DYNAMICAL BEHAVIOUR OF PREY-PREDATOR SYSTEMS: EXPLORING HERD MECHANISMS, PREY REFUGES, AND THE DISPERSAL PROCESS

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by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

LIST OF SYMBOLS

a	Handling time of the predator
b	Attack rate of the predator
c	Each individual prey converts into the newborn of predators
d	Death rate of the predator
m	Refuge of the prey
r	Growth rate of prey
k	Carrying capacity of the prey
D_x	Dispersal strength of the prey
D_y	Dispersal strength of the predator
$E(x, y)$	Equilibrium points or critical points
$J(E)$	The Jacobian at any equilibrium point E
x	Prey population
y	Predator population
t	time
$\frac{dx}{dt}$	The rate of change of prey population with respect to time
$\frac{dy}{dt}$	The rate of change of predator population with respect to time
λ	Eigenvalues
I	Identity matrix
$\Re_2^+$	2-D positive domain

LIST OF APPENDICES

DINAMIK TINGKAH LAKU SISTEM MANGSA-PEMANGSA: MENEROKA MEKANISME KAWANAN, PERLINDUNGAN MANGSA, DAN PROSES PENYEBARAN

ABSTRAK

Interaksi kompleks antara dinamik mangsa dan pemangsa merupakan teras utama dalam bidang ekologi kerana ia mempengaruhi kepelbagaian biologi serta kestabilan ekosistem. Tesis ini meneliti aspek yang masih kurang diterokai dengan mengkaji kesan tiga mekanisme ekologi penting, iaitu mekanisme kawanan, perlindungan mangsa, dan proses penyebaran. Objektif utama kajian ini adalah untuk menganalisis bagaimana sistem mangsa-pemangsa bertindak balas terhadap kehadiran dan ketiadaan faktor-faktor tersebut. Bagi mencapai tujuan ini, empat model persamaan pembezaan biasa (ODE) ekologi sedia ada dianalisis, dengan fokus kepada sistem mangsa–pemangsa yang dicirikan oleh respons fungsian jenis II dan punca kuasa dua. Berdasarkan analisis ini, tiga model ekologi baharu dicadangkan. Model pertama menggabungkan mekanisme kawanan hanya dalam populasi pemangsa, sekali gus mengisi jurang kajian dalam literatur mengenai tingkah laku berkumpulan pemangsa. Model kedua menambah kesan perlindungan mangsa untuk menilai pengaruh gabungannya bersama kawanan pemangsa. Model ketiga pula melanjutkan sistem mangsa–pemangsa dengan mekanisme kawanan pemangsa ke dalam sistem persamaan pembezaan separa (PDE), membolehkan kajian aspek ruang dan proses penyebaran dalam sistem ekologi ini dijalankan. Melalui kaedah teori dan analisis, titik keseimbangan telah ditentukan, analisis kestabilan dilakukan, dan kewujudan titik bifurkasi setempat dibuktikan. Simulasi berangka mengesahkan dapatan teori dengan menunjukkan kemunculan pelbagai bifurkasi termasuk transkritikal, Hopf subkritikal,

Hopf superkritikal, dan homoklinik, masing-masing menandakan ambang kritikal perubahan dinamik populasi. Sumbangan utama tesis ini adalah dalam membuktikan bahawa mekanisme kawanan mampu meningkatkan kewujudan bersama dan mengurangkan risiko kepupusan; bahawa kesan gabungan perlindungan mangsa dan kawanan pemangsa berupaya mengurangkan tekanan pemangsaan serta menyokong kepelbagaian biologi jangka panjang; dan bahawa penyebaran ruang dalam kerangka PDE memainkan peranan penting dalam mencegah kepupusan setempat, menggalakkan penjajahan, meningkatkan kewujudan bersama, serta memperkukuh kestabilan sistem ekologi. Secara keseluruhannya, tesis ini memperluas pemahaman teori mengenai sistem mangsa-pemangsa dengan mengintegrasikan mekanisme kawanan pemangsa, perlindungan mangsa, dan penyebaran ruang dalam satu kerangka pemodelan yang menyeluruh. Dapatan ini memberikan pandangan ekologi baharu dengan implikasi langsung terhadap pemuliharaan biodiversiti, pengurusan populasi mangsa–pemangsa, serta perancangan strategi bagi mengekalkan keseimbangan ekologi.

DYNAMICAL BEHAVIOUR OF PREY-PREDATOR SYSTEMS: EXPLORING HERD MECHANISMS, PREY REFUGES, AND THE DISPERSAL PROCESS

ABSTRACT

The complex interactions between prey and predator dynamics are a central concern in ecology, influencing both biodiversity and ecosystem stability. This thesis addresses relatively underexplored aspects of these interactions by investigating the effects of three crucial ecological mechanisms: herd mechanism, prey refuges, and dispersal processes. The primary objective is to analyse how prey-predator systems respond to the presence and absence of these factors. To achieve this, an analysis of four existing ecological ordinary differential equation (ODE) models is conducted, focusing on prey-predator systems characterised by type II and square-root functional responses. Based on these analyses, three new ecological models are proposed. The first model uniquely incorporates herd behaviour exclusively in predator populations, directly addressing the literature gap on predator herding. The second model extends this by incorporating prey refuge effects to explore their joint influence with predator herding. The third model further extends the prey-predator model with predator herd behaviours into a partial differential equation (PDE) system, enabling the examination of spatial and dispersal process in this ecological system. Through theoretical and analytical methods, equilibrium points are calculated, stability analyses are performed, and the existence of local bifurcation points is demonstrated. Numerical simulations validate the theoretical findings, revealing the emergence of various bifurcations, including transcritical, subcritical Hopf, supercritical Hopf and homoclinic, each marking critical thresholds where shifts in population dynamics occur. The novelty of

this thesis lies in demonstrating that species herding can enhance species coexistence and reduce extinction risk; that the combined effects of prey refuge and predator herding can mitigate predation pressure and foster long-term biodiversity; and that spatial dispersal within the PDE framework plays a pivotal role in preventing local extinctions, promoting colonisation, enhancing coexistence outcomes and stability of ecological system. In conclusion, this thesis advances the theoretical understanding of prey-predator systems by integrating predator herd behaviour, prey refuge, and spatial dispersal within a unified modelling framework. These findings offer new ecological insights with direct implications for biodiversity conservation, management of prey-predator populations, and the design of strategies to sustain ecological balance.

CHAPTER 1

INTRODUCTION

1.1 Preliminary

This thesis begins by outlining key ecological mechanisms that govern prey-predator interactions and influence population stability. These mechanisms shape survival strategies, spatial distribution, and the long-term balance between species. The discussion establishes the ecological context, identifies existing knowledge gaps, and presents the research questions, objectives, scope, and significance. It also situates the work within the broader field of mathematical ecology, providing the conceptual foundation for the modelling approaches developed in this study.

1.2 General Background

The dynamics of prey-predator interactions have long attracted the attention of ecologists, biologists, and scholars across multiple disciplines (Jolles et al., 2022; Premate et al., 2021; Djilali & Ghanbari, 2021; Mohd & Noorani, 2021; Arancibia-Ibarra et al., 2019; Braza, 2012). Exploring these dynamics extends well beyond academic interest, serving as an essential approach to understanding the complexity of ecosystem functioning (Pike et al., 2023). Thus, this thesis aims to examine key aspects of prey-predator relationships, with particular focus on herd behaviour, the role of refuge, and the dispersal process.

1.2.1 Prey-predator interactions

Interactions between prey and predator involve the mutual influence of two or more organisms, with consequences for their respective populations and the ecosystems they inhabit (Saha et al., 2025b; R. Wang et al., 2025; Lennox et al., 2025; Verma et al., 2023; Stanicka et al., 2023). In such ecosystems, one organism assumes the role of predator, actively seeking to capture and consume another organism, the prey. For example, in the African savannah, the dynamics between lions (predators) and zebras (prey) demonstrate how predation can significantly affect population sizes and behaviours, leading to adaptations over generations (Singh, 2021; Deng et al., 2019) These interactions evolve over time, shaping the coexistence and evolutionary trajectories of species (Diz-Pita & Otero-Espinar, 2021). Within the field of population dynamics, research has consistently shown that prey-predator relationships have a substantial impact on species demographics (Naik et al., 2023; Paul et al., 2021; Ahn & Yoon, 2021; Saha & Samanta, 2021b).

From an ecological perspective, these interactions function as a regulatory mechanism for governing population dynamics. The existence or absence of predators exerts a direct influence on the population sizes of prey species, subsequently impacting the ecological dynamics at a broader scale (Bassing et al., 2025; Tye et al., 2024; Samuel et al., 2023). In circumstances where predators are limited or non-existent, there tends to be a notable increase in prey populations, leading to overgrazing and disruptions in the natural ecological cycles (Beschta & Ripple, 2016). Conversely, if the prey population experiences a decline or disappears, predators encounter a scarcity of food resources, resulting in a reduction in their own population size and jeopardizing their long-term survival (Datta et al., 2025; Tiwari & Rani, 2025; Parsons et al., 2022). These interactions highlight the delicate balance that is dependent on the presence and vitality of both prey and predator populations.

1.2.2 Herd behaviours

Herd behaviour refers to the coordinated and collective actions of individuals within a species in response to external stimuli. It constitutes a fundamental aspect of animal survival, shaping prey-predator interactions in diverse ecosystems (Perez et al., 2020; Sk & Alam, 2017; Maiti et al., 2016; Bera et al., 2015). Central to this phenomenon is the principle of "safety in numbers," which vividly manifests in the natural world. Species such as wildebeests roaming the African savannah or schools of fish in marine environments often aggregate into herds or shoals as a defensive strategy (Falgueras-Cano et al., 2022; Kotrschal et al., 2020; Moreno García et al., 2020). By forming large, coordinated groups, individuals reduce the likelihood of being singled out, making it considerably more difficult for predators to isolate and capture a target (Kasumyan & Pavlov, 2023; Chakraborty, 2023; Hamilton, 1971).

The basis of herd behaviour in prey populations lies in innate survival instincts. Prey species typically maintain heightened vigilance and react swiftly to perceived threats (Slovikosky & Montgomery, 2024; Crane et al., 2024; Suraci et al., 2022; Burton et al., 2022). Synchronisation within herds is facilitated through auditory and visual signals, which enable rapid coordination (Olczak et al., 2023; Lamontagne & Gaunet, 2023; Hoehl et al., 2021). When a potential threat is detected by one individual, it can trigger a cascading chain reaction, producing a collective and immediate response from the entire group (Shi et al., 2025; Blank, 2025). Such cohesion enhances survival prospects by reducing predator success rates.

It is important to note, however, that herd behaviour is not confined to prey alone. Predators also adopt cooperative strategies that mirror herd-like behaviour during hunting (Thirthar et al., 2024; Hansen et al., 2023; Shimelmitz et al., 2023; Torres Ortiz et al., 2021; MacNulty et al., 2014). For example, wolf packs coordinate their efforts to bring down prey that would be unmanageable for a solitary hunter (Beschta & Ripple, 2016). In these cases, predators display their own form of herd behaviour, relying on collaboration to improve hunting success (Bhargava & Dubey, 2023; Shimelmitz et al., 2023; Cram et al., 2022). The interaction of these strategies, such as defensive herding in prey and cooperative hunting in predators, plays a critical role in maintaining ecological balance and sustaining ecosystem stability.

1.2.3 Prey refuge

Within the context of prey-predator interactions, the concept of prey refuge refers to the strategies adopted by prey species, through both spatial positioning and behavioural adjustments, to secure protection against potential predators (Jana et al., 2016; Ma et al., 2009; Kar, 2005, 2006; González-Olivares & Ramos-Jiliberto, 2003). This notion is fundamental to species survival dynamics, as it enables prey to successfully avoid predation and sustain their existence over time (Alsulami et al., 2025; Cherif et al., 2024; Boon et al., 2023; Arevalo et al., 2023; Lima & Dill, 1990). Refuge can be expressed in multiple forms, including the use of physical shelters such as burrows, thick vegetation, or other protective habitats that limit predator accessibility (Ahmad & Bhat, 2025; Cowan et al., 2021). It may also involve behavioural responses, for example, remaining motionless or using camouflage to escape detection by predators (Tan et al., 2024; Barman, 2022). In aquatic ecosystems, small fish and invertebrates often conceal themselves beneath leaves, while certain bird species construct nests in dense undergrowth to safeguard their offspring from predators (Searcy et al., 2023; Staeck, 2022). By employing such strategies, prey species enhance their prospects for long-term survival, allowing them to flourish and reproduce despite ongoing predation threats (Lennox et al., 2025; Manaf & Mohd, 2023).

The ecological importance of prey refuge lies in its essential role as a survival mechanism that reduces predation risk (Lennox et al., 2025; Manaf & Mohd, 2023; Boon et al., 2023; Sabal et al., 2021). This function not only supports the persistence and growth of prey populations but also has broader implications for biodiversity, ecological balance, and ecosystem health. Moreover, refuges influence the dynamics of prey-predator systems by shaping behavioural patterns and spatial distributions within both populations (Ning et al., 2025; Takyi et al., 2023). Their presence alters predator hunting strategies, reduces predator efficiency, and at the same time maintains prey stability, thereby preserving the intricate balance of prey-predator interactions.

1.2.4 Dispersal

Within ecological dynamics, dispersal refers to the process by which species relocate from their native habitats in search of more favourable environments or geographic regions (Morton et al., 2018; Doebeli, 1995; Hastings, 1983). This process is pivotal for understanding species distribution, population abundance, and genetic diversity within ecosystems (Peniston et al., 2024; De Kort et al., 2021; Choo et al., 2021; Schlägel et al., 2020; Lawrence & Fraser, 2020). Importantly, dispersal operates across multiple spatial and temporal scales, generating distinct consequences for both prey and predator populations (Chakraborty, 2021; Morton et al., 2018). These consequences often differ markedly between prey and predator species (Peniston et al., 2024; Schlägel et al., 2020).

For prey populations, dispersal is typically an adaptive response to changing environmental conditions. When faced with unfavourable circumstances, prey may disperse to avoid predation, to secure essential resources such as food and shelter, or to establish themselves in new habitats (Hermann et al., 2021; Sabal et al., 2021). Such prey dispersal often produces a dilution effect, whereby predators find it more difficult to concentrate on a single prey type, ultimately leading to reduced predation pressure (Webber et al., 2023; Creed et al., 2022; Culshaw-Maurer et al., 2020).

Predator species likewise engage in dispersal, albeit for different reasons. Predators commonly disperse when local prey populations become scarce, seeking out regions with higher prey densities (Twining et al., 2022; Grupstra et al., 2021;

McGregor et al., 2020). This redistribution of predators across landscapes redistributes predation pressure and exerts significant influence on prey population dynamics.

Dispersal patterns can be broadly classified into two forms: symmetric and asymmetric (Dey et al., 2014; Yakubu, 2007; Doebeli, 1995). Symmetric dispersal occurs when individuals from both prey and predator communities move from their current locations (Bani-Yaghoub et al., 2014; Dey et al., 2014; Yakubu, 2007; Doebeli, 1995). For instance, prey may relocate in search of new feeding grounds, while predators disperse in pursuit of richer prey sources. This mutual dispersal contributes to dynamic variations in population distributions and interactions. This reciprocal movement reshapes population distributions and modifies ecological interactions. In contrast, asymmetric dispersal describes unidirectional movement (Meng et al., 2025; Fang et al., 2020; Wu et al., 2020; Arditi et al., 2018). In wildlife systems, prey species frequently exhibit stronger tendencies toward dispersal (Lawton et al., 2024; Ji et al., 2022; Choo et al., 2021; Morton et al., 2018; Goodwin et al., 2005). Typically, prey disperse away from habitats marked by high predation risk or limited resources, altering their spatial configuration and influencing subsequent prey-predator interactions. Predator dispersal, by contrast, is usually motivated by the pursuit of prey rather than avoidance of threats (Ji et al., 2022; Kim & Choi, 2020).

Overall, dispersal plays a central role in structuring the spatial distributions and population dynamics of prey and predator species. For prey, it facilitates escape from predation, opens opportunities to exploit new resources, and enables colonisation of unoccupied habitats. Collectively, these mechanisms enhance survival prospects and enrich the genetic diversity of prey populations.

1.3 Problem statement

The interactions between prey and predators are essential for sustaining community dynamics within ecological systems (Rind & Bels, 2024; Yasin et al., 2023; Pokhrel & Lamsal, 2020; Savoca et al., 2020). These interactions are strongly influenced by various ecological mechanisms, including herding strategies, prey refuges, and dispersal behaviour (Mohd & Noorani, 2021; Das, A., & Samanta, 2020; Luo et al., 2020; Bera et al., 2015; Braza, 2012). While these mechanisms have been studied individually, a comprehensive understanding of how they jointly shape prey-predator dynamics remains incomplete.

Herding strategies play a vital role in shaping prey-predator interactions (Souna et al., 2020). The ecological consequences of prey herd behaviour are relatively well established (Acotto & Venturino, 2024; Berardo et al., 2021; Bera et al., 2015, 2016a; Schwarzl et al., 2016; Matia & Alam, 2013), but the mechanisms and implications of predator herd behaviour remain underexplored. In particular, little is known about how predator herding interacts with ecological parameters such as conversion rates, attack rates, and stability thresholds.

Similarly, prey refuges, which allow species to avoid predation through spatial hiding or reduced accessibility, have been widely examined (Mahapatra et al., 2021; Jana et al., 2016; Guin et al., 2015; Sarwardi et al., 2012; Ma et al., 2009; Kar, 2005; González-Olivares & Ramos-Jiliberto, 2003). However, limited attention has been given to the combined influence of prey refuge and prey herd behaviour under predator pressure (Tripathi et al., 2024; Manaf & Mohd, 2022). Moreover, the interplay between predator herding and prey refuge has rarely been studied, especially in terms of their joint effects on bifurcation structures, coexistence conditions, and transient oscillations.

Dispersal processes further complicate prey-predator dynamics by shaping spatial and temporal outcomes (Manaf & Mohd, 2023; Cheng & Zou, 2021; Mohd & Noorani, 2021; Kang et al., 2017). Despite substantial progress, the combined influence of predator herd behaviour and spatial dispersal, particularly within partial differential equation (PDE) frameworks, remains largely unexamined. This gap limits the ability to explain ecological patterns such as spatial clustering, range shifts, localised extinction, and their implications for long-term stability and coexistence.

To address these gaps, this thesis formulates, analyses, and compares a series of mathematical models, encompassing both ODE and PDE frameworks, to examine the roles of predator herd behaviour, prey refuges, and spatial dispersal. The analysis begins with comparative evaluations of existing models and progresses toward extended and integrated frameworks. The central aim is to determine the conditions under which stability in prey-predator systems is maintained or destabilised, while also identifying the bifurcation behaviours that emerge under different ecological scenarios.

1.4 Research Questions

Several research questions have been formulated to gain a more comprehensive understanding of the dynamics between prey and predator species as follows:

1. How does the incorporation of predator herd mechanisms, as an extension of classical prey-predator models limited to prey herding, alter the system's stability and generate distinct bifurcation phenomena under variations in conversion rates, attack rates and other ecological parameters?

2. In what ways do the combined effects of prey refuge and predator herding influence the dynamical behaviours of prey-predator systems, and do these mechanisms act in a reinforcing or counteractive manner compared to models with isolated mechanisms?

3. How does extending the prey-predator framework into a reaction-diffusion setting with predator herd behaviour and local dispersal elucidate the role of symmetric versus asymmetric dispersal in shaping coexistence mechanisms and system stability?

These research questions serve as the fundamental framework for exploring the complex dynamics of prey-predator interactions. In the subsequent section, the research objectives are clearly defined to guide the inquiry into these complex issues.

1.5 Objectives

This thesis aims to demonstrate the essential role of mathematical models in describing and understanding the dynamic behaviour of species under various ecological factors. The main objectives are:

1. To formulate a new prey-predator model incorporating predator herding, extending classical prey-herding systems and analysing its bifurcational dynamics under key ecological parameters. (Chapters 4 - 5)

2. To synthesise and compare extended prey-predator models incorporating prey refuge and predator herding, evaluating their joint effects on stability, coexistence and bifurcation structures. (Chapters 6 - 7)

3. To extend the prey-predator framework with predator herding into a reaction-diffusion model, investigating how symmetric and asymmetric dispersal patterns shape coexistence and stability of ecological system. (Chapter 8)

1.6 Scope of the study

This thesis investigates the dynamics of ecological systems using ODEs, with particular emphasis on extensions of the classical Lotka-Volterra framework incorporating Type II and square-root functional responses. These two forms were chosen because they are widely recognised in ecological modelling for realistically representing prey-predator interactions, particularly predator saturation effects and handling time. In this thesis, the square-root functional response is specifically applied in models with herd behaviour, as it reflects the reduced predation rate when prey or predators move in coordinated groups, which is one of the key ecological mechanisms examined in this thesis.

The scope of this thesis centres on three fundamental ecological mechanisms that significantly influence prey-predator systems: herd behaviour, prey refuge strategies, and species dispersal. These mechanisms are explored systematically through both comparative analysis of existing models and the formulation of extended models. Initially, the thesis conducts a comparative analysis of ODE models to assess the influence of prey herd behaviour and varying conversion rates in the presence and absence of predator herd behaviour. This is followed by the development and analysis of extended ODE models that incorporate predator herd mechanisms, prey refuge effects, and their combined impact on the system's bifurcation structure, equilibrium points, and qualitative behaviour.

To account for spatial movement and the resulting ecological heterogeneity, the thesis extends the ODE framework to a PDE model. This extension enables the investigation of how different dispersal patterns, such as prey-driven or predator-driven movement, influence the emergence of spatiotemporal dynamics, including oscillatory structures, spatial patterning, and long-term system stability.

The analysis relies heavily on numerical simulations supported by specialised software tools. XPPAUT and AUTO are employed to detect bifurcation points, perform numerical continuation, and construct bifurcation diagrams. These tools are widely employed in dynamical systems research due to their reliability and user-friendly interfaces. For symbolic computations and local stability analysis, Maple is used to evaluate steady-state stability and calculate eigenvalue spectra. MATLAB is utilised to visualise model behaviour through phase portraits, time series graphs for the ODE systems, and surface plots for the PDE models, allowing the spatial evolution of species densities to be tracked over time.

All parameter values used in simulations are drawn from ecologically validated studies, particularly the work by (Chen & Wang, 2018), ensuring that the models remain relevant to real-world prey-predator interactions and grounded in biological realism. Through this integrated approach, the study offers a comprehensive framework for understanding how local and spatial ecological mechanisms shape the stability, coexistence, and long-term dynamics of interacting species.

1.7 Significance of research

This study is significant as it applies mathematical modelling frameworks to advance the understanding of complex ecosystem dynamics, particularly in the context of prey-predator interactions. By systematically incorporating ecological mechanisms such as herd behaviour, prey refuge strategies, and species dispersal into ordinary and partial differential equation models, the research enhances current theoretical insights and provides a more holistic perspective on species coexistence and stability.

The findings contribute meaningfully to ecological theory by revealing how these mechanisms influence equilibrium states, bifurcation structures, and spatiotemporal patterns. Such knowledge can inform decision-making processes in biodiversity conservation and ecosystem regulation. In particular, the insights gained from this study may guide policymakers, ecologists, and conservation practitioners in designing more effective strategies for managing species interactions and mitigating ecological instability under changing environmental conditions.

Moreover, this research provides an analytical foundation that can be integrated into environmental science education, supporting curriculum development in mathematical ecology. By offering a structured and quantitative approach to studying ecological interactions, the study also serves as a valuable reference for future research in nonlinear modelling and theoretical ecology. Ultimately, the outcomes of this thesis may contribute to the development of ecologically sound policies and modelling tools that promote species persistence and long-term ecosystem sustainability.

1.8 Outline of the thesis

This thesis is organised into nine chapters. **Chapter 1** introduces the study by providing a general overview of prey-predator interactions and the ecological mechanisms of interest: herd behaviour, prey refuge, and dispersal processes. It also presents the problem statement, research questions, objectives, scope, and significance of the study.

Chapter 2 reviews the relevant literature, focusing on prey-predator systems and functional responses, particularly Type II and square-root forms. It also examines key ecological factors such as herd behaviour, prey refuge mechanisms, and dispersal processes that form the basis of this research.

Chapter 3 outlines the mathematical theories and analytical methods employed, with emphasis on stability and bifurcation analysis. The discussion covers local and global stability concepts, the Routh-Hurwitz criterion, and the Bendixson-Dulac theorem, along with key bifurcation types such as transcritical and Hopf bifurcations relevant to the models analysed.

Chapter 4 provides a comparative analysis of ODE models incorporating prey herd behaviour under two distinct scenarios: the absence and presence of predator herd behaviour. The analysis examines how variations in conversion rate affect equilibrium states, oscillatory patterns, and bifurcation structures using one- and two-parameter bifurcation analyses. The ecological implications of prey and predator herd behaviour are explored through dynamical comparisons across scenarios.

Chapter 5 introduces an ODE model that explicitly incorporates predator herd behaviour. The model is examined for equilibrium points, local and global stability, and bifurcation patterns. The effects of varying conversion rate and other ecological factors on system dynamics are assessed using one- and two-parameter bifurcation analyses, supported by numerical simulations to illustrate population trends, persistence, and the ecological role of predator herding.

Chapter 6 offers an analysis and comparison of ODE models that include prey refuge mechanisms, both with and without prey herd behaviour. The study investigates how prey refuge rate and predator handling time affect coexistence and oscillatory dynamics using one- and two-parameter bifurcation analyses. The joint influence of refuge and prey herding is evaluated in terms of qualitative dynamics and stability outcomes.

Chapter 7 develops an ODE model that integrates prey refuge and predator herd behaviour. Stability and bifurcation analyses are conducted to assess how these combined mechanisms influence system dynamics. Numerical simulations investigate the ecological consequences of integrating both mechanisms, while comparative analyses evaluate the differences between models containing one or both mechanisms.

Chapter 8 extends the predator-herd ODE framework into a PDE model incorporating species dispersal through spatial diffusion terms. The study examines how symmetrical and asymmetrical dispersal patterns affect spatiotemporal dynamics, stability, and species persistence. Numerical simulations and pattern analyses highlight spatial heterogeneity and long-term ecological outcomes.

Chapter 9 concludes the thesis by summarising the key findings and their contributions to ecological modelling. Broader implications for ecosystem management and conservation strategies are discussed, along with potential directions for future research, particularly in applying these modelling approaches to real-world ecological systems.

1.9 Summary

The discussion has introduced herd behaviour, prey refuge, and dispersal as central ecological mechanisms shaping prey-predator dynamics. By influencing survival strategies and regulating population stability, these mechanisms provide the conceptual foundation for the modelling approaches employed in this thesis. Building on this foundation, the next chapter reviews established mathematical models and synthesises earlier research on these mechanisms, tracing current knowledge, highlighting methodological developments, and identifying unresolved questions that set the direction for the present study.

CHAPTER 2

LITERATURE REVIEW

2.1 Preliminary

This chapter reviews the historical development of prey-predator models and functional responses, with particular emphasis on the integration of ecological factors such as herd behaviour, refuge mechanisms, and dispersal processes. It also identifies gaps in existing research, providing the basis for the development of new models and analytical approaches in the later stages of this thesis.

2.2 Prey-predator model

The development of the prey-predator model marks a significant milestone in both ecology and mathematical biology. Known as the Lotka-Volterra equations, this model provides a framework for analysing the dynamics of populations involved in prey-predator interactions. An exploration of the historical context and key principles that form the basis of these equations is essential.

Population modelling dates to the early 20th century when Lotka (1925) and Volterra (1926) independently introduced mathematical formulations to describe species interactions within ecosystems. Their work emerged during a period of growing interest in understanding the mechanisms driving population dynamics and the desire to represent these complex relationships mathematically. Several biological assumptions are fundamental to modelling a prey-predator system, including the following:

1. In the absence of predators, the prey population exhibits Malthusian growth, characterized by its growth equation, $\dfrac{dx}{dt} = rx$ where r is a positive constant.

2. In the absence of prey, the predator population experiences Malthusian decay, governed by the decay equation, $\frac{dy}{dt} = -\gamma y$ where γ is a positive constant.

3. The dynamics of prey and predator populations involve chance encounters, leading to a decrease in the prey population at a rate of $-\beta xy$ where β is a positive constant. Simultaneously, the predator population increases due to these chance interactions at a rate of δxy where δ is a positive constant.

The inclusion of the interaction terms δxy and $-\beta xy$ can be substantiated through the rationale that the occurrence of random encounters between prey and predators is directly related to the product of their respective populations, denoted as xy. Biologists rationalize this proportionality by positing that doubling either the prey or predator population should result in a twofold increase in the frequency of random encounters. Combining the Malthusian growth rates and the rates of chance encounters yields the mathematical framework known as the Volterra prey-predator system:

$$\frac{dx}{dt} = rx - \beta xy,$$
$$\frac{dy}{dt} = \delta xy - \gamma x.$$

The presented form of the differential equations serves to underscore that both x and y adhere to a fundamental scalar first-order differential equation, expressed as $\frac{du}{dt} = ru$, where the temporal rate function r is contingent upon time. When considering initial population sizes in proximity to zero, the behaviour of these two differential equations closely resembles the Malthusian growth model, represented as $\frac{dx}{dt} = rx$, and the Malthusian decay model, expressed as $\frac{dy}{dt} = -\gamma y$. This fundamental growth or decay characteristic enables us to identify either the predator variable y or the prey variable x, regardless of the sequence in which the differential equations are arranged.

To summarise, the Lotka-Volterra equations provide a fundamental framework for understanding the dynamics of prey-predator interactions in ecological systems. Rooted in biological principles, this model reveals the intricate interdependence between predator and prey populations, addressing factors like growth, decline, and random encounters. It stands as a significant contribution to ecology, acting as an essential tool for researchers and ecologists to explore species relationships in natural environments. As knowledge of ecological dynamics evolves, the Lotka-Volterra model continues to play a crucial role in elucidating these complex interactions.

2.3 Functional Responses

Functional response describes how a predator's rate of prey consumption changes with varying prey density. This concept is crucial in developing models that illustrate prey-predator interactions. Functional responses are classified into three main types: type-I, type II and type-III as proposed by Holling in a series of studies (Holling, 1965). Figure 2.1 illustrates these functional responses.

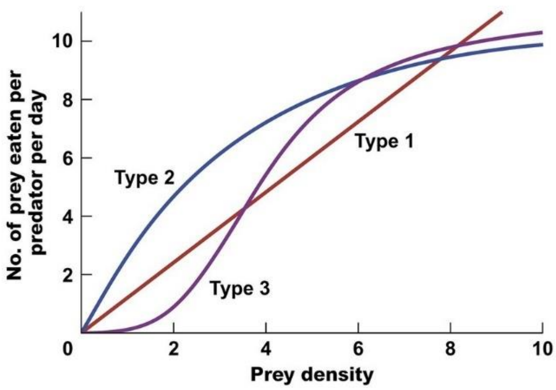

Figure 2.1: Holling types of functional response (Krebs, 2022).

2.3.1 Type I Functional Response

Consider the function $p(x)$ denoting a predator's response concerning a specific prey. This response is characterized as a functional response when the following conditions are satisfied:

i) $p(0)=0$, indicating that all responses originate from the origin.

ii) $p(x)\geq 0$, signifying that all responses are monotonically increasing.

Type I functional response is characterized by a linear relationship between the rate of predation and prey density. This response assumes that the rate at which predators consume prey is directly proportional to prey density, without accounting for a saturation point. The functional response for Type I is given by:

$$p(x)=\beta x\,; \quad \beta>0\,,$$

where $p(x)$ denotes the predation rate, β represents a constant proportion, and x, is the prey density. However, this model neglects the biological reality of predator satiation, as predators cannot consume prey at an indefinitely increasing rate. The lack of a saturation effect leads to unrealistic predictions, especially under high predation pressure, where the model implies unlimited prey consumption. Ali et al. (2016) highlights the limitations of such linear models in accurately capturing the complexities of ecological interactions, particularly in predicting population stability and resilience.

2.3.2 Type II Functional Response

Type II functional response introduces the concept of a saturation effect, where the predation rate increases with prey density but eventually levels off as predators reach their consumption limits. The functional response for Type II is described by the equation:

$$p(x) = \frac{\beta x}{1 + \alpha x}; \quad \beta, \alpha > 0,$$

where β increases with higher prey density, but the rate eventually levels off as the prey density reaches higher levels. The saturation constant, α signifies the point at which the predation rate plateaus. In this model, the rate of predation initially rises with increasing prey density, but eventually, the rate levels off due to handling time limitations, leading to a saturation effect. This response better reflects real-world prey-predator dynamics by accounting for predator satiation, making it essential for modeling ecological systems where predators have consumption limits.

2.3.3 Type III Functional Response

The exploration of alternative functional responses reveals significant differences in ecological predictions and outcomes compared to the Holling Type II response. The Holling Type III functional response introduces a sigmoidal relationship between prey density and predation rates:

$$p(x) = \frac{\beta x^2}{1 + \alpha x^2}; \quad \beta, \alpha > 0.$$

This response signifies that the predation rate experiences a gradual increase at low prey densities, followed by a more rapid escalation, and eventually plateaus as prey density further rises. The term α symbolizes the density-dependent saturation impact on the predation rate, where β acts as the saturation constant determining the magnitude of this quadratic inhibition with the increase in prey density x.

This model suggests that at low prey densities, predation rates increase slowly, allowing prey populations to escape predation pressure. However, as prey availability rises, the rate of predation accelerates, creating a sigmoidal curve. While this response can provide insights into certain ecological scenarios, it may misrepresent dynamics in environments where prey populations are under significant predation pressure. For example, Beroual and Sari (2020) illustrate that the Type III response can lead to an inflection point in predation rates, which may not accurately reflect the behaviour of predators in high-density prey situations. This misrepresentation can skew predictions regarding population interactions and stability, particularly in systems where prey is heavily exploited.

2.3.4 Square Root Functional Response

An alternative functional response that addresses some limitations of the Type II and Type III models is the square root functional response, expressed as:

$$p(x) = \beta\sqrt{x}, \quad \beta, x > 0,$$

where β is a proportionality constant, and $\sqrt{x}$ represents the gradual increase in predation rate relative to prey density. This response is particularly relevant in systems where predator consumption efficiency diminishes as prey density increases. Unlike the aggressive saturation seen in Type II, the square root response reflects a more moderated, nonlinear growth in predation rates, especially in species where herding behaviour or group-defense mechanisms play a significant role. This functional response has been applied to various prey-predator systems (Samanta et al., 2019; Braza, 2012). For instance, Braza (2012) explored its use in nonlinear prey-predator models, demonstrating how this response stabilizes ecological systems by moderating the increase in predation rates as prey density rises. Additionally, Figure 2.2 illustrates the curves of the Holling type II functional response (blue) and the modified type II (square root) functional response (red), as studied by Samanta et al. (2019).

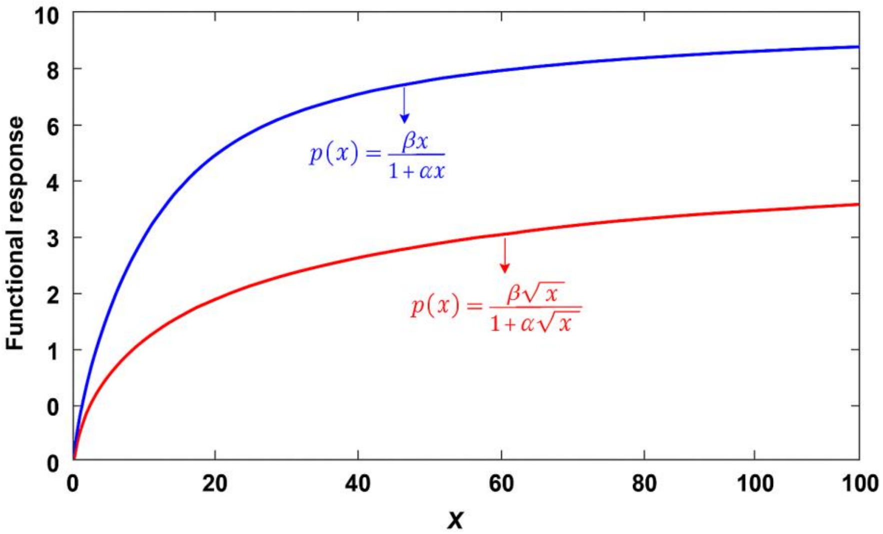

Figure 2.2: Holling type II and modified type II (square root) functional responses.

The square root functional response is particularly relevant in systems where prey exhibit herd behaviour, such as large mammals or schooling fish, which use collective actions to reduce predation risk (Santra, 2021; Kooi & Venturino, 2016). In prey-predator systems, this response captures the diminishing returns in predation efficiency as prey density rises. Specifically, it becomes evident in models where prey populations utilize herd behaviour, reducing individual predation risk through collective defense mechanisms. For instance, Lin et al. (2019) demonstrated that in a homogeneous diffusive prey-predator system, incorporating herd behaviour with a square root functional response generates complex spatiotemporal patterns, underscoring the role of such behavioural adaptations in ecological modelling. Similarly, Kooi and Venturino (2016) explored an ecoepidemic prey-predator model, showing how prey herd behaviour affects population stability and dynamics.

Moreover, the square root functional response enables a more realistic representation of prey-predator interactions by considering the effects of prey aggregation. Santra (2021) showed in discrete models how herd behaviour complicates predator dynamics, as dense prey populations can lower predator efficiency. This idea is reinforced by Xu et al. (2016), who found that predator responses to prey are altered when factoring in defense mechanisms like herding. Such findings indicate that traditional models may underestimate prey-predator system stability when behavioural factors are neglected. Additionally, this response has been shown to stabilize prey-predator interactions by preventing over-predation at high prey densities. For example, Tang et al. (2016) and Song and Tang (2017) analysed a model with herd behaviour and demonstrated that the square root response promotes stable coexistence of predator and prey populations, even under varying environmental conditions. This stability is key to understanding ecological resilience and long-term dynamics.

Motivated by the discussion on various functional responses, this thesis will employ a combination of Type II and the square root functional responses for ecological system modelling. The Type II response is essential for capturing predator satiation, as it reflects how predation rates increase with prey density but eventually plateau due to handling time limitations (Krebs, 2022). This response provides an accurate depiction of prey-predator interactions where predators have a limited capacity to process and consume prey. Complementing this, the square root functional response adds a layer of nuance to the model by accounting for diminishing predation efficiency as prey density increases, which is particularly relevant in ecosystems with herd behaviour or collective defense mechanisms (Peng et al., 2024). By incorporating both functional responses, the model will better capture the complex dynamics of prey-predator systems, allowing for the exploration of both individual predator limits and the complexities introduced by herd behaviours in species. Thus, this dual approach ensures a more realistic and comprehensive understanding of ecological interactions.

2.4 Herd Behaviour

Herd behaviour refers to the coordinated actions of individuals within a species, typically in response to threats such as predation. Prey often rely on group-based strategies to enhance survival, where clustering around leaders creates synchronised movement that reduces individual exposure. This is exemplified by Hamilton's (1971) "selfish herd" hypothesis, in which individuals seek central positions within the group to minimise predation risk (Matia & Alam, 2013).

The ecological implications of herd behaviour have been explored through various mathematical models (Cao, Qian and Bao, Xiongxiong and Yi, 2024; Ahmed & Almatrafi, 2023; Shivam et al., 2022; Laurie et al., 2020; Vijaya Lakshmi, 2020; Samanta et al., 2019; Bera et al., 2016b, 2016a). Strong prey herding can, under certain conditions, drive predator populations to extinction, particularly in systems with aggressive predators (Bera et al., 2016b, 2016a). Similarly, Schwarzl et al. (2016) showed that solitary predators are less successful against tightly grouped prey, confirming that aggregation can substantially reshape prey-predator dynamics.

When herding is restricted to prey alone, its effects are often twofold. On one hand, group defence lowers individual predation risk and creates a refuge-like effect, enhancing prey persistence (López et al., 2023; Samanta et al., 2019; Schwarzl et al., 2016). On the other, over-concentration can intensify competition for resources, increasing susceptibility to disease and destabilising the population (Venturino, 2022; Belvisi & Venturino, 2013). Several modelling studies show that prey-only herding tends to stabilise dynamics under moderate pressure but may trigger predator extinction or oscillatory outbreaks when combined with strong nonlinear feedback (Jain et al., 2024; Bera et al., 2016b). This suggests that prey herding is not universally protective, but its stabilising role depends on ecological context and parameter thresholds.

When both prey and predators herd simultaneously, dynamics become more complex. Dual social behaviour generates nonlinear feedback loops in which prey clustering reduces capture success while predator coordination counters this defence (Rahman et al., 2023; Du et al., 2022). Such interactions may shift coexistence boundaries, modify bifurcation points, and even create new attractors in the system (Acotto & Venturino, 2024; Bondi et al., 2023). Ecologically, this reflects real systems where prey adopt collective defence and predators respond with cooperative hunting, producing outcomes that alternate between stability and chaotic oscillations.

More complex interpretations emerge when disease dynamics are incorporated (Venturino, 2022; Wu & Meng, 2021; Banerjee et al., 2017; Khan et al., 2015; Belvisi & Venturino, 2013; Braza, 2005). Banerjee et al. (2017), through an ecoepidemic model, found that certain predator mortality thresholds lead to system collapse, amplified by the protective effect of prey herding. In contrast, Kooi and Venturino (2016) discovered that the weakening of infected prey in a herd could support predator survival, suggesting that the ecological outcome of herding depends on additional factors such as infection dynamics. Similarly, Belvisi and Venturino (2013) incorporated group defence into their model and observed that, although herding reduces predation, it does not always prevent disease-induced collapse. Taken together, these findings suggest that herding can contribute to ecological stability, but its effect is contingent on additional factors and cannot universally guarantee system persistence.

Recent mathematical models have also highlighted a connection between herding and oscillatory population dynamics (Jain et al., 2024; Acotto & Venturino,