in any small neighborhood of a fixed point. Global bifurcations are those bifurcations that cannot be detected by looking at small neighborhoods of equilibrium (fixed) points or cycles.

Remark 1.1. There are global bifurcations in which certain local bifurcations are involved. In such cases, looking at the local bifurcation provides only partial information on the behavior of the system. (e.g. Saddle-node homoclinic bifurcation ([107] p. 59).

In what follows, we recall particular bifurcations. We give only their normal forms and the impact of the parameter of the system. But before, we give some notes on the normal form theory.

The method of normal forms provides a way of finding a coordinate system in which the dynamical system takes the simplest form. The method is local in the sense that, the coordinate transformations are generated in a neighborhood of a known solution, which is generally an equilibrium point. In general, the coordinate transformations will be nonlinear functions of the dependent variables. However, the important point is that, these coordinate transformations are found by solving a sequence of linear problems. The structure of the normal form is determined entirely by the nature of the linear part of the vector field.

1. Saddle-node or Fold bifurcations.

The normal form for saddle-node bifurcations is given by the following first order differential equation :

$$\dot{x} = \mu \pm x^2 \quad x, \mu \in \mathbb{R} \quad (1.5)$$

The sign of the parameter μ determines the number of fixed points. It is possible to have zero, one or two fixed points. When two fixed points exist, one is stable and the other is unstable.

2. Transcritical bifurcations

The normal form for transcritical bifurcations is given by the following first order differential equation :

$$\dot{x} = \mu x \pm x^2 \quad x, \mu \in \mathbb{R} \quad (1.6)$$

Two fixed points always exist with one stable and the other unstable. Their stability change with the sign of the parameter μ . Thus, an exchange of stability has occurred at $\mu = 0$. This type of bifurcation is also called "change of stability bifurcation".

3. Pitchwork or Flip bifurcations

The normal form for Pitchwork bifurcations is given by the following first order differential equation :

$$\dot{x} = \mu x \pm x^3 \quad x, \mu \in \mathbb{R} \quad (1.7)$$

It is possible to have one ($x = 0$) or three fixed points when the sign of the parameter varies. When there exist three fixed points (including the origin), if the origin is stable (resp. unstable) then the other fixed points are unstable (resp. stable).

In figure 1.1 , we have bifurcation diagrams of the above three types of bifurcations (saddle-node bifurcation ($\dot{x} = \mu - x^2$), transcritical bifurcation ($\dot{x} = \mu x - x^2$) and pitchwork bifurcation ($\dot{x} = \mu x - x^3$)).

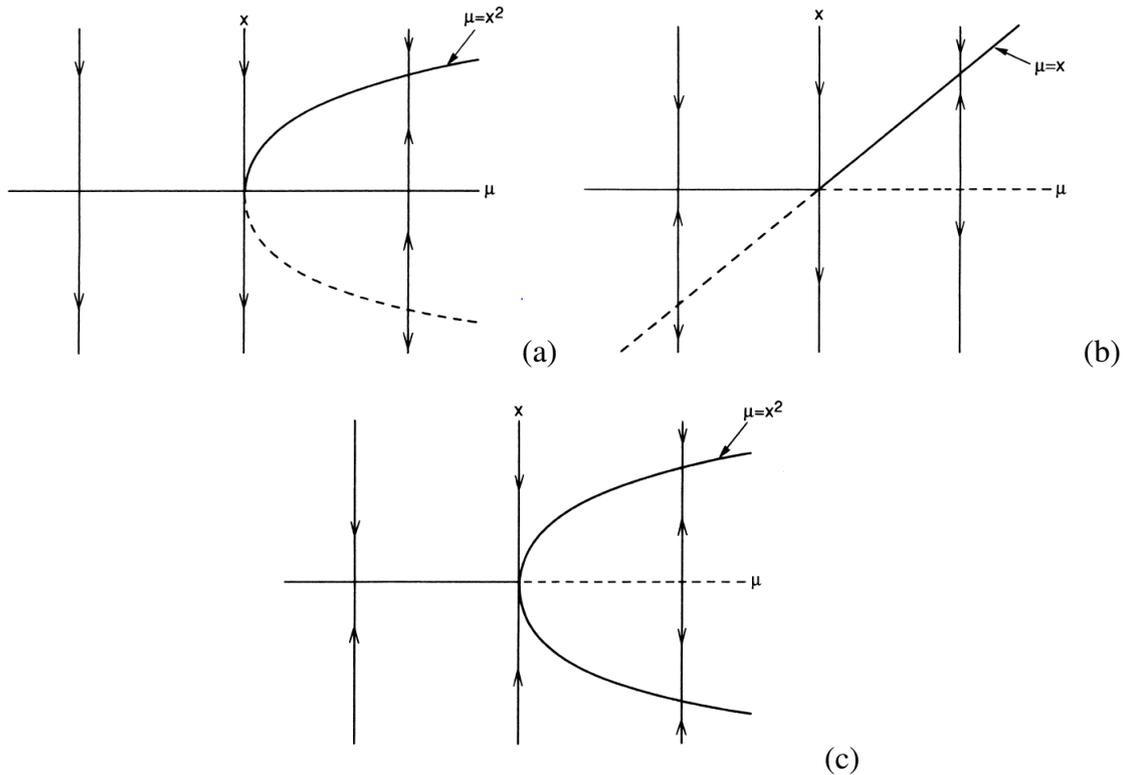


Figure 1.1: (a) Bifurcation diagram of a saddle-node bifurcation in the phase-parameter space. (b) Bifurcation diagram of transcritical bifurcation in the phase-parameter space. (c) Bifurcation diagram of a pitchfork bifurcation in the phase-parameter space. Continuous line represents stable points while discontinuous line represents unstable points. The arrows along the vertical lines represent the flow generated by each equation along the x -direction.

4. The Poincaré - Andronov - Hopf bifurcation.

All the type of bifurcation discussed above have involved motion on a one-dimensional centre manifold on which fixed points can exist or not as the parameter varies. The Hopf bifurcation rather involves a non-hyperbolic fixed point for which the linearized system has purely eigenvalues, and thus a two-dimensional center manifold, and the bifurcating solutions are periodic rather than stationary. In what follows, we give the so-called Hopf bifurcation theorem. But before, let's recall the definition of a limit cycle.

Definition 1.13. (Limit cycle) ([63])

A limit cycle is a closed trajectory in \mathbb{R}^2 which has the property that at least one other trajectory spirals into it either as time approaches infinity or as time approaches negative infinity.

In other words, the limit cycle is an isolated trajectory (isolated in the sense that neighboring trajectories are not closed, but they spiral either toward or away from the limit cycle).

If all neighboring trajectories approach the limit cycle, the limit cycle is said to be stable or attractive, that is, all the neighboring trajectories approach the limit cycle as time approaches infinity. Otherwise, the limit cycle is said to be unstable, that is, all neighboring trajectories approach it as time approaches negative infinity.

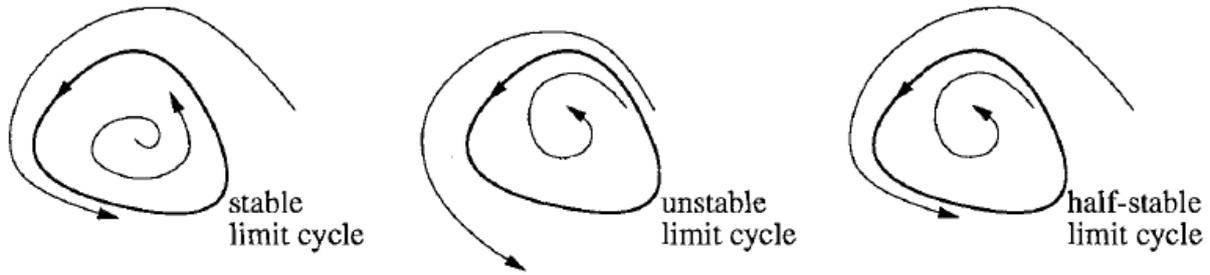


Figure 1.2: Illustration of stable, unstable and half-stable limit cycle. From Strogatz (1994) ([167])

Stable limit cycles are very important scientifically. They model systems that exhibit self-sustained oscillations. In other words, these systems oscillate even in the absence of external periodic forcing. Among the countless examples that could be given, we mention only a few: the beating of a heart; the periodic firing of a pacemaker neuron; daily rhythms in human body temperature and hormone secretion; chemical reactions that oscillate spontaneously; and dangerous self-excited vibrations in bridges and airplane wings. In each case, there is a standard oscillation of some preferred period, waveform, and amplitude. If the system is perturbed slightly, it always returns to the standard cycle. (From Strogatz (1994) ([167]))

The following theorems are usually used to prove that a system of two ordinary differential equations in the space \mathbb{R}^2 does not admit a limit cycle.

Theorem 1.8. (Bendixson’s negative criterion)([95])

Given the system $\dot{x} = X(x, y), \dot{y} = Y(x, y)$. There is no closed paths in a simply connected region of the phase plane on which $\frac{\partial X}{\partial x} + \frac{\partial Y}{\partial y}$ is of one sign.

Theorem 1.9. (Dulac’s test)([95])

Given the system $\dot{x} = X(x, y), \dot{y} = Y(x, y)$. There is no closed paths in a simply connected region of the phase plane on which $\frac{\partial \rho X}{\partial x} + \frac{\partial \rho Y}{\partial y}$ is of one sign, where $\rho(x, y)$ is any function having continuous first partial derivatives.

For more details on the Poincaré-Bendixson theorem and its six corollaries on closed paths, one can refer to M. W. Hirsch et al. (2004)([77])

Theorem 1.10. (Hopf Bifurcation Theorem)([28])

Consider a second-order nonlinear autonomous ODE of the form

$$\dot{x} = f(x, \mu), x \in \mathbb{R}^2, \mu \in \mathbb{R}, \tag{1.8}$$

where f is a C^1 nonlinear vector field.

Suppose that the nonlinear autonomous system (1.8) has an equilibrium point $x = x^*(\mu)$, and that the associate Jacobian $(Df)_{x=x^*}$ has a pair of complex eigenvalues $\lambda_{1,2}(\mu) = \alpha(\mu) \pm \beta(\mu)i$. Assume that there exists a critical value μ_0 of μ such that :

1.1. Some mathematical notes

- (i) $\alpha(\mu_0) = 0$,
- (ii) $\beta(\mu_0) \neq 0$,
- (iii) $\left(\frac{\partial\alpha(\mu)}{\partial\mu}\right)_{\mu=\mu_0} \neq 0$.

Then, if particularly,

- (iv) $\left(\frac{\partial\alpha(\mu)}{\partial\mu}\right)_{\mu=\mu_0} > 0$,

the following results hold :

- (a) when $\mu = \mu_0$, there exists concentric trajectories around the equilibrium $x^*(\mu_0)$ which is then a center. The Hopf bifurcation is said to be degenerate.
- (b) when $\mu = \mu_0$, the equilibrium $x^*(\mu_0)$ is asymptotically stable and there exists a value $\bar{\mu} > \mu_0$ such that for any $\mu \in]\mu_0, \bar{\mu}[$, such that it exists around the unstable equilibrium $x^*(\mu_0)$, a limit cycle asymptotically stable with an amplitude proportional to $\sqrt{\mu - \mu_0}$. The Hopf bifurcation is said to be supercritical.
- (c) when $\mu = \mu_0$, the equilibrium $x^*(\mu_0)$ is unstable and there exists a value $\bar{\mu} > \mu_0$ such that for any $\mu \in]\mu_0, \bar{\mu}[$, such that there exists around the asymptotically stable equilibrium $x^*(\mu_0)$, a limit cycle unstable with an amplitude proportional to $\sqrt{\mu - \mu_0}$. The Hopf bifurcation is said to be subcritical.

Remark 1.2. If $\left(\frac{\partial\alpha(\mu)}{\partial\mu}\right)_{\mu=\mu_0} < 0$, then the conclusions of the above theorem are reversed.

Figures (1.3) and (1.4) are bifurcation diagrams of the following systems with one parameter α , $[\dot{x}_1 = \alpha x_1 - x_2 - x_1(x_1^2 + x_2^2), \dot{x}_2 = x_1 + \alpha x_2 - x_2(x_1^2 + x_2^2)]$, $[\dot{x}_1 = \alpha x_1 - x_2 + x_1(x_1^2 + x_2^2), \dot{x}_2 = x_1 + \alpha x_2 + x_2(x_1^2 + x_2^2)]$. They illustrate the two different types (supercritical and subcritical) of Hopf bifurcations.

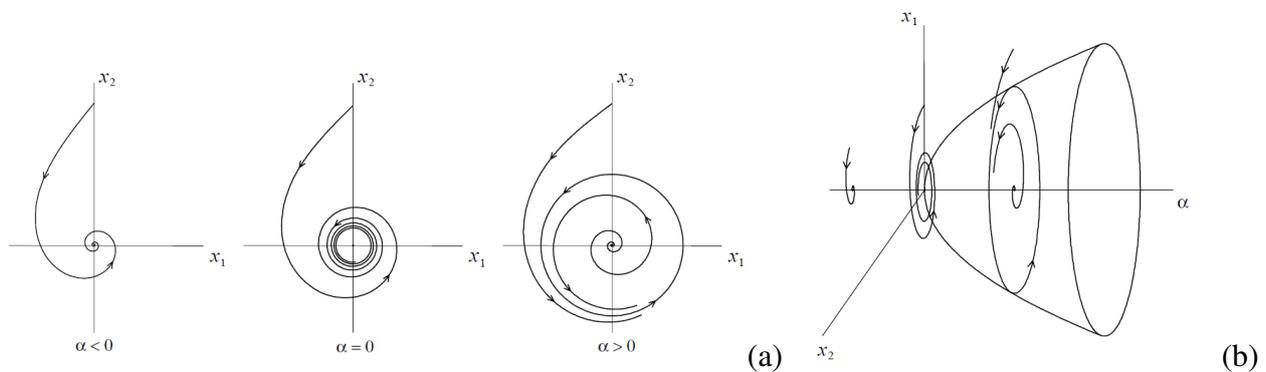


Figure 1.3: (a) Bifurcation diagram for the system in the phase space. (b) Bifurcation diagram for the system in the phase-parameter space. Supercritical Hopf bifurcation.

1.1. Some mathematical notes

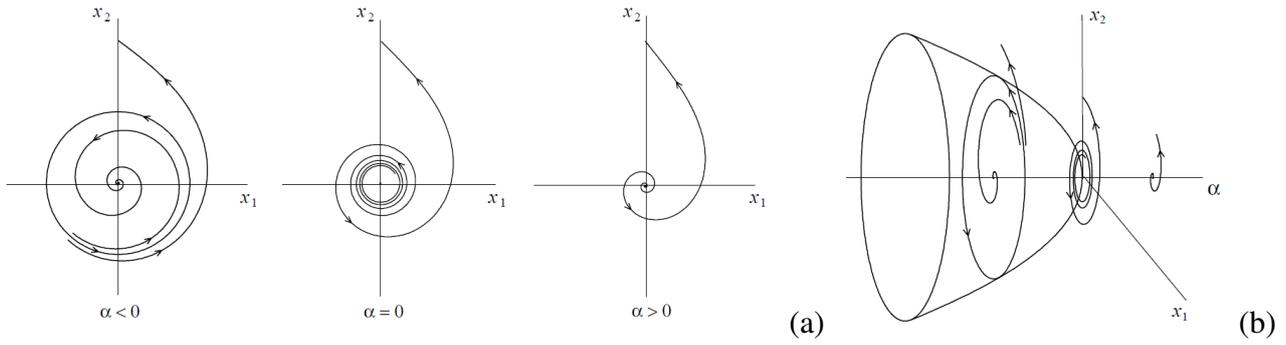


Figure 1.4: (a) Bifurcation diagram for the system in the phase space. (b) Bifurcation diagram for the system in the phase-parameter space. Subcritical Hopf bifurcation.

In the following table, we give a list of the different types of one parameter's bifurcations and their normal forms.

Table 1.1: Different Types of bifurcations

Type of bifurcation	Normal Form
Saddle-node	$\dot{x} = \mu \pm x^2 \quad x, \mu \in \mathbb{R}$
Transcritical	$\dot{x} = \mu x \pm x^2 \quad x, \mu \in \mathbb{R}$
Pitchwork	$\dot{x} = \mu x \pm x^3 \quad x, \mu \in \mathbb{R}$
Hopf	$\dot{z} = (\alpha + i)z + \beta z^2 \bar{z} \quad z \in \mathbb{C}, \mu \in \mathbb{R}$

Some authors refer the Hopf bifurcation theorem as the Poincaré-Andronov-Hopf bifurcation theorem because, the Hopf bifurcation theorem is named after Hopf, who gave the first proof in \mathbb{R}^n in 1942. But the theorem had been proved by Andronov and Léontovich in the late 1930s using techniques du to Poincaré and Bendixon.

Remark 1.3. In the above bifurcations, we have only one bifurcation parameter. There exists some more complicated types of bifurcations with two bifurcation parameters. Among those bifurcations with two parameters, we have the Cusp bifurcation, the Bautin (generalized Hopf) bifurcation, the Bogdanov-Takens (double-zero) bifurcation, the Fold-Hopf (zero-pair) bifurcation and the Hopf-Hopf bifurcation. For more details concerning those bifurcations, one can refer to Y. A. Kuznetsov (1998)([107]).

1.1.5 Optimal control theory

Consider a system in some applications, where the dynamics are captured by a model, whether it is by ordinary differential equations (ODEs), partial differential equations (PDEs), or discrete difference equations. Assume also that this system has a variable, or variables, which can be controlled from the outside. The question which naturally arises is how exactly to control this element in order to

produce the best outcome, as measured by some predetermined goal or goals. The mathematical theory behind answering these questions, often called optimal control theory or dynamic optimization, has found applications in a myriad of fields, from the biological sciences, to economics, to business and management, to physics and engineering. The objective of optimal control theory is to determine the control signals that will cause a process to satisfy the physical constraints and at the same time minimize (or maximize) some performance criterion. In this thesis, we apply optimal control theory to a delayed predator-prey model. That is why in what follows, we shall just give the result on the necessary optimality conditions for the delayed optimal control problem with mixed control-state constraints ([172]).

Let $[t_0, t_f]$ be the time interval, and τ_1 and τ_2 two positive constants less than $t_f - t_0$. We consider a retarded optimal control problem (ROCP) with two constants delays τ_1 and τ_2 in the state variable $x \in \mathbb{R}^n$. Without loss of generality, we assume that $\tau_1 < \tau_2$. The problem (ROCP) can be written as follows: Minimize

$$J(u, x) = g(x(t_f)) + \int_{t_0}^{t_f} L(t, x(t), x(t - \tau_1), x(t - \tau_2), u(t))dt, \quad (1.9)$$

subject to the retarded differential equation, boundary conditions and mixed-control state inequality constraints :

$$\dot{x} = f(t, x(t), x(t - \tau_1), x(t - \tau_2), u(t))dt, \quad (1.10)$$

$$x(t) = \varphi(t), \quad t \in [t_0 - \tau_1, t_0], \quad (1.11)$$

$$x(t) = \psi(t), \quad t \in [t_0 - \tau_2, t_0 - \tau_1], \quad (1.12)$$

$$W(x(t_f)) = 0, \quad (1.13)$$

$$\mathcal{C}(x(t), u(t)) \leq 0, \quad t \in [t_0, t_f], \quad (1.14)$$

where the functions :

$$g : \mathbb{R}^n \longrightarrow \mathbb{R}, L : [t_0, t_f] \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^m \longrightarrow \mathbb{R}, W : \mathbb{R}^n \longrightarrow \mathbb{R}^d, \\ L : [t_0, t_f] \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^m \longrightarrow \mathbb{R}^n, \mathcal{C} : [t_0, t_f] \times \mathbb{R}^n \times \mathbb{R}^m \longrightarrow \mathbb{R}^p$$

are assumed to be twice continuously differentiable with respect to their arguments.

Definition 1.14. (Admissible pair)([172])

A pair $p(\cdot) = (u(\cdot), x(\cdot))$ is an admissible pair for a given problem (ROCP) if the state $x(\cdot)$ and the control $u(\cdot)$ satisfy conditions (1.10)-(1.14).

Definition 1.15. (Locally optimal pair)([172])

An admissible pair (\hat{u}, \hat{x}) is a locally optimal pair or weak minimum for a given problem (ROCP) if the inequality $J(\hat{u}, \hat{x}) \leq J(u, x)$ holds for all (u, x) admissible in a neighborhood of (\hat{u}, \hat{x}) with $\|u(t) - \hat{u}(t)\| < \epsilon$ and $\|x(t) - \hat{x}(t)\| < \epsilon$ for $t \in [t_0, t_f]$ and ϵ sufficiently small.

Instead of considering a weak minimum, we could use the more general notion of Pontryagin minimum, thus admitting neighborhood of (\hat{u}, \hat{x}) in the L^1 -norm.

1.1. Some mathematical notes

Remark 1.4. In the absence of delays (i.e. $\tau_1 = \tau_2 = 0$), the initial value profiles given by conditions (1.11) and (1.12) are omitted. Moreover, condition (1.13) is replaced by a general condition of mixed type of the form $w(x(t_0), x(t_f)) = 0$. In this case, the Hamiltonian or Pontryagin function without constraints (1.14) is given by :

$$H(t; x; u; \lambda) := L(t, x, u) + \lambda^* f(t, x, u). \quad (1.15)$$

The augmented Hamiltonian is defined by adjoining the mixed control-state constraint (1.14) by multiplier $\mu \in \mathbb{R}^p$ to the Hamiltonian (1.16), that is,

$$\mathcal{H}(t; x; u; \lambda, \mu) := L(t, x, u) + \lambda^* f(t, x, u) + \mu^* \mathcal{C}(t, x, u) \quad (1.16)$$

where the symbol “*” denotes the transposition.

The following theorem deals with necessary optimality conditions for the optimal control of the delayed differential system (1.10) with mixed control-state constraints (1.11)-(1.14).

Theorem 1.11. ([172])

Let (\hat{u}, \hat{x}) be locally optimal for a ROCP with two delays $\tau_1 \neq 0$ and $\tau_2 \neq 0$ such that $\frac{\tau_1}{\tau_2} \in \mathbb{Q}$ for $(\tau_2 > 0)$ and $\frac{\tau_2}{\tau_1} \in \mathbb{Q}$ for $(\tau_1 > 0)$. Then, there exist an adjoint function $\hat{\lambda} \in W^{1,\infty}([t_0, t_f], \mathbb{R}^n)$, a multiplier function $\hat{\mu} \in L^\infty([t_0, t_f], \mathbb{R}^p)$ and a multiplier $\hat{\nu} \in \mathbb{R}^q$ such that for all $t \in [t_0, t_f]$, the following conditions hold :

1. Adjoint differential equation :

$$\begin{aligned} \dot{\hat{\lambda}}(t)^* &= -\mathcal{H}_x(t, x(t), x(t - \tau_1), x(t - \tau_2), u(t)) \\ &\quad - \mathcal{X}_{[t_0, t_f - \tau_1]}(t) \mathcal{H}_y(t + \tau_1, x(t + \tau_1), x(t + \tau_1 - \tau_2), u(t + \tau_1)) \\ &\quad - \mathcal{X}_{[t_0, t_f - \tau_2]}(t) \mathcal{H}_z(t + \tau_2, x(t + \tau_2), x(t + \tau_2 - \tau_1), u(t + \tau_2)). \end{aligned} \quad (1.17)$$

2. Transversality condition :

$$\lambda^*(t_f) = g_x(x(t_f)) + \nu^* W_x(t_f). \quad (1.18)$$

3. Minimum condition for Hamiltonian :

$$H(t, \hat{x}(t), \hat{x}(t - \lambda_1), \hat{x}(t - \lambda_2), \hat{u}(t), \hat{\lambda}(t)) \leq H(t, \hat{x}(t), \hat{x}(t - \lambda_1), \hat{x}(t - \lambda_2), u(t), \hat{\lambda}(t)), \quad (1.19)$$

$\forall u \in \mathbb{R}^m$ such that $\mathcal{C}(t, x(t), u) \leq 0$.

4. Local minimum for augmented Hamiltonian :

$$\mathcal{H}(t, \hat{x}(t), \hat{x}(t - \lambda_1), \hat{x}(t - \lambda_2), \hat{u}(t), \hat{\lambda}(t), \hat{\mu}(t)) = 0.$$

5. Nonnegativity of multiplier and complementarity condition :

$$\hat{\mu}(t) \geq 0 \quad \text{and} \quad \hat{\mu}_i(t) \mathcal{C}_i(t, \hat{x}(t), \hat{u}(t)) = 0, \quad \forall i = 1, \dots, p. \quad (1.21)$$

1.2 Predator-prey modelling

In the first subsection of this section, we give the basic models for the growth of single species. Those models are always used to formulate models for the interacting species. In the second subsection, we give the basic Lotka-Volterra and logistic Lotka-Volterra models for interacting species (the case of two populations) which are nowadays used for the formulation of most of the predator-preys models.

1.2.1 Simple single species models

1.2.1.1 Exponential Growth Population Model

The population density of a single species at time t will be denoted by $x(t)$, where it is assumed that x is everywhere differentiable, that is, x is a smooth function of t . Although unrealistic since $x(t)$ is an integer-valued function and thus not continuous, for populations with a large number of members, the assumptions of continuity and differentiability provide reasonable approximations. In many biological experiments the population biomass, which one might expect to be more nearly described by a smooth function than the population size, is often taken as the definition of $x(t)$. The rate of change of population density can be computed if the birth, death, and migration rates are known. A closed population has, by definition, no migration neither into nor out of the population. In this case, the population size changes only through births and deaths and the rate of change of population size is simply the birth rate minus the death rate. The formulation of a specific model requires explicit assumptions on the birth and death rates. Ideally, these assumptions are made with the goal of addressing specific biological questions such as under what conditions will interference competition (competition for hosts) and pathogen virulence lead to host-pathogen long-term coexistence. For micro-organisms, which reproduce by splitting, it is reasonable to assume that the rate of birth of new organisms is proportional to the number of organisms present. In mathematical terms, this assumption may be expressed by saying that if the population size at time t is x , then over a short time interval of duration h from time t to time $(t + h)$, the number of births is approximately bhx for some constant b , the per capita birth rate. Similarly, we may assume that the number of deaths over the same time interval is approximately μhx for some constant μ the per capita death rate. Hence, the net change in population size from time t to time $(t + h)$, which is $x(t + h) - x(t)$, may be approximated by $[(bh - \mu h)]x(t)$. The duration h of the time interval must be short to ensure that the population size does not change very much and thus that the numbers of births and deaths are approximately proportional to $x(t)$. We obtain the approximate equality :

$$x(t + h) - x(t) \approx (b - \mu)x(t)h. \quad (1.22)$$

The division by h gives :

$$\frac{x(t + h) - x(t)}{h} = (b - \mu)x(t), \quad (1.23)$$

and passage to the limit as h tends to 0 gives :

$$\frac{dx(t)}{dt} = (b - \mu)x(t) = rx(t), \quad (1.24)$$

1.2. Predator-prey modelling

where $r = b - \mu$ is the net growth rate. The equation (1.24) is called the exponential or Malthusian population model.

The approximate equality in (1.22) means that the difference between the two sides of (1.22) is so small that the result of dividing this difference by h gives a quantity that approaches zero as h tends to 0. This differential equation has the infinite family of solutions given by the one parameter family of functions $x(t) = ke^{rt}$; hence, this one parameter family gives a solution of (1.24) for every choice of the constant k . The most convenient way to impose a condition that will describe the population dynamics of a specific population is by specifying the initial population size at time $t = 0$ as $x(t_0) = x_0$. This choice selects the solution, $x(t) = x_0e^{rt}$. When $r > 0$ (or equivalently $b > \mu$) implies that the population size will grow unboundedly as t tends to $+\infty$, while $r < 0$ (or $b < \mu$) implies that the population size will approach zero as t tends to $+\infty$.

1.2.1.2 Logistic Growth Population Model

The assumption that the rate of growth of a population is proportional to its size (linear assumption) is usually unrealistic on longer time scales. In what follows, nonlinear assumptions are considered on the rate of population growth rates. Those assumptions lead to quite different qualitative predictions. It is assumed that total growth rates are not constants and depend on the size of the population. It is assumed that the birth rate $b = b_0 - b_x x$ is a decreasing function of x and the death rate $\mu = \mu_0 + \mu_x x$ is an increasing function of x where b_0 and μ_0 are respectively the birth rate and the death rate when x is too small. b_x and μ_x are respectively the strength of density-dependant of the birth and death rates. Replacing $b = b_0 - b_x x$ and $\mu = \mu_0 + \mu_x x$ in (1.24) gives :

$$\frac{dx(t)}{dt} = r \left(1 - \frac{x}{K}\right) x(t) \quad (1.25)$$

where $K = \frac{r}{b_x + \mu_x} = \frac{b_0 - \mu_0}{b_x + \mu_x}$ and is called the carrying capacity of the environment, which is usually determined by the available sustaining resources. It represents the population size that available resources can continue to support. The value r is called the intrinsic growth rate, because it represents the per capita growth rate achieved if the population size were small enough to ensure negligible resource limitations. Equation (1.25) is called the logistic model for population growth. This model was first studied by Belgian Mathematician Pierre Franois Verhulst in the middle of the 19th century. In this model, like the exponential model, the only mechanisms for changing the population size are births and deaths. There is nothing to account for migration into or out of the population.

Solving equation (1.25) with initial value $x(t_0) = x_0 > 0$ gives :

$$x(t) = \frac{x_0 K e^{rt}}{K + x_0 (e^{rt} - 1)}$$

with $0 < x_0 < K$.

The solution of the logistic initial value problem shows that the population size $x(t)$ approaches the limit K as t tends to $+\infty$. The logistic model predicts rapid initial growth for $0 < x_0 < K$, then a decrease in growth rate as time passes so that the size of the population approaches a limit. This

1.2. Predator-prey modelling

behavior is in agreement with the observed behavior of many populations, and for this reason, the logistic model is often used as a means of describing population size.

1.2.1.3 Generalized Logistic Growth Population Model

Although the logistic growth equation generates a curve that tends towards an exponential form at low values, its maximum slope, or "point of inflexion", is always at half the value of the upper asymptote, $\frac{K}{2}$. This is unsatisfactory, because the factors that determine the density at which the species x grows fastest are complex, so it is unlikely that all species grow fastest in monoculture when they are at half their maximum standing crop. Introducing another parameter into the equation could allow the shape of the upper part of the curve to be independent of the shape of the lower part, while still having an equation that tends towards an exponential form at low values of x . One option is the following generalized logistic growth population model or the Richards (1959)([145]) growth equation

$$\frac{dx(t)}{dt} = r \left(1 - \left(\frac{x}{K} \right)^q \right) x(t), \quad (1.26)$$

where q is a constant that allows the shape of the sigmoid curve to be varied.

When $q = 1$ the Richards equation matches the logistic equation, but for $q > 1$ the maximum slope of the curve is when $x > \frac{K}{2}$, and when $q < 1$ the maximum slope of the curve is when $x < \frac{K}{2}$. This allows a wider range of curves to be produced, but as q tends towards zero, the lowest value of y at the point of inflexion remains greater than $\frac{K}{e}$, where e represents the universal constant, the base of the natural logarithm.

For $q > 0$, the integrated form of the Richards equation (1.26) is

$$x(t) = K \left(1 + \exp(d - rqt) \right)^{-1/q},$$

where d is a parameter that indirectly defines the value of t (time) at which $x = \frac{K}{2}$.

Let's mention the fact that a new generalized logistic Sigmoid growth equation has been proposed by C. P. D. . Birsch (1999)([22]), with a comparison to the Richards growth equation.

There exist in the literature some others growth equations for single species (The Gompertz growth model, the model with Allee effects, . . .).

1.2.2 Models for interacting species

1.2.2.1 The Lotka-Volterra Predator-Prey Model

In 1925, Vito Volterra's son-in-law named Dr. Umberto Ancona has a conversation with Volterra. Dr. Umberto Ancona pointed out the fact that in the years following the First World War, the proportion of predator fish caught in the Upper Adriatic was up from before, whereas the proportion of prey fish was down. Inspired by his future son-in-law, Vito Volterra wrote a paper, entitled Fluctuations in the abundance of a species considered mathematically. Volterra (1926)([176]) developed a model to describe the interaction between a predator and a prey, based on the following assumptions :

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1. prey would multiply indefinitely (i.e. grow exponentially) in the absence of predators,
2. predator densities will decay exponentially to zero in the absence of the prey, due to starvation,
3. the proportional increase rate of the preys decreases as the number of predators increases,
4. the growth rate of predators increases when the number of preys increases.

During the same year, Alfred James Lotka (1925)([123]) published a book entitled Elements of Physical Biology in which he discussed the Volterra model for predator-prey interactions. It is safe to assume, of course that, the two was completely unaware of each other's work. It is this model that is known as the Lotka-Volterra predator-prey model. Taking into account the above assumptions made by V. Volterra, the Lotka-Volterra predator-prey model is governed by the following set of ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx - axy, \\ \dot{y}(t) = \epsilon axy - \mu y. \end{cases} \quad (1.27)$$

In those equations $x(t)$ and $y(t)$ denote the abundance of preys (food) and predators (consumers) at the time t , respectively. The parameter r represents the exponential growth rate of prey in the absence of the predator, while μ represents the death or mortality rate of the predators in the absence of prey. The parameter a represents the attack rate of predators, which equals the area or volume that a predator searches through during a single unit of time. The parameter ϵ represents the conversion efficiency, i.e. the efficiency with which predators convert consumed prey into offspring.

The analysis of model (1.27) ([147]) leads to the following results :

1. The two species fluctuate periodically in abundance, the period only depending on the coefficients of increase and of destruction of the two species, and on the initial numbers of the individuals of the two species.
2. The average numbers of the two species tend to constant values, whatever the initial may have been, so long as the coefficients of increase or of destruction of the two species and also the coefficients of protection and attack remain constant.
3. If we try to destroy individuals of both species uniformly and proportionally to their number, the average number of individuals of the eaten species grows and the average number of the eating species diminishes. But increased protection of the eaten species increases the average numbers of both.

Despite the brevity of the document and the modest closing sentence, Volterra established with his study a corner-stone for the theory about predator-prey interactions. The Lotka-Volterra predator-prey model, as it has been referred to since Volterra's contribution, forms a basis on which most if not all models of such interactions have been founded. In addition, it has become clear that predator-prey interactions are one of the most important causes of oscillations in species abundance. Hence, not only the model that Volterra studied, but also the fluctuations he reported are to the present day important

focal points for studying the dynamics of interacting species.

The Lotka-Volterra model represented one of the triumphs of early attempts at mathematical modelling in population biology. However, it turns out that there are serious flaws in the model. Any attempt at refinement by introducing self-limiting terms in the per capita growth rates such as in the logistic equation for single populations will lead to qualitatively different behavior of the solutions, orbits that spiral in toward the equilibrium rather than periodic orbits. The price of refinement of the model is loss of agreement with observation. In order to construct a model that predicts periodic solutions, we will have to assume nonlinear per capita growth rates for the two species.

1.2.2.2 The Logistic Lotka-Volterra Predator-Prey Model

The Lotka-Volterra predator-prey model assumes that, in the absence of predators, the prey population grows exponentially. This Malthusian growth is not realistic. Populations are often limited by their environment and usually use particular means to reach their carrying capacities respectively. So, it can be better to modify the Lotka-Volterra model by replacing the exponential growth of preys by a logistic growth. Hence, if we assume that, in the absence of predation, the growth of the prey population follows the logistic model, we obtain the following model :

$$\begin{cases} \dot{x}(t) = r \left(1 - \frac{x}{K}\right) x - axy, \\ \dot{y}(t) = \epsilon axy - \mu y, \end{cases} \quad (1.28)$$

where K is the carrying capacity of the prey population. One can remark that for large value of the carrying capacity K , this model is a small perturbation of the Lotka-Volterra model.

Let's set $K_c = \frac{\mu}{\epsilon a}$ and $K_s = \frac{\mu}{\epsilon a} \left(\frac{1}{2} + \frac{1}{2} \sqrt{1 + \frac{r}{\mu}} \right)$. Regarding the dynamic of the logistic Lotka-Volterra predator-prey model, the following conclusions hold ([147]) :

1. For $K < K_c$, the maximum prey abundance is insufficient to allow predators to persist. The internal steady state $\left(\frac{\mu}{\epsilon a}, \frac{r}{a} \left(1 - \frac{\mu}{\epsilon a K}\right) \right)$ adopts negative and hence biologically irrelevant values. The prey-only equilibrium $(K, 0)$ is a stable node.
2. For $K_c < K < K_s$, the internal steady state $\left(\frac{\mu}{\epsilon a}, \frac{r}{a} \left(1 - \frac{\mu}{\epsilon a K}\right) \right)$ is biologically feasible and is a stable node. The prey-only equilibrium $(K, 0)$ is a saddle point.
3. For $K > K_c$, the internal steady state $\left(\frac{\mu}{\epsilon a}, \frac{r}{a} \left(1 - \frac{\mu}{\epsilon a K}\right) \right)$ is still the only biologically feasible and stable steady state, but it has become a stable spiral. Hence, the approach to the steady state is always oscillatory.

Discussions

With respect to the two important predictions that were derived from the basic Lotka-Volterra predator-prey model, the model with logistic prey growth does not change the prediction that steady-state prey abundances are completely controlled by life-history characteristics of the predator. However, incorporating a logistic prey growth stabilizes the internal steady state, such that oscillation are not to be

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expected any longer. Even for very larger values of the prey carrying capacity the internal steady state is ultimately approached slowly. The slightest amount of density dependence in the prey growth hence stabilizes the oscillations of the basic Lotka-Volterra model. Because a very small perturbation of the model structure (i.e. adding even a tiny amount of density dependence in prey growth) changes the neutral stability of the steady state and the neutrally stable oscillations, the basic Lotka-Volterra model is not considered structurally stable.

In figure (1.5), we give an example of phase portraits of the Lotka-Volterra model ($\dot{N} = r_N N - \lambda_N N P$, $\dot{P} = \alpha_N N P - m P$) and that of the logistic Lotka-Volterra model ($\dot{N} = r_N (1 - \frac{N}{K_N}) - \lambda_N N P$, $\dot{P} = \alpha_N N P - m P$).

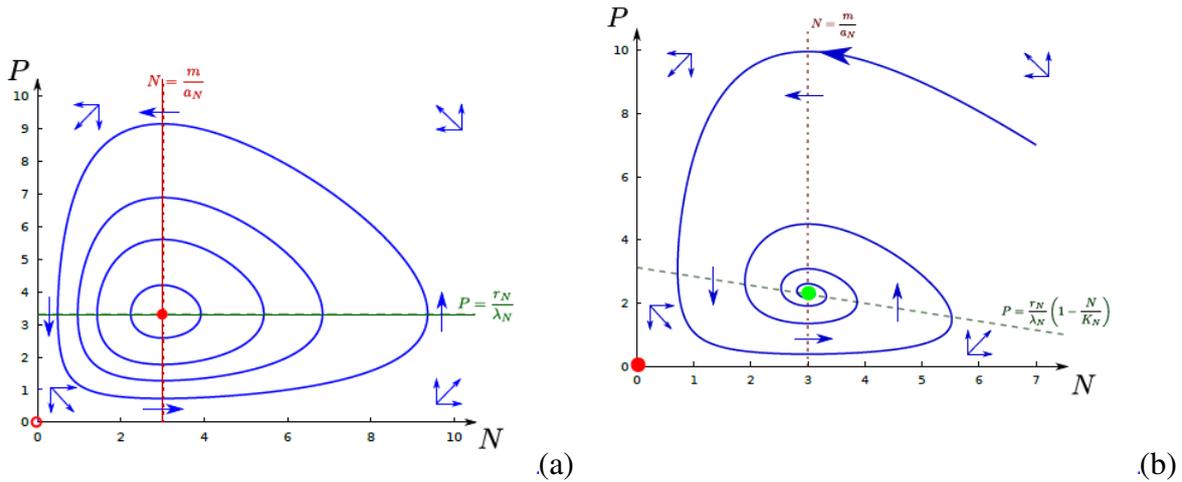


Figure 1.5: (a) Phase portrait of the Lotka-Volterra model where $r_N = 2$, $\lambda_N = 0.6$, $\alpha_N = 0.5$, $m = 1.5$ with initial conditions $(0.5, 4)$, $(1, 4)$, $(1.5, 4)$, $(2.5, 4)$, (b) Phase portrait of the logistic Lotka-Volterra model with $r_N = 2$, $r_P = 1.5$, $\lambda_N = 0.6$, $\alpha_N = 1$, $K_N = 10$, $m = 3$. From M. T. Alves ([3])

1.3 Functional Responses

After the modification of the Lotka-Volterra model by replacing the exponential growth of preys by the logistic growth, interactions between one population (predators) and another population (preys) eaten by the first one have been generalized by taking into account some assumptions. The set of ordinary differential equations for the dynamics of the interacting populations are then modified. In what follows, we recall assumptions and features for predator-prey models. Consider the class of predator-prey models that take as state variables the two total densities of the two populations, regarded as spatially homogeneous and without regard for age or size, and whose dynamics is based on continuous time. Considering the classical Gause type predator-prey system for the modelling of interacting species, the so-called Holling type functional responses are given in the first subsection and in the second subsection of this section, we give some others functional responses.

Let $x(t)$ and $y(t)$ denote densities of preys and predators at time t , respectively. The classical Gause

type predator-prey system takes the following form ([50]) :

$$\begin{cases} \dot{x}(t) = xg(x, K) - yp(x), \\ \dot{y}(t) = y(-d + cq(x)), \end{cases} \quad (1.29)$$

where :

1. $g(x, K)$ is a continuous and differentiable function describing the specific growth rate of the preys in the absence of predators and satisfying the following conditions :

(i) $g(0, K) = r > 0$

(ii) $g(K, K) = 0$

(iii) $g_x(K, K) < 0$

(iv) $g_x(x, K) \leq 0$

(v) $g_K(x, K) > 0$

where g_x and g_K are respectively the partial derivative of the function g with respect to x and K respectively.

2. $p(x)$ is the functional response of predators to the preys. It describes the change in the density of the prey attacked per unit time per predator as the prey density changes. It is continuous and differentiable and satisfies $p(0) = 0$. In general, it depends on many factors, for example, the various prey densities, the efficiency with which predators can search out and kill the prey, the handling time, etc. Some functional responses extensively used in modelling population dynamics will be given in a subsection below.
3. $q(x)$ is the numerical response. It describes how predators convert the consumed prey into the growth of predators. In most classical predator-prey models, $q(x) = p(x)$ (conversion of biomass law).
4. The parameter c indicates the efficiency of predators in converting consumed prey into their growth.
5. The parameter d is the predator mortality rate.

An interesting case is when the predator growth function is different from the predator predation function. Moreover, the predator growth term is described by a function of not the prey density only, instead it is assumed to be dependent on the ratio of predators and their prey $\frac{y}{x}$. We study intensively the Leslie-Gower predator-preys models which are examples of those particular models, in the third chapter. In what follows, we recall some particular functional responses used for predator-prey modelling.

1.3.1 Holling type Functional responses

In order to describe the change in the rate of consumption of prey by a predator when the density of prey varies, Holling introduced the term functional response in his papers on predator-prey dynamics ([78], ([79])). In the literature, there exist some functional responses with the name of Holling and, some other functional responses without Holling's name. In what follows, we give a non-exhaustive list of some functional responses.

1.3.1.1 The Holling type I functional response

It is given with the assumption that the number of preys eaten by a predator depends linearly to the density of the preys. This assumption is unrealistic due to the fact that, it is not possible for a predator to exceed a certain number of preys even if there is abundance of preys. The saturation effect needs to be taken into account. The Holling type I functional response which is also called the Lotka-Volterra functional response is given by :

$$p(x) = ax \quad (1.30)$$

where a is the handling rate of the predator and x denotes the density of preys.

The other Holling type functional responses have been formulated with the following assumptions :

1. The saturation effect of predator is taken into account. It means that a predator can eat preys up to a certain number which cannot be exceeded even if preys are abundant.
2. A predator divides its time for two activities. The predator has to look for preys so he needs searching time for it. After that, he needs handling time used to hunt, to catch, to kill and to eat the prey.

1.3.1.2 The Holling type II functional response

Also called Michaelis-Menten functional response, the Holling type II response function is given by the following equalities :

$$p(x) = \frac{B\alpha x}{1 + B\beta x} = \frac{ax}{x + D}, \quad (1.31)$$

where :

1. α is the searching time of preys for the predator
2. β is the handling time of preys for the predator
3. B is the predation rate per unit of time
4. $a = \frac{\alpha}{\beta}$ is the maximal growth rate of the predator. It is also the rate of saturation constant.
5. $D = \frac{1}{B\beta}$ is the rate of half saturation constant.

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1.3.1.3 The Holling type III functional response

The Holling type III functional response is given by the following equalities :

$$p(x) = \frac{B\alpha x^2}{1 + B\beta x^2} = \frac{ax^2}{x^2 + D}, \quad (1.32)$$

where the parameters α , β , B , a , D are the same used for the Holling type II functional response (1.31) with the same meanings.

The Holling type III functional response can be generalized ([89]) by the following equality (1.33) and we have the so-called Generalized Holling type III or sigmoidal functional response:

$$p(x) = \frac{mx^2}{ax^2 + bx + 1} \quad (1.33)$$

where m , a are positive constants and b a constant satisfying $b > -2\sqrt{a}$ (so that $ax^2 + bx + 1 > 0$ for all $x \geq 0$ and hence $p'(x) > 0$ for $x > 0$).

One can remark that when x approaches infinity, there exists a saturation constant $\frac{m}{a}$ for predators. When $b < 0$, the predation increases to a maximum and then decreases, thus $p(x)$ describes the situation where the preys can better defend or disguise themselves when their population density becomes large enough. When $b \geq 0$, the predators increase their feeding rates until some saturation level is reached.

1.3.1.4 The Generalized Holling type VI functional response

Also called the Monod-Haldane ([148]) functional response, the generalized Holling type IV ([171]) functional response is given by the following equality :

$$p(x) = \frac{mx}{ax^2 + bx + 1} \quad (1.34)$$

where m , a are positive constants and b a constant. When $b = 0$, the function is called the Holling type IV ([116]) functional response in the literature.

The generalized Holling type III functional response with $b < 0$ and the generalized Holling type IV functional response are nonmonotone functions.

Some other functional responses without the Holling name can be found in the literature with the name of authors. In the following subsection, we give some of them.

1.3.2 Some Other Functional Responses

1.3.2.1 The Ivlev functional response

The Ivlev type functional response is a prey-dependent functional response suggested by Ivlev (1961)([92]). It is both monotonically increasing and uniformly bounded. It is given by the following equality :

$$p(x) = a(1 - e^{-\gamma x}), \quad (1.35)$$

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where the parameters a and γ are positive constants standing respectively for the maximal growth rate of the predators or the saturation constant and the efficiency of the predators for capturing preys. Many authors([10], [103], [168]) have studied predator-prey models with the Ivlev type functional response.

1.3.2.2 The Hassell-Varley functional response

Most of the functional responses are functions depending only on the prey density. That is why they are called prey-dependent functional responses. But there exists in the literature some functional responses which are functions depending on both predator and prey densities called ratio-dependent functional responses. For example, Arditi and Ginzburg (1989)([4]) have proposed the following functional response (1.36) by modifying the well-known Holling type II functional response.

$$p(x, y) = \frac{ax}{x + Dy}, \quad (1.36)$$

where the parameters a and D are positive constants which stand respectively for capturing rate and half saturation constant.

The Hassell-Varley functional response is a ratio-dependent functional response proposed by Hassell and Varley (1969)([75]) by the following equality :

$$p(x, y) = \frac{ax}{x^\gamma + Dy}, \quad (1.37)$$

where the positive constant γ is called the Hassell-Varley constant.

In a typical predator-prey interaction where predators do not form groups, one can assume that $\gamma = 1$, producing the so-called ratio-dependent predator-prey dynamics. For terrestrial predators that form a fixed number of tight groups, it is often reasonable to assume that $\gamma = \frac{1}{2}$. For aquatic predators that form a fixed number of tight groups, $\gamma = \frac{1}{3}$ may be more appropriate. Since most predators do not form a fixed number of tight groups, it can be argued that for most realistic predator-prey interactions, $\gamma \in [\frac{1}{2}, 1)$. A predator-prey model with Hassell-Varley type functional response has been studied by S. B. Hsu et al. (2008)([85]).

1.3.2.3 The Beddington-DeAngelis functional response

The Beddington-DeAngelis functional response is a ratio-dependent functional response proposed by Beddington and DeAngelis ([13], [44]). It is given by the following equality :

$$p(x, y) = \frac{mx}{a + bx + cy}, \quad (1.38)$$

where :

1. m represents the maximum number of prey population that predator population can eat per time,
2. a represents the prey density, where the attack rate is half-saturated,

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3. b is a positive constant which denotes the effect of handling time for predators,
4. c is a positive constant and measures the magnitude of interference among predators.

It is obvious that two cases are possible as following. One case is that, if $b = 1$, $c = 0$ and $a > 0$, then it reduces to a Holling type II functional response (or Michaelis-Menten functional response). The other case is that, if $b = 0$, $c = 0$ and $a > 0$, then it reduces to a linear mass-action functional response (or Holling type I functional response).

1.3.2.4 The Crowley-Martin functional response

The Crowley-Martin type functional response is classified as one of predator-dependent functional responses, i.e., that are functions of both prey and predator abundance because of predator interference. It is assumed that predator-feeding rate decreases by higher predator density even when prey density is high, and therefore the effects of predator interference in feeding rate remain important all the time whether an individual predator is handling or searching for a prey at a given instant of time.

There may be a situation that an increase of consumer (predator) density implies the decrease in feeding rate of predator due to mutual interference among individual of predators. In this functional response, the predators do not interfere with one another's activities. So the competition among predators for food comes from the depletion of preys. But the functional response in prey-predator models must be predator dependent. Crowley and Martin (1989)([41]) proposed a predator-dependent functional response of the form :

$$p(x, y) = \frac{\alpha x}{1 + ax + by + abxy}, \quad (1.39)$$

where :

1. α is a positive parameter that describes the effects of capture rate,
2. a is a positive parameter that represents handling time,
3. b is a positive parameter which stands for the magnitude of interference among predators on the feeding rate.

The intuitive and experimental observations infer that a decrease in feeding rate of consumers (predators) per unit consumer is due to mutual interference among predators. This is a function of both prey and predator due to predator interference. If the prey density is high, then the predator feeding rate can decrease by higher predator density. Therefore, the effects of predator interference on feeding rate remain important all the time whether an individual predator is handling or searching for a prey at a given instant of time ([202]).

This represents the per capita feeding rate of predator. Depending on parameters a and b , the following cases arise :

- (i) When $a > 0$, $b = 0$, the Crowley-Martin type of functional response is simplified to Michaelis-Menten (or Holling type II) functional response;

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- (ii) When $a = 0, b > 0$, it expresses a saturation response;
- (iii) When $a = 0, b = 0$, the Crowley-Martin type of functional response is simplified to a linear mass action function response (or Holling type I).

In table (1.2), we summarize the functional responses listed in the section.

Table 1.2: Different Types of Predators Functional Responses

Holling I	ax
Holling II	$\frac{B\alpha x}{1 + B\beta x} = \frac{ax}{x + D}$
Holling III	$\frac{B\alpha x^2}{1 + B\beta x^2} = \frac{ax^2}{x^2 + D}$
Generalized Holling III	$\frac{mx^2}{ax^2 + bx + 1}$
Holling IV	$\frac{B\alpha x}{1 + B\beta x^2} = \frac{ax}{x^2 + D}$
Generalized Holling IV	$\frac{mx}{ax^2 + bx + 1}$
Ivlev	$a(1 - e^{-\gamma x})$
Crowley-Martin	$\frac{\alpha x}{1 + ax + by + abxy}$
Hassel-Varley	$\frac{ax}{x^\gamma + Dy}$
Beddington-DeAngelis	$\frac{mx}{a + bx + cy}$

EFFECTS OF PREY REFUGE, FUNCTIONAL RESPONSES, ADDITIONAL FOOD, HARVESTING AND TIME DELAY ON PREDATOR-PREY MODELS

Abstract

In this chapter, a brief literature review on predator-prey models is done. Based on the basic Lotka-Volterra predator-prey model, many others predator-prey models have been proposed by several authors using different assumptions, in other to have more realistic models which are close to the reality. The aim of this chapter is to recall results on effects of a prey refuge, a functional response, additional fixed food for predators, harvesting and time delay(s) on the dynamic of a predator-prey model. In what follows, we recall some predator-prey models incorporating a prey refuge and effects of prey refuge in the first section. Some models studied using different functional responses and effects of a functional response are presented in the second section. In the third section, some predator-prey models incorporating additional fixed food for predators and effects of additional fixed food for predators are presented. In the fourth section, some models incorporating different types of harvesting functions and effects of harvesting are given. In the fifth and last section, some predator-prey models incorporating discrete time delay(s) and effects of discrete time delay(s) are presented.

2.1 Effects Of Preys Refuge on Predator-Prey Models

In the presence of predator population, prey population shows a variety of defense mechanisms, such as changes in life history, morphological and behavioral traits. Among them, behavioral changes, e.g., migration and refuge are the most effective defense strategies observed in the prey population (Laforsch and Tollrian, (2004)([108]); Hanazoto et al. (2001) ([69]); Dodson (1988) ([48]); Lampert (1989) ([109]); Samanta et al. (2011) ([156]) (2013) ([157]); Samanta and Chattopadhyay (2013) ([157]); Abrams (2008) ([1]); Collings (1995) ([35]); Gonzalez-Olivares and Ramos-Jiliberto (2003) ([60])).

In the presence of predators, prey population often moves to areas where they are safe from their predators, which is better known as prey refuge. For example, mite predator-prey interactions often exhibit spatial refugia which afford the prey some degree of protection from predation (Collings (1995) ([35])). Zooplankton use macrophytes as day-time refuge areas when trying to escape from pelagic predators (Sagrario G. (2009) ([153])). Huffaker and Kennett (1956) ([90]) noted that strawberry plants provide physical barriers protecting part of the population of cyclamen mites, *Tarsonemus pallidus* Banks, from predation by *Typhlodromus* mites. Huffaker (1958) ([91]) experimentally showed that prey refuge in *Eotetranychus sex maculatus* Riley reduces the chance of extinction due to predation by *Metaseiulus occidentalis* Nesbitt. The effect of prey refuge on the dynamics of interacting populations is governed by the hypothesis that hiding behavior of prey reduces the prey mortality due to reduction in predation success (Gonzalez-Olivares and Ramos-Jiliberto, (2003) ([60])). In order to study effects of preys refuge on a predator-prey model, the following model (2.1) has been proposed using the generalized Gause formulation (1.29) for interactions between predators and their preys :

$$\begin{cases} \dot{x}(t) &= xg(x - x_R, K) - yp(x), \\ \dot{y}(t) &= y(-d + cq(x - x_R)), \end{cases} \quad (2.1)$$

where x_R is a quantity of prey population which incorporates refuges and which can be considered from two alternative points of view. The first one is when the quantity of hiding prey is proportional to the density of prey ($x_R = \beta x$). The parameter $\beta \in [0, 1[$ stands for the rate of refuge of prey population or the strength or prey refuge. This means that when $\beta = 0$, all the preys are available for predation. $\beta x(t)$ models the capacity of the refuge at the time t and so $(1 - \beta)x(t)$ of the preys are available for predation. The second one is when the quantity of hiding prey is a constant number ($x_R = R$). R is a fixed number of preys using refuge. It means that if we have R preys protected by the refuge, it will remain $x(t) - R$ preys available for predation at the time t . Obviously, we have $0 \leq R < x(t)$. In the literature, most of predator-prey models incorporating preys refuge are presented with the logistic growth for preys. In what follows, we present some predator-prey models incorporating prey refuges and effects of prey refuges.

2.1.1 Some predator-prey models incorporating prey refuges

2.1.1.1 The Z. Ma et al. model (2009)

Z. Ma et al. (2009)([124]) have studied the role of prey refuges on some predator-prey models. In their models, the refuges are considered as two types : a constant proportion of prey and a fixed number of preys using refuges. For applications, they used the Rosenzweig, the Ivlev and the Holling types functional responses.

1. A constant proportion of prey using refuges

When there is a constant proportion of preys using refuges ($x_R = \beta x$), the Ma et al. model is

the following set of ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - p\varphi(x - \beta x)y, \\ \dot{y}(t) = (q\varphi(x - \beta x) - d)y, \end{cases} \quad (2.2)$$

where r , K , p , q , d are all positive constants which have biological meanings accordingly. r is the intrinsic per capita growth rate of the prey population, K is the environmental carrying capacity of the prey population, p is the maximal per capita consumption rate of predators, d is the per capita death rate of predators, and q is the efficiency with which predators convert consumed preys into new predators. The term φ represents the functional response of the predator population. The following models have been obtained for the three different functional responses.

(a) Case of Rosenzweig functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - p(1 - \beta)^a x^a y, \\ \dot{y}(t) = (q(1 - \beta)^a x^a - d)y, \end{cases} \quad (2.3)$$

where $0 < a < 1$.

(b) Case of Ivlev functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - p(1 - e^{-a(1-\beta)x})y, \\ \dot{y}(t) = (q(1 - e^{-a(1-\beta)x}) - d)y. \end{cases} \quad (2.4)$$

(c) Case of Holling functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{p(1 - \beta)^\gamma x^\gamma y}{a + (1 - \beta)^\gamma x^\gamma}, \\ \dot{y}(t) = \left(\frac{q(1 - \beta)^\gamma x^\gamma}{a + (1 - \beta)^\gamma x^\gamma} - d\right) y. \end{cases} \quad (2.5)$$

2. A constant number of prey using refuges

(a) Case of Rosenzweig functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - p(x - R)^a y, \\ \dot{y}(t) = (q(x - R)^a - d)y, \end{cases} \quad (2.6)$$

where $0 < a < 1$.

(b) Case of Ivlev functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - p(1 - e^{-a(x-R)})y, \\ \dot{y}(t) = (q(1 - e^{-a(x-R)}) - d)y. \end{cases} \quad (2.7)$$

(c) Case of Holling functional response

For this case, the model is given by the following ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{p(x-R)^\gamma y}{a + (x-R)^\gamma}, \\ \dot{y}(t) = \left(\frac{q(x-R)^\gamma}{a + (x-R)^\gamma} - d\right) y. \end{cases} \quad (2.8)$$

2.1.1.2 The T. K. Kar model (2005)

T. K. Kar (2005)([98]) consider a prey-predator model with Holling type II response function incorporating a constant proportion prey refuge. His model which is then a modified Rosenzweig-MacArthur predator-prey model is the following one :

$$\begin{cases} \dot{x}(t) = \alpha x \left(1 - \frac{x}{K}\right) - \frac{\beta(1-m)xy}{1 + a(1-m)x}, \\ \dot{y}(t) = \left(\frac{c(1-m)x}{1 + a(1-m)x} - \gamma\right) y. \end{cases} \quad (2.9)$$

Here a denotes the intrinsic growth rate and K the carrying capacity of preys; γ is the death rate of predators; $\frac{\beta}{a}$ is the maximum number of preys that can be eaten by each predator in unit time; $\frac{1}{a}$ is the density of preys necessary to achieve one half that rate; c is the conversion factor denoting the number of newly born predators for each captured prey. The term $\frac{\beta x}{1 + ax}$ denotes the functional response of predators. The model incorporates refuge protecting mx of the preys, where $m \in [0; 1)$ is constant. This leaves $(1 - mx)$ of the prey available to predators.

2.1.1.3 The Y. Huang et al. model (2006)

Y. Huang et al. (2005)([98]) have proposed and studied a model by modifying a predator-prey model with the Holling type III functional response. They incorporated a constant proportion refuge of preys. Their model is given by the following set of two ordinary differential equations :

$$\begin{cases} \dot{x}(t) = ax - bx^2 - \frac{\alpha(1-m)^2 x^2 y}{\beta^2 + (1-m)^2 x^2}, \\ \dot{y}(t) = \left(\frac{k\alpha(1-m)^2 x^2}{\beta^2 + (1-m)^2 x^2} - c\right) y. \end{cases} \quad (2.10)$$

Here a denotes the intrinsic growth rate, b is the strength of competition among individual of preys (such that $\frac{a}{b}$ is the carrying capacity of the prey), c is the death rate of predators, α is the maximal growth rate or the saturation constant, β the half saturation constant, k is the conversion factor denoting the number of newly born predators for each captured prey. The term $\frac{\alpha(1-m)^2 x^2}{\beta^2 + (1-m)^2 x^2}$ denotes

the Holling type III functional response of predators with the incorporation of the prey refuge.

According to the analysis of the above models regarding effects of prey refuges on the dynamic of a predator-prey model, the following effects have been obtained.

2.1.2 Fluctuating population densities effects

From the analysis of the Z. Ma et al. (2009)([124]), we have the following conclusions :

1. The equilibrium density of prey population increases as refuges used by prey increases, while that of predators firstly increases and then decreases with prey refuges. In fact, it is easy to show that there is an increase in the equilibrium density of both prey and the predator population as the refuges increase under a very restricted set of conditions. This occurs when the equilibrium density of preys population is less than $\frac{K}{2}$ for either a constant proportion or a fixed number of preys using refuges.
2. When the refuges using by preys are high enough, prey population reaches its maximum environmental carrying capacity and predator population can go extinct.

According to T. K. Kar (2005)([98]), increasing the amount of refuge can increase preys densities and lead to populations outbreaks. So a refuge can be important for the biological control of a pest.

2.1.3 Stabilizing and destabilizing effects

For Z. Ma et al. (2009)([124]), the effects of prey refuges play an important role in determining the stability of the interior equilibrium point of the considered model. On the one hand, under a very restricted condition, the refuges used by preys have a stabilizing effect, that is, increases the local stability of the interior equilibrium. Here, stabilization or increase of stability refers to cases where an interior equilibrium point changes from repeller to an attractor due to changes in the value of a control parameter. On the other hand, the refuges have a destabilizing effect on the stability of the positive equilibrium point when a given assumption holds. In their paper, destabilization or decrease of stability is with regard to cases where a positive equilibrium point changes from locally stable state to an unstable state due to changes in the value of the controlled parameter.

According to Y. Huang et al. (2005)([98]), The prey refuge has a stabilizing effect on prey-predator interactions. If a small refuge is added to the model which is considered, the refuge will not alter the dynamical stability of the neutrally stable Lotka-Volterra model, adding a large refuge to the model replaced the oscillatory behavior with a stable equilibrium.

Remark 2.1. Comparing the conclusions obtained from analyzing stability properties of two types of refuges using by preys, Z. Ma et al. (2009)([124]) have obtained that the refuges which protect a constant number of preys have a stronger stabilizing effect on population dynamics than the refuges which protect a constant proportion of preys.

2.1.4 Appearance of limit cycles

According to T. K. Kar (2005)([98]), the following results hold :

1. If $m = 1 + \frac{\gamma a + c\beta}{ka(\gamma a - c\beta)}$, then system (2.9) enters into Hopf type small amplitude periodic solutions (limit cycles) near the interior equilibrium.
2. If $m \leq 1 + \frac{\gamma a + c\beta}{ka(\gamma a - c\beta)}$, then system (2.9) has exactly one limit cycle which is globally asymptotically stable.
3. If $c\beta > \gamma a$, the interior equilibrium exists if $+\frac{\gamma a + c\beta}{ka(\gamma a - c\beta)} < m < +\frac{\gamma + c\beta}{k(\gamma a - c\beta)}$ and a globally stable limit cycle exists when $m \leq 1 + \frac{\gamma a + c\beta}{ka(\gamma a - c\beta)}$.

The following results has been obtained by Y. Huang et al. (2005)([98])from the model (2.10) :

1. If $m < 1 + \frac{2bc\beta}{a(k\alpha - 2c)}\sqrt{\frac{c}{k\alpha - c}}$, then system (2.10) admits at least one limit cycle.
2. If $0 < m < 1 + \frac{2bc\beta}{a(k\alpha - 2c)}\sqrt{\frac{c}{k\alpha - c}}$, then system (2.10) admits only one limit cycle which is globally asymptotically stable.

2.2 Effects Of Functional Response on Predator-Prey Models

2.2.1 Some predator-prey models with different functional responses

2.2.1.1 Predator-prey model with Holling type II functional response

The predator-prey model with logistic growth for preys and a Holling type II functional response is also called the Roseinzweig-MacArthur predator-prey model. Interactions between prey and predator populations with the Holling type II functional response and logistic growth for preys are governed by the following set of ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx\left(1 - \frac{x}{K}\right) - \frac{axy}{1 + ahx}, \\ \dot{y}(t) = \left(\frac{cax}{1 + ahx} - m\right)y, \end{cases} \quad (2.11)$$

where K is the environmental capacity, a is the prey capture rate, h is the capture time, m is the predators intrinsic mortality, and c denotes the conversion efficiency of ingested preys into the predators.

2.2.1.2 Predator-prey model with Holling type III functional response

A predator-prey model with logistic growth for preys and Holling type III functional response has been studied by C. Jun-Ping and Z. Hong-De (1986)([97]). Their model is the following one :

$$\begin{cases} \dot{x}(t) = ax - bx^2 - \frac{\alpha x^2 y}{x^2 + \beta^2}, \\ \dot{y}(t) = \left(\frac{k^2}{x^2 + \beta^2} - c\right)y. \end{cases} \quad (2.12)$$

2.2. Effects Of Functional Response on Predator-Prey Models

where the parameters a, b, c, α, β and k are positive constants standing respectively for the intrinsic growth rate of the preys, the strength of competition among individual of preys (such that $\frac{a}{b}$ is the carrying capacity of the prey), the death rate for the predators, the maximal growth rate or the saturation constant, the half saturation constant, the conversion factor denoting the number of newly born predator for each captured prey.

2.2.1.3 Predator-prey model with Holling type IV functional response

S. Ruan and D. Xiao (2001)([148]) have considered a predator-prey system with nonmonotonic functional response. They considered only the system with the simplified Monod-Haldane or Holling type IV function $p(x) = \frac{mx}{a+x^2}$. Their model is the following one :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{xy}{a+x^2}, \\ \dot{y}(t) = \left(\frac{\mu x}{a+x^2} - D\right) y. \end{cases} \quad (2.13)$$

After S. Ruan and D. Xiao (2001)([148]), J. C. Huang and D. Xiao (2004)([86]) have studied the dynamics of a predator-prey system with the original Monod-Haldane or Holling type-IV function $p(x) = \frac{mx}{a+bx+x^2}$. Their model is given by the following set of two ordinary differential equations:

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{xy}{a+bx+x^2}, \\ \dot{y}(t) = \left(\frac{\mu x}{a+bx+x^2} - D\right) y, \end{cases} \quad (2.14)$$

where $K > 0$ is the carrying capacity of the prey population and $D > 0$ is the death rate of the predator population, and $r > 0$ is the maximum growth rate of the preys, $\mu > 0$ is the maximum predation rate, and $a > 0$ is the so-called half-saturation constant. The parameter b is such that the denominator of above system does not vanish for non-negative x and $b > -2\sqrt{a}$.

2.2.1.4 Predator-Prey Model with Ivlev type functional response

The Ivlev type functional response is among those functional responses which do not belong to the set of Holling type functional response. In an article on the dynamics of predator-prey models with the Ivlev type functional response, K. Ryu (2015)([150]) has studied the following model :

$$\begin{cases} \dot{x}(t) = rx(1-x) - (1-e^{-ax})y, \\ \dot{y}(t) = ((1-e^{-ax}) - D)y, \end{cases} \quad (2.15)$$

where r, a and D are positive constants that stand for the prey's intrinsic growth rate, the efficiency of the predator for capturing prey and the predator death rate, respectively. Here $x(t)$ and $y(t)$ are the population densities of prey and predator populations at time t , respectively.

2.2.1.5 Predator-Prey Model with Hassel-Varley type functional response

The Hassel-Varley functional response is one of those ratio-dependent functional response different from density dependent functional responses, which have been built for predator-prey interactions. The Hassel-varley type functional response has been used by SZE-Bi Hsu et al. (2008)([85]) in a model with logistic growth for preys. They argued that predator-prey models with Hassell-Varley type functional response are appropriate for interactions where predators form groups. Their model is the following set of two ordinary differential equations :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{x + my^\gamma}, \\ \dot{y}(t) = \left(\frac{fx}{x + my^\gamma} - D\right) y, \end{cases} \quad (2.16)$$

where $\gamma \in (0, 1)$ is the Hassell-Varley constant, the constants r, K, c, m, f, D are positive that stand for prey intrinsic growth rate, carrying capacity, capturing rate, half saturation constant, maximal predator growth rate, predator death rate, respectively.

2.2.2 Bifurcating effects and appearance of limit cycles

F. Wu and Y. Jiao (2019)([180]) have studied the model (2.11) with the following results :

Setting $X = \frac{x}{rK}, Y = \frac{y}{hKr^2}$ and $T = rt$. Then model (2.11) becomes :

$$\begin{cases} \dot{X}(T) = X(1 - X) - \frac{XY}{X + \alpha}, \\ \dot{Y}(T) = \left(\frac{RX}{X + \alpha} - \sigma\right) Y, \end{cases} \quad (2.17)$$

with $\alpha = \frac{1}{ahKr}, \sigma = \frac{m}{r}$ and $R = \frac{c}{hr}$,

1. System (2.17) enters transcritical bifurcation around $R = (1 + \alpha)\sigma$.
2. Let us assume $R > \sigma(\alpha + 1)$ and $\alpha < 1$. If $a(R_0) < 0$ ([180], p.9), the periodic solution of the Hopf bifurcation from the positive equilibrium point $E_*(x^*, y^*)$ is asymptotically stable, the Hopf bifurcation is subcritical. If $a(R_0) > 0$ ([180], p.9), the periodic solution of the bifurcation is unstable, and the Hopf bifurcation is supercritical.

C. Jun-Ping and Z. Hong-De (1986)([97]) have proposed a qualitative analysis of the model (2.12) and give conditions for the existence and uniqueness of limit cycles around the positive equilibrium point. They concluded that if $k\alpha - c > 0, \frac{k\alpha}{2} < c < k\alpha$ and $a > \frac{2bc\beta}{2c - k\alpha} \sqrt{\frac{c}{k\alpha - c}}$, then there is a stable limit cycle around the positive equilibrium point $E_*(x^*, y^*)$, where $x^* = \beta \sqrt{\frac{c}{k\alpha - c}}$ and $y^* = \left(a - b\beta \sqrt{\frac{c}{k\alpha - c}}\right) \frac{k\beta}{\sqrt{c(k\alpha - c)}}$.

S. Ruan and D. Xiao (2001)([148]) have shown that the model (2.13) exhibits the Bogdanov-Takens bifurcation. They have also shown that, by choosing the carrying capacity of the preys and the death rate of the predators as bifurcation parameters, the system (2.13) undergoes a series of bifurcations

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including the saddle-node bifurcation, the supercritical and subcritical Hopf bifurcations, and the homoclinic bifurcation.

After S. Ruan and D. Xiao (2001)([148]), J. C. Huang and D. Xiao (2004)([86]) have studied the dynamics of a predator-prey system with the original Monod-Haldane or Holling type-IV function $p(x) = \frac{mx}{a + bx + x^2}$. The qualitative analysis of the model (2.14) indicates that it has a unique stable limit cycle. The bifurcation analysis of the system (2.14) exhibits static and dynamical bifurcations including saddle-node bifurcation, Hopf bifurcation, homoclinic bifurcation and bifurcation of cusp-type with codimension two (ie, the Bogdanov-Takens bifurcation), and it also exists codimension three degenerated equilibrium and homoclinic orbit.

In an article on the dynamics of predator-prey models with the Ivlev type functional response, K. Ryu (2015)([150]) has studied the existence and the uniqueness of limit cycles. He has shown that if $D < 1 - e^{-a}$ and $a > -\frac{(2D+(1-D)\ln(1-D))\ln(1-D)}{D+(1-D)\ln(1-D)}$, then system (2.15) has a unique stable limit cycle. The Hassel-varley type functional response has been used by SZE-Bi Hsu et al. (2008)([85]) in a model with logistic growth for preys. For terrestrial predators that form a fixed number of tight groups, they have shown that the existence of an unstable positive equilibrium in the predator-prey model (2.16) implies the existence of a unique nontrivial positive limit cycle.

2.3 Effects Of Additional Food on Predator-Prey Models

2.3.1 Predator-Prey Models incorporating additional food

2.3.1.1 The P. D. N. Srinivasu et al. model (2007)

P. D. N. Srinivasu et al. (2007)([163]) has formulated a model representing predator-prey dynamics, when the predator is provided with some additional food, by modifying a predator-prey model with Holling type II functional response. They assumed that the predator is provided with additional food of constant biomass A , which is distributed uniformly in the habitat as in the case with the prey as well as the predator in the habitat. They also assume that the number of encounters per predator with the additional food is proportional to the density of the additional food. Here, the proportionality constant characterizes the ability of the predator to identify the additional food. The aim of their research is to study the consequences of providing additional food on the system dynamics. Thus their model representing predator-prey dynamics when the predator is provided with additional food is the following coupled differential system :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{e_1xy}{1 + e_1h_1x + e_2h_2A}, \\ \dot{y}(t) = \frac{n_1e_1xy + n_2e_2Ay}{1 + e_1h_1x + e_2h_2A} - my, \end{cases} \quad (2.18)$$

where h_1 (h_2), e_1 (e_2), n_1 (n_2) respectively represent the handling time of the predators per unit quantity of preys (additional food), ability for the predator to detect the preys (additional food) and the nutritional value of the prey (additional food).

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Setting $c = \frac{1}{h_1}$, $b = n_1 c$, $\eta = \frac{n_2 e_2}{n_1 e_1}$ and $\alpha = \frac{n_1 h_2}{n_2 h_1}$, system (2.18) becomes :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{a + x + \alpha\eta A}, \\ \dot{y}(t) = \frac{b(x + \eta A)}{a + x + \alpha\eta A} - my, \end{cases} \quad (2.19)$$

Setting $X = \frac{x}{a}$, $T = rt$, $Y = \frac{cy}{ar}$ and replacing X by x , Y by y and T by t , system (2.19) becomes :

$$\begin{cases} \dot{x}(t) = [g(x, \alpha, \xi) - y]f(x, \alpha, \xi), \\ \dot{y}(t) = \left[\beta f(x, \alpha, \xi) \left(1 + \frac{\xi}{X}\right) - \delta \right] y, \end{cases} \quad (2.20)$$

with $f(x, \alpha, \xi) = \frac{x}{1 + \alpha\xi + x}$, $g(x, \alpha, \xi) = (1 + \alpha\xi + x) \left(1 - \frac{x}{\gamma}\right)$ where $\gamma = \frac{K}{a}$, $\beta = \frac{b}{r}$, $\delta = \frac{m}{r}$ and $\xi = \frac{\eta A}{a}$.

2.3.1.2 The B. S. R. V. Prasad et al. model (2013)

Considering the Beddington-DeAngelis model representing the predator-prey dynamics with mutual interference among predators, and assuming that the predators are provided with additional food of biomass A , which is uniformly distributed in the habitat and that the number of encounters per predator with the additional food is proportional to the density of the additional food, B. S. R. V. Prasad et al. (2013)([143]) formulated the following model :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{a + x + \alpha\eta A + \rho y}, \\ \dot{y}(t) = \frac{b(x + \eta A)}{a + x + \alpha\eta A + \rho y} - my, \end{cases} \quad (2.21)$$

where $c = \frac{1}{h_1}$ stands for maximum rate of predation. $a = \frac{1}{e_1 h_1}$ is the normalization coefficient that relates the densities of the predator and prey populations (in the absence of additional food) to the environment in which they interact. $\rho = \frac{e_2 h_2}{e_1 h_1}$ measures the strength of mutual interference among the predators. $b = \epsilon c$ the maximum growth rate of the predators. $\alpha = \frac{h_A}{h_1}$ (the ratio between the handling times towards the additional food and the preys) denotes the quality of the additional food relative to the preys. h_1 , h_2 and h_A represent the handling time of the predators per prey item, interaction time between predators and the handling time of the predator per unit quantity of the additional food respectively. e_1 , e_2 and e_A represent respectively constants that would depend on factors such as the predators movement rate while searching to detect preys or other predators and the constant that signifies the predators movement rate while searching to detect the additional food. $\epsilon \in (0, 1)$ represents the efficiency with which the food consumed by the predator gets converted into predator biomass. Here, authors term the additional food to be of low quality if the ratio of handling times between additional food and preys is greater than the ratio between the maximum predator growth rate and its death rate and it termed as high quality food if the above inequality reverses.

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Thus the quality of the additional food is decided by the value of α relative to the ratio $\frac{\beta}{\alpha}$. From the definition of $\eta = \frac{e_A}{e_1}$ authors infer that it represents effectual ability of the predator to detect additional food relative to the prey. Thus, the term ηA represents quantity of additional food perceptible to the predator relative to prey.

Setting $X = \frac{x}{a}$, $T = rt$, $Y = \frac{cy}{ar}$ and replacing X by x , Y by y and T by t , system (2.19) becomes the following non-dimensionless model which reduce the number of parameters as well as the complexity associated with the analysis :

$$\begin{cases} \dot{x}(t) = x \left(1 - \frac{x}{\gamma} \right) - \frac{xy}{1 + \alpha\xi + x + \epsilon y}, \\ \dot{y}(t) = \frac{\beta(x + \xi)y}{1 + \alpha\xi + x + \epsilon y} - \delta y, \end{cases} \quad (2.22)$$

where $\gamma = \frac{K}{a}$, $\beta = \frac{b}{r}$, $\delta = \frac{m}{r}$, $\epsilon = \frac{\rho}{c}$ and $\xi = \frac{\eta A}{a}$.

Here it is pertinent to note that the parameter ξ represents the normalized quantity of additional food perceptible to predator relative to prey.

2.3.2 Distraction effect

From the analysis of their models (2.18-2.19-2.20), Srinivasu et al. (2007)([163]) have concluded that:

If the handling time for the additional food is supposed to be higher than that of preys. Here, they find that, if the predators population goes extinct in the absence of additional food, it is not possible to bring in eventual predator-prey coexistence by providing additional food to predators. Therefore, if in the absence of additional food, the births due to consumption of preys are not compensating the deaths, then adding any amount of additional food cannot improve the situation. This is due to the distraction effect caused by the addition of low-quality food which takes more time to consume when compared with that of a prey item and the predators are time limited. Thus, in this situation biological control is not possible through additional food.

From the analysis of their models (2.21-2.22), B. S. R. V. Prasad et al. (2013)([143]) have concluded that :

When the strength of mutual interference is assumed to be greater than unity (signifying stronger mutual interference), it is possible to control and limit the prey population by the predators with provision of high quality additional food to predators. However, the high mutual interference in predators deters the prey from going extinct. This is due to distraction effect caused on predators due to higher mutual interference and availability of large quantities of high quality additional food. It is noted worthy that in the absence of additional food, if the prey can not support the predators towards coexistence due to its poor nutritive value, it is possible to bring in stable coexistence by provision of high quality food to predators, and thus control the preys in the system although it can not be driven to extinction.

2.3.3 Fluctuating individual populations effect

From the analysis of their models (2.21-2.22), B. S. R. V. Prasad et al. (2013)([143]) have concluded that :

1. In the case where the interference between the predators is weak (less than 1), along with bringing in coexistence and controlling the preys by providing additional food to predators, it becomes possible to eradicate the preys from the system by appropriate choice on quality and quantity of additional food and strength of interference between predators. In this case, providing the predators with additional food may either cause an increase in the eventual predator population, and decrease eventual prey population or it may even bring in oscillations into the system depending on the characteristics of the high quality additional food.
2. In the considered models (2.21-2.22), the additional food of high quality acts as supplement to the predators, enhancing their growth at low prey concentrations. But, because of the self-limiting behavior of the predators, this growth is limited. Thus, the provision of additional food (of high quality) stabilizes the system at low prey populations. With further increase in the quantity of the high quality additional food, the predators eradicate the prey from the system and get stabilized on the predator axis. In this case the eradication becomes possible due to the ability for the predators to spend more time with the high quality additional food, which results in numerical abundance of predators and losing less time due to mutual interference.

From the analysis of their models (2.18-2.19-2.20), Srinivasu et al. (2007)([163]) have concluded that:

If the ratio between the handling times of the additional food and the preys is less than the ratio between the maximum predator growth rate and its starvation rate, several subcases are possible. If the predator population goes extinct in the system without additional food, then we can bring in coexistence of predators and preys by providing the predators with additional food with concentration level belonging to a specified interval. Here, the additional food increases the consumption of the predator population which reflects in the numerical abundance of the predator which in turn increases the per capita consumption of preys. As a result, there is a decrease in the equilibrium prey population.

2.3.4 Stabilizing effect

From the analysis of their models (2.18-2.19-2.20), Srinivasu et al. (2007)([163]) have concluded that:

If in the absence of additional food, the system admits an interior equilibrium, then introduction of additional food leaves the prey equilibrium level unaltered and the predator equilibrium increases with food supply. The nature of the equilibrium depends on the nature of the interior equilibrium in the absence of additional food. If it is asymptotically stable when there is no food supply, then it will continue to be asymptotically stable with increase in food supply. On the other hand, if it is unstable

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when there is no food supply, then the amplitude of the oscillations due to instability of the interior equilibrium decreases with increase in the food level and after a critical food level, the equilibrium turns asymptotically stable and it will remain in that state for all higher food levels.

From the analysis of their models (2.21-2.22), B. S. R. V. Prasad et al. (2013)([143]) have concluded that :

For a chosen high quality additional food, if the population cycles eventually, then by increasing the quantity of additional food, not only the amplitude of these cycles can be reduced but the system can be stabilized at low prey population. This observation is in contrast to the other classical predator-prey models with Holling type II functional response, where in the interior equilibrium exhibits instability nature at low prey population density, which induces limit cycles in the system dynamics [32,83,88]. The occurrence of limit cycles in these cases can be accounted for, by the fact that the predators are not able to reproduce enough at lower prey concentrations.

2.3.5 Appearance of limit cycles

For Srinivasu et al. (2007)([163]), and according to the analysis of their models (2.18-2.19-2.20) :

If, in the absence of additional food, the system has stable coexistence, then providing additional food may either cause monotonic increase in the eventual value of the predator while maintaining stability, or it may bring in oscillations into the system when the supply goes beyond a specified level, leading to a stable limit cycle. These cycles move towards the predator axis with increase in the additional food supply. Beyond a certain level of food supply, the prey population goes extinct and predators are solely supported by the additional food. Even in the case where the eventual predator population is monotone with respect to food supply, the prey gets eradicated beyond a specific level of food supply. At this stage the predators can also be eliminated by with-drawing the additional food supply to the predators.

2.4 Effects Of Harvest On Predator-Prey Models

Predators and preys are ecological resources. So, they can be used either for human being needs or for commercial industries. It can then be exploited and harvested in fishery, forestry and wildlife management. There is a wide range of interest in the use of bioeconomic models to gain insight into the scientific management of the renewable resources like fisheries and forestries. To study effects of harvesting in the dynamic of relationship between species, some harvesting functions have been considered by several researchers. While incorporating harvesting of one or both species in the generalized Gause formulation of predator-preys models (1.29), the new model takes the following form :

$$\begin{cases} \dot{x}(t) = xg(x, K) - yp(x) - \varphi(x(t)), \\ \dot{y}(t) = y(-d + cq(x)) - \psi(y(t)), \end{cases} \quad (2.23)$$

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where $\varphi(x(t))$ and $\psi(y(t))$ are respectively the harvesting functions for the prey and the predator populations. When only preys are harvested, we have $\varphi(x(t)) = 0$ and when only predators are harvested we have $\psi(y(t))$.

In the literature, it exists some harvesting functions :

1. **Constant harvesting functions.** For such functions, a constant number of individuals being harvested are harvested per unit of time.
2. **Linear harvesting functions.** It means that the number of individuals harvested per unit of time is proportional to the current population. Thus if $\varphi(x) = qEx$ where q is the catchability coefficient, E is the effort applied to harvest individuals x , which is measured in terms of number of (standard) vessels being used to harvest the individual population. It has been noticed that the proportionate harvesting embodies several unrealistic features like random search for the harvested population and equal likelihood of being captured for every species of the harvested population.
3. **Nonlinear harvesting functions.** For example ([65]), we have the Michaelis-Menten $\varphi(x) = \frac{qEx}{m_1E + m_2x}$ where q is the catchability coefficient, E is the effort applied to harvest individuals which is measured in terms of number of (standard) vessels being used to harvest the individual population and m_1, m_2 are suitable positive constants. The nonlinear harvesting function exhibits saturation effects with respect to both the stock abundance and the effort-level. The parameter m_1 is proportional to the ratio of the stock-level to the harvesting rate (catch-rate) at higher levels of effort, and m_2 is proportional to the ratio of the effort-level to the harvesting rate (catch-rate) at higher stock-levels.
4. **Continuous Threshold Harvesting functions.** For this family of harvesting functions, it is assumed that harvesting which starts at $t = 0$, independently of the population size, is not very realistic. In this regard, threshold policy (TP) harvesting considers starting harvesting only when a population x has reached a certain threshold value T . Those harvesting functions are usually defined with constant, linear or nonlinear functions when the harvested population is greater than the threshold T . Such harvesting functions are defined as ([23]) :

$$\varphi(x) = \begin{cases} 0 & \text{if } x < T, \\ h & \text{if } x \geq T. \end{cases} \quad (2.24)$$

$$\varphi(x) = \begin{cases} 0 & \text{if } x < T, \\ \frac{h(x - T)}{h + x - T} & \text{if } x \geq T. \end{cases} \quad (2.25)$$

$$\varphi(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x - T_1)}{T_2 - T_1} & \text{if } T_1 \leq x \leq T_2, \\ h & \text{if } x > T_2. \end{cases} \quad (2.26)$$

2.4.1 Predator-prey models incorporating harvesting

2.4.1.1 The P. Lenzini and J. Rebaza model (2010)

P. Lenzini and J. Rebaza ([112]) have formulated and studied a ratio-dependent predator-prey model with two different non-constant harvesting functions depending on the predator population. The first harvesting policy involves a linear harvesting rate in terms of the predator species. The model is the following one :

$$\begin{cases} \dot{x}(t) = x(1-x) - \frac{axy}{x+y}, \\ \dot{y}(t) = \left(\frac{bx}{x+y} - d\right)y - hy, \end{cases} \quad (2.27)$$

Where x and y denote the prey and predator populations, respectively, a is the capture rate of the prey, b is the prey conversion rate, d is the natural death rate of the predator and h represents a constant harvesting effort. As the abundance of the predator species increases, the number of predator harvested will increase linearly.

In a more realistic approach, P. Lenzini and J. Rebaza take into account the assumption of diminishing marginal returns of the harvesting organization. This gives the second harvesting policy which is a rational harvesting rate in terms of the predator species :

$$\begin{cases} \dot{x}(t) = x(1-x) - \frac{axy}{x+y}, \\ \dot{y}(t) = \left(\frac{bx}{x+y} - d\right)y - \frac{hy}{c+y}, \end{cases} \quad (2.28)$$

Where x and y denote the prey and predator populations, respectively, a is the capture rate of the prey, b is the prey conversion rate, d is the natural death rate of the predator, h is the maximum harvesting rate of the predator species and c is the number of predator species it takes to reach one-half of the maximum harvesting rate. This model characterizes the behavior of a commercial harvesting company when their decision to harvest depends on both the revenue and cost of harvesting. As more species become available, harvesting more at a linear rate might not be profitable, due to supply and demand factors.

2.4.1.2 The T. K. Kar and K. Chakraborty model (2010)

T. K. Kar and K. Chakraborty ([101]) study is mainly concerned with a predator-prey model, the ecological set up of which is as follows. There is a prey which is harvested continuously and a predator living on the prey. It is assumed that the predator is not harvested and hence harvesting does not affect the growth of the predator population directly. However, there is a conflict for common resource i.e. prey between predators and harvesting agency though the predators have competition among themselves for their survival. The growth of prey is assumed to be logistic. Let us assume x and y are respectively the size of the prey and predator population at time t . Keeping these in view,

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the model proposed and studied by T. K. Kar and K. Chakraborty is the following one :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{\alpha xy}{a+x} - h(t), \\ \dot{y}(t) = \left(-d + \frac{\beta \alpha x}{a+x}\right) y - \gamma y^2, \end{cases} \quad (2.29)$$

where r is the intrinsic growth rate of the prey, K is the environmental carrying capacity of prey, α is the maximal relative increase of predation, a is Michaelis-Menten constant, $h(t)$ is the harvesting at time t , d is the death rate of predator, β is conversion factor (we assume $0 < \beta < 1$, since the whole biomass of the prey is not transformed to the biomass of the predator). Density dependent mortality rate γy^2 describes either a self limitation of consumers or the influence of predation. Self limitation can occur if there is some other factor (other than food) which becomes limiting at high population densities.

T. K. Kar and K. Chakraborty take the harvest rate $h(t)$ in the form :

$$h = m q x E$$

where q is the catchability coefficient, E is the effort used to harvest the population and m ($0 < m < 1$) is the fraction of the stock available for harvesting.

T. K. Kar and K. Chakraborty extend the model system (2.30), assuming that fishery effort E itself is a dynamic variable that satisfies :

$$\frac{dE}{dt} = \dot{E}(t) = \lambda(p m q x - c) E$$

where c is the constant fishing cost per unit effort, p is the constant price per unit biomass of landed fish and λ is stiffness parameter.

Thus, the final model becomes :

$$\begin{cases} \dot{x}(t) = rx \left(1 - \frac{x}{K}\right) - \frac{\alpha xy}{a+x} - m q x E, \\ \dot{y}(t) = \left(-d + \frac{\beta \alpha x}{a+x}\right) y - \gamma y^2, \\ \dot{E}(t) = \lambda(p m q x - c) E \end{cases} \quad (2.30)$$

2.4.1.3 The L. Chen et al. model (2011)

Recently Haque ([70]) modified the prey-dependent Michaelis-Menten or Holling type II functional response $p(x) = \frac{bx}{1+Ax}$ in the classical Bazykin's model to the ratio-dependent functional response $p\left(\frac{x}{y}\right) = \frac{bx}{y+Ax}$ proposed by Arditi and Ginzburg ([4]) by modifying the Holling type II functional response. Haque ([70]) obtained the following system :

$$\begin{cases} \dot{x}(t) = ax - \frac{bxy}{y+Ax} - ex^2, \\ \dot{y}(t) = -cy + \frac{dxy}{y+Ax} - fy^2, \end{cases} \quad (2.31)$$

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where x and y are scaled prey and predator population densities, respectively. Parameter $a > 0$ is the prey natural growth rate, $b/A > 0$ is the prey maximal consumption rate by predators, $d/A > 0$ is the maximal growth rate of predators, $1/A > 0$ is the half-saturation constant of predators, $e > 0$ and $f > 0$ are the prey and predator intraspecies competition rates, respectively, and $c > 0$ is the predator natural mortality rate.

Both harvesting and predation are processes in which members of a population are removed by an external agency, sometimes for population management, but more often for the benefit of the harvester from the point of view of human needs. Hence, the exploitation of biological resources and the harvesting of populations are commonly practiced in fishery, forestry, and wildlife management, which is related to the optimal management of renewable resources.

L. Chen et al. ([30]) have formulated and studied a model assuming that the prey population is subjected to harvesting at a constant rate in model (2.31) as follows :

$$\begin{cases} \dot{x}(t) = ax - \frac{bxy}{y + Ax} - ex^2 - H, \\ \dot{y}(t) = -cy + \frac{dxy}{y + Ax} - fy^2, \end{cases} \quad (2.32)$$

where $H > 0$ is a constant harvesting rate.

For simplicity, L. Chen et al. ([30]) rescaled the state and time variables of model (2.31) as follows :

$$\bar{t} = at, \quad \bar{x} = \left(\frac{e}{a}\right)x, \quad \bar{y} = \left(\frac{be}{ad}\right)y$$

Dropping the bars, they obtained the following system :

$$\begin{cases} \dot{x}(t) = x - \frac{\epsilon xy}{\alpha x + y} - x^2 - h, \\ \dot{y}(t) = -\gamma y + \frac{\epsilon xy}{\alpha x + y} - \delta y^2, \end{cases} \quad (2.33)$$

where

$$\gamma = c/a, \quad \alpha = Ab/d, \quad \epsilon = b/a, \quad \delta = fd/be, \quad h = He/a^2.$$

2.4.1.4 The J. Bohn et al. model (2011)

J. Bohn et al. ([23]) proposed a modified predator-prey model with Michaelis-Menten functional response and continuous threshold policy harvesting functions on preys. They also assumed that preys are harvested by using the continuous threshold policy defined by equations (2.25) and (2.26). Their model is given by :

$$\begin{cases} \dot{x}(t) = x(1-x) - \frac{axy}{1+mx} - \varphi(x(t)), \\ \dot{y}(t) = \left(\frac{bx}{1+mx} - d\right)y(t), \end{cases} \quad (2.34)$$

Where x and y denote the prey and predator populations, respectively. The parameters a, b, d, m are all positive constants : a is the capture rate of the prey, b is the prey conversion rate, d is the natural death rate of the predator. The term $\frac{x}{1+mx}$ is known as a Holling type II functional response. φ is the continuous threshold policy defined by equations (2.25) and (2.26).

2.4.1.5 The Belkhodja et al. model (2018)

Recently, Chiboub et al. (2012)([31]) proposed a new functional response, in order to explain the influence of changing water level fluctuations in an artificial lake on fish predator-prey dynamics. In the studied lake, two interdependent species are considered; the pike (brochet in French) which is the most important predator and the roach (gardon in French) which is the prey. This functional response is based on the following general considerations. When a predator attacks a prey, it has access to a certain quantity of food depending on the water level. When the water level is low, during the autumn, the predator is more in contact with the prey, and the predation increases. Conversely, when the water level is high, in the spring, it is more difficult for the predator to find a prey and the predation decreases. Chiboub et al. (2012)([31]) assumed that the accessibility function $b(t)$ for the prey is continuous and 1-periodic, the minimum value b_1 is reached in spring and the maximum value b_2 is attained during autumn. The predator needs a quantity γ as food, but it has access to a quantity $g(x, y) = \frac{b(t)x}{y + D}$ which depends on the water level, where D measures other causes of mortality outside of predation. Thus, if $g(x, y) \geq \gamma$, then the predator will be satisfied with the quantity γ of his food. Otherwise, if $g(x, y) < \gamma$, the predator will content himself with $g(x, y) = \frac{b(t)x}{y + D}$. To summarize, the quantity of food received per predator and per unit of time is $\min\left(\frac{b(t)x}{y + D}, \gamma\right)$. Chiboub et al. (2012)([31]) proposed and studied the following predator-preys model :

$$\begin{cases} \dot{x}(t) = rx\left(1 - \frac{x}{K}\right) - \min\left(\frac{b(t)x}{y + D}, \gamma\right) y(t), \\ \dot{y}(t) = \left(e \min\left(\frac{b(t)x}{y + D}, \gamma\right) - d\right) y(t), \end{cases} \quad (2.35)$$

where r, e, d are positive constants.

In order to investigate the effects of harvesting on the prey-predator ecosystem, Belkhodja et al. (2018)([15]) incorporate a linear harvest of preys in the model (2.35) proposed by Chiboub et al. (2012)([31]). Belkhodja et al. (2018)([15]) focused on the autonomous case and use as predation rate, the mean function $b = \int_0^1 b(1 + 0.5\cos(2\pi t))dt$. Belkhodja et al. (2018)([15]) aimed to obtain some results which are theoretically beneficial to maintaining the sustainable development of the prey-predator system as well as keeping the economic interest of harvesting at an ideal level. Therefore, they studied the following prey-predator model :

$$\begin{cases} \dot{x}(t) = rx\left(1 - \frac{x}{K}\right) - \min\left(\frac{bx}{y + D}, \gamma\right) y(t) - qEx(t), \\ \dot{y}(t) = \left(e \min\left(\frac{bx}{y + D}, \gamma\right) - d\right) y(t). \end{cases} \quad (2.36)$$

Assuming that $b < \min\left(\frac{\gamma(y_0 + D)}{x_0}, \frac{4a\gamma Dd}{K(a + d - qE)^2}\right)$, with $x_0 = x(0)$ and $y_0 = y(0)$, the model (2.36) becomes the following reduce model :

$$\begin{cases} \dot{x}(t) = rx\left(1 - \frac{x}{K}\right) - \frac{bxy}{y + D} - qEx(t), \\ \dot{y}(t) = \left(e \frac{bxy}{y + D} - d\right) y(t), \end{cases} \quad (2.37)$$

where q is the catchability coefficient of the prey species and E denotes the effort devoted to the harvesting.

2.4.2 Fluctuating in individual population effect

Belkhdja et al. (2018)([15]) have concluded that, the presence of harvesting can impact the existence and the behavior of the positive equilibrium, that is for $0 \leq E \leq \frac{a}{q} \left(1 - \frac{dD}{ebK}\right)$, the two fish populations can be maintained at an appropriate equilibrium level in the habitat. As harvesting becomes larger than the level $\frac{a}{q} \left(1 - \frac{dD}{ebK}\right)$, overharvesting can lead to the extinction of the predators. Indeed, the density of the prey population decreases with increasing effort used to harvesting, which leads to a more difficult situation for the predator to find a prey, and to possible extinction.

J. Bohn et al. ([23]) have shown that when the harvesting function (2.26) is used, the predator population density increases as h increases if the prey conversion rate b and the predator death rate d satisfy the relation $T_1 b > (mT_1 + 1)d$. The predator population decreases if the inequality is reversed.

2.4.3 Stabilizing effect

J. Bohn et al. ([23]) have shown that harvesting has a stabilizing effect on the ecosystem. A stable equilibrium remains to be stable when threshold harvesting is applied, and an unstable equilibrium becomes stable for some sets of parameters. With the harvesting function (2.25), a stable focus of the system without harvesting, moves to the stable focus of the system with harvesting. An unstable focus moves to a stable node. With the harvesting function (2.26), a stable focus of the system without harvesting moves to a stable node and an unstable focus moves to a stable focus.

2.4.4 Bifurcating effects and appearance of limits cycles

J. Bohn et al. ([23]) have proved that when the harvesting function (2.26) is used, it is possible to have saddle-node and transcritical bifurcations for some values of the parameter h . And when the two different type of harvesting functions (2.25) and (2.26) are used, it is possible to have subcritical and supercritical Hopf bifurcations around the coexistence equilibria when those equilibria satisfy the conditions that permit them to be of center-type.

According to P. Lenzini and J. Rebaza ([112]), system (2.27) undergoes a transcritical bifurcation involving the two equilibria (The coexistence equilibrium and the one without predators). The transcritical bifurcation occurs when the predator conversion rate b matches the sum of its death rate d and the harvesting rate h . P. Lenzini and J. Rebaza ([112]) have also shown that, under certain conditions for the coexisting equilibrium to be a center, the system (2.27) exhibits subcritical and supercritical Hopf bifurcations. According to P. Lenzini and J. Rebaza ([112]), a pitchfork bifurcation is detected for the parameter value $h = 1/3$ for the system (2.28).

It is proved by L. Chen et al. ([30]) that their model (2.32) can undergo Hopf bifurcation and

Bogdanov-Takens bifurcation near the corresponding positive equilibrium as some parameters of the model vary.

2.5 Effects Of Discrete Time Delay On Predator-Prey Models

For reasons like maturing time, gestation time or capturing time, time delays of one type or another have been incorporated into predator-prey models. It has been shown that, generally delay differential equations can exhibit much more complicated dynamics than ordinary differential equations.

Time delays can be incorporated into the generalized Gause-type predator-prey model (1.29) (assuming that $p(x) = q(x)$) in five different ways as follows :

1. A time delay τ standing for maturation time for prey population in the prey specific growth term $g(x(t), K)$, that is,

$$\begin{cases} \dot{x}(t) = x(t)g((x - \tau), K) - yp(x), \\ \dot{y}(t) = y(t)(-d + cp(x)). \end{cases} \quad (2.38)$$

2. A time delay τ standing for gestation time or reaction time of predator population in the predator response term $p(x(t))$ in the predator equation, that is,

$$\begin{cases} \dot{x}(t) = x(t)g(x(t), K) - yp(x), \\ \dot{y}(t) = y(t)(-d + cp(x(t - \tau))). \end{cases} \quad (2.39)$$

3. A time delay τ in the interaction term $y(t)p(x(t))$ of the predator equation, assuming that the change rate of predators depends on the number of prey and of predators present at some previous time, that is,

$$\begin{cases} \dot{x}(t) = x(t)g(x(t), K) - yp(x), \\ \dot{y}(t) = -dy(t) + cy(t - \tau)p(x(t - \tau)). \end{cases} \quad (2.40)$$

The last two models are obtained by incorporating one delay for the prey dynamic and another one for the predator dynamic. The two delays can be assumed different or equal.

4. A time delay τ_1 standing for maturation time for prey population and a time delay τ_2 representing gestation time or reaction time of predator population

$$\begin{cases} \dot{x}(t) = x(t)g(x(t - \tau_1), K) - yp(x), \\ \dot{y}(t) = y(t)(-d + cp(x(t - \tau_2))). \end{cases} \quad (2.41)$$

5. A time delay τ_1 representing maturation time for prey population and a time delay τ_2 assuming that the change rate of predators depends on the number of prey and of predators present at some previous time

$$\begin{cases} \dot{x}(t) = x(t)g(x(t - \tau_1), K) - yp(x), \\ \dot{y}(t) = -dy(t) + cy(t - \tau_2)p(x(t - \tau_2)). \end{cases} \quad (2.42)$$

In what follows, four examples of modified predator-prey models incorporating one or two discrete time delays are proposed, with different functional responses taking into account density-dependence and ratio-dependence.

2.5.1 Predator-prey models incorporating discrete time delay

2.5.1.1 The S. Gakkhar et al. model (2009)

S. Gakkhar et al. ([52]) have formulated a Beddington-DeAngelis ratio-dependent predator-prey model with discrete time delay. The delay terms occur in growth as well as in interaction terms. For this, they assumed that the prey takes time τ_1 to convert the food into its growth, whereas the predator takes time τ_2 for the same. Their delayed predator-prey model is the following one :

$$\begin{cases} \dot{x}(t) = x(t) \left(1 - x(t - \tau_1) - \frac{a_1 x(t)y(t)}{a + x(t) + by(t)} \right), \\ \dot{y}(t) = d_1 y(t) \left(-d + \frac{a_a x(t - \tau_2)}{a + x(t - \tau_2) + by(t - \tau_2)} \right). \end{cases} \quad (2.43)$$

The model (2.43) has been studied by S. Gakkhar et al. with the assumption that $\tau_1 = \tau_2$. The case $\tau_1 \neq \tau_2$ has been studied later by C. Xu and P. Li ([185]).

2.5.1.2 The Z. Jiang et al. model (2010)

A delayed predator-prey system with Holling II functional response has been formulated and studied by Z. Jiang et al. ([94]) for the stability, local Hopf bifurcation the global Hopf bifurcation. Their model is the following one :

$$\begin{cases} \dot{x}(t) = x(t) \left(r_1 - a_{11}x(t - \tau) - \frac{a_{12}y(t)}{1 + mx(t)} \right), \\ \dot{y}(t) = y(t) \left(-r_2 + \frac{a_{21}x(t)}{1 + mx(t)} - a_{22}y(t) \right). \end{cases} \quad (2.44)$$

Where $x(t)$ and $y(t)$ denote the density of prey and predator at time t , respectively. m denotes the search rate multiplied by the handling time; r_1 denotes the intrinsic growth rate of prey; r_2 denotes the death rate of the predator; a_{11} denotes the intraspecific competitions rate of the prey; a_{12} denotes the capturing rate of the predator; $\frac{a_{21}}{a_{12}}$ is the conversion rate of nutrients into the reproduction of the predator; a_{22} is the interspecies competitions rate of the prey and predator; τ is the generation time of the prey species. In biological terms, τ, r_i, a_{ij} ($i, j = 1, 2$) are positive constants.

2.5.1.3 The H. Zhao et al. model (2013)

H. Zhao et al. (2013) ([200]) incorporates two discrete time delays in a predator-prey model with a ratio-dependent Holling type III functional response. By means of an iteration technique, they have obtained sufficient conditions for the global attractiveness of the positive equilibrium. By comparison arguments, they address the global stability of the semi-trivial equilibrium. By using the theory of

functional equation and Hopf bifurcation, they have obtained conditions on which positive equilibrium exists and the quality of Hopf bifurcation. Using a global Hopf bifurcation result of Wu (1998) for functional differential equations, they have also obtained the global existence of the periodic solutions. Their model is the following set of two ordinary differential equations :

$$\begin{cases} \dot{x}(t) = x(t) \left(r_1 - a_{11}x(t) - \frac{a_{12}x(t)y(t - \tau_2)}{my^2(t - \tau_2) + x^2(t)} \right), \\ \dot{y}(t) = \frac{a_{21}x^2(t - \tau_1)y(t)}{my^2(t) + x^2(t - \tau_1)} - r_2y(t). \end{cases} \quad (2.45)$$

From the biological sense, we assume that $x^2 + y^2 \neq 0$. $r_1, r_2, a_{11}, a_{12}, a_{21}$, and m are positive constants, in which r_1 denotes the intrinsic growth rate of the prey, a_{11} is the intraspecific competition rate of the prey, a_{12} is the capturing rate of the predator, $\frac{a_{21}}{a_{12}}$ describes the efficiency of the predator in converting consumed prey into predator offspring, m is the interference coefficient of the predators, and r_2 is the predator mortality rate. The delay $\tau_1 \geq 0$ denotes the gestation period of the predator and $\tau_2 \geq 0$ is the hunting delay of the predator to prey.

2.5.1.4 The B. Barman and B. Ghosh models (2019)

Two well known Lotka-Volterra type and Rosenzweig-MacArthur predator-prey models have been modified by B. Barman and B. Ghosh (2019) ([12]) in their paper on explicit impacts of harvesting in delayed predator-prey models. They have incorporated time delay into the logistic growth term of preys for each model. Authors have analyzed the dynamics of both the models, by considering the time delay as the bifurcation parameter. The two models proposed and analyzed are the following :

$$\begin{cases} \dot{x}(t) = rx(t) \left(1 - \frac{x(t - \tau)}{K} \right) - \alpha x(t)y(t), \\ \dot{y}(t) = \beta x(t)y(t) - my(t). \end{cases} \quad (2.46)$$

$$\begin{cases} \dot{x}(t) = rx(t) \left(1 - \frac{x(t - \tau)}{K} \right) - \frac{\alpha x(t)y(t)}{h + x(t)}, \\ \dot{y}(t) = \frac{\beta x(t)y(t)}{h + x(t)} - my(t), \end{cases} \quad (2.47)$$

2.5.2 Stability switching effect

B. Barman and B. Ghosh (2019) ([12]) have proved that time delay can induce instability, for some critical value, and the instability persists if the delay exceeds the critical threshold. Hence, stability switching is not the only phenomenon in Lotka-Volterra type and Rosenzweig-MacArthur models. In addition, they observed that time delay certainly causes instability in Lotka-Volterra type system. However, Martin and Ruan (2001)([128]) and Kar and Pahari (2006)([100]) proved that there exists parametric condition, for which, time delay does not change the asymptotic stability behavior of the coexisting equilibrium. Here, they have shown that such a parameter condition is not possible in Rosenzweig-MacArthur model, for which steady state remain stable for increasing time delay. Likewise, the Lotka-Volterra model, Rosenzweig-MacArthur model also experiences instability for

2.6. Conclusion

some critical value and the coexisting equilibrium stays unstable for larger time delay. Therefore, authors can suggest that both the models have qualitatively similar dynamics under time delay.

C. Xu and P. Li ([185]) have proved that when some conditions depending on parameters of model (2.43) are satisfied, there exists some critical values for the discrete time delay. For the parameters values greater or smaller than those critical values, the stability of the coexistence equilibrium can switch.

2.5.3 Bifurcating effect and Appearance of limit cycles

The bifurcation analysis done by S. Gakkhar et al. ([52]), C. Xu and P. Li ([185]), Z. Jiang et al. ([94]), H. Zhao et al. (2013) ([200]), B. Barman and B. Ghosh (2019) ([12]) have revealed that there exist critical values of the discrete time delay for which, the formulated and studied models undergo Hopf bifurcations around the possible coexistence equilibrium and, consequently it is possible to have the existence of some limit cycles.

2.5.4 Fluctuating in individual population effect

From theoretical analysis of their model (2.45), H. Zhao et al. (2013) ([200]) have shown that the larger values of gestation time delay cause fluctuation in individual population density and hence the system becomes unstable.

2.6 Conclusion

At the end of this chapter, we can conclude that the refuges used by preys can have a stabilizing effect, that is, increases the local stability of the interior equilibrium. The prey refuge can induce a destabilizing impact on the stability of the positive equilibrium point. Adding a small refuge to a predator-prey model, the refuge will not alter the dynamical stability of the neutrally stable Lotka-Volterra model, adding a large refuge to the model replaced the oscillatory behavior with a stable equilibrium. By comparing the conclusions obtained from analyzing stability properties of two types of refuges used by preys, we can conclude that the refuges which protect a constant number of preys have a stronger stabilizing effect on population dynamics than the refuges which protect a constant proportion of preys. The refuges used by preys can induce appearance of limit cycles.

Replacing the Holling type I functional response by any other functional response in a predator-prey model can induce appearance of different types of bifurcation and limit cycles.

Talking about providing additional fixed food to predator, It has been shown that incorporating additional fixed food for predators can induce distraction effect, fluctuation of individual populations, stabilizing effects and appearance of limit cycles.

The presence of harvesting of prey species, predator species or both prey and predator species can induce fluctuating in individual population effect, stabilizing effect, bifurcating effects with different

2.6. Conclusion

type of bifurcations and appearance of limits cycles.

In most of the delayed predator-preys models, the effect of the delay is studied by considering the time delay as the bifurcation parameter. It is proved that the time delay can induce instability for some critical values, and the instability persists if the delay exceeds the critical thresholds. Incorporating a discrete time delay in a predator-prey model can also induce appearance of Hopf bifurcation and limit cycles.

OPTIMAL HARVESTING AND STABILITY ANALYSIS IN A LESLIE-GOWER DELAYED PREDATOR-PREY MODEL

Abstract

A delayed Leslie-Gower predator-prey model with continuous threshold prey harvesting is formulated and studied. Existence and local stability of the positive equilibrium of the system with and without the discrete time delay are completely determined in the parameter plane. Considering the discrete time delay as parameter, we investigate the effect of delay on stability of the coexisting equilibrium. It is observed that there are stability switches and a Hopf bifurcation occurs when the delay crosses some critical values. Applying the normal form theory and the centre manifold theorem, the direction and stability of the Hopf bifurcations are explicitly determined by the parameters of the system. Optimal harvesting is also investigated and some numerical simulations are given to support and extend our theoretical results.

3.1 Introduction

Leslie has introduced a predator-prey model ([113]), including support capability that the environment provides predators is proportional to the number of prey. Leslie advances that the growth rate of predators and preys admits an upper limit which can be approached under certain conditions : for the predator when the number of prey is high, for the prey when predator numbers (can be also the number of prey) is low ([113], [114]). The Leslie-Gower term means in absence of preys, the predators have an oscillatory behavior. There are many predator-prey models in the literature with Leslie-Gower term or a modified Leslie-Gower term and Holling type II functional response ([84], [80], [187], [64], [191]). Some of them analyze bifurcations ([84], [194], [66]), persistence ([139]) or seasonally varying parameters ([51]). The Leslie-Gower predator-prey model has not yet been analyzed as in this chapter, considering optimal harvest and response function of type III. Profit, over-exploitation and extinction of a species being harvested are primary concerns in ecology and commercial harvesting industries. Thus, current research incorporates a harvesting component in mathematical models to

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study the effects it has on one or multiple species. This has attracted interest from the commercial harvesting industry and from many scientific communities including biology, ecology, and economics. Most predator-prey models in the literature consider either constant or linear harvesting functions ([93], [99], [111], [182]). Recently, Tchinda et al., Tankam et al. ([173], [169]) considered a system of delay differential equations modelling the predator-prey dynamics with continuous threshold prey harvesting and Holling response function of type III. In ([173]), the model system was given by :

$$\begin{cases} \dot{x}(t) = \varphi(x(t)) - mp(x(t)) - H(x(t)), \\ \dot{y}(t) = [-d + cmp(x(t - \tau))]y(t), \end{cases} \quad (3.1)$$

where $x(t)$ and $y(t)$ denote the population of preys and predators at time t respectively. The parameter d is the natural mortality rate of predators. Parameters c and m are positive constants. The function

$$\varphi(x) = rx \left(1 - \frac{x}{K}\right) \quad (3.2)$$

models the behavior of preys in absence of predators, where r denote the growth rate of preys when x is small, and K is the capacity of the environment to support the preys. The functions $H(x)$ and $p(x)$ which are the harvesting function of the preys and the response function of predators to preys respectively, are defined by

$$H(x) = \begin{cases} 0 & \text{if } x < T, \\ \frac{h(x - T)}{h + x - T} & \text{if } x \geq T. \end{cases} \quad (3.3)$$

and

$$p(x) = \frac{x^2}{ax^2 + bx + 1} \quad (3.4)$$

where a is a positive constant and b is a nonnegative constant. This function is one of potential response function of predators to preys, modelling the consumption of preys by predators. It reflects very small predation when the number of preys is small, and a group of advantage for the preys when the number of prey is high ($p(x)$ tends to $\frac{1}{a}$ when x tends to infinity). For the harvesting function, T is the threshold value. In this way, once the prey population reaches the size $x = T$, then harvesting starts and increases smoothly to a limit value h . Here, a discrete time delay τ is in the predator response term $p(x(t))$ in the predator equation. This delay can be regarded as a gestation period or reaction time of the predators. In ([169]), System (3.1) has been investigated, but with a piecewise linear threshold policy harvesting given by

$$H(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x - T_1)}{T_2 - T_1} & \text{if } T_1 \leq x \leq T_2, \\ h & \text{if } x > T_2. \end{cases} \quad (3.5)$$

This piecewise linear threshold policy harvesting has been previously introduced in ([23]) in a predator-prey model without discrete time delay where a Holling response function of type II was considered. In these models, global qualitative and bifurcation analysis are combined to determine

the global dynamics of the model. But, note that, all those models do not take into account the fact that reduction in a predator population has a reciprocal relationship with per capita availability of its preferred food. This assumption leads the Leslie-Gower formulation. On the other hand, time delay plays an important role in many biological dynamical systems, being particularly relevant in ecology, where time delays have been recognized to contribute critically to the stable or unstable outcome of prey densities due to predation. The introduction of time delay into the population model is more realistic to model the interaction between the predator and prey populations and the population models with time delay are of current research interest in mathematical biology ([106], [149]). There is extensive literature about the effects of delay on the dynamics of predator-prey models. In this chapter, we consider a delayed Leslie-Gower predator-prey model both with refuge and the piecewise linear threshold policy harvesting given by (3.5). The Leslie-Gower formulation is based on the assumption that reduction in a predator population has a reciprocal relationship with per capita availability of its preferred food. Indeed, Leslie introduced a predator-prey model where the carrying capacity of the predator environment is proportional to the number of prey ([113], [114]). He stresses the fact that there are upper limits to the rates of increase of both prey x and predator y , which are not recognized in the Lotka-Volterra model. This chapter is organized as follows. In the second section, a brief literature of the Leslie-Gower predator-prey models and effects of prey refuge, different functional responses, harvesting and discrete time delay are given. In the third section, we give a description of the newly formulated model. In the fourth section, some preliminary results on the boundedness of solutions for System (3.28) with the harvesting function (3.5) is given. Existence and stability of equilibria of the non-delayed model are investigated in the fifth section. The sixth section deals with the linear stability and the Hopf analysis of the model system with discrete time delay. In the seventh section, direction and stability of Hopf bifurcation are presented. In the eighth section, optimal harvest policy of population model is derived. Numerical results to illustrate the analytical findings are presented in the ninth section and, finally, a summary is presented in the tenth section.

3.2 Leslie-Gower predator-prey models and Modified Leslie-Gower predator-prey models

3.2.1 Leslie-Gower predator-prey models

The Leslie-Gower predator-prey model is one of those modified predator-prey models from the basic one proposed by Lotka (1920)([122]) and Volterra (1931)([177]) for relationship between predator and their preys. A dynamic of predators is proposed by Leslie after an analysis of some results obtained by Gause (1934) ([54]). In fact, Gause (1934)([54]) has studied the growth of two protozoa named *Paramecia Caudatum* and *Paramecia Aurelia*. The two protozoa have been cultivated separately on the buffered medium (Half loop and One loop) concentration of bacteria. The main observation which has been used by Leslie is that when the two protozoa are cultivated separately, their

3.2. Leslie-Gower predator-prey models and Modified Leslie-Gower predator-prey models

growth is logistic and the maximal number of each protozoa depends on the concentration of what is considered as their food. So according to that observation, Leslie concluded that one can modelled interactions between predator and preys, by assuming that the dynamic of predators can be modelled by a logistic growth in which the carrying capacity of the predator depends directly on its source of food. The carrying capacity of the predator's environment is proportional to the number of preys. This interesting formulation for the predator dynamics has been discussed by Leslie and Gower in (1960)([115]) and by Pielou in (1969)([141]). In the formulation of his model, Leslie stresses the fact that there are upper limits to the rate of increase of both predators and their preys populations. This hypothesis is not recognized in the Lotka-Volterra model. Predators and their preys can reach to those upper limits in presence of favorable conditions which can be : for the predator, when the number of preys per predator is large and for the prey when the number of predators is small. When all those considerations are taken into account and in the case of continuous time, we have the so called Leslie-Gower predator-prey models as follows :

$$\begin{cases} \dot{x}(t) = (r_1 - a_1 y(t))x(t), \\ \dot{y}(t) = \left(r_2 - \frac{a_2 y(t)}{x(t)} \right) y(t), \end{cases} \quad (3.6)$$

and

$$\begin{cases} \dot{x}(t) = (r_1 - a_1 y(t) - b_1 x(t))x(t), \\ \dot{y}(t) = \left(r_2 - \frac{a_2 y(t)}{x(t)} \right) y(t), \end{cases} \quad (3.7)$$

where $x(t)$ and $y(t)$ represent respectively the preys and the predators populations at the time t . The parameters r_1 and r_2 are the intrinsic growth rates of the prey and the predator respectively, b_1 measures the strength of competition among individuals of preys, a_2 is a measure of the food quantity that the prey provides converted to predator birth. The quantity $\frac{r_1}{b_1}$ is the carrying capacity of the prey in the absence of predation. The term $\frac{y}{x}$ is the Leslie-Gower term which measures the loss in the predator population due to the fact that its favorite food becomes rare. Those systems are known respectively as the first and the second Leslie-Gower predator-prey models. In the first model, the influence of the within-species competition on the prey population is negligible ($b_1 = 0$). So the first model is the simplification of the second one.

Setting $K = \frac{r_1}{b_1}$ and $\alpha = \frac{r_2}{a_2}$ which represent respectively the environmental carrying capacity of preys and the measure of the food quality that the preys provides towards the predator births, the Leslie-Gower predator-prey models (3.6) and (3.7) take the following forms (3.8) and (3.9) which are often used by some authors.

$$\begin{cases} \dot{x}(t) = (r_1 - a_1 y(t))x(t), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)} \right) y(t), \end{cases} \quad (3.8)$$

and

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t)}{K}\right) x(t) - a_1 x(t)y(t), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.9)$$

Table 3.1: Parameter of the Leslie-Gower predator-prey model

Parameter	Interpretation (Definition)
r_1	Intrinsic growth rate of preys
r_2	Intrinsic growth rate of preys
a_1	Predation rate per unit of time
a_2	The food quantity that the prey provides converted to predator birth
b_1	Strength of competition among individuals of preys
$K = \frac{r_1}{b_1}$	Environmental carrying capacity of preys
α	The food quality that the preys provides towards the predator births

The Leslie-Gower predator preys models has some particularities. They are models without proportionality between the functional response and the numerical response, the principle of the biomass conversion is not taken into account ([20], [57]). Those models are also among models considering that during predation, preys are not always killed. So predation can only reduce the growth of the fecundity of preys ([19]). For example, parasites and herbivorous as predators eat their preys without killing them.

A. Korobeinikov (2001) ([104]) has established the global stability of the unique coexisting equilibrium of the Leslie-gower predator-prey models by defining a Lyapounov function. The Leslie-Gower predator-prey models do not admit any limit cycle.

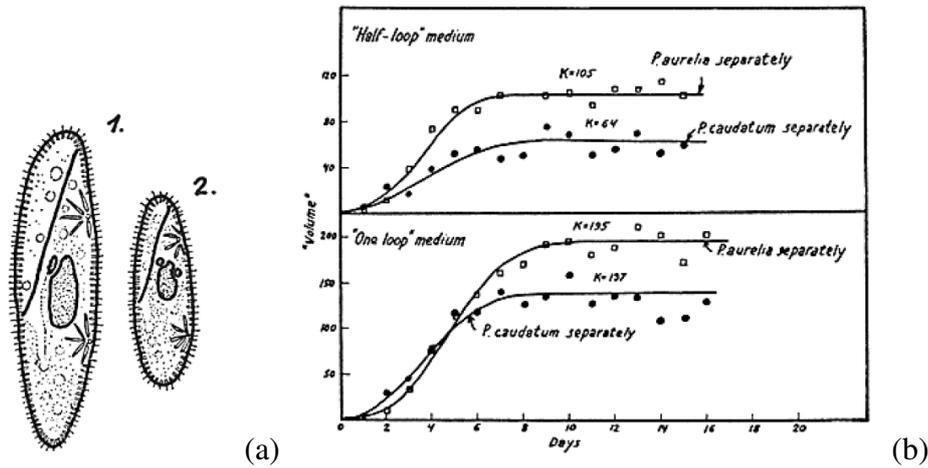


Figure 3.1: (a) Paramecium Caudatum (1), (b) Paramecium Aurelia (2), (b) The growth of the "volume" in Paramecium Caudatum and Paramecium Aurelia cultivated separately on the buffered medium ("half-loop" and "one-loop" concentrations of bacteria). From G. F. Gause ([54])

In figure (3.2.1), we have the phase portrait of the Leslie-Gower model

$$\dot{N} = r_N \left(1 - \frac{N}{K_N}\right) - \lambda_N NP, \quad \dot{P} = r_P \left(1 - \frac{P}{\alpha_N N}\right)$$

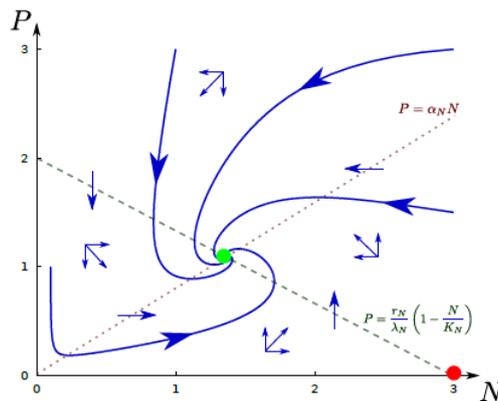


Figure 3.2: Phase portrait of the Leslie-Gower model with $r_N = 2$, $r_P = 1.5$, $\lambda_N = 1$, $\alpha_N = 0.8$, $K_N = 3$. From M. T. Alves ([3])

3.2.2 Modified Leslie-Gower predator-prey models

3.2.2.1 The Leslie-Gower predator-prey model incorporating prey refuge

The F. Chen et al. model (2009)

Prey refuge usually plays two important roles, serving both to reduce the chance of extinction due to predation and to damp prey-predator oscillations. Theoretical studies of prey refuge in interactive populations have shown that it has a stabilizing effect on the system dynamics and the addition of prey refuge substantially reduces the risk of prey extinction (Taylor (1984) ([171]); Krivan (1998) ([105]); Sih (1987) ([159]); Kar (2005) ([98]); Huang et al. (2006) ([87]); Ma et al. (2009) ([124]).

3.2. Leslie-Gower predator-prey models and Modified Leslie-Gower predator-prey models

Hassell (1978) ([76]) shows that adding a sufficiently large refuge to a discrete-time Nicholson-Bailey model (Nicholson (1933) ([136]); Nicholson and Bailey, 1935 ([137])) stabilizes the system from oscillations to stable equilibrium. Many other empirical studies have also suggested that refuges for prey are crucial in explaining prey persistence (Huffaker (1958) ([91]); Gause et al., (1936) ([55]); Connell (1970) ([36]); Macan, (1976) ([126])). Prey refuge is potentially important for increasing species richness in natural communities and of stabilizing population sizes, biomass and productivity (Pal and Samanta, (2013) ([140])).

In contrast, McNair (1986) ([131]) showed that refuge can exert a locally destabilizing effect and create large-amplitude oscillations. Ma et al. (2009) ([124]) showed that if the refuge used by prey is high enough, then the prey population reaches its maximum environmental carrying capacity, and the predators go extinct.

The following modified Leslie-Gower predator-prey model incorporating prey refuge has been proposed and studied by F. Chen et al. (2009) ([29]).

$$\begin{cases} \dot{x}(t) = (r_1 - a_1(1-m)y(t) - b_1x(t))x(t), \\ \dot{y}(t) = \left(r_2 - \frac{a_2y(t)}{(1-m)x(t)} \right) y(t), \end{cases} \quad (3.10)$$

where the parameter m stands for the measure of the strength of refuge ($0 \leq m < 1$). When $m = 0$, all the preys are available to predation. $mx(t)$ models the capacity of a refuge at the time t . So if $mx(t)$ represents the population of preys that are protected by the refuge, it remains $(1-m)x(t)$ of preys that are available to predation.

Influence of prey refuge in a Leslie-Gower predator-prey model

F. Chen et al. (2009) ([29]) have investigated the influence of prey refuge in a Leslie-Gower predator-prey model. The mathematic analysis of their model (3.10) has shown that increasing the amount of refuge can increase prey densities. As far as the predator species is concerned, when the assumption $a_1r_2 \leq a_2b_1$ holds, increasing the amount of prey refuge can decrease the predator densities; when the assumption $a_1r_2 > a_2b_1$ holds, there exists a threshold m^* , such that for the prey refuge smaller than this threshold, increasing the amount of prey refuge can increase the predator densities and if the prey refuge is larger than the threshold, increasing the amount of prey refuge can decrease the predator densities.

3.2.2.2 Leslie-Gower predator-prey models with different functional responses

Some modified Leslie-Gower predator-prey models have been formulated and studied, by incorporating a functional response different from the Holling type I, in order to investigate effects of the functional response on the dynamic of the Leslie-Gower predator-preys model. In this section, modified Leslie-Gower predator-prey with Holling type II, III, IV, Crowley-Martin and Beddington-DeAngelis functional responses, and effects of those functional responses are given.

The Holling-Tanner (1959-1975) model.

Holling-Tanner model for predator-prey interactions is a modified Leslie-Gower predator-prey model

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proposed by (1975)([170]) by replacing the functional response in the Leslie-Gower model by a Holling type II functional response. The Holling-Tanner predator-prey model is governed by the following nonlinear coupled ordinary differential equations :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \frac{\lambda xy}{A + x}, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.11)$$

The parameter λ denotes the maximal predator per capita consumption rate. A is a saturation value which corresponds to the number of prey necessary to achieve one half the maximum rate λ .

The ratio-dependent Holling-Tanner (2007) model.

Z. Liang and H. Pan (2007) ([117]) have done a qualitative analysis of a ratio-dependent Holling-Tanner model. Their model with ratio-dependance is the following :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \frac{\lambda xy}{Ay + x}, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.12)$$

The M. A. Aziz-Alaoui and M. D. Okiye model (2003).

M. A. Aziz-Alaoui and Okiye (2003) ([8]) have proposed a Leslie-Gower predator-prey model with the Holling type II functional response. The difference between their model and the Holling-Tanner model (3.11) is on the predator dynamic. In the Holling-Tanner model (3.11), the carrying capacity of the predator is proportional to prey abundance ($C = \alpha x$ where α is the conversion factor of prey into predators). The term $\frac{y}{\alpha x}$ of the predator dynamic of (3.11) is called the Leslie-Gower term. It measures the loss in the predator population due to rarity (per capita $\frac{y}{x}$) of its favorite food. In the case of severe scarcity, y can switch over to other populations but its growth will be limited by the fact that its most favorite food (x) is not available in abundance. This situation can be taken care of by adding a positive constant d to the denominator. Hence, the second equation of (3.11) becomes

$$\dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t) + d}\right) y(t) = \left(r_2 - \frac{r_2 y(t)}{\alpha x(t) + d/\alpha}\right) y(t).$$

Then, the model proposed and studied by M. A. Aziz-Alaoui and Okiye (2003) ([8]) is the following two-dimensional system of ordinary differential equations :

$$\begin{cases} \dot{x}(t) = \left(r_1 - b_1 x - \frac{a_1 y}{x + k_1}\right) x, \\ \dot{y}(t) = \left(r_2 - \frac{a_2 y(t)}{x + k_2}\right) y, \end{cases} \quad (3.13)$$

where x and y denotes the population densities at time t ; r_1 , a_1 , b_1 , k_1 , r_2 , a_2 , and k_2 are model parameters assuming only positive values. These parameters are defined as follows : r_1 is the growth rate of prey x , b_1 measures the strength of competition among individuals of species x , a_1 is the maximum value which per capita reduction rate of x can attain, k_1 (respectively, k_2) measures the extent to which environment provides protection to prey x (respectively, to predator y), r_2 describes

the growth rate of y , and a_2 has a similar meaning to a_1 .

Effects of the Holling type II functional response.

Replacing the linear functional response of the Leslie-Gower model by the Holling type II functional response can have effects on the dynamic of the Leslie-Gower predator-prey model. The Holling-Tanner model has been studied by May (1973) ([129]), Tanner (1975), Murray (1989) ([135]) and Gasull et al. (1997) ([53]). With the Holling type II functional response, there is no more any global asymptotically stable equilibrium and limit cycles can exist (Methods of Coppel (1991) ([38]) and some critical transformations have been used to show the existence of a unique limit cycle for (3.12)).

The J. Huang et al. model (2014).

The model proposed and analyzed by J. Huang et al. (2014) ([89]) is a predator-prey system of Leslie type with generalized Holling type III or sigmoidal functional response. Their model is governed by the following nonlinear coupled ordinary differential equations :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \frac{\lambda x^2 y}{Ax^2 + Bx + 1}, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.14)$$

Effects of the Holling type III functional response.

J. Huang et al. (2014) ([89]) have shown that when the Holling type I functional response is replaced by the Holling type III functional response, the newly formulated model (3.14) has very rich and complicated dynamics. There exist a stable limit cycle enclosing two non-hyperbolic positive equilibria, a stable limit cycle enclosing an unstable homoclinic loop, two limit cycles enclosing a hyperbolic positive equilibrium, or one stable limit cycle enclosing three hyperbolic positive equilibria. The model (3.14) also undergoes degenerate focus type Bogdanov-Takens bifurcation of codimension 3, and it is possible to have the coexistence of three stable states (two stable equilibria and a stable limit cycle).

The Y. Li and D. Xiao model (2007).

A Leslie type model with a simplified Holling type IV functional response has been proposed and studied by Y. Li and D. Xiao (2007)([183]). Their model is the following one :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \frac{\lambda xy}{x^2 + B}, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.15)$$

Effects of the Holling type IV functional response.

The study of the model (3.15) has shown that replacing the Holling type I functional response by a Holling type IV functional response has some effects on the dynamics of the model. It is possible to have a stable limit cycle enclosing two equilibria, a unstable limit cycle enclosing a hyperbolic equilibrium, a unstable homoclinic loop enclosing a hyperbolic equilibrium, or two limit cycles enclosing a hyperbolic equilibrium by choosing different values of parameters. However, the model never has two limit cycles enclosing a hyperbolic equilibrium for all values of parameters.

The N. Ali and M. Jazar model (2013).

3.2. Leslie-Gower predator-prey models and Modified Leslie-Gower predator-prey models

N. Ali and M. Jazar (2013)([2]) have considered and studied a predator-prey model which incorporates a modified version of the Leslie-Gower with Crowley- Martin functional response. Their model is the following :

$$\begin{cases} \dot{x}(t) = a_1 \left(1 - \frac{x}{K}\right) x - \frac{bxy}{(1+cx)(1+dy)}, \\ \dot{y}(t) = \left(a_2 - \frac{ey}{x+f}\right) y(t), \end{cases} \quad (3.16)$$

where x and y denotes the population densities at time t ; a_1, a_2, b, c, d, e, f and K are model parameters assuming only positive values and are defined as follows : a_1 and K are the intrinsic growth rate and the carrying capacity of prey population x respectively. The constants b, c and d are the saturating Crowley-Martin type functional response parameters, in which c measures the magnitude of interference among preys. Further, a_2 describes the growth rate of predator y ; e is the maximum value which per capita reduction rate of y can attain, f measures the extent to which environment provides protection to predator y .

Effects of the Crowley- Martin functional response.

Replacing the Holling type I functional response by the Crowley- Martin functional response can induce the existence of Hopf-bifurcation of nonconstant periodic solutions surrounding the interior equilibrium. Under suitable conditions, it is possible to establish the existence and non-existence of periodic solutions.

The S. Yu model (2014).

Based on the model proposed and analyzed by Alaoui (2003) ([8]), the model studied by S. Yu (2014) ([192]) incorporates the Beddington-DeAngelis functional response and can be considered as a generalization of the Alaoui et al. model. The model studied by S. Yu is the following set of two ordinary differential equations :

$$\begin{cases} \dot{x}(t) = \left(r_1 - px(t) - \frac{\alpha y(t)}{a + bx + cy} \right) x(t), \\ \dot{y}(t) = \left(r_2 - \frac{\beta y(t)}{x(t) + k} \right) y(t), \end{cases} \quad (3.17)$$

where x and y denotes the population densities at time t ; $r_1, r_2, p, \alpha, \beta, a, b, c$ and k are model parameters assuming only positive values. These parameters are defined as follows : r_1 is the growth rate of prey x , p measures the strength of competition among individuals of species x , a_1 is the maximum value which per capita reduction rate of x can attain, k measures the extent to which environment provides protection to predator y , r_2 describes the growth rate of y , and a_2 has a similar meaning to a_1 .

Effects of the Beddington-DeAngelis functional response.

The author discuss the structure of nonnegative equilibria and their local stability. Also, the permanence of the system is investigated. By applying the fluctuation lemma, qualitative analysis and Lyapunov direct method, respectively, three sufficient conditions on the global asymptotic stability of a positive equilibrium have been obtained.

3.2.2.3 Leslie-Gower predator-prey models with harvesting

Predators and preys can be harvested for human being needs or for commercial reasons. In what follows, and in order to study effects of harvesting, modified Leslie-Gower predator-preys models incorporating constant harvesting, linear harvesting and nonlinear harvesting of one species (predator or prey) or both species (predator and prey) studied by different authors are presented.

The C. Zhu and K. Lan model (2010).

C. Zhu and K. Lan (2010) ([203]) considered a Leslie-Gower predator-preys model with a positive constant harvesting rate h . They assume that preys are continuously harvested at the constant rate h by a harvesting agency and the predators are not of commercial importance. Their model is of the form :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy - h, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.18)$$

Effects of constant harvesting of preys.

C. Zhu and K. Lan (2010) ([203]) have proved that when preys are continuously harvested at the constant rate h , and when the positive equilibria on the x -axis exists, there are saddle-nodes, saddles or unstable nodes depending on the choices of the parameters involved, while the interior positive equilibria in the first quadrant are saddles, stable or unstable nodes, foci, centers, saddle-nodes or cusps. C. Zhu and K. Lan (2010) ([203]) have shown that there are two saddle node bifurcations and by computing the Liapunov numbers and determining its signs, the existence of the supercritical or subcritical Hopf bifurcations and limit cycles for the weak centers are proved.

The J. Huang et al. model (2013).

The effect of constant-yield predator harvesting on the dynamics of a Leslie-Gower predator-prey model is studied by J. Huang et al. (2013) ([88]). Their model is the following one :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t) - h, \end{cases} \quad (3.19)$$

where h denotes the constant-yield predator harvesting.

Effects of constant harvesting of predators.

J. Huang et al. (2013) ([88]) have shown that when predators are continuously harvested at the constant rate h , the newly formulated model (3.19) has a Bogdanov-Takens singularity (cusp case) of codimension 3 or a weak focus of multiplicity two for some parameter values, respectively. It is also possible to have saddle-node bifurcation, repelling and attracting Bogdanov-Takens bifurcations, supercritical and subcritical Hopf bifurcations, and degenerate Hopf bifurcation as the values of parameters vary. Hence, there are different parameter values for which their model has a homoclinic loop or two limit cycles. J. Huang et al. (2013) ([88]) concluded that their results indicate that the dynamical behavior of the model is very sensitive to the constant-yield predator harvesting and the

initial densities of both species. It requires careful management in the applied conservation and renewable resource contexts.

The N. Zhang et al. model (2011).

N. Zhang et al. (2011) ([198]) proposed and analyzed a Leslie-Gower predator-prey model with the assumption that predator and prey species in their model are both of commercial importance. So, they are subjected to constant effort harvesting. The parameters c_1 and c_2 measure the effort being spent by a harvesting agency. Thus, they formulated the following system with linear harvesting function :

$$\begin{cases} \dot{x}(t) &= r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy - c_1 x, \\ \dot{y}(t) &= r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t) - c_2 y, \end{cases} \quad (3.20)$$

Effects of linear harvesting of preys and predators.

It has been shown by N.zhang et al. (2011) ([198]) that the unique positive equilibrium of the system is globally stable, which means that suitable harvesting has no influence on the persistent property of the harvesting system. They found that harvesting can have fluctuating effect on the predator density. Under some suitable restriction, harvesting has no influence on the final density of the prey species, while the density of predator species is strictly decreasing function of the harvesting efforts.

The R. P. Gupta et al. model(2012).

A modified version of the Leslie-Gower type predator-prey model is proposed and analyzed by R. P. Gupta et al. (2012) ([65]). Their model is a bidimensional system of ordinary differential equation predator-prey model with a nonlinear prey-harvesting function, the Michaelis-Menten harvesting function. Their model is the following set of two differential equations :

$$\begin{cases} \dot{x}(t) &= r_1 \left(1 - \frac{x}{K}\right) x - \frac{qEx}{m_1 E + m_2 x}, \\ \dot{y}(t) &= r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t), \end{cases} \quad (3.21)$$

where q is the catchability coefficient, E is the effort applied to harvest individuals which is measured in terms of number of (standard) vessels being used to harvest the individual population and m_1, m_2 are suitable positive constants.

Effects of nonlinear harvesting of preys.

R. P. Gupta et al. (2012) ([65]) have shown that the nonlinear harvesting of preys significantly modifies the dynamics of the system in comparison to the proportionate harvesting of prey. It is possible to have bifurcating effects. The model (3.21) can have two, one or no interior equilibrium point in the first quadrant, where two interior equilibria collapse to one interior equilibrium point and then disappear through saddle-node bifurcation considering the rate of harvesting as bifurcation parameter. The local existence of limit cycle appearing through local Hopf bifurcation is also possible.

The M. K. Singh et al. model (2016).

M. K. Singh et al. (2016) ([160]) have modelled a Leslie-Gower predator-prey model with Michaelis-Menten type predator nonlinear harvesting. They have the study the stability and the bifurcation

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analysis of their following model :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t)}\right) y(t) - \frac{qEy}{m_1 E + m_2 y}, \end{cases} \quad (3.22)$$

where q is the catchability coefficient, E is the effort applied to harvest individuals which is measured in terms of number of (standard) vessels being used to harvest the individual population and m_1, m_2 are suitable positive constants.

Effects of nonlinear harvesting of predators.

M. K. Singh et al. (2016) ([160]) have shown that their proposed model exhibits the bistability for certain parametric conditions. They have shown that nonlinear harvesting of predators can induced a bifurcating effect. Their model (3.22) exhibits different kinds of bifurcations (e.g., the saddle-node bifurcation, the subcritical and supercritical Hopf bifurcations, Bogdanov-Takens bifurcation, and the homoclinic bifurcation) whenever the values of parameters of the model vary. Their analytical findings and numerical simulations reveal far richer and complex dynamics in comparison to the models with no harvesting and with constant-yield predator harvesting.

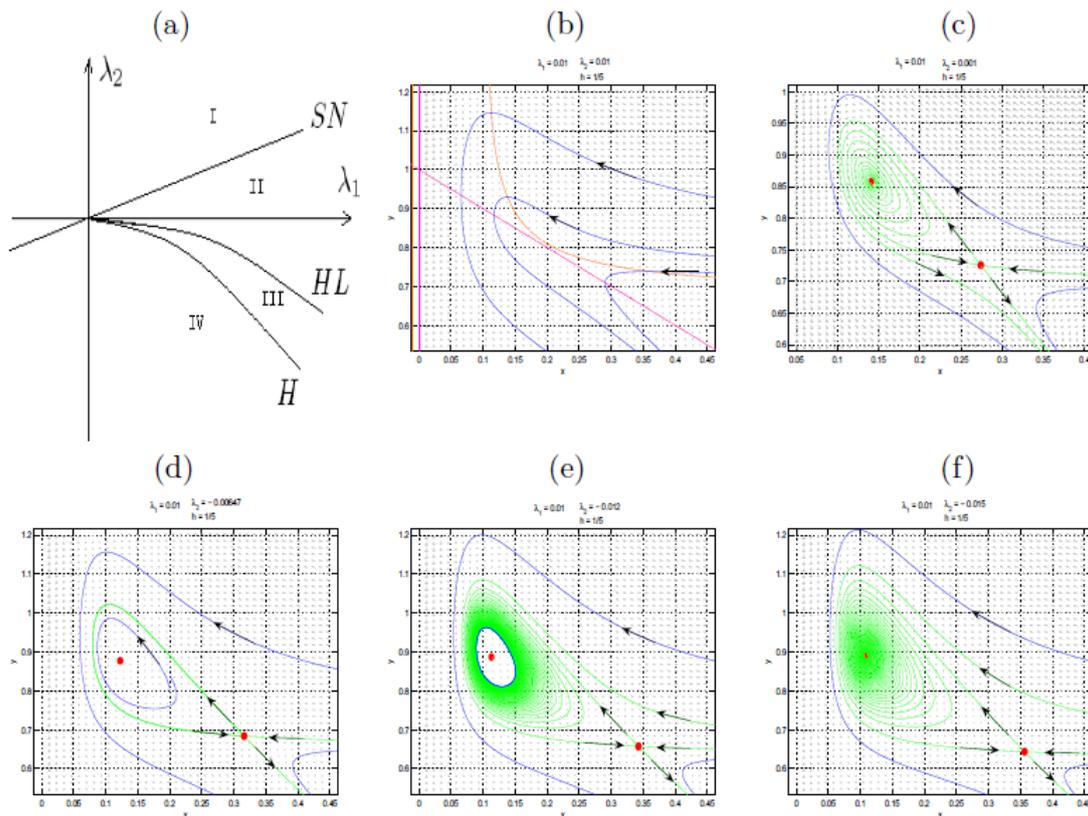


Figure 3.3: The attracting Bogdanov-Takens bifurcation diagram and corresponding phase portraits of system (3.19). (a) Bifurcation diagram; (b) No equilibria when the parameters lies in region I; (c) An unstable focus when the parameters lies in region II; (d) A stable homoclinic loop when the parameters lies on the curve HL; (e) A stable limit cycle when the parameters lies in region III; (f) A stable focus when the parameters lies in region IV. From J. Huang et al. ([88])

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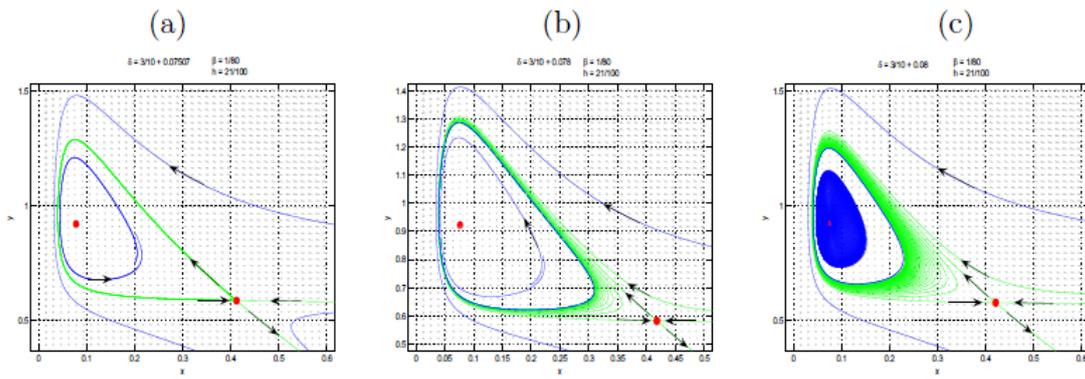


Figure 3.4: Phase portraits of system (3.19) , (a) A stable homoclinic cycle enclosing an unstable hyperbolic focus; (b) A stable limit cycle enclosing an unstable hyperbolic focus and arising from the attracting homoclinic bifurcation (c) Two limit cycles enclosing a stable hyperbolic focus. From J. Huang et al. ([88])

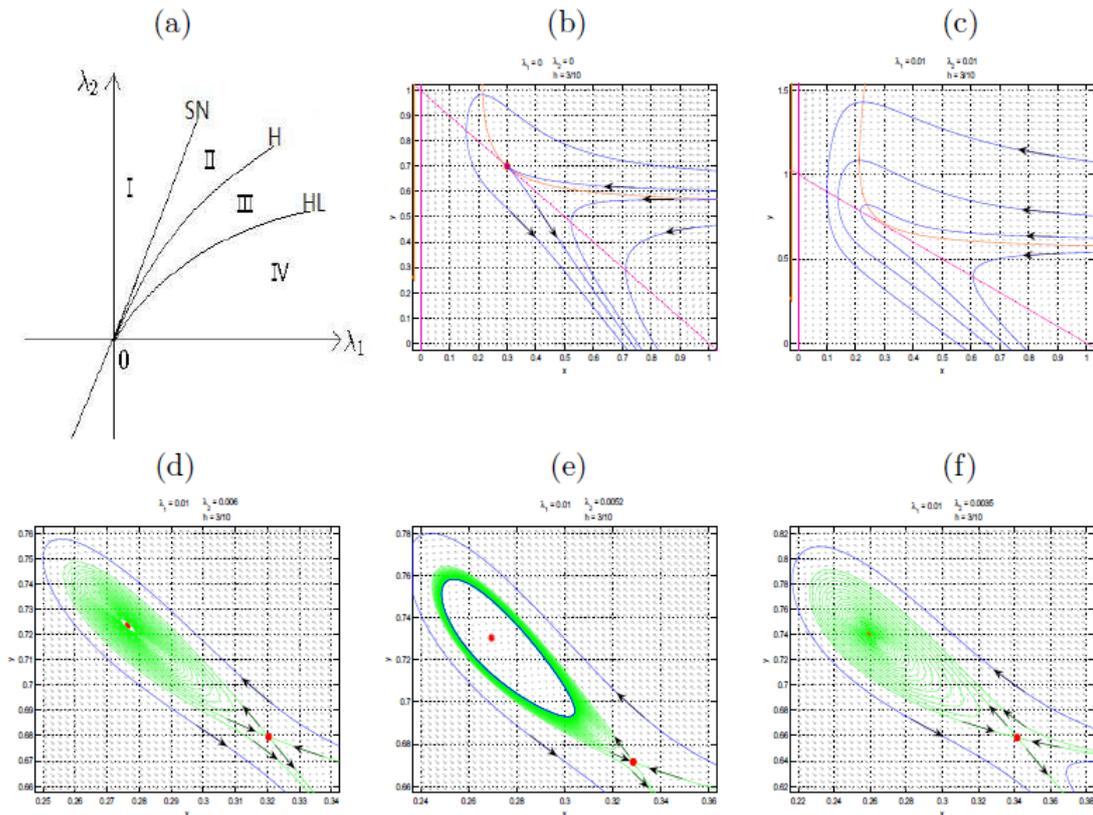


Figure 3.5: The repelling Bogdanov-Takens bifurcation diagram and corresponding phase portraits of system (3.19). (a) Bifurcation diagram; (b) A cusp of codimension 2 for the value (0, 0) of parameters; (c) No equilibria when the couple of parameters lies in region I; (d) An unstable focus when the couple of parameters lies in region II; (e) An unstable limit cycle when the couple of parameters lies in region III; (f) A stable focus when the couple of parameters lies in region IV. From J. Huang et al.([88])

With figures (3.3), (3.4) and (3.5), we can see how complex can become the dynamic of a Leslie-

3.2. Leslie-Gower predator-prey models and Modified Leslie-Gower predator-prey models

Gower predator-prey model incorporating a constant harvest of predators.

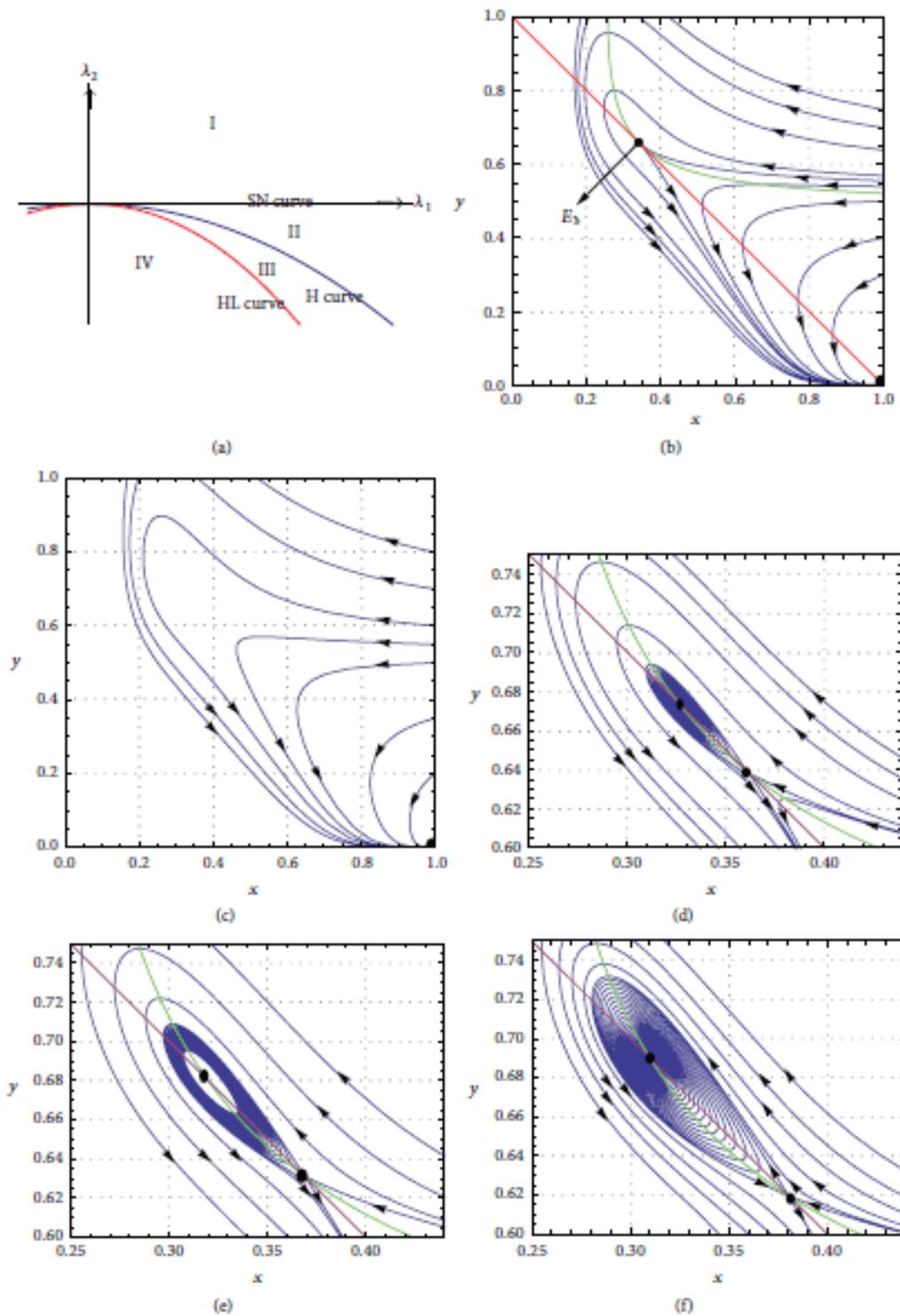


Figure 3.6: The Bogdanov-Takens bifurcation diagram and corresponding phase portraits of system (3.22). (a) Bogdanov-Takens bifurcation diagram. (b) The equilibrium point is a cusp. (c) No interior equilibrium point for parameters lying in region I. (d) An unstable focus for parameters lying in region II. (e) An unstable limit cycle for parameters lying in region III. (f) A stable focus for parameters lying in region IV. From M. K. Singh et al. ([160])

Figure (3.6) is an illustration of an example of complex dynamics that can arise from the incorpo-

ration of nonlinear harvesting of predators.

3.2.2.4 Leslie-Gower predator-prey models with discrete time delay

In what follows, some modified Leslie-Gower predator-preys models incorporating discrete time delay(s) are presented in order to recall the effect of discrete time delay on the initial Leslie-Gower predator-prey models.

The E. Beretta and Y. Kuang model (1998).

A characteristic behavior of predator-prey dynamics is the often observed oscillatory phenomenon of the population densities. A common mechanism to do this is to introduce time delays in the models, which is, indeed, a more realistic approach to the understanding of the predator-prey dynamics. A simple and natural way to do this is to incorporate a single discrete delay into the predator equations. In their paper, E. Beretta and Y. Kuang (1998) ([17]) perform global qualitative analyses on some delayed ratio-dependent predator-prey systems. Although the ratio-dependent systems do have negative feedbacks in the predator equations, they are not very helpful if one wants to use the traditional approaches of constructing Liapunov functionals or make use of suitable Razumikhin type arguments. Their approach make use of a rather novel and nontrivial way of constructing proper Liapunov functionals, used first in their recent work on the traditional Lotka-Volterra type predator-prey system with a single discrete delay in the predator equation ([16]).

The following Leslie-Gower predator-prey model incorporating a discrete time delay is a particular case of the models studied by E. Beretta and Y. Kuang (1998) ([17]).

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t-\tau)}{\alpha x(t-\tau)}\right) y(t), \end{cases} \quad (3.23)$$

The S. Yuan and Y. Song model (2009).

S. Yuan and Y. Song (2009) ([194]) consider the following delayed Leslie-Gower predator-prey model

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t-\tau)}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x}\right) y(t), \end{cases} \quad (3.24)$$

The S. Yuan and Y. Song model (2009).

S. Yuan and Y. Song (2009) ([195]) has proposed and studied a delayed LeslieGower predatorprey system in which they assumed that the predator and the prey species have the same feedback delay to their growth. Their model is the following one :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t-\tau)}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t-\tau)}{\alpha x}\right) y(t), \end{cases} \quad (3.25)$$

The Y. Ma model (2012).

Y. Ma (2012) ([125]) has proposed the following model in which he has assumed that only an adult

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predator has the ability to predate. Using the time taken for digestion of the prey, he has introduced the above Leslie-Gower model with two delays.

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x}{K}\right) x - \lambda xy(t - \tau_1), \\ \dot{y}(t) = r_2 \left(1 - \frac{y}{\alpha x(t - \tau_2)}\right) y(t), \end{cases} \quad (3.26)$$

where τ_1 denotes the maturation delay of the predator, while τ_2 denotes the time taken for digestion of the prey.

The W. Zhang et al. model (2013).

The model (3.27) proposed by W. Zhang et al. (2013) (zhang 2013) is a two species Leslie-Gower predator-prey system with a discrete time delay (maturation time).

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t - \tau)}{K}\right) x - \lambda xy, \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{\alpha x(t - \tau)}\right) y(t), \end{cases} \quad (3.27)$$

Effects of discrete time delay.

E. Beretta and Y. Kuang (1998) ([17]), S. Yuan and Y. Song (2009) ([195]), S. Yuan and Y. Song (2009) ([195]), Y. Ma (2012) ([125]) and W. Zhang et al. (2013) (zhang 2013) have shown that the discrete time delay can induced Hopf bifurcating effect, appearance of limit cycles and stability switching of the positive equilibrium when the positive equilibrium is stable for the models without the discrete time delay. Using the discrete time delay as a bifurcation parameter, their results show that the positive equilibrium can only be asymptotically stable or unstable depending on the delays. They have also obtained that Hopf bifurcations can occur as the delay crosses some critical values. In addition, they have paid special attention to the global continuation of local Hopf bifurcations. Using a global Hopf bifurcation result of Wu (1998) ([179]) for functional differential equations, they have showed the global existence of periodic solutions and Hopf bifurcations are demonstrated.

3.3 Formulation of a Modified Leslie-Gower Predator-Prey Model

Considering the Leslie-Gower predator-prey model (3.7), we assume a possible constant proportion of prey refuge $x_R = mx(t)$. m is such that $0 \leq m < 1$. This parameter is the rate of refuge of prey population. This means that when $m = 0$, all preys are available for predation. $mx(t)$ models the capacity of a refuge at time t and so refuge protecting $mx(t)$ of the prey population. It therefore remains $(1 - m)x(t)$ of the preys available for predation. We also assume that preys are harvested with the continuous threshold harvesting function $H(x(t))$ (3.5) defined as follows :

$$H(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x - T_1)}{T_2 - T_1} & \text{if } T_1 \leq x \leq T_2, \\ h & \text{if } x > T_2. \end{cases}$$

3.4. Positivity and Boundedness of solutions

Due to the fact that a time delay can play an important role in biological dynamical systems, where it has been recognized to contribute critically to the stable or unstable outcome of prey densities due to predation, we introduce a discrete time delay τ for the predator dynamic in order to take into account the gestation or the maturation of the predator. So our newly formulated predator-prey model incorporating prey refuge, discrete time delay and harvesting of preys, is given by the following set of two ordinary differential equations :

$$\begin{cases} \dot{x}(t) &= (r_1 - b_1 x(t)) x(t) - a_1(1 - m)x(t)y(t) - H(x(t)), \\ \dot{y}(t) &= \left(r_2 - \frac{a_2 y(t - \tau)}{(1 - m)x(t - \tau)} \right) y(t), \end{cases} \quad (3.28)$$

Let us denote by \mathbb{R}_+^2 the nonnegative quadrant and by $\text{int}(\mathbb{R}_+^2)$ the positive quadrant. For $\theta \in [-\tau, 0]$, we use the following conventional notation :

$$x_t(\theta) = x(t + \theta)$$

Then the initial conditions for system (3.28) take the form :

$$\begin{cases} \dot{x}_0(\theta) &= \phi_1(\theta), \\ \dot{y}_0(\theta) &= \phi_2(\theta), \end{cases} \quad (3.29)$$

for all $\theta \in [-\tau, 0]$, where $(\phi_1, \phi_2) \in \mathcal{C}([-\tau, 0], \mathbb{R}_+^2)$, $x(0) = \phi_1(0) > 0$ and $y(0) = \phi_2(0) > 0$.

In model (3.28), $x(t)$ denotes the prey population at time t and $y(t)$ the predator population at time t . All parameters are positive and Parameters r_1 and r_2 are the intrinsic growth rate of the preys and predators respectively, a_1 denotes the predation rate per unit of time, $\frac{r_1}{b_1}$ is the carrying capacity of the prey's environment and $\frac{r_2}{a_2}$ is the carrying capacity of the predator's environment which is proportional to the number of prey. Here, we incorporate a single discrete time delay $\tau > 0$ in the negative feedback of the predator's density.

For ecological reason as in ([169]), we make the following assumptions:

(i) $0 < x(0) \leq \frac{r_1}{b_1} \equiv K$

(ii) $T_1 < T_2 < K$

In fact, the first assumption comes from the fact that it is not plausible to have an initial value of the preys $x(0)$ at time $t = 0$ which is greater than the carrying capacity K of the preys. Moreover if $T_1 = T_2$, then the harvesting function becomes a discrete harvesting. In other hand, if we assume $T_2 \geq K$, then we will not have some harvest after T_2 since the first assumption leads to $0 \leq x(t) \leq K$.

3.4 Positivity and Boundedness of solutions

3.4.1 Positivity of solutions

In what follows, we show that solutions of system (3.28-3.29) and system (3.5) that start in \mathbb{R}_+^2 will remain there. Indeed, we have the following theorem.

3.4. Positivity and Boundedness of solutions

Theorem 3.1. Every solution of System (3.28) that starts in \mathbb{R}_+^2 will remain there.

Proof. Let $(x_0; y_0) \in \mathbb{R}_+^2$ be given and let us denote for each $t \geq 0$, $(x(t); y(t))$ the orbit of System (3.28) passing through $(x_0; y_0)$ at $t = 0$. Then, we can find that $(x(t); y(t)) \in \mathbb{R}_+^2$ for all $t \geq 0$. Thus, every solution of System (3.28) that starts in \mathbb{R}_+^2 will remain there. \square

3.4.2 Boundedness of solutions

In the following theorem, we show that solutions of system (3.28-3.29) and system (3.5) are uniformly bounded.

Theorem 3.2. Let Assumption (ii) holds. Then, every solution of System (3.28) is uniformly bounded.

Proof. Let $(x_0; y_0) \in \mathbb{R}_+^2$ be given.

From the \dot{x} -equation of System (3.28), we have

$$\dot{x}(t) \leq (r_1 - b_1 x(t))x(t).$$

which implies

$$x(t) \leq \frac{1}{\frac{b_1}{r_1} + \left(\frac{1}{x(0)} - \frac{b_1}{r_1}\right) e^{-r_1 t}}$$

for all $t \geq 0$. Since $0 < x(0) \leq \frac{r_1}{b_1}$ from Assumption 2 – (i), it follows that $x(t) \leq \frac{r_1}{b_1}$ for all $t \geq 0$.

Now, let us check for the boundedness of $y(t)$.

From the predator equation, we have $\dot{y}(t) \leq r_2 y(t)$. Hence, for $t > \tau$, $y(t) \leq y(t - \tau)e^{r_2 \tau}$. This equation is equivalent for $t > \tau$, to

$$y(t - \tau) \geq y(t)e^{-r_2 \tau}. \quad (3.30)$$

Moreover, for any $\delta > 1$, there exists a positive T_δ such that for $t > T_\delta$, $x(t) < \delta \frac{r_1}{b_1}$. Eq.(3.30) gives for $t > T_\delta + \tau$,

$$\dot{y}(t) < y(t) \left(r_2 - \frac{a_2 e^{-r_2 \tau}}{\delta(1-m) \frac{r_1}{b_1}} y(t) \right),$$

which implies, by the same arguments use for x , that

$$\limsup_{t \rightarrow +\infty} y(t) < \frac{r_2}{a_2 \delta(1-m) \frac{r_1}{b_1} e^{r_2 \tau}}$$

. The conclusion of this theorem holds for $\delta \rightarrow 1$. \square

3.5 Equilibria of the model without delay and their stability

3.5.1 Equilibria of the model without delay

In this subsection we analyze some equilibria properties of System (3.5)-(3.28). These steady states, which are determined analytically by setting $\dot{x} = \dot{y} = 0$, are independent of the delay τ . The following results holds :

Theorem 3.3. :

1. System (3.5)-(3.28) has one, two or three equilibria with $y = 0$ (without predators).

• System (3.5)-(3.28) has one equilibrium in $\mathbb{R}_+^* \times \{0\}$ which is :

- $E_1(x_1, 0)$ if $(r_1 - b_1 T_2)T_2 > h$, with $x_1 \in \left[\frac{K}{2}, K\right]$ if $T_2 \leq \frac{K}{2}$, or $x_1 \in [T_2, K]$ if $T_2 \geq \frac{K}{2}$.

- $\tilde{F}(\tilde{x}, 0)$ if $(r_1 - b_1 T_2)T_2 \leq h$ and $T_2 \geq \frac{K}{2}$. $\tilde{x} \in [T_1, T_2]$.

• System (3.5)-(3.28) has two equilibria in $\mathbb{R}_+^* \times \{0\}$: $\tilde{F}(\tilde{x}, 0)$ and $\tilde{E}\left(\frac{K}{2}, 0\right)$.

$\tilde{x} \in [T_1, T_2]$ under the conditions $T_2 \leq \frac{K}{2}$, $(r_1 - b_1 T_2)T_2 \leq h$ and $\frac{r_1 K}{4} = h$.

• System (3.5)-(3.28) has three equilibria in $\mathbb{R}_+^* \times \{0\}$: $\tilde{F}(\tilde{x}, 0)$, $E_1(x_1, 0)$ and $E_2(x_2, 0)$.

$\tilde{x} \in [T_1, T_2]$, $x_1 \in \left[\frac{K}{2}, K\right]$, $x_2 \in \left[T_2, \frac{K}{2}\right]$ under the conditions $T_2 \leq \frac{K}{2}$, $(r_1 - b_1 T_2)T_2 \leq h$ and $\frac{r_1 K}{4} > h$.

x_1 and x_2 are solutions of equation $-b_1 x^2 + r_1 x - h = 0$.

\tilde{x} is a solution of equation $-b_1 x^2 + \left(r_1 - \frac{h}{T_2 - T_1}\right) x + \frac{h T_1}{T_2 - T_1} = 0$,

2. System (3.5)-(3.28) has one, two or three coexisting equilibria.

• System (3.5)-(3.28) has one coexisting equilibrium which is :

- $G_0\left(\frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1 - m)^2}, y_0\right)$ if $\frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1 - m)^2} < T_1$.

- $G(x^*, y^*)$ if $\frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1 - m)^2} \in [T_1, T_2]$. $x^* \in [T_1, T_2]$ and $y^* = \frac{r_2 (1 - m) x^*}{a_2}$.

- $G_1(x_1^*, y_1^*)$ if $\frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1 - m)^2} \geq T_2$ and $(r_1 - b_1 T_2)T_2 > h$. $x_1^* \in \left[T_2, \frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1 - m)^2}\right]$ and $y_1^* = \frac{r_2 (1 - m) x_1^*}{a_2}$.

• System (3.5)-(3.28) has two coexisting equilibria :

- $G(x^*, y^*) \in [T_1, T_2] \times \mathbb{R}_+^*$

3.5. Equilibria of the model without delay and their stability

$$- \tilde{G}_0 \left(\frac{a_2 r_1}{2(a_2 b_1 + r_2 a_1 (1-m)^2)}, \tilde{y}_0 \right) \text{ when } \frac{a_2 r_1}{2(a_2 b_1 + r_2 a_1 (1-m)^2)} > T_2, \\ \left(\frac{a_2 r_1 - (a_2 b_1 + r_2 a_1 (1-m)^2) T_2}{a_2} \right) T_1 \leq h \text{ and } \left(\frac{a_2 r_1^2}{4(a_2 b_1 + a_1 r_1 (1-m)^2)} \right) = h.$$

• System (3.5)-(3.28) has three coexisting equilibria :

$$- G(x^*, y^*) \in [T_1, T_2] \times \mathbb{R}_+^* \\ - G_1(x_1^*, y_1^*) \in \left] \frac{a_2 r_1}{2(a_2 b_1 + r_2 a_1 (1-m)^2)}, \frac{a_2 r_1}{a_2 b_1 + r_2 a_1 (1-m)^2} \right] \times \mathbb{R}_+^* \\ - G_2(x_2^*, y_2^*) \in \left[T_2, \frac{a_2 r_1}{2(a_2 b_1 + r_2 a_1 (1-m)^2)} \right] \times \mathbb{R}_+^* \text{ when } \frac{a_2 r_1}{2(a_2 b_1 + r_2 a_1 (1-m)^2)} > T_2, (r_1 - b_1 T_2) T_2 \leq h \text{ and } \frac{a_2 r_1^2}{4(a_2 b_1 + a_1 r_1 (1-m)^2)} > h.$$

x_1^* and x_2^* are solutions of equation $-\frac{a_2 b_1 + a_1 r_2 (1-m)^2}{a_2} x^2 + r_1 x - h = 0$.

x^* is a solution of equation $-\frac{a_2 b_1 + a_1 r_2 (1-m)^2}{a_2} x^2 + \left(r_1 - \frac{h}{T_2 - T_1} \right) x + \frac{h T_1}{T_2 - T_1} = 0$,

Remark 3.1. : Concerning parameters $K = \frac{r_1}{b_1} b_0 = b_1 + \frac{r_2 a_1 (1-m)^2}{a_2}$ and $K_0 = \frac{r_1}{b_0}$, we always have $K_0 \leq K$.

Proof. : Let $K = \frac{r_1}{b_1}$, $b_0 = b_1 + \frac{r_2 a_1 (1-m)^2}{a_2}$, $K_0 = \frac{r_1}{b_0}$, $\varphi : x \mapsto (r_1 - b_1 x)x$ and $\varphi_0 : x \mapsto (r_1 - b_0 x)x$.

An equilibrium $S(x, y)$ of the model is solution of Eq.(3.31) when $x < T_1$, Eq. (3.32) when $T_1 \leq x \leq T_2$ and Eq. (3.33) when $x \geq T_2$, where

$$\begin{cases} (r_1 - b_1 x)x - a_1(1-m)xy = 0, \\ \left[r_2 - \frac{a_2 y}{(1-m)x} \right] y = 0, \end{cases} \quad (3.31)$$

$$\begin{cases} (r_1 - b_1 x)x - a_1(1-m)xy - \frac{h(x - T_1)}{T_2 - T_1} = 0, \\ \left[r_2 - \frac{a_2 y}{(1-m)x} \right] y = 0, \end{cases} \quad (3.32)$$

and

$$\begin{cases} (r_1 - b_1 x)x - a_1(1-m)xy - h = 0, \\ \left[r_2 - \frac{a_2 y}{(1-m)x} \right] y = 0. \end{cases} \quad (3.33)$$

From the second equation of System (3.31), System (3.32) or System (3.33), we have $y = 0$ or $y = \frac{r_2(1-m)x}{a_2}$.

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When $y = 0$, the equilibria $(0, 0)$ and $\left(\frac{r_1}{b_1}, 0\right)$ exist on $[0, T_1[$. This is impossible since $\frac{r_1}{b_1} = K > T_1$. Moreover, we have the following equations,

$$(r_1 - b_1x)x - a_1(1 - m)xy - \frac{h(x - T_1)}{T_2 - T_1} = 0 \text{ on } [T_1, T_2],$$

and

$$(r_1 - b_1x)x - a_1(1 - m)xy - h = 0 \text{ on } [T_2, K].$$

- On $[T_1, T_2]$, the identity at the equilibrium gives equation $-b_1x^2 + \left(r_1 - \frac{h}{T_2 - T_1}\right)x + \frac{hT_1}{T_2 - T_1} = 0$ which admits a unique positive solution.

Let us consider $f(x) = -b_1x^2 + \left(r_1 - \frac{h}{T_2 - T_1}\right)x + \frac{hT_1}{T_2 - T_1}$. Then $f(T_1) > 0$ and $f(T_2) = \varphi(T_2) - h$. Hence, if $\varphi(T_2) \leq h$, a unique solution exists on $[T_1, T_2]$.

- On $[T_2, K]$, the identity at the equilibrium gives equation $-b_1x^2 + r_1x - h = 0$. Its discriminant is

$$\Delta = r_1^2 - 4b_1h = 4b_1 \left(\varphi\left(\frac{K}{2}\right) - h \right).$$

Hence, if $\frac{K}{2} > h$, there are two positive solutions, which are both on $[T_2, K]$, when $T_2 < \frac{K}{2}$ and $\varphi(T_2) \leq h$. Besides, when $\varphi(T_2) > h$, just one of the solutions is on $[T_2, K]$.

Still according to the sign of the discriminant Δ , if $\varphi\left(\frac{K}{2}\right) = h$, $x = \frac{K}{2}$ is the unique solution on $[T_2, K]$ when $\frac{K}{2} \geq T_2$.

There is no solution when $\frac{K}{2} < T_2$.

When $y \neq 0$, from the second equation of System (3.31), System (3.32) and System (3.33), we have $y = \frac{r_2(1 - m)}{a_2}x$. Replacing it in the first equation gives $(r_1 - b_0x)x - H(x) = 0$. On $[0, T_1]$, the unique solution of this equation is $x = K_0$, which exists if and only if $K_0 \leq T_1$. Moreover, we have the following equations,

$$(r_1 - b_0x)x - \frac{h(x - T_1)}{T_2 - T_1} = 0 \text{ on } [T_1, T_2]$$

and

$$(r_1 - b_0x)x - h = 0 \text{ on } [T_2, K].$$

- On $[T_1, T_2]$, if $K_0 < T_1$, there is no equilibrium on $[T_1, T_2]$. Else, the identity at the equilibrium gives equation $-b_0x^2 + \left(r_1 - \frac{h}{T_2 - T_1}\right)x + \frac{hT_1}{T_2 - T_1} = 0$ which admits a unique positive solution.

Let us consider $f_0(x) = -b_0x^2 + \left(r_1 - \frac{h}{T_2 - T_1}\right)x + \frac{hT_1}{T_2 - T_1}$. Then $f_0(T_1) = b_0T_1(K_0 - T_1) > 0$ and $f_0(T_2) = \varphi_0(T_2) - h$. Hence, if $\varphi_0(T_2) \leq h$, a unique solution exists on $[T_1, T_2]$.

- On $[T_2, K]$, the identity at the equilibrium gives $-b_0x^2 + r_1x - h = 0$. Its discriminant is $\Delta_0 = r_1^2 - 4b_0h = 4b_0 \left(\varphi_0\left(\frac{K_0}{2}\right) - h \right)$. Hence, when $\frac{K_0}{2} > h$, there are two positive solutions, which are both on $[T_2, K_0]$, when $T_2 < \frac{K_0}{2}$ and $\varphi_0(T_2) \leq h$. Besides, when $\varphi_0(T_2) > h$, just one of the solutions is on $[T_2, K]$ (particularly on $[T_2, K_0]$).

3.5. Equilibria of the model without delay and their stability

Still according to the sign of the discriminant, when $\varphi_0\left(\frac{K_0}{2}\right) = h$, $x = \frac{K_0}{2}$ is the unique solution on $[T_2, K]$ when $\frac{K_0}{2} \geq T_2$. There is no solution when $\frac{K_0}{2} < T_2$.

□

Remark 3.2. : We summarize the results about equilibria in Fig. 3.7 and Fig. 3.8.

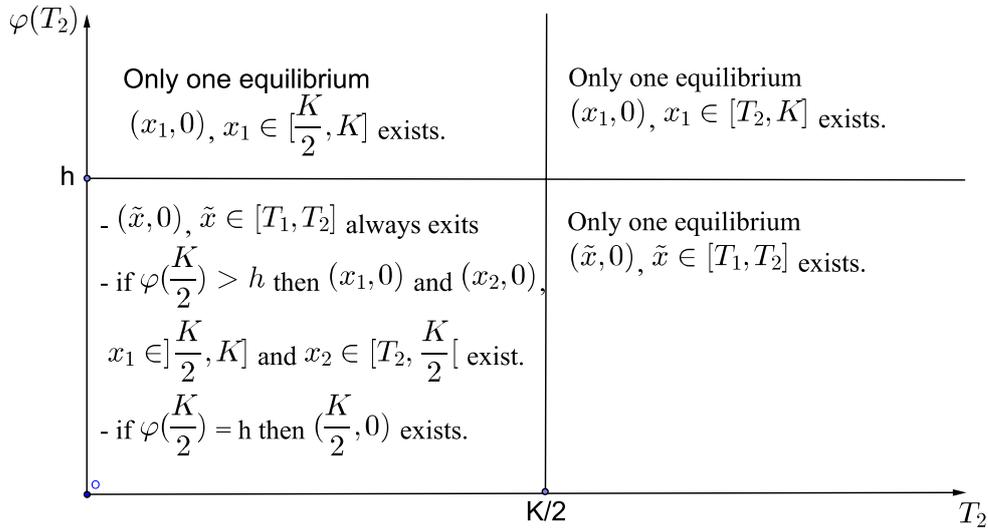


Figure 3.7: Existence and number of equilibria when $y = 0$.

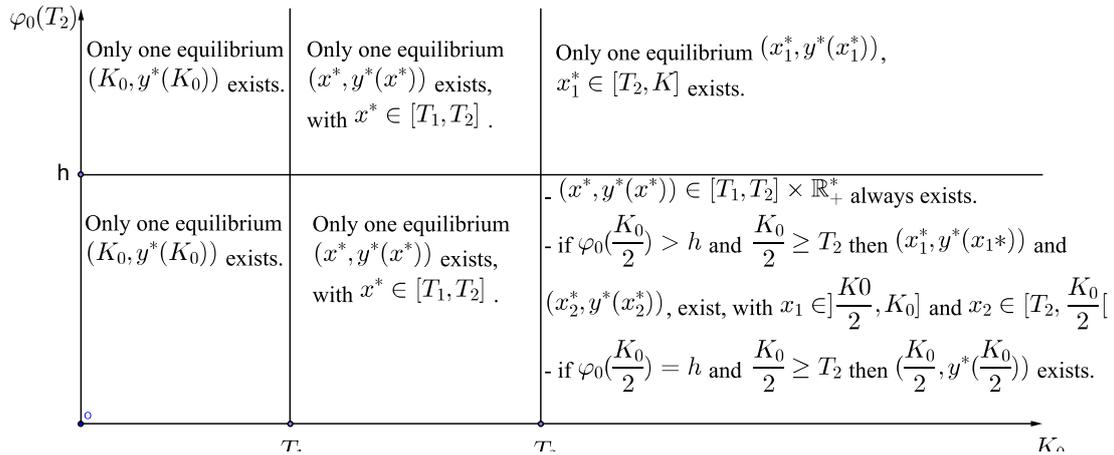


Figure 3.8: Existence and number of equilibria when $y \neq 0$ and $y^*(x^*) = \frac{r_2(1-m)x^*}{a_2}$.

3.5.2 Stability of Equilibria of the model without delay

The Jacobian matrix $J(x, y)$ of System (3.28) at the equilibrium (x, y) when $T_1 \leq x \leq T_2$, is given by

$$\begin{pmatrix} \varphi'(x) - \frac{h}{T_2 - T_1} - a_1(1 - m)y & -a_1(1 - m)x, \\ \frac{a_2 y^2}{(1 - m)x^2} & r_2 - \frac{2a_2 y}{(1 - m)x} \end{pmatrix}.$$

We notice that $r_2 \geq 0$ is always an eigenvalue of any equilibrium $E(x, 0)$, which is therefore unstable.

Concerning stability of any equilibrium $G(x^*, y^*)$ with $y^* \neq 0$, the following theorem holds.

Theorem 3.4. : Let consider

$$\Delta_1 = \left[\varphi'(x^*) - a_1(1 - m)y^* - r_2 \right]^2 - 4 \left[2a_1(1 - m)r_2 y^* - r_2 \varphi'(x^*) \right],$$

$$\Delta_2 = \left[\varphi'(x^*) - a_1(1 - m)y^* - \frac{h}{T_2 - T_1} - r_2 \right]^2 - 4 \left[2a_1(1 - m)r_2 y^* - r_2 \left[\varphi'(x^*) - \frac{h}{T_2 - T_1} \right] \right].$$

1. Let consider an equilibrium $G(x^*, y^*)$ with $x^* \in [0, T_1 \cup T_2, K]$.
 - If $\Delta_1 > 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1 - m)y^* + r_2 > 0$ and $2a_1(1 - m)r_2 y^* - r_2 \varphi'(x^*) > 0$.
 - If $\Delta_1 = 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1 - m)y^* + r_2 > 0$.
 - If $\Delta_1 < 0$, then the equilibrium is a stable focus when $-\varphi'(x^*) + a_1(1 - m)y^* + r_2 > 0$.
 - If $-\varphi'(x^*) + a_1(1 - m)y^* + r_2 = 0$ and $2a_1(1 - m)r_2 y^* - r_2 \varphi'(x^*) > 0$, then the equilibrium is a center.
2. Let consider an equilibrium $G(x^*, y^*)$ with $x^* \in [T_1, T_2]$.
 - If $\Delta_2 > 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1 - m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$ and $2a_1(1 - m)r_2 y^* - r_2 \left(\varphi'(x^*) - \frac{h}{T_2 - T_1} \right) > 0$.
 - If $\Delta_2 = 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1 - m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$.
 - If $\Delta_2 < 0$, then the equilibrium is a stable focus when $-\varphi'(x^*) + a_1(1 - m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$.
 - If $-\varphi'(x^*) + a_1(1 - m)y^* + \frac{h}{T_2 - T_1} + r_2 = 0$ and $2a_1(1 - m)r_2 y^* - r_2 \left(\varphi'(x^*) - \frac{h}{T_2 - T_1} \right) > 0$, then the equilibrium is a center.

Proof. : The Jacobian matrix $J(x^*, y^*)$ of System (3.28) at the equilibrium (x^*, y^*) becomes

$$\begin{pmatrix} \varphi'(x^*) - a_1(1 - m)y^* - H'(x^*) & -a_1(1 - m)x^* \\ r_2 \frac{y^*}{x^*} & -r_2 \end{pmatrix},$$

3.6. Hopf bifurcation and stability analysis of the delayed model

where $H'(x) = 0$ for $x \in [0, T_1[\cup]T_2, K]$ and $H'(x) = \frac{h}{T_2 - T_1}$ for $x \in [T_1, T_2]$.

Therefore, the eigenvalues are given by the following equation:

$$\begin{aligned} \lambda^2 + \lambda \left[-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 \right] \\ + 2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) = 0. \end{aligned} \quad (3.34)$$

The discriminant of this equation is given by

$$\begin{aligned} \Delta = \left[\varphi'(x^*) - a_1(1-m)y^* - H'(x) - r_2 \right]^2 \\ - 4 \left[2a_1(1-m)r_2y^* - r_2[\varphi'(x^*) - H'(x)] \right], \end{aligned}$$

which is equal to Δ_1 on $[0, T_1[\cup]T_2, K]$ and Δ_2 on $[T_1, T_2]$.

- When $\Delta > 0$, $J(x^*, y^*)$ has two positive eigenvalues which are both negatives if $-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 > 0$ and $2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) > 0$.
- When $\Delta = 0$, $J(x^*, y^*)$ has one positive eigenvalue which is negative if $-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 > 0$.
- When $\Delta < 0$, $J(x^*, y^*)$ has two conjugated complex eigenvalues with a positive real part equal to $\varphi'(x^*) - a_1(1-m)y^* - H'(x) - r_2$.
- When $-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 = 0$ and $2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) > 0$, $J(x^*, y^*)$ has pure imaginary eigenvalues.

Hence, the conclusions follow. \square

Remark 3.3. : The importance of this section is due to the fact that, if an equilibrium of System (3.5)- (3.28) is unstable for $\tau = 0$, it remains unstable for $\tau > 0$ ([42], [128]). Then, any equilibrium of System (3.28) in the form $E(x, 0)$ is unstable when $\tau > 0$. Concerning stability of equilibria when $\tau > 0$, we only consider the coexistence equilibria.

3.6 Hopf bifurcation and stability analysis of the delayed model

In order to analyze the stability of coexistence equilibria $G(x^*, y^*)$, let us define new variables $u(t) = x(t) - x^*$ and $v(t) = y(t) - y^*$. Then the linearization of System (3.28) at G^* gives

$$\begin{cases} \dot{u}(t) = \left[r_1 - 2b_1x^* - a_1(1-m)y^* - H'(x^*) \right] u(t) \\ \quad - a_1(1-m)x^*v(t), \\ \dot{v}(t) = -\Psi'(x^*)y^{*2}u(t - \tau) - r_2v(t - \tau), \end{cases} \quad (3.35)$$

where $H'(x^*) = 0$ for $x^* \in [0, T_1[\cup]T_2, K]$, $H'(x^*) = \frac{h}{T_2 - T_1}$ for $x^* \in [T_1, T_2]$ and $\Psi(x^*) = \frac{a_2}{(1-m)x^*}$.

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The characteristic equation of System (3.35) at $G^*(x^*, y^*)$ is given by

$$\lambda^2 - \alpha\lambda + r_2\lambda e^{-\lambda\tau} - r_2(\alpha - a_1(1-m)y^*)e^{-\lambda\tau} = 0, \quad (3.36)$$

where $\alpha = r_1 - 2b_1x^* - a_1(1-m)y^* - H'(x^*)$.

Note that for $\tau = 0$, the characteristic equations (3.36) becomes

$$\lambda^2 + (r_2 - \alpha)\lambda - r_2(\alpha - a_1(1-m)y^*) = 0. \quad (3.37)$$

Since the sum and product of roots are $-(r_2 - \alpha)$ and $-r_2(\alpha - a_1(1-m)y^*)$ respectively, the two roots of (3.37) are real and negative or complex conjugate with negative real parts if and only if

$$r_2 - \alpha > 0 \quad \text{and} \quad \alpha - a_1(1-m)y^* < 0. \quad (3.38)$$

Hence, in the absence of time delay, the system is locally asymptotically stable if and only if $r_2 - \alpha > 0$ and $\alpha - a_1(1-m)y^* < 0$.

Now, for $\tau > 0$, if $\lambda = i\omega$ is a root of equation (3.36), then we have

$$-\omega^2 + \alpha\omega + r_2i\omega(\cos\omega\tau - i\sin\omega\tau) - c(\cos\omega\tau - i\sin\omega\tau) = 0,$$

where $c = r_2(\alpha - a_1(1-m)y^*)$.

Separating real and imaginary parts gives

$$r_2\omega \sin\omega\tau - c \cos\omega\tau = \omega^2 \quad \text{and} \quad r_2\omega \cos\omega\tau + c \sin\omega\tau = \alpha\omega. \quad (3.39)$$

Eliminating τ by squaring and adding equations of (3.39), we get the algebraic equation

$$r_2^2\omega^6 + [c^2 + r_2^2(\alpha^2 - r_2^2)]\omega^4 + c^2(\alpha^2 - 2r_2^2)\omega^2 - c^4 = 0. \quad (3.40)$$

Substituting $\omega^2 = \eta$ in the above equation gives a cubic equation in η of the form

$$r_2^2\eta^3 + [c^2 + r_2^2(\alpha^2 - r_2^2)]\eta^2 + c^2(\alpha^2 - 2r_2^2)\eta - c^4 = 0. \quad (3.41)$$

Observe that conditions (3.38) implies $\alpha < r_2$. Since $r_2^2 > 0$ and $-c^4 < 0$, if $c^2 + r_2^2(\alpha^2 - r_2^2) > 0$ or $\alpha^2 - 2r_2^2 < 0$, then by Descartes' rule of sign, Eq.(3.41) has at least one positive root.

If $\alpha \in]-r_2, r_2[$, then $\alpha^2 - 2r_2^2 < 0$ and Eq.(3.41) has only one positive root. If $\alpha < -r_2$, then $c^2 + r_2^2(\alpha^2 - r_2^2) > 0$ and Eq.(3.41) has at least one positive root. So, for any cases, Eq.(3.41) has at least one positive root.

The following theorem gives a criterion for the switching in the stability behavior of $G^*(x^*, y^*)$ in terms of the delay parameter τ .

Theorem 3.5. : Suppose that $G^*(x^*, y^*)$ exists and is locally asymptotically stable for System (3.28) with $\tau = 0$. Also let $\eta_0 = \omega_0^2$ be a positive root of Eq.(3.41). Then there exists a value $\tau = \tau_0$ such that G^* is locally asymptotically stable for $\tau \in (0, \tau_0]$ and unstable for $\tau > \tau_0$. Furthermore, the system undergoes a Hopf bifurcation at G^* when $\tau = \tau_0$.

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Proof. : Since ω_0 is a solution of Eq.(3.40), the characteristic Eq.(3.36) has the pair of purely imaginary roots $\pm i\omega_0$. From Eq.(3.39), τ_n^0 for $n = 0, 1, \dots$ as a function of ω_0 is given by

$$\tau_n^0 = \frac{1}{\omega_0} \arccos \left\{ \frac{w_0^2(-c + \alpha r_2)}{c^2 + r_2^2 w_0^2} \right\} + \frac{2\pi n}{\omega_0}. \quad (3.42)$$

For $\tau = 0$, theorem 3.4 ensures that G^* is locally asymptotically stable. Hence, by Butler's lemma [27], G^* remains stable up to the minimum value of τ_n^0 , obtained here for $n = 0$, i.e. for $\tau < \tau_0^0$, so that $\tau^0 = \min_{n \geq 0} \tau_n^0 \equiv \tau_0^0$. The theorem can be completely proved if we can show that

$$\text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\lambda=i\omega_0} > 0.$$

Differentiating equation (3.36) with respect to τ yields

$$\left[2\lambda - \alpha + (r_2 - r_2\tau\lambda + c\tau)e^{-\lambda\tau} \right] \frac{d\lambda}{d\tau} = (r_2\lambda^2 - c\lambda)e^{-\lambda\tau}, \quad (3.43)$$

which gives

$$\begin{aligned} \left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1} &= \frac{2\lambda - \alpha + (r_2 - r_2\tau\lambda + c\tau)e^{-\lambda\tau}}{(r_2\lambda^2 - c\lambda)e^{-\lambda\tau}}, \\ &= -\frac{2\lambda^2 - \alpha\lambda}{\lambda^2(\lambda^2 - \alpha\lambda)} - \frac{r_2}{\lambda(c - r_2\lambda)} - \frac{\tau}{\lambda}, \\ &= -\frac{1}{\lambda^2 - \alpha\lambda} - \frac{1}{\lambda^2} - \frac{r_2}{\lambda(c - r_2\lambda)} - \frac{\tau}{\lambda}. \end{aligned}$$

Thus, $\mu_0 = \text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\lambda=i\omega_0}$ is given by

$$\begin{aligned} \mu_0 &= \text{sign} \left\{ \text{Re} \left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1} \right\} \Big|_{\lambda=i\omega_0}, \\ &= \text{sign} \left\{ \text{Re} \left[-\frac{1}{\lambda^2 - \alpha\lambda} - \frac{1}{\lambda^2} - \frac{r_2}{\lambda(c - r_2\lambda)} \right] \right\} \Big|_{\lambda=i\omega_0}, \\ &= \text{sign} \left\{ \frac{w_0^2}{w_0^4 + \alpha^2 w_0^2} + \frac{1}{w_0^2} - \frac{r_2^2 w_0^2}{r_2^2 w_0^4 + w_0^2 c^2} \right\} \\ &= \text{sign} \left\{ \frac{r_2^2 w_0^4 + 2c^2 w_0^2 + \alpha^2 c^2}{(w_0^4 + \alpha^2 w_0^2)(r_2 w_0^2 + c^2)} \right\} > 0. \end{aligned}$$

Hence, $\text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\tau=\tau^0, \lambda=i\omega_0} > 0$. The transversality condition is satisfied and a Hopf bifurcation occurs at $\tau = \tau^0$. This achieves the proof. \square

3.7 Direction and stability of Hopf bifurcation

In this section, we give some properties of the Hopf bifurcation presented in Theorem (3.5). We also analyze the stability of bifurcated periodic solutions occurring through Hopf bifurcations, by using the normal form theory and the center manifold reduction for retarded functional differential equations (RFDEs) due to Hassard, Kazarinoff and Wan ([74]). We assume that System (3.28) undergoes

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Hopf bifurcation at the positive equilibrium $G(x^*; y^*)$ for $\tau = \tau_0^j$, ($j = 0, 1, 2, \dots$) and then $i\omega_0$ is corresponding purely imaginary roots of the characteristic equation. Let $x_1(t) = x(t) - x^*$ and $x_2(t) = y(t) - y^*$. Then, system (3.5)-(3.28) is equivalent to :

$$\begin{cases} \dot{x}_1(t) = (r_1 - 2b_1x^* - a_1(1-m)y^*)x_1(t) - H'(x^*)x_1(t) - a_1(1-m)x^*x_2(t) \\ \quad + f_1(x_1(t), x_2(t)), \\ \dot{x}_2(t) = -\Psi'(x^*)y^{*2}x_1(t-\tau) - r_2x_2(t-\tau) + f_2(x_2(t), x_1(t-\tau), x_2(t-\tau)), \end{cases} \quad (3.44)$$

where

$$f_1(x_1(t), x_2(t)) = -a_1(1-m)x_1(t)x_2(t) - b_1x_1^2(t)$$

and

$$\begin{aligned} f_2(x_2(t), x_1(t-\tau), x_2(t-\tau)) = r_2(x_2(t) + y^*) - (\Psi(x_1(t-\tau) + x^*)(x_2(t-\tau) + y^*)) (x_2(t) + y^*) \\ + \Psi'(x^*)y^{*2}x_1(t-\tau) + r_2x_2(t-\tau) \end{aligned}$$

Let $\tau = \tau_j^0 + \mu$. Then, $\mu = 0$ corresponds to Hopf bifurcation value of System (3.28) at the positive equilibrium $G(x^*; y^*)$. Since System (3.28) is equivalent to System (3.44), in the following discussion we use System (3.44).

In System (3.44), let $\bar{x}_k(t) = x_k(\tau t)$ and drop the bars for simplicity of notation. Then, System (3.44) can be rewritten as a system of RFDEs in $\mathcal{C}([-1, 0], \mathbb{R}^2)$ of the form :

$$\begin{cases} \dot{x}_1(t) = (\tau_j^0 + \mu)(r_1 - 2b_1x^* - a_1(1-m)y^*)x_1(t) - (\tau_j^0 + \mu)H'(x^*)x_1(t) \\ \quad - (\tau_j^0 + \mu)a_1(1-m)x^*x_2(t) + (\tau_j^0 + \mu)f_1(x_1(t), x_2(t)), \\ \dot{x}_2(t) = -(\tau_j^0 + \mu)\Psi'(x^*)y^{*2}x_1(t-\tau) \\ \quad - (\tau_j^0 + \mu)r_2x_2(t-\tau) \\ \quad + (\tau_j^0 + \mu)f_2(x_2(t), x_1(t-\tau), x_2(t-\tau)), \end{cases} \quad (3.45)$$

Define the linear operator $L(\mu) : \mathcal{C} \rightarrow \mathbb{R}^2$ and the nonlinear operator $f(\cdot, \mu) : \mathcal{C} \rightarrow \mathbb{R}^2$ by:

$$L_\mu\phi = (\tau_j^0 + \mu) \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + (\tau_0 + \mu) \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix}, \quad (3.46)$$

and

$$f(\phi, \mu) = (\tau_j^0 + \mu) \begin{pmatrix} f_1(\phi_1(0), \phi_2(0)) \\ f_2(\phi_2(0), \phi_1(-1), \phi_2(-1)) \end{pmatrix}, \quad (3.47)$$

respectively, where $\phi = (\phi_1, \phi_2)^T \in \mathcal{C}$, $J_0 = r_1 - 2b_1x^* - a_1(1-m)y^* - H'(x^*)$, $J_1 = -a_1(1-m)x^*$. By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \mu)$, $-1 \leq \theta \leq 0$ whose elements are of bounded variation such that :

$$L_\mu(\phi) = \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta) \quad \text{for } \phi \in \mathcal{C}([-1, 0], \mathbb{R}^2) \quad (3.48)$$

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In fact, we can choose

$$\eta(\theta, \mu) = (\tau_j^0 + \mu) \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} \delta(\theta) + (\tau_j^0 + \mu) \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix} \delta(\theta+1), \quad (3.49)$$

where δ is the Dirac delta function defined by

$$\delta(\theta) = \begin{cases} 0 & \text{if } \theta \neq 0, \\ 1 & \text{if } \theta = 0. \end{cases} \quad (3.50)$$

For $\phi \in \mathcal{C}([-1, 0], \mathbb{R}^2)$, define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \text{if } -1 \leq \theta < 0 \\ \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta), & \text{if } \theta = 0 \end{cases} \quad (3.51)$$

and

$$R(\mu)\phi = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & \text{if } -1 \leq \theta < 0, \\ f(\mu, \phi), & \text{if } \theta = 0. \end{cases} \quad (3.52)$$

Then, System (3.45) is equivalent to

$$\dot{x}(t) = A(\mu)x_t + Rx_t. \quad (3.53)$$

where $x_t(\theta) = x(t + \theta)$, $\theta \in [-1, 0]$.

For $\psi \in \mathcal{C}^1([0, 1], \mathbb{R}^2)$, define

$$A^*(\mu)\psi = \begin{cases} -\frac{d\psi(s)}{ds} & \text{if } 0 < s \leq 1, \\ \int_{-1}^0 d\eta^T(s, \mu)\psi(-s) & \text{if } s = 0. \end{cases} \quad (3.54)$$

and a bilinear inner product

$$\langle \psi, \phi \rangle = \bar{\psi}(0) \cdot \phi(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \bar{\psi}^T(\xi - \theta) d\eta(\theta)\phi(\xi) d\xi, \quad (3.55)$$

where $\eta(\theta) = \eta(\theta, 0)$.

In addition, by Theorem (3.5) we know that $\pm i\omega_0\tau_j^0$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^* . Let us assume that $q(\theta)$ is the eigenvector of $A(0)$ corresponding to $i\omega_0\tau_j^0$ and $q^*(s)$ is the eigenvector of A^* corresponding to $-i\omega_0\tau_j^0$

Let $q(\theta) = \begin{pmatrix} 1, & \nu_1 \end{pmatrix}^T e^{i\omega_0\tau_j^0\theta}$ and $q^*(s) = D \begin{pmatrix} 1, & \nu_1^* \end{pmatrix}^T e^{i\omega_0\tau_j^0 s}$. From the above discussion, it is easy to know that $A(0)q(0) = i\omega_0\tau_j^0 q(0)$ and $A^*(0)q^*(0) = -i\omega_0\tau_j^0 q^*(0)$. That is

$$\tau_j^0 \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} q(0) + \tau_j^0 \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} q(-1) = i\omega_0\tau_j^0 q(0)$$

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and

$$\tau_j^0 \begin{pmatrix} J_0 & 0 \\ J_1 & -r_2 \end{pmatrix} q^*(0) + \tau_j^0 \begin{pmatrix} 0 & -\Psi'(x^*)y^{*2} \\ 0 & -r_2 \end{pmatrix} q^*(-1) = -i\omega_0\tau_j^0 q^*(0).$$

Thus, we can easily obtain

$$q(\theta) = \left(1, \frac{J_0 - i\omega_0}{a_1(1-m)x^*} \right)^T e^{i\omega_0\tau_j^0\theta}, \quad (3.56)$$

$$q^*(s) = D \left(1, \frac{J_0 + i\omega_0}{\Psi'(x^*)y^{*2}e^{-i\omega_0\tau_j^0}} \right)^T e^{i\omega_0\tau_j^0 s}. \quad (3.57)$$

In order to assure $\langle \bar{q}^*(s), q(\theta) \rangle = 1$, we need to determine the value of D . From (3.55), we have

$$\begin{aligned} \langle \bar{q}^*(s), q(\theta) \rangle &= \bar{q}^*(0)q(0) - \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{q}^*(\xi - \theta) d\eta(\theta) q(\xi) d\xi \\ &= \bar{q}^*(0)q(0) - \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{D} \left(1, \bar{\nu}_1^* \right) e^{-i\omega_0\tau_j^0(\xi-\theta)} d\eta(\theta) \left(1, \nu_1 \right)^T e^{i\omega_0\tau_j^0\xi} d\xi \\ &= \bar{q}^*(0)q(0) - \bar{q}^*(0) \int_{-1}^0 \theta e^{i\omega_0\tau_j^0\theta} d\eta(\theta) q(0) \\ &= \bar{q}^*(0)q(0) - \bar{q}^*(0)\tau_j^0 \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \left(-e^{-i\omega_0\tau_j^0} \right) q(0) \\ &= \bar{D} \left[1 + \nu_1 \bar{\nu}_1^* - \tau_j^0 e^{-i\omega_0\tau_j^0} \bar{\nu}_1^* (\Psi'(x^*)y^{*2} + r_2) \right]. \end{aligned}$$

Therefore, we have

$$\begin{aligned} \bar{D} &= \frac{1}{1 + \nu_1 \bar{\nu}_1^* - \tau_j^0 e^{-i\omega_0\tau_j^0} \bar{\nu}_1^* (\Psi'(x^*)y^{*2} + r_2)}, \\ D &= \frac{1}{1 + \bar{\nu}_1 \nu_1^* - \tau_j^0 e^{i\omega_0\tau_j^0} \nu_1^* (\Psi'(x^*)y^{*2} + r_2)}. \end{aligned} \quad (3.58)$$

Using the same notations as in [74], we first compute the coordinates to describe the center manifold \mathcal{C}_0 at $\mu = 0$. Let x_t be the solution of Eq. (3.44) when $\mu = 0$. Define

$$\begin{aligned} z(t) &= \langle q^*, x_t \rangle, \\ W(t, \theta) &= x_t(\theta) - 2\mathcal{R}_e \left(z(t)q(\theta) \right) \\ &= x_t(\theta) - \left(z(t)q(\theta) + \bar{z}(t)\bar{q}(\theta) \right). \end{aligned} \quad (3.59)$$

On the center manifold \mathcal{C}_0 , we have

$$W(t, \theta) = W(z, \bar{z}, \theta), \quad (3.60)$$

where

$$W(z, \bar{z}, \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + W_{30}(\theta) \frac{z^3}{6} + \dots, \quad (3.61)$$

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z and \bar{z} are local coordinates for center manifold C_0 in the direction of q^* and \bar{q}^* . Note that W is real if x_t is real. We only consider real solutions. For solution $x_t \in C_0$ of Eq.(3.44), since $\mu = 0$, we have

$$\begin{aligned}\dot{z}(t) &= i\omega_0\tau_j^0 z + \bar{q}^*(0)f\left(0, W(z, \bar{z}, 0) + 2\mathcal{R}_e(z(t)q(\theta))\right) \\ &\equiv i\omega_0\tau_j^0 z + \bar{q}^*(0)f_0(z, \bar{z}).\end{aligned}\quad (3.62)$$

We rewrite this equation as

$$\dot{z}(t) = i\omega_0\tau_j^0 z + g(z, \bar{z}), \quad (3.63)$$

where

$$g(z, \bar{z}) = g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta)z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}(\theta)\frac{z^2\bar{z}}{2} + \dots \quad (3.64)$$

Then, $x_t(\theta) = (x_{1t}(\theta), x_{2t}(\theta))$ and $q(\theta) = (1, \nu_1)^T e^{i\omega_0\tau_j^0\theta}$. So, from Eq.(3.59) and Eq.(3.61), it follows that

$$\begin{aligned}x_t(\theta) &= W(t, \theta) + 2\mathcal{R}_e\left(z(t)q(\theta)\right) \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}\frac{\bar{z}^2}{2} \\ &\quad + (1, \nu_1)^T e^{i\omega_0\tau_j^0\theta} z(t) + (1, \bar{\nu}_1)^T e^{-i\omega_0\tau_j^0\theta} \bar{z}(t) + \dots\end{aligned}\quad (3.65)$$

Then, we have

$$\begin{aligned}x_{1t}(0) &= z + \bar{z} + W_{20}^{(1)}(0)\frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + \dots \\ x_{2t}(0) &= \nu_1 z + \bar{\nu}_1 \bar{z} + W_{20}^{(2)}(0)\frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + \dots \\ x_{1t}(-1) &= ze^{-i\omega_0\tau_j^0} + \bar{z}e^{i\omega_0\tau_j^0} + W_{20}^{(1)}(-1)\frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1)\frac{\bar{z}^2}{2} + \dots \\ x_{2t}(-1) &= \nu_1 ze^{-i\omega_0\tau_j^0} + \bar{\nu}_1 \bar{z}e^{i\omega_0\tau_j^0} + W_{20}^{(2)}(-1)\frac{z^2}{2} + W_{11}^{(2)}(-1)z\bar{z} + W_{02}^{(2)}(-1)\frac{\bar{z}^2}{2} + \dots\end{aligned}\quad (3.66)$$

It follows together with Eq.(3.47) that

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$$\begin{aligned}
g(z, \bar{z}) &= \bar{q}^*(0)f_0(z, \bar{z}) \\
&= \bar{q}^*(0)f(0, x_t) = \tau_j^0 \bar{D} \left(1, \bar{\nu}_1^* \right) \times \\
&\quad \left(\begin{array}{l} -b_1 x_{1t}^2(0) - a_1(1-m)x_{1t}(0)x_{2t}(0); \\ \\ -\Psi'(x^*)x_{2t}(-1)x_{2t}(0) \\ -\Psi'(x^*)x_{1t}(-1)x_{2t}(-1)x_{2t}(0); \\ -\Psi'(x^*)y^*x_{1t}(-1)x_{2t}(-1) \\ -\Psi'(x^*)y^*x_{1t}(-1)x_{2t}(0); \\ -\frac{\Psi''(x^*)}{2}y^*x_{1t}^2(-1)x_{2t}(-1) \\ -\frac{\Psi''(x^*)}{2}y^*x_{1t}^2(-1)x_{2t}(0); \\ -\frac{\Psi''(x^*)}{2}y^{*2}x_{1t}^2(-1)x_{2t}(0) \\ -\frac{\Psi^{(3)}(x^*)}{6}y^{*2}x_{1t}^3(-1) - \dots \end{array} \right) \\
&= \frac{z^2}{2} \left\{ 2\tau_j^0 \bar{D}[-b_1 - \nu_1 a_1(1-m) - \bar{\nu}_1^*(\Psi(x^*)\nu_1^2 e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*\nu_1 e^{-2i\omega_0\tau_j^0}) \right. \\
&\quad \left. - y^*\nu_1 e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2}y^{*2}e^{-2i\omega_0\tau_j^0} \right\} \\
&+ \frac{\bar{z}^2}{2} \left\{ 2\tau_j^0 \bar{D}[-b_1 - \bar{\nu}_1 a_1(1-m) - \bar{\nu}_1^*(\Psi(x^*)\bar{\nu}_1^2 e^{i\omega_0\tau_j^0} - \Psi'(x^*)y^*\bar{\nu}_1 e^{2i\omega_0\tau_j^0}) \right. \\
&\quad \left. - y^*\bar{\nu}_1 e^{i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2}y^{*2}e^{2i\omega_0\tau_j^0} \right\} \\
&+ z\bar{z} \left\{ 2\tau_j^0 \bar{D}[-b_1 - \Re_e(\nu_1)a_1(1-m) - \bar{\nu}_1^*(\Re_e(\nu_1\bar{\nu}_1 e^{-i\omega_0\tau_j^0})\Psi(x^*) - \Re_e(\bar{\nu}_1)y^*\Psi'(x^*)) \right. \\
&\quad \left. - y^*\Re_e(\nu_1 e^{i\omega_0\tau_j^0}) - y^{*2}\Psi''(x^*) \right\} \\
&+ \frac{z^2\bar{z}}{2} \left\{ \tau_j^0 \bar{D} \left[-b_1 \left(2W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0) \right) - a_1(1-m)(2W_{11}^{(2)}(0) + W_{20}^{(2)}(0) + \bar{\nu}_1 W_{20}^{(1)}(0)) \right. \right. \\
&\quad + 2\nu_1 a_1(1-m)W_{11}^{(1)}(0) - \bar{\nu}_1^* \Psi(x^*)(2\nu_1 W_{11}^{(2)}(0) + \bar{\nu}_1 W_{20}^{(2)}(0)e^{i\omega_0\tau_j^0}) \\
&\quad + \bar{\nu}_1^* \Psi(x^*)(\bar{\nu}_1 W_{20}^{(2)}(-1) + 2\nu_1 W_{11}^{(2)}(-1)) - \bar{\nu}_1^* \Psi'(x^*)(2\nu_1 \bar{\nu}_1 e^{-2i\omega_0\tau_j^0}) \\
&\quad + \bar{\nu}_1^* \Psi'(x^*)(2\nu_1 \bar{\nu}_1 + 2\nu_1^2 e^{-2i\omega_0\tau_j^0}) - \bar{\nu}_1^* \Psi'(x^*)y^*(2W_{11}^{(2)}(-1)e^{-i\omega_0\tau_j^0}(1 + \nu_1) \\
&\quad + \bar{\nu}_1^* \Psi'(x^*)y^*W_{20}^{(1)}(-1)e^{i\omega_0\tau_j^0}(1 + \bar{\nu}_1) - 2W_{11}^{(2)}(0)e^{-i\omega_0\tau_j^0} + W_{20}^{(2)}(0)e^{i\omega_0\tau_j^0} \\
&\quad + \bar{\nu}_1 W_{20}^{(1)}(-1) + 2\nu_1 W_{11}^{(1)}(-1)) - \bar{\nu}_1^* \frac{\Psi''(x^*)y^*}{2}(6\nu_1 e^{-i\omega_0\tau_j^0} + 4\nu_1 + 2\bar{\nu}_1 e^{-2i\omega_0\tau_j^0}) \\
&\quad \left. \left. + 4y^*\bar{\nu}_1^* \frac{\Psi''(x^*)y^*}{2}W_{11}^{(1)}(-1)e^{-i\omega_0\tau_j^0} + 2y^*e^{i\omega_0\tau_j^0}W_{20}^{(1)}(-1) - \bar{\nu}_1^* \frac{\Psi'''(x^*)y^*}{3}(2e^{-i\omega_0\tau_j^0} + e^{i\omega_0\tau_j^0}) \right\}. \tag{3.67}
\end{aligned}$$

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Comparing the coefficient with Eq.(3.64) gives :

$$\begin{aligned}
g_{20} &= 2\tau_j^0 \bar{D}(-b_1 - \nu_1 a_1(1 - m)) - 2\tau_j^0 \bar{D} \bar{\nu}_1^* \Psi(x^*) \nu_1^2 e^{-i\omega_0 \tau_j^0} \\
&\quad - 2\tau_j^0 \bar{D} \Psi'(x^*) y^* \nu_1 e^{-2i\omega_0 \tau_j^0} - 2\tau_j^0 \bar{D} y^* \nu_1 e^{-i\omega_0 \tau_j^0} - 2\tau_j^0 \bar{D} \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0}, \\
g_{02} &= 2\tau_j^0 \bar{D}(-b_1 - \nu_1 a_1(1 - m)) - 2\tau_j^0 \bar{D} \bar{\nu}_1^* \Psi(x^*) \nu_1^2 e^{-i\omega_0 \tau_j^0} - 2\tau_j^0 \bar{D} \Psi'(x^*) y^* \nu_1 e^{-2i\omega_0 \tau_j^0} \\
&\quad - 2\tau_j^0 \bar{D} y^* \nu_1 e^{-i\omega_0 \tau_j^0} - 2\tau_j^0 \bar{D} \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0}, \\
g_{11} &= 2\tau_j^0 \bar{D}(-b_1 - \Re_e(\nu_1) a_1(1 - m)) - 2\tau_j^0 \bar{D} \bar{\nu}_1^* \Re_e(\nu_1 \bar{\nu}_1 e^{-i\omega_0 \tau_j^0}) \Psi(x^*) - 2\tau_j^0 \bar{D} \bar{\nu}_1^* \Re_e(\bar{\nu}_1) y^* \Psi'(x^*) \\
&\quad - 2\tau_j^0 \bar{D} \bar{\nu}_1^* y^* \Re_e(\nu_1 e^{i\omega_0 \tau_j^0}) - 2\tau_j^0 \bar{D} \bar{\nu}_1^* y^{*2} \Psi''(x^*), \\
g_{21} &= -\tau_j^0 \bar{D} b_1 (2W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)) - \tau_j^0 \bar{D} a_1 (1 - m) (2W_{11}^{(2)}(0) + W_{20}^{(2)}(0)) \\
&\quad + \tau_j^0 \bar{D} \bar{\nu}_1 a_1 (1 - m) W_{20}^{(1)}(0) + 2\nu_1 W_{11}^{(1)}(0) - \bar{\nu}_1^* \Psi(x^*) (2\nu_1 W_{11}^{(2)}(0) + \bar{\nu}_1 W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0}) \\
&\quad + \bar{\nu}_1^* \Psi(x^*) (\bar{\nu}_1 W_{20}^{(2)}(-1) + 2\nu_1 W_{11}^{(2)}(-1)) - \bar{\nu}_1^* \Psi'(x^*) (2\nu_1 \bar{\nu}_1 e^{-2i\omega_0 \tau_j^0} + 2\nu_1 \bar{\nu}_1 \\
&\quad - 2\bar{\nu}_1^* \Psi'(x^*) \nu_1^2 e^{-2i\omega_0 \tau_j^0} - \bar{\nu}_1^* \Psi'(x^*) y^* 2W_{11}^{(2)}(-1) e^{-i\omega_0 \tau_j^0} (1 + \nu_1) \\
&\quad + \bar{\nu}_1^* \Psi'(x^*) y^* W_{20}^{(1)}(-1) e^{i\omega_0 \tau_j^0} (1 + \bar{\nu}_1) - 2\bar{\nu}_1^* \Psi'(x^*) y^* W_{11}^{(2)}(0) e^{-i\omega_0 \tau_j^0} \\
&\quad + \bar{\nu}_1^* \Psi'(x^*) y^* W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0} + \bar{\nu}_1 W_{20}^{(1)}(-1) + 2\bar{\nu}_1^* \Psi'(x^*) y^* \nu_1 W_{11}^{(1)}(-1) \\
&\quad - \bar{\nu}_1^* \frac{\Psi''(x^*) y^*}{2} (6\nu_1 e^{-i\omega_0 \tau_j^0} + 4\nu_1) + 2\bar{\nu}_1^* \frac{\Psi''(x^*) y^*}{2} \bar{\nu}_1 e^{-2i\omega_0 \tau_j^0} \\
&\quad + 4\bar{\nu}_1^* \frac{\Psi''(x^*) y^*}{2} y^* W_{11}^{(1)}(-1) e^{-i\omega_0 \tau_j^0} + 2y^* e^{i\omega_0 \tau_j^0} W_{20}^{(1)}(-1) \\
&\quad - \bar{\nu}_1^* \frac{\Psi'''(x^*) y^*}{3} (2e^{-i\omega_0 \tau_j^0} + e^{i\omega_0 \tau_j^0})
\end{aligned} \tag{3.68}$$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21} , we still need to compute them. From Eq.(3.53) and Eq.(3.59), we have

$$\begin{aligned}
\dot{W} &= \dot{x}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\
&= \begin{cases} AW - 2\mathcal{R}_e\{\bar{q}^*(0)f_0q(\theta)\} & \text{if } \theta \in [-1; 0), \\ AW - 2\mathcal{R}_e\{\bar{q}^*(0)f_0q(\theta)\} + f_0 & \text{if } \theta = 0, \end{cases} \\
&\stackrel{\text{def}}{=} AW + \mathcal{H}(z, \bar{z}, \theta),
\end{aligned} \tag{3.69}$$

where

$$\mathcal{H}(z, \bar{z}, \theta) = \mathcal{H}_{20}(\theta) \frac{z^2}{2} + \mathcal{H}_{11}(\theta) z\bar{z} + \mathcal{H}_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \tag{3.70}$$

Substituting the corresponding series into Eq.(3.69) and comparing the coefficients give

$$(A - 2i\omega_0 \tau_j^0) W_{20}(\theta) = -\mathcal{H}_{20}(\theta), \tag{3.71}$$

$$AW_{11}(\theta) = -\mathcal{H}_{11}(\theta).$$

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From Eq.(3.69), we know that for $\theta \in [-1, 0)$,

$$\begin{aligned}\mathcal{H}(z, \bar{z}, \theta) &= -\bar{q}^*(0)f_0q(\theta) - q^*(0)\bar{f}_0\bar{q}(\theta) \\ &= -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta).\end{aligned}\quad (3.72)$$

Comparing the coefficient with Eq.(3.70) gives

$$-g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta) = H_{20}(\theta), \quad (3.73)$$

$$-g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta) = H_{11}(\theta). \quad (3.74)$$

From Eq.(3.71) and Eq.(3.73) and the definition of A , it follows that

$$\dot{W}(\theta) = 2i\omega_0\tau_j^0W_{20} + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta). \quad (3.75)$$

Notice that $q(\theta) = \begin{pmatrix} 1 \\ \nu_1 \end{pmatrix}^T e^{i\omega_0\tau_j^0\theta}$. Hence,

$$W_{20}(\theta) = \frac{ig_{20}}{w_0\tau_j^0}q(0)e^{i\omega_0\tau_j^0\theta} + \frac{i\bar{g}_{02}}{3w_0\tau_j^0}\bar{q}(0)e^{-i\omega_0\tau_j^0\theta} + E_1e^{2i\omega_0\tau_j^0\theta}, \quad (3.76)$$

where $E_1 = (E_1^{(1)}, E_1^{(2)}) \in \mathbb{R}^2$ is a constant vector.

Similarly, from Eq.(3.71) and Eq.(3.74), we obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{w_0\tau_j^0}q(0)e^{i\omega_0\tau_j^0\theta} + \frac{i\bar{g}_{11}}{w_0\tau_j^0}\bar{q}(0)e^{-i\omega_0\tau_j^0\theta} + E_2, \quad (3.77)$$

where $E_2 = (E_2^{(1)}, E_2^{(2)}) \in \mathbb{R}^2$ is also a constant vector.

In what follows, we will seek appropriate E_1 and E_2 . From the definition of A and Eq.(3.71), we obtain

$$\int_{-1}^0 d\eta(\theta)W_{20}(\theta) = 2i\omega_0\tau_jW_{20}(0) - H_{20}(0), \quad (3.78)$$

$$\int_{-1}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0), \quad (3.79)$$

where $\eta(\theta) = \eta(0, \theta)$. By Eq.(3.69), we have

$$\begin{aligned}H_{20}(0) &= -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2\tau_j^0 \times \\ &\left(\begin{array}{c} -b_1 - \nu_1 a_1(1-m) \\ -\Psi(x^*)\nu_1^2 e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*\nu_1 e^{-2i\omega_0\tau_j^0} \\ -y^*\nu_1 e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2}y^{*2}e^{-2i\omega_0\tau_j^0} \end{array} \right),\end{aligned}\quad (3.80)$$

$$\begin{aligned}H_{11}(0) &= -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + 2\tau_j^0 \times \\ &\left(\begin{array}{c} -b_1 - \Re_e(\nu_1)a_1(1-m) \\ -\Re_e(\nu_1\bar{\nu}_1 e^{-i\omega_0\tau_j^0})\Psi(x^*) - \Re_e(\bar{\nu}_1)y^*\Psi'(x^*) \\ -y^*\Re_e(\nu_1 e^{i\omega_0\tau_j^0}) - y^{*2}\Psi''(x^*) \end{array} \right).\end{aligned}\quad (3.81)$$

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Substituting Eq.(3.76) and Eq.(3.80) into Eq.(3.78) and using the fact that

$$\begin{aligned} \left(i\omega_0\tau_j^0 I - \int_{-1}^0 e^{i\omega_0\tau_j^0\theta} d\eta(\theta) \right) q(0) &= 0, \\ \left(-i\omega_0\tau_j^0 I - \int_{-1}^0 e^{-i\omega_0\tau_j^0\theta} d\eta(\theta) \right) \bar{q}(0) &= 0, \end{aligned} \tag{3.82}$$

we obtain

$$\begin{aligned} \left(2i\omega_0\tau_j^0 I - \int_{-1}^0 e^{2i\omega_0\tau_j^0\theta} d\eta(\theta) \right) E_1 &= 2\tau_j^0 \times \\ &\begin{pmatrix} -b_1 - \nu_1 a_1(1-m) \\ -\Psi(x^*)\nu_1^2 e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*\nu_1 e^{-2i\omega_0\tau_j^0} \\ -y^*\nu_1 e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0\tau_j^0} \end{pmatrix}. \end{aligned}$$

This leads to

$$\begin{aligned} &\begin{pmatrix} 2i\omega_0 - J_0 & -J_1 \\ \Psi'(x^*)y^{*2}e^{-2i\omega_0\tau_j^0} & 2i\omega_0 + r_2 e^{-2i\omega_0\tau_j^0} \end{pmatrix} E_1 = \\ &2 \begin{pmatrix} -b_1 - \nu_1 a_1(1-m) \\ -\Psi(x^*)\nu_1^2 e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*\nu_1 e^{-2i\omega_0\tau_j^0} \\ -y^*\nu_1 e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0\tau_j^0} \end{pmatrix}. \end{aligned}$$

Solving this system for E_1 gives

$$E_1^{(1)} = \frac{2}{\sigma} \begin{vmatrix} -b_1 - \nu_1 a_1(1-m) & a_1(1-m)x^* \\ e_0 & 2i\omega_0 + r_2 e^{-2i\omega_0\tau_j^0} \end{vmatrix},$$

where

$$e_0 = -\Psi(x^*)\nu_1^2 e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*\nu_1 e^{-2i\omega_0\tau_j^0} - y^*\nu_1 e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0\tau_j^0},$$

$$E_1^{(2)} = \frac{2}{\sigma} \begin{vmatrix} 2i\omega_0 - J_0 & -b_1 - \nu_1 a_1(1-m) \\ \Psi'(x^*)y^{*2}e^{-2i\omega_0\tau_j^0} & e_0 \end{vmatrix},$$

where

$$\sigma = \begin{vmatrix} 2i\omega_0 - J_0 & a_1(1-m)x^* \\ \Psi'(x^*)y^{*2}e^{-2i\omega_0\tau_j^0} & 2i\omega_0 + r_2 e^{-2i\omega_0\tau_j^0} \end{vmatrix}.$$

3.7. Direction and stability of Hopf bifurcation

Similarly, substituting Eq.(3.77) and Eq.(3.81) into (3.79) gives

$$E_2 = \begin{pmatrix} -J_0 & -J_1 \\ \Psi'(x^*)y^{*2} & r_2 \end{pmatrix} \begin{pmatrix} -b_1 - \Re_e(\nu_1)a_1(1-m) \\ -\Re_e(\nu_1\bar{\nu}_1e^{-i\omega_0\tau_j^0})\Psi(x^*) - \Re_e(\bar{\nu}_1)y^*\Psi'(x^*) \\ -y^*\Re_e(\nu_1e^{i\omega_0\tau_j^0}) - y^{*2}\Psi''(x^*) \end{pmatrix}.$$

Therefore,

$$E_2^{(1)} = \frac{2}{\varrho} \begin{vmatrix} -b_1 - \Re_e(\nu_1)a_1(1-m) & -J_1 \\ e_1 & r_2 \end{vmatrix},$$

where

$$e_1 = -\Re_e(\nu_1\bar{\nu}_1e^{-i\omega_0\tau_j^0})\Psi(x^*) - \Re_e(\bar{\nu}_1)y^*\Psi'(x^*) - y^*\Re_e(\nu_1e^{i\omega_0\tau_j^0}) - y^{*2}\Psi''(x^*)$$

$$E_2^{(2)} = \frac{2}{\varrho} \begin{vmatrix} -J_0 & -b_1 - \Re_e(\nu_1)a_1(1-m) \\ \Psi'(x^*)y^{*2} & e_1 \end{vmatrix},$$

where

$$\varrho = \begin{vmatrix} -J_0 & a_1(1-m)x^* \\ \Psi'(x^*)y^{*2} & r_2 \end{vmatrix}.$$

Thus, we can determine W_{20} and W_{11} from Eq.(3.76) and Eq.(3.77). Furthermore, g_{21} in Eq.(3.68) can be expressed in terms of parameters and delay. Thus, we can compute the following values

$$\begin{aligned} C_1(0) &= \frac{i}{2w_0\tau_j^0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}, \\ \nu_2 &= -\frac{\Re_e\{C_1(0)\}}{\Re_e\{\lambda'(\tau_j^0)\}}, \\ \beta_2 &= 2\Re_e\{C_1(0)\}, \\ T_2 &= -\frac{\mathcal{I}_m\{C_1(0)\} + \nu_2\mathcal{I}_m\{\lambda'(\tau_j^0)\}}{w_0\tau_j^0}, \end{aligned} \tag{3.83}$$

which determine the qualities of bifurcating periodic solution in the center manifold at the critical value τ_j^0 .

Theorem 3.6. [74] In Eq. (3.83), the sign of ν_2 determines the direction of the Hopf bifurcation. Thus, if $\nu_2 > 0$, then the Hopf bifurcation is supercritical and the bifurcating periodic solution exists for $\tau_1 > \tau_1^0$. If $\nu_2 < 0$, then the Hopf bifurcation is subcritical and the bifurcating periodic solution exists for $\tau_1 < \tau_1^0$. β_2 determines the stability of the bifurcating periodic solution: The bifurcating periodic solutions are stable if $\beta_2 < 0$ and unstable if $\beta_2 > 0$. T_2 determines the period of the bifurcating periodic solutions: the period increase if $T_2 > 0$ and decrease if $T_2 < 0$.

3.8 Bioeconomic equilibrium and optimal harvest policy

The first part of this section deals with the bionomic equilibrium of System (3.28). The term bionomic equilibrium is an amalgamation of the concepts of biological equilibrium and economic equilibrium. As we already saw, a biological equilibrium is given by $\dot{x} = 0 = \dot{y}$. The economic equilibrium is said to be achieved when TR (the total revenue obtained by selling the harvested biomass) equals TC (the total cost for the effort devoted to harvesting). To discuss the bionomic equilibrium of the prey-predator model, we consider the parameters such as c = cost per unit effort for prey; p = price per unit biomass for the prey. The net economic rent or net revenue (R) at any time is given by :

$$R(x, h, t) = \left(p \frac{x - T_1}{T_2 - T_1} - c \right) h \quad \text{if } T_1 \leq x \leq T_2, \quad (3.84)$$

and

$$R(x, h, t) = (p - c)h \quad \text{if } x \geq T_2, \quad (3.85)$$

The bionomic equilibrium is $P_\infty(x_\infty, y_\infty, h_\infty)$ where x_∞, y_∞ and h_∞ are the positive solutions of the following simultaneous equations :

$$\begin{cases} (r_1 - b_1x)x - a_1(1 - m)xy - \frac{h(x - T_1)}{T_2 - T_1} = 0, \\ \left(r_2 - \frac{a_2y}{(1 - m)x} \right) y = 0 \quad \text{if } T_1 \leq x \leq T_2, \\ \left(p \frac{x - T_1}{T_2 - T_1} - c \right) h = 0 \end{cases} \quad (3.86)$$

and

$$\begin{cases} (r_1 - b_1x)x - a_1(1 - m)xy - h = 0, \\ \left(r_2 - \frac{a_2y}{(1 - m)x} \right) y \quad \text{if } x \geq T_2, \\ (p - c)h = 0 \end{cases} \quad (3.87)$$

It may be noted here that if $c > p \frac{x - T_1}{T_2 - T_1}$ when $T_1 \leq x \leq T_2$ or if $c > p$ when $x \geq T_2$, i.e. if the prey cost exceeds the revenue obtained from it, then the economic rent obtained from the prey becomes negative. Hence the prey will be closed and no bionomic equilibrium exists. Therefore, for

3.8. Bioeconomic equilibrium and optimal harvest policy

the existence of bionomic equilibrium, it is natural to assume $c < p \frac{x - T_1}{T_2 - T_1}$ when $T_1 \leq x \leq T_2$ and $c < p$ when $x \geq T_2$. Then for $T_1 \leq x \leq T_2$,

$$x_\infty = T_1 + \frac{c}{p}(T_2 - T_1), \quad (3.88)$$

$$y_\infty = \frac{r_2(1 - m)x_\infty}{a_2}, \quad (3.89)$$

$$h_\infty = \frac{p(r_1 - b_1x_\infty - a_1(1 - m)y_\infty)x_\infty}{c}, \quad (3.90)$$

It is clear that $h_\infty > 0$ if

$$r_1 - b_1x_\infty - a_1(1 - m)y_\infty > 0 \quad (3.91)$$

Thus, the bionomic equilibrium $P_\infty(x_\infty, y_\infty, h_\infty)$ exists if $x_\infty \leq T_2$ and inequality (3.91) holds.

In what follows, our objective is to maximize the total discounted net revenues from the fishery. In commercial exploitation of renewable resources, the fundamental problem from the economic point of view, is to determine the optimal trade-off between present and future harvests. If we look at the problem, it is observed that the marine fishery sectors become more important not only for domestic demand but also from the imperatives of exports. Symbolically our strategy is to maximize the present value J given by

$$J(h) = \int_0^{t_f} R(x(t), h(t), t)e^{-\delta t} dt \quad (3.92)$$

where $R(x(t), h(t), t)$ is defined by (3.84) and (3.85), and δ denotes the instantaneous annual rate of discount. Our problem is to maximize J subject to the state System (3.28) by invoking Pontryagins Maximum principle for retarded optimal control problem (2013)([172]). The control variable $h(t)$ is subjected to the constraints $0 \leq h(t) \leq K$. So, in other words, our problem now is to find h^* such that

$$J(h^*) = \max_{h \in \Omega} J(h) \quad (3.93)$$

where $\Omega = \{h \in L^1(0; t_f); 0 \leq h \leq K\}$.

The existence of an optimal harvesting is due to the concavity of integrand of J with respect to h , a boundedness of the state solutions $(x(t); y(t))$, and the Lipschitz property of the state system (3.28) with respect to the state variables (see L. S. Pontryagin et al. ([142])).

Using the Pontryagins maximum principle for delayed control problem [[142], [172]], problem (3.93) is reduced to maximize the Hamiltonian \mathcal{H} defined by :

$$\begin{aligned} \mathcal{H}(x(t), y(t), x(t - \tau), y(t - \tau), h(t), (t)) &= R(x(t), h(t), t)e^{-\delta t} + \lambda_1(t)\dot{x}(t) + \lambda_2(t)\dot{y}(t) \\ &= e^{-\delta t}R(x(t), h(t), t) + \lambda_1(t)((r_1 - b_1x(t) - a_1(1 - m)y(t))x(t) - H(x(t))) \\ &\quad + \lambda_2(t)y(t) \left(r_2 - \frac{a_2y(t - \tau)}{(1 - m)x(t - \tau)} \right) \end{aligned}$$

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where $\lambda(t) = (\lambda_1(t), \lambda_2(t))$. By the maximal principle, there exists adjoint variables $\lambda_1(t)$ and $\lambda_2(t)$ for all $t \geq 0$ such that

$$\begin{cases} \frac{d\lambda_1}{dt}(t) = -\frac{\partial \mathcal{H}}{\partial x(t)}(t) - \mathcal{X}_{[0, t_f - \tau]}(t) \frac{\partial \mathcal{H}}{\partial x(t - \tau)}(t + \tau), \\ \frac{d\lambda_2}{dt}(t) = -\frac{\partial \mathcal{H}}{\partial y(t)}(t) - \frac{\partial \mathcal{H}}{\partial y(t - \tau)}(t + \tau), \end{cases} \quad (3.94)$$

and

$$\frac{\partial \mathcal{H}}{\partial h(t)}(x(t), y(t), x(t - \tau), y(t - \tau), h(t), (t)) = 0 \quad (3.95)$$

where $\mathcal{X}_{[0, t_f - \tau]}(t)$ is the indicatrice function on $[0, t_f - \tau]$. Therefore, we obtain the adjoint system :

$$\begin{cases} \dot{\lambda}_1(t) = -\frac{ph}{T_2 - T_1} e^{-\delta t} + \lambda_1(t)(-r_1 + 2b_1x(t)) \\ \quad + \lambda_1(t) \left(a_1(1 - m)y(t) + \frac{h}{T_2 - T_1} \right) \\ \quad - \mathcal{X}_{[0, t_f - \tau]}(t) \frac{a_2y(t + \tau)\lambda_2(t + \tau)y(t)}{(1 - m)x^2(t)}, \\ \dot{\lambda}_2(t) = -a_1(1 - m)x(t)\lambda_1(t) - r_2\lambda_2(t) \\ \quad + \mathcal{X}_{[0, t_f - \tau]}(t) \frac{a_2y(t + \tau)\lambda_2(t + \tau)}{(1 - m)x(t)}, \end{cases} \quad (3.96)$$

The transversality conditions of system (3.96) are

$$\lambda_1(t_f) = \lambda_2(t_f) = 0$$

Since \mathcal{H} is linear in the control variable h , the optimal control will be a combination of bang-bang control and singular control. Let

$$\sigma(t) = e^{-\delta t} \left(\frac{p(x - T_1)}{T_2 - T_1} - c \right) - \lambda_1(t) \left(\frac{x - T_1}{T_2 - T_1} \right)$$

The optimal control $h(t)$ which maximizes \mathcal{H} must satisfy the following conditions :

$$h(t) = K \quad \text{if} \quad \sigma(t) > 0 \quad (3.97)$$

equivalent to

$$e^{\delta t} \lambda_1(t) < p - \frac{c}{\frac{x - T_1}{T_2 - T_1}} \quad (3.98)$$

$$h(t) = 0 \quad \text{if} \quad \sigma(t) < 0 \quad (3.99)$$

equivalent to

$$e^{\delta t} \lambda_1(t) > p - \frac{c}{\frac{x - T_1}{T_2 - T_1}} \quad (3.100)$$

where $e^{\delta t} \lambda_1(t)$ is the usual shadow price ([33]) and $p - \frac{c}{\frac{x - T_1}{T_2 - T_1}}$ is the net economic revenue on a unit harvest. This shows that $h = K$ or zero according to the shadow price is less than or greater than the net economic revenue on a unit harvest. Economically, condition (3.98) implies that if the profit after

3.9. Numerical simulations

paying all the expenses is positive, then it is beneficial to harvest up to the limit of available effort. Condition (3.100) implies that when the shadow price exceeds the fisherman's net economic revenue on a unit harvest, then the fisherman will not exert any effort.

When $\sigma(t)$, i.e. when the shadow price equals the net economic revenue on a unit harvest, then the Hamiltonian \mathcal{H} becomes independent of the control variable $h(t)$, i.e. $\frac{\partial \mathcal{H}}{\partial h}$. This is the necessary condition for the singular control $h(t)$ to be optimal over the control set $0 \leq h \leq K$. Thus, the optimal harvesting policy is

$$h(t) = \begin{cases} 0 & \text{if } \sigma(t) < 0, \\ h^* & \text{if } \sigma(t) = 0, \\ K & \text{if } \sigma(t) > 0. \end{cases}$$

Solving $\sigma(t) = 0$, we get

$$\lambda_1(t) = e^{-\delta t} p - \left(\frac{c}{\frac{x-T_1}{T_2-T_1}} \right) \quad (3.101)$$

Substituting equation (3.101) into system (3.96) gives :

$$\left\{ \begin{array}{l} \dot{\lambda}_1(t) = -\frac{ph}{T_2-T_1} e^{-\delta t} + e^{-\delta t} \left(p - \frac{c}{\frac{x-T_1}{T_2-T_1}} \right) \times \\ \quad \left(-r_1 + 2b_1x(t) + a_1(1-m)y(t) + \frac{h}{T_2-T_1} \right) \\ \quad - \mathcal{X}_{[0,t_f-\tau]}(t) \frac{a_2y(t+\tau)\lambda_2(t+\tau)y(t)}{(1-m)x^2(t)}, \\ \dot{\lambda}_2(t) = -a_1(1-m)x(t)e^{-\delta t} \left(p - \frac{c}{\frac{x-T_1}{T_2-T_1}} \right) - r_2\lambda_2(t) \\ \quad + \mathcal{X}_{[0,t_f-\tau]}(t) \frac{a_2y(t+\tau)\lambda_2(t+\tau)}{(1-m)x(t)}, \end{array} \right. \quad (3.102)$$

Using equilibrium conditions and integrating System (3.102), we obtain $\lambda_1(t)$ and $\lambda_2(t)$. Solving equation

$$\lambda_1(t) = p - \left(\frac{c}{\frac{x-T_1}{T_2-T_1}} \right);$$

we obtain the optimal harvesting efforts h^* .

3.9 Numerical simulations

In this section, we give some numerical simulations for a special case of System (3.28) with harvesting function (3.5) to support our analytical results in this chapter. As an example, we consider systems (3.28) and (3.5) with the coefficients $r_1 = 1.1$, $b_1 = 1.1/300$, which gives $K = 300$, $m = 0.1$, $a_1 = 0.11$, $r_2 = 0.2$, $a_2 = 1$, $h = 0.2 * K$, $T_1 = 60$, $T_2 = 90$ and $t = 20$. When there is no delay, we choose $x(0) = 40$ and $y(0) = 25$. That is,

$$\left\{ \begin{array}{l} \dot{x}(t) = \left(1.1 - \frac{1.1}{300} * x(t) \right) * x(t) - 0.11 * (1 - 0.1) * x(t) * y(t) - H(x(t)), \\ \dot{y}(t) = \left(0.2 - \frac{1.2 * y(t-\tau)}{(1-0.1) * x(t-\tau)} \right) * y(t), \end{array} \right. \quad (3.103)$$

3.9. Numerical simulations

In figure (3.9), we have $\Delta_1 = 117.5377 > 0$, $-\varphi'(K_0) + a_1(1 - m)y_0 + r_2 = 11.2751 > 0$ and $2a_1(1 - m)r_2y_0 - r_2\varphi'(K_0) = 2.3975 > 0$. So the conditions of stability of equilibrium $G_0(K_0, y_0)$ are satisfied and G_0 is locally asymptotically stable.

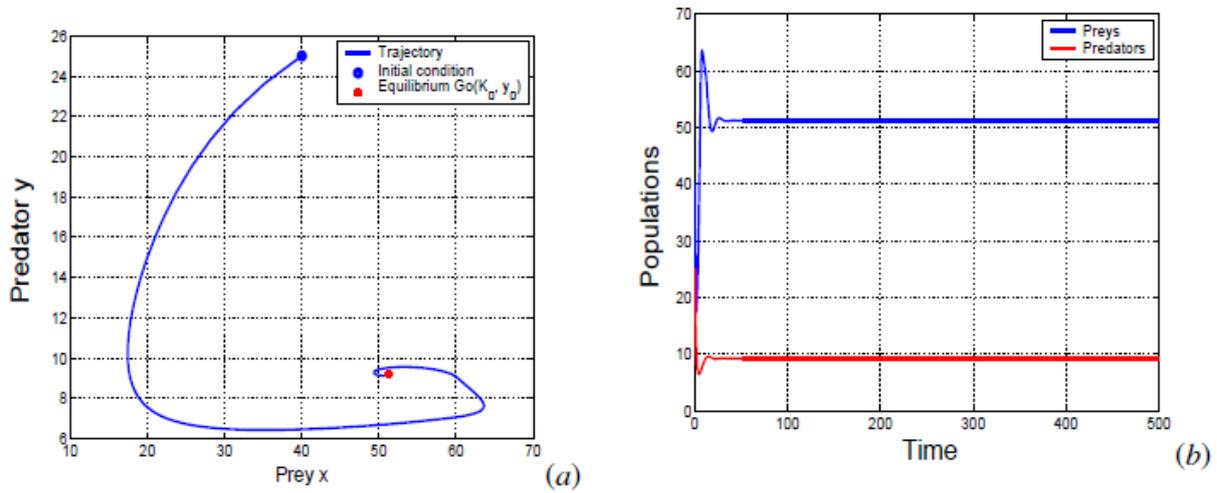


Figure 3.9: The numerical approximations of (3.28) when $\tau = 0$ and $K_0 = 51.1945 < T_1$. The positive equilibrium $G_0(51.1945; 9.2150)$ is locally asymptotically stable.

Figure (3.10) shows that under some conditions, equilibrium $G_1(x_1^*, y_1^*)$ is the only equilibrium of the model system (3.28) and is locally asymptotically stable. More precisely, we have $x_1^* - T_2 = 68.065$, $K_0 - x_1^* = 83.28$, $\varphi(T_2) - h = 9.3$, $\Delta_1 = 1.14 \times 10^3$, $-\varphi'(x_1^*) + a_1(1 - m)y_1^* + r_2 = 33.8253 > 0$ and $2a_1(1 - m)r_2y_1^* - r_2\varphi'(x_1^*) = 0.3396 > 0$. So, we have $T_2 < x_1^* < K_0$, $\varphi(T_2) > h$. Thus, all the conditions for the stability of equilibrium G_1 are satisfied.

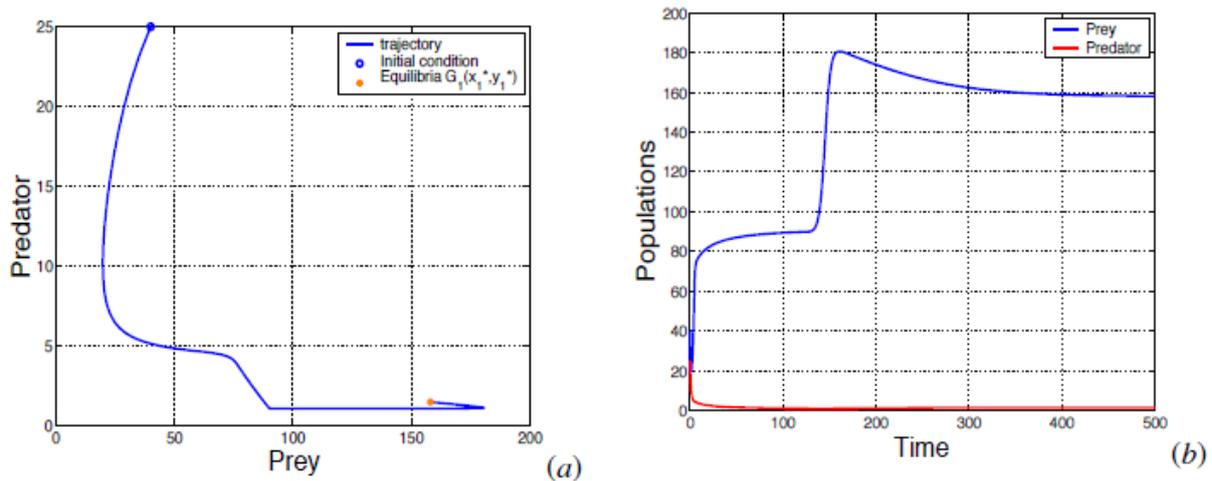


Figure 3.10: The numerical approximations of (3.28) when $\tau = 0$, $r_2 = 0.01$ and $K_0 = 51.1945 > T_2$. The positive equilibrium $G_1(158.0658; 1.4226)$ is asymptotically stable.

Now, we present some numerical results of the system for different values of t . From the above discussion, we may determine the direction of Hopf-bifurcation and the direction of bifurcating periodic solution. We consider the system when the parameter values are given as in Figure (3.11). So, the

3.9. Numerical simulations

model has a positive equilibrium $G_0(51.1945; 9.2150)$ which is locally asymptotically stable for $\tau = 0$. When τ passes through the critical value $\tau = \tau_1^0 = 95.2311$ and $\frac{d(\mathcal{R}_e \lambda(\tau))}{d\tau} \Big|_{\lambda=i\omega_0, \tau=\tau_1^0} = 7.6799 > 0$, the equilibrium G_0 loses its stability and the system (3.28) experiences Hopf-bifurcation. From Sect. 7, we can determine the nature of the stability and direction of the periodic solution bifurcating from the interior equilibrium at the critical point τ_1^0 .

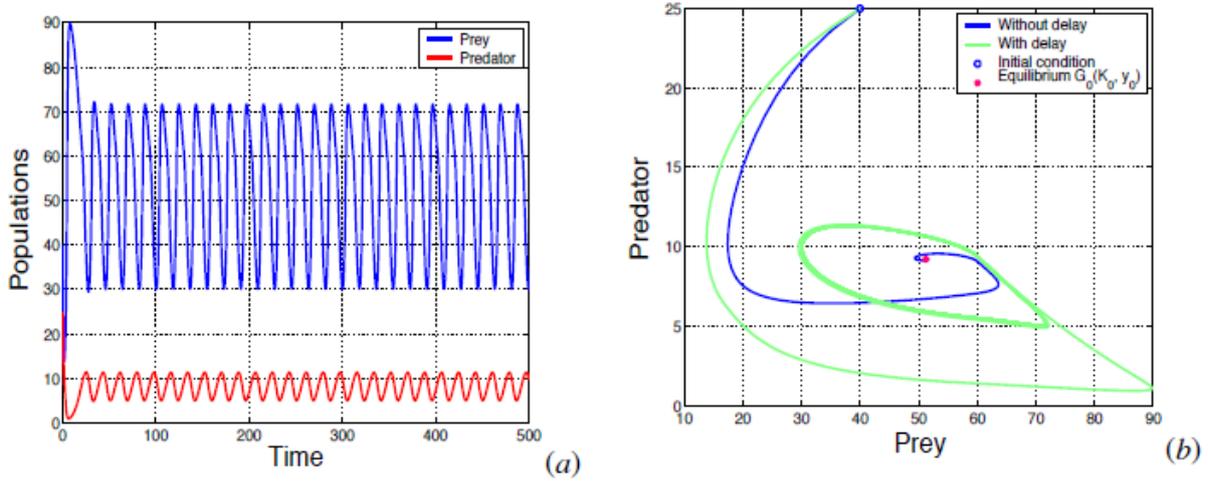


Figure 3.11: Hopf bifurcation behavior of the system (3.28) around the interior equilibrium $G_0(51.1945; 9.2150)$ when $\tau = \tau_1^0 = 95.2311$. The other parameter are the same as in Figure (3.9). We obtain the existence of unstable supercritical bifurcating periodic solution around the interior equilibrium G_0 with the same parameter values as in Figure (3.9).

Using (3.83), we can compute $C_1(0) = 69.7625 - 28.9307i$, $\nu_2 = 968.6446 > 0$, $\beta_2 = 139.5250 > 0$ and $T_2 = -120.1525$. Hence, the bifurcating periodic solution exists when τ crosses τ_1^0 from left to right and the corresponding periodic solution is supercritical and unstable (as $\beta_2 > 0$) as evident from Figure (3.11) (a) – (b). The negative sign of T_2 indicates the decreasing period of the periodic solution of the system. Moreover, this system is locally asymptotically stable around the interior equilibrium G_0 , which is clearly depicted from Figure (3.11)(a) – (b) for $\tau = 16 < \tau_1^0$.

3.9. Numerical simulations

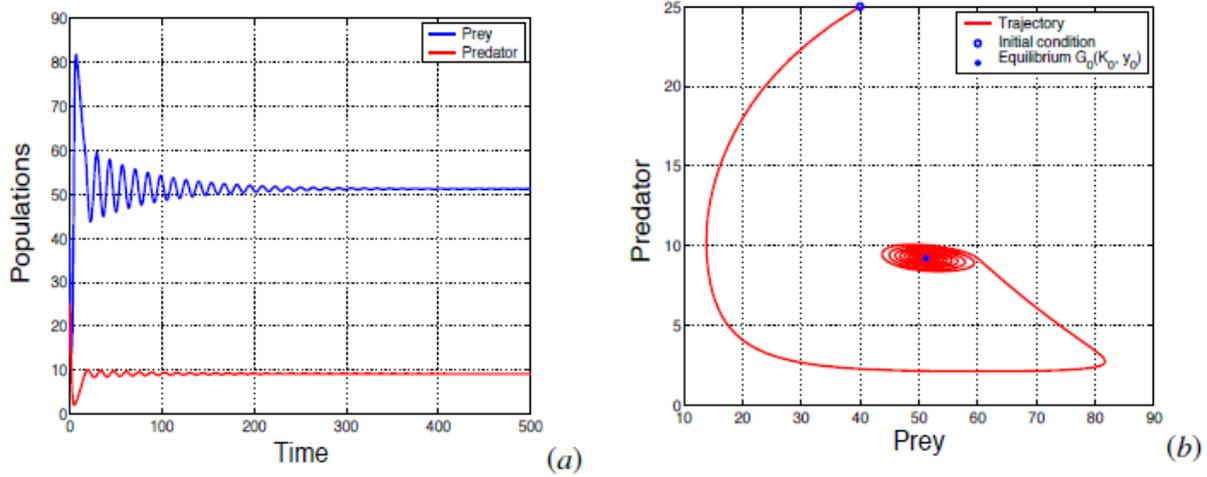


Figure 3.12: System (3.28) is globally asymptotically stable around the interior equilibrium G_0 at $\tau = 16 < \tau_0^0 = 95.2311$. The other parameter values are given in the previous figure.

Figure (3.13) gives the optimal harvesting of prey in the presence of the two population. We observe that the control increase the period of limit cycle (see Figure (3.13)(a)) and also increase the predator and prey population (see Figure Figure (3.13)(b)-(c)). In order to obtain this result, the harvesting will be made periodically (see Figure Figure (3.13)(d)). From this figure, it is clear that as the time progresses the prey and predator populations fluctuate in different period depending on the values of the optimal harvesting. We observe that when we harvest, the predator population decrease quickly and the prey population starts to rise rapidly. On the other hand as the predator population rises, the prey population descends speedily. This figure is obtained when $p = 30$, $c = 35$ and $\delta = 0.1$.

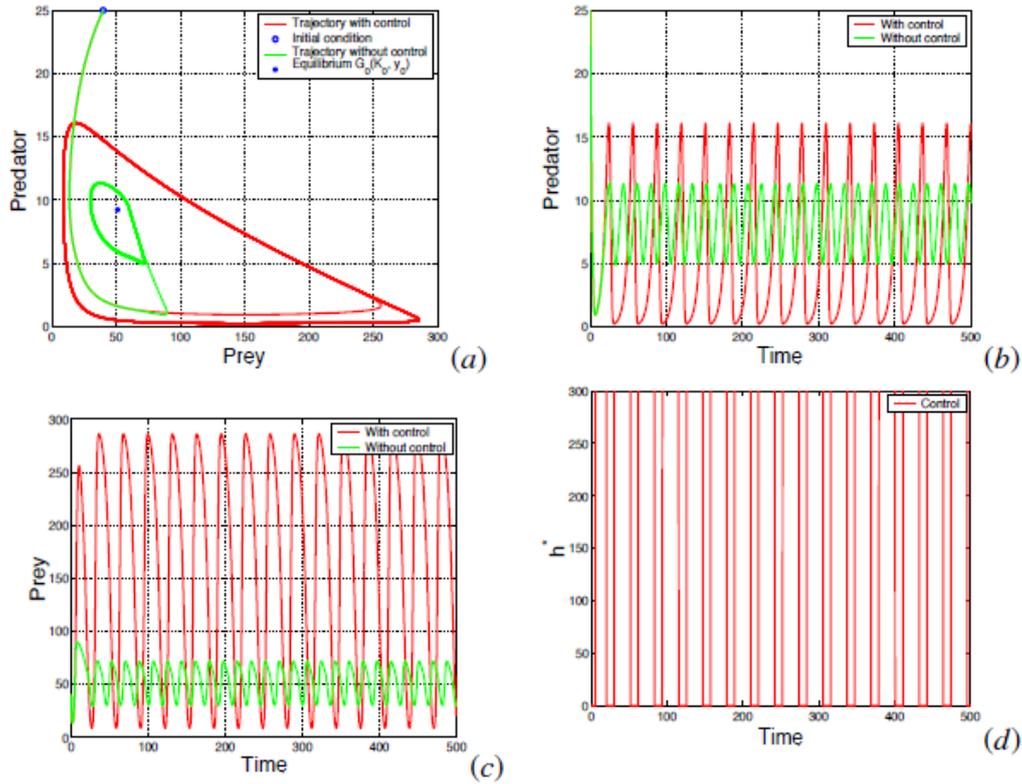


Figure 3.13: Trajectory of system (3.28) with and without control.

3.10 Conclusion

In this chapter, the properties of Hopf bifurcations in a Leslie-Gower Predator-Prey model with discrete time delay in predators equation have been studied. We have also investigated optimal harvesting when the harvesting is given by a continuous function in this model. Although bifurcations in a population dynamics without delay have been investigated by many researchers, there are few papers on the bifurcations of a population dynamics with delay, which have shown direction of global Hopf-bifurcation and optimal harvesting simultaneously. We have obtained sufficient conditions on the parameters for which the delay-induced system is asymptotically stable around the positive equilibrium for all values of the delay parameter and if the conditions are not satisfied, then there exists a critical value of the delay parameter below which the system is stable and above which the system is unstable. By applying the normal form theory and the center manifold theorem, the explicit formulae which determine the stability and direction of the bifurcating periodic solutions have been determined. Our analytical and simulation results show that when the delay τ passes through the critical value τ_0^0 , the coexisting equilibrium G_0 losses its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from G_0 . Also, the amplitude of oscillations increases with increasing t . For the considered parameter values, it is observed that the Hopf bifurcation is supercritical and the bifurcating periodic solution is unstable. The problem of optimal harvesting policy has been solved by using the new result of retarded optimal control which is an extension of Pontryagins Maximal principle theory. We hope that the theoretical investigations which have been carried out in this chapter

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will certainly help the experimental ecologists to do some experimental studies and as a consequence the theoretical ecology may be developed to some extent. In this chapter, the modified Leslie-Gower predator-preys model incorporates a harvested function with two thresholds. In the next chapter, I'll formulate a modified Leslie-Gower predator-prey model with additional fixed food for predators and the harvesting functions used for harvesting of preys will be define with only one threshold.

HOPF BIFURCATION ANALYSIS IN A DELAYED LESLIE-GOWER PREDATOR-PREY MODEL INCORPORATING ADDITIONAL FIXED FOOD FOR PREDATORS

Abstract

In this chapter, we formulate and analyze a modified Leslie-Gower predator-prey model. Our model incorporates refuge of preys, additional fixed food for predators, harvesting of preys through a continuous threshold policy (CTP) and a time-delay as to account for predators maturity time. We first carry out a qualitative analysis of the model without time-delay, showing existence of extinction, preys-free, predators-free and coexistence equilibria. We further study their stability conditions. Relying only on theoretical results of the model, we construct bifurcation diagrams involving refuge and harvest limit parameters. This led to summarize different scenarios for the model including elimination of one species or competition of both species, that are proven possible. Furthermore, considering the time-delay as bifurcation parameter, we analyze the stability of the coexistence equilibria and prove the system can undergoes a Hopf bifurcation. The direction of that Hopf bifurcation and the stability of the bifurcated periodic solution are determined by applying the normal form theory and the center manifold theorem. Numerical simulations are presented to illustrate our theoretical results.

4.1 Introduction

Relationship between predators and their preys has been modelled by Lotka (1920) [122] and Volterra (1931) [177]. Their model, which is nowadays considered as the simplest predator-prey model, has been modified by authors like Leslie ((1948) [113], (1958) [114]). In their researches, they considered that a predator consumes only one type of prey and does not have another resource of food. This hypothesis has been modified by several authors who considered that a predator can be provided

with additional food. In this way, many experimentalists and theoreticians have studied the consequences of providing a predator with additional food, the corresponding effects on the predator-prey dynamics, its utility on controllability of ecosystems such as integrated pest management and species conservation which employ biological control as one of the tools. Bilde and Toft (1998) [21], Coll and Guershon (2002) [34], Harmon (2003) [72], Hardwood et al. (2005) [73], Murdoch et al. (1985) [134], Sabelis and Van Rijn (2006) [151], Srinivasu et al. (2007) [163], Van Baalen et al. (2001) [9], Van Rijn et al. ((2002) [146], (2005) [152]), H.M. Ulfa et al. (2017) [174] have investigated the consequences of providing additional food to predators in a predator-prey system. Recently, Srinivasu et al. (2011) [165] studied the qualitative behavior of a predator-prey system incorporating additional food for the predator. The conclusion of their investigation was that handling times for the available foods to the predator play a key role in the determination of the eventual state of the ecosystem. For Haque and Greenhalgh (2010) [71], providing alternative food to predators can play an important role in promoting the persistence of predator-prey systems. M. T. Alves (2013) [3] studied a model with additional food and a preference rate of the predator for one or the other food. M. T. (2013) [3] concluded that providing alternative fixed food to predator cause a distraction effect. That distraction effect has been identified as a mechanism which can favor positive indirect effects on the principal prey in the long term. For M. T. (2013) [3], due to the presence of alternative food, the predator does not spend all its searching time on its favorite food, so its consumption of that favorite food is no more at the maximal rate. Then there is a negative impact on the growth rate of the predator. Because the use of spatial refuges by the prey population is one of the more relevant behavioral traits that affect the dynamics of predator-prey system, F. Chen et al. (2009) [29], Y. Huang et al. (2006) [87], T.K. Kar (2006) [99] have investigated the influence of prey refuge in predator-prey models. They concluded that the prey refuge has a stabilizing effect on the predator prey relationship. It is more realistic to assume that, after predating the prey, the reproduction of the predator is not instantaneous. It is necessary to take into account the fact that the reproduction of predator is mediated through some time lag which is required for gestation. The conversion of prey energy to predator energy is not instantaneous. For the above reasons, models with delays are more realistic than those without delays. For example, a time delay can cause the change of the stability of an equilibrium, making a stable equilibrium to become unstable (For more details, see Brauer (1977) [25], Kar et al. (2011) [102], Beretta et al. (1998) [17], Kuang (1993) [106], Gopalsamy (1992) [61], Azbelev et al. (2006) [7], Balachandran et al. (2006) [11], Arino et al. (2006) [5], C. Liu et al. (2016) [118], Q. Liu et al. (2014) [120], J. Liu (2014) [119], J. liu et al. (2012) [121], Y. F. Ma (2012)[125], A.F. Nindjin et al. (2006) [138], D. Xiao and W. Li (2003) [181], C. Xu et al. (2011) [188], R. Yafia et al. (2007) [186], C. Xu et al. (2011) [188], X. Yan and W. Li (2006) [189], S. Yuan et al. (2009) [194], R. Yuan et al. (2015) [193], S.L. Yuan and Y. L. Song (2009) [195], S. L. Yuan et al. (2009) [196], Zhang zi-zhen and Yang hui-zhong (2013) [201]). Banshidhar Sahoo and Swarup Poria (2015) [155] has studied the effects of additional food and time delay due to gestation time.

Predators and preys are ecological resources. So they can be used either for human being needs or for commercial industries. It can then be exploited and harvested in fishery, forestry and wildlife

4.2. Leslie-Gower predator-prey models incorporating additional food and some applications of Leslie-Gower predator-prey models

management. There is a wide range of interest in the use of bioeconomic models to gain insight into the scientific management of the renewable resources like fisheries and forestries. To study the effect of harvesting in the dynamic of relationship between species, some harvesting functions have been considered by researchers. We can cite constant harvesting function, linear harvesting functions, quadratic harvesting functions (Leard et al. (2008) [111], Kar and al. (2006) [99], Kar et al. (2011) [102], Gazi et al. (2008) [56], Lenzini et al. (2010) [112], Feng et al. (2006) [49], Liu et al. (2016) [118]), M. Rayungsari et al. (2014) [144]) and the so-called continuous threshold policy (CTP) which use one or more than one threshold and, with which the harvesting starts when the population of the species being harvested has reached a certain threshold (Bohn et al. (2011) [23], R.S. Lashkarian and D.B. Sharifabad (2016) [110], Meza and al. (2005) [132], Tankam et al. (2015) [169]).

In what follows, we formulate and analyze a Leslie-Gower predator-prey model derived from the one proposed by Mickael Teixeira Alves (2013) [3]. After the predation of preys, the reproduction of the predator population is not an instantaneous phenomenon. The use of spatial refuges by the preys population can affect the dynamic of a predator prey model system. Preys can be harvested either for human being needs or for commercial industries. So, our model incorporates a time delay τ in the predator equation which represents the time lag for gestation (or maturation) of predator, a refuge for preys and a CTP harvesting function for preys.

The organization of this chapter is as follows : in the second section, some models incorporating additional fixed food for predators and some applications of Leslie-Gower predator-prey models for practical ecological problems concerning the predator-prey interactions are given. We formulate the modified Leslie-Gower predator-prey model in the third section. In the fourth section, we prove that each solution of the system is positive and bounded. The fifth section contains the equilibria of the model without the time delay and their stability. The investigation for a Hopf bifurcation is done in the sixth section. We analyze the stability and the direction of the existing Hopf bifurcation in the seventh section. Numerical simulations results are supplied in the eighth section in support of the theoretical analysis.

4.2 Leslie-Gower predator-prey models incorporating additional food and some applications of Leslie-Gower predator-prey models

In this section, two modified Leslie-Gower predator-prey models incorporating additional fixed food for predators are given in order to have informations about effects of additional food on the dynamic of the initial Leslie-Gower predator-prey model. Some applications of the Leslie-Gower predator-prey models for concrete ecological problems are also presented in this section.

4.2.1 The M. T. Alves (2013) model

M. T. Alves (2013) ([3]) has formulated a model from the Leslie-Gower predator-prey model by assuming that, the predator is provided with additional food. He assumes that the additional food is not dynamic but maintained at a constant level and the encounters between the predators and additional food is proportional to the density of additional food. His model is the following two-dimensional system of ordinary differential equations:

$$\begin{cases} \dot{N}(t) = r_N \left(1 - \frac{N}{K_N}\right) N - q\lambda_N NP, \\ \dot{P}(t) = r_P \left(1 - \frac{P}{q\alpha_N N + (1-q)\alpha_A K_A}\right) P, \end{cases} \quad (4.1)$$

The variables $N(t)$ and $P(t)$ denote respectively the preys and predators populations at the time t . The positive parameter q represents the preference rate of the predator due to the fact that the predator has two sources of food. It means that if $q = 0$, the predator consumes only the additional food A . Thus the carrying capacity of the predator is $\alpha_A K_A$. If $q = 1$, the predator consumes only the prey N . So the carrying capacity of the predator is $\alpha_N N$. If $q \in (0, 1)$, the predator consumes the two sources of food according to proportions defined by the parameter q . The carrying capacity of the predator is $q\alpha_N N + (1-q)\alpha_A K_A$ according to the formalism of Stephens and Krebs (1986) ([166]). The parameter α_A is the measure of the amount of energy in the form of biomass of the additional food assimilate into the predator’s energy in term of biomass and the parameter K_A represents the constant density of the additional food. Those three parameters have been introduced for additional fixed food. The other parameters are those always present in a classical Leslie-Gower predator-prey model.

The aim of his work on model (4.1) was to study the effects of shared predation, that is the situation in which a predator has a choice between two sources of food. Such predation usually induces negative indirect interactions between prey, or apparent competition, through an increase of predator density and thus of predation pressure. Two mechanisms can however weaken apparent competition and lead to equivocal signs of indirect interactions. On the one hand, predator distraction, which stems from the difficulty to efficiently forage for different prey at the same moment in time and diminishes the number of prey captured per predator. On the other hand, predator negative density dependence limits predator growth. The following conclusions have been obtained by M. T. Alves.

1. Indirect effects of the additional fixed food A over the preys N strictly depend on equilibria of the predator depending on preys ($\overline{P}_N^* = \alpha_N K_N$, $\overline{P}_A^* = \alpha_A K_A$, $P_N^* = \frac{r_N \alpha_N K_N}{r_N + \alpha_N K_N \lambda_N}$). The distraction of the predator by the additional food can induce and favorite positive indirect effect on the prey.
2. On the one hand, if the predator has a fixed preference its preys, a positif indirect effect of the additional food A on the prey N is possible if $\overline{P}_A^* < (1 + \frac{1}{q})P_N^*$. Moreover, if $\overline{P}_A^* < 2P_N^*$ then the positif indirect effect is possible for any value of the preference rate q .

4.2. Leslie-Gower predator-prey models incorporating additional food and some applications of Leslie-Gower predator-prey models

3. On the other hand, if the predator has an adaptative preference for its preys, a positif indirect effect is possible if $\overline{P}_A^* > P_N^*$. The additional fixed food A can cause a partial or a total distraction on the predator. That distraction has a negative effect on the growth rate of the predator.
4. Comparing the adaptative and the fixed preferences, the positive effect of the additional fixed food A is easily achievable when the predator has an adaptative preference.

Let's mention that M. T. Alves has also studied effect of additional fixed food by modifying the Holling-Tanner predator-prey model. He has also studied effects of dynamic additional food. He has formulated and study the following models.

$$\begin{cases} \dot{N}(t) = r_N N - \frac{q\lambda_N NP}{1 + h_N N}, \\ \dot{P}(t) = r_P \left(1 - \frac{P}{q\alpha_N N + (1-q)\alpha_A K_A} \right) P, \end{cases} \quad (4.2)$$

$$\begin{cases} \dot{N}(t) = r_N \left(1 - \frac{N}{K_N} \right) N - q\lambda_N NP, \\ \dot{A}(t) = r_A \left(1 - \frac{A}{K_A} \right) A - (1-q)\lambda_A AP, \\ \dot{P}(t) = r_P \left(1 - \frac{P}{q\alpha_N N + (1-q)\alpha_A K_A} \right) P, \end{cases} \quad (4.3)$$

For more details on the study of models (4.2) and (4.3), the reader can refer to M. T. Alves (2013) ([3]).

4.2.2 The H. M. Ulfa et al. (2017) model

M. A. Aziz-Alaoui and M. D. Okiye (2003) ([8]) have formulated the following (4.4) modified Leslie-Gower predator-prey model. The Holling type II functional response is used for predator functional response. Their model is of the following set of two ordinary differential equations :

$$\begin{cases} \dot{X}(t) = (1-X)X - \frac{\delta XY}{X+m}, \\ \dot{Y}(t) = \beta \left(1 - \frac{Y}{X+e} \right) P, \end{cases} \quad (4.4)$$

The nature of actively moving predators becomes a reason that they can target on more than one prey or switch to other food sources. Considering the limited prey population will require additional food for predators, the M. A. Aziz-Alaoui and M. D. Okiye (2003) ([8]) model (4.4) is reconsidered. H. M. Ulfa et al. have modified model (4.4) by including the additional food to predators in terms of the handling time and the nutritional value of additional food. The Leslie-Gower predator- prey model with additional food for predators is stated as :

$$\begin{cases} \dot{X}(t) = (1-X)X - \frac{\delta XY}{X+m+nA}, \\ \dot{Y}(t) = \beta \left(1 - \frac{Y}{X+e} \right) P + \frac{\sigma nAY}{X+m+nA}, \end{cases} \quad (4.5)$$

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where δ , m , n , A , β , e and σ are positive parameters. The term nA represents quantity of additional food perceptible to the predator relative to prey.

The following results hold for the H. M. Ulfa et al. model (4.5).

1. The Leslie-Gower predator-prey model with additional food for predator (4.5) is a permanence system, indicating that the solution of system is bounded.
2. The model (4.5) has four equilibrium points, namely the extinction of both populations point (E_0), the extinction of predator point (E_1), the extinction of prey point (E_2), and both populations are able to survive (E_3).
3. E_0 and E_2 are always unstable, whereas E_1 and E_3 are stable under certain conditions.
4. Increasing the coefficient of additional food for predator (n) may stabilize equilibrium E_3 and at the same time destabilize equilibrium E_1 .

4.2.3 Some applications of Leslie-Gower predator-prey models

Some Leslie-Gower predator-prey model have been used for practical ecological problems concerning the predator-prey interactions. In what follows, I give two examples in which Leslie-Gower predator-prey models are used.

4.2.3.1 Management of multispecies fisheries

Management of multispecies is the title of the R. M. May et al (1979) ([130]) paper's on problems of fisheries as mentioned on the title. For R. M. May et al., with the overexploitation of many conventional fish stocks, and growing interest in harvesting new kinds of food from the sea, there is an increasing need for managers of fisheries to take into account of interactions among species. In particular as Antarctic krill-fishing industries grow, there is a need to agree upon sound principles for managing the Southern Ocean ecosystem. Using simple models (Leslie-Gower models), authors discuss the way multispecies (krills, baleen whales, seals, cephalopods, sperms whales) food webs respond to the harvesting of species at different trophic levels. The biological and economic insights are applied for a discussion of fisheries in the Southern Ocean and the North Sea and to enunciate some general principles for harvesting in multispecies systems. The very important study done by the authors have reached to many conclusions. For more details on the models used, their analysis, studies with economics (maximum sustainable yield (MSY)) and biological considerations, comparative conclusions, the reader can refer to R. M. May et al. paper ([130]).

4.2.3.2 Cats protecting birds : Modelling the mesopredator release effect

F. Courchamp et al. (1999) ([39]) have built a mathematical model of Leslie-Gower type describing a three-species system (prey-mesopredator-superpredator). The aim of their work is to examine the fate of prey species (endemic birds) in an insular ecosystem in which a mesopredator (rats) and a superpredator (feral cats) have been introduced. They have formulated the fourth following models for their studies.

According to F. Courchamp et al. (1999) ([39]), the two models (4.6) and (4.7) consist of two simple coupled differential equations each representing the dynamic of one population. Each population is described by a simple logistic equation, modified to take into account its relationship with the other species. It is assumed that all the prey species form a single "bird" population, with average characteristics. The carrying capacities of the environment for the mesopredator and superpredator populations are not constant, but depend partially (rats and omnivores) or totally (cats and carnivores) on the number of available individual prey on which their populations can feed at the time t . The carrying capacity is thus the quantity of non-avian food S divided by the consumption rate η_S , plus the number of prey B divided by the mesopredator predation rate η_b , $\frac{S}{\eta_S} + \frac{B}{\eta_b}$, that is $\frac{\eta_b S + \eta_S B}{\eta_b \eta_S}$. Instead of $\eta_b R$, the predation rate of rats on birds is $\frac{B \eta_b R}{S + B}$.

In order to take into account the three species simultaneously, further assumptions have been made for the third model (4.8). Taking as example a domestic cat which is an opportunist predator which switches prey species according to their availability, the number of birds and rats preyed upon by cats will depend on their respective numbers. Thus, instead of $\mu_b C$ and $\mu_S C$, one will find $\frac{\mu_b B C}{B + R}$ and $\frac{\mu_r R C}{B + R}$. The cat carrying capacity is : $\frac{B}{\mu_b} + \frac{R}{\mu_c}$

The first one (4.6) representing interactions between the preys (birds) and mesopredators (rats) is the following coupled ordinary differential equations :

$$\begin{cases} \dot{B}(t) = r_b B \left(1 - \frac{B}{K_b} \right) - \frac{\eta_b B R}{S + B}, \\ \dot{R}(t) = r_r R \left(1 - \frac{\eta_b \eta_S R}{\eta_b S + \eta_S B} \right), \end{cases} \quad (4.6)$$

The second one (4.7) representing interactions between the preys (birds) and superpredators (cats) is the following coupled ordinary differential equations :

$$\begin{cases} \dot{B}(t) = r_b B \left(1 - \frac{B}{K_b} \right) - \mu_b C, \\ \dot{C}(t) = r_c C \left(1 - \frac{\mu_b C}{B} \right), \end{cases} \quad (4.7)$$

The third one (4.8) stating for the dynamic between the three species preys (birds), mesopredators (rats) and superpredators (cats) is the following set of three ordinary differential equations

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:

$$\begin{cases} \dot{B}(t) = r_b B \left(1 - \frac{B}{K_b} \right) - \frac{\eta_b BR}{S+B} - \frac{\mu_b BC}{B+R}, \\ \dot{R}(t) = r_r C \left(1 - \frac{\eta_b \eta_s R}{\eta_b S + \eta_s B} \right) - \frac{\mu_r RC}{B+R}, \\ \dot{C}(t) = r_c C \left(1 - \frac{\mu_b \mu_r C}{\mu_r B + \mu_b R} \right) \end{cases} \quad (4.8)$$

The fourth one (4.9) stating for the dynamic between the three species preys (birds), meso-predators (rats) and superpredators (cats) and used for strategy control is the following set of three ordinary differential equations :

$$\begin{cases} \dot{B}(t) = r_b B \left(1 - \frac{B}{K_b} \right) - \frac{\eta_b BR}{S+B} - \frac{\mu_b BC}{B+R}, \\ \dot{R}(t) = r_r C \left(1 - \frac{\eta_b \eta_s R}{\eta_b S + \eta_s B} \right) - \frac{\mu_r RC}{B+R} - \lambda_r R, \\ \dot{C}(t) = r_c C \left(1 - \frac{\mu_b \mu_r C}{\mu_r B + \mu_b R} \right) - \lambda_c C \end{cases} \quad (4.9)$$

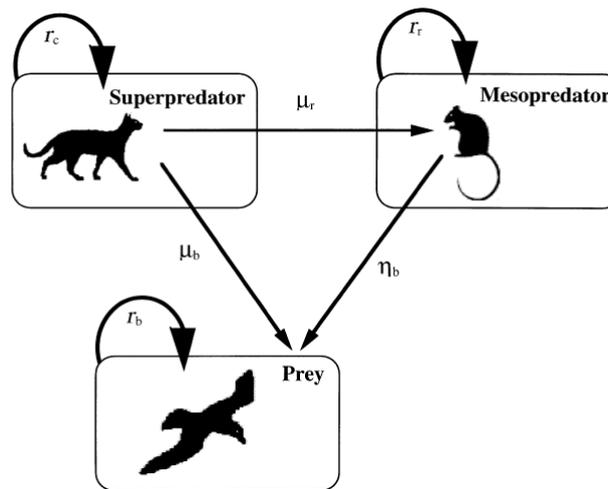


Figure 4.1: Compartmental representation of the mathematical model (4.9). The arrows represent the flux within and are between compartments. Curved arrows are intrinsic rates. From F. Courchamp et al. ([39])

4.2. Leslie-Gower predator-prey models incorporating additional food and some applications of Leslie-Gower predator-prey models

Table 4.1: Parameters and variables of models (4.6)-(4.7)-(4.8)-(4.9)

Variables/parameters	Interpretation (Definition)
B	Preys population (birds) at the time t
R	Mesopredators population (rats) at the time t
C	Superpredators population (cats) at the time t
r_b	Intrinsic growth rate of preys (birds)
r_r	Intrinsic growth rate of mesopredators (rats)
r_c	Intrinsic growth rate of superpredators (cats)
μ_b	Predation rate of superpredators on preys
μ_r	Predation rate of superpredators on mesopredators
η_b	Predation rate of mesopredators on preys
η_s	Predation rate of mesopredators on other foods
λ_r	Control effort on the rat population
λ_c	Control effort on the cat population
K_b	Carrying capacity of the environment of preys

For more details for the formulation of the above models, the reader can refer to F. Courchamp et al. ([39], [40]). The following conclusions hold for model (4.8 - 4.9) :

- (a) The presence of one predator only is sufficient to induce the extinction of the endemic prey.
- (b) When both the mesopredator and the superpredator are present, seven situations may arise, among which is the case where the three species are present with stable dynamics.
- (c) Interestingly, there is a case where both predator species can coexist indefinitely, even after the eradication of the prey species.
- (d) More interestingly is the case where the superpredator causes the extinction of the mesopredator but not of the prey.
- (e) It has been shown that the presence of a superpredator may have a global positive effect in insular ecosystems in which, an introduced mesopredator threatens an endemic prey.
- (f) The presence of the superpredator may preclude the elimination of the prey by the mesopredator.
- (g) The eradication of the superpredator should be avoided, as a means to prevent what is termed " mesopredator release : a sudden burst of mesopredator, once the superpredator pressure is suppressed".

- (h) The study of the control strategy clearly shows that the fate of the prey will depend on the superpredator control level. Although counterintuitive, if the superpredator control is too high, the prey will disappear.

4.3 Formulation of a modified Leslie-Gower predator-prey model

M. T. Alves (2013) [3] formulated and analyzed the following model :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t)}{K_1} \right) x(t) - q\lambda_1 x(t)y(t), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{q\alpha_1 x(t) + (1-q)\alpha_A K_A} \right) y(t), \end{cases} \quad (4.10)$$

where the variables $x(t)$ and $y(t)$ are respectively the preys and the predators populations at time t . In the model (4.10), we have two categories of parameters. The parameters r_1 and r_2 are the intrinsic growth rates of preys and predators respectively. λ_1 measures the strength of competition among individuals of preys population, K_1 is the carrying capacity of the preys when there is no predation, α_1 measures the amount of energy in the form of biomass of the prey $x(t)$ assimilate into the predator's energy in the term of biomass. The parameters r_1 , r_2 , λ_1 , α_1 and K_1 always exist in a Leslie-Gower predator-prey model. The parameters q , K_A and α_A has been introduced by M.T. Alves (2013) [3] with the assumption of additional food for predators. M.T. Alves (2013) [3] assumes that the predator is provided with additional food of constant density K_A . The parameter α_A measures the amount of energy in the form of biomass of the additional food assimilate into the predator's energy in the term of biomass. The parameter q is the preference rate of the predator due to the fact that the predator has two sources of food. It means that if $q = 0$, the predator consumes only the additional food A . Thus the carrying capacity of the predator is $\alpha_A K_A$. If $q = 1$, the predator consumes only the prey x . So the carrying capacity of the predator is $\alpha_1 x(t)$. If $q \in (0, 1)$, the predator consumes the two sources of food according to proportions defined by the parameter q . The carrying capacity of the predator is given by $q\alpha_1 x(t) + (1-q)\alpha_A K_A$ according to the formalism of Stephens and Krebs (1986) [166].

Our model, incorporating prey refuge, time delay and harvesting of preys, reads as :

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t)}{K_1} \right) x(t) - q\lambda_1(1-m)x(t)y(t) - \varphi(x(t)), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t-\tau)}{q\alpha_1(1-m)x(t-\tau) + (1-q)\alpha_A K_A} \right) y(t), \end{cases} \quad (4.11)$$

Due to the fact that the reproduction of the predator population after the predation of preys is not an instantaneous phenomenon, we introduced a time delay τ in the predator equation which

4.3. Formulation of a modified Leslie-Gower predator-prey model

represents the time lag for gestation (or maturation) of predator.

The term $m \in [0, 1)$ measures the strength of refuge. It means that $mx(t)$ models the capacity of a refuge at the time t and so refuge protecting $mx(t)$ quantity of the prey population at the time t , it remains $(1 - m)x(t)$ quantity of preys available to the predation.

$\varphi(x(t))$ denotes the continuous threshold prey harvesting function defined as follows:

$$\varphi(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x - T_1)}{h + x - T_1} & \text{if } x \geq T_1. \end{cases} \quad (4.12)$$

In this way, if the prey population is less than the threshold T_1 , there is not harvesting of preys. Once the prey population reaches the size $x = T_1$, their harvesting starts and increases smoothly to a limit value h . From both biological and practical point of views such harvesting function is more sound than its constant or linear counterparts (Bohn et al. (2011) [23], Tankam et al. (2015) [169]). For biological reason, it is natural to assume

$$T_1 < K_1 \quad (K_1 = \frac{r_1}{b_1}). \quad (4.13)$$

Due to the fact that it is not plausible to have the number of preys (respectively the number of predators) at time $t = 0$ greater than the carrying capacity $K_1 = \frac{r_1}{b_1}$ (respectively $K_2 = q\alpha_1(1 - m)K_1 + \alpha_A K_A$) of preys (respectively predators), we assume :

$$0 \leq x(0) < \frac{r_1}{b_1}. \quad (4.14)$$

and

$$0 \leq y(0) < q\alpha_1(1 - m)K_1 + \alpha_A K_A. \quad (4.15)$$

The initial conditions for the system (4.11)- (4.12) are chosen as :

$$x(0) \geq 0, \quad y(0) \geq 0. \quad (4.16)$$

For $\theta \in [-\tau, 0]$, we use the notation :

$$x_t(\theta) = x(t + \theta) \quad (4.17)$$

Then the initial conditions for the system take the form :

$$x_0(\theta) = \phi_1(\theta), y_0(\theta) = \phi_2(\theta), \quad (4.18)$$

for all $\theta \in [-\tau, 0]$, where $(\phi_1, \phi_2) \in \mathcal{C}([-\tau, 0], \mathbb{R}_+^2)$, $x(0) = \phi_1 > 0$ and $y(0) = \phi_2 > 0$.

$\mathcal{C} = \mathcal{C}([-\tau, 0], \mathbb{R}_+^2)$ is the Banach space of continuous functions from the interval $[-\tau, 0]$ into $\mathbb{R}_+^2 = \{(x, y) : x \geq 0, y \geq 0\}$.

4.4 Positivity and Boundedness of solutions

4.4.1 Positivity of solutions

In this subsection, we prove that our model is biologically meaningful. It means that the variable $x(t)$ and $y(t)$ which represent the population of preys and predators respectively are always positive. We have the following theorem.

Theorem 4.1. When assumptions (4.14) and (4.15) hold, the positive quadrant \mathbb{R}_+^2 is invariant for system (4.11)-(4.12).

Proof. We must show that for each solution (x, y) of system (4.11)-(4.12), defined and continuous on $[-\tau, A[$ where $A \in]0, +\infty[$, $x(t) > 0$ and $y(t) > 0$ for all $t \in [0, A[$. Suppose that it is not true. Then there exists a value of T in $]0, A[$ such that for all $t \in [0, T[$, $x(t) > 0$ and $y(t) > 0$, and either $x(T) = 0$ or $y(T) = 0$.

For all $t \in [0, T[$ and from equations of (4.11), we have,

$$x(t) > x(0) \exp \left(\int_0^t \left(r_1 - b_1 x(s) - q \lambda_1 (1 - m) y(s) - \frac{h}{h + x(s) - T_1} \right) ds \right)$$

and

$$y(t) = y(0) \exp \left(\int_0^t \left(r_2 \left(1 - \frac{y(s - \tau)}{q \alpha_1 (1 - m) x(s - \tau) + (1 - q) \alpha_A K_A} \right) \right) ds \right)$$

As x and y are defined and continuous on the compact $[-\tau, T]$, there exists $M \geq 0$ such that :

$$x(t) > x(0) \exp \left(\int_0^t \left(r_1 - b_1 x(s) - a_1 (1 - m) y(s) - \frac{h}{h + x(s) - T_1} \right) ds \right) \geq x(0) \exp(-TM)$$

and

$$y(t) = y(0) \exp \left(\int_0^t \left(r_2 \left(1 - \frac{y(s - \tau)}{q \alpha_1 (1 - m) x(s - \tau) + (1 - q) \alpha_A K_A} \right) \right) ds \right) \geq y(0) \exp(-TM)$$

Let us take the limit as $t \rightarrow T$, we get

$$x(T) \geq x(0) \exp(-TM) > 0$$

and

$$y(T) \geq y(0) \exp(-TM) > 0$$

which contradicts the fact that either $x(T) = 0$ or $y(T) = 0$. Then, a solution of system (4.11)-(4.12) which starts in the positive quadrant \mathbb{R}_+^2 remains there. \square

4.4.2 Boundedness of solutions

In this subsection, we prove that each solution of system (4.11) is bounded. The following theorem holds.

Theorem 4.2. When the assumptions (4.14) and (4.15) hold, each solution of system (4.11)-(4.12) is uniformly bounded.

Proof. Using the first equation of system (4.11), we always have

$$\dot{x}(t) \leq r_1 x(t) \left(1 - \frac{x(t)}{K_1} \right)$$

which implies

$$x(t) \leq \frac{1}{\frac{1}{K_1} + \left(\frac{1}{x(0)} - \frac{1}{K_1} \right) e^{-r_1 t}}.$$

Using the assumption (4.14), we have $x(t) \leq K_1$, for all positive value of t . It means that $x(t)$ is bounded.

We use the second equation of system (4.12) to prove that $y(t)$ is bounded.

For all $t \geq 0$, we have

$$\dot{y}(t) \leq r_2 y(t).$$

Integrating that differential inequality from $t - \tau$ to t gives :

$$y(t - \tau) \geq y(t) e^{-r_2 \tau}.$$

Using the fact that $x(t) \leq K_1$, we have the following differential inequality

$$\dot{y}(t) \leq r_2 y(t) \left(1 - \frac{y(t)}{K} \right),$$

where $K = \frac{(1 - m)q\alpha_1 K_1 + (1 - q)\alpha_A K_A}{e^{-r_2 \tau}}$.

The above differential inequality with unknown y implies:

$$y(t) \leq \frac{1}{\frac{1}{K} + \left(\frac{1}{y(0)} - \frac{1}{K} \right) e^{-r_2 t}}.$$

Using the assumption (4.15), we have $y(t) \leq K$, for all positive value of t . Thus $y(t)$ is bounded. One can easily verify that, using assumption (4.15), the inequalities $x(t) \leq K_1$ and $e^{r_2 \tau} \geq 1$, we have $y(0) \leq K$. \square

4.5 Equilibria of the model without delay and their stability

4.5.1 Equilibria of the model without delay

In the following theorem, we give equilibria of system (4.11)-(4.12).

Theorem 4.3.

(a) When $x < T_1$, the system (4.11)-(4.12) has four equilibria which are :

- $E_1^0(0, 0)$ which means that both predators and preys are absent.
- $E_2^0(0, (1 - q)\alpha_A K_A)$ for which there is no prey while the predator population reaches its carrying capacity.
- $E_3^0(K_1, 0)$ for which there is no predator and the prey population reaches its carrying capacity.
- $E_4^0\left(\frac{r_1 - \lambda_1(1 - m)q(1 - q)\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}, \frac{r_1\alpha_1(1 - m)q + (1 - m)b_1\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}\right)$.
The coexistence equilibrium E_4^0 is biologically meaningful if $r_1 > \lambda_1(1 - m)q(1 - q)\alpha_A K_A$.

(b) When $x \geq T_1$, the system (4.11)-(4.12) is such that :

- $E_1^\varphi(x_1^\varphi, 0)$ is an equilibrium for which there is no predator and the number x_1^φ of preys is a positive solution on the interval $[T_1, K_1]$ of equation (4.19) :

$$-b_1x^3 + (r_1 - b_1(h - T_1))x^2 + (r_1(h - T_1) - h)x + hT_1 = 0. \quad (4.19)$$

- $E_2^\varphi(x_2^\varphi, y_2^\varphi)$ is an equilibrium where $y_2^\varphi = (1 - m)q\alpha_1x_2^\varphi + (1 - q)\alpha_A K_A$ and the number x_2^φ of preys is a positive solution on the interval $[T_1, K_1]$ of equation (4.20).

$$A_1^\varphi x^3 + A_2^\varphi x^2 + A_3^\varphi x + hT_1 = 0, \quad (4.20)$$

where :

$$A_1^\varphi = -b_1 - q^2\lambda_1\alpha_1(1 - m)^2,$$

$$A_2^\varphi = r_1 - q(1 - q)(1 - m)\lambda_1\alpha_A K_A - (h - T_1)(b_1 + q^2\lambda_1\alpha_1(1 - m)^2),$$

$$A_3^\varphi = (r_1 - q(1 - q)(1 - m)\lambda_1\alpha_A K_A)(h - T_1) - h.$$

Proof. A couple of variables (x, y) is an equilibrium of system (4.11)-(4.12) if it is a solution of the following systems on $[0, T_1] \times \mathbb{R}_+$ and on $[T_1, K_1] \times \mathbb{R}_+$ respectively.

$$\begin{cases} r_1 \left(1 - \frac{x(t)}{K_1}\right) x(t) - q\lambda_1(1 - m)x(t)y(t) & = 0, \\ r_2 \left(1 - \frac{y(t)}{q\alpha_1(1 - m)x(t) + (1 - q)\alpha_A K_A}\right) y(t) & = 0, \end{cases} \quad (4.21)$$

$$\begin{cases} r_1 \left(1 - \frac{x(t)}{K_1}\right) x(t) - q\lambda_1(1 - m)x(t)y(t) - \frac{h(x - T_1)}{h + x - T_1} & = 0, \\ r_2 \left(1 - \frac{y(t)}{q\alpha_1(1 - m)x(t) + (1 - q)\alpha_A K_A}\right) y(t) & = 0, \end{cases} \quad (4.22)$$

4.5. Equilibria of the model without delay and their stability

Firstly, we solve the system (4.21) on $[0, T_1] \times \mathbb{R}_+$. Using the first equation of the system (4.21), we have $x = 0$ or $x = \frac{r_1 - q\lambda_1(1-m)y}{b_1}$.

Replacing x by 0 in the second equation of the system (4.21) gives $y = 0$ or $y = (1-q)\alpha_A K_A$. Then we have the equilibria E_1^0 and E_2^0 .

Replacing x by $\frac{r_1 - q\lambda_1(1-m)y}{b_1}$ in the second equation of the system (4.21) gives $y = 0$ or $y = (1-m)q\alpha_1 x + (1-q)\alpha_A K_A$. If $y = 0$, we have $x = \frac{r_1}{b_1}$. If $y = (1-m)q\alpha_1 x + (1-q)\alpha_A K_A$, we have $x = \frac{r_1 - \lambda_1(1-m)q(1-q)\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1-m)^2}$ and $y = \frac{r_1\alpha_1(1-m)q + (1-m)b_1\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1-m)^2}$. Then we have the equilibria E_3^0 and E_4^0 .

Secondly, we solve the system (4.22) on $[T_1, K_1] \times \mathbb{R}_+$.

Using the second equation of system (4.22) gives $y = 0$ or $y = (1-m)q\alpha_1 x + (1-q)\alpha_A K_A$. If $y = 0$, we find that x is a solution of equation (4.19). Moreover if we consider the function f defined by $f(x) = -b_1x^3 + (r_1 - b_1(h - T_1))x^2 + (r_1(h - T_1) - h)x + hT_1$, then we have $f(T_1) = hT_1(r_1 - b_1T_1) > 0$ using assumption (4.13). We also have $f(K_1) = -h(K_1 - T_1) < 0$ because $T_1 < K_1$. Thus, by the intermediate value theorem (H. Boualeu et al. (2007) [24], F. Moulin et al. (2007) [133]), it exists at least one solution of equation (4.19). So we have the equilibria E_1^φ . If $y = (1-m)q\alpha_1 x + (1-q)\alpha_A K_A$, x is a solution of equation (4.20). Moreover, if we consider the function g defined by $g(x) = A_1^\varphi x^3 + A_2^\varphi x^2 + A_3^\varphi x + hT_1$, we have $g(T_1) = hT_1(r_1 - b_1T_1 - q\lambda_1(1-m)(1-q)\alpha_A K_A + q\alpha_1(1-m)T_1)$. We have $g(K_1) = -(K_1(K_1 - T_1) + hT_1)(q\lambda_1(1-m)(1-q)\alpha_A K_A + q^2\lambda_1\alpha_1 K_1(1-m)^2) < 0$ because $T_1 < K_1$. Thus, if $r_1 - b_1T_1 - q\lambda_1(1-m)(1-q)\alpha_A K_A + q(1-m)\alpha_1 T_1 > 0$ then $g(T_1) > 0$. By the intermediate value theorem (H. Boualeu et al. (2007) [24], F. Moulin et al. (2007) [133]), (4.20) has at least one solution in $[K_1, T_1]$. Thus we have the equilibrium E_2^φ . \square

Note that if $(CONDEX(x_2^\varphi))$ below holds

$$CONDEX(x_2^\varphi) : r_1 - b_1T_1 - q\lambda_1(1-m)(1-q)\alpha_A K_A + q(1-m)\alpha_1 T_1 > 0$$

then equation (4.20) will have at least one solution in the interval $[T_1, K_1]$. So, we have a sufficient condition for the existence of the coexistence equilibrium E_2^φ .

Discussion

In what follows, we make a discussion on the results in terms of the rate preference q , the threshold of harvesting T_1 and the intrinsic growth rate of preys r_1 . The aim of that discussion is to analyze the impact of the preference rate q , the threshold of harvesting T_1 and the intrinsic growth rate of preys r_1 on the equilibria of the model. As it has been done in the theorem, we distinguish two cases:

- (a) *Case 1* : $x < T_1$, there is no harvesting of preys.

1.1. $q = 0$, the predator consumes only the additional food A .

- Equilibria E_1^0 and E_3^0 remain unchanged.
- The equilibrium $E_2^0 = (0, \alpha_A K_A)$ is such that the predator reaches its carrying capacity.
- The coexistence equilibrium $E_4^0 = (K_1, (1 - m)\alpha_A K_A)$ always exists (the condition of its existence given in the theorem is satisfied), the preys x which are not consumed reach their carrying capacity while the predator also reaches its carrying capacity taking into account the refuge of the preys x .

1.2. $q = 1$, the predators consume only the preys.

- Equilibria E_1^0 and E_3^0 remain unchanged.
- The predator population does not more reach its carrying capacity when the predators consume only the preys. The equilibrium $E_2^0 = (0, 0) = E_1^0$.
- The coexisting equilibrium $E_4^0 \left(\frac{r_1}{b_1 + \lambda_1 \alpha_1 (1 - m)^2}, \frac{r_1 \alpha_1 (1 - m) + (1 - m) b_1 \alpha_A K_A}{b_1 + \lambda_1 \alpha_1 (1 - m)^2} \right)$ always exists (the condition of its existence $r_1 > \lambda_1 (1 - m) q (1 - q) \alpha_A K_A$ given in the theorem is satisfied). Preys and predators do not more reach their carrying capacities as when $q = 0$.

We remark that when the predators consume only one source of food, the coexisting equilibrium always exists.

1.3. $q \in (0, 1)$, the predators consume the two sources of food according to the preference rate q .

- Equilibria E_1^0 , E_2^0 and E_3^0 always exist with the possibility for the preys or the predators to reach their carrying capacities.
- The coexisting equilibrium does not more always exists. Its existence depends on the intrinsic growth rate r_1 of preys, the density of additional fixed food for predators K_A , the amount of energy in the form of biomass of additional food assimilate into the predator's energy α_A , the strength of refuge m and the strength of competition among individuals of preys. So if

$r_1 \geq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then the coexisting equilibrium E_4^0 always exists for any value of the preference rate q in $(0, 1)$. If $r_1 \leq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then the coexisting equilibrium E_4^0 exists only for the values of the preference rate

$$q \text{ in } (0, q_1] \cup [q_2, 1) \text{ where } q_1 = \frac{1}{2} - \frac{1}{2} \sqrt{1 - \frac{4r_1}{\lambda_1 \alpha_A K_A (1 - m)}} \text{ and } q_2 = \frac{1}{2} + \frac{1}{2} \sqrt{1 - \frac{4r_1}{\lambda_1 \alpha_A K_A (1 - m)}}.$$

(b) *Case 2* : $x \geq T_1$, there is harvesting of preys.

2.1. $q = 0$, the predator consumes only the additional food A .

- Equilibrium E_1^φ always exists.
- The coexisting equilibrium $E_2^\varphi = (x_2^\varphi, \alpha_A K_A)$ always exists (Using assumption (4.13) gives $r_1 - b_1 T_1 > 0$ and $CONDEX(x_2^\varphi)$ holds), the predator population reaches its carrying capacity.

2.2. $q = 1$, the predators consume only the preys.

- The equilibrium E_1^φ always exists.
- The coexisting equilibrium $E_2^\varphi = (x_2^\varphi, (1 - m)\alpha_1 x_2^\varphi)$ always exists (Using assumption (4.13) gives $r_1 - b_1 T_1 + (1 - m)\alpha_1 T_1 > 0$ and $CONDEX(x_2^\varphi)$ holds). Predators reach their carrying capacity.

2.3. $q \in (0, 1)$, the predators consume the two sources of food according the preference rate q .

- Equilibrium E_1^φ always exists.
- The coexisting does not always exist. Its existence can be discussed in terms of the threshold of harvesting T_1 . Then, we have the following cases.
 If $T_1 \geq \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$, then using assumption (4.13) gives $r_1 - b_1 T_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A + q(1 - m)\alpha_1 T_1 > r_1 - b_1 T_1 + (1 - m)\alpha_1 T_1 > 0$. Thus, $CONDEX(x_2^\varphi)$ holds and the coexisting equilibrium E_2^φ exists.
 If $T_1 < \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$ and $r_1 \geq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then E_2^φ exists.
 If $T_1 < \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$ and $r_1 < \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then the coexistence equilibria E_2^φ doesn't always exist.

4.5.2 Stability of equilibria of the model without delay

The following theorem holds :

Theorem 4.4.

- The equilibrium E_1^0 is an unstable node.
- The equilibrium E_2^0 is a stable node if $r_1 < q\lambda_1(1 - m)(1 - q)\alpha_A K_A$ and a saddle (unstable) if $r_1 > q\lambda_1(1 - m)(1 - q)\alpha_A K_A$. We have a saddle-node bifurcation.
- The equilibrium E_3^0 is a saddle (unstable).

4.5. Equilibria of the model without delay and their stability

(d) The equilibrium E_4^0 is locally asymptotically stable. More precisely, let us set :

$$\Delta_{E_4^0} = (b_1x_4^0 - r_2)^2 - 4(1 - m)^2\alpha_1r_2q^2x_4^0$$

- If $\Delta_{E_4^0} > 0$, then E_4^0 is a stable node.
- If $\Delta_{E_4^0} < 0$, then E_4^0 is a stable spiral.
- If $\Delta_{E_4^0} = 0$, then E_4^0 is a stable degenerate node.

(e) The equilibrium E_1^φ is unstable. More precisely,

- if $\frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} < b_1x_1^\varphi$, then E_1^φ is a saddle.
- if $\frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} > b_1x_1^\varphi$, then E_1^φ is an unstable node.

(f) Let us set :

$$\begin{aligned} Tr(J(E_2^\varphi)) &= -r_2 - b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2}, \\ |J(E_2^\varphi)| &= -r_2 \left(-b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) + (1 - m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi, \\ \Delta_{E_2^\varphi} &= \left(r_2 - b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right)^2 - 4(1 - m)^2q^2\lambda_1\alpha_1r_2x_2^\varphi. \end{aligned}$$

i. When $\Delta_{E_2^\varphi} > 0$, the equilibrium E_2^φ is :

- a saddle if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi > 0$;
- a stable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi < 0$;
- an unstable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi > 0$.

ii. When $\Delta_{E_2^\varphi} < 0$, the equilibrium x_2^φ is :

- a stable spiral if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi < 0$;
- an unstable spiral if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi > 0$;

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- a centre if $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1 x_2^\varphi - (1 - m)^2 q^2 \lambda_1 \alpha_1 x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1 x_2^\varphi = 0$.

iii. When $\Delta_{E_2^\varphi} = 0$, the equilibrium x_2^φ is :

- a degenerate stable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1 x_2^\varphi - (1 - m)^2 q^2 \lambda_1 \alpha_1 x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1 x_2^\varphi < 0$;
- a degenerate unstable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1 x_2^\varphi - (1 - m)^2 q^2 \lambda_1 \alpha_1 x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1 x_2^\varphi > 0$.

Proof.

(a) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_1^0 is :

$$J_{E_1^0} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_1^0}$ has two positive eigenvalues (r_1 and r_2). So the equilibrium E_1^0 is an unstable node.

(b) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_2^0 is :

$$J_{E_2^0} = \begin{pmatrix} r_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A & 0 \\ r_2(1 - m)\alpha_1 q & -r_2 \end{pmatrix}.$$

$J_{E_2^0}$ has one negative eigenvalue ($-r_2$). The stability of the equilibrium E_2^0 depends on the sign of the second eigenvalue $r_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A$. Moreover the discriminant of the characteristic equation is $\Delta_{E_2^0} = (r_1 + r_2 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A)^2 > 0$. Thus if $r_1 < q\lambda_1(1 - m)(1 - q)\alpha_A K_A$, then the equilibrium E_2^0 is stable node and the equilibrium E_4^0 does not exist. If $r_1 > q\lambda_1(1 - m)(1 - q)\alpha_A K_A$, the equilibrium E_2^0 is a saddle (unstable).

(c) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_3^0 is :

$$J_{E_3^0} = \begin{pmatrix} -r_1 & -q\lambda_1(1 - m)K_1 \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_3^0}$ has one positive eigenvalue (r_2). The equilibrium E_3^0 is a saddle (unstable).

(d) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_4^0 is :

$$J_{E_4^0} = \begin{pmatrix} -b_1 x_4^0 & -q\lambda_1(1 - m)x_4^0 \\ (1 - m)\alpha_1 r_2 q & -r_2 \end{pmatrix}.$$

$$Tr(J_{E_4^0}) = -(b_1 x_4^0 + r_2) < 0,$$

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$$|(J_{E_4^0})| = r_2 b_1 x_4^0 + (1 - m)^2 \alpha_1 \lambda_1 r_2 q^2 x_4^0 > 0.$$

Moreover the discriminant of the characteristic equation is $\Delta_{E_4^0} = (b_1 x_4^0 - r_2)^2 - 4(1 - m)^2 \alpha_1 \lambda_1 r_2 q^2 x_4^0$. Therefore, if $\Delta_{E_4^0} > 0$, then the equilibrium E_4^0 is a stable node. If $\Delta_{E_4^0} < 0$, then the equilibrium E_4^0 is a stable spiral. If $\Delta_{E_4^0} = 0$, then the equilibrium E_4^0 is a stable degenerate node.

(e) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_1^φ is :

$$J_{E_1^\varphi} = \begin{pmatrix} -b_1 x_1^\varphi + \frac{\varphi(x_1^\varphi)}{x_1^\varphi} - \varphi'(x_1^\varphi) & -q \lambda_1 (1 - m) x_2^\varphi \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_1^\varphi}$ has one positive eigenvalue (r_2). Thus the equilibrium E_1^φ is unstable. Moreover, if $-b_1 x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2 T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} < 0$, then the equilibrium E_1^φ is a saddle.

If $-b_1 x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2 T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} > 0$, then the equilibrium E_1^φ is an unstable node.

If $-b_1 x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2 T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} = 0$, then the equilibrium E_1^φ is an unstable non hyperbolic point.

(f) The jacobian matrix of the system (4.11)-(4.12) at the equilibrium E_2^φ is :

$$J_{E_2^\varphi} = \begin{pmatrix} -b_1 x_2^\varphi + \frac{\varphi(x_2^\varphi)}{x_2^\varphi} - \varphi'(x_2^\varphi) & -q \lambda_1 (1 - m) x_2^\varphi \\ (1 - m) \alpha_1 r_2 q & -r_2 \end{pmatrix}.$$

$$Tr(J_{E_2^\varphi}) = -b_1 x_2^\varphi - r_2 + \frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2},$$

$$|J_{E_2^\varphi}| = -r_2 \left(-b_1 x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) + (1 - m)^2 q^2 \alpha_1 \lambda_1 r_2 x_2^\varphi.$$

The discriminant of the characteristic equation is :

$$\Delta_{E_2^\varphi} = \left(r_2 + b_1 x_2^\varphi - \frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right)^2 - 4(1 - m)^2 q^2 \alpha_1 \lambda_1 r_2 x_2^\varphi.$$

Then using the signs of $Tr(J_{E_2^\varphi})$, $|J_{E_2^\varphi}|$ and $\Delta_{E_2^\varphi}$, and the table given in (Jordan et al. (2007) [95]), we have the type and the stability of the equilibrium E_2^φ as in theorem (4.4). (For stability of equilibria in the plane, one can also refer to Auger et al. (2010) [6], Hirsch et al. (2004) [77]).

□

Remark 4.1. When the equilibrium E_2 is locally asymptotically stable, the equilibrium E_4 doesn't exist. When E_4 exists, it is always locally asymptotically stable and E_2 is unstable.

Remark 4.2. If $\frac{h(x_2^\varphi - T_1)^2 - h^2 T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \leq 0$ or $h \geq \frac{(x_2^\varphi - T_1)^2}{T_1}$, then the equilibrium E_2^φ is always stable. More precisely, x_2^φ is a stable node if $\Delta_{E_2^\varphi} > 0$, a stable spiral if $\Delta_{E_2^\varphi} < 0$ and a degenerate stable node if $\Delta_{E_2^\varphi} = 0$.

4.6 Hopf bifurcation and stability analysis of the delayed model

In this section, we study the stability of system (4.11)-(4.12) for $\tau > 0$. Before going further, let us recall the fact that if an equilibrium is unstable for $\tau = 0$, it remains unstable for $\tau > 0$ (see Martin and al. (2001) [128], Culshaw et al. (2000) [42]). Thus, we shall study the stability of the coexisting equilibrium without harvesting E_4^0 which is always stable when it exists, and the stability of the coexisting equilibrium with harvesting E_2^φ . Let us recall that E_2^φ exists if $CONDEX(x_2^\varphi)$ is satisfied and is stable if

$$-b_1x_2^\varphi - r_2 + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} < 0$$

and

$$-r_2 \left(-b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) + (1 - m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi > 0.$$

We recall that the equilibrium E_4^0 exists if,

$$r_1 - \lambda_1(1 - m)q(1 - q)\alpha_A K_A > 0$$

To linearize system (4.11)-(4.12) around an equilibrium $E(x_e, y_e)$ which can be E_4^0 or E_2^φ , let us set $X = x - x_e$ and $Y = y - y_e$. Then the linearized system of system (4.11)-(4.12) reads as :

$$\begin{cases} \dot{X}(t) = \left(-b_1x_e + \frac{\varphi(x_e)}{x_e} - \varphi'(x_e) \right) X(t) - q\lambda_1(1 - m)x_eY(t), \\ \dot{Y}(t) = r_2(1 - m)q\alpha_1X(t - \tau) - r_2Y(t - \tau). \end{cases} \quad (4.23)$$

From the linearized system (4.23), we have the following characteristic equation :

$$\lambda^2 + A_{1\varphi}\lambda + r_2\lambda e^{-\lambda\tau} + A_{2\varphi}e^{-\lambda\tau} = 0, \quad (4.24)$$

where

$$A_{1\varphi} = b_1x_e - \frac{h(x_e - T_1)^2 - h^2T_1}{x_e(x_e + h - T_1)^2},$$

$$A_{2\varphi} = A_{1\varphi}r_2 + r_2\lambda_1\alpha_1q^2(1 - m)^2x_e.$$

Now, let us investigate conditions under which the characteristic equation (4.24) has purely imaginary roots $\lambda = i\omega$.

Replacing λ by $i\omega$ in equation (4.24) gives :

$$-\omega^2 + A_{1\varphi}i\omega + A_{2\varphi}e^{-i\omega\tau} + r_2e^{-i\omega\tau}i\omega = 0. \quad (4.25)$$

Then separating the real and the imaginary parts in equation (4.25) gives :

$$-\omega^2 + A_{2\varphi}\cos\tau\omega + r_2\omega\sin\tau\omega = 0, \quad (4.26)$$

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and

$$A_{1\varphi}\omega - A_{2\varphi}\sin\tau\omega + r_2\omega\cos\tau\omega = 0. \quad (4.27)$$

From equations (4.26) and (4.27), we have :

$$\cos\tau\omega = \frac{(A_{2\varphi} - r_2A_{1\varphi})\omega^2}{A_{2\varphi}^2 + r_2^2\omega^2} = \frac{r_2\lambda_1\alpha_1q^2(1-m)^2x_e}{A_{2\varphi}^2 + r_2^2\omega^2} \quad (4.28)$$

and

$$\sin\tau\omega = \frac{A_{1\varphi}A_{2\varphi}\omega + r_2\omega^3}{A_{2\varphi}^2 + r_2^2\omega^2} \quad (4.29)$$

From equations (4.28) and (4.29) and using the equation $\cos^2\tau\omega + \sin^2\tau\omega = 1$, we obtain the following equation :

$$r_2^2\omega^6 + (A_{2\varphi}^2 + r_2^2A_{1\varphi}^2 - r_2^4)\omega^4 + (A_{1\varphi}^2A_{2\varphi}^2 - 2r_2^2A_{2\varphi}^2)\omega^2 - A_{2\varphi}^4 = 0. \quad (4.30)$$

Setting $W = \omega^2$, equation (4.30) becomes :

$$r_2^2W^3 + (A_{2\varphi}^2 + r_2^2A_{1\varphi}^2 - r_2^4)W^2 + (A_{1\varphi}^2A_{2\varphi}^2 - 2r_2^2A_{2\varphi}^2)W - A_{2\varphi}^4 = 0,$$

which has, by the Descartes's rule of sign at least one positive root because $r_2^2 > 0$ and $-A_{2\varphi}^4 < 0$. Then, we have at least two opposite values $\omega_0 > 0$ and $\omega_1 < 0$ of ω .

Moreover, from (4.28) and (4.29) and for $\omega = \omega_0$, we obtain :

$$\tau_k = \frac{1}{\omega_0} \arctan \left(\frac{A_{1\varphi}A_{2\varphi}\omega_0 + r_2\omega_0^3}{r_2\lambda_1\alpha_1q^2(1-m)^2x_e\omega_0^2} \right) + \frac{k\pi}{\omega_0} = \tau_0 + \frac{k\pi}{\omega_0}, k \in \mathbb{Z},$$

where

$$\tau_0 = \frac{1}{\omega_0} \arctan \left(\frac{A_{1\varphi}A_{2\varphi}\omega_0 + r_2\omega_0^3}{r_2\lambda_1\alpha_1q^2(1-m)^2x_e\omega_0^2} \right).$$

In order to see if a Hopf bifurcation can occur, we verify the transversality condition (Diekmann et al. (1995) [46]).

When differentiating equation (4.24) with respect to τ , we obtain :

$$[2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau + r_2e^{-\lambda\tau} - r_2\lambda\tau e^{-\lambda\tau}] \frac{d\lambda}{d\tau} - (A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau} = 0,$$

from which we obtain,

$$\begin{aligned} \left(\frac{d\lambda}{d\tau} \right)^{-1} &= \frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau + r_2e^{-\lambda\tau} - r_2\lambda\tau e^{-\lambda\tau}}{(A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau}} \\ &= \frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{(A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda} \\ &= -\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{\lambda(\lambda^2 + A_{1\varphi}\lambda)} - \frac{\tau}{\lambda} \\ &= -\frac{1}{\lambda} \left[\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{\lambda^2 + A_{1\varphi}\lambda} + \tau \right]. \end{aligned}$$

Following Cooke and Grossman (1982) [37], we therefore obtain by using (4.28) and (4.29),

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$$\begin{aligned}
 \operatorname{sign} \left\{ \frac{d(\operatorname{Re}\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} &= \operatorname{sign} \left\{ \operatorname{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega_0} \\
 &= \operatorname{sign} \left\{ \operatorname{Re} \left(-\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}}{\lambda(\lambda^2 + A_{1\varphi}\lambda)} \right) \right\}_{\lambda=i\omega_0} \\
 &= \operatorname{sign} \left\{ \frac{r_2^2\omega_0^4 + 2\omega_0^2 A_{2\varphi}^2 + A_{1\varphi}^2 A_{2\varphi}^2}{(\omega_0^4 + A_{1\varphi}^2\omega_0^2)(A_{2\varphi}^2 + r_2^2\omega_0^2)} \right\}.
 \end{aligned}$$

Hence, we have:

$$\operatorname{sign} \left\{ \frac{d(\operatorname{Re}\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} > 0.$$

It means that the transversality condition is satisfied. Then, a Hopf bifurcation can occur when $\tau = \tau_0$.

The following theorem holds for the stability of the coexisting equilibrium E of system (4.11)-(4.12):

Theorem 4.5.

- (a) If $\tau \in [0, \tau_0)$, then the equilibrium $E(x_e, y_e)$ is locally asymptotically stable.
- (b) If $\tau > \tau_0$, then the equilibrium $E(x_e, y_e)$ is unstable.
- (c) If $\tau = \tau_k$ with $k \in \mathbb{Z}$, then the system (4.11)-(4.12) undergoes a Hopf bifurcation.

Proof. We proved that it is possible to have purely imaginary roots for the characteristic equation (4.24) and the transversality condition is satisfied. Thus we have the third item of theorem (4.5). In what follows, we prove the first and the second items of theorem (4.5).

By Rouche's theorem (1960) [47] and the continuity in τ , the characteristic equation (4.24) has roots with positive real parts if and only if it has purely imaginary roots.

Let $\lambda(\tau) = \mu(\tau) + i\omega(\tau)$ where μ and ω are reals depending on τ . For $\tau = 0$, the equilibrium E is stable. Thus we have $\mu(0) < 0$. By continuity, if τ is sufficiently small, we still have $\mu(\tau) < 0$ and E is still stable. The change of stability will occur for some values of τ for which $\mu(\tau) = 0$ and $\omega(\tau) \neq 0$, it means that λ will be purely imaginary. Let τ_e be such that $\mu(\tau_e) = 0$ and $\omega(\tau_e) = \omega_e \neq 0$ with $\lambda = i\omega(\tau_e)$. In this case, the steady state loses stability and eventually becomes unstable when $\mu(\tau)$ becomes positive. In other words, if such a value ω_e does not exist, then the steady state E will remain stable for all τ . \square

4.7 Direction and stability of Hopf bifurcation

In this section, we compute some formulas by using the normal form theory and the center manifold theorem introduced by Hassard et al. (1981) ([74]). These formulas are used to determine the direction of the Hopf bifurcation and the stability of the bifurcating periodic solution of system (4.11)-(4.12) which occurs when the delay τ takes the critical value τ_0 .

4.7. Direction and stability of Hopf bifurcation

For convenience, let $t = s\tau$, $x(s\tau) = x_1(s)$, $y(s\tau) = x_2(s)$ and $\tau = \tau_0 + \mu$, $\mu \in \mathbb{R}$ so that $\mu = 0$ is the Hopf bifurcating value for system (4.11)-(4.12). Then the system (4.11)-(4.12) becomes equivalent to the system :

$$\dot{u}(t) = L_\mu(u_t) + f(\mu, u_t), \quad (4.31)$$

where $u_t = (x_1(t), x_2(t))^T \in \mathcal{C}$ and $u_t(\theta) = u(t + \theta) = (x_1(t + \theta), x_2(t + \theta))^T \in \mathcal{C}$.

$L_\mu : \mathcal{C} \rightarrow \mathbb{R}^2$ is defined as follows :

$$L_\mu \phi = (\tau_0 + \mu) \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + (\tau_0 + \mu) \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix}, \quad (4.32)$$

where $A_{A\varphi} = -b_1 x_e + \frac{\varphi(x_e)}{x_e} - \varphi'(x_e)$, $B_{A\varphi} = -q\lambda_1(1 - m)x_e$, $C_{A\varphi} = qr_2\alpha_1(1 - m)$, $D_{A\varphi} = -r_2$.

$f : \mathcal{R} \times \mathcal{C} \rightarrow \mathbb{R}^2$ is defined as follows :

$$f(\mu, \phi) = (\tau_0 + \mu)(f_1, f_2)^T, \quad (4.33)$$

where $\phi(\theta) = (\phi_1(\theta), \phi_2(\theta))^T \in \mathcal{C}$

$$f_1 = a_{11}\phi_1^2(0) + a_{12}\phi_1(0)\phi_2(0) + a_{13}\phi_1^3(0),$$

and

$$f_2 = a_{21}\phi_1^2(-1) + a_{22}\phi_1(-1)\phi_2(0) + a_{23}\phi_1(-1)\phi_2(-1) + a_{24}\phi_2(-1)\phi_2(0) + a_{25}\phi_1^3(-1) \\ + a_{26}\phi_1^2(-1)\phi_2(0) + a_{27}\phi_1^2(-1)\phi_2(-1) + a_{28}\phi_1(-1)\phi_2(0)\phi_2(-1),$$

with,

$$a_{11} = -b_1 + \frac{h^2}{(x_e + h - T_1)^2}, \quad a_{12} = -q\lambda_1(1 - m), \quad a_{13} = \frac{h^2}{(x_e + h - T_1)^4} \\ a_{21} = -\frac{r_2(1 - m)^2 q^2 \alpha_1^2}{y_e^2}, \quad a_{22} = \frac{r_2(1 - m)q\alpha_1}{y_e}, \quad a_{23} = \frac{r_2(1 - m)q\alpha_1}{y_e}, \quad a_{24} = -\frac{r_2}{y_e}, \quad a_{25} = \\ -\frac{r_2(1 - m)^3 q^3 \alpha_1^3}{y_e^2}, \quad a_{26} = -\frac{r_2(1 - m)^2 q^2 \alpha_1^2}{y_e^2}, \quad a_{27} = -\frac{r_2(1 - m)^2 q^2 \alpha_1^2}{y_e^2}, \quad a_{28} = \frac{r_2(1 - m)q\alpha_1}{y_e^2}.$$

L_μ is a one parameter family of bounded linear operators in $\mathcal{C}[-1, 0] \rightarrow \mathbb{R}^2$. Then by the Riesz representation theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta, \mu)$ in $[-1, 0] \rightarrow \mathbb{R}^2$ such that

$$L_\mu(\phi) = \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta). \quad (4.34)$$

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In fact, we can choose

$$\eta(\theta, \mu) = (\tau_0 + \mu) \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} \delta(\theta) + (\tau_0 + \mu) \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix} \delta(\theta+1), \quad (4.35)$$

where δ is the Dirac function. Then equation (4.31) is satisfied.

For $\phi \in C^1[-1, 0]$, let us define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \text{if } -1 \leq \theta < 0 \\ \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta), & \text{if } \theta = 0 \end{cases} \quad (4.36)$$

and

$$R(\mu)\phi = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & \text{if } -1 \leq \theta < 0, \\ f(\mu, \phi), & \text{if } \theta = 0. \end{cases} \quad (4.37)$$

The system (4.11)-(4.12) is then transformed into the operator equation of the form (4.38) as follows, in order to study the Hopf bifurcation problem

$$\dot{u}(t) = A(\mu)u_t + Ru_t. \quad (4.38)$$

Define the adjoint operator for $\psi \in C^1([0, 1], (\mathbb{R}^2)^*)$,

$$A^*(\mu)\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds} & \text{if } 0 < s \leq 1, \\ \int_{-1}^0 d\eta^T(s, \mu)\psi(-s) & \text{if } s = 0. \end{cases} \quad (4.39)$$

In order to normalize the eigenvectors of the operator A and the adjoint operator A^* , we need to introduce the following bilinear form:

$$\langle \psi, \phi \rangle = \bar{\psi}(0) \cdot \phi(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \bar{\psi}^T(\xi - \theta) d\eta(\theta) \phi(\xi) d\xi, \quad (4.40)$$

where $\eta(\theta) = \eta(\theta, 0)$.

By the discussion and the transformation $t = s\tau$, we know that $i\tau_0\omega_0$ and $-i\tau_0\omega_0$ are the eigenvalues of $A(0)$ and other eigenvalues have strictly negative real parts. Hence they are also eigenvalues of A^* . Now we are going to compute the eigenvectors of $A(0)$ and A^* corresponding to their respective eigenvalues $i\tau_0\omega_0$ and $-i\tau_0\omega_0$. If we suppose that $q(\theta) = (q^{(1)}(\theta), q^{(2)}(\theta))^T = (1, q_1)^T e^{i\tau_0\omega_0\theta}$ is the eigenvector of $A(0)$ corresponding to the eigenvalue $i\tau_0\omega_0$, then by the definition we have $A(0)q(0) = i\tau_0\omega_0q(0)$. Then using the definition of $A(0)$ and the expressions given by (4.31), (4.33) and (4.34), gives :

$$\tau_0 \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} q(0) + \tau_0 \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} q(-1) = i\tau_0\omega_0q(0),$$

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or equivalently $\tau_0 \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ q_1 \end{pmatrix} + \tau_0 \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} 1 \\ q_1 \end{pmatrix} e^{-i\tau_0\omega_0} = i\tau_0\omega_0 \begin{pmatrix} 1 \\ q_1 \end{pmatrix}$

This implies $\begin{cases} A_{A\varphi} + B_{A\varphi}q_1 & = i\omega_0, \\ (C_{A\varphi} + D_{A\varphi}q_1)e^{-i\tau_0\omega_0} & = q_1i\omega_0, \end{cases}$

and $q_1 = \frac{C_{A\varphi}}{-D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}$.

Thus, $q^{(1)}(\theta) = e^{i\tau_0\omega_0\theta}$ and $q^{(2)}(\theta) = \frac{C_{A\varphi}e^{i\tau_0\omega_0\theta}}{-D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}$.

Now let us compute the eigenvector q^* of A^* . Suppose that we have $q^*(s) = G_{A\varphi}(1, q_1^*)^T e^{i\tau_0\omega_0 s}$, $0 \leq s \leq 1$. Then we have the following relation

$$\tau_0 \begin{pmatrix} A_{A\varphi} & 0 \\ B_{A\varphi} & 0 \end{pmatrix} q^*(0) + \tau_0 \begin{pmatrix} 0 & C_{A\varphi} \\ 0 & D_{A\varphi} \end{pmatrix} q^*(-1) = -i\tau_0\omega_0 q^*(0),$$

which is equivalent to $\tau_0 \begin{pmatrix} A_{A\varphi} & 0 \\ B_{A\varphi} & 0 \end{pmatrix} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} + \tau_0 \begin{pmatrix} 0 & C_{A\varphi} \\ 0 & D_{A\varphi} \end{pmatrix} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} e^{-i\tau_0\omega_0} = -i\tau_0\omega_0 \begin{pmatrix} 1 \\ q_1^* \end{pmatrix}$.

This implies $\begin{cases} A_{A\varphi} + C_{A\varphi}q_1^*e^{-i\tau_0\omega_0} & = -i\omega_0, \\ B_{A\varphi} + D_{A\varphi}q_1^*e^{-i\tau_0\omega_0} & = -q_1^*i\omega_0, \end{cases}$

and $q_1^* = -\frac{B_{A\varphi}}{D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}$.

Now let's compute $G_{A\varphi}$ by using the orthogonality condition $\langle q^*(s), q(\theta) \rangle = 1$. By using (4.39), we have :

$$\begin{aligned} \langle q^*(s), q(\theta) \rangle &= \overline{q^*(0)} \cdot q(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \overline{q^*}^T(\xi - \theta) d\eta(\theta) q(\xi) d\xi \\ &= \overline{q^*(0)} \cdot q(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \overline{G_{A\varphi}}(1, \overline{q_1^*}) e^{-i\omega_0\tau_0(\xi-\theta)} d\eta(\theta) (1, q_1)^T e^{i\omega_0\tau_0\xi} \\ &= \overline{G_{A\varphi}} \left\{ 1 + q_1 \overline{q_1^*} - (1, \overline{q_1^*}) \int_{-1}^0 \theta e^{i\omega_0\tau_0\theta} d\eta(\theta) (1, q_1)^T \right\} \\ &= \overline{G_{A\varphi}} \{ 1 + q_1 \overline{q_1^*} + \tau_0 e^{-i\omega_0\tau_0} (C_{A\varphi} + D_{A\varphi}q_1) \overline{q_1^*} \cdot \} \end{aligned}$$

Then,

$$G_{A\varphi} = [1 + \overline{q_1}q_1^* + \tau_0 e^{i\omega_0\tau_0} (C_{A\varphi} + D_{A\varphi}\overline{q_1})q_1^*]^{-1}.$$

Now, we are going to compute the coordinates to describe the center manifold \mathcal{C}_0 at $\mu = 0$. Let us define

$$z(t) = \langle q^*, u_t \rangle \tag{4.41}$$

and

$$W(t, \theta) = u_t(\theta) - 2\text{Re}\{z(t)q(\theta)\}, \tag{4.42}$$

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where u_t is a solution of (4.37) when $\mu = 0$.

On the center manifold \mathcal{C}_0 , we have :

$$W(t, \theta) = W(z(t), \bar{z}(t), \theta),$$

where,

$$W(t, \theta) = W(z(t), \bar{z}(t), \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \quad (4.43)$$

In (4.42), z and \bar{z} represent the local coordinates of the centre manifold \mathcal{C}_0 in the direction of q and q^* respectively.

Now let us reduce equation (4.37) to an ordinary differential equation using a single complex variable on the centre manifold. Since $\mu = 0$ and for u_t a solution of (4.37) belonging to the centre manifold \mathcal{C}_0 , we have :

$$\begin{aligned} \dot{z}(t) &= \langle q^*, \dot{u}(t) \rangle = \langle q^*, Au_t + Ru_t \rangle \\ &= \langle q^*, Au_t \rangle + \langle q^*, Ru_t \rangle = \langle A^* q^*, u_t \rangle + \langle q^*, Ru_t \rangle . \\ &= i\tau_0\omega_0 z + \bar{q}^* f_0(z, \bar{z}) \end{aligned}$$

The following equation :

$$\dot{z}(t) = i\tau_0\omega_0 z + \bar{q}^* f_0(z, \bar{z}) \quad (4.44)$$

can be rewritten as :

$$\dot{z}(t) = i\tau_0\omega_0 z + g(z, \bar{z}), \quad (4.45)$$

where,

$$g(z, \bar{z}) = g_{20} \frac{z^2}{2} + g_{11} z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{z^2\bar{z}}{2} + \dots \quad (4.46)$$

In what follows, we are going to expand g in powers of z and \bar{z} in order to obtain from the first three coefficients of this expansion, the value of μ_2 which indicates the direction of the Hopf bifurcation (that is to say if the Hopf bifurcation is supercritical or subcritical), and the value of β_2 which determines the stability. To do so, we use the algorithm presented by Hassard and al. (Hassard and al. (1981) [74]).

A substitution of (4.37) in (4.45) leads to :

$$\begin{aligned} \dot{W}(t) &= \dot{u}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= A(\mu)u_t + Ru_t - [i\tau_0\omega_0 z + \bar{q}^*(0)f_0(z, \bar{z})]q - [-i\tau_0\omega_0\bar{z} + q^*(0)\bar{f}_0(z, \bar{z})]\bar{q} \\ &= AW + 2ARe(zq) + Ru_t - 2Re[\bar{q}^*(0)f_0(z, \bar{z})q(\theta)] - 2Re[i\tau_0\omega_0 zq(\theta)] \\ &= AW - 2Re[\bar{q}^*(0)f_0(z, \bar{z})q(\theta)] + Ru_t. \end{aligned}$$

Then we obtain the following equations

$$\dot{W} = \begin{cases} AW - 2Re[\bar{q}^*(0)f_0(z, \bar{z})q(\theta)] & \text{if } -1 \leq \theta < 0, \\ AW - 2Re[\bar{q}^*(0)f_0(z, \bar{z})q(\theta)] + f & \text{if } \theta = 0. \end{cases} \quad (4.47)$$

Equations (4.46) can be rewritten as :

$$\dot{W} = AW + H(z, \bar{z}, \theta), \quad (4.48)$$

where

$$H(z, \bar{z}, \theta) = H_{20}(\theta) \frac{z^2}{2} + H_{11}(\theta) z\bar{z} + H_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \quad (4.49)$$

Derivating W in (4.42) with respect to t , we have :

$$\dot{W} = W_z \dot{z} + W_{\bar{z}} \dot{\bar{z}}. \quad (4.50)$$

Then using (4.42), (4.47) and (4.48), gives :

$$(A - 2i\tau_0\omega_0)W_{20}(\theta) = -H_{20}(\theta), \quad (4.51)$$

and

$$AW_{11}(\theta) = -H_{11}(\theta). \quad (4.52)$$

Using equations (4.43) and (4.44) gives :

$$g(z, \bar{z}) = \bar{q}^*(0) f_0(z, \bar{z}) = \tau_0 \overline{G_{A\varphi}} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} = \tau_0 \overline{G_{A\varphi}} (f_1 + q_1^* f_2), \quad (4.53)$$

where

$$f_1 = a_{11}x_1^2(t) + a_{12}x_1(t)x_2(t) + a_{13}x_1^3(t),$$

$$f_2 = a_{21}x_1^2(t-1) + a_{22}x_1(t-1)x_2(t) + a_{23}x_1(t-1)x_2(t-1) + a_{24}x_2(t-1)x_2(t) + a_{25}x_1^3(t-1) \\ + a_{26}x_1^2(t-1)x_2(t) + a_{27}x_1^2(t-1)x_2(t-1) + a_{28}x_1(t-1)x_2(t)x_2(t-1),$$

and

$$x_{1t}(0) = q^{(1)}(0)z + \bar{q}^{(1)}(0)\bar{z} + W_{20}^{(1)}(0) \frac{z^2}{2} + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0) \frac{\bar{z}^2}{2} + \dots$$

$$x_{2t}(0) = q^{(2)}(0)z + \bar{q}^{(2)}(0)\bar{z} + W_{20}^{(2)}(0) \frac{z^2}{2} + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0) \frac{\bar{z}^2}{2} + \dots$$

$$x_{1t}(-1) = q^{(1)}(-1)z + \bar{q}^{(1)}(-1)\bar{z} + W_{20}^{(1)}(-1) \frac{z^2}{2} + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1) \frac{\bar{z}^2}{2} + \dots$$

$$x_{2t}(-1) = q^{(2)}(-1)z + \bar{q}^{(2)}(-1)\bar{z} + W_{20}^{(2)}(-1) \frac{z^2}{2} + W_{11}^{(2)}(-1)z\bar{z} + W_{02}^{(2)}(-1) \frac{\bar{z}^2}{2} + \dots$$

An identification by using (4.43) and (4.52) gives us the following coefficients of g :

$$g_{20} = 2\tau_0 \overline{G_{A\varphi}} \{ a_{11}(q^{(1)}(0))^2 + a_{12}q^{(1)}(0)q^{(2)}(0) + q_1^*(a_{21}(q^{(1)}(-1))^2 + a_{22}q^{(1)}(-1)q^{(2)}(0) \\ + a_{23}q^{(1)}(-1)q^{(2)}(-1) + a_{24}q^{(2)}(0)q^{(2)}(-1)) \},$$

$$g_{11} = \tau_0 \overline{G_{A\varphi}} \{ 2a_{11}q^{(1)}(0)\bar{q}^{(1)}(0) + a_{12}(q^{(1)}(0)q^{(2)}(0) + \bar{q}^{(1)}(0)q^{(2)}(0)) \\ + q_1^*(2a_{21}q^{(1)}(-1)\bar{q}^{(1)}(-1) + a_{22}(q^{(1)}(-1)\bar{q}^{(2)}(0) + q^{(2)}(0)\bar{q}^{(1)}(-1)) \\ + a_{23}(q^{(1)}(-1)\bar{q}^{(2)}(-1) + q^{(2)}(-1)\bar{q}^{(1)}(-1)) + a_{24}(q^{(2)}(-1)\bar{q}^{(2)}(0) + q^{(2)}(0)\bar{q}^{(2)}(-1)) \},$$

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$$\begin{aligned}
 g_{02} &= 2\tau_0 \overline{G_{A\varphi}} \{a_{11}(\overline{q}^{(1)}(0))^2 + a_{21}\overline{q}^{(1)}(0)\overline{q}^{(2)}(0) + q_1^*(a_{21}(\overline{q}^{(2)}(-1))^2 + a_{22}\overline{q}^{(1)}(-1)\overline{q}^{(2)}(0) \\
 &\quad + a_{23}\overline{q}^{(1)}(-1)\overline{q}^{(2)}(-1) + a_{24}\overline{q}^{(2)}(0)\overline{q}^{(2)}(-1))\}, \\
 g_{21} &= 2\tau_0 \overline{G_{A\varphi}} \{a_{11}(\overline{q}^{(1)}(0)W_{20}^{(1)}(0) + 2q^{(1)}(0)W_{11}^{(1)}(0)) + a_{12}(q^{(1)}(0)W_{11}^{(2)}(0) + \frac{1}{2}\overline{q}^{(1)}(0)W_{20}^{(2)}(0) \\
 &\quad + \frac{1}{2}\overline{q}^{(2)}(0)W_{20}^{(1)}(0) + \overline{q}^{(2)}(0)W_{11}^{(1)}(0)) + 3a_{13}(q^{(1)}(0))^2\overline{q}^{(1)}(0) + q_1^*(a_{21}(\overline{q}^{(1)}(-1)W_{20}^{(1)}(-1) \\
 &\quad + 2q^{(1)}(-1)W_{11}^{(1)}(-1)) + a_{22}(q^{(1)}(-1)W_{11}^{(2)}(0) + \frac{1}{2}\overline{q}^{(1)}(-1)W_{20}^{(2)}(0) + \frac{1}{2}\overline{q}^{(2)}(0)W_{20}^{(1)}(-1) \\
 &\quad + q^{(2)}(0)W_{11}^{(1)}(-1)) + a_{23}(q^{(1)}(-1)W_{11}^{(2)}(-1) + \frac{1}{2}\overline{q}^{(1)}(-1)W_{20}^{(2)}(-1) + q^{(2)}(-1)W_{11}^{(1)}(-1) \\
 &\quad + \frac{1}{2}\overline{q}^{(2)}(-1)W_{20}^{(1)}(-1)) + a_{24}(q^{(2)}(0)W_{11}^{(2)}(-1) + \frac{1}{2}\overline{q}^{(2)}(0)W_{20}^{(2)}(-1) + q^{(2)}(-1)W_{11}^{(2)}(0) \\
 &\quad + \frac{1}{2}\overline{q}^{(2)}(-1)W_{20}^{(2)}(0)) + 3a_{25}(q^{(1)}(-1))^2\overline{q}^{(1)}(-1) + a_{26}((q^{(1)}(-1))^2\overline{q}^{(2)}(0) \\
 &\quad + 2q^{(1)}(-1)\overline{q}^{(1)}(-1)q^{(2)}(0)) + a_{27}((q^{(1)}(-1))^2\overline{q}^{(2)}(-1) + 2q^{(1)}(-1)\overline{q}^{(1)}(-1)q^{(2)}(-1)) \\
 &\quad + a_{28}(q^{(1)}(-1)\overline{q}^{(2)}(0)q^{(2)}(-1)) + q^{(1)}(-1)\overline{q}^{(2)}(-1)q^{(1)}(0) + q^{(2)}(-1)\overline{q}^{(1)}(-1)q^{(2)}(0)\}.
 \end{aligned}$$

Now we reach to the step of computation of $W_{20}(\theta)$. Using (4.36) and (4.47) gives :

$$\begin{aligned}
 H(z, \bar{z}, \theta) &= -2\text{Re}[\overline{q}^*(0)f_0(z, \bar{z})q(\theta)] + Ru_t = -gq(\theta) - \overline{gq}(\theta) + Ru_t \\
 &= -\left(g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2}\right)q(\theta) - \left(\overline{g}_{20}\frac{\bar{z}^2}{2} + \overline{g}_{11}z\bar{z} + \overline{g}_{02}\frac{z^2}{2}\right)\overline{q}(\theta) + Ru_t, \quad (4.54)
 \end{aligned}$$

where

$$Ru_t = \tau_0 \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} = 2\tau_0 A^{A\varphi} \frac{z^2}{2} + \tau_0 B^{A\varphi} z\bar{z},$$

with,

$$\begin{aligned}
 A^{A\varphi} &= \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix}, \\
 B^{A\varphi} &= \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix},
 \end{aligned}$$

Where,

$$\begin{aligned}
 A_{11}^{A\varphi} &= a_{11}(q^{(1)}(0))^2 + a_{12}q^{(1)}(0)q^{(2)}(0), \\
 A_{21}^{A\varphi} &= a_{21}(q^{(1)}(-1))^2 + a_{22}q^{(1)}(-1)q^{(2)}(0) + a_{23}q^{(1)}(-1)q^{(2)}(-1) + a_{24}q^{(2)}(-1)q^{(2)}(0), \\
 B_{11}^{A\varphi} &= 2a_{11}q^{(1)}(0)\overline{q}^{(1)}(0) + a_{12}(q^{(1)}(0)\overline{q}^{(2)}(0) + \overline{q}^{(1)}(0)q^{(2)}(0)), \\
 B_{21}^{A\varphi} &= 2a_{21}q^{(1)}(-1)\overline{q}^{(1)}(-1) + a_{22}(q^{(1)}(-1)\overline{q}^{(2)}(0) + \overline{q}^{(1)}(-1)q^{(2)}(0)) \\
 &\quad + a_{23}(q^{(1)}(-1)\overline{q}^{(2)}(-1) + \overline{q}^{(1)}(-1)q^{(2)}(-1)) + a_{24}(q^{(2)}(-1)\overline{q}^{(2)}(0) + \overline{q}^{(2)}(-1)q^{(2)}(0)).
 \end{aligned}$$

A comparison of the coefficients of equations (4.48) and (4.53) gives the following equalities :

$$H_{20}(\theta) = \begin{cases} -gq(\theta) - \overline{gq}(\theta) & \text{if } -1 \leq \theta < 0, \\ -gq(\theta) - \overline{gq}(\theta) + 2\tau_0 A & \text{if } \theta = 0. \end{cases} \quad (4.55)$$

$$H_{11}(\theta) = \begin{cases} -gq(\theta) - \overline{gq}(\theta) & \text{if } -1 \leq \theta < 0, \\ -gq(\theta) - \overline{gq}(\theta) + \tau_0 B & \text{if } \theta = 0. \end{cases} \quad (4.56)$$

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When we substitute (4.54) in (4.50) and (4.55) in (4.51) respectively, we obtain the following differential equations :

$$\begin{cases} \dot{W}_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{20}\bar{q}(\theta), \\ \dot{W}_{11}(\theta) = g_{11}q(\theta) + \bar{g}_{11}\bar{q}(\theta), \end{cases} \quad (4.57)$$

which have the following solutions :

$$\begin{cases} W_{20}(\theta) = \frac{ig_{20}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{\bar{g}_{02}}{3i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + E_{1A\varphi}e^{2i\tau_0\omega_0\theta}, \\ W_{11}(\theta) = \frac{g_{11}}{i\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + E_{2A\varphi}, \end{cases} \quad (4.58)$$

where $E_{1A\varphi} = (E_{1A\varphi}^{(1)}, E_{1A\varphi}^{(2)})^T$ and $E_{2A\varphi} = (E_{2A\varphi}^{(1)}, E_{2A\varphi}^{(2)})^T$ are constant vectors belonging to \mathbb{R}^2 .

Now, let us compute the constant vectors $E_{1A\varphi}$ and $E_{2A\varphi}$ by using (4.50) and (4.51). We have

$$\int_{-1}^0 d\eta(\theta)W_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(0) - H_{20}(0), \quad (4.59)$$

and

$$\int_{-1}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0). \quad (4.60)$$

Then, using the fact that,

$$\begin{aligned} \left(i\tau_0\omega_0 I - \int_{-1}^0 e^{i\tau_0\omega_0\theta} d\eta(\theta) \right) q(0) &= 0, \\ \left(-i\tau_0\omega_0 I - \int_{-1}^0 e^{-i\tau_0\omega_0\theta} d\eta(\theta) \right) \bar{q}(0) &= 0, \end{aligned}$$

and, using the first equation of (4.57), equations (4.53) and (4.58), we have :

$$\left(2i\tau_0\omega_0 I - \int_{-1}^0 e^{2i\tau_0\omega_0\theta} d\eta(\theta) \right) E_1 = 2\tau_0 \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix}$$

which implies $\begin{pmatrix} 2i\omega_0 - A_{A\varphi} & -B_{A\varphi} \\ -C_{A\varphi}e^{-2i\tau_0\omega_0} & 2i\omega_0 - D_{A\varphi}e^{-2i\tau_0\omega_0} \end{pmatrix} \begin{pmatrix} E_{1A\varphi}^{(1)} \\ E_{1A\varphi}^{(2)} \end{pmatrix} = 2 \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix}$

and finally

$$\begin{cases} E_{1A\varphi}^{(1)} = \frac{2B_{A\varphi}A_{21}^{A\varphi} + 2A_{11}^{A\varphi}(2i\omega_0 - D_{A\varphi}e^{-2i\tau_0\omega_0})}{(A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi})e^{-2i\tau_0\omega_0} - 2i\omega_0D_{A\varphi}e^{-2i\tau_0\omega_0} - 2i\omega_0A_{A\varphi} - 4\omega_0^2}, \\ E_{1A\varphi}^{(2)} = \frac{2A_{11}^{A\varphi}C_{A\varphi}e^{-2i\tau_0\omega_0} + 2A_{21}^{A\varphi}(2i\omega_0 - A_{A\varphi})}{(A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi})e^{-2i\tau_0\omega_0} - 2i\omega_0D_{A\varphi}e^{-2i\tau_0\omega_0} - 2i\omega_0A_{A\varphi} - 4\omega_0^2}. \end{cases} \quad (4.61)$$

Similarly, using the second equation of (4.57), (4.55) and (4.59), gives :

$$\left(\int_{-1}^0 e^{-i\tau_0\omega_0\theta} d\eta(\theta) \right) E_{2A\varphi} = \tau_0 \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix} \Rightarrow \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} E_{2A\varphi}^{(1)} \\ E_{2A\varphi}^{(2)} \end{pmatrix} = - \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix},$$

and finally

$$\begin{cases} E_{2A\varphi}^{(1)} = \frac{B_{A\varphi}B_{21}^{A\varphi} - D_{A\varphi}B_{11}^{A\varphi}}{A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi}}, \\ E_{2A\varphi}^{(2)} = \frac{C_{A\varphi}B_{11}^{A\varphi} - A_{A\varphi}B_{21}^{A\varphi}}{A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi}}. \end{cases} \quad (4.62)$$

Finally, from (4.57), (4.59) and (4.61) we can now calculate values which are useful for the determination of the period of the bifurcating solution and its stability. We have the following values:

$$\begin{aligned} C_1(0) &= \frac{i}{2\tau_0\omega_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{1}{2}g_{21}, \\ \mu_2 &= -\frac{ReC_1(0)}{Re\left(\frac{d\lambda}{d\tau}(\tau_0)\right)}, \\ \beta_2 &= 2ReC_1(0), \\ T_2 &= -\frac{Im(C_1(0)) + \mu_2 Im\left(\frac{d\lambda}{d\tau}(\tau_0)\right)}{\tau_0\omega_0}. \end{aligned}$$

The following result gives us a description of the Hopf bifurcating periodic solutions of equations (4.11)-(4.12)

Theorem 4.6.

- (a) The sign of μ_2 determines the direction of the Hopf bifurcation. If $\mu_2 > 0$, then the Hopf bifurcation is supercritical. If $\mu_2 < 0$, then the Hopf bifurcation is subcritical.
- (b) The sign of β_2 determines the stability of the bifurcating periodic solutions. If $\beta_2 > 0$, then the bifurcating periodic solutions are unstable. If $\beta_2 < 0$, then the bifurcating periodic solutions are stable.
- (c) T_2 determines the period of the bifurcating periodic solutions. If $T_2 > 0$, then the period increases. If $T_2 < 0$, then period decreases.

4.8 Numerical simulations

In this section, some numerical simulations are provided in order to illustrate our theoretical analysis and also to support our discussion. The values of the parameters $r_1, r_2, \alpha_1, \alpha_A, K_1, K_A$ and q are those which have been used for Fig.4.1 in ([3]). We recall that initial conditions values $x(0)$ and $y(0)$ must satisfy (4.14) and (4.15) respectively. For our numerical treatments, we consider parameter values summarized in Table 4.2. Note that for the cases without harvesting, we have used $h = 0$ and for the impact of refuge strength m , preference rate q and harvesting limit value h , we have used some other values of those parameters.

Table 4.2: Parameter values for the Leslie-Gower predator-prey model (4.11)-(4.12)

Parameter	Value	Reference
r_1	2	M. T. Alves (2013) [3]
r_2	1.5	M. T. Alves (2013) [3]
λ_1	5	Assumed
α_1	0.8	M. T. Alves (2013) [3]
h	1	Assumed
T_1	2	Assumed
α_A	1.2	M. T. Alves (2013) [3]
K_1	3	M. T. Alves (2013) [3]
K_A	3	M. T. Alves (2013) [3]
q	0.7	M. T. Alves (2013) [3]
m	0.7	Assumed

In figure 4.2, we have the bifurcation diagram and phase portraits of system (4.11)-(4.12) without the time delay and without harvesting. We are interested in the effects of the prey refuge strength m and the preference rate q on the dynamic of system (4.11)-(4.12) without the time delay. For some values of m and q , it is possible to have either the extinction of the prey population or the coexistence of the prey and predator populations.

4.8. Numerical simulations

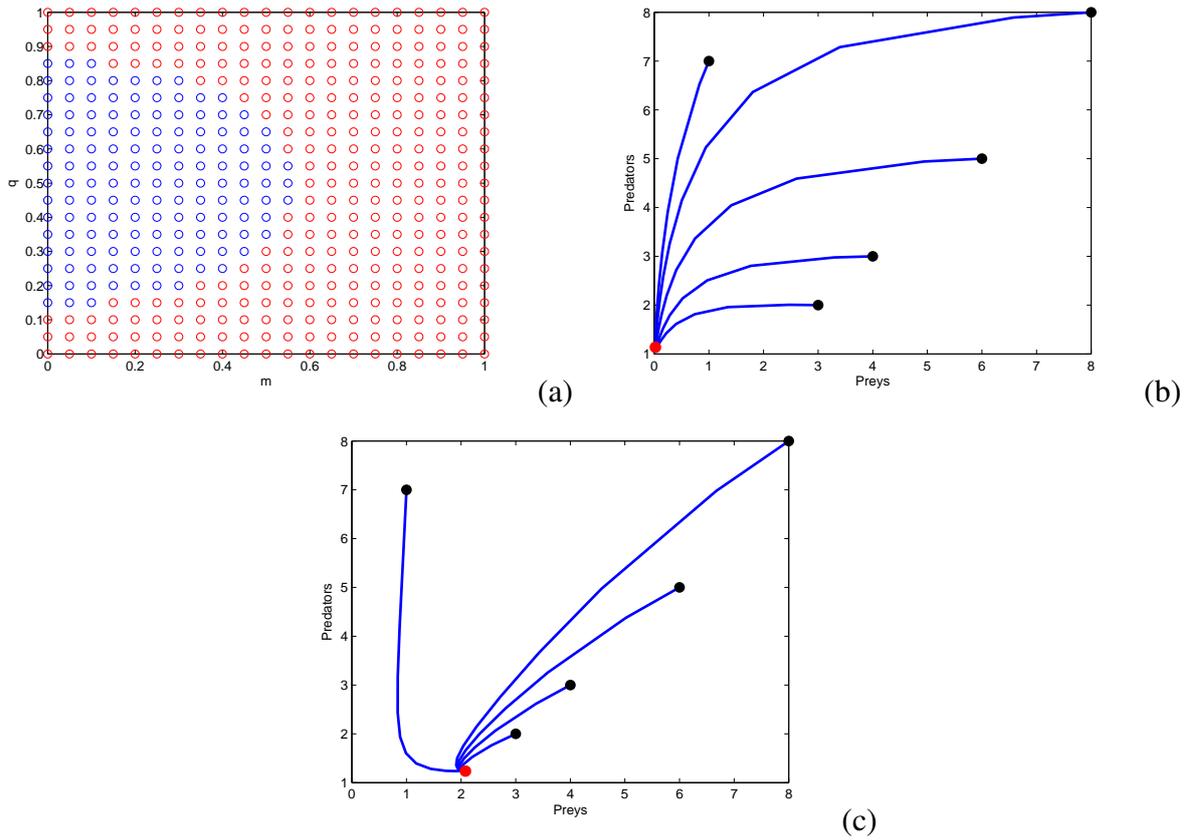


Figure 4.2: (a) Bifurcation diagram of the system (4.11)-(4.12) without harvesting and when the time delay $\tau = 0$. The red circles mean that the prey-free equilibrium E_2^0 is unstable for the corresponding values of the parameter m and q . For those values of m and q , the coexisting equilibrium E_4^0 exists and is locally asymptotically stable. The blue circles mean that the prey-free equilibrium E_2^0 is locally asymptotically stable for the corresponding values of the parameter m and q . For those values of m and q , the coexisting equilibrium E_4^0 doesn't exist. (b) Phase portrait of system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.3$, $q = 0.7$. The prey-free equilibrium $E_2^0(0; 1.08)$ is locally asymptotically stable. (c) Phase portrait of system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$. The coexisting equilibrium $E_4^0(2.016; 1.2494)$ is locally asymptotically stable. Black bullets denote the initial data while the red bullet denotes the equilibrium.

In figure 4.3, we have the bifurcation diagram and phase portraits of system (4.11)-(4.12) without the time delay, with and without harvesting. We are interested in the effects of prey refuge strength m and the limit value of harvesting h on the dynamic of system (4.11)-(4.12) without the time delay. For a fixed value on the preference rate q and for some values of m and h , it is possible to have either the extinction of the prey population or the coexistence of the prey and predator populations.

4.8. Numerical simulations

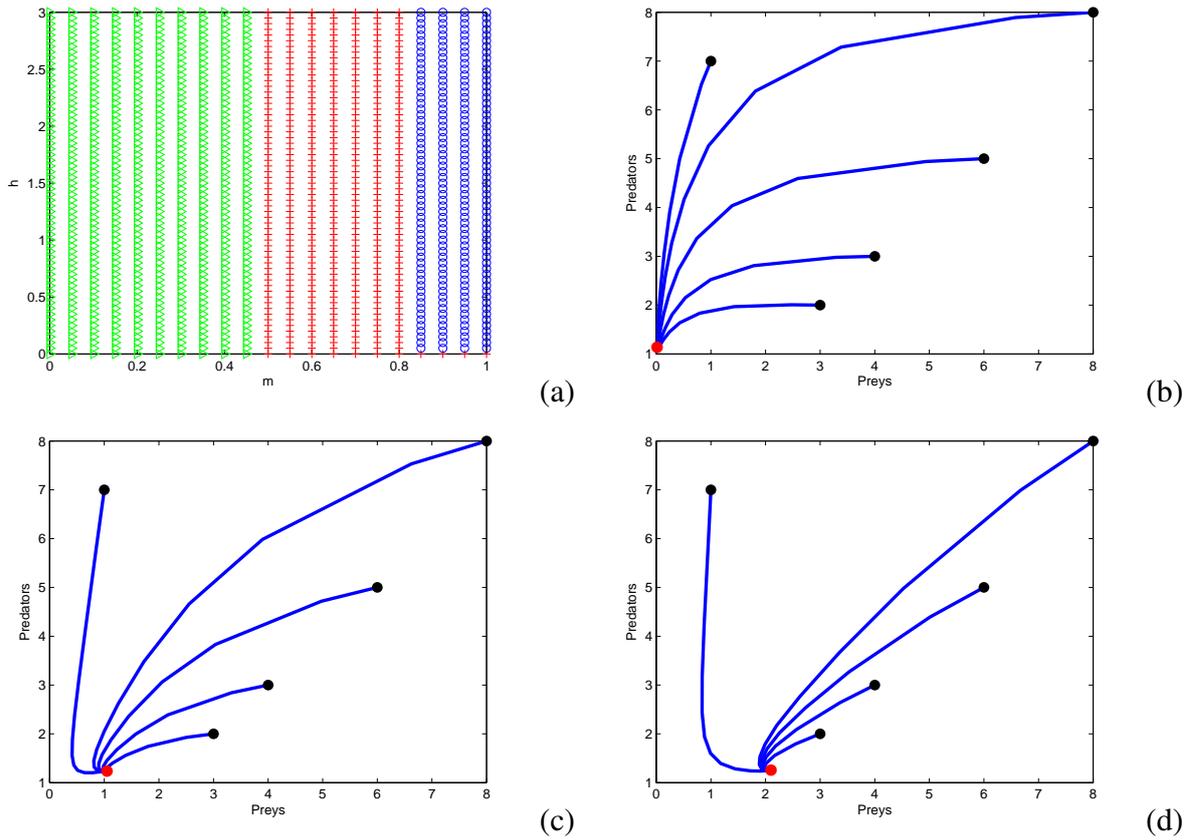


Figure 4.3: (a) Bifurcation diagram of system (4.11)-(4.12) with harvesting and when the time delay $\tau = 0$. The green triangle means that the system (4.11)-(4.12) doesn't have a coexisting equilibrium but the prey-free equilibrium E_2^0 of the model without harvesting exists and is locally asymptotically stable. The red plus means that the system (4.11)-(4.12) doesn't have a coexisting equilibrium but the coexisting equilibrium E_4^0 of the model without harvesting exists and is locally asymptotically stable. The blue circle means that the system (4.11)-(4.12) has one coexisting equilibrium E_2^φ which is locally asymptotically stable. (b) Phase portrait of system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.3$, $q = 0.7$ et $h = 1$. (c) Phase portrait of the system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.7$, $q = 0.7$ and $h = 1$. (d) Phase portrait of system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$ and $h = 1$. Black bullets denote the initial data while the red bullet denotes the equilibrium.

In figure 4.4, we have the phase portraits of system (4.11)-(4.12) without and with the time delay. We are interested in the effect of the time delay on the dynamic of system (4.11)-(4.12). Panel (b) illustrates the fact that when the time delay $\tau = 0.8 < \tau_0 = 1.0088$, the coexisting equilibrium $E_2^\varphi(2.0095; 1.2488)$ is always stable. Thus for this case, the time delay doesn't have any effect on the stability of the equilibrium. Panel (c) is an illustration of the existence of a Hopf bifurcation for the critical value $\tau_0 = 1.0088$ of the time delay. We have a stable subcritical bifurcating periodic solution around the coexisting equilibrium $E_2^\varphi(2.0095; 1.2488)$ ($\beta_2 = 0.7056$, $\mu_2 = -0.5078$, $T_2 = 2.8505$). With panel (d), one can see that for the value $\tau = 1.5 > \tau_0 = 1.0088$, the coexisting equilibrium become unstable. So for those values of the time delay τ , the coexisting equilibrium

4.8. Numerical simulations

$E_2^\varphi(2.0095; 1.2488)$ is destabilized.

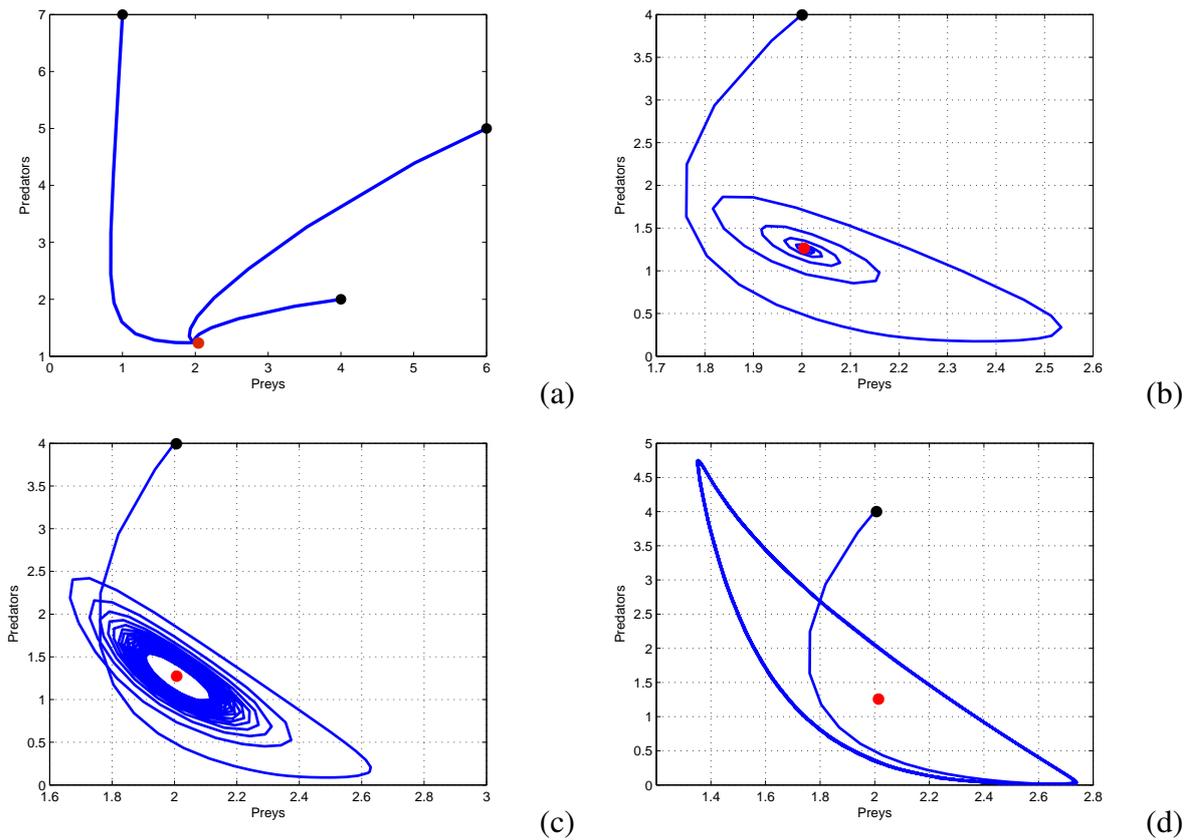


Figure 4.4: (a) Phase portrait of the system (4.11)-(4.12) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$ and $h = 1$. (b) Phase portrait of the system (4.11)-(4.12) when the time delay $\tau = 0.8$, $m = 0.85$, $q = 0.7$ and $h = 1$. (c) Phase portrait of the system (4.11)-(4.12) when the time delay $\tau = 1.0088$, $m = 0.85$, $q = 0.7$ and $h = 1$. (d) Phase portrait of the system (4.11)-(4.12) when the time delay $\tau = 1.5$, $m = 0.85$, $q = 0.7$ and $h = 1$. Black bullets denote the initial data while the red bullet denotes the equilibrium.

Table 4.3: values of x_2^φ and y_2^φ for system (4.11)-(4.12) for $m = 0.7$ and $h = 1$

value of q	x_2^φ	y_2^φ
0.1	2.6308	3.3031
0.2	2.5253	3.0012
0.3	2.4467	2.6961
0.4	2.3930	2.3897
0.5	2.3623	2.0834
0.6	2.3532	1.7788
0.7	2.3650	1.4773
0.8	2.3972	1.1802
0.9	2.4498	0.8891

According to Table 4.3, one can see that when the preference rate q increases, the number of predators at the coexisting equilibrium of system (4.11)-(4.12) always decreases while we have a fluctuation of the number of preys. The number of preys decreases up to a value of the preference rate q and begin to increase after that value.

4.9 Conclusion

In this chapter, we have incorporated a time delay, a continuous threshold policy harvesting of preys and a refuge of preys in a Leslie-Gower predator-prey model with additional fixed food . The theoretical analysis shows that when the threshold and the harvesting limit value satisfy a condition depending on the preference rate of predators, the carrying capacity of the additional fixed food, the refuge strength of preys, there always exists a coexistence equilibrium for the studied model. Considering the time delay as a bifurcation parameter, it has been shown that there exists a critical values of the time delay depending on the threshold of harvesting and the rate of harvesting, the preference rate, the carrying capacity of the additional fixed food. For those critical values of the time delay, a Hopf bifurcation occurs around the coexistence equilibrium and for the values of the time delay greater than that critical value, the coexistence equilibrium becomes unstable. An application of the normal form theory and the center manifold theorem allowed us to study the stability and determine the direction of the bifurcating periodic solutions. So the time delay as effect on the stability of the system around the coexistence equilibrium. We also remark that increasing the preference rate of predators decreases the numbers of predators but does not reach to extinction while the number of preys decreases firstly and increases after. By using a bifurcation diagram, we also observe that the existence and the stability of equilibria of the system without time delay depend on the refuge strength, the preference rate and the harvesting limit value. According to our theoretical analysis, we can conclude that quantitatively, taking into account harvesting increases the number of equilibria with at least one more coexistence equilibrium which can be stable.

GENERAL CONCLUSION

On earth, almost all single species lives with interacting with other species. It is the particular case of predator-prey interactions. Using mathematical methods of modelling, Vito Volterra and A. J. Lotka has formulated a mathematical model for interactions between predators and their preys. Their model has been modified by several authors with many different functional responses for the number of preys eaten by the predator per unit of time. Many other predator-prey models including two different types of prey refuges, additional fixed food for predators, four different types of harvesting of preys, predators or both species, discrete time delay(s) have been formulated from the basic Lotka-Volterra predator-preys models. In this thesis, I have given a non-exhaustive list of functional responses, some models with each of those functional responses, some models taking into account the two different types of preys refuge, models with additional food, models with harvesting and models with discrete time delay with different functional responses. It has been seen that formulating models including assumptions in order to be close to the reality can be sometimes easily done but, one of the problem after the formulation of those models is their theoretical analysis (stability or bifurcation) with mathematical tools. For all the models presented in the literature review of our thesis, theoretical analysis reveal very rich, complex, interesting conclusions and results on effects of prey refuges, functional responses, harvesting of species, discrete time delay and additional fixed food.

Among modified Lotka-Volterra predator-prey models, we have those particular predator-prey models named Leslie-Gower models. They are particular for reasons as the non-respect of the principle of the biomass conversion, the carrying capacity of the predator which is proportional to the preys population. Our brief literature review on Leslie-Gower predator-prey models has revealed that modified Leslie-Gower predator-prey models formulated with harvesting of species, don't use harvesting functions with threshold(s), some of those models with harvesting don't study the problem of optimal harvesting and, even when those modified models incorporate discrete time delay(s), the problem of the direction and the stability of the bifurcating solution is not always solved. In the third chapter of this these, we have formulated a Leslie-Gower predator-prey model incorporating continuous harvesting function with two thresholds, prey refuge and discrete time delay for the dynamic of the predator population. Preliminaries concerning the positivity and the boundedness have been done for biological reasons. We have done the stability analysis of the newly formulated model, when the discrete time delay is not taken into account, after a laborious work on the determination of equilibria of the

model without the discrete time delay. Because the stability of equilibria of the model with discrete time delay depends to that of the same equilibria for the model without discrete time delay, due to the fact, an unstable equilibrium for the model without the time delay remains unstable for the model with discrete time delay, we have studied the stability of only stable equilibria of the non-delayed model. We have showed that, under sufficient conditions on the parameters, the delay-induced system is asymptotically stable around the positive equilibrium for all values of the delay parameter and if the conditions are not satisfied, then there exists a critical value of the delay parameter below which the system is stable and above which the system is unstable. We conclude that the discrete time delay have a destabilizing effect on the model. Considering the discrete time delay as the bifurcation parameter, we have done a bifurcation analysis of our model. We have showed the existence of critical values of the discrete time delay such that when the delay passes through one of those critical values, the coexisting equilibrium losses its stability and a Hopf bifurcation occurs. By applying the normal form theory and the center manifold theorem, the explicit formulae for the stability and direction of the bifurcating periodic solutions have been determined. We have also solved the problem of optimal harvesting policy by using the new result of retarded optimal control which is an extension of Pontryagin's Maximal principle theory.

In the fourth and last chapter of our thesis, another modified Leslie-Gower predator-prey model incorporating additional fixed food for predators, discrete time delay in the predator equation, refuge and continuous threshold (with one delay) harvesting of preys has been formulated and studied. For biological reasons, we have proved that solutions of our model are always positive and uniformly bounded. Through a discussion based on the parameters of the newly formulated model, we have studied the existence and the stability of equilibria of the model without the discrete time delay. We have studied effects of the prey refuge, harvesting, additional fixed food using respectively the strength of refuge, the limit value of preys harvesting and the preference rate of the predator. With the help of some bifurcation diagrams, we obtained that different scenarios for the model including elimination of one species or competition of both species are possible. We also remark that increasing the preference rate of predators decreases the number of predators but does not reach to extinction while the number of preys decreases firstly and increases after. Considering the time delay as a bifurcation parameter, we have shown the existence of critical values of the time delay depending on the threshold of harvesting and the rate of harvesting, the preference rate, the carrying capacity of the additional fixed food. For those critical values of the discrete time delay, a Hopf bifurcation occurs around the coexistence equilibrium and for the values of the time delay greater than those critical values, the coexistence equilibrium becomes unstable. So the discrete time delay has a destabilizing effect on the model. Applying the normal form theory and the center manifold theorem, we obtained the stability and the direction of the bifurcating periodic solutions.

Perspectives

In this thesis, we have seen with our formulated models and all the models incorporating discrete time delay(s) formulated by many others authors, for Lotka-Volterra predator-prey models type or Leslie-Gower predator-prey models, that discrete time delay(s) can have effects as destabilizing an equilibrium of the models. In the model formulated and studied in the third and fourth chapters of our thesis, a discrete time delay has been incorporated in the predators equation for the predator dynamic. Those models can be modified by incorporating a discrete time delay in the preys equation (in the growth function of preys for example) for the dynamic of the prey population. We shall then have a model with two discrete time delays and investigate effects of those discrete time delays.

It is well known that the choice of the functional response is very important for a model formulation, because it has been proved that the functional response can induce effects on a model. So, our formulated model can be modified by replacing the Lotka-Volterra functional response used in the models by any other functional response of Holling type or not. It is possible to obtain results and conclusions on effects of the functional response.

The model formulated in the last chapter incorporates fixed food for predators. Due to the fact that it is also possible to provide predators with dynamic additional food, one can formulate a model assuming that predators are provided with dynamic additional food, in order to study effects of that additional food and even, make a comparison with results of the model with additional fixed food. If it is assumed that there is incorporation of dynamic food for predators, harvesting of one of the species or both species, discrete time delay(s), it is possible to formulate many others interesting models very close to the existing reality.

Due to the fact that species (predators and preys) can move from one area to another, it can be more realistic to formulate and study spatio-temporal predator-prey models by modifying the models formulated in our thesis, in order to study effects of taking into account the spatial aspect.

The models formulated and studied in our thesis can be reformulated with the assumption of mature and immature preys among the prey population. It is then possible to formulate the so-called staged structured models and look for effects of taking into account the presence of mature and immature preys.

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OPTIMAL HARVESTING AND STABILITY ANALYSIS IN A LESLIE-GOWER DELAYED PREDATOR-PREY MODEL

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Abstract. A delayed Leslie-Gower predator-prey model with continuous threshold prey harvesting is studied. Existence and local stability of the positive equilibrium of the system with or without delay are completely determined in the parameter plane. Considering delay as parameter, we investigate the effect of delay on stability of the coexisting equilibrium. It is observed that there are stability switches and a Hopf bifurcation occurs when the delay crosses some critical values. Employing the normal form theory, the direction and stability of the Hopf bifurcations are explicitly determined by the parameters of the system. Optimal harvesting is also investigated and some numerical simulations are given to support and extend our theoretical results.

Keywords: harvesting; Hopf bifurcation; retarded optimal control; stability analysis.

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1. INTRODUCTION

Leslie has introduced a predator-prey model [1], including support capability that the environment provides predators is proportional to the number of prey. Leslie advances that the growth rate of predators and preys admits an upper limit which can be approached under certain conditions: for the predator when the number of prey is high, for the prey when predator numbers (can be also the number of prey) is low [1, 2]. The Leslie-Gower term means in absence of preys, the predators have an oscillatory behavior.

There are many predator-prey models in the literature with Leslie-Gower term or a modified Leslie-Gower term and Holling type II functional response [3, 5–8, 11–13]. Some of them analyze bifurcations [3,4, 14], persistence [9] or seasonally varying parameters [10]. The Leslie-Gower predator-prey model has not yet been analyzed as in this paper, considering optimal harvest and response function of type III.

Profit, over-exploitation and extinction of a species being harvested are primary concerns in ecology and commercial harvesting industries. Thus, current research incorporates a harvesting component in mathematical models to study the effects it has on one or multiple species. This has attracted interest from the commercial harvesting industry and from many scientific communities including biology, ecology, and economics.

Most predator-prey models in the literature consider either constant or linear harvesting functions [15, 16, 19, 20]. Recently, Tchinda et al., Tankam et al. [21, 23] considered a system of delay differential equations modeling the predator-prey dynamics with continuous threshold prey harvesting and Holling response function of type III. In [21], the model system was given by

$$(1) \quad \begin{cases} \dot{x}(t) = \varphi(x(t)) - my(t)p(x(t)) - H(x(t)), \\ \dot{y}(t) = [-d + cmp(x(t - \tau))]y(t), \end{cases}$$

where $x(t)$ and $y(t)$ represent the population of preys and predators at time t respectively. The parameter d is the natural mortality rate of predators. Parameters c and m are positive constants. The function

$$(2) \quad \varphi(x) = rx \left(1 - \frac{x}{K}\right)$$

models the behavior of preys in absence of predators, where r denote the growth rate of preys when x is small, and K is the capacity of the environment to support the preys. The functions $H(x)$ and $p(x)$ which are the harvesting function of the preys and the response function of predators to preys respectively, are defined by

$$(3) \quad H(x) = \begin{cases} 0 & \text{if } x < T, \\ \frac{h(x-T)}{h+x-T} & \text{if } x \geq T, \end{cases}$$

and

$$(4) \quad p(x) = \frac{x^2}{ax^2 + bx + 1},$$

where a is a positive constant and b is a nonnegative constant. This function is one of potential response function of predators to preys, modeling the consumption of preys by predators. It reflects very small predation when the number of preys is small ($p'(0) = 0$), and a group of advantage for the preys when the number of prey is high ($p(x)$ tends to $\frac{1}{a}$ when x tends to infinity). For the harvesting function, T is the threshold value. In this way, once the prey population reaches the size $x = T$, then harvesting starts and increases smoothly to a limit value h . Here, a time delay τ is in the predator response term $p(x(t))$ in the predator equation. This delay can be regarded as a gestation period or reaction time of the predators.

In [23], System (1) has been investigated, but with a piecewise linear threshold policy harvesting given by

$$(5) \quad H(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x-T_1)}{T_2-T_1} & \text{if } T_1 \leq x \leq T_2, \\ h & \text{if } x \geq T_2. \end{cases}$$

This piecewise linear threshold policy harvesting has been previously introduced in [22] in a predator prey model without delay where a Holling response function of type II was considered.

In these models, global qualitative and bifurcation analysis are combined to determine the global dynamics of the model. But, note that, all these models do not take into account the fact that reduction in a predator population has a reciprocal relationship with per capita availability of its preferred food. This assumption leads the Leslie- Gower formulation.

On the other hand, time delay plays an important role in many biological dynamical systems, being particularly relevant in ecology, where time delays have been recognized to contribute critically to the stable or unstable outcome of prey densities due to predation. The introduction of time delay into the population model is more realistic to model the interaction between the predator and prey populations and the population models with time delay are of current research interest in mathematical biology [29,31]. There is extensive literature about the effects of delay on the dynamics of predator-prey models.

In this paper, we consider a delayed Leslie-Grower predator-prey model both with refuge and the piecewise linear threshold policy harvesting given by Eq. (5). The Leslie-Gower formulation is based on the assumption that reduction in a predator population has a reciprocal relationship with per capita availability of its preferred food. Indeed, Leslie introduced a predator-prey model where the carrying capacity of the predator environment is proportional to the number of prey [1, 2]. He stresses the fact that there are upper limits to the rates of increase of both prey x and predator y , which are not recognized in the Lotka-Volterra model.

This paper is organized as follows. In the Section 2, we give a description of the model. In Section 3, some preliminary results on the boundedness of solutions for System (6) when Eq.(5) are given. Existence and unicity of equilibria are investigated. Section 4 deals with the linear stability analysis of the model system with and without time delay. In Section 5, direction and stability of Hopf bifurcation are presented. In Section 6, optimal harvest policy of population model is derived. Numerical results to illustrate the analytical findings are presented in Section 7 and, finally, a summary is presented in Section 8.

2. THE MODEL

It is well known that time delay can play an important role in biological dynamical systems, where it has been recognized to contribute critically to the stable or unstable outcome of prey densities due to predation. Therefore, let us analyze the following delayed predator-prey model:

$$(6) \quad \begin{cases} \dot{x}(t) &= (r_1 - b_1 x(t))x(t) - a_1(1-m)x(t)y(t) \\ &- H(x(t)), \\ \dot{y}(t) &= \left[r_2 - \frac{a_2 y(t-\tau)}{(1-m)x(t-\tau)} \right] y(t), \end{cases}$$

where $x(t)$ denotes the Prey population at time t and $y(t)$ the Predator population at time t . All parameters are positive and m is such that $0 \leq m < 1$. This parameter is the rate of refuge of prey population. This means that when $m = 0$, all preys are available for predation. $m x(t)$ models the capacity of a refuge at time t and so refuge protecting $m x(t)$ of the prey population. It therefore remains $(1-m)x(t)$ of the preys available for predation. Parameters r_1 and r_2 are the intrinsic growth rate of the preys and predators respectively, a_1 denotes the predation rate per unit of time, $\frac{r_1}{b_1}$ is the carrying capacity of the prey's environment and $\frac{r_2}{a_2} x(t)$ is the carrying capacity of the predator's environment which is proportional to the number of prey. Here, we incorporate a single discrete delay $\tau > 0$ in the negative feedback of the predator's density.

Let us denote by \mathbb{R}_2^+ the nonnegative quadrant and by $\text{int}(\mathbb{R}_2^+)$ the positive quadrant. For $\theta \in [-\tau, 0]$, we use the following conventional notation:

$$x_t(\theta) = x(t + \theta).$$

Then the initial conditions for this system take the form

$$(7) \quad \begin{cases} \dot{x}_0(\theta) &= \phi_1(\theta), \\ \dot{y}_0(\theta) &= \phi_2(\theta), \end{cases}$$

for all $\theta \in [-\tau, 0]$, where $(\phi_1, \phi_2) \in C([-\tau, 0], \mathbb{R}_+^2)$, $x(0) = \phi_1(0) > 0$ and $y(0) = \phi_2(0) > 0$.

For ecological reason, as in [23], we make the following assumption. We assume that:

- : (i) $0 < x(0) \leq \frac{r_1}{b_1} \equiv K$;
- : (ii) $T_1 < T_2 < K$.

In fact, the first assumption comes from the fact that it is not plausible to have an initial value of the preys $x(0)$ at time $t = 0$ which is greater than the carrying capacity K of the preys. Moreover if $T_1 = T_2$, then the harvesting function becomes a discrete harvesting. In other hand,

if we assume $T_2 \geq K$, then we will not have some harvest after T_2 since the first assumption leads to $0 \leq x(t) \leq K$.

3. PRELIMINARY RESULTS

3.1. Boundedness of solutions. We start by showing that solutions of System (6) and System (5) that start in \mathbb{R}_+^2 will remain there and are uniformly bounded. Indeed, we have the following theorem.

Theorem 1. : *Let Assumption 2-(i) holds. Then, every solution of System (6) that starts in \mathbb{R}_+^2 will remain there and is uniformly bounded.*

Proof. : Let $(x_0, y_0) \in \mathbb{R}_+^2$ be given and let us denote for each $t \geq 0$, $(x(t), y(t))$ the orbit of System (6) passing through (x_0, y_0) at $t = 0$. Then, we can find that $(x(t), y(t)) \in \mathbb{R}_+^2$ for all $t \geq 0$. Thus, every solution of System (1) that starts in \mathbb{R}_+^2 will remain there. From the \dot{x} -equation of System (6), we have

$$\dot{x}(t) \leq (r_1 - b_1 x(t))x(t).$$

Applying a differential inequality [28] gives

$$x(t) \leq \frac{1}{\frac{b_1}{r_1} + \left(\frac{1}{x(0)} - \frac{b_1}{r_1} \right) e^{-r_1 t}}$$

for all $t \geq 0$. Since $0 < x(0) \leq \frac{r_1}{b_1}$ from Assumption 2-(i), it follows that $x(t) \leq \frac{r_1}{b_1}$ for all $t \geq 0$. Now, let us check for the boundedness of $y(t)$.

From the predator equation, we have $\dot{y}(t) \leq r_2 y(t)$. Hence, for $t > \tau$, $y(t) \leq y(t - \tau) e^{r_2 \tau}$. This equation is equivalent for $t > \tau$, to

$$(8) \quad y(t - \tau) \geq y(t) e^{-r_2 \tau}.$$

Moreover, for any $\delta > 1$, there exists a positive T_δ such that for $t > T_\delta$, $x(t) < \delta \frac{r_1}{b_1}$. Eq.(8) gives for $t > T_\delta + \tau$,

$$\dot{y}(t) < y(t) \left(r_2 - \frac{a_2 e^{-r_2 \tau}}{\delta(1-m) \frac{r_1}{b_1}} y(t) \right),$$

which implies, by the same arguments use for x , that $\limsup_{t \rightarrow +\infty} y(t) < \frac{r_2}{a_2 \delta(1-m) \frac{r_1}{b_1} e^{r_2 \tau}}$. The conclusion of this lemma holds for $\delta \rightarrow 1$. \square

3.2. Equilibria of the model. In this section we analyze some equilibria properties of System (6)-(5). These steady states, which are determined analytically by setting $\dot{x} = \dot{y} = 0$, are independent of the delay τ . The following results holds:

Proposition 1. : Let $K = \frac{r_1}{b_1}$, $b_0 = b_1 + \frac{r_2 a_1 (1-m)^2}{a_2}$, $K_0 = \frac{r_1}{b_0}$, $\varphi : x \mapsto (r_1 - b_1 x)x$ and $\varphi_0 : x \mapsto (r_1 - b_0 x)x$.

(1) System (6)-(5) has one or more equilibria with $y = 0$ (without predators).

- One equilibrium in $\mathbb{R}_+^* \times \{0\}$ under some conditions. More precisely,
 - if $\varphi(T_2) > h$, then $E_1(x_1, 0)$ is the unique equilibrium of the model with $x_1 \in \left[\frac{K}{2}, K\right]$ if $T_2 \leq \frac{K}{2}$, or $x_1 \in [T_2, K]$ if $T_2 \geq \frac{K}{2}$.
 - if $\varphi(T_2) \leq h$ and $T_2 \geq \frac{K}{2}$, then $\tilde{F}(\tilde{x}, 0)$ is the unique equilibrium of the model with $\tilde{x} \in [T_1, T_2]$.
- Two equilibria $\tilde{F}(\tilde{x}, 0)$ and $\tilde{E}\left(\frac{K}{2}, 0\right)$ in $\mathbb{R}_+^* \times \{0\}$, where $\tilde{x} \in [T_1, T_2]$ under the conditions $T_2 \leq \frac{K}{2}$, $\varphi(T_2) \leq h$ and $\varphi\left(\frac{K}{2}\right) = h$.
- Three equilibria $\tilde{F}(\tilde{x}, 0)$, $E_1(x_1, 0)$ and $E_2(x_2, 0)$ in $\mathbb{R}_+^* \times \{0\}$, where $\tilde{x} \in [T_1, T_2]$, $x_1 \in \left[\frac{K}{2}, K\right]$, $x_2 \in \left[T_2, \frac{K}{2}\right]$ under the conditions $T_2 \leq \frac{K}{2}$, $\varphi(T_2) \leq h$ and $\varphi\left(\frac{K}{2}\right) > h$.

(2) Under some conditions, System (6)-(5) has one or more coexistence equilibria.

- A unique equilibrium in these different cases:
 - if $K_0 < T_1$, then $G_0(K_0, y_0)$ is the equilibrium of the model.
 - if $K_0 \in [T_1, T_2]$, then $G(x^*, y^*)$ is the equilibrium of the model, with $x^* \in [T_1, T_2]$ and $y^* = \frac{r_2(1-m)x^*}{a_2}$.
 - if $K_0 \geq T_2$ and $\varphi(T_2) > h$, then $G_1(x_1^*, y_1^*)$ is the equilibrium of the model with $x_1^* \in [T_2, K_0]$ and $y_1^* = \frac{r_2(1-m)x_1^*}{a_2}$.
- Two equilibria $G(x^*, y^*) \in [T_1, T_2] \times \mathbb{R}_+^*$ and $\tilde{G}_0\left(\frac{K_0}{2}, \tilde{y}_0\right)$ when $\frac{K_0}{2} > T_2$, $\varphi_0(T_2) \leq h$ and $\varphi_0\left(\frac{K_0}{2}\right) = h$.
- Three equilibria $G(x^*, y^*) \in [T_1, T_2] \times \mathbb{R}_+^*$, $G_1(x_1^*, y_1^*) \in \left[\frac{K_0}{2}, K_0\right] \times \mathbb{R}_+^*$ and $G_2(x_2^*, y_2^*) \in \left[T_2, \frac{K_0}{2}\right] \times \mathbb{R}_+^*$ when $\frac{K_0}{2} > T_2$, $\varphi_0(T_2) \leq h$ and $\varphi_0\left(\frac{K_0}{2}\right) > h$.

Remark 1. : Concerning parameters K and K_0 , we always have $K_0 \leq K$.

Proof. : An equilibrium $S(x,y)$ of the model is solution of Eq.(9) when $x < T_1$, Eq. (10) when $T_1 \leq x \leq T_2$ and Eq. (11) when $x \geq T_2$, where

$$(9) \quad \begin{cases} (r_1 - b_1x)x - a_1(1-m)xy = 0, \\ \left[r_2 - \frac{a_2y}{(1-m)x} \right] y = 0, \end{cases}$$

$$(10) \quad \begin{cases} (r_1 - b_1x)x - a_1(1-m)xy - \frac{h(x-T_1)}{T_2-T_1} = 0, \\ \left[r_2 - \frac{a_2y}{(1-m)x} \right] y = 0, \end{cases}$$

and

$$(11) \quad \begin{cases} (r_1 - b_1x)x - a_1(1-m)xy - h = 0, \\ \left[r_2 - \frac{a_2y}{(1-m)x} \right] y = 0. \end{cases}$$

From the second equation of System (9), System (10) or System (11), we have $y = 0$ or $y = \frac{r_2(1-m)x}{a_2}$.

When $y = 0$, the equilibria $(0,0)$ and $\left(\frac{r_1}{b_1}, 0\right)$ exist on $[0, T_1[$. This is impossible since $\frac{r_1}{b_1} = K > T_1$. Moreover, we have the following equations,

$$(r_1 - b_1x)x - a_1(1-m)xy - \frac{h(x-T_1)}{T_2-T_1} = 0 \text{ on } [T_1, T_2],$$

and

$$(r_1 - b_1x)x - a_1(1-m)xy - h = 0 \text{ on } [T_2, K].$$

- On $[T_1, T_2]$, the identity at the equilibrium gives equation $-b_1x^2 + \left(r_1 - \frac{h}{T_2-T_1}\right)x + \frac{hT_1}{T_2-T_1} = 0$ which admits a unique positive solution.

Let us consider $f(x) = -b_1x^2 + \left(r_1 - \frac{h}{T_2-T_1}\right)x + \frac{hT_1}{T_2-T_1}$. Then $f(T_1) > 0$ and $f(T_2) = \varphi(T_2) - h$. Hence, if $\varphi(T_2) \leq h$, a unique solution exists on $[T_1, T_2]$.

- On $[T_2, K]$, the identity at the equilibrium gives equation $-b_1x^2 + r_1x - h = 0$. Its discriminant is

$$\Delta = r_1^2 - 4b_1h = 4b_1 \left(\varphi\left(\frac{K}{2}\right) - h \right).$$

Hence, if $\frac{K}{2} > h$, there are two positive solutions, which are both on $[T_2, K]$, when $T_2 < \frac{K}{2}$ and $\varphi(T_2) \leq h$. Besides, when $\varphi(T_2) > h$, just one of the solutions is on $[T_2, K]$.

Still according to the sign of the discriminant Δ , if $\varphi(\frac{K}{2}) = h$, $x = \frac{K}{2}$ is the unique solution on $[T_2, K]$ when $\frac{K}{2} \geq T_2$. There is no solution when $\frac{K}{2} < T_2$.

When $y \neq 0$, from the second equation of System (9), System (10) and System (11), we have $y = \frac{r_2(1-m)}{a_2}x$. Replacing it in the first equation gives $(r_1 - b_0x)x - H(x) = 0$. On $[0, T_1]$, the unique solution of this equation is $x = K_0$, which exists if and only if $K_0 \leq T_1$. Moreover, we have the following equations,

$$(r_1 - b_0x)x - \frac{h(x - T_1)}{T_2 - T_1} = 0 \text{ on } [T_1, T_2]$$

and

$$(r_1 - b_0x)x - h = 0 \text{ on } [T_2, K].$$

- On $[T_1, T_2]$, if $K_0 < T_1$, there is no equilibrium on $[T_1, T_2]$. Else, the identity at the equilibrium gives equation $-b_0x^2 + (r_1 - \frac{h}{T_2 - T_1})x + \frac{hT_1}{T_2 - T_1} = 0$ which admits a unique positive solution.

Let us consider $f_0(x) = -b_0x^2 + (r_1 - \frac{h}{T_2 - T_1})x + \frac{hT_1}{T_2 - T_1}$. Then $f_0(T_1) = b_0T_1(K_0 - T_1) > 0$ and $f_0(T_2) = \varphi_0(T_2) - h$. Hence, if $\varphi_0(T_2) \leq h$, a unique solution exists on $[T_1, T_2]$.

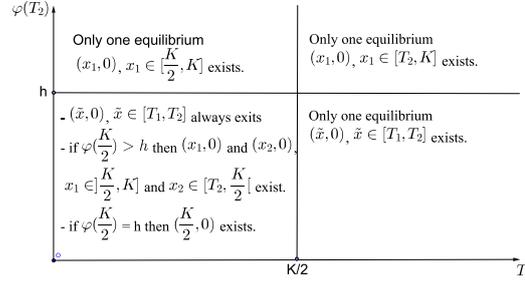
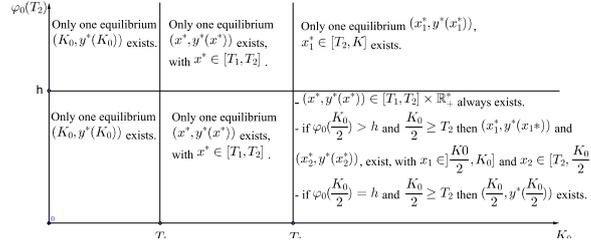
- On $[T_2, K]$, the identity at the equilibrium gives $-b_0x^2 + r_1x - h = 0$. Its discriminant is $\Delta_0 = r_1^2 - 4b_0h = 4b_0\left(\varphi_0(\frac{K_0}{2}) - h\right)$. Hence, when $\frac{K_0}{2} > h$, there are two positive solutions, which are both on $[T_2, K_0]$, when $T_2 < \frac{K_0}{2}$ and $\varphi_0(T_2) \leq h$. Besides, when $\varphi_0(T_2) > h$, just one of the solutions is on $[T_2, K]$ (particularly on $[T_2, K_0]$).

Still according to the sign of the discriminant, when $\varphi_0(\frac{K_0}{2}) = h$, $x = \frac{K_0}{2}$ is the unique solution on $[T_2, K]$ when $\frac{K_0}{2} \geq T_2$. There is no solution when $\frac{K_0}{2} < T_2$.

□

Remark 2. : We summarize the results about equilibria in Fig. 1 and Fig. 2.

4. STABILITY ANALYSIS

FIGURE 1. Existence and number of equilibria when $y = 0$.FIGURE 2. Existence and number of equilibria when $y \neq 0$ and $y^*(x^*) = \frac{r_2(1-m)x^*}{a_2}$.

4.1. Stability of equilibria when $\tau = 0$. The Jacobian matrix $J(x, y)$ of System (6) at the equilibrium (x, y) when $T_1 \leq x \leq T_2$, is given by

$$\begin{pmatrix} \varphi'(x) - \frac{h}{T_2 - T_1} - a_1(1-m)y & -a_1(1-m)x, \\ \frac{a_2 y^2}{(1-m)x^2} & r_2 - \frac{2a_2 y}{(1-m)x} \end{pmatrix}.$$

We notice that $r_2 \geq 0$ is always an eigenvalue of any equilibrium $E(x, 0)$, which is therefore unstable.

Concerning stability of any equilibrium $G(x^*, y^*)$ with $y^* \neq 0$, the following theorem holds.

Theorem 2. : Let consider

$$\Delta_1 = \left[\varphi'(x^*) - a_1(1-m)y^* - r_2 \right]^2 - 4 \left[2a_1(1-m)r_2 y^* - r_2 \varphi'(x^*) \right],$$

$$\Delta_2 = \left[\varphi'(x^*) - a_1(1-m)y^* - \frac{h}{T_2 - T_1} - r_2 \right]^2 - 4 \left[2a_1(1-m)r_2 y^* - r_2 \left[\varphi'(x^*) - \frac{h}{T_2 - T_1} \right] \right].$$

(1) Let consider an equilibrium $G(x^*, y^*)$ with $x^* \in [0, T_1 \cup T_2, K]$.

- If $\Delta_1 > 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1-m)y^* + r_2 > 0$ and $2a_1(1-m)r_2 y^* - r_2 \varphi'(x^*) > 0$.

- If $\Delta_1 = 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1-m)y^* + r_2 > 0$.
- If $\Delta_1 < 0$, then the equilibrium is a stable focus when $-\varphi'(x^*) + a_1(1-m)y^* + r_2 > 0$.
- If $-\varphi'(x^*) + a_1(1-m)y^* + r_2 = 0$ and $2a_1(1-m)r_2y^* - r_2\varphi'(x^*) > 0$, then the equilibrium is a center.

(2) Let consider an equilibrium $G(x^*, y^*)$ with $x^* \in [T_1, T_2]$.

- If $\Delta_2 > 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1-m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$ and $2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - \frac{h}{T_2 - T_1}) > 0$.
- If $\Delta_2 = 0$, then the equilibrium is a stable node when $-\varphi'(x^*) + a_1(1-m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$.
- If $\Delta_2 < 0$, then the equilibrium is a stable focus when $-\varphi'(x^*) + a_1(1-m)y^* + \frac{h}{T_2 - T_1} + r_2 > 0$.
- If $-\varphi'(x^*) + a_1(1-m)y^* + \frac{h}{T_2 - T_1} + r_2 = 0$ and $2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - \frac{h}{T_2 - T_1}) > 0$, then the equilibrium is a center.

Proof. : The Jacobian matrix $J(x^*, y^*)$ of System (6) at the equilibrium (x^*, y^*) becomes

$$\begin{pmatrix} \varphi'(x^*) - a_1(1-m)y^* - H'(x^*) & -a_1(1-m)x^* \\ r_2 \frac{y^*}{x^*} & -r_2 \end{pmatrix},$$

where $H'(x) = 0$ for $x \in [0, T_1 \cup T_2, K]$ and $H'(x) = \frac{h}{T_2 - T_1}$ for $x \in [T_1, T_2]$.

Therefore, the eigenvalues are given by the following equation:

$$(12) \quad \lambda^2 + \lambda \left[-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 \right] + 2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) = 0.$$

The discriminant of this equation is given by

$$\Delta = \left[\varphi'(x^*) - a_1(1-m)y^* - H'(x) - r_2 \right]^2 - 4 \left[2a_1(1-m)r_2y^* - r_2[\varphi'(x^*) - H'(x)] \right],$$

which is equal to Δ_1 on $[0, T_1 \cup T_2, K]$ and Δ_2 on $[T_1, T_2]$.

- When $\Delta > 0$, $J(x^*, y^*)$ has two positive eigenvalues which are both negatives if $-\varphi'(x^*) + a_1(1-m)y^* + H'(x^*) + r_2 > 0$ and $2a_1(1-m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) > 0$.

- When $\Delta = 0$, $J(x^*, y^*)$ has one positive eigenvalue which is negative if $-\varphi'(x^*) + a_1(1 - m)y^* + H'(x^*) + r_2 > 0$.
- When $\Delta < 0$, $J(x^*, y^*)$ has two conjugated complex eigenvalues with a positive real part equal to $\varphi'(x^*) - a_1(1 - m)y^* - H'(x^*) - r_2$.
- When $-\varphi'(x^*) + a_1(1 - m)y^* + H'(x^*) + r_2 = 0$ and $2a_1(1 - m)r_2y^* - r_2(\varphi'(x^*) - H'(x^*)) > 0$, $J(x^*, y^*)$ has pure imaginary eigenvalues.

Hence, the conclusions follow. \square

Remark 3. : *The importance of this section is due to the fact that, if an equilibrium of System (6)-(5) is unstable for $\tau = 0$, it remains unstable for $\tau > 0$ [24, 25]. Then, any equilibrium of System (6) in the form $E(x, 0)$ is unstable when $\tau > 0$. Concerning stability of equilibria when $\tau > 0$, we only consider the coexistence equilibria.*

4.2. Stability of coexistence Equilibria for $\tau > 0$ and Hopf Bifurcation. In order to analyze the stability of coexistence equilibria $G(x^*, y^*)$, let us define new variables $u(t) = x(t) - x^*$ and $v(t) = y(t) - y^*$. Then the linearization of System (6) at G gives

$$(13) \quad \begin{cases} \dot{u}(t) &= [r_1 - 2b_1x^* - a_1(1 - m)y^* - H'(x^*)]u(t) \\ &- a_1(1 - m)x^*v(t), \\ \dot{v}(t) &= -\Psi'(x^*)y^{*2}u(t - \tau) - r_2v(t - \tau), \end{cases}$$

where $H'(x^*) = 0$ for $x^* \in [0, T_1] \cup [T_2, K]$, $H'(x^*) = \frac{h}{T_2 - T_1}$ for $x^* \in [T_1, T_2]$ and $\Psi(x^*) = \frac{a_2}{(1 - m)x^*}$.

The characteristic equation of System (13) at $G(x^*, y^*)$ is given by

$$(14) \quad \lambda^2 - \alpha\lambda + r_2\lambda e^{-\lambda\tau} - r_2(\alpha_1 - a_1(1 - m)y^*)e^{-\lambda\tau} = 0,$$

where $\alpha = r_1 - 2b_1x^* - a_1(1 - m)y^* - H'(x^*)$.

Note that for $\tau = 0$, the characteristic equations (14) becomes

$$(15) \quad \lambda^2 + (r_2 - \alpha)\lambda - r_2(\alpha - a_1(1 - m)y^*) = 0.$$

Since the sum and product of roots are $-(r_2 - \alpha)$ and $-r_2(\alpha - a_1(1 - m)y^*)$ respectively, the two roots of (15) are real and negative or complex conjugate with negative real parts if and only

if

$$(16) \quad r_2 - \alpha > 0 \quad \text{and} \quad \alpha - a_1(1-m)y^* < 0.$$

Hence, in the absence of time delay, the system is locally asymptotically stable if and only if $r_2 - \alpha > 0$ and $\alpha - a_1(1-m)y^* < 0$.

Now, for $\tau > 0$, if $\lambda = i\omega$ is a root of equation (14), then we have

$$-\omega^2 + \alpha\omega + r_2i\omega(\cos \omega\tau - i\sin \omega\tau) - c(\cos \omega\tau - i\sin \omega\tau) = 0,$$

where $c = r_2(\alpha - a_1(1-m)y^*)$.

Separating real and imaginary parts gives

$$(17) \quad r_2\omega \sin \omega\tau - c \cos \omega\tau = \omega^2 \quad \text{and} \quad r_2\omega \cos \omega\tau + c \sin \omega\tau = \alpha\omega.$$

Eliminating τ by squaring and adding equations of (17), we get the algebraic equation

$$(18) \quad r_2^2\omega^6 + [c^2 + r_2^2(\alpha^2 - r_2^2)]\omega^4 + c^2(\alpha^2 - 2r_2^2)\omega^2 - c^4 = 0.$$

Substituting $\omega^2 = \eta$ in the above equation gives a cubic equation in η of the form

$$(19) \quad r_2^2\eta^3 + [c^2 + r_2^2(\alpha^2 - r_2^2)]\eta^2 + c^2(\alpha^2 - 2r_2^2)\eta - c^4 = 0.$$

Observe that conditions (16) implies $\alpha < r_2$. Since $r_2^2 > 0$ and $-c^4 < 0$, if $c^2 + r_2^2(\alpha^2 - r_2^2) > 0$ or $\alpha^2 - 2r_2^2 < 0$, then by Descartes' rule of sign, Eq.(19) has at least one positive root.

If $\alpha \in]-r_2, r_2[$, then $\alpha^2 - 2r_2^2 < 0$ and Eq.(19) has only one positive root. If $\alpha < -r_2$, then $c^2 + r_2^2(\alpha^2 - r_2^2) > 0$ and Eq.(19) has at least one positive root. So, for any cases, Eq.(19) has at least one positive root.

The following theorem gives a criterion for the switching in the stability behavior of $G^*(x^*, y^*)$ in terms of the delay parameter τ .

Theorem 3. : *Suppose that $G(x^*, y^*)$ exists and is locally asymptotically stable for System (6) with $\tau = 0$. Also let $\eta_0 = \omega_0^2$ be a positive root of Eq.(19). Then there exists a value $\tau = \tau_0$ such that G is locally asymptotically stable for $\tau \in (0, \tau_0]$ and unstable for $\tau > \tau_0$. Furthermore, the system undergoes a Hopf bifurcation at G when $\tau = \tau_0$.*

Proof. : Since ω_0 is a solution of Eq.(18), the characteristic Eq.(14) has the pair of purely imaginary roots $\pm i\omega_0$. From Eq.(17), τ_n^0 for $n = 0, 1, \dots$ as a function of ω_0 is given by

$$(20) \quad \tau_n^0 = \frac{1}{w_0} \arccos \left\{ \frac{w_0^2(-c + \alpha r_2)}{c^2 + r_2^2 w_0^2} \right\} + \frac{2\pi n}{w_0}.$$

For $\tau = 0$, theorem 2 ensures that G is locally asymptotically stable. Hence, by Butler's lemma [27], G remains stable up to the minimum value of τ_n^0 , obtained here for $n = 0$, i.e. for $\tau < \tau_0^0$, so that $\tau^0 = \min_{n \geq 0} \tau_n^0 \equiv \tau_0^0$. The theorem can be completely proved if we can show that

$$\text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\lambda=i\omega_0} > 0.$$

Differentiating equation (14) with respect to τ yields

$$(21) \quad [2\lambda - \alpha + (r_2 - r_2\tau\lambda + c\tau)e^{-\lambda\tau}] \frac{d\lambda}{d\tau} = (r_2\lambda^2 - c\lambda)e^{-\lambda\tau},$$

which gives

$$\begin{aligned} \left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1} &= \frac{2\lambda - \alpha + (r_2 - r_2\tau\lambda + c\tau)e^{-\lambda\tau}}{(r_2\lambda^2 - c\lambda)e^{-\lambda\tau}}, \\ &= -\frac{2\lambda^2 - \alpha\lambda}{\lambda^2(\lambda^2 - \alpha\lambda)} - \frac{r_2}{\lambda(c - r_2\lambda)} - \frac{\tau}{\lambda}, \\ &= -\frac{1}{\lambda^2 - \alpha\lambda} - \frac{1}{\lambda^2} - \frac{r_2}{\lambda(c - r_2\lambda)} - \frac{\tau}{\lambda}. \end{aligned}$$

Thus, $\mu_0 = \text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\lambda=iw_0}$ is given by

$$\begin{aligned} \mu_0 &= \text{sign} \left\{ \text{Re} \left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1} \right\} \Big|_{\lambda=iw_0}, \\ &= \text{sign} \left\{ \text{Re} \left[-\frac{1}{\lambda^2 - \alpha\lambda} - \frac{1}{\lambda^2} - \frac{r_2}{\lambda(c - r_2\lambda)} \right] \right\} \Big|_{\lambda=iw_0}, \\ &= \text{sign} \left\{ \frac{w_0^2}{w_0^4 + \alpha^2 w_0^2} + \frac{1}{w_0^2} - \frac{r_2^2 w_0^2}{r_2^2 w_0^4 + w_0^2 c^2} \right\} \\ &= \text{sign} \left\{ \frac{r_2^2 w_0^4 + 2c^2 w_0^2 + \alpha^2 c^2}{(w_0^4 + \alpha^2 w_0^2)(r_2 w_0^2 + c^2)} \right\} > 0. \end{aligned}$$

Hence, $\text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\} \Big|_{\tau=\tau^0, \lambda=i\omega_0} > 0$. The transversality condition is satisfied and a Hopf bifurcation occurs at $\tau = \tau^0$. This achieves the proof. \square

5. PROPERTIES OF HOPF BIFURCATION

In this section, we give some properties of the Hopf bifurcation presented in Theorem 3 and analyse the stability of bifurcated periodic solutions occurring through Hopf bifurcations by using the normal form theory and the center manifold reduction for retarded functional differential equations (RFDEs) due to Hassard, Kazarinoff and Wan [17]. We assume that System (6) undergoes Hopf bifurcation at the positive equilibrium $G(x^*, y^*)$ for $\tau = \tau_j^0$, ($j = 0, 1, 2, \dots$) and then $\pm i\omega_0$ is corresponding purely imaginary roots of the characteristic equation.

Let $x_1(t) = x(t) - x^*$ and $x_2(t) = y(t) - y^*$. Then, system (6)-(5) is equivalent to :

$$(22) \quad \begin{cases} \dot{x}_1(t) = \left[r_1 - 2b_1x^* - a_1(1-m)y^* \right] x_1(t) \\ \quad - H'(x^*)x_1(t) - a_1(1-m)x^*x_2(t) \\ \quad + f_1(x_1(t), x_2(t)), \\ \dot{x}_2(t) = -\Psi'(x^*)y^{*2}x_1(t-\tau) - r_2x_2(t-\tau) \\ \quad + f_2(x_2(t), x_1(t-\tau), x_2(t-\tau)), \end{cases}$$

where

$$\begin{aligned} f_1(x_1(t), x_2(t)) &= -a_1(1-m)x_1(t)x_2(t) \\ &\quad - b_1x_1^2(t), \end{aligned}$$

and

$$\begin{aligned} f_2(x_2(t), x_1(t-\tau), x_2(t-\tau)) &= r_2(x_2(t) + y^*) \\ &\quad - \left[\Psi(x_1(t-\tau) + x^*)(x_2(t-\tau) + y^*) \right] (x_2(t) + y^*) \\ &\quad + \Psi'(x^*)y^{*2}x_1(t-\tau) + r_2x_2(t-\tau). \end{aligned}$$

Let $\tau = \tau_j^0 + \mu$. Then, $\mu = 0$ corresponds to Hopf bifurcation value of System (6) at the positive equilibrium $G(x^*, y^*)$. Since System (6) is equivalent to System (22), in the following discussion we use System (22).

In System (22), let $\bar{x}_k(t) = x_k(\tau t)$ and drop the bars for simplicity of notation. Then, System (22) can be rewritten as a system of RFDEs in $\mathcal{C}([-1, 0], \mathbb{R}^2)$ of the form:

$$(23) \quad \begin{cases} \dot{x}_1(t) = (\tau_j^0 + \mu) \left[r_1 - 2b_1x^* - a_1(1-m)y^* \right] x_1(t) \\ \quad - (\tau_j^0 + \mu)H'(x^*)x_1(t) \\ \quad - (\tau_j^0 + \mu)a_1(1-m)x^*x_2(t) \\ \quad + (\tau_j^0 + \mu)f_1(x_1(t), x_2(t)), \\ \dot{x}_2(t) = -(\tau_j^0 + \mu)\Psi'(x^*)y^{*2}x_1(t - \tau) \\ \quad - (\tau_j^0 + \mu)r_2x_2(t - \tau) \\ \quad + (\tau_j^0 + \mu)f_2(x_2(t), x_1(t - \tau), x_2(t - \tau)). \end{cases}$$

Define the linear operator $L(\mu) : \mathcal{C} \rightarrow \mathbb{R}^2$ and the nonlinear operator $f(\cdot, \mu) : \mathcal{C} \rightarrow \mathbb{R}^2$ by:

$$(24) \quad \begin{aligned} L_\mu(\phi) &= (\tau_j^0 + \mu) \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} \\ &+ (\tau_j^0 + \mu) \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix} \end{aligned}$$

and

$$(25) \quad f(\phi, \mu) = (\tau_j^0 + \mu) \begin{pmatrix} f_1(\phi_1(0), \phi_2(0)) \\ f_2(\phi_2(0), \phi_1(-1), \phi_2(-1)) \end{pmatrix}$$

respectively, where $\phi = (\phi_1, \phi_2)^T \in \mathcal{C}$, $J_0 = r_1 - 2b_1x^* - a_1(1-m)y^* - H'(x^*)$, $J_1 = -a_1(1-m)x^*$.

By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \mu)$, $-1 \leq \theta \leq 0$ whose elements are of bounded variation such that

$$(26) \quad L_\mu(\phi) = \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta) \quad \text{for } \phi \in \mathcal{C}([-1, 0], \mathbb{R}^2).$$

In fact, we can choose

$$(27) \quad \begin{aligned} \eta(\theta, \mu) = & (\tau_j^0 + \mu) \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} \delta(\theta) \\ & + (\tau_j^0 + \mu) \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \delta(\theta + 1), \end{aligned}$$

where δ is the Dirac delta function defined by

$$(28) \quad \delta(\theta) = \begin{cases} 0 & \text{if } \theta \neq 0, \\ 1 & \text{if } \theta = 0. \end{cases}$$

For $\phi \in \mathcal{C}([-1, 0], \mathbb{R}^2)$, define

$$(29) \quad A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta} & \text{if } \theta \in [-1, 0), \\ \int_{-1}^0 d\eta(\mu, s)\phi(s) & \text{if } \theta = 0, \end{cases}$$

and

$$(30) \quad R(\mu)\phi = \begin{cases} 0 & \text{if } \theta \in [-1, 0), \\ f(\mu, \phi) & \text{if } \theta = 0. \end{cases}$$

Then, System (23) is equivalent to

$$(31) \quad \dot{x}(t) = A(\mu)x_t + R(\mu)x_t,$$

where $x_t(\theta) = x(t + \theta)$, $\theta \in [-1, 0]$.

For $\psi \in \mathcal{C}^1([0, 1], \mathbb{R}^2)$, define

$$(32) \quad A^* \psi = \begin{cases} -\frac{d\psi(s)}{ds} \text{ if } s \in (0, 1], \\ \int_1^0 d\eta(t, 0)\phi(-t) \text{ if } s = 0, \end{cases}$$

and a bilinear inner product

$$(33) \quad \begin{aligned} \langle \psi(s), \phi(\theta) \rangle &= \bar{\psi}(0)\phi(0) \\ &\quad - \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{\psi}(\xi - \theta)d\eta(\theta)\phi(\xi)d\xi, \end{aligned}$$

where $\eta(\theta) = \eta(\theta, 0)$. In addition, by Theorem 3 we know that $\pm i\omega_0 \tau_j^0$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^* . Let us assume that $q(\theta)$ is the eigenvector of $A(0)$ corresponding to $i\omega_0 \tau_j^0$ and $q^*(s)$ is the eigenvector of A^* corresponding to $-i\omega_0 \tau_j^0$.

Let $q(\theta) = \begin{pmatrix} 1 & v_1 \end{pmatrix}^T e^{i\omega_0 \tau_j^0 \theta}$ and $q^*(s) = D \begin{pmatrix} 1 & v_1^* \end{pmatrix}^T e^{i\omega_0 \tau_j^0 s}$. From the above discussion, it is easy to know that $A(0)q(0) = i\omega_0 \tau_j^0 q(0)$ and $A^*(0)q^*(0) = -i\omega_0 \tau_j^0 q^*(0)$. That is

$$\begin{aligned} &\tau_j^0 \begin{pmatrix} J_0 & J_1 \\ 0 & 0 \end{pmatrix} q(0) \\ &+ \tau_j^0 \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} q(-1) = i\omega_0 \tau_j^0 q(0) \end{aligned}$$

and

$$\begin{aligned} &\tau_j^0 \begin{pmatrix} J_0 & 0 \\ J_1 & -r_2 \end{pmatrix} q^*(0) \\ &+ \tau_j^0 \begin{pmatrix} 0 & -\Psi'(x^*)y^{*2} \\ 0 & -r_2 \end{pmatrix} q^*(-1) = -i\omega_0 \tau_j^0 q^*(0). \end{aligned}$$

Thus, we can easily obtain

$$(34) \quad q(\theta) = \left(1, \frac{J_0 - i\omega_0}{a_1(1-m)x^*}\right)^T e^{i\omega_0\tau_j^0\theta},$$

$$(35) \quad q^*(s) = D \left(1, \frac{J_0 + i\omega_0}{\Psi'(x^*)y^{*2}e^{-i\omega_0\tau_j^0}}\right)^T e^{i\omega_0\tau_j^0s}.$$

In order to assure $\langle \bar{q}^*(s), q(\theta) \rangle = 1$, we need to determine the value of D . From (33), we have

$$\begin{aligned} \langle q^*(s), q(\theta) \rangle &= \bar{q}^*(0)q(0) \\ &- \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{q}^*(\xi - \theta) d\eta(\theta) q(\xi) d\xi \\ &= \bar{q}^*(0)q(0) \\ &- \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{D} \left(1, \bar{v}_1^*\right) e^{-i\omega_0\tau_j^0(\xi-\theta)} d\eta(\theta) \left(1, v_1\right)^T e^{i\omega_0\tau_j^0\xi} d\xi \\ &= \bar{q}^*(0)q(0) \\ &- \bar{q}^*(0) \int_{-1}^0 \theta e^{i\omega_0\tau_j^0\theta} d\eta(\theta) q(0) \\ &= \bar{q}^*(0)q(0) \\ &- \bar{q}^*(0) \tau_j^0 \begin{pmatrix} 0 & 0 \\ -\Psi'(x^*)y^{*2} & -r_2 \end{pmatrix} \begin{pmatrix} -e^{-i\omega_0\tau_j^0} \\ 1 \end{pmatrix} q(0) \\ &= \bar{D} \left[1 + v_1 \bar{v}_1^* - \tau_j^0 e^{-i\omega_0\tau_j^0} \bar{v}_1^* (\Psi'(x^*)y^{*2} + r_2)\right]. \end{aligned}$$

Therefore, we have

$$(36) \quad \begin{aligned} \bar{D} &= \frac{1}{1 + v_1 \bar{v}_1^* - \tau_j^0 e^{-i\omega_0\tau_j^0} \bar{v}_1^* (\Psi'(x^*)y^{*2} + r_2)}, \\ D &= \frac{1}{1 + \bar{v}_1 v_1^* - \tau_j^0 e^{i\omega_0\tau_j^0} v_1^* (\Psi'(x^*)y^{*2} + r_2)}. \end{aligned}$$

Using the same notations as in [17], we first compute the coordinates to describe the center manifold \mathcal{C}_0 at $\mu = 0$. Let x_t be the solution of Eq. (22) when $\mu = 0$. Define

$$(37) \quad \begin{aligned} z(t) &= \langle q^*, x_t \rangle, \\ W(t, \theta) &= x_t(\theta) - 2\mathcal{R}_e \left(z(t) q(\theta) \right) \\ &= x_t(\theta) - \left(z(t) q(\theta) + \bar{z}(t) \bar{q}(\theta) \right). \end{aligned}$$

On the center manifold \mathcal{C}_0 , we have

$$(38) \quad W(t, \theta) = W(z, \bar{z}, \theta),$$

where

$$(39) \quad \begin{aligned} W(z, \bar{z}, \theta) &= W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02} \frac{\bar{z}^2}{2} \\ &+ W_{30}(\theta) \frac{z^3}{6} + \dots, \end{aligned}$$

z and \bar{z} are local coordinates for center manifold C_0 in the direction of q^* and \bar{q}^* . Note that W is real if x_t is real. We only consider real solutions. For solution $x_t \in \mathcal{C}_0$ of Eq.(22), since $\mu = 0$, we have

$$(40) \quad \begin{aligned} \dot{z}(t) &= i\omega_0 \tau_j^0 z \\ &+ \bar{q}^*(0) f\left(0, W(z, \bar{z}, 0) + 2\mathcal{R}_e(z(t)q(\theta))\right) \\ &\equiv i\omega_0 \tau_j^0 z + \bar{q}^*(0) f_0(z, \bar{z}). \end{aligned}$$

We rewrite this equation as

$$(41) \quad \dot{z}(t) = i\omega_0 \tau_j^0 z + g(z, \bar{z}),$$

where

$$(42) \quad \begin{aligned} g(z, \bar{z}) &= g_{20}(\theta) \frac{z^2}{2} + g_{11}(\theta) z\bar{z} + g_{02} \frac{\bar{z}^2}{2} \\ &+ g_{21}(\theta) \frac{z^2 \bar{z}}{2} + \dots \end{aligned}$$

Then, $x_t(\theta) = (x_{1t}(\theta), x_{2t}(\theta))$ and $q(\theta) = (1, v_1)^T e^{i\omega_0 \tau_j^0 \theta}$. So, from Eq.(37) and Eq.(39), it follows that

$$(43) \quad \begin{aligned} x_t(\theta) &= W(t, \theta) + 2\mathcal{R}_e\left(z(t)q(\theta)\right) \\ &= W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02} \frac{\bar{z}^2}{2} \\ &+ (1, v_1)^T e^{i\omega_0 \tau_j^0 \theta} z(t) + (1, \bar{v}_1)^T e^{-i\omega_0 \tau_j^0 \theta} \bar{z}(t) + \dots \end{aligned}$$

Then, we have

$$\begin{aligned}
x_{1t}(0) &= z + \bar{z} + W_{20}^{(1)}(0) \frac{z^2}{2} + W_{11}^{(1)}(0) z\bar{z} \\
&+ W_{02}^{(1)}(0) \frac{\bar{z}^2}{2} + \dots \\
x_{2t}(0) &= v_1 z + \bar{v}_1 \bar{z} + W_{20}^{(2)}(0) \frac{z^2}{2} + W_{11}^{(2)}(0) z\bar{z} \\
&+ W_{02}^{(2)}(0) \frac{\bar{z}^2}{2} + \dots \\
(44) \quad x_{1t}(-1) &= z e^{-i\omega_0 \tau_j^0} + \bar{z} e^{i\omega_0 \tau_j^0} + W_{20}^{(1)}(-1) \frac{z^2}{2} \\
&+ W_{11}^{(1)}(-1) z\bar{z} + W_{02}^{(1)}(-1) \frac{\bar{z}^2}{2} + \dots \\
x_{2t}(-1) &= v_1 z e^{-i\omega_0 \tau_j^0} + \bar{v}_1 \bar{z} e^{i\omega_0 \tau_j^0} + W_{20}^{(2)}(-1) \frac{z^2}{2} \\
&+ W_{11}^{(2)}(-1) z\bar{z} + W_{02}^{(2)}(-1) \frac{\bar{z}^2}{2} + \dots
\end{aligned}$$

It follows together with Eq.(25) that

$$\begin{aligned}
g(z, \bar{z}) &= \bar{q}^*(0) f_0(z, \bar{z}) \\
&= \bar{q}^*(0) f(0, x_t) = \tau_j^0 \bar{D} \left(1, \bar{v}_1^* \right) \times \\
&\quad \left(\begin{array}{l} -b_1 x_{1t}^2(0) - a_1(1-m)x_{1t}(0)x_{2t}(0); \\ \\ -\Psi'(x^*)x_{2t}(-1)x_{2t}(0) \\ -\Psi'(x^*)x_{1t}(-1)x_{2t}(-1)x_{2t}(0); \\ -\Psi'(x^*)y^*x_{1t}(-1)x_{2t}(-1) \\ -\Psi'(x^*)y^*x_{1t}(-1)x_{2t}(0); \\ -\frac{\Psi''(x^*)}{2}y^*x_{1t}^2(-1)x_{2t}(-1) \\ -\frac{\Psi''(x^*)}{2}y^*x_{1t}^2(-1)x_{2t}(0); \\ -\frac{\Psi''(x^*)}{2}y^{*2}x_{1t}^2(-1)x_{2t}(0) \\ -\frac{\Psi^{(3)}(x^*)}{6}y^{*2}x_{1t}^3(-1) - \dots \end{array} \right)
\end{aligned}$$

$$\begin{aligned}
&= \frac{z^2}{2} \left\{ 2\tau_j^0 \bar{D} [-b_1 - v_1 a_1 (1-m) \right. \\
&- \bar{v}_1^* (\Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} - \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\
&- \left. y^* v_1 e^{-i\omega_0 \tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0}) \right] \left. \right\} \\
&+ \frac{\bar{z}^2}{2} \left\{ 2\tau_j^0 \bar{D} [-b_1 - \bar{v}_1 a_1 (1-m) \right. \\
&- \bar{v}_1^* (\Psi(x^*) \bar{v}_1^2 e^{i\omega_0 \tau_j^0} - \Psi'(x^*) y^* \bar{v}_1 e^{2i\omega_0 \tau_j^0} \\
&- \left. y^* \bar{v}_1 e^{i\omega_0 \tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{2i\omega_0 \tau_j^0}) \right] \left. \right\} \\
&+ z\bar{z} \left\{ 2\tau_j^0 \bar{D} [-b_1 - \mathfrak{R}_e(v_1) a_1 (1-m) \right. \\
&- \bar{v}_1^* (\mathfrak{R}_e(v_1) \bar{v}_1 e^{-i\omega_0 \tau_j^0}) \Psi(x^*) - \mathfrak{R}_e(\bar{v}_1) y^* \Psi'(x^*) \\
&- \left. y^* \mathfrak{R}_e(v_1 e^{i\omega_0 \tau_j^0}) - y^{*2} \Psi''(x^*) \right] \left. \right\} \\
&+ \frac{z^2 \bar{z}}{2} \left\{ \tau_j^0 \bar{D} \left[-b_1 \left((2W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)) \right) \right. \right. \\
&- a_1 (1-m) (2W_{11}^{(2)}(0) + W_{20}^{(2)}(0) + \bar{v}_1 W_{20}^{(1)}(0)) \\
&+ 2v_1 a_1 (1-m) W_{11}^{(1)}(0) \\
&- \bar{v}_1^* \Psi(x^*) (2v_1 W_{11}^{(2)}(0) + \bar{v}_1 W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0}) \\
&+ \bar{v}_1^* \Psi(x^*) (\bar{v}_1 W_{20}^{(2)}(-1) + 2v_1 W_{11}^{(2)}(-1)) \\
&- \bar{v}_1^* \Psi'(x^*) (2v_1 \bar{v}_1 e^{-2i\omega_0 \tau_j^0}) \\
&+ \bar{v}_1^* \Psi'(x^*) (2v_1 \bar{v}_1 + 2v_1^2 e^{-2i\omega_0 \tau_j^0}) \\
&- \bar{v}_1^* \Psi'(x^*) y^* (2W_{11}^{(2)}(-1) e^{-i\omega_0 \tau_j^0} (1+v_1) \\
&+ \bar{v}_1^* \Psi'(x^*) y^* W_{20}^{(1)}(-1) e^{i\omega_0 \tau_j^0} (1+\bar{v}_1) \\
&- 2W_{11}^{(2)}(0) e^{-i\omega_0 \tau_j^0} + W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0} \\
&+ \bar{v}_1 W_{20}^{(1)}(-1) + 2v_1 W_{11}^{(1)}(-1)) \\
&- \bar{v}_1^* \frac{\Psi''(x^*) y^*}{2} (6v_1 e^{-i\omega_0 \tau_j^0} + 4v_1 + 2\bar{v}_1 e^{-2i\omega_0 \tau_j^0}) \\
&+ 4y^* \bar{v}_1^* \frac{\Psi''(x^*) y^*}{2} W_{11}^{(1)}(-1) e^{-i\omega_0 \tau_j^0} \\
&+ 2y^* e^{i\omega_0 \tau_j^0} W_{20}^{(1)}(-1) \\
&- \left. \bar{v}_1^* \frac{\Psi'''(x^*) y^*}{3} (2e^{-i\omega_0 \tau_j^0} + e^{i\omega_0 \tau_j^0}) \right. \left. \right\}.
\end{aligned}$$

Comparing the coefficient with Eq.(42) gives

$$\begin{aligned}
g_{20} &= 2\tau_j^0 \bar{D} (-b_1 - v_1 a_1 (1-m)) \\
&- 2\tau_j^0 \bar{D} \bar{v}_1^* \Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} \\
&- 2\tau_j^0 \bar{D} \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\
&- 2\tau_j^0 \bar{D} y^* v_1 e^{-i\omega_0 \tau_j^0} \\
&- 2\tau_j^0 \bar{D} \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0},
\end{aligned}$$

$$\begin{aligned}
g_{02} &= 2\tau_j^0 \bar{D}(-b_1 - v_1 a_1(1-m)) \\
&\quad - 2\tau_j^0 \bar{D} \bar{v}_1^* \Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} \\
&\quad - 2\tau_j^0 \bar{D} \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\
&\quad - 2\tau_j^0 \bar{D} y^* v_1 e^{-i\omega_0 \tau_j^0} \\
&\quad - 2\tau_j^0 \bar{D} \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0}, \\
g_{11} &= 2\tau_j^0 \bar{D}(-b_1 - \Re_e(v_1) a_1(1-m)) \\
&\quad - 2\tau_j^0 \bar{D} \bar{v}_1^* \Re_e(v_1 \bar{v}_1 e^{-i\omega_0 \tau_j^0}) \Psi(x^*) \\
&\quad - 2\tau_j^0 \bar{D} \bar{v}_1^* \Re_e(\bar{v}_1) y^* \Psi'(x^*) \\
&\quad - 2\tau_j^0 \bar{D} \bar{v}_1^* y^* \Re_e(v_1 e^{i\omega_0 \tau_j^0}) \\
&\quad - 2\tau_j^0 \bar{D} \bar{v}_1^* y^{*2} \Psi''(x^*), \\
g_{21} &= -\tau_j^0 \bar{D} b_1 (2W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)) \\
&\quad - \tau_j^0 \bar{D} a_1 (1-m) (2W_{11}^{(2)}(0) + W_{20}^{(2)}(0)) \\
&\quad + \tau_j^0 \bar{D} \bar{v}_1 a_1 (1-m) W_{20}^{(1)}(0) + 2v_1 W_{11}^{(1)}(0) \\
&\quad - \bar{v}_1^* \Psi(x^*) (2v_1 W_{11}^{(2)}(0) + \bar{v}_1 W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0}) \\
&\quad + \bar{v}_1^* \Psi(x^*) (\bar{v}_1 W_{20}^{(2)}(-1) + 2v_1 W_{11}^{(2)}(-1)) \\
&\quad - \bar{v}_1^* \Psi'(x^*) (2v_1 \bar{v}_1 e^{-2i\omega_0 \tau_j^0} + 2v_1 \bar{v}_1 \\
&\quad - 2\bar{v}_1^* \Psi'(x^*) v_1^2 e^{-2i\omega_0 \tau_j^0}) \\
&\quad - \bar{v}_1^* \Psi'(x^*) y^* 2W_{11}^{(2)}(-1) e^{-i\omega_0 \tau_j^0} (1 + v_1) \\
&\quad + \bar{v}_1^* \Psi'(x^*) y^* W_{20}^{(1)}(-1) e^{i\omega_0 \tau_j^0} (1 + \bar{v}_1) \\
&\quad - 2\bar{v}_1^* \Psi'(x^*) y^* W_{11}^{(2)}(0) e^{-i\omega_0 \tau_j^0} \\
&\quad + \bar{v}_1^* \Psi'(x^*) y^* W_{20}^{(2)}(0) e^{i\omega_0 \tau_j^0} + \bar{v}_1 W_{20}^{(1)}(-1) \\
&\quad + 2\bar{v}_1^* \Psi'(x^*) y^* v_1 W_{11}^{(1)}(-1) \\
&\quad - \bar{v}_1^* \frac{\Psi''(x^*) y^*}{2} (6v_1 e^{-i\omega_0 \tau_j^0} + 4v_1) \\
&\quad + 2\bar{v}_1^* \frac{\Psi''(x^*) y^*}{2} \bar{v}_1 e^{-2i\omega_0 \tau_j^0} \\
&\quad + 4\bar{v}_1^* \frac{\Psi''(x^*) y^*}{2} y^* W_{11}^{(1)}(-1) e^{-i\omega_0 \tau_j^0} \\
&\quad + 2y^* e^{i\omega_0 \tau_j^0} W_{20}^{(1)}(-1) \\
&\quad - \bar{v}_1^* \frac{\Psi'''(x^*) y^*}{3} (2e^{-i\omega_0 \tau_j^0} + e^{i\omega_0 \tau_j^0})
\end{aligned}
\tag{46}$$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21} , we still need to compute them. From Eq.(31) and Eq.(37), we have

$$\begin{aligned}
 \dot{W} &= \dot{x}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\
 (47) \quad &= \begin{cases} AW - 2\mathcal{R}_e\{\bar{q}^*(0)f_0q(\theta)\} & \text{if } \theta \in [-1;0), \\ AW - 2\mathcal{R}_e\{\bar{q}^*(0)f_0q(\theta)\} + f_0 & \text{if } \theta = 0, \end{cases} \\
 &\stackrel{\text{def}}{=} AW + \mathcal{H}(z, \bar{z}, \theta),
 \end{aligned}$$

where

$$\begin{aligned}
 (48) \quad \mathcal{H}(z, \bar{z}, \theta) &= \mathcal{H}_{20}(\theta)\frac{z^2}{2} + \mathcal{H}_{11}(\theta)z\bar{z} \\
 &\quad + \mathcal{H}_{02}(\theta)\frac{\bar{z}^2}{2} + \dots
 \end{aligned}$$

Substituting the corresponding series into Eq.(47) and comparing the coefficients give

$$(49) \quad (A - 2i\omega_0\tau_j^0)W_{20}(\theta) = -\mathcal{H}_{20}(\theta),$$

$$AW_{11}(\theta) = -\mathcal{H}_{11}(\theta).$$

From Eq.(47), we know that for $\theta \in [-1, 0)$,

$$\begin{aligned}
 (50) \quad \mathcal{H}(z, \bar{z}, \theta) &= -\bar{q}^*(0)f_0q(\theta) - q^*(0)\bar{f}_0\bar{q}(\theta) \\
 &= -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta).
 \end{aligned}$$

Comparing the coefficient with Eq.(48) gives

$$(51) \quad -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta) = H_{20}(\theta),$$

$$(52) \quad -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta) = H_{11}(\theta).$$

From Eq.(49) and Eq.(51) and the definition of A , it follows that

$$(53) \quad \dot{W}(\theta) = 2i\omega_0\tau_j^0W_{20} + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

Notice that $q(\theta) = \left(1, v_1\right)^T e^{i\omega_0\tau_j^0\theta}$. Hence,

$$(54) \quad W_{20}(\theta) = \frac{ig_{20}}{w_0\tau_j^0}q(0)e^{i\omega_0\tau_j^0\theta} + \frac{i\bar{g}_{02}}{3w_0\tau_j^0}\bar{q}(0)e^{-i\omega_0\tau_j^0\theta} + E_1e^{2i\omega_0\tau_j^0\theta},$$

where $E_1 = \left(E_1^{(1)}, E_1^{(2)}\right) \in \mathbb{R}^2$ is a constant vector. Similarly, from Eq.(49) and Eq.(52), we obtain

$$(55) \quad W_{11}(\theta) = -\frac{ig_{11}}{w_0\tau_j^0}q(0)e^{i\omega_0\tau_j^0\theta} + \frac{i\bar{g}_{11}}{w_0\tau_j^0}\bar{q}(0)e^{-i\omega_0\tau_j^0\theta} + E_2,$$

where $E_2 = \left(E_2^{(1)}, E_2^{(2)}\right) \in \mathbb{R}^2$ is also a constant vector.

In what follows, we will seek appropriate E_1 and E_2 . From the definition of A and Eq.(49), we obtain

$$(56) \quad \int_{-1}^0 d\eta(\theta)W_{20}(\theta) = 2i\omega_0\tau_jW_{20}(0) - H_{20}(0),$$

$$(57) \quad \int_{-1}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0),$$

where $\eta(\theta) = \eta(0, \theta)$. By Eq.(47), we have

$$(58) \quad H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + 2\tau_j^0 \times \begin{pmatrix} -b_1 - v_1a_1(1-m) \\ -\Psi(x^*)v_1^2e^{-i\omega_0\tau_j^0} - \Psi'(x^*)y^*v_1e^{-2i\omega_0\tau_j^0} \\ -y^*v_1e^{-i\omega_0\tau_j^0} - \frac{\Psi''(x^*)}{2}y^{*2}e^{-2i\omega_0\tau_j^0} \end{pmatrix},$$

$$(59) \quad H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + 2\tau_j^0 \times \begin{pmatrix} -b_1 - \Re_e(v_1)a_1(1-m) \\ -\Re_e(v_1\bar{v}_1e^{-i\omega_0\tau_j^0})\Psi(x^*) - \Re_e(\bar{v}_1)y^*\Psi'(x^*) \\ -y^*\Re_e(v_1e^{i\omega_0\tau_j^0}) - y^{*2}\Psi''(x^*) \end{pmatrix}.$$

Substituting Eq.(54) and Eq.(58) into Eq.(56) and using the fact that

$$(60) \quad \begin{aligned} \left(i\omega_0 \tau_j^0 I - \int_{-1}^0 e^{i\omega_0 \tau_j^0 \theta} d\eta(\theta) \right) q(0) &= 0, \\ \left(-i\omega_0 \tau_j^0 I - \int_{-1}^0 e^{-i\omega_0 \tau_j^0 \theta} d\eta(\theta) \right) \bar{q}(0) &= 0, \end{aligned}$$

we obtain

$$\begin{aligned} &\left(2i\omega_0 \tau_j^0 I - \int_{-1}^0 e^{2i\omega_0 \tau_j^0 \theta} d\eta(\theta) \right) E_1 = 2\tau_j^0 \times \\ &\begin{pmatrix} -b_1 - v_1 a_1 (1-m) \\ -\Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} - \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\ -y^* v_1 e^{-i\omega_0 \tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0} \end{pmatrix}. \end{aligned}$$

This leads to

$$\begin{aligned} &\begin{pmatrix} 2i\omega_0 - J_0 & -J_1 \\ \Psi'(x^*) y^{*2} e^{-2i\omega_0 \tau_j^0} & 2i\omega_0 + r_2 e^{-2i\omega_0 \tau_j^0} \end{pmatrix} E_1 = \\ &2 \begin{pmatrix} -b_1 - v_1 a_1 (1-m) \\ -\Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} - \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\ -y^* v_1 e^{-i\omega_0 \tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0} \end{pmatrix}. \end{aligned}$$

Solving this system for E_1 gives

$$E_1^{(1)} = \frac{2}{\sigma} \begin{vmatrix} -b_1 - v_1 a_1 (1-m) & a_1 (1-m) x^* \\ e_0 & 2i\omega_0 + r_2 e^{-2i\omega_0 \tau_j^0} \end{vmatrix},$$

where

$$\begin{aligned} e_0 &= -\Psi(x^*) v_1^2 e^{-i\omega_0 \tau_j^0} - \Psi'(x^*) y^* v_1 e^{-2i\omega_0 \tau_j^0} \\ &\quad - y^* v_1 e^{-i\omega_0 \tau_j^0} - \frac{\Psi''(x^*)}{2} y^{*2} e^{-2i\omega_0 \tau_j^0}, \end{aligned}$$

$$E_1^{(2)} = \frac{2}{\sigma} \begin{vmatrix} 2i\omega_0 - J_0 & -b_1 - v_1 a_1 (1 - m) \\ \Psi'(x^*) y^{*2} e^{-2i\omega_0 \tau_j^0} & e_0 \end{vmatrix},$$

where

$$\sigma = \begin{vmatrix} 2i\omega_0 - J_0 & a_1(1 - m)x^* \\ \Psi'(x^*) y^{*2} e^{-2i\omega_0 \tau_j^0} & 2i\omega_0 + r_2 e^{-2i\omega_0 \tau_j^0} \end{vmatrix}.$$

Similarly, substituting Eq.(55) and Eq.(59) into (57) gives

$$E_2 = \begin{pmatrix} -J_0 & -J_1 \\ \Psi'(x^*) y^{*2} & r_2 \end{pmatrix} 2 \begin{pmatrix} -b_1 - \Re_e(v_1) a_1 (1 - m) \\ -\Re_e(v_1 \bar{v}_1 e^{-i\omega_0 \tau_j^0}) \Psi(x^*) - \Re_e(\bar{v}_1) y^* \Psi'(x^*) \\ -y^* \Re_e(v_1 e^{i\omega_0 \tau_j^0}) - y^{*2} \Psi''(x^*) \end{pmatrix}.$$

Therefore,

$$E_2^{(1)} = \frac{2}{\rho} \begin{vmatrix} -b_1 - \Re_e(v_1) a_1 (1 - m) & -J_1 \\ e_1 & r_2 \end{vmatrix},$$

where

$$e_1 = -\Re_e(v_1 \bar{v}_1 e^{-i\omega_0 \tau_j^0}) \Psi(x^*) - \Re_e(\bar{v}_1) y^* \Psi'(x^*) \\ - y^* \Re_e(v_1 e^{i\omega_0 \tau_j^0}) - y^{*2} \Psi''(x^*)$$

$$E_2^{(2)} = \frac{2}{\rho} \begin{vmatrix} -J_0 & -b_1 - \Re_e(v_1) a_1 (1 - m) \\ \Psi'(x^*) y^{*2} & e_1 \end{vmatrix},$$

where

$$\rho = \begin{vmatrix} -J_0 & a_1(1-m)x^* \\ \Psi'(x^*)y^{*2} & r_2 \end{vmatrix}.$$

Thus, we can determine W_{20} and W_{11} from Eq.(54) and Eq.(55). Furthermore, g_{21} in Eq.(46) can be expressed in terms of parameters and delay. Thus, we can compute the following values

$$\begin{aligned} C_1(0) &= \frac{i}{2w_0\tau_j^0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}, \\ v_2 &= -\frac{\Re\{C_1(0)\}}{\Re\{\lambda'(\tau_j^0)\}}, \\ \beta_2 &= 2\Re\{C_1(0)\}, \\ T_2 &= -\frac{\Im\{C_1(0)\} + v_2\Im\{\lambda'(\tau_j^0)\}}{w_0\tau_j^0}, \end{aligned} \tag{61}$$

which determine the qualities of bifurcating periodic solution in the center manifold at the critical value τ_j^0 .

Theorem 4. [17]: *In Eq. (61), the sign of v_2 determines the direction of the Hopf bifurcation. Thus, if $v_2 > 0$, then the Hopf bifurcation is supercritical and the bifurcating periodic solution exists for $\tau_1 > \tau_1^0$. If $v_2 < 0$, then the Hopf bifurcation is subcritical and the bifurcating periodic solution exists for $\tau_1 < \tau_1^0$. β_2 determines the stability of the bifurcating periodic solution: The bifurcating periodic solutions are stable if $\beta_2 < 0$ and unstable if $\beta_2 > 0$. T_2 determines the period of the bifurcating periodic solutions: the period increase if $T_2 > 0$ and decrease if $T_2 < 0$.*

6. BIONOMIC EQUILIBRIUM AND OPTIMAL HARVEST POLICY

The first part of this section deals with the *bionomic equilibrium* of System (6). The term bionomic equilibrium is an amalgamation of the concepts of biological equilibrium and economic equilibrium. As we already saw, a biological equilibrium is given by $\dot{x} = 0 = \dot{y}$. The economic

equilibrium is said to be achieved when TR (the total revenue obtained by selling the harvested biomass) equals TC (the total cost for the effort devoted to harvesting).

To discuss the bionomic equilibrium of the prey-predator model, we consider the parameters such as c = cost per unit effort for prey; p = price per unit biomass for the prey.

The net economic rent or net revenue (R) at any time is given by

$$(62) \quad R(x, h, t) = \left(p \frac{x - T_1}{T_2 - T_1} - c \right) h \text{ if } T_1 \leq x \leq T_2,$$

and

$$(63) \quad R(x, h, t) = (p - c)h \text{ if } x \geq T_2.$$

The bionomic equilibrium is $P_\infty(x_\infty, y_\infty, h_\infty)$, where x_∞ , y_∞ and h_∞ are the positive solutions of the following simultaneous equations

$$(64) \quad \begin{cases} (r_1 - b_1x)x - a_1(1 - m)xy - \frac{h(x - T_1)}{T_2 - T_1} = 0, \\ [r_2 - \frac{a_2y}{(1 - m)x}]y = 0, \quad \text{if } T_1 \leq x \leq T_2 \\ \left(p \frac{x - T_1}{T_2 - T_1} - c \right) h = 0, \end{cases}$$

and

$$(65) \quad \begin{cases} (r_1 - b_1x)x - a_1(1 - m)xy - h = 0, \\ [r_2 - \frac{a_2y}{(1 - m)x}]y = 0, \quad \text{if } x \geq T_2 \\ (p - c)h = 0, \end{cases}$$

It may be noted here that if $c > p \frac{x - T_1}{T_2 - T_1}$ when $T_1 \leq x \leq T_2$ or if $c > p$ when $x \geq T_2$, i.e. if the prey cost exceeds the revenue obtained from it, then the economic rent obtained from the prey becomes negative. Hence the prey will be closed and no bionomic equilibrium exists. Therefore, for the existence of bionomic equilibrium, it is natural to assume $c < p \frac{x - T_1}{T_2 - T_1}$ when

$T_1 \leq x \leq T_2$ and $c < p$ when $x \geq T_2$. Then, for $T_1 \leq x \leq T_2$,

$$(66) \quad x_\infty = T_1 + \frac{c}{p}(T_2 - T_1),$$

$$(67) \quad y_\infty = \frac{r_2(1-m)x_\infty}{a_2},$$

$$(68) \quad h_\infty = \frac{p(r_1 - b_1x_\infty - a_1(1-m)y_\infty)x_\infty}{c}.$$

It is clear that $h_\infty > 0$ if

$$(69) \quad r_1 - b_1x_\infty - a_1(1-m)y_\infty > 0.$$

Thus, the bionomic equilibrium $P_\infty(x_\infty, y_\infty, h_\infty)$ exists if $x_\infty \leq T_2$ and inequality (69) holds.

In what follows, our objective is to maximize the total discounted net revenues from the fishery. In commercial exploitation of renewable resources, the fundamental problem from the economic point of view, is to determine the optimal trade-off between present and future harvests. If we look at the problem, it is observed that the marine fishery sectors become more important not only for domestic demand but also from the imperatives of exports.

Symbolically our strategy is to maximize the present value J given by

$$(70) \quad J(h) = \int_0^{t_f} R(x(t), h(t), t) e^{-\delta t} dt,$$

where $R(x, h, t) = \left(p \frac{x - T_1}{T_2 - T_1} - c\right)h$ if $T_1 \leq x \leq T_2$, $R(x, h, t) = (p - c)h$ if $x \geq T_2$ and δ denotes the instantaneous annual rate of discount. Our problem is to maximize J subject to the state System (6) by invoking Pontryagin's Maximum principle for retarded optimal control problem [26]. The control variable $h(t)$ is subjected to the constraints $0 \leq h(t) \leq K$. So, in other words, our problem now is to find h^* such that

$$(71) \quad J(h^*) = \max_{h \in \Omega} J(h),$$

where $\Omega = \{h \in L^1(0, t_f); 0 \leq h \leq K\}$.

The existence of an optimal harvesting is due to the concavity of integrand of J with respect to h , a boundedness of the state solutions $(x(t), y(t))$, and the Lipschitz property of the state system (6) with respect to the state variables (see [32]).

Using the Pontryagin's maximum principle for delayed control problem [26, 30], problem (71) is reduced to maximize the Hamiltonian \mathcal{H} defined by:

$$\begin{aligned} \mathcal{H}(x(t), y(t), x(t-\tau), y(t-\tau), h(t), \lambda(t)) = & \\ e^{-\delta t} R(x(t), h(t), t) + \lambda_1(r_1 - b_1 x(t))x(t) & \\ + \lambda_1 \left[-a_1(1-m)x(t)y(t) - H(x(t)) \right] & \\ + \lambda_2 \left[r_2 y(t) - \frac{a_2 y(t-\tau)y(t)}{(1-m)x(t-\tau)} \right], & \end{aligned}$$

where $\lambda = (\lambda_1, \lambda_2)$. By the maximal principle, there exists adjoint variables $\lambda_1(t)$ and $\lambda_2(t)$ for all $t \geq 0$ such that

$$(72) \quad \begin{cases} \frac{d\lambda_1(t)}{dt} = -\chi_{[0, t_f - \tau]}(t) \frac{\partial \mathcal{H}}{\partial x(t-\tau)}(t + \tau), \\ \quad \quad \quad - \frac{\partial \mathcal{H}}{\partial x(t)}(t) \\ \frac{d\lambda_2(t)}{dt} = -\chi_{[0, t_f - \tau]}(t) \frac{\partial \mathcal{H}}{\partial y(t-\tau)}(t + \tau), \\ \quad \quad \quad - \frac{\partial \mathcal{H}}{\partial y(t)}(t) \end{cases}$$

and

$$(73) \quad \frac{\partial \mathcal{H}}{\partial h(t)}(x(t), y(t), x(t-\tau), y(t-\tau), h(t), \lambda(t)) = 0,$$

where $\chi_{[0, t_f - \tau]}(t)$ is the indicatrice function on $[0, t_f - \tau]$.

Therefore, we obtain the adjoint system:

$$(74) \quad \begin{cases} \dot{\lambda}_1(t) = -\frac{ph}{T_2 - T_1} e^{-\delta t} + \lambda_1(t)(-r_1 + 2b_1 x(t)) \\ \quad + \lambda_1(t) \left(a_1(1-m)y(t) + \frac{h}{T_2 - T_1} \right) \\ \quad - \chi_{[0, t_f - \tau]}(t) \frac{a_2 y(t+\tau) \lambda_2(t+\tau) y(t)}{(1-m)x^2(t)}, \\ \dot{\lambda}_2(t) = -a_1(1-m)x(t)\lambda_1(t) - r_2 \lambda_2(t) \\ \quad + \chi_{[0, t_f - \tau]}(t) \frac{a_2 y(t+\tau) \lambda_2(t+\tau)}{(1-m)x(t)}. \end{cases}$$

The transversality conditions of System (74) are

$$\lambda_1(t_f) = \lambda_2(t_f) = 0.$$

Since \mathcal{H} is linear in the control variable h , the optimal control will be a combination of bang-bang control and singular control. Let

$$\sigma(t) = e^{-\delta t} \left(\frac{p(x-T_1)}{T_2-T_1} - c \right) - \lambda_1(t) \frac{(x-T_1)}{T_2-T_1}.$$

The optimal control $h(t)$ which maximizes \mathcal{H} must satisfy the following conditions:

$$(75) \quad h(t) = K \quad \text{if} \quad \sigma(t) > 0$$

$$(76) \quad \text{i.e.} \quad e^{\delta t} \lambda_1(t) < p - \frac{c}{\frac{x-T_1}{T_2-T_1}},$$

$$(77) \quad h(t) = 0 \quad \text{if} \quad \sigma(t) < 0$$

$$(78) \quad \text{i.e.} \quad e^{\delta t} \lambda_1(t) > p - \frac{c}{\frac{x-T_1}{T_2-T_1}},$$

where $e^{\delta t} \lambda_1(t)$ is the usual shadow price [18] and $p - \frac{c}{\frac{x-T_1}{T_2-T_1}}$ is the net economic revenue on a unit harvest. This shows that $h = K$ or zero according to the shadow price is less than or greater than the net economic revenue on a unit harvest. Economically, condition (76) implies that if the profit after paying all the expenses is positive, then it is beneficial to harvest up to the limit of available effort. Condition (78) implies that when the shadow price exceeds the fisherman's net economic revenue on a unit harvest, then the fisherman will not exert any effort.

When $\sigma(t) = 0$, i.e. when the shadow price equals the net economic revenue on a unit harvest, then the Hamiltonian \mathcal{H} becomes independent of the control variable $h(t)$, i.e. $\partial \mathcal{H} / \partial h = 0$. This is the necessary condition for the singular control $h(t)$ to be optimal over the control set $0 \leq h \leq K$. Thus, the optimal harvesting policy is

$$h(t) = \begin{cases} 0 & \text{if } \sigma(t) < 0, \\ h^* & \text{if } \sigma(t) = 0, \\ K & \text{if } \sigma(t) > 0. \end{cases}$$

Solving $\sigma(t) = 0$, we get

$$(79) \quad \lambda_1(t) = e^{-\delta t} \left(p - \frac{c}{\frac{x-T_1}{T_2-T_1}} \right).$$

Substituting Eq(79) into System (74) gives

$$(80) \quad \left\{ \begin{array}{l} \dot{\lambda}_1(t) = -\frac{ph}{T_2 - T_1} e^{-\delta t} + e^{-\delta t} \left(p - \frac{c}{\frac{x - T_1}{T_2 - T_1}} \right) \times \\ \left(-r_1 + 2b_1x(t) + a_1(1 - m)y(t) + \frac{h}{T_2 - T_1} \right) \\ - \mathcal{X}_{[0, t_f - \tau]}(t) \frac{a_2y(t + \tau)\lambda_2(t + \tau)y(t)}{(1 - m)x^2(t)}, \\ \dot{\lambda}_2(t) = -a_1(1 - m)x(t)e^{-\delta t} \left(p - \frac{c}{\frac{x - T_1}{T_2 - T_1}} \right) \\ - r_2\lambda_2(t) + \mathcal{X}_{[0, t_f - \tau]}(t) \frac{a_2y(t + \tau)\lambda_2(t + \tau)}{(1 - m)x(t)}. \end{array} \right.$$

Using equilibrium conditions and integrating System (80), we obtain $\lambda_1(t)$ and $\lambda_2(t)$. Solving equation

$$\lambda_1(t) = p - \frac{c}{\frac{x - T_1}{T_2 - T_1}},$$

we obtain the optimal harvesting efforts h^* .

7. NUMERICAL SIMULATIONS

In this section, we give some numerical simulations for a special case of System (6) with harvesting function (5) to support our analytical results in this paper. As an example, we consider systems (6) and (5) with the coefficients $r_1 = 1.1$, $b_1 = 1.1/300$, which gives $K = 300$, $m = 0.1$, $a_1 = 0.11$, $r_2 = 0.2$, $a_2 = 1$, $h = 0.2 * K$, $T_1 = 60$, $T_2 = 90$ and $\tau = 20$. When there is no delay, we choose $x(0) = 40$ and $y(0) = 25$. That is,

$$(81) \quad \left\{ \begin{array}{l} \dot{x}(t) = \left(1.1 - \frac{1.1}{300} * x \right) * x \\ - 0.11 * (1 - 0.1) * x * y - H(x(t)), \\ \dot{y}(t) = \left(0.2 - \frac{1.2 * y(t - \tau)}{(1 - 0.1) * x(t - \tau)} \right) * y(t). \end{array} \right.$$

In Figure 3, we have $\Delta_1 = 117.5377 > 0$, $-\varphi'(K_0) + a_1(1-m)y_0 + r_2 = 11.2751 > 0$ and $2a_1(1-m)r_2y_0 - r_2\varphi'(K_0) = 2.3975 > 0$. So, the conditions of stability of equilibrium $G_0(K_0, y_0)$ are satisfied and G_0 is locally asymptotically stable.

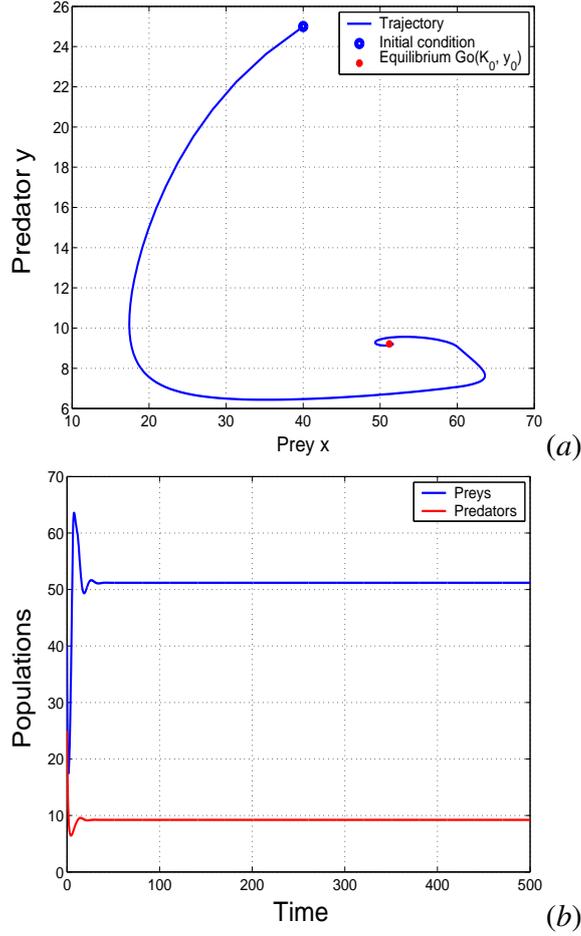


FIGURE 3. The numerical approximations of system (6) when $\tau = 0$ and $K_0 = 51.1945 < T_1$. The positive equilibrium $G_0(51.1945, 9.2150)$ is a asymptotically stable.

Fig. 4 shows that under some conditions, equilibrium $G_1(x_1^*, y_1^*)$ is the only equilibrium of the model system (6) and is locally asymptotically stable. More precisely, we have $x_1^* - T_2 = 68.065$, $K_0 - x_1^* = 83.28$, $\varphi(T_2) - h = 9.3$, $\Delta_1 = 1.14 \times 10^3$,

$$-\varphi'(x_1^*) + a_1(1-m)y_1^* + r_2 = 33.8253 > 0$$

and $2a_1(1-m)r_2y_1^* - r_2\phi'(x_1^*) = 0.3396 > 0$. So, we have $T_2 < x_1^* < K_0$, $\phi(T_2) > h$ and all conditions which give the stability of G_1 .

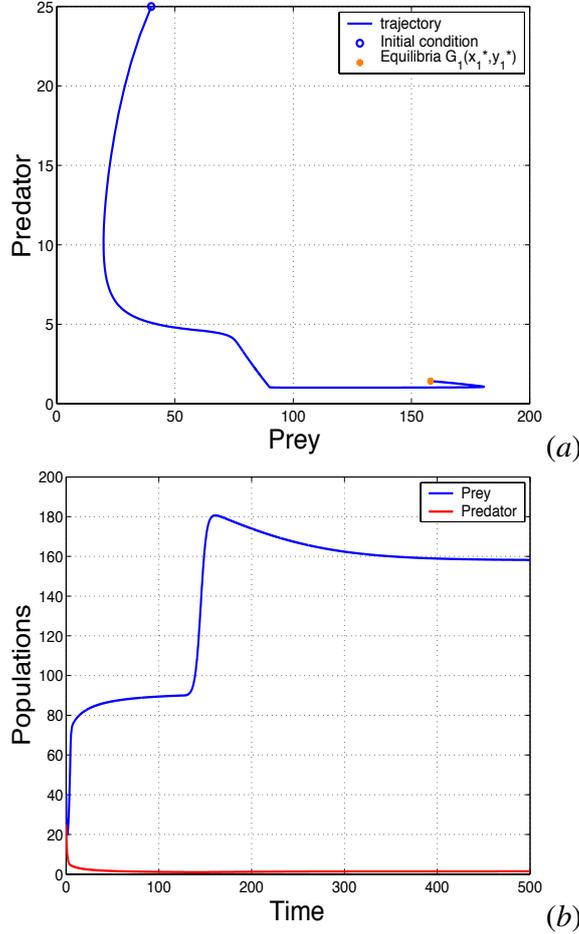


FIGURE 4. The numerical approximations of system (6) when $\tau = 0$, $r_2 = 0.01$ and $K_0 = 241.35 > T_2$. The positive equilibrium $G_1(158.0658, 1.4226)$ is a asymptotically stable.

We now present some numerical results of the system for different values of τ . From the above discussion, we may determine the direction of Hopf-bifurcation and the direction of bifurcating periodic solution. We consider the system when the parameter values are given as in Figure (3). So, the model has a positive equilibrium $G_0(51.1945, 9.2150)$ which is locally asymptotically stable for $\tau = 0$. When τ passes through the critical value $\tau = \tau_1^0 = 95.2311$ and $\left. \frac{d(R_e\lambda(\tau))}{d\tau} \right|_{\lambda=i\omega_0, \tau=\tau_1^0} = 7.6799 > 0$, the equilibrium G_0 losses its stability and the system (6) experiences Hopf-bifurcation. From Sect. 5 we can determine the nature of the stability and

direction of the periodic solution bifurcating from the interior equilibrium at the critical point τ_0^0 .

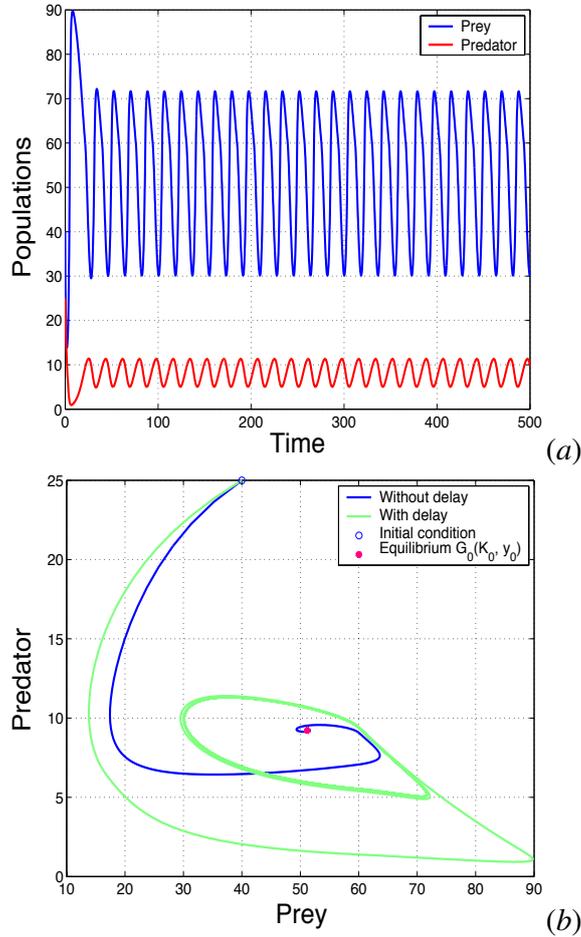


FIGURE 5. Hopf bifurcation behavior of the system (6) around the interior equilibrium $G_0(51.1945, 9.2150)$ when $\tau = \tau_0^0 = 95.2311$. The other parameter are the same as in Fig. (3). We obtain the existence of unstable supercritical bifurcating periodic solution around the interior equilibrium G_0 with the same parameter values as in Fig. (3).

Using (61), we can compute $C_1(0) = 69.7625 - 28.9307i$, $\nu_2 = 968.6446 > 0$, $\beta_2 = 139.5250 > 0$ and $T_2 = -120.1525$. Hence, the bifurcating periodic solution exists when τ crosses τ_1^0 from left to right and the corresponding periodic solution is supercritical and unstable (as $\beta_2 > 0$) as evident from Fig. 5 (a)-(b). The negative sign of T_2 indicates the decreasing period of the

periodic solution of the system. Moreover, this system is locally asymptotically stable around the interior equilibrium G_0 , which is clearly depicted from Fig. 6(a).(b) for $\tau = 16 < \tau_0^0$.

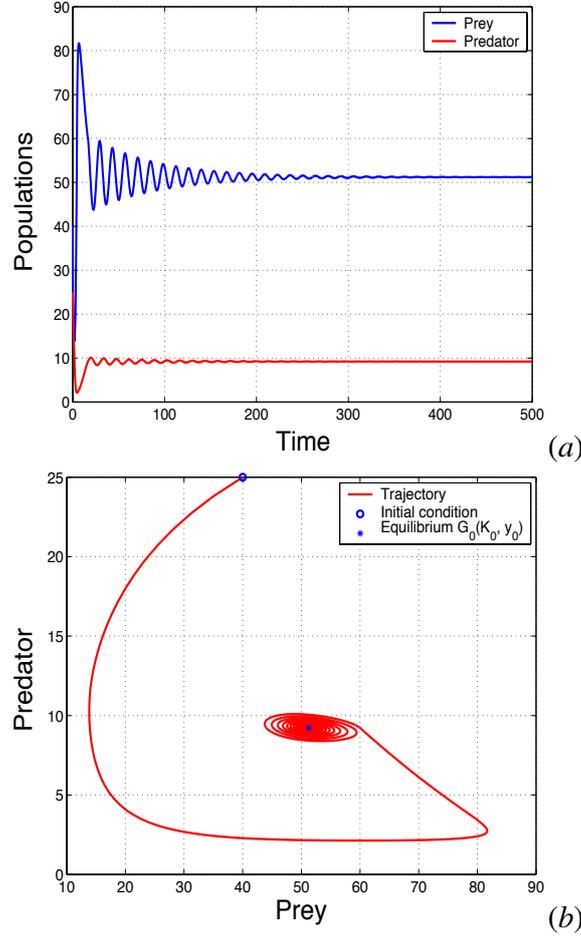


FIGURE 6. The system (6) is globally asymptotically stable around the interior equilibrium G_0 at $\tau = 16 < \tau_0 = 95.2311$. The other parameter values are given in the previous figure.

Figure (7) gives the optimal harvesting of prey in the presence of the two population. We observe that the control increase the period of limit cycle (see Figure (7 a)) and also increase the predator and prey population (see Figure (7 b and c)). In order to obtain this result, the harvesting will be made periodically (see Figure (7 d)). From this figure, it is clear that as the time progresses the prey and predator populations fluctuate in different period depending on the values of the optimal harvesting. We observe that when we harvest, the predator population decrease quickly and the prey population starts to rise rapidly. On the other hand as the predator

population rises, the prey population descends speedily. This figure is obtained when $p = 30$, $c = 35$ and $\delta = 0.1$.

8. CONCLUSIONS

In this paper, the properties of Hopf bifurcations in a Leslie-Gower Predator-Prey model with delay in predator's equation have been studied. We have also investigated optimal harvesting when the harvesting is given by a continuous function in this model. Although bifurcations in a population dynamics without delay have been investigated by many researchers, there are few papers on the bifurcations of a population dynamics with delay, which have shown direction of global Hopf-bifurcation and optimal harvesting simultaneously. We have obtained sufficient conditions on the parameters for which the delay-induced system is asymptotically stable around the positive equilibrium for all values of the delay parameter and if the conditions are not satisfied, then there exists a critical value of the delay parameter below which the system is stable and above which the system is unstable. By applying the normal form theory and the center manifold theorem, the explicit formulae which determine the stability and direction of the bifurcating periodic solutions have been determined. Our analytical and simulation results show that when the delay τ passes through the critical value τ_0^0 , the coexisting equilibrium G_0 loses its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcate from G_0 . Also, the amplitude of oscillations increases with increasing τ . For the considered parameter values, it is observed that the Hopf bifurcation is supercritical and the bifurcating periodic solution is unstable. The problem of optimal harvesting policy has been solved by using the new result of retarded optimal control which is an extension of Pontryagin's Maximal principle theory. We hope that the theoretical investigations which have been carried out in this paper will certainly help the experimental ecologists to do some experimental studies and as a consequence the theoretical ecology may be developed to some extent.

Conflict of Interests

The author(s) declare that there is no conflict of interests.

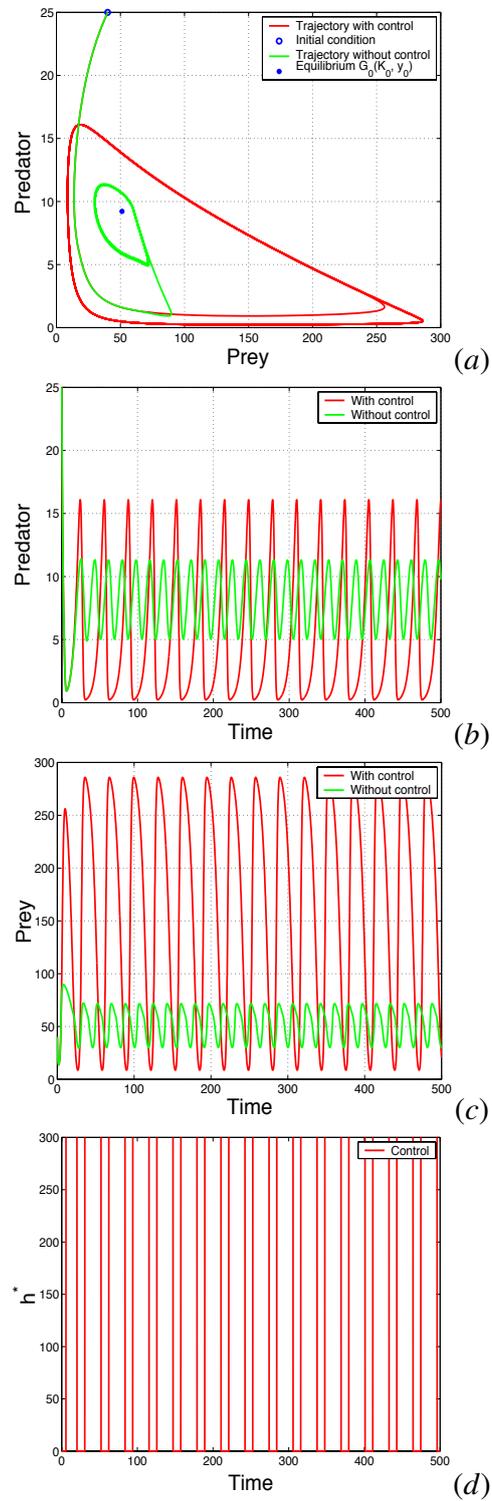


FIGURE 7. Trajectory of the model system (6) with and without the control.

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Hopf bifurcation analysis in a delayed Leslie–Gower predator–prey model incorporating additional food for predators, refuge and threshold harvesting of preys

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Abstract In this paper, we formulate and analyze a modified Leslie–Gower predator–prey model. Our model incorporates refuge of preys, additional fixed food for predators, harvesting of preys through a continuous threshold policy and a time delay as to account for predators maturity time. We first carry out a qualitative analysis of the model without time delay, showing existence of extinction, prey-free, predator-free and coexistence equilibria. We further study their stability conditions. Relying only on theoretical results of the model, we construct bifurcation diagrams involving refuge and harvest limit parameters. This led to summarize different scenarios for the model including elimination of one species or competition of both species that are proved possible. Furthermore, considering the time delay as bifurcation parameter, we analyze the stability of the coexistence equilibria and prove the system can undergoes a Hopf bifurcation. The direction

of that Hopf bifurcation and the stability of the bifurcated periodic solution are determined by applying the normal form theory and the center manifold theorem. Numerical simulations are presented to illustrate our theoretical results.

Keywords Hopf bifurcation · Center manifold · Delayed Leslie–Gower model · Normal form · Continuous threshold policy · Additional food

1 Introduction

Relationship between predators and their preys has been modeled by Lotka [42] and Volterra [64]. Their model, which is nowadays considered as the simplest predator–prey model, has been modified by authors like Leslie [36, 37]. In their researches, they considered that a predator consumes only one type of prey and does not have another source of food. This hypothesis has been modified by authors who consider that a predator can be provided with additional food [49, 54, 55]. In this way, many experimentalists and theoreticians have studied the consequences of providing a predator with additional food, the corresponding effects on the predator–prey dynamics, its utility on controllability of ecosystems such as integrated pest management and species conservation which employ biological control as one of the tools [7, 14, 24, 25, 47, 52, 57, 62]. Van Rijn et al. [63], Sabelis and van Rijn [51]), and Ulfa et al. [60] have investigated the consequences of providing additional

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food to predators in a predator–prey system. Recently, Srinivasu et al. [56] have studied the qualitative behavior of a predator–prey system incorporating additional food for the predator. The conclusion of their investigation was that handling times for the available foods to the predator play a key role in the determination of the eventual state of the ecosystem. For Haque and Greenhalgh [23], providing alternative food to predators can play an important role in promoting the persistence of predator–prey systems. Alves [1] studied a model with additional food and a preference rate of the predator for one or the other food. He concluded that providing alternative fixed food to predator causes a distraction effect. That distraction effect has been identified as a mechanism which can favor positive indirect effects on the principal prey in the long term. According to Alves [1], due to the presence of alternative food, the predator does not spend all its searching time on its favorite food, so its consumption of that favorite food is no more at the maximal rate. Then, there is a negative impact on the growth rate of the predator [53].

Spatial refuges by the prey population is one of the more relevant behavioral traits that affect the dynamics of predator–prey system. Several authors, including Chen et al. [11], Huang et al. [28] and Kar [30], investigated the influence of prey refuge in predator–prey models. They concluded that the prey refuge has a stabilizing effect on the predator–prey relationship. However, it is questionable to consider that prey consumed is instantaneously converted into predator biomass as in aforementioned works. Hence, it may be more realistic to assume that, after predating the prey, the reproduction of the predator is not instantaneous. It is necessary to take into account the fact that the reproduction of predator is mediated through some time lag which is required for gestation. For the above reasons, models with delays are more realistic than those without delays. For example, a time delay can cause the change of the stability of an equilibrium, making a stable equilibrium to become unstable through a Hopf bifurcation (see, e.g., Brauer [10], Kar et al. [31], Beretta et al. [6], Kuang [32], Gopalsamy [22], Azbelev et al. [4], Balachandran et al. [5], Arino et al. [2], Liu et al. [41], Liu et al. [38,40], Liu [39], Datta et al. [17], Ma [43], Nindjin et al. [48], Xiao and Li [65], Xu et al. [66], Yafia et al. [67], Xu et al. [66], Yan and Li [69], Yuan et al. [70], Yuan et al. [72,73], Yuan and Song [71], Zi-Zhen and Hui-Zhong [75]).

Predators and preys are ecological resources. So they can be used either for human being needs or for commercial industries. It can then be exploited and harvested in fishery, forestry and wildlife management. There is a wide range of interest in the use of bioeconomic models to gain insight into the scientific management of the renewable resources like fisheries and forestries [13]. To study the effect of harvesting in the dynamic of relationship between species, some harvesting functions have been considered by researchers. We can cite constant harvesting function, linear harvesting functions, nonlinear harvesting functions, quadratic harvesting functions [17,20,21,30,31,34,35,41,50,61,74] and the so-called continuous threshold policy (CTP) which use one or more than one threshold and with which harvesting starts when the population of the species being harvested has reached a certain threshold [8,33,45,59].

In what follows, we formulate and analyze a Leslie–Gower predator–prey model derived from the one proposed by Alves [1], but with some improvements. Notably, we take into account time delay τ for the conversion time from prey biomass to predator biomass after predation. In addition, a prey refuge is also considered. Finally, a CTP harvesting function for preys is taken into account. The organization of our paper is as follows: We formulate the model in Sect. 2. In Sect. 3, we prove that each solution of the system is positive and bounded. Section 4 contains the equilibria of the model without the time delay and their stability. Considering the time delay as bifurcation parameter, the investigation for a Hopf bifurcation is done and the stability of equilibria is studied in Sect. 5. We analyze the stability and the direction of the existing Hopf bifurcation in Sect. 6. Numerical simulations results are supplied in Sect. 7 in support of the theoretical analysis.

2 The model formulation

Alves [1] formulated and analyzed the following model:

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t)}{K_1} \right) x(t) - q\lambda_1 x(t)y(t), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t)}{q\alpha_1 x(t) + (1-q)\alpha_A K_A} \right) y(t), \end{cases} \quad (1)$$

where the variables $x(t)$ and $y(t)$ are, respectively, the preys and the predators population at time t . In

model (2), we have two categories of parameters. The parameters r_1 and r_2 are the intrinsic growth rates of preys and predators, respectively. λ_1 measures the strength of competition among individuals of preys population, K_1 is the carrying capacity of the preys when there is no predation, α_1 measures the amount of energy in the form of biomass of the prey $x(t)$ assimilate into the predator's energy in terms biomass. The parameters $r_1, r_2, \lambda_1, \alpha_1$ and K_1 always exist in a Leslie–Gower predator–prey model. The parameters q, K_A and α_A have been introduced by Alves [1] with the assumption of additional food for predators. He assumes that the predator is provided with additional food of constant density K_A . The parameter α_A measures the amount of energy in the form of biomass of the additional food assimilate into the predator's energy in terms of biomass. The parameter q is the preference rate of the predator due to the fact that the predator has two sources of food. It means that if $q = 0$, the predator consumes only the additional food A . Thus the carrying capacity of the predator is $\alpha_A K_A$. If $q = 1$, the predator consumes only the prey x . So the carrying capacity of the predator is $\alpha_1 x(t)$. If $q \in (0, 1)$, the predator consumes two sources of food according to proportions defined by the parameter q . The carrying capacity of the predator population is then given by $q\alpha_1 x(t) + (1 - q)\alpha_A K_A$ according to the formalism of Stephens and Krebs [58]. Our model, incorporating prey refuge, additional food for predators, time delay and harvesting of preys, is given by the following set of ordinary differential equations:

$$\begin{cases} \dot{x}(t) = r_1 \left(1 - \frac{x(t)}{K_1}\right) x(t) - q\lambda_1(1 - m)x(t)y(t) - \varphi(x(t)), \\ \dot{y}(t) = r_2 \left(1 - \frac{y(t - \tau)}{q\alpha_1(1 - m)x(t - \tau) + (1 - q)\alpha_A K_A}\right) y(t). \end{cases} \quad (2)$$

Due to the fact that the reproduction of the predator population after the predation of preys is not an instantaneous phenomenon, we introduced a time delay τ in the predator equation which represents the time lag for gestation or maturation of the predator. The parameter $m \in [0, 1)$ measures the strength of refuge. It means that $m x(t)$ models the capacity of a refuge at the time t . Hence, refuge protecting $m x(t)$ quantity of the prey population at the time t , it remains $(1 - m)x(t)$ quantity of preys available to the predation. $\varphi(x(t))$ denotes the continuous threshold prey harvesting function defined as follows:

$$\varphi(x) = \begin{cases} 0 & \text{if } x < T_1, \\ \frac{h(x - T_1)}{h + x - T_1} & \text{if } x \geq T_1. \end{cases} \quad (3)$$

In this way, if the prey population is less than the threshold T_1 , there is not harvesting of preys. Once the prey population reaches the size $x = T_1$, their harvesting starts and increases smoothly to a limit value h . From both biological and practical point of views, such harvesting function is more sound than its constant or linear counterparts [8, 59]. For biological reason, it is natural to assume

$$T_1 < K_1 \quad \left(K_1 = \frac{r_1}{b_1}\right). \quad (4)$$

Due to the fact that it is not plausible to have the number of preys (respectively, the number of predators) at time $t = 0$ greater than the carrying capacity $K_1 = \frac{r_1}{b_1}$ (respectively, $K_2 = q\alpha_1(1 - m)K_1 + \alpha_A K_A$) of preys (respectively, predators), we assume:

$$0 \leq x(0) < \frac{r_1}{b_1} \quad (5)$$

and

$$0 \leq y(0) < q\alpha_1(1 - m)K_1 + \alpha_A K_A. \quad (6)$$

The initial conditions for system (2)–(3) are chosen as:

$$x(0) \geq 0, \quad y(0) \geq 0. \quad (7)$$

For $\theta \in [-\tau, 0]$, we use the notation:

$$x_t(\theta) = x(t + \theta). \quad (8)$$

Then the initial conditions for the system take the form:

$$x_0(\theta) = \phi_1(\theta), \quad y_0(\theta) = \phi_2(\theta), \quad (9)$$

for all $\theta \in [-\tau, 0]$, where $(\phi_1, \phi_2) \in \mathcal{C}([-\tau, 0], \mathbb{R}_+^2)$, $x(0) = \phi_1 > 0$ and $y(0) = \phi_2 > 0$.

$\mathcal{C} = \mathcal{C}([-\tau, 0], \mathbb{R}_+^2)$ is the Banach space of continuous functions from the interval $[-\tau, 0]$ into $\mathbb{R}_+^2 = \{(x, y) : x \geq 0, y \geq 0\}$.

3 Positivity and boundedness of solutions

3.1 Positivity of solutions

In this subsection, we prove that our model is biologically meaningful. It means that the variables $x(t)$ and $y(t)$ which represent the population of preys and predators, respectively, are always positive. We have the following theorem.

Theorem 1 When assumptions (5) and (6) hold, the positive quadrant \mathbb{R}_+^2 is invariant for system (2)–(3).

Proof See “Appendix A.” □

3.2 Boundedness of solutions

In this subsection, we prove that each solution of system (2)–(3) is bounded. The following theorem holds.

Theorem 2 When assumptions (5) and (6) hold, each solution of system (2)–(3) is uniformly bounded.

Proof See “Appendix B.” □

4 Equilibria of the model and their stability when $\tau = 0$

4.1 Equilibria of the model when $\tau = 0$

In the following theorem, we give equilibria of system (2)–(3).

Theorem 3 1. When $x < T_1$, system (2)–(3) has four equilibria which are:

- $E_1^0(0, 0)$ which means that both predators and preys are absent.
- $E_2^0(0, (1 - q)\alpha_A K_A)$ for which there is no prey, while the predator population reaches its carrying capacity.
- $E_3^0(K_1, 0)$ for which there is no predator and the prey population reaches its carrying capacity.
- $E_4^0\left(\frac{r_1 - \lambda_1(1 - m)q(1 - q)\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}, \frac{r_1\alpha_1(1 - m)q + (1 - q)b_1\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}\right)$.

The coexistence equilibrium E_4^0 is biologically meaningful if $r_1 > \lambda_1(1 - m)q(1 - q)\alpha_A K_A$.

2. When $x \geq T_1$, system (2)–(3) is such that:

- $E_1^\varphi(x_1^\varphi, 0)$ is an equilibrium for which there is no predator and the number x_1^φ of preys is a positive solution on the interval $[T_1, K_1]$ of equation (10):

$$-b_1x^3 + (r_1 - b_1(h - T_1))x^2 + (r_1(h - T_1) - h)x + hT_1 = 0. \tag{10}$$

- $E_2^\varphi(x_2^\varphi, y_2^\varphi)$ is an equilibrium where $y_2^\varphi = (1 - m)q\alpha_1x_2^\varphi + (1 - q)\alpha_A K_A$ and the number x_2^φ of preys is a positive solution on the interval $[T_1, K_1]$ of equation (11)

$$A_1^\varphi x^3 + A_2^\varphi x^2 + A_3^\varphi x + hT_1 = 0, \tag{11}$$

where

$$\begin{aligned} A_1^\varphi &= -b_1 - q^2\lambda_1\alpha_1(1 - m)^2, \\ A_2^\varphi &= r_1 - q(1 - q)(1 - m)\lambda_1\alpha_A K_A - (h - T_1)(b_1 + q^2\lambda_1\alpha_1(1 - m)^2), \\ A_3^\varphi &= (r_1 - q(1 - q)(1 - m)\lambda_1\alpha_A K_A)(h - T_1) - h. \end{aligned}$$

Proof See “Appendix C.” □

Note that if *CONDEX*(x_2^φ) below holds

$$\begin{aligned} \text{CONDEX}(x_2^\varphi) : r_1 - b_1T_1 - q\lambda_1(1 - m) \\ (1 - q)\alpha_A K_A + q(1 - m)\alpha_1T_1 > 0 \end{aligned}$$

then equation (11) will have at least one solution in the interval $[T_1, K_1]$. So, we have a sufficient condition for the existence of the coexistence equilibrium E_2^φ .

In what follows, we discuss on the results of the above theorem in terms of the preference rate q , the threshold of harvesting T_1 and the intrinsic growth rate of preys r_1 . The aim of that discussion is to analyze the impact of the preference rate q , the threshold of harvesting T_1 and the intrinsic growth rate of preys r_1 on the equilibria of the model. As it has been done in the theorem, we distinguish two cases:

1. *Case 1* : $x < T_1$, there is no harvesting of preys.

1.1. $q = 0$, the predator consumes only the additional food A .

- Equilibria E_1^0 and E_3^0 remain unchanged.
- The equilibrium $E_2^0 = (0, \alpha_A K_A)$ is such that the predator reaches its carrying capacity.
- The coexistence equilibrium $E_4^0 = (K_1, (1 - m)\alpha_A K_A)$ always exists (the condition of its existence given in the theorem is satisfied); the preys x which are not consumed reach their carrying capacity, while the predator also reaches its carrying capacity taking into account the refuge of the preys x .

1.2. $q = 1$, the predators consume only the preys.

- Equilibria E_1^0 and E_3^0 remain unchanged.
- The predator population does not more reach its carrying capacity when the preda-

tors consume only the preys. The equilibrium $E_2^0 = (0, 0) = E_1^0$.

- The coexistence equilibrium E_4^0 $\left(\frac{r_1}{b_1 + \lambda_1 \alpha_1 (1 - m)^2}, \frac{r_1 \alpha_1 (1 - m) + (1 - m) b_1 \alpha_A K_A}{b_1 + \lambda_1 \alpha_1 (1 - m)^2} \right)$ always exists. (The condition of its existence $r_1 > \lambda_1 (1 - m) q (1 - q) \alpha_A K_A$ given in the theorem is satisfied.) Preys and predators do not more reach their carrying capacities as when $q = 0$.

We remark that when the predators consume only one source of food, the coexistence equilibrium always exists.

- 1.3. $q \in (0, 1)$, the predators consume the two sources of food according to the preference rate q .

- Equilibria E_1^0, E_2^0 and E_3^0 always exist with the possibility for the preys or the predators to reach their carrying capacities.

- The coexistence equilibrium does not more always exists. Its existence depends on the intrinsic growth rate r_1 of preys, the density of additional fixed food for predators K_A , the amount of energy in the form of biomass of additional food assimilate into the predator's energy α_A , the strength of refuge m and the strength of competition among individuals of preys.

So if $r_1 \geq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then the coexistence equilibrium E_4^0 always exists for any value of the preference rate q in $(0, 1)$. If $r_1 \leq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then

the coexistence equilibrium E_4^0 exists only for the values of the preference rate q in $(0, q_1] \cup [q_2, 1)$ where $q_1 = \frac{1}{2} - \frac{1}{2} \sqrt{1 - \frac{4r_1}{\lambda_1 \alpha_A K_A (1 - m)}}$ and $q_2 = \frac{1}{2} + \frac{1}{2} \sqrt{1 - \frac{4r_1}{\lambda_1 \alpha_A K_A (1 - m)}}$.

2. Case 2 : $x \geq T_1$, there is harvesting of preys.

- 2.1. $q = 0$, the predator consumes only the additional food A .

- Equilibrium E_1^0 always exists.

- The coexistence equilibrium $E_2^0 = (x_2^0, \alpha_A K_A)$ always exists (using assumption (4) gives $r_1 - b_1 T_1 > 0$ and $CONDEX(x_2^0)$ holds); the predator population reaches its carrying capacity.

- 2.2. $q = 1$, the predators consume only the preys.

- The equilibrium E_1^0 always exists.
- The coexistence equilibrium $E_2^0 = (x_2^0, (1 - m) \alpha_1 x_2^0)$ always exists. (Using assumption (4) gives $r_1 - b_1 T_1 + (1 - m) \alpha_1 T_1 > 0$ and $CONDEX(x_2^0)$ holds.) Predators reach their carrying capacity.

- 2.3. $q \in (0, 1)$, the predators consume the two sources of food according to the preference rate q .

- Equilibrium E_1^0 always exists.
- The coexistence does not always exist. Its existence can be discussed in terms of the threshold of harvesting T_1 . Then, we have the following cases.

If $T_1 \geq \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$, then using assumption (4) gives $r_1 - b_1 T_1 - q \lambda_1 (1 - m) (1 - q) \alpha_A K_A + q (1 - m) \alpha_1 T_1 > r_1 - b_1 T_1 + (1 - m) \alpha_1 T_1 > 0$. Thus, $CONDEX(x_2^0)$ holds and the coexistence equilibrium E_2^0 exists.

If $T_1 < \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$ and $r_1 \geq \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then E_2^0 exists.

If $T_1 < \frac{\lambda_1 \alpha_A K_A}{\alpha_1}$ and $r_1 < \frac{\lambda_1 \alpha_A K_A (1 - m)}{4}$, then the coexistence equilibria E_2^0 does not always exist.

4.2 Stability of equilibria of the model without delay

The following theorem holds:

Theorem 4 1. The equilibrium E_1^0 is an unstable node.

2. The equilibrium E_2^0 is a stable node if $r_1 < q \lambda_1 (1 - m) (1 - q) \alpha_A K_A$ and a saddle (unstable) if $r_1 > q \lambda_1 (1 - m) (1 - q) \alpha_A K_A$. We have a saddle-node bifurcation.

3. The equilibrium E_3^0 is a saddle (unstable).

4. The equilibrium E_4^0 is locally asymptotically stable. More precisely, let us set:

$$\Delta_{E_4^0} = (b_1x_4^0 - r_2)^2 - 4(1 - m)^2\alpha_1r_2q^2x_4^0$$

- If $\Delta_{E_4^0} > 0$, then E_4^0 is a stable node.
- If $\Delta_{E_4^0} < 0$, then E_4^0 is a stable spiral.
- If $\Delta_{E_4^0} = 0$, then E_4^0 is a stable degenerate node.

5. The equilibrium E_1^φ is unstable. More precisely,

- if $\frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} < b_1x_1^\varphi$, then E_1^φ is a saddle.
- if $\frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} > b_1x_1^\varphi$, then E_1^φ is an unstable node.

6. Let us set:

$$\begin{aligned} Tr(J(E_2^\varphi)) &= -r_2 - b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2}, \\ |J(E_2^\varphi)| &= -r_2 \left(-b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) \\ &\quad + (1 - m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi, \\ \Delta_{E_2^\varphi} &= \left(r_2 - b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right)^2 \\ &\quad - 4(1 - m)^2q^2\lambda_1\alpha_1r_2x_2^\varphi. \end{aligned}$$

(a) When $\Delta_{E_2^\varphi} > 0$, the equilibrium E_2^φ is:

- a saddle if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi > 0$;
- a stable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi < 0$;
- an unstable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi > 0$.

(b) When $\Delta_{E_2^\varphi} < 0$, the equilibrium x_2^φ is:

- a stable spiral if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi < 0$;
- an unstable spiral if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi > 0$;
- a center if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi = 0$.

(c) When $\Delta_{E_2^\varphi} = 0$, the equilibrium x_2^φ is:

- a degenerate stable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi < 0$;
- a degenerate unstable node if $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - b_1x_2^\varphi - (1 - m)^2q^2\lambda_1\alpha_1x_2^\varphi < 0$ and $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} - r_2 - b_1x_2^\varphi > 0$.

Proof See ‘‘Appendix D.’’

□

Remark 1 When the equilibrium E_2 is locally asymptotically stable, the equilibrium E_4 does not exist. When E_4 exists, it is always locally asymptotically stable and E_2 is unstable.

Remark 2 If $\frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \leq 0$ or $h \geq \frac{(x_2^\varphi - T_1)^2}{T_1}$, then equilibrium E_2^φ is always stable. More precisely, x_2^φ is a stable node if $\Delta_{E_2^\varphi} > 0$, a stable spiral if $\Delta_{E_2^\varphi} < 0$ and a degenerate stable node if $\Delta_{E_2^\varphi} = 0$.

5 Hopf bifurcation and stability analysis of the delayed model

In this section, we study the stability of system (2)–(3) for $\tau > 0$. Before going further, let us recall the fact that if an equilibrium is unstable for $\tau = 0$, it remains unstable for $\tau > 0$ (see Martin et al. [44], Culshaw et al. [16]). Thus, we shall study the stability of the coexistence equilibrium without harvesting E_4^0 which is always stable when it exists and the stability of the coexistence equilibrium with harvesting E_2^φ . Let us recall that when equilibrium E_2^φ exists, it is stable if

$$-b_1x_2^\varphi - r_2 + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} < 0$$

and

$$-r_2 \left(-b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) + (1 - m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi > 0.$$

We recall that the equilibrium E_4 exists if

$$r_1 - \lambda_1(1 - m)q(1 - q)\alpha_A K_A > 0.$$

To linearize system (2)–(3) around an equilibrium $E(x_e, y_e)$ which can be E_4^0 or E_2^φ , let us set $X = x - x_e$ and $Y = y - y_e$. Then the linearized system of system (2)–(3) reads as:

$$\begin{cases} \dot{X}(t) = \left(-b_1x_e + \frac{\varphi(x_e)}{x_e} - \varphi'(x_e) \right) X(t) \\ \quad - q\lambda_1(1 - m)x_e Y(t), \\ \dot{Y}(t) = r_2(1 - m)q\alpha_1 X(t - \tau) - r_2Y(t - \tau). \end{cases} \quad (12)$$

From the linearized system (12), we have the following characteristic equation:

$$\lambda^2 + A_{1\varphi}\lambda + r_2\lambda e^{-\lambda\tau} + A_{2\varphi}e^{-\lambda\tau} = 0, \quad (13)$$

where

$$A_{1\varphi} = b_1x_e - \frac{h(x_e - T_1)^2 - h^2T_1}{x_e(x_e + h - T_1)^2},$$

$$A_{2\varphi} = A_{1\varphi}r_2 + r_2\lambda_1\alpha_1q^2(1 - m)^2x_e.$$

Now, let us investigate conditions under which the characteristic equation (13) has purely imaginary roots $\lambda = i\omega$.

Replacing λ by $i\omega$ in equation (13) gives:

$$-\omega^2 + A_{1\varphi}i\omega + A_{2\varphi}e^{-i\omega\tau} + r_2e^{-i\omega\tau}i\omega = 0. \quad (14)$$

Then separating the real and the imaginary parts in equation (14) gives:

$$-\omega^2 + A_{2\varphi}\cos\tau\omega + r_2\omega\sin\tau\omega = 0, \quad (15)$$

and

$$A_{1\varphi}\omega - A_{2\varphi}\sin\tau\omega + r_2\omega\cos\tau\omega = 0. \quad (16)$$

From equations (15) and (16), we have:

$$\cos\tau\omega = \frac{r_2\lambda_1\alpha_1q^2(1 - m)^2x_e\omega^2}{A_{2\varphi}^2 + r_2^2\omega^2} \quad (17)$$

and

$$\sin\tau\omega = \frac{A_{1\varphi}A_{2\varphi}\omega + r_2\omega^3}{A_{2\varphi}^2 + r_2^2\omega^2}. \quad (18)$$

From equations (17) and (18) and using the equation $\cos^2\tau\omega + \sin^2\tau\omega = 1$, we obtain the following equation:

$$r_2^2\omega^6 + (A_{2\varphi}^2 + r_2^2A_{1\varphi}^2 - r_2^4)\omega^4 + (A_{1\varphi}^2A_{2\varphi}^2 - 2r_2^2A_{2\varphi}^2)\omega^2 - A_{2\varphi}^4 = 0. \quad (19)$$

Setting $W = \omega^2$, equation (19) becomes:

$$r_2^2W^3 + (A_{2\varphi}^2 + r_2^2A_{1\varphi}^2 - r_2^4)W^2 + (A_{1\varphi}^2A_{2\varphi}^2 - 2r_2^2A_{2\varphi}^2)W - A_{2\varphi}^4 = 0,$$

which has at least one positive root because $r_2^2 > 0$ and $-A_{2\varphi}^4 < 0$. Then, we have at least two opposite values $\omega_0 > 0$ and $\omega_1 < 0$ of ω .

Moreover, from (17) and (18) and for $\omega = \omega_0$, we obtain:

$$\tau_k = \frac{1}{\omega_0} \arctan \left(\frac{A_{1\varphi}A_{2\varphi}\omega_0 + r_2\omega_0^3}{r_2\lambda_1\alpha_1q^2(1 - m)^2x_e\omega_0^2} \right) + \frac{k\pi}{\omega_0} = \tau_0 + \frac{k\pi}{\omega_0}, \quad k \in \mathbb{Z},$$

where

$$\tau_0 = \frac{1}{\omega_0} \arctan \left(\frac{A_{1\varphi}A_{2\varphi}\omega_0 + r_2\omega_0^3}{r_2\lambda_1\alpha_1q^2(1 - m)^2x_e\omega_0^2} \right).$$

In order to see whether a Hopf bifurcation can occur, we verify the transversality condition [18]. When differentiating equation (13) with respect to τ , we obtain:

$$[2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau + r_2e^{-\lambda\tau} - r_2\lambda\tau e^{-\lambda\tau}]\frac{d\lambda}{d\tau} - (A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau} = 0,$$

from which we obtain,

$$\begin{aligned} \left(\frac{d\lambda}{d\tau}\right)^{-1} &= \frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau + r_2e^{-\lambda\tau} - r_2\lambda\tau e^{-\lambda\tau}}{(A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau}} \\ &= \frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{(A_{2\varphi} + r_2\lambda)\lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda} \\ &= -\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{\lambda(\lambda^2 + A_{1\varphi}\lambda)} - \frac{\tau}{\lambda} \\ &= -\frac{1}{\lambda} \left[\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{\lambda^2 + A_{1\varphi}\lambda} + \tau \right]. \end{aligned}$$

Following Cooke and Grossman [15], we therefore obtain by using (17) and (18),

$$\begin{aligned} &sign \left\{ \frac{d(Re\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} \\ &= sign \left\{ Re \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\}_{\lambda=i\omega_0} \\ &= sign \left\{ Re \left(-\frac{2\lambda + A_{1\varphi} - A_{2\varphi}e^{-\lambda\tau}\tau}{\lambda(\lambda^2 + A_{1\varphi}\lambda)} \right) \right\}_{\lambda=i\omega_0} \\ &= sign \left\{ \frac{r_2^2\omega_0^4 + 2\omega_0^2A_{2\varphi}^2 + A_{1\varphi}^2A_{2\varphi}^2}{(\omega_0^4 + A_{1\varphi}^2\omega_0^2)(A_{2\varphi}^2 + r_2^2\omega_0^2)} \right\}. \end{aligned}$$

Hence, we have:

$$sign \left\{ \frac{d(Re\lambda)}{d\tau} \right\}_{\lambda=i\omega_0} > 0.$$

It means that the transversality condition is satisfied. Then, a Hopf bifurcation can occur when $\tau = \tau_0$.

The following theorem holds for the stability of the coexistence equilibrium of system (2)–(3):

- Theorem 5** 1. If $\tau \in [0, \tau_0)$, then the coexistence equilibrium $E(x_e, y_e)$ is locally asymptotically stable.
 2. If $\tau > \tau_0$, then the equilibrium $E(x_e, y_e)$ is unstable.
 3. If $\tau = \tau_k$ with $k \in \mathbb{Z}$, then system (2)–(3) undergoes a Hopf bifurcation.

Proof See “Appendix E.” □

Remark 3 According to results obtained for the transversality condition and the existence of the critical value τ_0 , the Hopf bifurcation always exists for any values the refuge strength m , the preference rate q and the harvesting limit value h .

6 Direction and stability of Hopf bifurcation

In this section, we compute some formulas by using the normal form theory [12, 70] and the center manifold theorem introduced by Hassard et al. [26]. These formulas are used to determine the direction of the Hopf bifurcation and the stability of the bifurcating periodic solution of system (2)–(3) which occurs when the delay τ takes the critical value τ_0 . The following result gives us a description of the Hopf bifurcating periodic solutions of system (2)–(3)

Theorem 6 Let us consider System (2)–(3). There exists three real numbers μ_2 , β_2 and T_2 such that the followings hold true.

1. The sign of μ_2 determines the direction of the Hopf bifurcation. If $\mu_2 > 0$, then the Hopf bifurcation is supercritical. If $\mu_2 < 0$, then the Hopf bifurcation is subcritical.
2. The sign of β_2 determines the stability of the bifurcating periodic solutions. If $\beta_2 > 0$, then the bifurcating periodic solutions are unstable. If $\beta_2 < 0$, then the bifurcating periodic solutions are stable.

Table 1 Parameter values for the Leslie–Gower predator–prey model (2)–(3)

Parameter	Value	References
r_1	2	Alves [1]
r_2	1.5	Alves [1]
λ_1	5	Assumed
α_1	0.8	Alves [1]
h	1	Assumed
T_1	2	Assumed
α_A	1.2	Alves [1]
K_1	3	Alves [1]
K_A	3	Alves [1]
q	0.7	Alves [1]
m	0.7	Assumed

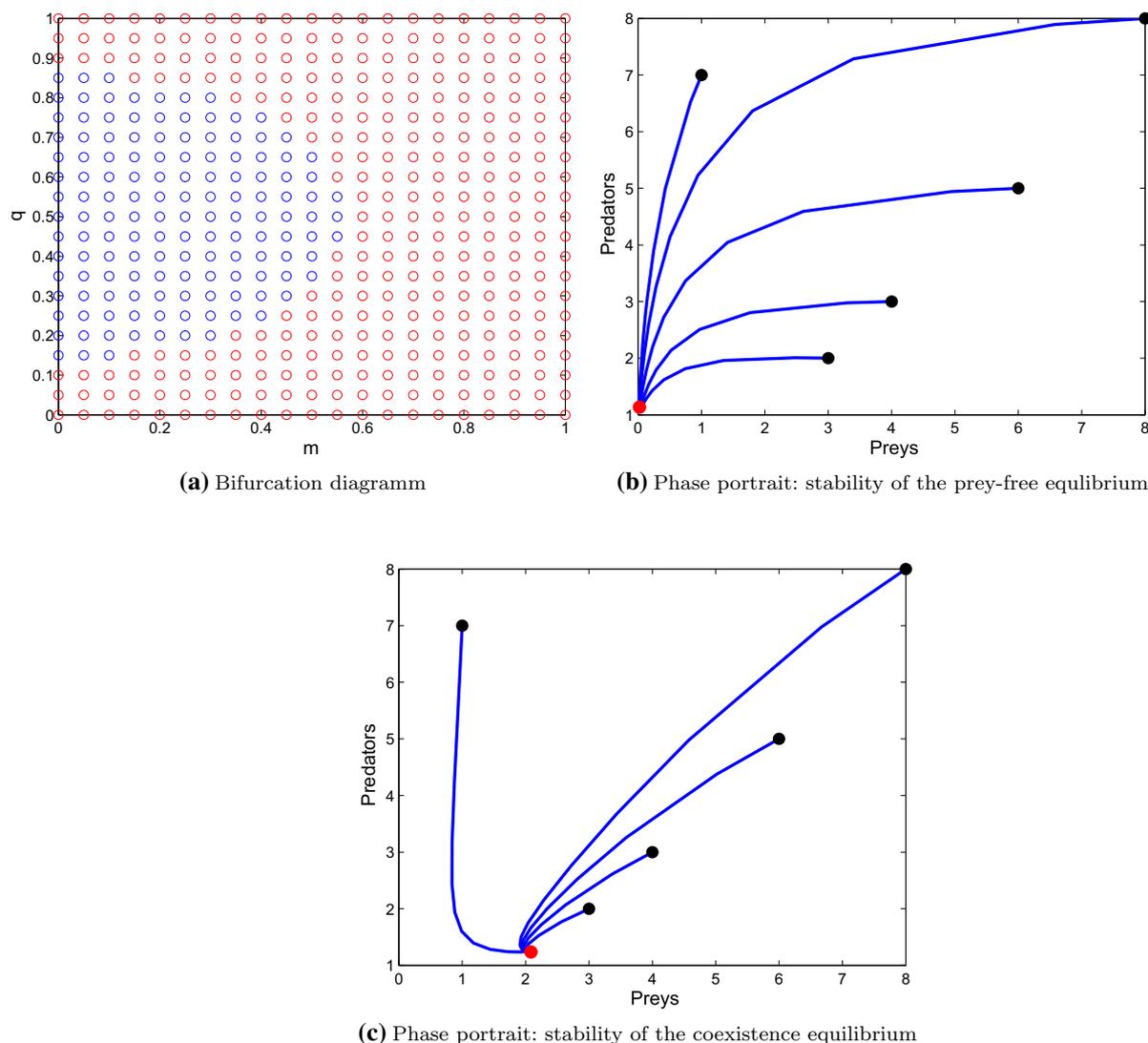


Fig. 1 **a** Bifurcation diagram of system (2)–(3) without harvesting and when the time delay $\tau = 0$. The red circles mean that the prey-free equilibrium E_2^0 is unstable for the corresponding values of the parameter m and q . For those values of m and q , the coexistence equilibrium E_4^0 exists and is locally asymptotically stable. The blue circles mean that the prey-free equilibrium E_2^0 is locally asymptotically stable for the corresponding values of the parameter m and q . For those values of m and

q , the coexistence equilibrium E_4^0 does not exist. **b** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.3$, $q = 0.7$. The prey-free equilibrium $E_2^0(0; 1.08)$ is locally asymptotically stable. **c** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$. The coexistence equilibrium $E_4^0(2.016; 1.2494)$ is locally asymptotically stable. Black bullets denote the initial data, while the red bullet denotes the equilibrium

3. T_2 determines the period of the bifurcating periodic solutions. If $T_2 > 0$, then the period increases. If $T_2 < 0$, then period decreases.

Proof See “Appendix F.”

□

7 Numerical simulations

In this section, some numerical simulations are provided in order to illustrate our theoretical analysis and also to support our discussion. The values of the parameters $r_1, r_2, \alpha_1, \alpha_A, K_1, K_A$ and q are those which have

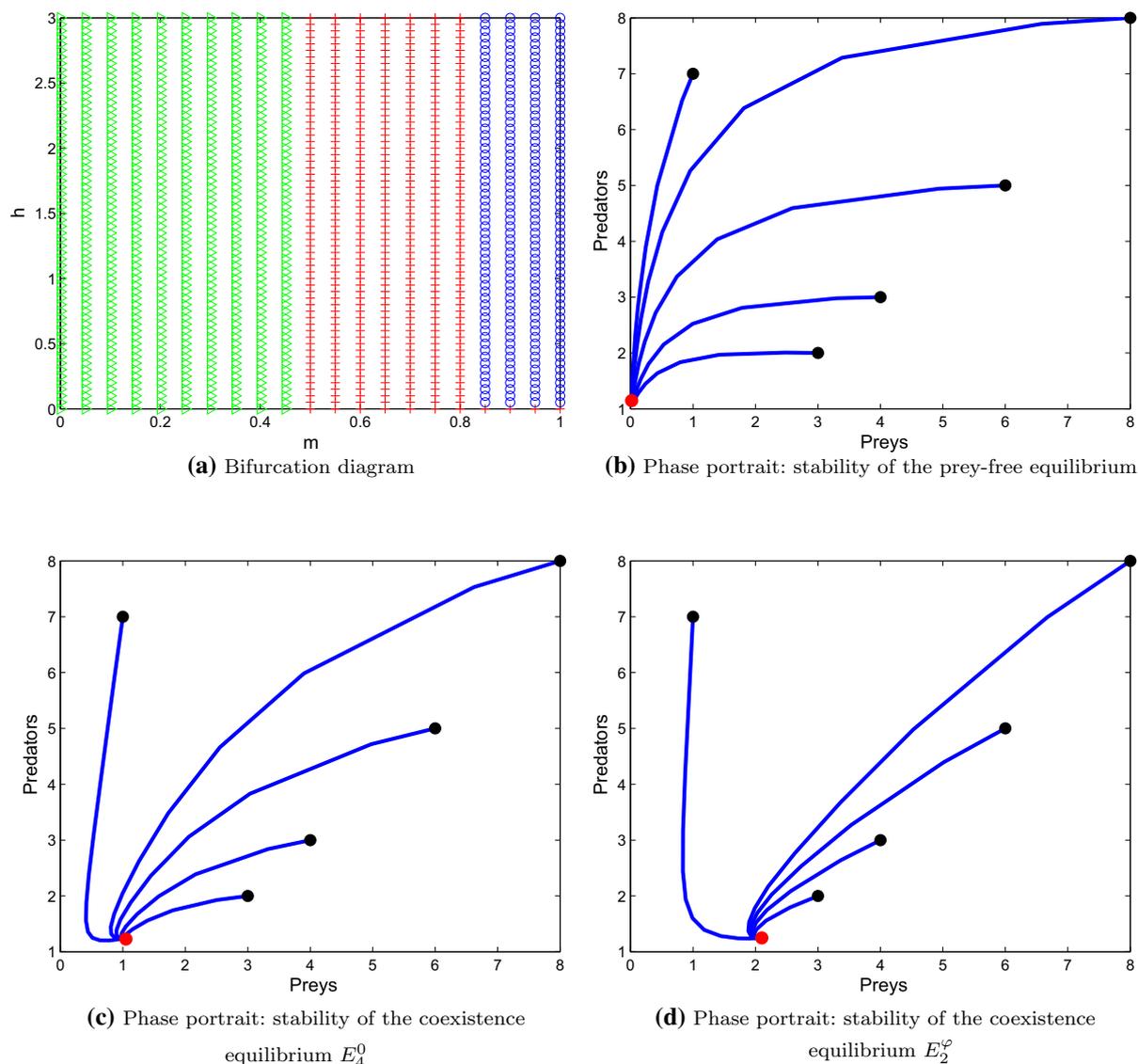


Fig. 2 **a** Bifurcation diagram of system (2)–(3) with harvesting and when the time delay $\tau = 0$. The green triangle means that system (2)–(3) does not have a coexistence equilibrium, but the prey-free equilibrium E_2^0 of the model without harvesting exists and is locally asymptotically stable. The red plus means that system (2)–(3) does not have a coexistence equilibrium, but the coexistence equilibrium E_4^0 of the model without harvesting exists and is locally asymptotically stable. The blue circle means

that system (2)–(3) has one coexistence equilibrium E_2^ϕ which is locally asymptotically stable. **b** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.3$, $q = 0.7$ et $h = 1$. **c** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.7$, $q = 0.7$ and $h = 1$. **d** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$ and $h = 1$. Black bullets denote the initial data, while the red bullet denotes the equilibrium. (Color figure online)

been used by [1, Fig. 4.1]. We recall that initial condition values $x(0)$ and $y(0)$ must satisfy (5) and (6), respectively. For our numerical treatments, we consider parameter values summarized in Table 1. Note that for the cases without harvesting, we use $h = 0$.

Figure 1 depicts the bifurcation diagram, in terms of the prey refuge and the preference rate, and phase portraits of system (2)–(3) without the time delay and without harvesting. We are interested in the effects of the prey refuge strength m and the preference rate q on

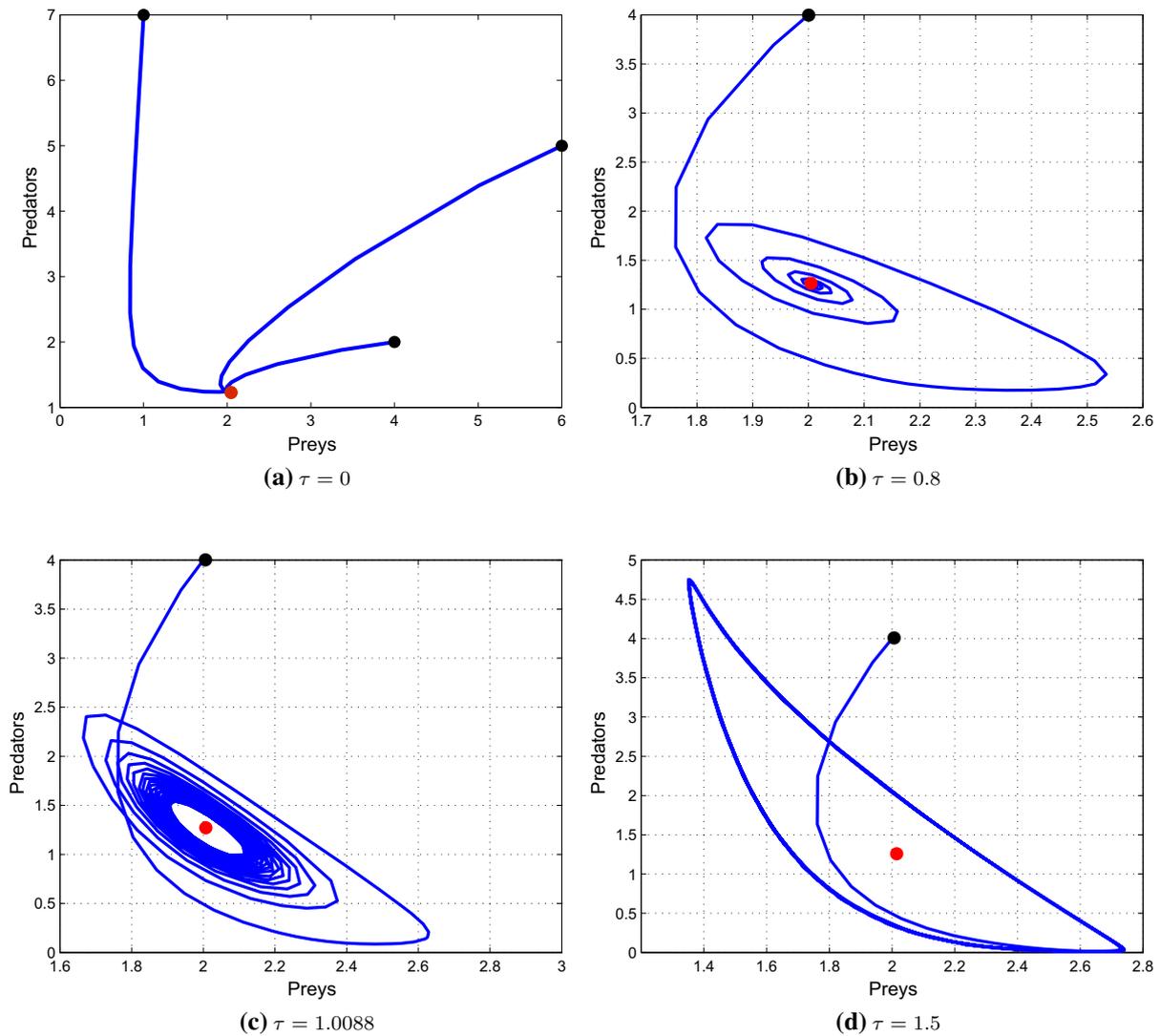


Fig. 3 **a** Phase portrait of system (2)–(3) when the time delay $\tau = 0$, $m = 0.85$, $q = 0.7$ and $h = 1$. **b** Phase portrait of system (2)–(3) when the time delay $\tau = 0.8$, $m = 0.85$, $q = 0.7$ and $h = 1$. **c** Phase portrait of system (2)–(3) when the time delay

$\tau = 1.0088$, $m = 0.85$, $q = 0.7$ and $h = 1$. **d** Phase portrait of system (2)–(3) when the time delay $\tau = 1.5$, $m = 0.85$, $q = 0.7$ and $h = 1$. Black bullets denote the initial data, while the red bullet denotes the equilibrium

the dynamic of system (2)–(3) without the time delay. For some values of m and q , it is possible to have either the extinction of the prey population or the coexistence of the prey and predator populations.

Figure 2 represents the bifurcation diagram, in terms of the prey refuge and harvest limit rate, and phase portraits of system (2)–(3) without the time delay, with and without harvesting. We are interested in the effects of prey refuge strength m and the limit value of harvesting

h on the dynamic of system (2)–(3) without the time delay. For a fixed value on the preference rate q and for some values of m and h , it is possible to have either the extinction of the prey population or the coexistence of the prey and predator populations (Fig. 2).

In Fig. 3, we have the phase portraits of system (2)–(3) without and with the time delay. We are interested in the effect of the time delay on the dynamic of system (2)–(3). Panel (b) illustrates the fact that when the time

Table 2 Values of x_2^φ and y_2^φ for system (2)–(3) for $m = 0.7$ and $h = 1$

Value of q	x_2^φ	y_2^φ
0.1	2.6308	3.3031
0.2	2.5253	3.0012
0.3	2.4467	2.6961
0.4	2.3930	2.3897
0.5	2.3623	2.0834
0.6	2.3532	1.7788
0.7	2.3650	1.4773
0.8	2.3972	1.1802
0.9	2.4498	0.8891

delay $\tau = 0.8 < \tau_0 = 1.0088$, the coexistence equilibrium $E_2^\varphi(2.0095; 1.2488)$ is always stable. Thus for this case, the time delay does not have any effect on the stability of the equilibrium. Panel (c) is an illustration of the existence of a Hopf bifurcation for the critical value $\tau_0 = 1.0088$ of the time delay. We have a stable subcritical bifurcating periodic solution around the coexistence equilibrium $E_2^\varphi(2.0095; 1.2488)$ ($\beta_2 = 0.7056$, $\mu_2 = -0.5078$, $T_2 = 2.8505$). With panel (d), one can see that for the value $\tau = 1.5 > \tau_0 = 1.0088$, the coexistence equilibrium becomes unstable. So for those values of the time delay τ , the coexistence equilibrium $E_2^\varphi(2.0095; 1.2488)$ is destabilized.

According to Table 2, one can see that when the preference rate q increases, the number of predators at the coexistence equilibrium of system (2)–(3) always decreases, while we have a fluctuation of the number of preys. The number of preys decreases up to a value of the preference rate q and begin to increase after that value.

8 Conclusion

In this paper, we have incorporated a time delay, a continuous threshold policy harvesting of preys and a refuge of preys in a Leslie–Gower predator–prey model with additional fixed food. The theoretical analysis shows that when the threshold and the harvesting limit value satisfy a condition depending on the preference rate of predators, the carrying capacity of the additional fixed food and the refuge strength of preys, there always exists a coexistence equilibrium for the studied model. Considering the time delay as a bifur-

cation parameter, it has been shown that it exists a critical value of the time delay depending on the threshold of harvesting and the rate of harvesting, the preference rate and the carrying capacity of the additional fixed food. For that critical value of the time delay, a Hopf bifurcation occurs around the coexistence equilibrium, and for the values of the time delay greater than that critical value, the coexistence equilibrium becomes unstable. An application of the normal form theory and the center manifold theorem allowed us to study the stability and determine the direction of the bifurcating periodic solutions. So the time delay is an impact on the stability of the system around the coexistence equilibrium. We also remark that increasing the preference rate of predators decreases the numbers of predators, but does not reach to extinction, while the number of preys decreases firstly and increases after. By using a bifurcation diagram, we also observe that the existence and the stability of equilibria of the system without time delay depend on the refuge strength, the preference rate and the harvesting limit value. According to our theoretical analysis, we can conclude that qualitatively, taking into account harvesting increases the number of equilibria with at least one more coexistence equilibrium which can be stable. In this paper, the time delay has been taken into account only for the dynamic of predators. For our further investigation, we shall formulate a model with two delays by introducing a time delay in the dynamic of preys in the model we have analyzed in this paper. Because the response function also has a significant role in a predator–prey model and particularly in a Leslie–Gower predator–prey model, we shall also formulate and investigate Leslie–Gower predator prey models with additional fixed food with different response functions as Holling type II, Holling type III and Holling type IV. What we have done in our paper can also be extended to Leslie–Gower predator–prey models with two preys and with one or more than one time delays, without or with any type of harvesting function.

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Compliance with ethical standards

Conflict of interest The authors Maximilien Onana, Boulchard Mewoli and Jean Jules Tewa declare that they have no conflict of interest.

A Proof of Theorem 1

We must show that each solution (x, y) of system (2)–(3), defined and continuous on $[-\tau, A[$ where $A \in]0, +\infty[$, $x(t) > 0$ and $y(t) > 0$ for all $t \in [0, A[$. Suppose that it is not true. Then there exists a value of T in $]0, A[$ such that for all $t \in [0, T[$, $x(t) > 0$ and $y(t) > 0$, and either $x(T) = 0$ or $y(T) = 0$.

For all $t \in [0, T[$ and from equations of (2), we have,

$$x(t) > x(0) \exp \left(\int_0^t (r_1 - b_1x(s) - q\lambda_1(1 - m)y(s) - \frac{h}{h + x(s) - T_1}) ds \right)$$

and

$$y(t) = y(0) \exp \left(\int_0^t \left(r_2 \left(1 - \frac{y(s - \tau)}{q\alpha_1(1 - m)x(s - \tau) + (1 - q)\alpha_A K_A} \right) \right) ds \right).$$

As x and y are defined and continuous on the compact $[-\tau, T]$, there exists $M \geq 0$ such that:

$$x(t) > x(0) \exp \left(\int_0^t (r_1 - b_1x(s) - a_1(1 - m)y(s) - \frac{h}{h + x(s) - T_1}) ds \right) \geq x(0) \exp(-TM)$$

and

$$y(t) = y(0) \exp \left(\int_0^t \left(r_2 \left(1 - \frac{y(s - \tau)}{q\alpha_1(1 - m)x(s - \tau) + (1 - q)\alpha_A K_A} \right) \right) ds \right) \geq y(0) \exp(-TM).$$

Taking the limit as $t \rightarrow T$ gives

$$x(T) \geq x(0) \exp(-TM) > 0$$

and

$$y(T) \geq y(0) \exp(-TM) > 0,$$

which contradicts the fact that either $x(T) = 0$ or $y(T) = 0$. Then, a solution of System (2)–(3) which starts in the positive quadrant \mathbb{R}_+^2 remains there.

B Proof of Theorem 2

Using the first equation of System (2), we always have

$$\dot{x}(t) \leq r_1 x(t) \left(1 - \frac{x(t)}{K_1} \right).$$

Applying a differential inequality [Hale, 1980] gives

$$x(t) \leq \frac{1}{\frac{1}{K_1} + \left(\frac{1}{x(0)} - \frac{1}{K_1} \right) e^{-r_1 t}}.$$

Using assumption (5) gives $x(t) \leq K_1$, for all positive value of t . It means that $x(t)$ is bounded.

Let us use the second equation of System (3) to prove that $y(t)$ is bounded. For all $t \geq 0$, we have

$$\dot{y}(t) \leq r_2 y(t).$$

Integrating that differential inequality from $t - \tau$ to t gives

$$y(t - \tau) \geq y(t) e^{-r_2 \tau}.$$

Using the fact that $x(t) \leq K_1$ gives the following differential inequality

$$\dot{y}(t) \leq r_2 y(t) \left(1 - \frac{y(t)}{K} \right)$$

where $K = \frac{(1 - m)q\alpha_1 K_1 + (1 - q)\alpha_A K_A}{e^{-r_2 \tau}}$. Once more, applying a differential inequality [Hale, 1980] gives

$$y(t) \leq \frac{1}{\frac{1}{K} + \left(\frac{1}{y(0)} - \frac{1}{K} \right) e^{-r_2 t}}.$$

Using assumption (6) gives $y(t) \leq K$, for all positive value of t . Thus $y(t)$ is bounded. One can easily verify that, using assumption (6), the inequalities $x(t) \leq K_1$ and $e^{r_2 \tau} \geq 1$ lead to $y(0) \leq K$.

C Proof of Theorem 3

A couple of variables (x, y) is an equilibrium of system (2)–(3) if it is a solution of the following systems on $[0, T_1] \times \mathbb{R}_+$ and on $[T_1, K_1] \times \mathbb{R}_+$, respectively.

$$\begin{cases} 0 = r_1 \left(1 - \frac{x(t)}{K_1} \right) x(t) - q\lambda_1(1 - m)x(t)y(t), \\ 0 = r_2 \left(1 - \frac{y(t)}{q\alpha_1(1 - m)x(t) + (1 - q)\alpha_A K_A} \right) y(t), \end{cases} \tag{20}$$

$$\begin{cases} 0 = r_1 \left(1 - \frac{x(t)}{K_1} \right) x(t) - q\lambda_1(1 - m)x(t)y(t) - \frac{h(x - T_1)}{h + x - T_1}, \\ 0 = r_2 \left(1 - \frac{y(t)}{q\alpha_1(1 - m)x(t) + (1 - q)\alpha_A K_A} \right) y(t). \end{cases} \tag{21}$$

Firstly, we solve system (20) on $[0, T_1] \times \mathbb{R}_+$. Using the first equation of the system (20), we have $x = 0$ or $x = \frac{r_1 - q\lambda_1(1 - m)y}{b_1}$.

Replacing x by 0 in the second equation of system (20) gives $y = 0$ or $y = (1 - q)\alpha_A K_A$. Then we have the equilibria E_1^0 and E_2^0 .

Replacing x by $\frac{r_1 - q\lambda_1(1 - m)y}{b_1}$ in the second equation of system (20) gives $y = 0$ or $y = (1 - m)q\alpha_1 x + (1 - q)\alpha_A K_A$. If $y = 0$, we have $x = \frac{r_1}{b_1}$. If $y = (1 - m)q\alpha_1 x + (1 - q)\alpha_A K_A$, we have $x = \frac{r_1 - \lambda_1(1 - m)q(1 - q)\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}$ and $y = \frac{r_1\alpha_1(1 - m)q + (1 - m)b_1\alpha_A K_A}{b_1 + q^2\lambda_1\alpha_1(1 - m)^2}$. Then we have the equilibria E_3^0 and E_4^0 .

Secondly, we solve system (21) on $[T_1, K_1] \times \mathbb{R}_+$.

Using the second equation of system (21) gives $y = 0$ or $y = (1 - m)q\alpha_1 x + (1 - q)\alpha_A K_A$. If $y = 0$, we find that x is a solution of equation (10). Moreover, if we consider the function f defined by $f(x) = -b_1x^3 + (r_1 - b_1(h - T_1))x^2 + (r_1(h - T_1) - h)x + hT_1$, then we have $f(T_1) = hT_1(r_1 - b_1T_1) > 0$ using assumption (4). We also have $f(K_1) = -h(K_1 - T_1) < 0$ because $T_1 < K_1$. Thus, by the intermediate value theorem [9, 46], there exists at least one solution of equation (10). So we have the equilibria E_1^φ . If $y = (1 - m)q\alpha_1 x + (1 - q)\alpha_A K_A$, x is a solution of equation (11). Moreover, if we consider the function g defined by $g(x) = A_1^\varphi x^3 + A_2^\varphi x^2 + A_3^\varphi x + hT_1$, we have $g(T_1) = hT_1(r_1 - b_1T_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A + q\alpha_1(1 - m)T_1)$. We have $g(K_1) = -(K_1(K_1 - T_1) + hT_1)(q\lambda_1(1 - m)(1 - q)\alpha_A K_A + q^2\lambda_1\alpha_1 K_1(1 - m)^2) < 0$ because $T_1 < K_1$. Thus, if $r_1 - b_1T_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A + q(1 - m)\alpha_1 T_1 > 0$ then $g(T_1) > 0$. By the intermediate value theorem [9, 46], (11) has at least one solution in $[K_1, T_1]$. Thus we have the equilibrium E_2^φ .

D Proof of Theorem 4

1. The Jacobian matrix of system (2)–(3) at the equilibrium E_1^0 is:

$$J_{E_1^0} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_1^0}$ has two positive eigenvalues (r_1 and r_2). So the equilibrium E_1^0 is an unstable node.

2. The Jacobian matrix of system (2)–(3) at the equilibrium E_2^0 is:

$$J_{E_2^0} = \begin{pmatrix} r_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A & 0 \\ r_2(1 - m)\alpha_1 q & -r_2 \end{pmatrix}.$$

$J_{E_2^0}$ has one negative eigenvalue ($-r_2$). The stability of the equilibrium E_2^0 depends on the sign of the second eigenvalue $r_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A$. Moreover, the discriminant of the characteristic equation is $\Delta_{E_2^0} = (r_1 - q\lambda_1(1 - m)(1 - q)\alpha_A K_A)^2 > 0$. Thus if $r_1 < q\lambda_1(1 - m)(1 - q)\alpha_A K_A$, then the equilibrium E_2^0 is stable node and the equilibrium E_4^0 does not exist. If $r_1 > q\lambda_1(1 - m)(1 - q)\alpha_A K_A$, the equilibrium E_2^0 is a saddle (unstable).

3. The Jacobian matrix of system (2)–(3) at the equilibrium E_3^0 is:

$$J_{E_3^0} = \begin{pmatrix} -r_1 & -q\lambda_1(1 - m)K_1 \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_3^0}$ has one positive eigenvalue (r_2). The equilibrium E_3^0 is a saddle (unstable).

4. The Jacobian matrix of system (2)–(3) at the equilibrium E_4^0 is:

$$J_{E_4^0} = \begin{pmatrix} -b_1x_4^0 & -q\lambda_1(1 - m)x_4^0 \\ (1 - m)\alpha_1 r_2 q & -r_2 \end{pmatrix}.$$

$$Tr(J_{E_4^0}) = -(b_1x_4^0 + r_2) < 0,$$

$$|(J_{E_4^0})| = r_2b_1x_4^0 + (1 - m)^2\alpha_1\lambda_1r_2q^2x_4^0 > 0.$$

Moreover, the discriminant of the characteristic equation is $\Delta_{E_4^0} = (b_1x_4^0 - r_2)^2 - 4(1 - m)^2\alpha_1\lambda_1r_2q^2x_4^0$. Therefore, if $\Delta_{E_4^0} > 0$, then the equilibrium E_4^0 is a stable node. If $\Delta_{E_4^0} < 0$, then the equilibrium E_4^0 is a stable spiral. If $\Delta_{E_4^0} = 0$, then the equilibrium E_4^0 is a stable degenerate node.

5. The Jacobian matrix of system (2)–(3) at the equilibrium E_1^φ is:

$$J_{E_1^\varphi} = \begin{pmatrix} -b_1x_1^\varphi + \frac{\varphi(x_1^\varphi)}{x_1^\varphi} - \varphi'(x_1^\varphi) & -q\lambda_1(1 - m)x_2^\varphi \\ 0 & r_2 \end{pmatrix}.$$

$J_{E_1^\varphi}$ has one positive eigenvalue (r_2). Thus, the equilibrium E_1^φ is unstable. Moreover, if $-b_1x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} < 0$, then the equilibrium E_1^φ is a saddle. If $-b_1x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} > 0$,

then the equilibrium E_1^φ is an unstable node. If $-b_1x_1^\varphi + \frac{h(x_1^\varphi - T_1)^2 - h^2T_1}{x_1^\varphi(x_1^\varphi + h - T_1)^2} = 0$, then the equilibrium E_1^φ is an unstable nonhyperbolic point.

- The Jacobian matrix of system (2)–(3) at the equilibrium E_2^φ is:

$$J_{E_2^\varphi} = \begin{pmatrix} -b_1x_2^\varphi + \frac{\varphi(x_2^\varphi)}{x_2^\varphi} - \varphi'(x_2^\varphi) & -q\lambda_1(1-m)x_2^\varphi \\ (1-m)\alpha_1r_2q & -r_2 \end{pmatrix}.$$

$$Tr(J_{E_2^\varphi}) = -b_1x_2^\varphi - r_2 + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2},$$

$$|J_{E_2^\varphi}| = -r_2 \left(-b_1x_2^\varphi + \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right) + (1-m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi.$$

The discriminant of the characteristic equation is:

$$\Delta_{E_2^\varphi} = \left(r_2 + b_1x_2^\varphi - \frac{h(x_2^\varphi - T_1)^2 - h^2T_1}{x_2^\varphi(x_2^\varphi + h - T_1)^2} \right)^2 - 4(1-m)^2q^2\alpha_1\lambda_1r_2x_2^\varphi.$$

Then using the signs of $Tr(J_{E_2^\varphi})$, $|J_{E_2^\varphi}|$ and $\Delta_{E_2^\varphi}$, and the table given in Jordan et al. [29], we have the type and the stability of the equilibrium E_2^φ as in theorem (4). (For stability of equilibria in the plane, one can also refer to Auger et al. [3] and Hirsch et al. [27].)

E Proof of Theorem 5

We proved that it is possible to have purely imaginary roots for the characteristic equation (13) and the transversality condition is satisfied. Thus, we have the third item of theorem 5. In what follows, we prove the first and the second items of theorem 5. By Rouché's theorem [19] and the continuity in τ , the characteristic equation (13) has roots with positive real parts if and only if it has purely imaginary roots. Let $\lambda(\tau) = \mu(\tau) + i\omega(\tau)$ where μ and ω are real depending on τ . For $\tau = 0$, the equilibrium E is stable. Thus, we have $\mu(0) < 0$. By continuity, if τ is sufficiently small, we still have $\mu(\tau) < 0$ and E is still stable. The change of stability will occur for some values of τ for which $\mu(\tau) = 0$ and $\omega(\tau) \neq 0$; it means that λ will be purely imaginary. Let τ_e be such that $\mu(\tau_e) = 0$ and $\omega(\tau_e) = \omega_e \neq 0$ with $\lambda = i\omega(\tau_e)$. In this case, the steady state loses stability and eventually becomes unstable when $\mu(\tau)$ becomes positive. In other words,

if such a value ω_e does not exist, then the steady state E will remain stable for all τ .

F Proof of Theorem 6

For convenience, let $t = s\tau$, $x(s\tau) = x_1(s)$, $y(s\tau) = x_2(s)$ and $\tau = \tau_0 + \mu$, $\mu \in \mathbb{R}$ so that $\mu = 0$ is the Hopf bifurcating value for system (2)–(3). Then system (2)–(3) becomes equivalent to the system:

$$\dot{u}(t) = L_\mu(u_t) + f(\mu, u_t), \tag{22}$$

where $u_t = (x_1(t), x_2(t))^T \in \mathcal{C}$ and $u_t(\theta) = u(t + \theta) = (x_1(t + \theta), x_2(t + \theta))^T \in \mathcal{C}$.

$L_\mu : \mathcal{C} \rightarrow \mathbb{R}^2$ is defined as follows:

$$L_\mu\phi = (\tau_0 + \mu) \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} + (\tau_0 + \mu) \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix}, \tag{23}$$

where $A_{A\varphi} = -b_1x_e + \frac{\varphi(x_e)}{x_e} - \varphi'(x_e)$, $B_{A\varphi} = -q\lambda_1(1-m)x_e$, $C_{A\varphi} = qr_2\alpha_1(1-m)$, $D_{A\varphi} = -r_2$. $f : \mathbb{R} \times \mathcal{C} \rightarrow \mathbb{R}^2$ is defined as follows:

$$f(\mu, \phi) = (\tau_0 + \mu)(f_1, f_2)^T, \tag{24}$$

where $\phi(\theta) = (\phi_1(\theta), \phi_2(\theta))^T \in \mathcal{C}$

$$f_1 = a_{11}\phi_1^2(0) + a_{12}\phi_1(0)\phi_2(0) + a_{13}\phi_1^3(0),$$

and

$$f_2 = a_{21}\phi_1^2(-1) + a_{22}\phi_1(-1)\phi_2(0) + a_{23}\phi_1(-1)\phi_2(-1) + a_{24}\phi_2(-1)\phi_2(0) + a_{25}\phi_1^3(-1) + a_{26}\phi_1^2(-1)\phi_2(0) + a_{27}\phi_1^2(-1)\phi_2(-1) + a_{28}\phi_1(-1)\phi_2(0)\phi_2(-1),$$

with

$$a_{11} = -b_1 + \frac{h^2}{(x_e + h - T_1)^2}, a_{12} = -q\lambda_1(1-m),$$

$$a_{13} = \frac{h^2}{(x_e + h - T_1)^4}$$

$$a_{21} = -\frac{r_2(1-m)^2q^2\alpha_1^2}{y_e}, a_{22} = \frac{r_2(1-m)q\alpha_1}{y_e},$$

$$a_{23} = \frac{r_2(1-m)q\alpha_1}{y_e}, a_{24} = -\frac{r_2}{y_e},$$

$$a_{25} = -\frac{r_2(1-m)^3 q^3 \alpha_1^3}{y_e^2}, a_{26} = -\frac{r_2(1-m)^2 q^2 \alpha_1^2}{y_e^2},$$

$$a_{27} = -\frac{r_2(1-m)^2 q^2 \alpha_1^2}{y_e^2}, a_{28} = \frac{r_2(1-m) q \alpha_1}{y_e^2}.$$

L_μ is a one parameter family of bounded linear operators in $C[-1, 0] \rightarrow \mathbb{R}^2$. Then by the Riesz representation theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta, \mu)$ in $[-1, 0] \rightarrow \mathbb{R}^2$ such that

$$L_\mu = \int_{-1}^0 d\eta(\theta, \mu) \phi(\theta). \tag{25}$$

In fact, we can choose

$$\eta(\theta, \mu) = (\tau_0 + \mu) \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} \phi_1(0) \\ \phi_2(0) \end{pmatrix} \delta(\theta)$$

$$+ (\tau_0 + \mu) \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} \phi_1(-1) \\ \phi_2(-1) \end{pmatrix} \delta(\theta + 1), \tag{26}$$

where δ is the Dirac function. Then equation (22) is satisfied.

For $\phi \in C^1[-1, 0]$, let us define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \text{if } -1 \leq \theta < 0 \\ \int_{-1}^0 d\eta(\theta, \mu)\phi(\theta), & \text{if } \theta = 0 \end{cases} \tag{27}$$

and

$$R(\mu)\phi = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & \text{if } -1 \leq \theta < 0, \\ f(\mu, \phi), & \text{if } \theta = 0. \end{cases} \tag{28}$$

System (2)–(3) is then transformed into the operator equation of the form (29) as follows, in order to study the Hopf bifurcation problem

$$\dot{u}(t) = A(\mu)u_t + Ru_t. \tag{29}$$

Define the adjoint operator for $\psi \in C^1([0, 1], (\mathbb{R}^2)^*)$,

$$A^*(\mu)\psi(s) = \begin{cases} -\frac{d\psi(s)}{ds} & \text{if } 0 < s \leq 1, \\ \int_{-1}^0 d\eta^T(s, \mu)\psi(-s) & \text{if } s = 0. \end{cases} \tag{30}$$

In order to normalize the eigenvectors of the operator A and the adjoint operator A^* , we need to introduce the following bilinear form:

$$\langle \psi, \phi \rangle = \overline{\psi}(0) \cdot \phi(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \overline{\psi}^T(\xi - \theta) d\eta(\theta) \phi(\xi) d\xi, \tag{31}$$

where $\eta(\theta) = \eta(\theta, 0)$.

By the discussion and the transformation $t = s\tau$, we know that $i\tau_0\omega_0$ and $-i\tau_0\omega_0$ are the eigenvalues of $A(0)$ and other eigenvalues have strictly negative real parts. Hence, they are also eigenvalues of A^* . Now we are going to compute the eigenvectors of $A(0)$ and A^* corresponding to their respective eigenvalues $i\tau_0\omega_0$ and $-i\tau_0\omega_0$. If we suppose that $q(\theta) = (q^{(1)}(\theta), q^{(2)}(\theta))^T = (1, q_1)^T e^{i\tau_0\omega_0\theta}$ is the eigenvector of $A(0)$ corresponding to the eigenvalue $i\tau_0\omega_0$, then by the definition we have $A(0)q(0) = i\tau_0\omega_0q(0)$. Then using the definition of $A(0)$ and the expressions given by (22), (24) and (25) gives:

$$\tau_0 \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} q(0) + \tau_0 \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} q(-1) = i\tau_0\omega_0q(0),$$

or equivalently

$$\tau_0 \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ q_1 \end{pmatrix} + \tau_0 \begin{pmatrix} 0 & 0 \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} 1 \\ q_1 \end{pmatrix} e^{-i\tau_0\omega_0} = i\tau_0\omega_0 \begin{pmatrix} 1 \\ q_1 \end{pmatrix}$$

$$\text{This implies } \begin{cases} A_{A\varphi} + B_{A\varphi}q_1 = i\omega_0, \\ (C_{A\varphi} + D_{A\varphi}q_1)e^{-i\tau_0\omega_0} = q_1i\omega_0, \end{cases}$$

$$\text{and } q_1 = \frac{C_{A\varphi}}{-D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}.$$

$$\text{Thus, } q^{(1)}(\theta) = e^{i\tau_0\omega_0\theta} \text{ and } q^{(2)}(\theta) = \frac{C_{A\varphi} e^{i\tau_0\omega_0\theta}}{-D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}.$$

Now let us compute the eigenvector q^* of A^* . Suppose that we have $q^*(s) = G_{A\varphi}(1, q_1^*)^T e^{i\tau_0\omega_0 s}$, $0 \leq s \leq 1$. Then we have the following relation

$$\tau_0 \begin{pmatrix} A_{A\varphi} & 0 \\ B_{A\varphi} & 0 \end{pmatrix} q^*(0) + \tau_0 \begin{pmatrix} 0 & C_{A\varphi} \\ 0 & D_{A\varphi} \end{pmatrix} q^*(-1) = -i\tau_0\omega_0q^*(0),$$

$$\text{which is equivalent to } \tau_0 \begin{pmatrix} A_{A\varphi} & 0 \\ B_{A\varphi} & 0 \end{pmatrix} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} + \tau_0 \begin{pmatrix} 0 & C_{A\varphi} \\ 0 & D_{A\varphi} \end{pmatrix} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} e^{-i\tau_0\omega_0} = -i\tau_0\omega_0 \begin{pmatrix} 1 \\ q_1^* \end{pmatrix}.$$

$$\text{This implies } \begin{cases} A_{A\varphi} + C_{A\varphi}q_1^* e^{-i\tau_0\omega_0} = -i\omega_0, \\ B_{A\varphi} + D_{A\varphi}q_1^* e^{-i\tau_0\omega_0} = -q_1^* i\omega_0, \end{cases}$$

$$\text{and } q_1^* = -\frac{B_{A\varphi}}{D_{A\varphi} + i\omega_0 e^{i\tau_0\omega_0}}.$$

Now let's compute $G_{A\varphi}$ by using the orthogonality condition $\langle q^*(s), q(\theta) \rangle = 1$. By using (30), we have:

$$\begin{aligned} &\langle q^*(s), q(\theta) \rangle \\ &= \overline{q^*}(0) \cdot q(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \overline{q^*}^T \\ &\quad (\xi - \theta) d\eta(\theta) q(\xi) d\xi \\ &= \overline{q^*}(0) \cdot q(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \overline{G_{A\varphi}}(1, \overline{q_1^*}) e^{-i\omega_0\tau_0(\xi-\theta)} \\ &\quad d\eta(\theta)(1, q_1)^T e^{i\omega_0\tau_0\xi} \\ &= \overline{G_{A\varphi}} \left\{ 1 + q_1 \overline{q_1^*} - (1, \overline{q_1^*}) \right. \\ &\quad \left. \int_{-1}^0 \theta e^{i\omega_0\tau_0\theta} d\eta(\theta)(1, q_1)^T \right\} \\ &= \overline{G_{A\varphi}} \left\{ 1 + q_1 \overline{q_1^*} + \tau_0 e^{i\omega_0\tau_0} (C_{A\varphi} + D_{A\varphi} q_1) \overline{q_1^*} \right\}. \end{aligned}$$

Then,

$$G_{A\varphi} = [1 + \overline{q_1} q_1^* + \tau_0 e^{-i\omega_0\tau_0} (C_{A\varphi} + D_{A\varphi} \overline{q_1}) q_1^*]^{-1}.$$

Now we are going to compute the coordinates to describe the center manifold \mathcal{C}_0 at $\mu = 0$. Let us define

$$z(t) = \langle q^*, u_t \rangle \tag{32}$$

and

$$W(t, \theta) = u_t(\theta) - 2Re\{z(t)q(\theta)\}, \tag{33}$$

where u_t is a solution of (28) when $\mu = 0$.

On the center manifold \mathcal{C}_0 , we have:

$$W(t, \theta) = W(z(t), \overline{z}(t), \theta),$$

where

$$\begin{aligned} W(t, \theta) = W(z(t), \overline{z}(t), \theta) = &W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\overline{z} \\ &+ W_{02}(\theta) \frac{\overline{z}^2}{2} + \dots \end{aligned} \tag{34}$$

In (33), z and \overline{z} represent the local coordinates of the center manifold \mathcal{C}_0 in the direction of q and q^* , respectively.

Now let us reduce equation (28) to an ordinary differential equation using a single complex variable on the center manifold. Since $\mu = 0$ and for u_t a solution of (28) belonging to the center manifold \mathcal{C}_0 , we have:

$$\begin{aligned} \dot{z}(t) = \langle q^*, \dot{u}(t) \rangle &= \langle q^*, Au_t + Ru_t \rangle \\ &= \langle q^*, Au_t \rangle + \langle q^*, Ru_t \rangle \\ &= \langle A^* q^*, u_t \rangle + \langle q^*, Ru_t \rangle \\ &= i\tau_0\omega_0 z + \overline{q^*} f_0(z, \overline{z}). \end{aligned}$$

The following equation:

$$\dot{z}(t) = i\tau_0\omega_0 z + \overline{q^*} f_0(z, \overline{z}) \tag{35}$$

can be rewritten as:

$$\dot{z}(t) = i\tau_0\omega_0 z + g(z, \overline{z}), \tag{36}$$

where

$$g(z, \overline{z}) = g_{20} \frac{z^2}{2} + g_{11} z\overline{z} + g_{02} \frac{\overline{z}^2}{2} + g_{21} \frac{z^2\overline{z}}{2} + \dots \tag{37}$$

In what follows, we are going to expand g in powers of z and \overline{z} in order to obtain from the first three coefficients of this expansion, the value of μ_2 which indicates the direction of the Hopf bifurcation (that is to say if the Hopf bifurcation is supercritical or subcritical) and the value of β_2 which determines the stability. To do so, we use the algorithm presented by Hassard et al. [26].

A substitution of (28) in (36) leads to:

$$\begin{aligned} \dot{W}(t) = \dot{u}_t - \dot{z}q - \dot{\overline{z}}\overline{q} \\ &= A(\mu)u_t + Ru_t - [i\tau_0\omega_0 z + \overline{q^*}(0) f_0(z, \overline{z})]q \\ &\quad - [-i\tau_0\omega_0 \overline{z} + q^*(0) \overline{f_0}(z, \overline{z})] \overline{q} \\ &= AW + 2ARe\{zq\} + Ru_t - 2Re[\overline{q^*}(0) f_0(z, \overline{z})q(\theta)] \\ &\quad - 2Re[i\tau_0\omega_0 zq(\theta)] \\ &= AW - 2Re[\overline{q^*}(0) f_0(z, \overline{z})q(\theta)] + Ru_t. \end{aligned}$$

Then we obtain the following equations

$$\dot{W} = \begin{cases} AW - 2Re[\overline{q^*}(0) f_0(z, \overline{z})q(\theta)] & \text{if } -1 \leq \theta < 0, \\ AW - 2Re[\overline{q^*}(0) f_0(z, \overline{z})q(\theta)] + f & \text{if } \theta = 0. \end{cases} \tag{38}$$

Equations (37) can be rewritten as:

$$\dot{W} = AW + H(z, \overline{z}, \theta), \tag{39}$$

where

$$\begin{aligned} H(z, \overline{z}, \theta) = &H_{20}(\theta) \frac{z^2}{2} + H_{11}(\theta) z\overline{z} \\ &+ H_{02}(\theta) \frac{\overline{z}^2}{2} + \dots \end{aligned} \tag{40}$$

Derivating W in (33) with respect to t , we have:

$$\dot{W} = W_z \dot{z} + W_{\overline{z}} \dot{\overline{z}}. \tag{41}$$

Then using (33), (38) and (39) gives:

$$(A - 2i\tau_0\omega_0)W_{20}(\theta) = -H_{20}(\theta), \tag{42}$$

and

$$AW_{11}(\theta) = -H_{11}(\theta). \tag{43}$$

Using equations (34) and (35) gives:

$$g(z, \bar{z}) = \bar{q}^*(0) f_0(z, \bar{z}) = \tau_0 \overline{G_{A\varphi}} \begin{pmatrix} 1 \\ q_1^* \end{pmatrix} \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} = \tau_0 \overline{G_{A\varphi}} (f_1 + q_1^* f_2), \tag{44}$$

where

$$\begin{aligned} f_1 &= a_{11}x_1^2(t) + a_{12}x_1(t)x_2(t) + a_{13}x_1^3(t), \\ f_2 &= a_{21}x_1^2(t-1) + a_{22}x_1(t-1)x_2(t) \\ &\quad + a_{23}x_1(t-1)x_2(t-1) + a_{24}x_2(t-1)x_2(t) \\ &\quad + a_{25}x_1^3(t-1) \\ &\quad + a_{26}x_1^2(t-1)x_2(t) + a_{27}x_1^2(t-1)x_2(t-1) \\ &\quad + a_{28}x_1(t-1)x_2(t)x_2(t-1), \end{aligned}$$

and

$$\begin{aligned} x_{1t}(0) &= q^{(1)}(0)z + \bar{q}^{(1)}(0)\bar{z} + W_{20}^{(1)}(0) \frac{z^2}{2} \\ &\quad + W_{11}^{(1)}(0)z\bar{z} + W_{02}^{(1)}(0) \frac{\bar{z}^2}{2} + \dots \\ x_{2t}(0) &= q^{(2)}(0)z + \bar{q}^{(2)}(0)\bar{z} + W_{20}^{(2)}(0) \frac{z^2}{2} \\ &\quad + W_{11}^{(2)}(0)z\bar{z} + W_{02}^{(2)}(0) \frac{\bar{z}^2}{2} + \dots \\ x_{1t}(-1) &= q^{(1)}(-1)z + \bar{q}^{(1)}(-1)\bar{z} + W_{20}^{(1)}(-1) \frac{z^2}{2} \\ &\quad + W_{11}^{(1)}(-1)z\bar{z} + W_{02}^{(1)}(-1) \frac{\bar{z}^2}{2} + \dots \\ x_{2t}(-1) &= q^{(2)}(-1)z + \bar{q}^{(2)}(-1)\bar{z} + W_{20}^{(2)}(-1) \frac{z^2}{2} \\ &\quad + W_{11}^{(2)}(-1)z\bar{z} + W_{02}^{(2)}(-1) \frac{\bar{z}^2}{2} + \dots \end{aligned}$$

An identification by using (34) and (43) gives us the following coefficients of g :

$$\begin{aligned} g_{20} &= 2\tau_0 \overline{G_{A\varphi}} \{a_{11}(q^{(1)}(0))^2 + a_{12}q^{(1)}(0)q^{(2)}(0) \\ &\quad + q_1^*(a_{21}(q^{(1)}(-1))^2 + a_{22}q^{(1)}(-1)q^{(2)}(0) \\ &\quad + a_{23}q^{(1)}(-1)q^{(2)}(-1) + a_{24}q^{(2)}(0)q^{(2)}(-1)\}, \\ g_{11} &= \tau_0 \overline{G_{A\varphi}} \{2a_{11}q^{(1)}(0)\bar{q}^{(1)}(0) \\ &\quad + a_{12}(q^{(1)}(0)q^{(2)}(0) + \bar{q}^{(1)}(0)q^{(2)}(0)) \\ &\quad + q_1^*(2a_{21}q^{(1)}(-1)\bar{q}^{(1)}(-1) \\ &\quad + a_{22}(q^{(1)}(-1)\bar{q}^{(2)}(0) + q^{(2)}(0)\bar{q}^{(1)}(-1)) \\ &\quad + a_{23}(q^{(1)}(-1)\bar{q}^{(2)}(-1) + q^{(2)}(-1)\bar{q}^{(1)}(-1)) \\ &\quad + a_{24}(q^{(2)}(-1)\bar{q}^{(2)}(0) + q^{(2)}(0)\bar{q}^{(2)}(-1))\}, \\ g_{02} &= 2\tau_0 \overline{G_{A\varphi}} \{a_{11}(\bar{q}^{(1)}(0))^2 \\ &\quad + a_{21}\bar{q}^{(1)}(0)\bar{q}^{(2)}(0) + q_1^*(a_{21}(\bar{q}^{(2)}(-1))^2 \end{aligned}$$

$$\begin{aligned} &\quad + a_{22}\bar{q}^{(1)}(-1)\bar{q}^{(2)}(0) \\ &\quad + a_{23}\bar{q}^{(1)}(-1)\bar{q}^{(2)}(-1) \\ &\quad + a_{24}\bar{q}^{(2)}(0)\bar{q}^{(2)}(-1)\}, \\ g_{21} &= 2\tau_0 \overline{G_{A\varphi}} \{a_{11}(\bar{q}^{(1)}(0)W_{20}^{(1)}(0) \\ &\quad + 2q^{(1)}(0)W_{11}^{(1)}(0)) + a_{12}(q^{(1)}(0)W_{11}^{(2)}(0) \\ &\quad + \frac{1}{2}\bar{q}^{(1)}(0)W_{20}^{(2)}(0) \\ &\quad + \frac{1}{2}\bar{q}^{(2)}(0)W_{20}^{(1)}(0) \\ &\quad + \bar{q}^{(2)}(0)W_{11}^{(1)}(0)) + 3a_{13}(q^{(1)}(0))^2\bar{q}^{(1)}(0) \\ &\quad + q_1^*(a_{21}(\bar{q}^{(1)}(-1)W_{20}^{(1)}(-1) \\ &\quad + 2q^{(1)}(-1)W_{11}^{(1)}(-1)) + a_{22}(q^{(1)}(-1)W_{11}^{(2)}(0) \\ &\quad + \frac{1}{2}\bar{q}^{(1)}(-1)W_{20}^{(2)}(0) \\ &\quad + \frac{1}{2}\bar{q}^{(2)}(0)W_{20}^{(1)}(-1) \\ &\quad + q^{(2)}(0)W_{11}^{(1)}(-1)) + a_{23}(q^{(1)}(-1)W_{11}^{(2)}(-1) \\ &\quad + \frac{1}{2}\bar{q}^{(1)}(-1)W_{20}^{(2)}(-1) + q^{(2)}(-1)W_{11}^{(1)}(-1) \\ &\quad + \frac{1}{2}\bar{q}^{(2)}(-1)W_{20}^{(1)}(-1)) + a_{24}(q^{(2)}(0)W_{11}^{(2)}(-1) \\ &\quad + \frac{1}{2}\bar{q}^{(2)}(0)W_{20}^{(2)}(-1) + q^{(2)}(-1)W_{11}^{(2)}(0) \\ &\quad + \frac{1}{2}\bar{q}^{(2)}(-1)W_{20}^{(2)}(0)) \\ &\quad + 3a_{25}(q^{(1)}(-1))^2\bar{q}^{(1)}(-1) \\ &\quad + a_{26}((q^{(1)}(-1))^2\bar{q}^{(2)}(0) \\ &\quad + 2q^{(1)}(-1)\bar{q}^{(1)}(-1)q^{(2)}(0)) \\ &\quad + a_{27}((q^{(1)}(-1))^2\bar{q}^{(2)}(-1) \\ &\quad + 2q^{(1)}(-1)\bar{q}^{(1)}(-1)q^{(2)}(-1)) \\ &\quad + a_{28}(q^{(1)}(-1)\bar{q}^{(2)}(0)q^{(2)}(-1) \\ &\quad + q^{(1)}(-1)\bar{q}^{(2)}(-1)q^{(1)}(0) \\ &\quad + q^{(2)}(-1)\bar{q}^{(1)}(-1)q^{(2)}(0))\}. \end{aligned}$$

Now we reach to the step of computation of $W_{20}(\theta)$. Using (27) and (38) gives:

$$\begin{aligned} H(z, \bar{z}, \theta) &= -2\text{Re}[\bar{q}^*(0) f_0(z, \bar{z})q(\theta)] + Ru_t \\ &= -gq(\theta) - \bar{g}\bar{q}(\theta) + Ru_t \\ &= - \left(g_{20} \frac{z^2}{2} + g_{11}z\bar{z} + g_{02} \frac{\bar{z}^2}{2} \right) q(\theta) \\ &\quad - \left(\bar{g}_{20} \frac{\bar{z}^2}{2} + \bar{g}_{11}z\bar{z} + \bar{g}_{02} \frac{z^2}{2} \right) \bar{q}(\theta) + Ru_t, \tag{45} \end{aligned}$$

where

$$Ru_t = \tau_0 \begin{pmatrix} f_1 \\ f_2 \end{pmatrix} = 2\tau_0 A^{A\varphi} \frac{z^2}{2} + \tau_0 B^{A\varphi} z\bar{z},$$

with

$$A^{A\varphi} = \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix},$$

$$B^{A\varphi} = \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix},$$

where

$$A_{11}^{A\varphi} = a_{11}(q^{(1)}(0))^2 + a_{12}q^{(1)}(0)q^{(2)}(0),$$

$$A_{21}^{A\varphi} = a_{21}(q^{(1)}(-1))^2 + a_{22}q^{(1)}(-1)q^{(2)}(0) + a_{23}q^{(1)}(-1)q^{(2)}(-1) + a_{24}q^{(2)}(-1)q^{(2)}(0),$$

$$B_{11}^{A\varphi} = 2a_{11}q^{(1)}(0)\bar{q}^{(1)}(0) + a_{12}(q^{(1)}(0)\bar{q}^{(2)}(0) + \bar{q}^{(1)}(0)q^{(2)}(0)),$$

$$B_{21}^{A\varphi} = 2a_{21}q^{(1)}(-1)\bar{q}^{(1)}(-1) + a_{22}(q^{(1)}(-1)\bar{q}^{(2)}(0) + \bar{q}^{(1)}(-1)q^{(2)}(0)) + a_{23}(q^{(1)}(-1)\bar{q}^{(2)}(-1) + \bar{q}^{(1)}(-1)q^{(2)}(-1)) + a_{24}(q^{(2)}(-1)\bar{q}^{(2)}(0) + \bar{q}^{(2)}(-1)q^{(2)}(0)).$$

A comparison of the coefficients of equations (39) and (44) gives the following equalities:

$$H_{20}(\theta) = \begin{cases} -gq(\theta) - \bar{g}\bar{q}(\theta) & \text{if } -1 \leq \theta < 0, \\ -gq(\theta) - \bar{g}\bar{q}(\theta) + 2\tau_0 A & \text{if } \theta = 0. \end{cases} \tag{46}$$

$$H_{11}(\theta) = \begin{cases} -gq(\theta) - \bar{g}\bar{q}(\theta) & \text{if } -1 \leq \theta < 0, \\ -gq(\theta) - \bar{g}\bar{q}(\theta) + \tau_0 B & \text{if } \theta = 0. \end{cases} \tag{47}$$

$$\begin{cases} E_{1A\varphi}^{(1)} = \frac{2B_{A\varphi}A_{21}^{A\varphi} + 2A_{11}^{A\varphi}(2i\omega_0 - D_{A\varphi}e^{-2i\tau_0\omega_0})}{(A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi})e^{-2i\tau_0\omega_0} - 2i\omega_0D_{A\varphi}e^{-2i\tau_0\omega_0} - 2i\omega_0A_{A\varphi} - 4\omega_0^2}, \\ E_{1A\varphi}^{(2)} = \frac{2A_{11}^{A\varphi}C_{A\varphi}e^{-2i\tau_0\omega_0} + 2A_{21}^{A\varphi}(2i\omega_0 - A_{A\varphi})}{(A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi})e^{-2i\tau_0\omega_0} - 2i\omega_0D_{A\varphi}e^{-2i\tau_0\omega_0} - 2i\omega_0A_{A\varphi} - 4\omega_0^2}. \end{cases} \tag{52}$$

When we substitute (45) in (41) and (46) in (42), respectively, we obtain the following differential equations:

$$\begin{cases} \dot{W}_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{20}\bar{q}(\theta), \\ \dot{W}_{11}(\theta) = g_{11}q(\theta) + \bar{g}_{11}\bar{q}(\theta), \end{cases} \tag{48}$$

which have the following solutions:

$$\begin{cases} W_{20}(\theta) = \frac{ig_{20}}{\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{\bar{g}_{20}}{3i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + E_{1A\varphi}e^{2i\tau_0\omega_0\theta}, \\ W_{11}(\theta) = \frac{g_{11}}{i\tau_0\omega_0}q(0)e^{i\tau_0\omega_0\theta} + \frac{\bar{g}_{11}}{i\tau_0\omega_0}\bar{q}(0)e^{-i\tau_0\omega_0\theta} + E_{2A\varphi}, \end{cases} \tag{49}$$

where $E_{1A\varphi} = (E_{1A\varphi}^{(1)}, E_{1A\varphi}^{(2)})^T$ and $E_{2A\varphi} = (E_{2A\varphi}^{(1)}, E_{2A\varphi}^{(2)})^T$ are constant vectors belonging to \mathbb{R}^2 .

Now, let us compute the constant vectors $E_{1A\varphi}$ and $E_{2A\varphi}$ by using (41) and (42). We have:

$$\int_{-1}^0 d\eta(\theta)W_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(0) - H_{20}(0), \tag{50}$$

and

$$\int_{-1}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0). \tag{51}$$

Then, using the fact that,

$$\begin{cases} \left(i\tau_0\omega_0 I - \int_{-1}^0 e^{i\tau_0\omega_0\theta} d\eta(\theta)\right)q(0) = 0, \\ \left(-i\tau_0\omega_0 I - \int_{-1}^0 e^{-i\tau_0\omega_0\theta} d\eta(\theta)\right)\bar{q}(0) = 0, \end{cases}$$

and using the first equation of (48), equations (44) and (49), we have:

$$\left(2i\tau_0\omega_0 I - \int_{-1}^0 e^{2i\tau_0\omega_0\theta} d\eta(\theta)\right)E_1 = 2\tau_0 \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix}$$

which implies $\begin{pmatrix} 2i\omega_0 - A_{A\varphi} & -B_{A\varphi} \\ -C_{A\varphi}e^{-2i\tau_0\omega_0} & 2i\omega_0 - D_{A\varphi}e^{-2i\tau_0\omega_0} \end{pmatrix}$

$$\begin{pmatrix} E_{1A\varphi}^{(1)} \\ E_{1A\varphi}^{(2)} \end{pmatrix} = 2 \begin{pmatrix} A_{11}^{A\varphi} \\ A_{21}^{A\varphi} \end{pmatrix} \text{ and finally}$$

Similarly, using the second equation of (48), (46) and (50) gives:

$$\begin{aligned} \left(\int_{-1}^0 e^{-i\tau_0\omega_0\theta} d\eta(\theta)\right)E_{2A\varphi} &= \tau_0 \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix} \\ \Rightarrow \begin{pmatrix} A_{A\varphi} & B_{A\varphi} \\ C_{A\varphi} & D_{A\varphi} \end{pmatrix} \begin{pmatrix} E_{2A\varphi}^{(1)} \\ E_{2A\varphi}^{(2)} \end{pmatrix} &= - \begin{pmatrix} B_{11}^{A\varphi} \\ B_{21}^{A\varphi} \end{pmatrix}, \end{aligned}$$

and finally

$$\begin{cases} E_{2A\varphi}^{(1)} = \frac{B_{A\varphi}B_{21}^{A\varphi} - D_{A\varphi}B_{11}^{A\varphi}}{A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi}}, \\ E_{2A\varphi}^{(2)} = \frac{C_{A\varphi}B_{11}^{A\varphi} - A_{A\varphi}B_{21}^{A\varphi}}{A_{A\varphi}D_{A\varphi} - B_{A\varphi}C_{A\varphi}}. \end{cases} \quad (53)$$

Finally, from (48), (50) and (52) we can now calculate values which are useful for the determination of the period of the bifurcating solution and its stability. We have the following values:

$$\begin{aligned} C_1(0) &= \frac{i}{2\tau_0\omega_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{1}{2}g_{21}, \\ \mu_2 &= -\frac{ReC_1(0)}{Re\left(\frac{d\lambda}{d\tau}(\tau_0)\right)}, \\ \beta_2 &= 2ReC_1(0), \\ T_2 &= -\frac{Im(C_1(0)) + \mu_2 Im\left(\frac{d\lambda}{d\tau}(\tau_0)\right)}{\tau_0\omega_0}. \end{aligned}$$

This ends the proof.

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