THE NUMERICAL BIFURCATION ANALYSIS OF LESLIE-GOWER PREDATOR-PREY MODEL WITH DIFFERENT TYPES OF PREDATOR HARVESTING STRATEGIES

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UNIVERSITI SAINS MALAYSIA

2023

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by

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Thesis submitted in fulfilment of the requirements
for the degree of
Master of Science

May 2023

ACKNOWLEDGEMENT

I would like to express my deepest appreciation to my supervisor Associate Professor Dr. Noor Atinah binti Ahmad, for her guidance, encouragement, kindness, and dedication throughout this journey. I would like to thank my co-supervisor, Associate Professor Dr. Mohd Hafiz bin Mohd, for his valuable input and guidance.

My deepest gratitude to my family especially to my late father, my mother, my husband, Arif and my son, Ammar Yusuf who believed in and supported me throughout the experience and were always by my side through the ups and downs of this journey. Finally, to all involved. Your assistance shall be remembered forever. Thank you so much.

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LIST OF ABBREVIATIONS

BT	Bogdanov-Takens Bifurcations
DTC	Degenerate transcritical bifurcation
GH	Degenerate Hopf Bifurcation
H	Hopf Bifurcation
LP	Saddle-node bifurcation point
TC	Transcritical Bifurcation
MSY	Maximum sustainable yield

LIST OF SYMBOLS

$\boldsymbol{x}$	Prey population
$\boldsymbol{y}$	Predator population
$\boldsymbol{\delta}$	The ratio of the growth rate of predator and prey
$\boldsymbol{\beta}$	The growth rate of predator
$\boldsymbol{h}$	Predator harvesting rate for constant-yield model
$\boldsymbol{h_1}$	Critical predator harvesting rate for constant-yield predator harvesting model
$\boldsymbol{\alpha}$	Predator harvesting rate for linear and nonlinear predator harvesting model
$\boldsymbol{\alpha_1}$	Critical predator harvesting rate for linear and nonlinear predator harvesting model
$\boldsymbol{\alpha_H}$	Predator harvesting rate for nonlinear at Hopf bifurcation point
$\boldsymbol{\gamma}$	Carrying capacity of the predator in the absence of prey for a nonlinear model
$\boldsymbol{\sigma}$	Lyapunov number
$\boldsymbol{\lambda}$	Eigenvalues
$\boldsymbol{\Delta}$	Discriminant of the equation
$\boldsymbol{r_1}$	Intrinsic growth rates of prey
$\boldsymbol{r_2}$	Intrinsic growth rates of predator
$\boldsymbol{K}$	Carrying capacity of the prey in the absence of a predator
$\boldsymbol{n}$	Measurement of food quality for the prey
$\boldsymbol{q}$	Catchability coefficient
$\boldsymbol{E}$	Efforts applied to harvest individuals
$\boldsymbol{u}$	The population that presents the harvesting

ANALISIS PERCABANGAN BERANGKA MODEL PEMANGSA-MANGSA LESLIE-GOWER DENGAN BEBERAPA JENIS STRATEGI PENUAIAN PEMANGSA

ABSTRAK

Model pemangsa-mangsa adalah model yang melibatkan interaksi antara dua spesies. Dinamik model pemangsa-mangsa menarik perhatian ramai ahli ekologi dan ahli matematik. Kajian ini menunjukkan hasil teori dan berangka ke atas analisis model pemangsa-mangsa Leslie-Gower dengan pelbagai jenis strategi penuaian pemangsa iaitu model penuaian pemangsa linear, hasil-malar, dan tidak linear. Kami menggambarkan analisis percabangan berangka kodimensi-satu dan kodimensi-dua untuk menunjukkan kestabilan titik keseimbangan dan tingkah laku model apabila nilai penuaian berubah dengan strategi penuaian yang berbeza. Kami menganalisis setiap model untuk menentukan kewujudan percabangan berangka tempatan seperti pelana-nod, transkritikal, Hopf, dan percabangan berangka Bogdanov-Takens serta membandingkan jenis percabangan berangka yang berbeza yang berlaku untuk setiap strategi penuaian pemangsa. Kajian ini menyiasat dinamik model pemangsa-mangsa Leslie-Gower dengan strategi penuaian berbeza melalui analisis berangka yang menyokong kadar penuaian kritikal yang ditentukan daripada analisis secara teori. Kajian ini juga menemui kepentingan strategi penuaian pemangsa dalam pengurusan sumber yang optimum yang boleh diperbaharui menggunakan model mangsa-pemangsa Leslie-Gower. Pemilihan nilai parameter adalah sangat penting kerana ia melibatkan perbezaan nilai yang sangat kecil dan boleh mengakibatkan spesis pemangsa pupus jika nilai penuaian pemangsa lebih tinggi berbanding nilai kritikal penuaian pemangsa.

THE NUMERICAL BIFURCATION ANALYSIS OF LESLIE-GOWER PREDATOR-PREY MODEL WITH DIFFERENT TYPES OF PREDATOR HARVESTING STRATEGIES

ABSTRACT

The predator-prey model is the most common model dealing with the interaction between two species. The dynamics of a predator-prey model has attracted a lot of attention from many ecologists and mathematicians. This study shows theoretical and numerical results on the analysis of the Leslie-Gower predator-prey model with different types of predator harvesting strategies namely linear, constant-yield and nonlinear predator harvesting models. We illustrate the numerical bifurcations analysis of codimension-one and codimension-two to show the stability of the steady-states and the behaviour of the model when the harvesting rate change under different harvesting strategies. We analyse each model to determine the existence of local bifurcations such as saddle-node, transcritical, Hopf, and Bogdanov-Takens bifurcations and compare the different type of bifurcations that occurs for each predator harvesting strategy. This study investigates the dynamics of the Leslie-Gower predator-prey model with different harvesting strategies through numerical analysis that corroborate with the critical harvesting rate determined from the theoretical analysis. This study also discovers the significance of predator harvesting strategies in the optimal management of renewable resources using the Leslie-Gower predator-prey model. The choice of the parameter values is crucial with the small difference in the values may cause the predator species extinct if the harvesting rate is greater than the critical harvesting rate.

CHAPTER 1

INTRODUCTION

1.1 Background of the study

In the ecological system, there are many interactions between the species in their environment, such as competition, commensalism, and predation. In ecological studies, the term “predation” is defined as a biological interaction in which the hunting organism (that is, the predator) feeds on the organism that is being preyed on. The predator species may not kill their prey before feeding on them, but the act of predation always becomes the reason for the death of the prey. Lotka and Volterra first introduced the theory of predator-prey interaction in the 1920s, which presumed that predator-prey interactions depend on the size of the prey population. Therefore, the prey population grows exponentially in the absence of a predator, and the predator will seek other prey after the size of the prey decreases (Boyce and DiPrima, 2010).

Holling (1959) further described the way a predator responds to the changing density of its prey via three types of functional response; (i) in type I there is a linear relationship where the predator can keep up with the increasing density of prey by eating them in direct proportion to their abundance in the environment; (ii) in type II the rate of prey consumption per predator initially rises as the prey density increases but eventually remains constant regardless of a further increase in prey density; (iii) in type III, the functional response resembles type II in which at high levels of prey density, saturation occurs, and the response of predators to prey at low prey density is different.

Despite all the theoretical models and approaches, there is still a lack of understanding of the complex interactions between predators and prey and the effect of predation on prey populations. In general, predators can have impacts on prey populations, but under certain circumstances, predation has little or no effects on prey populations even though they are the main cause of death in those populations. These circumstances can include direct killing and risk effects by other factors such as human activities that cause an environmental disaster. The outcomes can vary greatly depending on the habitat characteristics, the number of predator species, the vulnerability of prey, weather, age population and hunting behaviour. Furthermore, the exploitation of biological resources and harvesting of populations that are commonly practised in fishery, forestry, and wildlife management further disturbed the ecological conditions.

In response to these challenges, there is a wide interest to investigate predator-prey systems and the impact of harvesting on populations. Many classic models have been developed to study the dynamics of species interactions and one of the earliest predator-prey models in mathematical ecology is the Lotka-Volterra model. This model becomes the basis of many models in the analysis of population dynamics, and it was discovered independently by Alfred Lotka (1925) and by Vito Volterra (1926).

Harvesting is an important and effective method to prevent and control the explosive growth of predators or prey when they reach sufficient population numbers.

The rate of harvesting has been used to control the increase in population and as a controller of the population density. In resource management applications, harvesting gives a great impact on the stability and dynamics of the population system when there are changes in steady-states, perturbations, and parameter values (Ouncharoen et al., 2010).

In ecological modelling, the focus of population dynamics is whether the unforeseen changes in the dynamics of the populations occur, and which values of parameters involved do occur. These changes are called bifurcations. Bifurcations also can be interpreted in terms of eigenvalues degeneracy. Local bifurcations involve the degeneracy of some eigenvalue to a small region of phase space containing the steady-state and associated with the changes in the stability of the steady-state. In first-order ODEs of predator-prey systems, the qualitative characterization of the behaviours of solutions depends on their initial conditions and parameter. This can be done by finding the steady-state solutions, and then using stability analysis.

The main focus of this study is to perform the bifurcation analysis of the Leslie-Gower predator-prey model by further investigating the dynamics of three different predator harvesting strategies namely, (i) the constant-yield predator harvesting, (ii) linear harvesting, and (iii) non-linear predator harvesting strategies. This study aims to provide a comparative analysis of the Leslie-Gower predator-prey model on these three different predator harvesting strategies, analyse the dynamical bifurcation types that affect harvesting strategies, and provide evidence on the bifurcation analysis to support the most effective predator-prey model incorporating harvesting, based on theoretical analysis done by previous studies.

1.2 Problem Description

The interaction between species such as predator-prey models play an important role in studying the environmental balance and the management of renewable sources. The harvesting strategies for the populations in predator-prey is important to balance the population in an ecosystem, preserve the ecological health system, and at the same time control the exploitation of the ecosystem.

The effects of harvesting in the dynamics of the predator-prey model have attracted great attention from researchers for prey harvesting because it is common nature to harvest the prey and developed a modified model to study prey harvesting. Harvesting in prey affects the population of predators indirectly because it reduces the food population available in the area. A different point of view should be given to investigate and compare their dynamic behaviour when it involved different predator harvesting strategies to give a clear picture of real-life applications such as the impact of harvesting on the management of renewable resources in fishery management and consider harvesting at a rate less than the maximum sustainable yield (MSY) to ensure the risk-free environment. The MSY level is the population size that occurs at the point where the population is increasing at its maximum rate.

1.3 Objectives of the Study

The objectives of this study are:

a) To provide a comprehensive summary of theoretical and numerical analysis results of the Leslie-Gower predator-prey model with constant-yield predator harvesting, linear harvesting, and nonlinear predator harvesting.

b) To analyse the different predator harvesting strategies and make the comparative analysis in the Leslie-Gower predator-prey model that affect the different types of bifurcation.

c) To corroborate the numerical bifurcation analysis with theoretical analysis and discuss the biological interpretation in the predator-prey model with different predator harvesting strategies.

1.4 Significance of the Study

The findings in this study are useful for future research in ecology especially in mathematical modelling because this study will give a better understanding of the Leslie-Gower predator-prey model with different types of predator harvesting and its effects on the stability of the population especially involving constant-yield predator harvesting, linear predator harvesting, and nonlinear predator harvesting. The comparative studies for different predator harvesting strategies of Leslie-Gower predator-prey models discussed in this study can guide new researchers to develop new research ideas on the dynamics of the different models.

The study of the different harvesting rate use for the different predator harvesting strategies in the Leslie-Gower model will contribute to the research performed on understanding the impact of the harvesting rate on the coexistence and extinction between prey and predator in such scenarios which consider the exploitation of the predator population through harvesting. The results from both theoretical and numerical analysis of the models used in this study, gained through computing for the steady states, determining the stability of the steady states, and checking for the existence of possible bifurcations in the systems will be beneficial for planning balanced harvesting of resources.

Thus, the conclusions derived from this study can be used in the management of renewable resources, specifically in the field of extinction prevention as stated in Malaysia's Sustainable Development Goal (SDGs) to conserve and sustainably use the oceans, seas, and marine resources for sustainable development. Moreover, this work discusses the impact of the harvesting rate on predator-prey species in the ecosystem. Overall, it is hoped to add to the existing predator-prey model's body of knowledge and fill the gap in the current literature.

1.5 Outlines of the Thesis

This thesis is organized into six chapters. Chapter 1 is the introduction to the study. In Chapter 2, the literature related to Leslie-Gower predator-prey model is presented. Chapter 3 outlines a detailed analysis of the model system. In Chapter 4, the analytical result of the Leslie-Gower model with different predator harvesting strategies is discussed. The numerical simulation result for bifurcation analysis of the Leslie-Gower predator-prey model with different predator harvesting strategies is presented in Chapter 5. Discussion and conclusion are presented in Chapter 6 which summarize our key findings.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

In this chapter, we will discuss the predator-prey model incorporating different types of predator harvesting strategies, namely, constant-yield, linear and nonlinear Michaelis-Menten type predator harvesting. Lotka-Volterra model was discovered independently by Alfred Lotka and by Vito Volterra (1926). The Lotka-Volterra model is written as

$$\frac{dx}{dt} = ax - bxy,$$

$$\frac{dy}{dt} = -cy + dxy, \tag{2.1}$$

where *x* is the population of prey at time *t* and *y* is the population of the predator at time *t* with *a, b, c,* and *d* are positive parameters. This model was derived and developed through the logistic equation in the theory of chemical reaction and observation of the fish population in the Adriatic Sea. The Lotka-Volterra model describes the predator population as having logistic growth but the carrying capacity of the predator is proportional to prey abundance, where the existence of the predator depends exclusively on the prey population (Leslie & Gower, 1960). Therefore, for this study, it was of interest to investigate one of the important predator-prey models which is a modification of the Lotka-Volterra model known as the Leslie-Gower model.

The Leslie-Gower predator-prey model is written by Leslie and Gower (1960), which is given by

$$\frac{dx}{dt} = r_1 x\left(1 - \frac{x}{K}\right) - axy,$$

$$\frac{dy}{dt} = r_2 y(1 - \frac{y}{bx}). \tag{2.2}$$

Both r_1 and r_2 are intrinsic growth rates of prey and predator. The maximum value at which the per capita reduction rate of the prey, *x* is represented by *a*. *K* is the carrying capacity of the prey in the absence of a predator and *bx* is a prey-dependent carrying capacity for a predator. The measurement of the quality of the food for a predator is *b* which *bx* is proportional to prey abundance. The term $\frac{y}{bx}$ is called the Leslie-Gower term. If a constant is added to the term as $\frac{y}{bx+c}$, then it was called the modified Leslie-Gower term. The modified Leslie-Gower term is used to avoid the singularities when $x = 0$.

In early 1972, the stability analysis of predator-prey models with their harvesting regimes was investigated using the Leslie-Gower predator-prey model (2.2). Leslie-Gower predator-prey model with prey and predator harvesting was proposed as in May et al. (1979):

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy - H_1,$$

$$\frac{dy}{dt} = r_2 y(1 - \frac{y}{bx}) - H_2, \tag{2.3}$$

where H_1 and H_2 are the effects of harvesting for the prey and predator, respectively. If H_1 and H_2 from the system (2.3) equals zero, then the Leslie-Gower predator-prey model has no harvesting as in (2.2).

Next, there are two types of harvesting which are constant-effort harvesting and constant-yield harvesting have been proposed. Beddington and May (1980) proposed constant-effort harvesting for both predator and prey which was described by a linear function with constant multiplication of the size of the population under harvest where $H_1 = r_1 h_1 x$ and $H_2 = r_2 h_2 y$. Then, from Beddington and May (1980),

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy - r_1 h_1 x,$$

$$\frac{dy}{dt} = r_2 y(1 - \frac{y}{bx}) - r_2 h_2 y, \tag{2.4}$$

which can be simplified to

$$\frac{dx}{dt} = r_1 x(1 - h_1 - \frac{x}{K}) - axy,$$

$$\frac{dy}{dt} = r_2 y(1 - h_2 - \frac{y}{bx}). \tag{2.5}$$

Later, Beddington and Cooke (1982) studied the constant-yield prey harvesting and constant-effort predator harvesting with $H_1 = h_1$ and $H_2 = r_2 h_2 y$, respectively. The constant-yield harvesting is described by a constant independent of the size of the population under harvest. The different type of predator-prey model with the harvesting rate leads to different dynamical behaviour. Thus, the model is written as (Beddington and Cooke (1982))

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy - h_1,$$

$$\frac{dy}{dt} = r_2 y(1 - h_2 - \frac{y}{bx}). \tag{2.6}$$

Since they found constant-yield harvesting in prey presented more dynamics for the population system, further research in constant-yield harvesting for both predator and prey has been done. They found that if the predators are in a state of heavy depletion the effect of the prey harvesting on predator replacement yields is not very great but as predators rise to higher levels the effect becomes substantial. This model is written in Beddington and Cooke (1982) as

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy - h_1,$$

$$\frac{dy}{dt} = r_2 y(1 - \frac{y}{bx}) - h_2. \tag{2.7}$$

Zhu and Lan (2010) studied constant-yield harvesting on the prey and found that constant-yield harvesting has more dynamic effects on the population system than constant-effort harvesting. The model with constant-yield prey harvesting as given by (Zhu and Lan (2010))

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy - h_1,$$

$$\frac{dy}{dt} = r_2 y(1 - \frac{y}{bx}). \tag{2.8}$$

Then, Huang et al. (2013) studied the bifurcations analysis for Leslie-Gower predator-prey model with constant-yield predator harvesting. They found richer dynamics in the model which inspired them to continue their studied and analysed of the bifurcations with their dynamics for the constant-yield harvesting in predators. The constant-yield predator harvesting is written as $H_2 = h_2$ as given by (Huang et al. (2013))

$$\frac{dx}{dt} = r_1 x(1 - \frac{x}{K}) - axy,$$

$$\frac{dy}{dt} = r_2 y\left(1 - \frac{y}{bx}\right) - h_2. \tag{2.9}$$

Gupta et al. (2012) discussed the bifurcation analysis of a Leslie-Gower predator-prey model for nonlinear prey harvesting and mentioned nonlinear harvesting as more realistic and exhibits saturation effects concerning both the stock abundance and the effort level. The Leslie-Gower predator-prey model with Michaelis-Manten type prey harvesting is (Gupta et al. (2012))

$$\frac{dx}{dt} = \left[r\left(1 - \frac{x}{K}\right) - \alpha y - \frac{qE}{m_1E + m_2x}\right]x,$$

$$\frac{dy}{dt} = \begin{cases} s\left(1 - \frac{y}{nx}\right)y, & \text{if } (x, y) \neq 0 \\ 0, & \text{if } (x, y) = (0, 0) \end{cases}, \tag{2.10}$$

where r and s are intrinsic growth rates of the prey and predators, respectively. K is the environmental carrying capacity for prey, α is the maximal predator per capita consumption rate, n is a measure of food quality that the prey provides towards the predator births, q is the catchability coefficient, E is the effort applied to harvest individuals, m_1 and m_2 are positive constants. Singh et al. (2016) studied the nonlinear predator harvesting for Leslie-Gower predator-prey model and showed more complex and rich dynamics when adopting a nonlinear harvesting method compared to the model with no harvesting and with constant-yield predator harvesting. The model is written as (Singh et al. (2016))

$$\frac{dx}{dt} = r\left(1 - \frac{x}{K}\right)x - mxy,$$

$$\frac{dy}{dt} = \begin{cases} s(1 - \frac{y}{nx})y - \frac{qE}{m_1E + m_2x}, & \text{if } (x, y) \neq 0 \\ 0 & , \text{ if } (x, y) = (0, 0) \end{cases}. \tag{2.11}$$

Then, Hu and Cao (2017) analysed the stability and bifurcation types in the Leslie-Gower predator-prey model with the Michaelis-Menten nonlinear type of predator harvesting. Their findings revealed that the nonlinear predator harvesting type has richer dynamics compared to the linear harvesting and the constant-yield harvesting methods.

2.2 Predator-Prey Model with Harvesting Strategy

Harvesting has a strong impact on the dynamics of a predator-prey population. The strategy for harvesting is necessary to develop an ecological system in bio-economics and MSY with minimum effort to protect the ecosystems and to get an insight into the optimal management of renewable resources. Clark (2005) studied the mathematical model of harvesting to interplay the economical and biological perspectives in renewable resource management.

Hoekstra and van den Bergh (2005) studied the conservation and harvesting of a population dynamics model. They illustrated that several types of optimal harvesting solutions are possible depending on economic and ecological parameters such as the maximum harvesting rate, the discount rate, the cost of fishing, and the predator's search and handling time of prey. The final optimal harvest rate can be constant, resulting in a steady-state, either with or without the predator species. Moreover, harvesting is an effective method to prevent and control the explosive growth of predators or prey. Therefore, it is essential to introduce the harvesting strategies of populations into models. According to Gupta et al. (2015), there are three types of harvesting strategies which are:

i) constant harvesting, $h(u) = h$,

ii) proportional harvesting, $h(u) = qEu$, and

iii) nonlinear harvesting (Holling type II), $\frac{qEu}{m_1E+m_2u}$

where u is the population that presents the harvesting, q is the catchability coefficient, E is the effort applied to harvest individual populations, and m_1, m_2 are suitable positive constants. Constant harvesting can be described by a constant number, h of individuals harvested per unit of time which is independent of the size of the population under harvest. Proportional harvesting means that the number of individuals harvested per unit of time is proportional to the current population. Nonlinear harvesting, which is also known as Michaelis-Menten type harvesting or Holling type-II function, is more realistic compared to constant harvesting and proportional harvesting from biological and economic points of view. It shows that the nonlinear harvesting function exhibits a saturation effect for both stock abundance and effort level.

2.2.1 Predator-Prey Model with Prey Harvesting

Harvesting of prey is common in the predator-prey model which is frequently used to describe the dynamic in the ecological system. If the prey is harvested, the predator is indirectly affected by the harvest and can go extinct if its resources are overexploited. The predator-prey model with constant-yield harvesting in prey was studied by Zhu and Lan (2010). They investigated how the harvesting rate affects the dynamics of Leslie-Gower predator-prey models with prey harvesting. They computed the Lyapunov-numbers to obtain the supercritical or subcritical Hopf bifurcation and limit cycles for the weak centre.

The discussion on nonlinear harvesting started when Xiao and Jenning (2005) studied the dynamical properties of the ratio-dependent predator-prey model with constant prey harvesting. There are numerous kinds of bifurcations such as saddle-node, subcritical and supercritical Hopf bifurcations, and Bogdanov-Takens bifurcation. They showed a limit cycle and a homoclinic or heteroclinic orbit exist at different parameter values. It has been shown that the nonzero constant prey harvesting rate prevents common extinction as a possible outcome of predator-prey interaction.

Rebaza (2012) studied the dynamics of prey threshold harvesting and refuge and showed that threshold harvesting is more efficient than using continuous harvesting. Gupta et al. (2013) studied a bifurcation analysis of a modified Leslie-Gower prey-predator model in the presence of nonlinear harvesting in prey with the Michaelis-Menten type. Then, found out that the system has up to five steady states including the origin and can be a saddle, nodes, focus, centres and saddle-node bifurcations. Since, the common nature to harvest prey, many researchers focused on the prey harvesting model from earlier. Avila-Vales et al. (2017) described the dynamics and bifurcations of the predator-prey system with a functional response of Holling type III, that considered a Michaelis-Menten harvesting term in the prey population. Zhang et al. (2018) studied the dynamics of a modified Leslie-Gower model with Holling type-IV functional response and nonlinear prey harvesting. They discussed the bionomical steady state of the model and the optimal harvesting policy that should be adopted by a regulatory agency. They established the stability of the limit cycle using the Lyapunov number around the steady states. A stable limit cycle is possible when the consumption of prey by the predator is bounded by some maximum value. Diza and Addawe (2018) used a threshold on the prey harvesting to control the harvesting done in the population to avoid extinction and Su (2019) studied linear harvesting and identified a weak focus in the prey harvesting system. The study revealed that there are at most three limit cycles bifurcated from Hopf bifurcation. The ongoing study of predator-prey models with prey harvesting keeps growing with different modifications of the model with their prey harvesting. Next, we will discuss the predator-prey model with predator harvesting.

2.2.2 Predator-Prey Model with Predator Harvesting

The predator-prey models with predator harvesting caught the researcher's attention after the prey harvesting. It is well-known that harvesting one species has a strong influence on the dynamics of the ecosystem. The most common predator harvesting form is a nonzero constant or a linear harvesting rate. Azar et al. (1995) studied the stability properties of these two harvesting strategies in a two-prey-one-predator for Lotka-Volterra type model with predator harvesting. Their study contributes to a qualitative understanding of the properties of different harvesting strategies. They also demonstrated switching from a linear to a constant harvesting rate may turn a stable stationary state into a periodic or chaotic oscillatory mode from a mathematical perspective. However, when deciding on the constant level of harvesting, the instability of the constant harvest strategy calls for great care because the result is counter intuitive and worth exploring more in detail. Lenzini and Rebaza (2010) also studied two predator-prey models with linear or nonzero constant predator harvesting and mentioned that these two types of harvesting rates seemingly have their advantages and disadvantages in fitting the harvest in the real world. They reported that when the density of the predator or prey is rather low, the nonzero constant harvesting rate is not as reasonable as the proportional type, while if the predator or prey is abundant, the linear harvesting rate is less possible than the constant harvesting rate. The predator conversion rate must exceed the sum of the death and the harvesting rate to exhibit interesting dynamics around the coexistence steady-state, including multiple bifurcations, periodic orbits, and connecting orbits.

The interaction between a predator and prey modelled by differential equations system as a logistic model for prey and a linear model for predator was studied by Li et al. (2016). They discussed that the model with a linear predator harvesting rate has either a stable steady-state or a stable limit cycle compared with more dynamics for a constant harvesting rate on the predator. The new predator-prey model with non-smooth switched harvest on predator depending on the density of the predator.

Huang et al. (2013) studied the effect of constant-yield predator harvesting on the dynamics of a Leslie-Gower type model and showed that the model has Bogdanov-Takens singularity of codimension-three or a weak focus of multiplicity two for some parameter values. They have shown that as the parameters changed, the model exhibits saddle-node bifurcation, repelling and attracting Bogdanov-Takens bifurcations, supercritical and subcritical Hopf bifurcation, and degenerate Hopf bifurcations. Then, Gong and Huang (2014) proved the Bogdanov-Takens bifurcation for the model and when the different parameter values varied the model had a limit cycle or a homoclinic loop. Then, Song et al. (2018) studied the modified predator-prey model with Michaelis-Menten type predator harvesting and diffusion term. They mentioned that it can induce Turing instability spatially in homogenous periodic solutions. The natural growth rate of the prey can also affect the stability of the positive steady-state and induce Hopf bifurcation.

2.3 Leslie-Gower Predator-Prey Model with Predator Harvesting Strategies

An abundance of research can be found on prey harvesting techniques because it has rich dynamics. The predator harvesting study is also important to see their impacts on species interaction. Three types of predator harvesting strategies are considered in this section, namely, linear, constant-yield, and nonlinear Michaelis-Menten strategies. The Leslie-Gower predator-prey model depicts the convergence of asymptotic solutions to a stable steady state. The steady-state depends on the intrinsic factors which govern the system dynamics. It marks a significant improvement over the Lotka-Volterra model which is limited in its explanatory capability.

Jianfeng and Zhao (2017) studied the predator-prey model with constant-yield prey harvesting and make a comparison with predator harvesting. They mentioned that Bogdanov-Takens bifurcation occurred only in the system with predator harvesting. Huang et al. (2016) studied the dynamical behaviour of the predator-prey model with constant-yield predator harvesting in which they discovered that the initial densities of both species need careful management in the renewable resource contexts. The critical harvesting value affected the predator species for all admissible initial densities of both species when the harvest rate is greater than the critical value, which leads to extinction. Their analytical study showed that when the constant-yield harvesting rate, h varies, the model has complex dynamics such as saddle-node bifurcation, repelling and attracting Bogdanov-Takens bifurcations, supercritical and subcritical Hopf bifurcation, and degenerate Hopf Bifurcations. Later, Huang et al. (2016) produced analytical proof that the model with constant-yield predator harvesting has a Bogdanov-Taken singularity (cusp) of codimension-three or a weak focus of multiplicity two for some parameter values as well as the existence of a stable homoclinic loop and unstable limit cycle, two limit cycles and semi-stable limit cycle. Su (2020) investigates Huang et al. (2013) and shows the existence of two limit cycles from the degenerate Hopf bifurcation.

Another harvesting strategy is nonlinear or Michaelis-Menten strategy. Singh et al. (2016) studied the dynamical analysis for nonlinear Michaelis-Menten predator harvesting of Leslie-Gower model and showed the existence of bistability for some parametric conditions by different kinds of bifurcations such as Bogdanov-Takens bifurcation and homoclinic bifurcation. Zhu and Kong (2017) found very rich bifurcations dynamics of the Leslie-Gower predator-prey model with Michaelis-Menten predator harvesting and proved up to five equilibria and their dynamics such as topological saddles, nodes, foci, centres, saddle-nodes, cusps of codimension-two or three. They also proved the transcritical bifurcation, pitchfork bifurcation, Bogdanov-Takens bifurcation and homoclinic bifurcation. Then, Hu and Cao (2017) proved that Leslie-Gower model with nonlinear predator harvesting has a more realistic and reasonable model than the constant-yield harvesting and constant-effort harvesting from biological and economic points of view since it can remove some limitations which arise from the catch-per-unit-effort hypothesis by varying the parameter values. The model is written as (Hu and Cao (2017))

$$\frac{dx}{dt} = r_1 x\left(1-\frac{x}{K}\right) - axy,$$

$$\frac{dy}{dt} = r_2 x\left(1-\frac{y}{bx}\right) - \frac{qEy}{CE+ly}, \tag{2.12}$$

where term $\frac{qEy}{CE+ly}$ is the Michaelis-Menten type harvesting and E, q, C and l are positive parameters.

In-depth theoretical studies were carried out by Huang et al. (2013 and 2016) and Su (2020) in proving the existence of saddle-node bifurcation, Hopf bifurcation, and Bogdanov-Takens bifurcation for constant-yield predator harvesting strategy. In addition, the occurrence of limit cycles, degenerate Hopf bifurcations, and homoclinic bifurcation are also discussed. Similarly, Singh et al. (2016), Hu and Cao (2017), and Zhu and Kong (2017) studied the Leslie-Gower predator-prey model with the nonlinear Michaelis-Menten harvesting strategy and proved a richer dynamic compared to constant-yield predator harvesting due to the existence of non-extinct prey population at steady-state (1, 0). The occurrence of steady-states, transcritical bifurcation, homoclinic bifurcation, and bistability shown in the nonlinear model have developed more ideas to discover the dynamical studies.

Inspired by the work of Huang et al. (2013) and Hu and Cao (2017), this study will focus on predator harvesting for the Leslie-Gower predator-prey model with constant-yield harvesting and nonlinear harvesting. The linear harvesting model may not get much interest in the predator-prey model study. However, to see from the point of view of harvesting strategies, we will include linear harvesting as part of the harvesting strategies in the models. Therefore, in the numerical bifurcation analysis study, we will discuss the number of steady states, local asymptotic stability, and type of bifurcations for the models mentioned. The phase portrait, codimension-one, and codimension-two bifurcation diagrams will be illustrated graphically and verified according to the theoretical analysis done from previous studies. Then, different bifurcation types that occurred for different harvesting strategies will be analysed together with the effects of management renewable resources application.

CHAPTER 3

RESEARCH METHODOLOGY

3.1 Introduction

In this chapter, we will discuss the methodology for this study. The model adopted in this study is the Leslie-Gower predator-prey model with three different types of predator harvesting strategies, namely, linear, constant-yield and nonlinear predator harvesting models. To study the dynamics of the Leslie-Gower predator-prey model, we need basic knowledge of the qualitative and bifurcation theory of the model. The behaviour of a nonlinear system can be characterised by standard steady states, stability, and bifurcation analysis (Strogatz, 1994).

This study begins with determining the steady states to describe the behaviour of the predator and prey populations. It also can be found in graphical illustrations called nullclines in the phase plane. The stability analysis and bifurcation analysis will be carried out to determine the dynamic behaviour of the system. The sign of the eigenvalues is important to analyse the stability of the steady states which descend from the Jacobian matrix. The theoretical and numerical analyses of the saddle-node, transcritical, Hopf, degenerate Hopf, Bogdanov-Takens, and homoclinic bifurcations were further discussed in this study. Finally, the numerical bifurcation analysis is supported by the phase plane, codimension-one, and codimension-two bifurcation diagrams using XPPAUT and MATLAB software.

3.2 Steady States and Nullclines

Consider the system of the differential equation,

$$\frac{dx}{dt} = f(x, y),$$

$$\frac{dy}{dt} = g(x, y). \tag{3.1}$$

In ordinary differential equations (ODEs), the steady state is defined as a point that does not change when the functions are continuously differentiable. The steady states can be found by a point of intersection of *x*-nullcline and *y*-nullcline curves in the phase plane where the director field defined by the differential equation points in a particular direction. The *x*-nullcline is the set of points (*x*, *y*) such that $f(x, y) = 0$ and the vector are either straight up or straight down. The *y*-nullcline is the set of points $(x, y) = 0$ where $g(x, y) = 0$ and the vectors are either to the left or to the right. The directions only can be changed at a steady state.

To find the steady-states, we solve the simultaneous equations (by setting $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$ in (3.1)),

$$f(x, y) = 0,$$

$$g(x, y) = 0. \tag{3.2}$$

The steady states are solutions to system (3.1) that do not change over time and we denote them as (x^*, y^*).

3.3 Stability

In a dynamical system, stability is important to predict how a dynamical system evolves overtime. If the model is stable, then a small variation to the parameter values will not change the system qualitatively. However, if the model is not stable, it may be susceptible to the changes in the parameter values. A steady state can be an attractor or repeller. An attractor means the variable is displaced and moves back to the steady state and is asymptotically stable, while a repeller is a variable that is moved away from steady states and is unstable. The trajectories cannot cross the steady states unless in a periodic solution.

3.3.1 Stability Analysis

To determine the stability of system (3.1), we expand system (3.1) using Taylor expansion about (x^*, y^*). We linearize the system near the steady-state (x^*, y^*) to gives

$$\begin{aligned} \frac{d\hat{x}}{dt} &= \frac{\partial f}{\partial x}(x^*, y^*)\hat{x} + \frac{\partial f}{\partial y}(x^*, y^*)\hat{y}, \\ \frac{d\hat{y}}{dt} &= \frac{\partial g}{\partial x}(x^*, y^*)\hat{x} + \frac{\partial g}{\partial y}(x^*, y^*)\hat{y}, \end{aligned} \tag{3.3}$$

where $\hat{x} = (x - x^*)$ and $\hat{y} = (y - y^*)$ are local variables. Equation (3.3) can be written as

$$\begin{pmatrix} \frac{d\hat{x}}{dt} \\ \frac{d\hat{y}}{dt} \end{pmatrix} = J(x^*, y^*)\begin{pmatrix} \hat{x} \\ \hat{y} \end{pmatrix} \tag{3.4}$$

where

$$J(x^*, y^*)\begin{pmatrix} \hat{x} \\ \hat{y} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{pmatrix}, \tag{3.5}$$

is the Jacobian matrix of the system evaluated at the steady state. Let

$$a_{11} = \frac{\partial f}{\partial x}(x^*, y^*),\ a_{12} = \frac{\partial f}{\partial y}(x^*, y^*),\ a_{21} = \frac{\partial g}{\partial x}(x^*, y^*),\ \text{and}\ a_{22} = \frac{\partial g}{\partial y}(x^*, y^*).$$

Then, the determinant of *J* can be denoted as

$$\text{Det}\ J = a_{11}a_{22} - a_{12}a_{21}, \tag{3.6}$$

and the trace of *J* is

$$\text{Tr}\, J = a_{11} + a_{22}. \tag{3.7}$$

Thus, the eigenvalues of *J* are given by

$$\lambda_{1,2} = \frac{\text{Tr}J \pm \sqrt{(\text{Tr}J)^2 - 4(\text{Det}\ J)}}{2}. \tag{3.8}$$

According to Strogatz (1994), the eigenvalues can provide explanations about the types and stability of a steady state. From (3.8), there are two possibilities; either both eigenvalues are real or they form a complex conjugate pair such that $\lambda_{1,2} = a \pm bi$. If the eigenvalues are real ($b = 0$), then

a) in the case $\lambda_1 < 0$and $\lambda_2 < 0$, the steady-state is a stable node (see Figure 3.1(a)),

b) in the case $\lambda_1 > 0$ and $\lambda_2 > 0$, the steady-state is an unstable node (see Figure 3.1(b)),

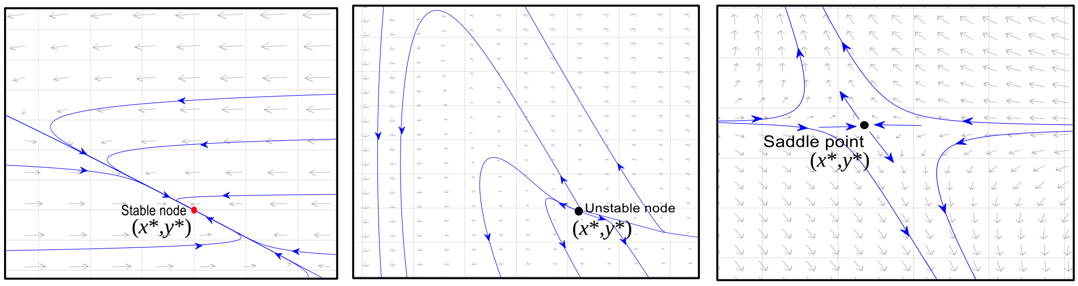
c) in the case $\lambda_1 > 0$ and $\lambda_2 < 0$ or $\lambda_1 < 0$ and $\lambda_2 > 0$, the steady-state is a saddle point (see Figure 3.1(c)).

However, if the eigenvalues are complex ($b \neq 0$), then

a) in the case $a < 0$, the steady-state is a stable spiral (see Figure 3.2(a)),

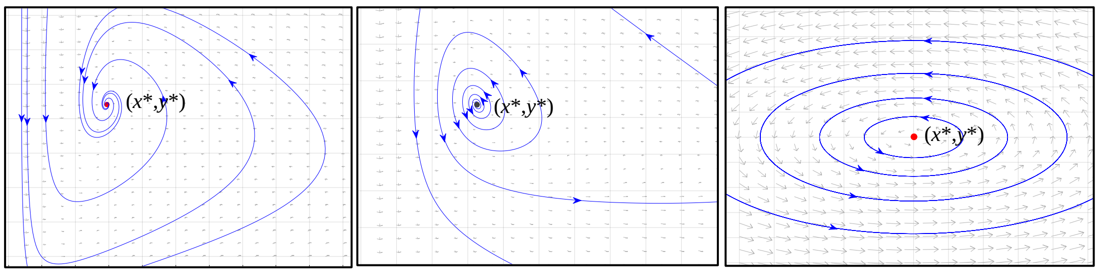
b) in the case $a > 0$, the steady-state is an unstable spiral (see Figure 3.2(b)),

c) in the case $a = 0$, the steady-state is a neutral centre (see Figure 3.2(c)).



(a): Stable node (b): Unstable node (c): Saddle Point

Figure 3.1: Phase portraits for real or distinct eigenvalues with the red dot denotes a stable steady state and the black dot denotes unstable steady states.



(a): Stable Spiral (b): Unstable Spiral (c): Neutral centre

Figure 3.2: Phase portraits for complex eigenvalues with the red dot denotes a stable steady state and the black dot denotes unstable steady states.

3.3.2 Lyapunov Method of Stability

In addition, the stability of the nonhyperbolic steady states can be determined by the Lyapunov number, σ for the steady-state at the origin. From Perko (1996), let

$$\frac{dx}{dt} = ax - by + p(x, y),$$

$$\frac{dy}{dt} = bx + ay + q(x, y)$$

with $b \neq 0$ where the power series expansions of p and q begin with second or higher-degree terms. Then, the Lyapunov number for the focus at the origin is