A Numerical Study of Modelling in a Predator–Prey System

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Abstract

The study in this thesis concerns the interactions of the two-spotted spider mite *Tetranychus urticae* and its predator *Phytoseiulus persimilis*. The logistic Lotka–Volterra predator–prey-taxis equations with diffusion and advection have been solved numerically to re-estimate parameters using three different response functions with two data sets. In order to observe the effect of prey-taxis on the periodicity of predator–prey dynamics, limits of prey-taxis parameter have been obtained using Routh-Hurwitz’s conditions for stability. It has been shown that for different values of prey-taxis it is possible to achieve periodic, quasi-periodic and chaotic nature of solutions in a predator–prey system. The formation of spatial patterns in the predator–prey system has been studied under various environmental conditions. First spatial patterns are generated with the inclusion of prey-taxis in the predator–prey system. Next spatial patterns are generated with the introduction of diffusion-driven instability and without prey-taxis in the predator–prey system. Among all parameters involved in predator–prey equations, only the predator interference parameter is varied to generate diffusion-driven instability leading to spatial patterns of population density. It has been shown that it is possible to generate spatial patterns with zero flux boundary conditions even in a smaller domain with a suitable value of the predator interference or prey–taxis. Next spatial patterns are generated with the presence of a habitat edge inside the domain. Here predators are sensitive to the presence of an internal edge while prey are free to forage in the entire domain. It has been shown that the sensivity of predators to remain in a favourable or in an unfavourable patch as well as the position of the internal edge have major impacts on the development of spatial patterns.

Finally biological control of two-spotted spider mite has been achieved with the introduction of prey-taxis in the predator–prey system. It has been shown that both response functions and initial conditions have major contributions in biological control of the prey population. It is possible to achieve successful biological control in space over a longer time-scale with prey population density below economic threshold provided the predator population density is at least twice that of the prey during most of the time.
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I extend gratitude to my parents who are responsible for the course my life has taken. Without doubt, their unwavering love and support have been fundamental throughout all stages leading up to, and during research towards this thesis.
Declaration

The candidate hereby declares that the work in this thesis, presented for the Degree of Doctorate in Mathematics submitted in the faculty of Engineering and Industrial Sciences, Swinburne University of Technology:

1. is that the candidate alone and has not been submitted previously, in whole or in part, in respect of any other academic award and has not been published in any form by other person except where due references are given, and

2. has been carried out during the period from February 2006 to June 2009 under the supervision of Dr. Manmohan Singh, Dr. David Lucy and Dr. Peter Ridland.

Aspriha Chakraborty Date: June, 2009
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Chapter 1

Summary of the Thesis

1.1 Overview

The aim of this thesis is to study the formation of spatial patterns of two-spotted spider mite leading to biological control under various environmental conditions. In order to investigate the formation of spatial patterns of two-spotted spider mite, the field data of two-spotted spider mite population on carnation has been used. The parameters governing the predator–prey system along with prey-taxis, have been estimated to obtain the best fit of numerical solutions to the field data.

In order to investigate the formation of spatial patterns with the inclusion of prey-taxis in the predator–prey system, it is essential to know the nature of predator–prey dynamics. In view of that, limits of prey-taxis parameter for which the predator–prey dynamics is periodic, quasi-periodic or chaotic have been obtained using different data sets and response functions. Results have further been verified numerically for each model considered.

Lotka–Volterra logistic predator–prey equations have been solved with the inclusion of prey-taxis. The predator–prey system has generated interesting spatial patterns. These spatial patterns have been obtained under different initial conditions and response functions.

In order to study the formation of spatial patterns further in a predator–prey system, in the absence of prey-taxis, diffusion–driven instability has been introduced in the system. Diffusion-driven instability can be achieved if the point of
equilibrium is stable without diffusion but unstable with diffusion. Predator interference $\beta$, plays a crucial role in inducing instability in the system. A limit on values of the parameter $\beta$, which introduces instability in the system is obtained. It has been observed that introduction of diffusion-driven instability incorporates aggregation of prey population density in the entire domain. In general, there is no real patch formation. In some cases, even if there is any, it is quite narrow.

With a view to develop the edge-mediated effect on the formation of spatial patterns, the predator–prey system has been considered in the absence of both prey-taxis and diffusion in predator velocity. It has been observed that prey population goes in refuge if the whole domain is divided into unequal sizes. As the whole domain is divided into equal size patches, the prey population comes out of refuge and gets spread all over or in a part of the whole domain. Spatial patterns have also been obtained by enlarging the domain size from $[-2, 2]$ to $[-4, 4]$. This increased size of the domain has produced marginal effect on the spatial patterns earlier produced with the smaller domain size.

The above study on the formation of spatial patterns has been extended to obtain biological control of two-spotted spider mites. A strategy has been developed to control the prey population density without adding any predator time to time from outside. It has been shown that it is possible to achieve the prey population density below economic threshold, that is, 2.5% of the carrying capacity provided the initial predator population density is at least twice than that of prey population in the entire domain. Lowering predator mortality and searching effectiveness of predator population density also help in achieving biological control of prey population.

**Main achievement of this thesis:**

- Estimation of parameters involved in the predator–prey system with prey-taxis.
- Effect of prey-taxis parameter on the periodicity of predator–prey dynamics.
- The formation of spatial patterns in the form of aggregation or small patches with the introduction of prey-taxis in the predator–prey system.
• Limits of predator interference parameter $\beta$ to induce diffusion–driven instability in the predator–prey system.

• The formation of the spatial patterns with the introduction of diffusion–driven instability in the predator–prey system.

• Nature of spatial patterns with the introduction of habitat edge inside a domain.

• Effects of initial conditions, response functions and data sets on the formation of spatial patterns.

• Biological control of two-spotted spider mite with prey-taxis.

MATHEMATICA has been used for numerical calculations. The other computer packages used are MICROSOFT WORD 2000, GHOSTVIEW. The whole document has been written using LATEX.

1.2 Structure of the thesis

• Chapter 1. Summary of the Thesis

This chapter gives a general introduction to the problems and briefly describes the content of the thesis.

• Chapter 2. Literature Survey

This chapter contains a review of research work relevant to the work presented in this thesis.

• Chapter 3. Estimation of Parameters with Prey-Taxis

This chapter describes the interactions of *Tetranychus urticae*, a serious pest of agricultural crops and its predacious mite *Phytoseiulus persimilis*. In order to improve the goodness of fit to the field data Kozlova et al.’s [89] models have been further extended by introducing prey-taxis in the Lotka–Volterra logistic predator–prey equations. The predator–prey-taxis equations are then solved numerically using the operator splitting method. Stability of equilibria
have been verified both with and without prey-taxis and diffusion. To examine the stability of equilibria without prey-taxis and diffusion, the variational matrix criteria have been used whereas for the equilibria with prey-taxis and diffusion, Routh–Hurwitz conditions have been used. Three different response functions along with two data sets as chosen by Kozlova et al. [89], have been used for investigation.

*This work has been accepted for publication in the Journal of “Mathematical and Computer Modelling”.*

- **Chapter 4. Effect of Prey-Taxis on the Periodicity of Predator-Prey Dynamics**

Using the data sets obtained in chapter 3, effect of prey-taxis $T$ on the periodicity of predator–prey dynamics have been observed in this chapter. Using Routh–Hurwitz’s stability criteria, limits of parameter $T$ have been obtained for which the predator–prey dynamics is periodic, quasi-periodic and chaotic. This has further been verified through numerical simulations. Effects of response functions, initial conditions and data sets on the periodic nature of predator–prey dynamics have also been investigated.

*This work has been accepted for publication in the Journal of “Canadian Applied Mathematics Quarterly”.*

- **Chapter 5. Spatial Patterns Generated by Prey-Taxis**

In this chapter, first of all, a value of prey-taxis $T$ has been chosen from the values obtained in chapter 4, for which the predator–prey dynamics is quasi-periodic. Using that value of $T$, bifurcation value of diffusivity in predator velocity $d_3$ has been obtained. The formation of spatial patterns are observed in a predator–prey system with the help of both prey-taxis and diffusion in predator velocity.

*This work is published in the Journal of “Mathematical and Computer Modelling”.*
• Chapter 6. **Spatial Patterns Generated by Diffusion-Driven Instability**

In this chapter, spatial patterns are generated through diffusion-driven instability in the predator–prey system. Though diffusion generally stabilizes a predator–prey dynamic system, under certain conditions, it can also destabilize a system. First of all, the conditions under which diffusion-driven instability can be introduced in a predator–prey system in the absence of prey-taxis have been derived. Next, the limits of predator interference parameter $\beta$ are obtained for which these conditions are satisfied. Results have been verified using numerical simulations.

*This work is published in the Journal of “Mathematical and Computer Modelling”.*

• Chapter 7. **Edge-Mediated Effects on the Formation of Spatial Patterns**

In this chapter the habitat edges have been introduced to restrict the movement of predator in the given domain while the prey is free to forage in the whole domain. The movement of the predator density is restricted by the relation $\alpha \frac{\partial v_1}{\partial x} = (1 - \alpha) \frac{\partial v_2}{\partial x}$, where $\alpha(0 < \alpha < 1)$ is the tendency of the predator to remain in the favourable patch. The minimum length of a patch in a domain for the development of spatial patterns has been calculated for different response functions and data sets. The spatial patterns have been generated for $\alpha = 0.2$ and 0.6. Various cases with different patch lengths have also been investigated.

• Chapter 8. **Effect of Prey-taxis on Biological Control**

In this chapter biological control of two-spotted spider mites throughout the domain over longer time-scale has been achieved with the help of prey-taxis. For successful biological control, the point of equilibrium is stable both with and without prey-taxis and the prey population density is below economic threshold, i.e., 2.5% of the carrying capacity for most of the time. In order to
fulfil these conditions, limits of predator mortality rate $\gamma$ and half-saturation constant $\phi$ are obtained. With particular values of parameters $\phi$ and $\gamma$, for which the point of equilibrium is stable with prey-taxis, bifurcation value of $T$ is obtained. Results have further been verified through numerical simulations.

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- **Chapter 9. Conclusions**

This chapter presents the conclusions and suggests opportunities for future developments.
Chapter 2

Literature Survey

2.1 Early history

Mathematical biology is a fast-growing, well-recognised and the most exciting modern application of mathematics. The increasing use of mathematics in biology is inevitable as biology becomes more quantitative. The complexity of the biological sciences makes interdisciplinary involvement essential. This new branch of science has a long and interesting history that starts from as early as fourth century B.C. (Salvatore [138]).

During fourth century B.C., Aristotle is possibly the first person to combine mathematics with biology. Also Archimedes of Syracuse (287–212 B.C.) was the first to combine mathematics with experimental enquiry, rather than philosophical questions. This trend continued to flourish until the time of Galen in the second century A.D. During the middle ages it flourished in the Arab world together with medicine and alchemy. Because of language barrier and the control of church, Arab knowledge spread out slowly in the western world. Thus biology underwent a period of decline during this time. But when renaissance came into Italy, the idea of combining mathematics with biology became stronger again.

Among all branches of biology, studies of population growth have interested many economists and politicians. Aristotle and Plato in ancient Greece considered the question of optimum population size in the city–states (state formed centering a city). Leonardo de Pisa, known as Fibonacci, is probably the first author who
applied mathematics to the growth of a population. In the year 1202 he showed the way to obtain number of offsprings of rabbits over certain time if initially there was only a pair. The sequence he obtained was named after him as ‘Fibonacci sequence’. After Fibonacci, there was not much progress in this field.

In the eighteenth century, population studies become more quantitative in nature and there was a tendency to explain it with mathematical formulas. Reverend Thomas Malthus (1766–1834), in his ‘Essay’, first tried to incorporate mathematics in population studies. He wrote that population, when unchecked, increase in geometric ratio where as subsistence increase in an arithmetic ratio (Salvatore [138]).

Nearly half a century later it was Charles Darwin (1809–1882), and, independently, Alfred R. Wallace (1823–1913), who from these two facts, the geometric ratio of increase and the tendency of the average number of individuals in a given species to remain constant, deduced the struggle for existence. The evolutionary theories of Darwin and Wallace were the subjects of numerous studies and endless controversy. Darwin emphasised the problem, one would encounter, if he were to pursue a mathematical solution of the problem because of the lack of quantitative data, the difficulty of securing it, and the enormous complexities of the problem. Alfred Wallace also had similar views concerning the possibility of using mathematics in describing the struggle for existence. He noted that the number of individuals of a given species remains approximately constant and attributed it to the limited supply of food and to the action of various enemies.

Later biologists, however, recognised the need to identify more clearly the many factors composing the problem of the struggle for existence so that each of them could be studied separately and their common essence could be identified. In 1877 K. Möbius introduced in biology the term ‘biocoenosis’ to indicate a biological association formed by all organisms living together in a given limited environment (Salvatore [138]). He noted that as a result of these associations certain interspecific relationships, such as competition for food, or space, or reciprocal domination, are created among the organisms. The ultimate effect of these interspecific relationships is to establish a state of equilibrium in their relative abundance. In the year 1903, A. Ghigi compared the state of dynamical equilibrium of the fluctuations of
the number of individuals of the species with the small oscillations of a pendulum, where the amplitude does not change as long as the external force remains the same (Salvatore [138]). He also pointed out that external factors like climate or human interference and internal factors related to food, space and the competition among species can affect the stability of a biological equilibrium.

The authors who attempted to give a quantitative formulation to the theory of natural selection were those, such as Francis Galton (1822–1911) and Karl Pearson (1857–1936), who founded the school of biometry and came to be known as the biometricians ([138]). They sought to give a numerical measure of the factors governing heredity and variation using the laws and methods of statistical inference at the time when Mendel’s [111] experiments in genetics were still undiscovered. In the late 1860, Galton [21] conceived the concept of standard deviation. He also invented the use of the regression line, and was the first to describe and explain the common phenomenon of regression toward the mean, which he first observed in his experiments on the size of the seeds of successive generations of sweet peas. He was a pioneer in the use of normal distribution to fit histograms of actual tabulated data. He invented the Quincunx, a pachinko-like device, also known as the bean machine, as a tool for demonstrating the law of error and the normal distribution [21]. He also discovered the properties of the bivariate normal distribution and its relationship to regression analysis. In 1901, with Walter Frank Raphael Weldon and Francis Galton, Karl Pearson founded the journal ‘Biometrika’ whose object was the development of statistical theory [132]. Pearson’s thinking underpins many of the ‘classical’ statistical methods which are in common use today. Some of his main contributions are: linear regression and correlation theory, classification of distributions especially probability distributions, exponential family of distributions, Pearson’s chi-square test, coefficient of correlation and coefficients of skewness [132]. These important contributions to the advancement of statistical methods form the basis of modern quantitative biology.

Theoretical population ecology emerged as a well-founded discipline between 1920 and 1935. In 1926 Humberto D’Ancona, son-in-law of famous Italian mathematician Vito Volterra, completed a statistical study of fish populations in the
Adriatic Sea. D’Ancona asked Volterra if there was a mathematical model that could explain the increase in certain kind of fish which he observed during the World War I period. In order to understand this phenomenon Volterra in 1926 constructed an analytical model describing a two–species predator–prey community. Volterra [153, 154, 155] showed that biological problems, like physical problems, can be made amenable to the mathematical method. In accordance to the conceptions of the naturalists, Volterra understood the fight for survival of the species to consist mainly of a struggle for the procurement of food. Therefore, he decided that the problem of the struggle for existence in a limited environment can be considered through the study of two distinct cases: – first, is the case of species competing for the same food supply, and second, is the case of the predator–prey interaction (Salvatore [138]).

At the same time, the same model, independently of Volterra [153, 154, 155], was produced by an American ecologist and mathematician Alfred J. Lotka in 1925. Lotka [100] has an immense contribution in mathematical biology. Unlike his predecessors, he tried to form a mathematical system from which all particular cases could be deduced, in the same sense that problems of motion can be studied through the use of Lagrange’s equations and problems of electrodynamics through Maxwell’s equations. In his mathematical system, he has three fundamental steps. Firstly, he formulated his own view of organic evolution which he expressed in terms analogous to the physical concepts of irreversibility in thermodynamics. Secondly, he identified biological parameters and introduced mathematical symbols so that evolution could be expressed quantitatively. Finally, he reinterpreted the mathematical models of physical chemistry particularly the law of mass action, to fit his views of evolution and renamed the chemical variables in terms of the biological parameters.

According to Bertuglia and Vaio [12], “Lotka–Volterra model is interesting in a conceptual level, but there are a number of problems regarding its real effectiveness. A fundamental characteristic of the dynamics envisaged by the basic model is that there are no points of stable equilibrium; the populations of the prey and the predators evolve according to endless cycles, without ever tending towards a situ-
The basic assumptions of this model are evidently not realistic; it does not consider any type of competition within the population of prey that is assumed to grow without any limits, if predators were not present. Furthermore, it assumes that the predators are never satiated, as the quantity of food they feed from is directly proportional to the number of existing prey. Therefore, it does not show any type of asymptotic stability. Moreover, the basic model does not consider the possibility of the extinction of the populations, which is a frequent result in laboratory tests of simple predator–prey systems (Gause [55]).

The basic Lotka–Volterra model has been improved with the introduction of various terms. One of the factors is carrying capacity of prey. ‘Carrying capacity’ is defined as the maximum number of prey available in the environment, in the absence of predator. May [106, 107] made various changes to the basic model. Firstly, he assumed a logistic growth for the prey. Secondly, he assumed that the predators could satiate themselves. With regard to the predators, May [106, 107] assumed that the limited availability of prey simply leads to a logistic growth for them. Therefore, the number of predators does not depend on the probability of their encounter with prey. Unlike the basic Lotka–Volterra model, this model can have a limit cycle as its solution.

According to Bertuglia and Vaio [12], “another variant of basic model, one of the most well–known and most used in Mathematical Biology, is that of Holling [73]. While studying several cases of predation by small mammals on pine sawflies, Holling [73] observed that the predation rate was not constant, but grew as the number of prey increased. Therefore not only the number of predators grew as that of the prey grew, but each predator increased its own consumption rate following the growth of prey. To describe this particular relationship, Holling [73] introduced two new terms, called the functional response and the numerical response of the predator. The functional response of the predator is the capture rate of prey for each individual predator. The numerical response of the predator is the predators’ growth rate. Holling [73] assumes that a predator divides its time into two parts:
the time employed in searching for the prey, called the *searching efficiency*, and the time employed digesting the prey, called the *handling time*. For each prey captured, there is an increase in the number of predators according to a constant of proportionality, called the *conversion efficiency*.

According to Kendall [82] “there have been numerous laboratory populations raised with the intent of reproducing the predator-prey cycles predicted by the Lotka–Volterra model. Most of these experiments were performed with interacting species (predators and prey) of protozoa or mites. Along with blowfly populations raised by Nicholson [122], Luckinbill [101] also demonstrated that population fluctuations could occur even in a constant environment. Constantino et al. [33] induced transitions between equilibrium and cyclic dynamics in laboratory populations of the flour beetle (*Tribolium castaneum*) by artificially increasing the adult mortality rate. In contrast, Nicholson stabilized the blowfly cycles by increasing the juvenile death rate. In the field, Krebs et al. [91] added food and reduced predation on snowshoe hares in 1km$^2$ enclosures during the course of a cycle. As a result each manipulation increased the peak density of snowshoe hares but delayed the peak. Density manipulations have also been used to prolong the cycle peak of Red Grouse (Moss et al. [113]). The results of these manipulations are often initially counter-intuitive, as most of us have intuition based on linear situations. Thus, these results can be best understood by making analogous manipulations to a nonlinear model. This empirical approaches greatly benefits from the thoughtful use of mechanistic models. For example, the conclusions about smallpox and measles were strengthened by the analysis of a nonlinear epidemiological model that supported the time-series analysis: with parameters appropriate to smallpox, the model produces stable limit cycles, whereas with measles parameters, it produces chaos (Olsen and Schaffer [127], Kendall et al. [83]). The *Tribolium* study used a mechanistic model to make predictions (which were sometimes confirmed) about the qualitative changes in dynamics as the mortality rate was varied (Constantino et al. [33])”.

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2.2 Some recent advances

Any living organism can sense the environment they live in and respond accordingly. This response generally involves movement towards or away from the external stimulus, and such a response is called \textit{taxis}, originated from Greek \textit{taxis}, which means to arrange. Taxis can be either positive or negative. When the pattern of movement of any living organism is toward the external stimulus, the taxis is called positive and when it is away from the stimulus, it is called negative. Many different types of taxis are known, including photo taxis, chemotaxis, geotaxis, magneto taxis, trophotaxis and so on. Photo taxis means light acts as a stimulus. Chemotaxis means chemical substance controls the movement of animals. In geotaxis acceleration due to gravity is the stimulating agent and in magneto taxis, a magnetic field acts as a taxis (Othmer and Stevens [129], Chakraborty et al. [29, 30]). According to Othmer and Stevens [129] “The purposes of taxis range from movement toward food and avoidance of noxious substances to large-scale aggregation for the survival”. In prey-taxis, prey population density acts as a stimulating agent. Thus prey-taxis can be defined as the pattern of movement of predator controlled by the non-uniform population density of prey while all other environmental factors are assumed to be homogeneous and constant (Kareiva and Odell [80], Turchin [151], Sapoukhina et al. [139]). That is, in space, predator tends to move where prey density is maximum and slowly predator population density builds up. Soon prey population falls down and predator has a tendency to search for new place with higher prey density leaving behind prey to grow again.

In the past two decades, a lot of work has been done on prey-taxis model. Among many mathematicians, Czárán [37], Grünbaum [62] and Turchin [151] have made significant contributions on prey-taxis modelling. They have used the conventional prey-taxis models where the directed movement of predator density is due to the advective velocity. But there are also many cases where the change or variation in velocity, i.e., individual acceleration depends on the stimulus gradient. Okubo and Chiang [124] and Okubo et al. [125] have shown that individual acceleration of swarming midges is zero at the center of the swarm, where the density of midges is maximum and the density gradient is zero. On the other hand, accelera-
tion increases with distance from the center and is maximum on the edge where the density is minimum and the gradient is maximum. Schooling fish demonstrate a similar response to their own density gradient. Parrish and Turchin [130] observed that at the center of the schooling fish, where the density gradient is zero, individual motion loses the directional component and becomes random. Observing another schooling fish, Flierl et al. [47] concluded that the probability of changing the direction of individual movement, that is, velocity variation, depends on the difference between the preferred and ambient temperatures. Analyzing herbivore movement, Karieva [78] detected that insects modify their migratory impulse, that is, accelerate, in response to the quality of food patch. Also in the existing field studies of the spatiotemporal predator–prey dynamics show that a strong aggregative response by the predator population to prey clusters are manifested by movements of coupled species patches.

Based on these observations, Sapoukhina et al. [139] have assumed that the phenomenon of accelerated predator movement take place along the prey density gradient at the individual level as well as at the level of population density. So, in their research, Sapoukhina et al. [139]) have modelled prey-taxis considering dependence of taxis velocity on prey density gradient as well as the inertial component of the directional movement.

At the large domain, the inertial movement of predator over longer time scale is determined by both mechanical laws as well as social and behavioural effects. Dixon [40] noticed that ladybirds are attracted to places where aphids are present as well as where they have recently been present. This kind of spatial behaviour is common among many species (McFarland [109]). Sapoukhina et al.’s [139] approach for modelling prey-taxis explains cases of successful biological controls as well as formation of different kinds of spatial patterns like aggregations, local extinctions, partial refuges and spatial heterogeneity.

There is also another type of interaction where the predators are ‘autocatalytic’ since when the densities are close to the steady state, an increase in predator density is temporarily amplified. As a result, hunting or reproductive efficiency of predator is improved. According to Murray [116] “suppose again there is a high
prey density area. Without diffusion the predator numbers would increase and eventually make both populations return to the steady state. However, it could happen that the predators grew and reduce the prey population to a level below the steady state value (the temporary increase in prey is enough to prompt the autocatalytic growth of predators to kick in). This would result in a net flux of prey from neighbouring regions which in turn would cause the predator density to drop in those regions (as autocatalysis works in the other direction) thereby letting the prey populations grow above their steady state value. In effect, autocatalytic predators benefit both from being at a high density locally and also because nearby there are regions containing few predators which thus supply them with a constant extra flux of prey. Prey continue to flow towards regions of high predation because of the random nature of diffusion.”

According to Murray [116] “A necessary condition for diffusion-driven instability in this predator–prey situations is that the predators disperse faster than the prey. Let us suppose there is a region of increased prey density. Without diffusion this would be damped out since the predators would temporarily increase and then drop back towards the steady state. However, with the predators diffusing it is possible that the local increase in predators (due to an increase in the prey) partially disperses and so is not strong enough to push the prey population back towards equilibrium. When predators disperse they lower the prey density in the neighbourhood. It is therefore possible to end up with clumps of high prey and predator populations interspersed with areas in which both densities are low. In the parasite analogy clumping of the sedentary prey (the host) coincides with areas of high prey density. Hosts can also exists at high levels because the parasites continue to disperse into the nearby ‘dead zone’ in which there are few of this type of host. The scale on which patterning takes place depends on the ratio of the diffusion coefficients.”

According to Cantrell and Cosner [24], “Area effects at the population level are often modeled by reaction–diffusion equations with spatially constant coefficients. Effects related to spatial heterogeneity and dispersal through different habitats are frequently studied via patch models. An example that we shall address in the
present thesis is critical patch size theory and its connections with environmental heterogeneity. The best-known models for critical patch size are called KISS models after Kierstead and Slobodkin [84] and Skellam [146]. In current usage, a KISS model is generally interpreted as a reaction–diffusion equation for a population density on a bounded region, with the coefficients of the equation being constant on the region and the density going to zero on the boundary of the region.”

Since the work of Skellam [146] and Kierstead and Slobodkin [84] there have been a number of variations and refinements on their basic models for critical patch size. Ludwig et al. [102] have considered situations where there might be multiple equilibria for the population density. In their models, Gurney and Nisbet [63] have considered the overall environment as to be infinite. But the quality of habitat was assumed to be good enough to induce a positive local growth rate on a central region and to become increasingly bad at greater distances from the center. Cantrell and Cosner [24] have assumed the overall environment to be finite with a boundary which is impermeable to the population inhabiting the environment but with arbitrarily arranged interior regions of favorable and unfavorable habitat among which the population may disperse. The distinction between patches with ‘hard edges’ across which there is no dispersal and those with ‘soft edges’ across which dispersal may occur is studied via simulations in Stamps et al. [150].

According to Fagan et al. [43], “Ecological edges often are treated as little more than ecological curiosities. Indeed, throughout much of ecology’s history, scientists have gone to great lengths to conduct research in homogeneous habitats devoid of edges and similar complicating factors.” Increasing recognition of the importance of edges has led many researchers (Dale et al. [38], Malcolm [103]) to call for studies of the functional links between habitat edges and community dynamics. A common theme is the critical need to understand the processes through which habitat edges make an impact on species dispersal and community composition in fragmented versus homogeneous landscapes. The simplest, and perhaps most widespread, class of edge-mediated effects involves habitat edges that facilitate or restrict the dispersal of organisms. Such effects are increasingly important because of the tangible connection between landscape modifications like habitat fragment-
tation and the creation or alteration of habitat edges (Groom and Schumaker [61], Chen et al. [31]).

Many authors like Bider [13], Wegner and Merriam [157], Wiens et al. [159], Schonewald-Cox and Bayless [141] have drawn comparisons between ecological edges and cellular membranes or other biological filters, noting that some edges, like membranes, can be differentially permeable to ecological flows. For a great diversity of taxa, edge permeability is often asymmetric (i.e., immigrants actively cross into patches but are quite hesitant to leave). Such unidirectional edge filtering often results in intense, but short-lived, ‘supersaturation’ of remnant patches as animals flee recently modified matrix habitat for nearby remnants, only to have their densities decline below pre-isolation levels as resources are exhausted (Whitcomb et al. [158]). Cantrell and Cosner [23] predicted that edge-sensitive skew Brownian motion (Harrison and Shepp [66]) may result in aggregation along habitat edges, producing spatial patterns similar to those obtained by Kaiser [76] and Bider [13] in laboratory and field studies, respectively.

Biological control of pests can be defined as: “the use of one or more organisms (agents) to maintain organism (pest) at a level at which it is no longer a problem”. One of the earliest successes in biological control was with the cottony cushion scale, a pest that was devastating the California citrus industry in the late 1800s. A predatory insect, the vedalia beetle, and a parasitoid fly were introduced from Australia. Within a few years the cottony cushion scale was completely controlled by these introduced natural enemies.

There has been much interest in the control of pests by a natural enemy. It has been shown by Bigger [14], Flaherty and Huffaker [46], Ghabbour [56], Helle and Sabelis [72], Huffaker and Kennet [74], Nachman [118], Nachman and Zemek [121], Sabelis [136] and others that pesticides may cause more problems than they cure by killing off a greater percentage of enemies than of the pests, or as Bigger has remarked, by shifting the system away from its equilibrium (Freedman [49]).

Nachman and Zemek [121] have shown that predators have high influence on the density of spider mites and on the plant injury they cause. According to Nachman and Zemek [121] “Plant injury increased with the initial number of spider
mites and decreased with the initial number of predators. Extinction of *T. urticae*, followed by extinction of *P. persimilis*, was the most likely outcome for most initial combinations of prey and predators”. On the other hand, Sabelis [136] has discussed about webbing and feeding of predators. When two-spotted spider mites attack any host plant, speckles appear on leaves plus the webbing is produced by protonymphs, deutonymphs and adult spider mites. In a few weeks time webbing covers the whole plant showing the presence of large pest population. The relationship between webbing and successful predatory activity of four predatory phytoseiids is analysed by Sabelis [136]. According to Sabelis [136], “the predators *M. occidentalis* and *A. bibens* (Bloomers [17]) have about the same rate of success on webbed as well as on un-webbed leaves, predator *A. potentillae* is better on un-webbed leaves, and predator *P. persimilis* is the best on webbed ones. The last species is the most efficient of all four on webbed leaves”.

The success of biological control depends on the behavioural response of predator to prey density variations. A successful biological control agent should remain in the prey colony until almost complete pest eradication. If the predator is an extremely active migrant, it leaves the location of low prey density saving the prey from local extinction. Therefore, a very high migration activity is not desirable in a successful biological control agent. Studying the life-history parameters of coccidophagous and aphidophagous ladybirds, Dixon [40] has shown that coccidophagous ladybirds are more successful biological control agents than aphidophagous species. This is because the life-history processes of aphidophagous ladybirds are much faster than the other species. Ferran et al. [44] have shown that it is possible to improve the efficiency of ladybirds by reducing its spatial activity. In turn, in their mathematical model with prey-taxis, Sapoukhina et al. [139] have shown that “predator with pronounced aggregated attack depresses the pest density to a very low level on which it can stay because of the emergence of a spatially heterogeneous dynamics.” They have also shown how “the degree of depression of pest abundance depends on the taxis coefficient of a potentially control agent. A low sensitivity of predators to the heterogeneity of pest density does not effect the dynamics qualitatively, but if it exceeds a certain bifurcation value, it promotes
persistence of the interacting populations”.

The present work is based on two-spotted spider mite and its predator. With the inclusion of prey-taxis in the predator–prey equations, parameters are re-estimated to obtain the best fit to the field data. Using prey-taxis further in the predator–prey system, periodicity of predator–prey dynamics as well as formation of spatial patterns are investigated. Next, formation of spatial patterns are achieved with diffusion–driven instability in the absence of prey-taxis. Formation of spatial patterns are further observed with the presence of habitat edge in a domain. Based on the above study, finally biological control of two-spotted spider mite is obtained with the help of prey-taxis.
Chapter 3

Estimation of Parameters with Prey-Taxis

3.1 Introduction

The two-spotted spider mite, commonly known as spider mite, belongs to the family Tetranychidae, genus Tetranychus and species urticae. The two-spotted spider mite, Tetranychus urticae is a serious pest of a variety of agricultural crops and ornamental plants. This mite has been recorded to feed on more than 180 different plant species in both greenhouse and outdoor environments. Spider mites are members of the Order Acarina, which includes spiders, ticks and mites. Whereas insects have three pairs of legs and three body regions (head, thorax, abdomen), spider mites have four pairs of legs and one body region. T. urticae can be recognized by the presence of two large dark green spots on the dorsal part of the abdomen. Depending on the host plant and other environmental factors, its colour varies from light green, dark green, brown, black, to orange.

Two-spotted spider mite feeds by using mouthparts modified to pierce plant cells. The contents of the plant cells are sucked up by the mite. This behavior leads to the characteristic speckled appearance of leaves attacked by T. urticae as shown in Figure 3.1. Outbreaks of spider mites often occur when the weather is hot and dry because the mite can lay more eggs under these conditions. Hot greenhouses and dry interior plants are very favourable environments for spider mites. Some
field crops are also vulnerable to mite attack. Strawberry fields, grape vineyards, almond orchards, apple orchards and mint fields are often attacked by spider-mites.

Populations of two-spotted spider mite tend to explode during periods of low humidity and high temperatures. High temperatures (up to 100° F) decrease the life cycle from three weeks to a mere seven days. Low humidity allows the mites to remove waste products more easily from their bodies through evaporation.

Predacious mites, such as *Phytoseiulus persimilis*, can be used to control two-spotted spider mites. These predacious mites feed exclusively on spider mites and consume 2 or 3 adults or several dozen eggs in a day. *P. persimilis* often need to be reintroduced as they rely exclusively on mites for food and can eventually consume all available prey. This beneficial mite is commercially available and is commonly released against *T. urticae* spider mites. *P. persimilis* tolerate hot climates as long as the relative humidity is between 60 and 90 percent.

Like other mites, *P. persimilis* do not have antennae, segmented bodies, or wings as shown in Figure 3.2. They pass through an egg stage, a six-legged larval stage and two eight-legged immature nymphal stages (protonymph and deutonymph) before becoming adults. *P. persimilis* mites are about the size of two-spotted spider mites, but lack spots, are orange in color, and are shinier and more pear-shaped than their prey. The shiny, oval eggs of *P. persimilis* are larger than spider mite eggs. In addition, predacious mites are much more active than pest mites, only stopping to feed.

Various experimental and theoretical developments have been done to study this pair of predator and prey. A number of researchers have used different ways of estimation of various parameters of experimental data. Nachman [118, 119, 120]
and Pearl et al. [131] have given stochastical approach to the model of *T. urticae* and *P. persimilis*. Shaw [143, 144] presents the discrete model for two-spotted spider mite and its predator mite *P. persimilis*. The system analysis of an acarine predator–prey system has been discussed by Fujita et al. [53]. Bernstein [11] has presented the deterministic model with emphasizing on French bean plant damages (Kozlova [88]).

It is well established that the predatory mite *P. persimilis* Athias-Henriot responds to odour emanating from leaves infested by its phytophagous prey, the two-spotted spider mite *T. urticae* Koch. Sabelis and Weel [137] have studied the behavioural mechanisms dominated by odour perception and how they contribute to find the prey. They also discussed about the influence of prey-related odour on orientation to wind direction (Sabelis and Weel [137]). Sabelis and Weel [137] have shown that well-fed predator females move upwind in presence of these stimuli, but downwind otherwise. The anemotactic responses of predator are both odour-conditioned and (feeding) state-dependent. Taxis, in fact, is defined as the stimulus–induced movement of animal and anemotaxis means the movement of any animal controlled by the acceleration due to odour. Prey-taxis is defined as the movement of predators controlled by prey density.

In the conventional prey-taxis models used by Czárán [37], Grünbaum [62] and Turchin [151], the directed movement of predator density is due to the advective velocity, which is assumed to be proportional to the gradient of prey density. As already mentioned in chapter 2, Sapoukhina et al. [139] have assumed that the directed movement of predator density is determined by the acceleration, which is proportional to the prey density gradient, or, in general, to the gradient of some
stimulus. The equations of reaction–diffusion–advection type have been used to obtain solutions of prey-taxis models (Arditi et al. [5]).

The study in this chapter is based on the glasshouse data of the two-spotted spider mite *T. urticae* and its predator *P. persimilis* on carnations as chosen by Kozlova [88] and Kozlova et al. [89]. Kozlova et al. [89] have used predator–prey deterministic equations to simulate the models for the estimation of various parameters. Using Sapoukhina et al.’s [139] approach for prey-taxis, Kozlova et al.’s [89] models have been extended here by introducing prey-taxis in Lotka–Volterra logistic predator–prey equations.

The aim is to improve the goodness of fit to the field data based on minimisation of errors. Errors have been calculated using the method of least squares. Three different response functions and two data sets as used by Kozlova et al. [89] have also been used here. The stabilities of equilibria have been verified using Routh–Hurwitz conditions.

### 3.2 Mathematical model

Let $u(x,t)$ be the population density (number per cubic centimeter) of prey *T. urticae*, $v(x,t)$ be the population density (number per cubic centimeter) of its predator *P. persimilis* and $w(x,t)$ be the velocity of predators.

Following Arditi et al. [5], it is assumed that the variation of the predator velocity is determined by the prey density gradient. This gives,

$$\left( \frac{\partial}{\partial t} + w \cdot \nabla \right) w = T \nabla u$$

(3.1)

where $T$ is used as the non–negative taxis coefficient throughout this study.

According to Arditi et al. [5], interactions like intraspecific competition for space equalize the velocities of neighbouring predators. Thus, introducing diffusion in the predator velocity, equation (3.1) becomes

$$\left( \frac{\partial}{\partial t} + w \cdot \nabla \right) w = T \nabla u + d_3 \nabla^2 w$$

(3.2)

where $d_3$ is the non–negative diffusivity constant of predator velocity.
For simplicity, it is assumed (Arditi et al. [5]) that the velocity, or its gradient is sufficiently small, thus neglecting \( w, \nabla w \), the predator velocity equation (3.2) becomes

\[
\frac{\partial w}{\partial t} = T \nabla u + d_3 \nabla^2 w. \tag{3.3}
\]

In one-dimensional form the predator–prey equations with prey-taxis (Arditi et al. [5], Harrison [65], Sapoukhina et al. [139]) can be written as:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \rho (1 - \frac{u}{K}) u - e f(u, v) v + d_1 \frac{\partial^2 u}{\partial x^2}, \tag{3.4} \\
\frac{\partial v}{\partial t} &= -\gamma v + \sigma f(u, v) v - \frac{\partial (vw)}{\partial x} + d_2 \frac{\partial^2 v}{\partial x^2}, \tag{3.5} \\
\frac{\partial w}{\partial t} &= T \frac{\partial u}{\partial x} + d_3 \frac{\partial^2 w}{\partial x^2}, \tag{3.6}
\end{align*}
\]

where \( \rho \) is the specific growth rate of prey in the absence of predators, \( K \) is the carrying capacity of the environment, \( \gamma \) is the mortality rate of the predators in the absence of prey, \( e \) is the maximum number of prey eaten by a predator per unit time, \( \sigma/e \) is the conversion efficiency to predator density, \( d_1 \) and \( d_2 \) are the non-negative diffusivity constants of prey and predator densities, \( d_3 \) is the non-negative diffusivity constant of predator velocity. \( T \) is used as the non-zero prey-taxis coefficient throughout this study.

All computations are carried out in the domain \([-1, 1]\) so that the effect of diffusion and prey-taxis can be observed. The boundary conditions of zero flux applied for this domain are

\[
\begin{align*}
\frac{\partial u(-1, t)}{\partial x} &= \frac{\partial v(-1, t)}{\partial x} = \frac{\partial u(1, t)}{\partial x} = \frac{\partial v(1, t)}{\partial x} = 0.
\end{align*}
\]

Also zero velocity of predator density movement on the boundary is

\[
w(-1, t) = w(1, t) = 0. \tag{3.7}
\]

### 3.3 Response functions

The response functions used (Kozlova et al. [90]) in equations (3.4) and (3.5) are:
Figure 3.3: Response function (a) with Data 1 and 2.

Figure 3.4: Response function (b) with Data 1 and 2.

\[
\begin{align*}
(a) \quad f(u, v) &= \frac{u}{\phi + u}, \\
(b) \quad f(u, v) &= \frac{u}{\phi + u + \beta v}, \\
(c) \quad f(u, v) &= \frac{u}{(\phi + u)(1 + \beta v)},
\end{align*}
\]

where \( \phi \) is the half-saturation constant, the level of prey at which half of the maximum consumption rate occurs, \( \beta \) is the predator interference constant.

The predator interference parameter \( \beta = 0.1 \), carrying capacity parameter \( K = 100 \), specific prey growth rate parameter \( \rho = 0.6 \), diffusion parameters \( d_1 = 0.0000125, d_2 = 0.02, d_3 = 0.0 \) have not been changed throughout this study (Kozlova et al. [89]). Different non-zero values of the prey-taxis coefficient, \( T \) are used in order to investigate the influence of prey-taxis on the predator–prey population. The remaining four parameters (Kozlova et al. [89]) are chosen here as
Figure 3.5: Response function (c) with Data 1 and 2.

(Data 1) \[ \phi = 19.409, \quad \gamma = 1.8, \quad \sigma = 2.9036, \quad e = 4.27, \]

(Data 2) \[ \phi = 20.524, \quad \gamma = 1.7, \quad \sigma = 3.1463, \quad e = 4.31. \]

The three response functions (a)–(c) are shown in Figures 3.3–3.5 for the values in Data 1 and Data 2 respectively. All of the three response functions have the basic features of having value zero when \( u = 0 \) and increases as \( u \) increases. The response functions (b) and (c) depend on the population density of the predator \( v \) as well as prey \( u \). But in the case of response function (b) the effect is marginal while in the case of response function (c), the response is significantly reduced for the larger values of the predator density \( v \) (Kozlova et al. [90]). In general, the values of the response functions (a)–(c) increase toward 1 as the population density of prey increases (Kozlova et al. [90]).

### 3.4 Initial conditions

Based on available field data, the initial conditions used (Kozlova [88], Kozlova et al. [89]) to solve equations (3.4)–(3.6) are

\[
\begin{align*}
u_0 &= 65. \exp(-x^4), \quad -1 \leq x \leq 1, \\
v_0 &= 1. \exp(-100x^2), \quad -1 \leq x \leq 1, \\
w_0 &= 0, \quad -1 \leq x \leq 1.
\end{align*}
\]
The initial conditions drawn in Figure 3.6 have interval steps of 0.1. These initial conditions are spatial distributions with the maximum prey population density as 65 and predator population density as 1. Here both populations are concentrated at the origin with \( v \) being more concentrated than \( u \).

### 3.5 Numerical scheme

The reaction–diffusion–advection equations (3.4), (3.5) and (3.6) have been solved numerically using an operator splitting method and both forward and central difference schemes (Marchuk [104], Kozlova et al. [89, 90], Chakraborty [27]). The system of equations (3.4)–(3.6) are split into two parts – one for first half time step and the second for the next half time step. The numerical method used for the reaction–diffusion–advection equations is the forward Euler scheme.

For the first half time step, nonlinear reaction part

\[
\frac{1}{2} \frac{\partial u}{\partial t} = \rho \left( 1 - \frac{u}{K} \right) u - ef(u,v) v, \tag{3.8}
\]
\[
\frac{1}{2} \frac{\partial v}{\partial t} = -\gamma v + \sigma f(u,v) v, \tag{3.9}
\]
\[
\frac{1}{2} \frac{\partial w}{\partial t} = 0, \tag{3.10}
\]

and for the second half time step, linear diffusion and advection parts

\[
\frac{1}{2} \frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2}, \tag{3.11}
\]
\[
\frac{1}{2} \frac{\partial v}{\partial t} = - \frac{\partial (vw)}{\partial x} + d_2 \frac{\partial^2 v}{\partial x^2}, \tag{3.12}
\]
\[ \frac{1}{2} \frac{\partial w}{\partial t} = T \frac{\partial u}{\partial x} + d_3 \frac{\partial^2 w}{\partial x^2} \] (3.13)

of the model are chosen.

Using the forward difference method, for the first half time step, the nonlinear part of equations (3.4)–(3.6) can be written as

\begin{align*}
    u_{i,j+\frac{1}{2}} &= u_{i,j} + \Delta t \left( \rho \left( 1 - \frac{u_{i,j}}{K} \right) u_{i,j} - e \, f \left( u_{i,j}, v_{i,j} \right) v_{i,j} \right), \quad (3.14) \\
    v_{i,j+\frac{1}{2}} &= v_{i,j} + \Delta t \left( -\gamma v_{i,j} + \sigma \, f \left( u_{i,j}, v_{i,j} \right) v_{i,j} \right), \quad (3.15) \\
    w_{i,j+\frac{1}{2}} &= w_{i,j}, \quad (3.16)
\end{align*}

where \( u_{i,j}, v_{i,j} \) and \( w_{i,j} \) are the approximate values of \( u, v \) and \( w \) at position \( x = -1 + i\Delta x, \ i = 0, 1, 2, \ldots \) and time \( j\Delta t, \ j = 0, 1, 2, \ldots \) and \( u_{i,j+\frac{1}{2}}, v_{i,j+\frac{1}{2}} \) and \( w_{i,j+\frac{1}{2}} \) indicate the representative values at the half time step.

Similarly, for the next half time step, the difference forms of the equations are:

\begin{align*}
    u_{i,j+1} &= u_{i,j+\frac{1}{2}} + d_1 \frac{\Delta t}{(\Delta x)^2} \left( u_{i-1,j+\frac{1}{2}} - 2u_{i,j+\frac{1}{2}} + u_{i+1,j+\frac{1}{2}} \right) + d_4 \frac{\Delta t}{(\Delta x)^2} \left( u_{i-1,j+\frac{1}{2}} - 2u_{i,j+\frac{1}{2}} + u_{i+1,j+\frac{1}{2}} \right), \quad (3.17) \\
    v_{i,j+1} &= v_{i,j+\frac{1}{2}} - v_{i,j+\frac{1}{2}} \frac{\Delta t}{2\Delta x} \left( w_{i+1,j+\frac{1}{2}} - w_{i-1,j+\frac{1}{2}} \right) - w_{i,j+\frac{1}{2}} \frac{\Delta t}{2\Delta x} \left( v_{i+1,j+\frac{1}{2}} - v_{i-1,j+\frac{1}{2}} \right) + d_2 \frac{\Delta t}{(\Delta x)^2} \left( v_{i-1,j+\frac{1}{2}} - 2v_{i,j+\frac{1}{2}} + v_{i+1,j+\frac{1}{2}} \right), \quad (3.18) \\
    w_{i,j+1} &= w_{i,j+\frac{1}{2}} + T \frac{\Delta t}{2\Delta x} \left( u_{i+1,j+\frac{1}{2}} - u_{i-1,j+\frac{1}{2}} \right) + d_3 \frac{\Delta t}{(\Delta x)^2} \left( w_{i-1,j+\frac{1}{2}} - 2w_{i,j+\frac{1}{2}} + w_{i+1,j+\frac{1}{2}} \right). \quad (3.19)
\end{align*}

The numerical schemes (3.17)–(3.19) for the diffusion and advection equations give stable solutions provided

\[ \left[ T \left( \frac{\Delta t}{\Delta x} \right) \right]^2 \leq 2d_i \frac{\Delta t}{(\Delta x)^2} \leq 1, \ i = 1, 2, 3. \]

These conditions are satisfied for the calculations of all cases considered in this study. In every case the increment value \( \Delta x = 0.1 \) centimeters and time step \( \Delta t = 0.00005 \) weeks are used after a preliminary convergence study.
In all these cases, the time sequences for the population densities $u$ and $v$ are chosen at the position $x = 0.5$, and the time sequences continue for 30 weeks.

### 3.6 Stability of equilibria without prey-taxis and diffusion

Different types of steady state solutions occur for different data sets. In order to examine the stability of different steady states, the variational matrix criterion has been used (Freedman [49], Chakraborty [27]).

The right-hand sides of equations (3.4) and (3.5) in absence of any diffusion, advection and prey-taxis terms can be written as

\[
F_1(u, v) = \rho \left(1 - \frac{u}{K}\right)u - ef(u, v)v,
\]
\[
F_2(u, v) = -\gamma v + \sigma f(u, v)v.
\]

Then the variational matrix $J$ is given by

\[
J = \begin{bmatrix}
\frac{\partial F_1}{\partial u} & \frac{\partial F_1}{\partial v} \\
\frac{\partial F_2}{\partial u} & \frac{\partial F_2}{\partial v}
\end{bmatrix}
\]

\[
= \begin{bmatrix}
\rho \left(1 - \frac{2u}{K}\right) - evf_u(u, v) & -ef(u, v) - evf_v(u, v) \\
\sigma vf_u(u, v) & -\gamma + \sigma f(u, v) + \sigma vf_v(u, v)
\end{bmatrix}.
\]

At the point of equilibrium $(u^*, v^*)$,

\[
J^* = \begin{bmatrix}
\rho \left(1 - \frac{2u^*}{K}\right) - evf_u(u^*, v^*) & -ef(u^*, v^*) - evf_v(u^*, v^*) \\
\sigma vf_u(u^*, v^*) & -\gamma + \sigma f(u^*, v^*) + \sigma vf_v(u^*, v^*)
\end{bmatrix}
\]

\[
= \begin{bmatrix}
a_{11} & a_{12} \\
a_{21} & a_{22}
\end{bmatrix}
\]
where

\[ a_{11} = \rho \left( 1 - \frac{2u^*}{K} \right) - ev^* f_u(u^*, v^*), \]
\[ a_{12} = -ef(u^*, v^*) - ev^* f_v(u^*, v^*), \]
\[ a_{21} = \sigma v^* f_u(u^*, v^*), \]
\[ a_{22} = -\gamma + \sigma f(u^*, v^*) + \sigma v^* f_v(u^*, v^*). \]  

(3.20)

In terms of response functions (a)–(c) given in section 3.3, \(a_{11}, a_{12}, a_{21}\) and \(a_{22}\) are expressed as follows:

(i) **Response function (a)**

The response function (a) is given as

\[ f(u, v) = \frac{u}{\phi + u}. \]

In terms of response function (a), equation (3.20) can be written as

\[ a_{11} = \rho \left( 1 - \frac{2u^*}{K} \right) - ev^* \frac{\phi}{(\phi + u^*)^2}, \]
\[ a_{12} = -\frac{ue^*}{\phi + u^*}, \]
\[ a_{21} = \sigma v^* \frac{\phi}{(\phi + u^*)^2}, \]
\[ a_{22} = -\gamma + \sigma \frac{ue^*}{\phi + u^*}. \]  

(3.21)

(ii) **Response function (b)**

The response function (b) is given as

\[ f(u, v) = \frac{u}{u + \phi + \beta v}. \]

In terms of response function (b), equation (3.20) can be written as

\[ a_{11} = \rho \left( 1 - \frac{2u^*}{K} \right) - ev^* \frac{\beta v^* + \phi}{(u^* + \phi + \beta v^*)^2}, \]
\[ a_{12} = -\frac{ue^*}{u^* + \phi + \beta v^*} - ev^* \frac{\beta u^*}{(u^* + \phi + \beta v^*)^2}, \]
\[ a_{21} = \sigma v^* \frac{\beta v^* + \phi}{(u^* + \phi + \beta v^*)^2}, \]
\[ a_{22} = -\gamma + \sigma \frac{ue^*}{u^* + \phi + \beta v^*} + \sigma v^* \frac{\beta u^*}{(u^* + \phi + \beta v^*)^2}. \]  

(3.22)

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(iii) Response function (c)

The response function (c) is given by
\[ f(u, v) = \frac{u}{(u + \phi)(1 + \beta v)}. \]

In terms of response function (c), equation (3.20) can be written as

\[ a_{11} = \rho \left( 1 - \frac{2u^*}{K} \right) - ev^* \frac{\phi}{(\phi + u^*)^2(1 + \beta v^*)}, \]
\[ a_{12} = -\frac{eu^*}{(\phi + u^*)(1 + \beta v^*)^2}, \]
\[ a_{21} = \sigma v^* \frac{\phi}{(\phi + u^*)^2(1 + \beta v^*)}, \]
\[ a_{22} = -\gamma + \frac{\sigma u^*}{(\phi + u^*)(1 + \beta v^*)^2}. \]  

(3.23)

3.7 Stability of equilibria with prey-taxis and diffusion

In order to derive the conditions of stability for the point of equilibrium with prey-taxis and diffusion, first of all the predator–prey-taxis equations (3.4)–(3.6) are linearised. To linearise equations (3.4)–(3.6) about the point of equilibrium \( E^* = (u^*, v^*, 0) \), small perturbations \( U(x, t), V(x, t) \) and \( W(x, t) \) are chosen.

Hence, equation (3.4) can be written as

\[ \frac{\partial (u + U)}{\partial t} = \rho \left( 1 - \frac{u + U}{K} \right)(u + U) - ef(u + U, v + V)(v + V) \]
\[ +d_1 \frac{\partial^2 u}{\partial x^2} \]
\[ \Rightarrow \frac{\partial U}{\partial t} + \frac{\partial U}{\partial t} = \rho \left( 1 - \frac{u}{K} - \frac{U}{K} \right)(u + U) - e(f(u, v) + Uf_u(u, v)) \]
\[ +VF_v(u, v)(v + V) + d_1 \frac{\partial^2 u}{\partial x^2} + d_1 \frac{\partial^2 U}{\partial x^2} \]
\[ = \rho \left( 1 - \frac{u}{K} \right)u + \rho \left( 1 - \frac{u}{K} \right)U - \rho \frac{U}{K} u - evf(u, v) \]
\[ -eUvf_u(u, v) - eVvf_v(u^*, v^*) - eVf^2(u, v) \]
\[ +d_1 \frac{\partial^2 u}{\partial x^2} + d_1 \frac{\partial^2 U}{\partial x^2} \]

neglecting higher order terms of \( U \) and \( V \).
At \((u^*, v^*, 0)\),

\[
\frac{\partial u^*}{\partial t} + \frac{\partial U}{\partial t} = \left( \rho \left( 1 - \frac{u^*}{K} \right) u^* - ev^* f(u^*, v^*) + d_1 \frac{\partial^2 u^*}{\partial x^2} \right) + \\
\left[ \rho \left( 1 - \frac{2u^*}{K} \right) U - eU v^* f_u(u^*, v^*) - eV v^* f_v(u^*, v^*) \right]
\]

\[
\frac{\partial U}{\partial t} = \rho \left( 1 - \frac{2u^*}{K} \right) U - ev^* f_u(u^*, v^*) U - e[f(u^*, v^*) + v^* f_v(u^*, v^*)] V + d_1 \frac{\partial^2 U}{\partial x^2} 
\]

\[
= \left[ \rho \left( 1 - \frac{2u^*}{K} \right) - ev^* f_u(u^*, v^*) \right] U + \\
\left[ -e(f(u^*, v^*) + v^* f_v(u^*, v^*)) \right] V + d_1 \frac{\partial^2 U}{\partial x^2} 
\]

\[
= a_{11} U + a_{12} V + d_1 \frac{\partial^2 U}{\partial x^2}, 
\]

since at the point of equilibrium \((u^*, v^*, 0)\), equation (3.4) gives

\[
\frac{\partial u^*}{\partial t} = \rho \left( 1 - \frac{u^*}{K} \right) u^* - e f(u^*, v^*) v^* + d_1 \frac{\partial^2 u^*}{\partial x^2}. 
\]

Equations (3.5) and (3.6) can be linearised about \((u^*, v^*, 0)\) in the same way as detailed above.

Hence equations (3.4)–(3.6) are reduced to a linear form (Sapoukhina et al. [139], Chakraborty [27]) as

\[
\frac{\partial U}{\partial t} = a_{11} U + a_{12} V + d_1 \frac{\partial^2 U}{\partial x^2}, \quad (3.24) 
\]

\[
\frac{\partial V}{\partial t} = a_{21} U + a_{22} V - v^* \frac{\partial W}{\partial x} + d_2 \frac{\partial^2 V}{\partial x^2}, \quad (3.25) 
\]

\[
\frac{\partial W}{\partial t} = T \frac{\partial U}{\partial x} + d_3 \frac{\partial^2 W}{\partial x^2}, \quad (3.26) 
\]

where \(a_{11}, a_{12}\) etc are the elements of the Jacobian matrix \(J^*\) at the point of equilibrium as defined in equation (3.20).
Assume a Fourier series solution of equations (3.24)–(3.26) of the form

\[ U(x, t) = \sum_k U_k \exp(\lambda t) \cos kx, \]  
\[ V(x, t) = \sum_k V_k \exp(\lambda t) \cos kx, \]  
\[ W(x, t) = \sum_k W_k \exp(\lambda t) \sin kx, \]

where \( k = n\pi/2, \) \( (n = 1, 2, 3, \ldots) \) is the wave number for the mode \( n. \) Equations (3.27)–(3.29) satisfy the boundary conditions (3.7).

With the substitution of \( U(x, t), \) \( V(x, t) \) and \( W(x, t) \) into equations (3.24)–(3.26), the equations are transformed as

\[ \sum_k U_k (a_{11} - \lambda - d_1 k^2) + \sum_k V_k (a_{12}) = 0, \]  
\[ \sum_k U_k (a_{21}) + \sum_k V_k (a_{22} - \lambda - d_2 k^2) - \sum_k W_k (v^* k) = 0, \]  
\[ \sum_k U_k (-Tk) + \sum_k W_k (-d_3 k^2 - \lambda) = 0. \]

### 3.7.1 Routh–Hurwitz conditions for stability

For a particular value of \( k, \) the variational matrix \( M_1 \) for equations (3.30)–(3.32) is given by

\[ M_1 = \begin{bmatrix}
    a_{11} - d_1 k^2 - \lambda & a_{12} & 0 \\
    a_{21} & a_{22} - d_2 k^2 - \lambda & -v^* k \\
    -Tk & 0 & -d_3 k^2 - \lambda
\end{bmatrix}. \]

The characteristic equation for the variational matrix \( M_1 \) is

\[ \lambda^3 + p(k^2) \lambda^2 + q(k^2) \lambda + r(k^2) = 0, \]  

where
\[ p(k^2) = k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22}), \quad (3.34) \]
\[ q(k^2) = k^2(d_1d_2 + d_2d_3 + d_3d_1) - c_1k^2 + c_2, \quad (3.35) \]
\[ r(k^2) = k^2(d_1d_2d_3k^4 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3
\]
\[ \quad -a_{12}v^*T + a_{11}a_{22}d_3 - a_{22}d_1d_3k^2). \quad (3.36) \]

Here \( c_1 \) and \( c_2 \) are given as
\[ c_1 = (a_{11}d_2 + a_{22}d_1 + a_{11}d_3 + a_{22}d_3), \quad (3.37) \]
\[ c_2 = (a_{11}a_{22} - a_{12}a_{21}). \quad (3.38) \]

Routh–Hurwitz conditions for the stability of the point of equilibrium are of the form (Sapoukhina et al. [139], Chakraborty [27])
\[ p(k^2) > 0, \quad (3.39) \]
\[ r(k^2) > 0, \quad (3.40) \]
\[ p(k^2)q(k^2) - r(k^2) > 0. \quad (3.41) \]

### 3.8 Bifurcation value of taxis coefficient

In this section, range of values of \( T \) is obtained for which the point of equilibrium is stable. First the predator–prey-taxis equations (3.4)–(3.6) have been solved, without prey-taxis and diffusion, to obtain the point of equilibrium \((u^*, v^*, 0)\) using response functions \((a)–(c)\) with Data 1 and Data 2. The values of \( u^*, v^* \) have been substituted in equation (3.20) to obtain the values of \( a_{11}, a_{12}, a_{21} \) and \( a_{22} \) in each case. The values of \( v^* \) along with \( a_{11}, a_{12} \) etc are substituted in condition (3.41) to obtain the expression in terms of \( T \). Solutions of this inequality in terms of \( T \) give the bifurcation value of \( T \) as detailed below. The first mode of excitation is 2, and the value of \( n \) is thus assumed to be 2 (Sapoukhina et al. [139], Chakraborty et al. [30]). Results are given in the form of two different cases called Case 1 and Case 2 in order to represent the interactions of Data 1 and 2 respectively with three response functions.

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Figure 3.7: Bifurcation value of $T$ for response function (a) with Data 1 and 2.

**Case 1a**

In the case of response function (a) with Data 1, the predator-prey-taxis equations (3.4)-(3.6) are solved, without prey-taxis, diffusion and advection, to obtain the point of equilibrium as $(u^*, v^*, 0) = (31.66, 4.9, 0)$. The values of $u^*$ and $v^*$ are then substituted in equation (3.21) to obtain the values of $a_{11}, a_{12}$ etc as $a_{11} = 0.06, a_{12} = -2.65, a_{21} = 0.106$ and $a_{22} = 0.0$. Substitution of all these values in condition (3.41) gives

$$p(k^2)q(k^2) - r(k^2) = 0.036 - 128.12T \triangleq s_1(T).$$

The graph has been drawn for $s_1(T)$, with $T$ as an unknown parameter, as shown in Figure 3.7. For a stable point of equilibrium, $s_1(T) > 0$. Thus $s_1(T) = 0$ gives the bifurcation value of $T$ for which the point of equilibrium becomes stable from unstable. For $s_1(T) = 0, T = 0.00028$. For any value of $T$ lower than the bifurcation value 0.00028, the point of equilibrium is stable as shown in Figure 3.7 and Table 3.1.

**Case 1b**

Similarly, in the case of response function (b) with Data 1, the point of equilibrium is obtained as $(u^*, v^*, 0) = (32.47, 4.97, 0)$. The values of $u^*, v^*$ are substituted in equation (3.22) to obtain the values of $a_{11}, a_{12}$ etc as $a_{11} = 0.06, a_{12} = -2.62, a_{21} = 0.105$ and $a_{22} = -0.017$. Substitution of all these values in condition (3.41) gives

$$p(k^2)q(k^2) - r(k^2) = 0.0415325 - 128.608T \triangleq s_1(T).$$

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Figure 3.8: Bifurcation value of $T$ for response function (b) with Data 1 and 2.

Figure 3.9: Bifurcation value of $T$ for response function (c) with Data 1 and 2.

The graph has been drawn for $s_1(T)$, with $T$ as an unknown parameter, as shown in Figure 3.8. For $s_1(T) = 0$, $T = 0.000323$. Thus for any value of $T$ lower than the bifurcation value 0.000323, the point of equilibrium is stable as shown in Figure 3.8 and Table 3.1.

**Case 1c**

In the case of response function (c) with Data 1, as in Case 1a, the point of equilibrium is obtained as $(u^*, v^*, 0) = (83.69, 3.09, 0)$. The values of $u^*, v^*$ are then substituted in equation (3.23) to obtain the values of $a_{11}, a_{12}$ etc as $a_{11} = -0.422681, a_{12} = -2.02154, a_{21} = 0.01253$ and $a_{22} = -0.42535$. Substitution of all these values in condition (3.41) gives

$$p(k^2)q(k^2) - r(k^2) = 0.301775 - 61.7363T \triangleq s_1(T).$$

The graph has been drawn for $s_1(T)$, with $T$ as an unknown parameter, as shown in Figure 3.9. For $s_1(T) = 0$, $T = 0.00489$. Thus for any value of $T$ lower than the bifurcation value 0.00489, the point of equilibrium is stable as shown in Figure 3.9 and Table 3.1.
Case 2a

In the case of response function (a) with Data 2, as in Case 1a, the point of equilibrium is \((u^*, v^*, 0) = (27.44, 4.84, 0)\). The values of \(a_{11}, a_{12}\) etc are obtained in the same way as in Case 1a where \(a_{11} = 0.084, a_{12} = -2.466, a_{21} = 0.136\) and \(a_{22} = 0.0\). Substitution of all these values in condition (3.41) gives

\[
p(k^2)q(k^2) - r(k^2) = 0.03604 - 117.906T \triangleq s_1(T).
\]

The graph has been drawn for \(s_1(T)\), with \(T\) as an unknown parameter, as shown in Figure 3.7. For \(s_1(T) = 0, T = 0.000306\). Thus for any value of \(T\) lower than the bifurcation value 0.000306, the point of equilibrium is stable as shown in Figure 3.7 and Table 3.1.

Case 2b

In the case of response function (b) with Data 2, as in Case 1a, the point of equilibrium is \((u^*, v^*, 0) = (28.1, 4.92, 0)\). As in Case 1b, the values of \(a_{11}, a_{12}\) etc are \(a_{11} = 0.078, a_{12} = -2.44, a_{21} = 0.135\) and \(a_{22} = -0.018\). Substitution of all these values in condition (3.41) gives

\[
p(k^2)q(k^2) - r(k^2) = 0.0428583 - 118.44T \triangleq s_1(T).
\]

The graph has been drawn for \(s_1(T)\), with \(T\) as an unknown parameter, as shown in Figure 3.8. For \(s_1(T) = 0, T = 0.000362\). Thus for any value of \(T\) lower than the bifurcation value 0.000362, the point of equilibrium is stable as shown in Figure 3.8 and Table 3.1.

Case 2c

In the case of response function (c) with Data 2, as in Case 1a, the point of equilibrium is \((u^*, v^*, 0) = (79.9, 3.91, 0)\). The values of \(a_{11}, a_{12}\) etc are \(a_{11} = -0.383, a_{12} = -1.773, a_{21} = 0.018\) and \(a_{22} = -0.506\). Substitution of all these values in condition (3.41) gives

\[
p(k^2)q(k^2) - r(k^2) = 0.327772 - 68.3724T \triangleq s_1(T).
\]

The graph has been drawn for \(s_1(T)\), with \(T\) as an unknown parameter, as shown in Figure 3.9. For \(s_1(T) = 0, T = 0.00479\). Thus for any value of \(T\) lower
than the bifurcation value 0.00479, the point of equilibrium is stable as shown in Figure 3.9 and Table 3.1.

In the next section, in order to estimate parameters with prey-taxis $T$, the point of equilibrium with prey-taxis has to be stable. In view of that, the value of $T$ is chosen to be less than the bifurcation value of the corresponding model.

Table 3.1: Characteristics of equilibria with prey-taxis

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp. func.</th>
<th>Point of Equilibrium</th>
<th>$T$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>$p(k^2).q(k^2)$</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(31.66,4.9,0)</td>
<td>0.00027</td>
<td>0.133</td>
<td>0.268</td>
<td>0.034</td>
<td>0.002</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.00029</td>
<td>0.133</td>
<td>0.268</td>
<td>0.036</td>
<td>-0.0003</td>
<td>Unstable</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(32.47,4.97,0)</td>
<td>0.00032</td>
<td>0.158</td>
<td>0.262</td>
<td>0.041</td>
<td>0.0004</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.00033</td>
<td>0.158</td>
<td>0.262</td>
<td>0.042</td>
<td>-0.0006</td>
<td>Unstable</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(83.69,3.09,0)</td>
<td>0.0048</td>
<td>1.045</td>
<td>0.289</td>
<td>0.296</td>
<td>0.006</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.0049</td>
<td>1.045</td>
<td>0.289</td>
<td>0.3025</td>
<td>-0.0005</td>
<td>Unstable</td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(27.44,4.84,0)</td>
<td>0.0003</td>
<td>0.113</td>
<td>0.319</td>
<td>0.035</td>
<td>0.001</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.00031</td>
<td>0.113</td>
<td>0.319</td>
<td>0.0365</td>
<td>-0.0004</td>
<td>Unstable</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(28.1,4.92,0)</td>
<td>0.00036</td>
<td>0.137</td>
<td>0.312</td>
<td>0.041</td>
<td>0.002</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.00037</td>
<td>0.137</td>
<td>0.312</td>
<td>0.044</td>
<td>-0.001</td>
<td>Unstable</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(79.9,3.91,0)</td>
<td>0.0047</td>
<td>1.087</td>
<td>0.302</td>
<td>0.321</td>
<td>0.007</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.0049</td>
<td>1.087</td>
<td>0.302</td>
<td>0.335</td>
<td>-0.007</td>
<td>Unstable</td>
</tr>
</tbody>
</table>
3.9 Estimation of parameters with prey-taxis and diffusion

Kozlova [88], Kozlova et al. [89] have estimated parameters for two-spotted spider mite with the inclusion of diffusion in the predator–prey system. In this section, the predator mortality rate $\gamma$ and predator birth rate $\sigma$ have been re-estimated with the inclusion of prey-taxis in the existing predator–prey system. The aim is to improve the goodness of fit with the field data (Kozlova [88]) given in Figure 3.10.

![Figure 3.10: Predator–prey graph from field data.](image)

In each case errors are calculated using the method of least squares as given by Harrison [65], Kozlova [88], Kozlova et al. [89], where the values of the goodness of fit indicator $R^2$ are given by

$$R^2 = \frac{\bar{S}^2 - S^2}{S^2},$$

with

$$\bar{S}^2 = \sum_{i=1}^{N} [(\bar{u} - u_{obs}(t_i))^2 + (\bar{v} - v_{obs}(t_i))^2]$$

and

$$S^2 = \sum_{i=1}^{N} \left[ \left( \frac{u(t_i) - u_{obs}(t_i)}{s_{u_i}} \right)^2 + \left( \frac{v(t_i) - v_{obs}(t_i)}{s_{v_i}} \right)^2 \right],$$

where $N$ is the total number of observations, $u(t_i)$ and $v(t_i)$ are numerically computed values of prey and predator respectively at observation time $t_i$, $u_{obs}(t_i)$ and $v_{obs}(t_i)$ are observed values of prey and predator at the same time $t_i$, $\bar{u}$ and $\bar{v}$ are the average values of the observed prey and predator populations. $S^2$ is the sum of squares of the differences between calculated and observed values. Values $s_{u_i}$ and $s_{v_i}$ are weights representing the relative measurement errors in the observations given by
Figure 3.11: Predator–prey solutions for response functions (a)–(c) with Data 1 in the absence of prey-taxis.

\[ s_{ui} = 1 + \alpha u_{obs}(t_i), \]
\[ s_{vi} = 1 + \alpha v_{obs}(t_i), \]

where \( \alpha = 0.02 \) is selected during the calculations as chosen by Kozlova [88].

Here the numerical computations are carried out for the minimization of \( S^2 \). Although the differential equations are nonlinear and there is no evidence that the residuals are normally distributed, however, the value of \( R^2 \) could be a good indication of the best fit. When \( R^2 \) is closer to 1, the best fit occurs (Harrison [65], Kozlova [88], Kozlova et al. [89]).

The estimated parameters for the simulated models are selected on the basis of (i) the value of the goodness of fit indicator \( R^2 \) and (ii) graphical comparison of the simulated values to the field data (Kozlova [88]).
Data 1

In the absence of prey-taxis, predator–prey solutions (Kozlova et al. [89]) for response functions (a)–(c) with Data 1 are shown in Figure 3.11. These solutions are referred to as model 1 in Table 3.2. It has been observed that in the case of response function (a), the error for model 1 is higher than that of response function (b) as given in Table 3.2. Thus in order to improve goodness of fit with Data 1, response function (b) is more suitable than response function (a). On the other hand, response function (c) does not show any fit with the field data as shown in Figure 3.11. Hence response function (c) also cannot be chosen to improve the goodness of fit. Finally response function (b) has been chosen to obtain better fit with Data 1.

In Figure 3.11, \( u_{\text{obs}} \) refers to the observed prey population density from the given field data (Kozlova et al. [89]), \( u \) refers to the numerical solutions of the prey population density. Similarly, \( v_{\text{obs}} \) refers to the observed predator population density from the field data and \( v \) refers to the numerical solutions of the predator population density. The same notation is used in Figures 3.12 and 3.13 as well.

Response function (b)

In order to improve the goodness of fit, \( T = 0.0003 \) has been introduced in the predator–prey-taxis equations (3.4)–(3.6). The corresponding model has been referred to as model 2 in Table 3.2 and shown in Figure 3.12. As already mentioned in section 3.8 and Table 3.1, for this value of \( T \), the point of equilibrium is always stable. Also errors are less at \( T = 0.0003 \) as compared to \( T = 0.0 \) given in Table 3.2. Next, the value of \( \gamma \) has been decreased steadily from 1.8 to 1.55, using a number of simulations, in order to improve the goodness of fit as shown in Figure 3.12. This has been referred to as model 3 in Table 3.2. As the value of \( \sigma \) is slowly increased from 2.9036 to 3.0744, using a number of simulations, the goodness of fit improves as shown in Figure 3.12 and referred to as model 4 in Table 3.2. This is further confirmed by error values as shown in Table 3.2.

Data 2

In the case of Data 2 with response functions (a) and (c), similar situations arise as that of Data 1. Thus the graphs for response functions (a) and (c) have
not been shown here. Hence here also response function (b) is chosen to obtain better fit with Data 2.

**Response function (b)**

In order to improve the goodness of fit, here also \( T = 0.0003 \) is introduced in the predator–prey–taxis equations (3.4)–(3.6). The corresponding model is referred to as model 2 in Table 3.2. The solutions are shown in Figure 3.13. In this case also, for this value of \( T \), the point of equilibrium is stable. The errors are less at \( T = 0.0003 \) as compared to \( T = 0.0 \) given in Table 3.2. Next, the value of \( \gamma \) is decreased steadily from 1.7 to 1.6, using a number of simulations, in order to improve the goodness of fit as shown in Figure 3.13 and referred to as model 3 in Table 3.2. As the value of \( \sigma \) is slowly increased from 3.1463 to 3.2756, using a number of simulations, the goodness of fit improves further as shown in Figure 3.13 and referred to as model 4 in Table 3.2. This is confirmed by error values as shown in Table 3.2.
Table 3.2: Estimation of parameters for Data 1 and Data 2 and response functions (a), (b) with prey-taxis

<table>
<thead>
<tr>
<th>Data</th>
<th>Response function</th>
<th>Model</th>
<th>$\gamma$</th>
<th>$\sigma$</th>
<th>$T$</th>
<th>$d_3$</th>
<th>$R^2$</th>
<th>$S^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>1</td>
<td>1.8</td>
<td>2.9036</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3722</td>
<td>32494.5</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>1</td>
<td>1.8</td>
<td>2.9036</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3931</td>
<td>31840.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1.8</td>
<td>2.9036</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.3953</td>
<td>31261.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>1.55</td>
<td>2.9036</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.4611</td>
<td>22733.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>1.55</td>
<td>3.0744</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.4842</td>
<td>20306.0</td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>1</td>
<td>1.7</td>
<td>3.1463</td>
<td>0.0</td>
<td>0.0</td>
<td>0.402</td>
<td>25841.3</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>1</td>
<td>1.7</td>
<td>3.1463</td>
<td>0.0</td>
<td>0.0</td>
<td>0.4521</td>
<td>23800.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1.7</td>
<td>3.1463</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.4561</td>
<td>23536.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>1.6</td>
<td>3.1463</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.4782</td>
<td>20974.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>1.6</td>
<td>3.2756</td>
<td>0.0003</td>
<td>0.0</td>
<td>0.4906</td>
<td>19655.5</td>
</tr>
</tbody>
</table>
Table 3.3: Characteristics of equilibria for modified Data 1 and Data 2 with response functions (a)–(c)

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp. func.</th>
<th>Point of Equilibrium</th>
<th>$T$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>$-r(k^2)$</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(19.73, 4.41, 0)</td>
<td>0.0003</td>
<td>0.073</td>
<td>0.3456</td>
<td>0.028</td>
<td>-0.0027</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>-ive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.19, 4.49, 0)</td>
<td>0.0003</td>
<td>0.095</td>
<td>0.338</td>
<td>0.004</td>
<td>0.028</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(71.97, 5.62, 0)</td>
<td>0.0003</td>
<td>1.055</td>
<td>0.262</td>
<td>0.023</td>
<td>0.253</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(19.6, 4.49, 0)</td>
<td>0.0003</td>
<td>0.18</td>
<td>0.38</td>
<td>0.009</td>
<td>0.06</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.03, 4.57, 0)</td>
<td>0.0003</td>
<td>0.101</td>
<td>0.364</td>
<td>0.028</td>
<td>0.009</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(70.92, 5.88, 0)</td>
<td>0.0003</td>
<td>1.08</td>
<td>0.269</td>
<td>0.023</td>
<td>0.268</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td></td>
</tr>
</tbody>
</table>

Hence the modified data sets 1 and 2 for $T = 0.0003$ are:

(Data 1) $\phi = 19.409, \quad \gamma = 1.55, \quad \sigma = 3.0744, \quad e = 4.27,$

(Data 2) $\phi = 20.524, \quad \gamma = 1.60, \quad \sigma = 3.2756, \quad e = 4.31.$

All other parameters as specified in section 3.3 remain unchanged. Characteristics of the point of equilibrium for modified data sets 1 and 2 along with response functions (a), (b) and (c) are given in Table 3.3.

From now onwards, these modified data sets 1 and 2 have been used and referred to as Data 1 and Data 2 respectively.

### 3.10 Discussion and conclusion

In this chapter, Lotka–Volterra logistic predator–prey-taxis equations (3.4)–(3.6) with $P. persimilis$ as the predator and $T. urticae$ as the prey are considered along with three response functions, two data sets and a set of initial conditions.
First of all, stabilities of equilibria are determined without prey-taxis and diffusion using the variational matrix criterion (Freedman [49]) described in section 3.6. Next, stabilities of equilibria are determined with prey-taxis and diffusion (Sapoukhina et al. [139]) using Routh–Hurwitz conditions described in section 3.7. Using Routh–Hurwitz conditions the bifurcation value of the prey-taxis coefficient for stable dynamics is determined for each response function, as described in section 3.8.

In order to improve the goodness of fit, as described in section 3.9, a non–zero value of prey-taxis, for which the point of equilibrium is stable, is chosen. The predator–prey-taxis equations with diffusion and advection are solved numerically with a non–zero value of prey-taxis along with different values of predator mortality rate \( \gamma \) and predator growth rate \( \sigma \). Here the value of \( \gamma \) is varied within the range of \( 1.5 < \gamma < 1.8 \) (Kozlova [88]). This range is chosen based on the information provided by Nachman [119], Bancroft and Margolies [7], Kozlova et al. [89]. Also the parameter \( \sigma \), predator growth rate, is less than \( e \) since conversion efficiency to predator density \( \sigma/e \) is less than 1. Here \( e \) is the number of prey eaten by a predator per unit time. Therefore \( \sigma = b e \), \( 0 < b < 1 \). According to Sabelis [136], the value of \( b \) is approximately 0.7 for \( P. Persimilis \). In this study, the range of \( b \) is chosen from 0.67 to 0.75 (Kozlova et al. [89]).

In the absence of prey-taxis, response function (a) has larger error than that of response function (b) as shown in Table 3.2. On the other hand, response function (c) does not fit at all with Data 1 as shown in Figure 3.11. Thus response function (b) is chosen to improve the goodness of fit in existing data sets with the inclusion of prey-taxis in the predator–prey system. With response function (b), using new values of \( \gamma \) and \( \sigma \) including non–zero value of prey-taxis, it is possible to improve the goodness of fit as shown in Figures 3.12, 3.13 as well as in Table 3.2.

Thus it can be concluded that it is possible to improve the goodness of fit with the inclusion of prey-taxis in a predator–prey system. Response functions play a major role in achieving the best fit to the field data.

The modified data sets Data 1 and Data 2 have been used in the next chapter to study the effects of prey-taxis on the periodicity of predator–prey dynamics.
Chapter 4

Effect of Prey-Taxis on the Periodicity of Predator–Prey Dynamics

4.1 Introduction

Regular fluctuations in population density, both periodic and chaotic, are found in a variety of species in nature. Although the exact causes of these cycles remain undetermined for most species, they generally involve strongly nonlinear trophic and competitive interactions among a small number of species. Experimentalists such as G. F. Gause [55] and A. J. Nicholson [122] produced cyclic dynamics in laboratory populations of protozoa and insects. In the meantime, Charles Elton [42] studied cyclic fluctuations in field populations of voles (small rodents) and in the numbers of furs of Canadian lynx and other large mammals traded by the Hudsons Bay Company. Foresters have long been dismayed by the periodic outbreaks of certain leaf-feeding insects, like spruce budworms, which can completely defoliate a forest when at peak density. However, it was not until Michael Rosenzweig [135], as a graduate student with Robert MacArthur [135] in the 1960s, added density dependence to the Lotka–Volterra equations that an ecological model capable of displaying true nonlinear limit cycles was developed (Kendall [82]).

In the early and mid 1970s, physicist Robert May [106, 107] produced a series of
papers demonstrating that complex dynamics (cycles and chaos) could be generated by the simplest ecological models, including the logistic map, an extremely simple model of density-dependent population growth with discrete generations.

The roots of chaos theory date back to about 1900, in the studies of Henri Poincaré on the problem of the motion of three objects in mutual gravitational attraction, the so-called three body problem. Later studies, also on the topic of non-linear differential equations, were carried out by G. D. Birkhoff [16], A. N. Kolmogorov [87], M. L. Cartwright [25, 26], J. E. Littlewood [26] and Stephen Smale [147]. Chaos was first knowingly observed in a mathematical model by meteorologist Edward Lorenz [99] in the early 1960s. According to Kendall [82] “Not only did he observe deterministic aperiodic fluctuations, but he also discovered sensitive dependence on initial conditions: restarting a simulation model without bothering to copy all of the significant digits, Lorenz observed a sequence of numbers that soon started to diverge from the original simulation.”

The term chaos as used in mathematics was coined in 1975 by the applied mathematicians James A. Yorke and T. Y. Li [96]. In mathematics and physics, chaos theory deals with the behaviour of certain non-linear dynamical systems that, under certain conditions, exhibit the phenomenon known as chaos. Examples of such systems include the atmosphere, the solar system, plate techtonics, turbulent fluids, economies and population growth.

Four qualitative types of dynamic attractors are observed: equilibrium, periodic cycles (also called limit cycles), quasi-periodic cycles, and chaos. Chaos is characterized by a positive Lyapunov exponent, which can be thought of as a measure of the long-term unpredictability of the system; equilibrium and periodic attractors have a negative exponent. As the systems parameters are changed, the dynamics may undergo an abrupt, qualitative change, known as a bifurcation (Kendall [82]).

The aim in this chapter is to investigate the effect of prey-taxis parameter on the periodicity of predator–prey dynamics. In view of that, limits of prey-taxis $T$ have been obtained for which the predator–prey dynamics is periodic, quasi-periodic or chaotic. Results have further been verified through numerical solutions using two data sets, three response functions and two initial conditions.
4.2 Mathematical model

In one-dimensional form the predator–prey-taxis equations (Arditi et al. [5], Har- rison [65], Sapoukhina et al. [139], Chakraborty et al. [30]) are written as:

\[
\frac{\partial u}{\partial t} = \rho (1 - \frac{u}{K}) u - e f(u, v) v + d_1 \frac{\partial^2 u}{\partial x^2}, \quad (4.1)
\]

\[
\frac{\partial v}{\partial t} = -\gamma v + \sigma f(u, v) v - \frac{\partial (vw)}{\partial x} + d_2 \frac{\partial^2 v}{\partial x^2}, \quad (4.2)
\]

\[
\frac{\partial w}{\partial t} = T \frac{\partial u}{\partial x} + d_3 \frac{\partial^2 w}{\partial x^2}, \quad (4.3)
\]

where all the symbols have their usual meanings as defined in section 3.2.

4.3 Response functions

The same response functions as used in chapter 3 have been used here. Data 1 and Data 2 obtained in section 3.9 have been used here. The predator interference parameter \( \beta = 0.1 \), carrying capacity parameter \( K = 100 \), specific prey growth rate parameter \( \rho = 0.6 \), diffusivity constants \( d_1 = 0.0000125 \), \( d_2 = 0.02 \) and \( d_3 = 0.0 \) have not been changed throughout this study. Different values of prey-taxis coefficient \( T \) have been chosen in order to observe its effect on the periodicity of the predator–prey dynamics.

Hence the two data sets are:

(Data 1) \( \phi = 19.409, \quad \gamma = 1.55, \quad \sigma = 3.0744, \quad e = 4.27, \)
(Data 2) \( \phi = 20.524, \quad \gamma = 1.60, \quad \sigma = 3.2756, \quad e = 4.31. \)

4.4 Initial conditions

The initial conditions used for numerical solutions of equations (4.1)–(4.3) are:
Figure 4.1: Initial condition (ii).

(i)

\[
\begin{align*}
    u_0 &= 65 \exp(-x^4), \ -1 \leq x \leq 1, \\
    v_0 &= 1. \exp(-100x^2), \ -1 \leq x \leq 1, \\
    w_0 &= 0, \ -1 \leq x \leq 1.
\end{align*}
\]

(ii)

\[
\begin{align*}
    u_0 &= \begin{cases} 
        65 \exp\left(-40 (x + 0.5)^2\right), & -1 \leq x \leq 0, \\
        0, & 0 < x \leq 1.
    \end{cases} \\
    v_0 &= \begin{cases} 
        0, & -1 \leq x < 0, \\
        1. \exp\left(-40 (x - 0.5)^2\right), & 0 \leq x \leq 1.
    \end{cases} \\
    w_0 &= 0, \ -1 \leq x \leq 1.
\end{align*}
\]

Initial condition (i) is already used in chapter 3. Initial condition (ii) is introduced in this chapter and shown in Figure 4.1. Initial condition (ii) has \( u \) concentrated at \( x = -0.5 \) and \( v \) concentrated about \( x = 0.5 \). The numerical scheme of the operator splitting method and the boundary conditions of zero flux as used in chapter 3 have also been used here.
Table 4.1: Characteristics of equilibria without prey-taxis

<table>
<thead>
<tr>
<th>Data</th>
<th>Response function</th>
<th>Point of Equilibrium</th>
<th>Eigenvalues</th>
<th>Nature of equilibrium</th>
<th>Characteristics of the solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(19.73, 4.41)</td>
<td>0.062 ± 0.605i</td>
<td>unstable</td>
<td>limit cycle</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.19, 4.49)</td>
<td>0.051 ± 0.6i</td>
<td>unstable</td>
<td>limit cycle</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(71.97, 5.62)</td>
<td>−0.43± 0.137i</td>
<td>stable</td>
<td>spiral</td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(19.6, 4.49)</td>
<td>0.059 ± 0.626i</td>
<td>unstable</td>
<td>limit cycle</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.03, 4.56)</td>
<td>0.048 ± 0.62i</td>
<td>unstable</td>
<td>limit cycle</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(70.92, 5.88)</td>
<td>−0.441± 0.13i</td>
<td>stable</td>
<td>spiral</td>
</tr>
</tbody>
</table>

4.5 Stability of equilibria with prey-taxis and diffusion

In this section, stability of equilibria both with and without prey-taxis have been investigated using the variational matrix criterion as detailed in 3.6. Eigenvalues obtained from the variational matrix $J^*$ corresponding to two data sets and each of the three response functions are given in Table 4.1.

In order to examine the existence of stable periodic solution with prey-taxis, the solutions of equations (3.24)–(3.26) are assumed of the form (Chakraborty et al. [28])

$$U(x,t) = \sum_k U_k \exp(\lambda t + ikx),$$  \hspace{1cm} (4.4)

$$V(x,t) = \sum_k V_k \exp(\lambda t + ikx),$$  \hspace{1cm} (4.5)

$$W(x,t) = \sum_k W_k \exp(\lambda t - ikx),$$  \hspace{1cm} (4.6)

where $k = n\pi/2$ is the wave number for the mode $n$.

With the substitution of $U(x,t)$, $V(x,t)$ and $W(x,t)$ into equations (3.24)–(3.26), for a particular value of $k$, the variational matrix $M_2$ is given by

$$M_2 = \begin{bmatrix}
\lambda - a_{11} + k^2 d_1 & -a_{12} & 0 \\
a_{21} & a_{22} - \lambda - d_2 k^2 & v^* k \\
T(i k) & 0 & -(d_3 k^2 + \lambda)
\end{bmatrix}. $$
The characteristic equation for the variational matrix $M_2$ is given by

$$
\lambda^3 + p(k^2)\lambda^2 + q(k^2)\lambda + r(k^2) = 0,
$$

where

$$
p(k^2) = k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22}), \quad (4.7)
$$

$$
q(k^2) = k^4(d_1d_2 + d_2d_3 + d_3d_1) - c_1k^2 + c_2, \quad (4.8)
$$

$$
r(k^2) = k^2(d_1d_2d_3k^4 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3
$$

$$+ a_{12}v^*T + a_{11}a_{22}d_3 - a_{22}d_1d_3k^2). \quad (4.9)
$$

Here $c_1$ and $c_2$ have already been defined earlier in equations (3.37) and (3.38) respectively.

Routh–Hurwitz conditions for the stability of the point of equilibrium are of the form (Sapoukhina et al. [139])

$$
p(k^2) > 0, \quad (4.10)
$$

$$
r(k^2) > 0, \quad (4.11)
$$

$$
p(k^2)q(k^2) - r(k^2) > 0. \quad (4.12)
$$

Substituting the values of $p(k^2), q(k^2)$ and $r(k^2)$ from equations (4.7)–(4.9) to inequality (4.12), it can be seen that

$$
(k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22})) \times [(a_{11}a_{22} - a_{12}a_{21}) +
$$

$$k^4(d_1d_2 + d_2d_3 + d_3d_1) - k^2(a_{11}d_2 + a_{22}d_1 + a_{11}d_3 + a_{22}d_3)] -
$$

$$k^2(d_1d_2d_3k^4 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3 + a_{12}v^*T) > 0.
$$

After some simplifications, the above inequality gives

$$
T > -\frac{k^2}{a_{12}v^*} \left\{ \frac{(a_{11} + a_{22})}{k^2} - (d_1 + d_2) \right\} \times \left\{ \frac{(a_{11}a_{22} - a_{12}a_{21})}{k^2} +
$$

$$k^2(d_1 + d_3)(d_2 + d_3) - a_{11}(d_2 + d_3) - a_{22}(d_1 + d_3)\right\}
$$

$$+ \frac{a_{11}a_{22}d_3}{k^2} - a_{11}d_2d_3 - a_{22}d_1d_3 + a_{11}d_2d_3k^2].
$$
Substituting $k = n\pi/2$ and after some simplifications, the above inequality gives

$$T > -\frac{n^2\pi^2}{16a_{12}v}\left[-4a_{22}d_1d_3 - 4a_{11}d_2d_3 + \frac{16a_{11}a_{22}d_3}{n^2\pi^2} + a_{11}d_2d_3n^2\pi^2 + \right.$$

$$\left.\{4a_{11} + 4a_{22} - (d_1 + d_2)n^2\pi^2\} \times \{16a_{12}a_{21} + (4a_{11} - (d_1 + d_3)n^2\pi^2)\} / (n^4\pi^4)\right]$$

$$\triangleq g(n).$$ (4.13)

Inequality (4.13) provides the limit of $T$ below which the point of equilibrium becomes unstable from stable and the value of $g(n)$ is negative.

In order to obtain the upper limit of $T$ beyond which the point of equilibrium becomes unstable from stable, equations (4.10)–(4.12) have been derived again for

\[
\begin{align*}
U(x, t) &= \sum_k U_k \exp(\lambda t + ikx) \\
V(x, t) &= \sum_k V_k \exp(\lambda t + ikx) \\
W(x, t) &= \sum_k W_k \exp(\lambda t + ikx).
\end{align*}
\]

With the substitution of $U(x, t)$, $V(x, t)$ and $W(x, t)$ into equations (3.24)–(3.26), for a particular value of $k$, the variational matrix $M_3$ is given by

\[
M_3 = \begin{bmatrix}
\lambda - a_{11} + k^2d_1 & -a_{12} & 0 \\
-a_{21} & a_{22} - \lambda - d_2k^2 & -v^*ik \\
T(ik) & 0 & -(d_3k^2 + \lambda)
\end{bmatrix}.
\]

The characteristic equation for the variational matrix $M_3$ is given by

$$\lambda^3 + p(k^2)\lambda^2 + q(k^2)\lambda + r(k^2) = 0,$$

where
respectively.

Substituting the values of \( p(k^2), q(k^2) \) and \( r(k^2) \) from equations (4.14)–(4.16) to inequality (4.12), it can be seen that

\[
(k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22})) \times \left\{ \frac{(a_{11}a_{22} - a_{12}a_{21})}{k^2} \right\} + k^4(d_1d_2 + d_2d_3 + d_3d_1) - k^2(a_{11}d_2 + a_{22}d_1 + a_{11}d_3 + a_{22}d_3) - k^2(d_1d_2d_3k^4 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3 - a_{12}v^*T) > 0.
\]

After some simplifications, the above inequality gives

\[
T < \frac{k^2}{a_{12}v^*} \left\{ \frac{(a_{11} + a_{22})}{k^2} - (d_1 + d_2) \right\} \times \left\{ \frac{(a_{11}a_{22} - a_{12}a_{21})}{k^2} \right\} + k^2(d_1 + d_3)(d_2 + d_3) - a_{11}(d_2 + d_3) - a_{22}(d_1 + d_3) + \frac{a_{11}a_{22}d_3}{k^2} - a_{11}d_2d_3 - a_{22}d_1d_3 + a_{11}d_2d_3k^2].
\]

Substituting \( k = n\pi/2 \) and after some simplifications, the above inequality gives

\[
T < \frac{n^2\pi^2}{16a_{12}v^*} \left\{ -4a_{22}d_1d_3 - 4a_{11}d_2d_3 + \frac{16a_{11}a_{22}d_3}{n^2\pi^2} + a_{11}d_2d_3n^2\pi^2 \right\} + \left\{ 4a_{11} + 4a_{22} - (d_1 + d_2)n^2\pi^2 \right\} \times \left\{ -16a_{12}a_{21} - (a_{11} - (d_1 + d_3)n^2\pi^2)(-4a_{22} + (d_2 + d_3)n^2\pi^2) / (n^4\pi^4) \right\} \Delta = f(n).
\]

Inequality (4.17) provides the upper limit of \( T \) beyond which the point of equilibrium becomes unstable from stable and the value of \( f(n) \) is positive.
4.6 Limits of prey-taxis parameter $T$

In order to observe the effect of $T$ on predator–prey dynamics, first of all, the limits of $T$ have been determined for which the predator–prey dynamics is periodic, quasi-periodic and chaotic. In view of that following steps have been used:

**Step 1:** Predator–prey-taxis equations (4.1)–(4.3) have been solved without prey-taxis, diffusion and advection to obtain the point of equilibrium $(u^*, v^*, 0)$.

**Step 2:** Values of $u^*$ and $v^*$ have been substituted in equation (3.20) to obtain the values of $a_{11}, a_{12}, a_{21}$ and $a_{22}$ respectively.

**Step 3:** In order to find the lower limit of $T$ for which the predator–prey dynamics is periodic, values of $a_{11}$ etc have been substituted in condition (4.13) to obtain an expression for $g(n)$.

**Step 4:** As mentioned earlier in section 4.5, $g(n)$ is always negative. Thus the value of $n$ for which the value of $g(n)$ is maximum, i.e. the closest one to zero, is the first excited mode. The corresponding value of $g(n)$ is the lower limit of $T$ for which the predator–prey dynamics is periodic.

**Step 5:** On the other hand, the value of $n$ for which the value of $g(n)$ is minimum, i.e. the farthest one to zero, is the highest excited mode. The corresponding value of $g(n)$ is the lower limit of $T$ for which the predator–prey dynamics is quasi-periodic. For any value of $T$ lower than this limit, the predator–prey dynamics is chaotic.

**Step 6:** In order to find the upper limit of $T$ for which the predator–prey dynamics is periodic, values of $a_{11}$ etc have been substituted in condition (4.17) to obtain an expression for $f(n)$.

**Step 7:** As mentioned earlier in section 4.5, $f(n)$ is always positive. Thus the value of $n$ for which the value of $f(n)$ is minimum, i.e. the closest one to zero, is the first excited mode. The corresponding value of $f(n)$ is the upper limit of $T$ for which the predator–prey dynamics is periodic.

**Step 8:** On the other hand, the value of $n$ for which the value of $f(n)$ is maximum, i.e. the farthest one to zero, is the highest excited mode. The corresponding value of $f(n)$ is the upper limit of $T$ for which the predator–prey dynamics is quasi-periodic. For any value of $T$ greater than this limit, the predator–prey dynamics
Case 1a

In the case of response function (a) with Data 1, the predator–prey-taxis equations (4.1)–(4.3) are solved without diffusion, advection and prey-taxis to obtain the point of equilibrium as \((u^*, v^*, 0) = (19.73, 4.41, 0)\). The values of \(u^*, v^*\) are substituted in equation (3.21) to obtain the values of \(a_{11}, a_{12}\) etc. as \(a_{11} = 0.124, a_{12} = -2.153, a_{21} = 0.172\) and \(a_{22} = 0.0\).

Lower limit of \(T\)

In order to find the lower limit of \(T\) for which the predator–prey dynamics is periodic, known values of \(a_{11}\) etc are substituted in condition (4.13) to obtain

\[
g(n) = -0.000812 + \frac{0.002}{n^2} + 0.000013n^2 - 3.2 \times 10^{-9}n^4.
\]

Graphs of \(g(n)\) have been drawn with \(n = 2, 3, 4\) and 5 as shown in Figure 4.2. Since for \(n = 1\) the value of \(g(n)\) is positive, the graph of \(g(n)\) for \(n = 1\) is not produced here and the case is not considered. From Figure 4.2, it can be seen that for \(n = 2\), the value of \(g(n)\) is maximum, i.e., the closest one to zero. Thus \(n = 2\) is the first excited mode and the corresponding value of \(g(n)\) is \(-0.000269414\). This gives the lower limit of prey-taxis parameter \(T\) for periodic dynamics. Thus for \(T > -0.000269414\), the predator–prey dynamics is periodic as shown in Table 4.2 and the point of equilibrium is stable.

For \(n = 4\), the value of \(g(n)\) is minimum, i.e. the farthest one from zero.
Thus $n = 4$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.000483096$. Thus for $-0.000483096 < T < -0.000269414$, the predator–prey dynamics is quasi-periodic. For $T < -0.000483096$, the dynamics is chaotic.

**Upper limit of $T$**

In order to find the upper limit of $T$ for which the predator–prey dynamics is periodic, known values of $a_{11}$ etc are substituted in condition (4.17) to obtain

$$f(n) = 0.000812 - \frac{0.002}{n^2} - 0.000013n^2 + 3.2 \times 10^{-9}n^4.$$

Graphs of $f(n)$ have been drawn for $n = 2, 3, 4$ and 5 as shown in Figure 4.2. Since for $n = 1$ the value of $f(n)$ is negative, the graph of $f(n)$ for $n = 1$ is not produced here and the case is not considered. From Figure 4.2, it can be seen that for $n = 2$, the value of $f(n)$ is minimum, i.e. the closest one to zero. Thus $n = 2$ is the first excited mode and the corresponding value of $f(n)$ is $0.000269414$. This gives the upper limit of prey-taxis parameter $T$ for periodic dynamics. Thus for $T < 0.000269414$, the predator–prey dynamics is periodic and the point of equilibrium is stable. It has been verified same way using Routh–Hurwitz conditions as described in the case of lower limit of $T$.

For $n = 4$, the value of $f(n)$ is maximum, i.e. the farthest one from zero. Thus $n = 4$ is the highest excited mode and the corresponding value of $f(n)$ is $0.000483096$. For $0.000269414 < T < 0.000483096$, the predator–prey dynamics is quasi-periodic. For $T > 0.000483096$, the predator–prey dynamics will be chaotic.

Hence

- for $-0.000269414 < T < 0.000269414$, the predator–prey dynamics is periodic and the point of equilibrium is stable.

- for $-0.000483096 < T < -0.000269414$ or $0.000269414 < T < 0.000483096$, the predator–prey dynamics is quasi-periodic.

- for $T < -0.000483096$ or $T > 0.000483096$, the predator–prey dynamics is chaotic.
Figure 4.3: Limits of $T$ for response function (b) with Data 1.

**Case 1b**

Similarly, in the case of response function (b) with Data 1, the point of equilibrium is $(u^*, v^*, 0) = (20.19, 4.49, 0)$. The values of $a_{11}, a_{12}$ etc are obtained from equation (3.22) as $a_{11} = 0.1203, a_{12} = -2.1286, a_{21} = 0.1709$ and $a_{22} = -0.0174$.

**Lower limit of $T$**

In order to find the lower limit of $T$ for which the predator–prey dynamics is periodic, known values of $a_{11}$ etc are substituted in condition (4.13) to obtain

$$g(n) = -0.000783237 + \frac{0.00157804}{n^2} + 0.0001243n^2 - 3.186 \times 10^{-9}n^4.$$  

Here also $n = 2$ is the first excited mode, as shown in Figure 4.3, and the corresponding value of $g(n)$ is $-0.000339061$. Thus for $T > -0.000339061$, the predator–prey dynamics is periodic as shown in Table 4.2 and the point of equilibrium is stable.

From Figure 4.3, it can be seen that $n = 3$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.000496294$. For $-0.000496294 < T < -0.000339061$, the predator–prey dynamics is quasi-periodic. For $T < -0.000496294$, the predator–prey dynamics is chaotic.

**Upper limit of $T$**

In order to find the upper limit of $T$, substitutions of known values of $a_{11}$ etc in condition (4.17) give
Here also \( n = 2 \) is the first excited mode, as shown in Figure 4.3, and the corresponding value of \( f(n) \) is 0.000339061. Thus for \( T < 0.000339061 \), the predator–prey dynamics is periodic and the point of equilibrium is stable. From Figure 4.3, it can be seen that \( n = 3 \) is the highest excited mode and the corresponding value of \( f(n) \) is 0.000496294. For 0.000339061 < \( T < 0.000496294 \), the predator–prey dynamics is quasi-periodic. For \( T > 0.000496294 \), the predator–prey dynamics is chaotic.

Hence

- for \(-0.000339061 < T < 0.000339061\), the predator–prey dynamics is periodic and the point of equilibrium is stable.
- for \(-0.000496294 < T < -0.000339061 \) or \( 0.000339061 < T < 0.000496294 \), the predator–prey dynamics is quasi-periodic.
- for \( T < -0.000496294 \) or \( T > 0.000496294 \), the predator–prey dynamics is chaotic.

**Case 1c**

In the case of response function (c) with Data 1, as in Cases 1a and 1b, the point of equilibrium is \((u^*, v^*, 0) = (71.97, 5.62, 0)\). The values of \( a_{11}, a_{12} \) etc are obtained from equation (3.23) as \( a_{11} = -0.299, a_{12} = -1.378, a_{21} = 0.026 \) and \( a_{22} = -0.558 \).

**Lower limit of \( T \)**

In order to find the lower limit of \( T \) for which the predator–prey dynamics is periodic, known values of \( a_{11} \) etc are substituted in condition (4.13) to obtain

\[
g(n) = -0.00118624 - \frac{0.00970813}{n^2} - 0.000382774n^2 - 0.393156 \times 10^{-9}n^4.
\]
Figure 4.4: Limits of $T$ for response function (c) with Data 1.

Here $n = 4$ is the first excited mode, as shown in Figure 4.4, and the corresponding value of $g(n)$ is $-0.00236707$. Thus for $T > -0.00236707$, the predator–prey dynamics is periodic as shown in Table 4.3 and the point of equilibrium is stable.

From Figure 4.4, it can be seen that $n = 1$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.0103026$. For $-0.0103026 < T < -0.00236707$, the predator–prey dynamics is quasi-periodic. For $T < -0.0103026$, the predator–prey dynamics is chaotic.

Upper limit of $T$

In order to find the upper limit of $T$, substitutions of known values of $a_{11}$ etc in condition (4.17) give

$$f(n) = 0.00118624 + \frac{0.00970813}{n^2} + 0.000382774n^2 + 0.393156 \times 10^{-9}n^4.$$

Here $n = 4$ is the first excited mode, as shown in Figure 4.4, and the corresponding value of $f(n)$ is $0.00236707$. Thus for $T > 0.00236707$, the predator–prey dynamics is periodic and the point of equilibrium is stable.

From Figure 4.4, it can be seen that $n = 1$ is the highest excited mode and the corresponding value of $f(n)$ is $0.0103026$. For $0.00236707 < T < 0.0103026$, the predator–prey dynamics is quasi-periodic. For $T < 0.0103026$, the predator–prey dynamics is chaotic.

Hence

- for $-0.00236707 < T < 0.00236707$, the predator–prey dynamics is periodic
Figure 4.5: Limits of $T$ for response function (a) with Data 2.

and the point of equilibrium is stable.

- for $-0.0103026 < T < -0.00236707$ or $0.00236707 < T < 0.0103026$, the predator–prey dynamics is quasi-periodic.

- for $T < -0.0103026$ or $T > 0.0103026$, the predator–prey dynamics is chaotic.

**Case 2a**

In the case of response function (a) with Data 2, the point of equilibrium is $(u^*, v^*, 0) = (19.6, 4.49, 0)$. The values of $a_{11}, a_{12}$ etc are $a_{11} = 0.118, a_{12} = -2.105, a_{21} = 0.187$ and $a_{22} = 0.0$.

**Lower limit of $T$**

In order to find the lower limit of $T$ for which the predator–prey dynamics is periodic, known values of $a_{11}$ etc are substituted in condition (4.13) to obtain

$$g(n) = -0.000865255 + \frac{0.0019981}{n^2} + 0.0000123391n^2 - 3.22174 \times 10^{-9}n^4.$$  

As in Case 1a, here also $n = 2$ is the first excited mode, as shown in Figure 4.5, and the corresponding value of $g(n)$ is $-0.000316425$. Thus for $T > -0.000316425$, the predator–prey dynamics is periodic as shown in Table 4.4 and the point of equilibrium is stable.

From Figure 4.5, it can be seen that $n = 4$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.000543774$. For $-0.000543774 < T <
−0.000316425, the predator–prey dynamics is quasi-periodic. For $T < -0.000543774$, the predator–prey dynamics is chaotic.

**Upper limit of $T$**

In order to find out the upper limit of $T$, substitutions of known values of $a_{11}$ etc in condition (4.17) give

$$f(n) = 0.000865255 - \frac{0.0019981}{n^2} - 0.0000123391n^2 + 3.22174 \times 10^{-9}n^4.$$  

As in Case 1a, here also $n = 2$ is the first excited mode, as shown in Figure 4.5, and the corresponding value of $f(n)$ is 0.000316425. Thus for $T < 0.000316425$, the predator–prey dynamics is periodic and the point of equilibrium is stable.

From Figure 4.5, it can be seen that $n = 4$ is the highest excited mode and the corresponding value of $f(n)$ is 0.000543774. For 0.000316425 < $T < 0.000543774$, the predator–prey dynamics is quasi-periodic. For $T > 0.000543774$, the predator–prey dynamics is chaotic.

Hence

- for $-0.000316425 < T < 0.000316425$, the predator–prey dynamics is periodic and the point of equilibrium is stable.
- for $-0.000543774 < T < -0.000316425$ or $0.000316425 < T < 0.000543774$, the predator–prey dynamics is quasi-periodic.
- for $T < -0.000543774$ or $T > 0.000543774$, the predator–prey dynamics is chaotic.

**Case 2b**

In the case of response function (b) with Data 2, the point of equilibrium is $(u^*, v^*, 0) = (20.03, 4.57, 0)$. The values of $a_{11}, a_{12}$ etc are $a_{11} = 0.114, a_{12} = -2.082, a_{21} = 0.186$ and $a_{22} = -0.018$. 

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Figure 4.6: Limits of $T$ for response function (b) with Data 2.

**Lower limit of $T$**

In order to find the lower limit of $T$ for which the predator–prey dynamics is periodic, known values of $a_{11}$ etc are substituted in condition (4.13) to obtain

$$g(n) = -0.000836445 + \frac{0.00158698}{n^2} + 0.0000118659n^2 - 3.20449 \times 10^{-9}n^4.$$  

As in Case 1b, here also $n = 2$ is the first excited mode, as shown in Figure 4.6, and the corresponding value of $g(n)$ is $-0.000392311$. Thus for $T > -0.000392311$, the predator–prey dynamics is periodic as shown in Table 4.4 and the point of equilibrium is stable.

From Figure 4.6, it can be seen that $n = 3$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.000553591$. For $-0.000553591 < T < -0.000392311$, the predator–prey dynamics is quasi-periodic. For $T < -0.000553591$, the predator–prey dynamics is chaotic.

**Upper limit of $T$**

In order to find the upper limit of $T$, substitutions of known values of $a_{11}$ etc in condition (4.17) give

$$f(n) = 0.000836445 - \frac{0.00158698}{n^2} - 0.0000118659n^2 + 3.20449 \times 10^{-9}n^4.$$  

As in Case 1b, here also $n = 2$ is the first excited mode, as shown in Figure 4.6, and the corresponding value of $f(n)$ is $0.000392311$. Thus for $T < 0.000392311$, 

63
the predator–prey dynamics is periodic and the point of equilibrium is stable.

From Figure 4.6, it can be seen that $n = 3$ is the highest excited mode and the corresponding value of $f(n)$ is $0.000553591$. For $0.000392311 < T < 0.000553591$, the predator–prey dynamics is quasi-periodic. For $T > 0.000553591$, the predator–prey dynamics is chaotic.

Hence

- for $-0.000392311 < T < 0.000392311$, the predator–prey dynamics is periodic and the point of equilibrium is stable.
- for $-0.000553591 < T < -0.000392311$ or $0.000392311 < T < 0.000553591$, the predator–prey dynamics is quasi-periodic.
- for $T < -0.000553591$ or $T > 0.000553591$, the predator–prey dynamics is chaotic.

**Case 2c**

In the case of response function (c) with Data 2, the point of equilibrium is $(u^*, v^*, 0) = (70.92, 5.88, 0)$. The values of $a_{11}, a_{12}$ etc are $a_{11} = -0.29, a_{12} = -1.326, a_{21} = 0.0298$ and $a_{22} = -0.592$.

**Lower limit of $T$**

In order to find the lower limit of $T$ for which the predator–prey dynamics is periodic, known values of $a_{11}$ etc are substituted in condition (4.13) to obtain

$$g(n) = -0.00120082 - \frac{0.00969961}{n^2} - 0.0000368923n^2 - 3.90839 \times 10^{-9}n^4.$$

Here $n = 4$ is the first excited mode, as shown in Figure 4.7, and the corresponding value of $g(n)$ is $-0.00239832$. Thus for $T > -0.00239832$, the predator–prey dynamics is periodic as shown in Table 4.5 and the point of equilibrium is stable.

From Figure 4.7, it can be seen that $n = 1$ is the highest excited mode and the corresponding value of $g(n)$ is $-0.0109373$. For $-0.0109373 < T < -0.00239832$, the predator–prey dynamics is quasi-periodic. For $T < -0.0109373$, the predator–prey dynamics is chaotic.
Figure 4.7: Limits of $T$ for response function (c) with Data 2.

Upper limit of $T$

In order to find the upper limit of $T$, substitutions of known values of $a_{11}$ etc
in condition (4.17) give

$$f(n) = 0.00120082 + \frac{0.00969961}{n^2} + 0.0000368923n^2 + 3.90839 \times 10^{-9}n^4.$$  

Here $n = 4$ is the first excited mode, as shown in Figure 4.7, and the corresponding value of $f(n)$ is 0.00239832. Thus for $T < 0.00239832$, the predator–prey dynamics is periodic and the point of equilibrium is stable.

From Figure 4.7, it can also be seen that $n = 1$ is the highest excited mode and
the corresponding value of $f(n)$ is 0.0109373. For $0.00239832 < T < 0.0109373$, the predator–prey dynamics is quasi-periodic. For $T > 0.0109373$, the predator–prey dynamics is chaotic.

Hence

- for $-0.00239832 < T < 0.00239832$, the predator–prey dynamics is periodic
  and the point of equilibrium is stable.
- for $-0.0109373 < T < -0.00239832$ or $0.00239832 < T < 0.0109373$, the predator–prey dynamics is quasi-periodic.
- for $T < -0.0109373$ or $T > 0.0109373$, the predator–prey dynamics is chaotic.
4.7 Numerical solutions

In order to verify graphically the various states of equilibrium, predator–prey-taxis equations (4.1)–(4.3) have been solved numerically using Data 1 and Data 2 for response functions (a)–(c) with three different values of $T$, obtained from the limits determined in section 4.6, along with initial conditions (i) and (ii). The time sequences continue for $t = 75$ weeks. In all the cases, phase–plane graphs of both prey and predator dynamics $u$ and $v$ have been shown at $x = 0.5$. Stabilities of equilibria with prey-taxis and diffusion along with different values of $T$ have been investigated using Routh–Hurwitz conditions (4.10)–(4.12) and are given in Tables 4.2–4.5 respectively.

Case 1a

Figure 4.8 shows the outputs for Data 1 with response function (a) along with two initial conditions and different values of the prey-taxis $T$.

In the case of initial condition (i), phase–plane graphs of both prey population density $u$ and predator population density $v$ with $T = -0.0001, -0.0004$ and $-0.0006$ have been shown in Figure 4.8.

At $T = -0.0001$, both prey population density $u$ and predator population
density \( v \) produce regular oscillations till 75 weeks. This is reflected in the corresponding phase–plane graph shown in Figure 4.8. In this case, the predator–prey dynamics produces limit cycle, thus, displays periodic nature of solutions. When the value of \( T \) is lowered to \(-0.0004\), each pulse of \( u \) and \( v \) becomes slightly wider than the previous one. This behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.8. As the value of \( T \) is further decreased to \(-0.0006\), chaotic dynamics develops after 60 weeks.

In the case of initial condition (ii), phase–plane graphs of both \( u \) and \( v \) with \( T = -0.00005, -0.0003 \) and \(-0.00051\) have been shown in Figure 4.8.

At \( T = -0.00005\), the first pulse of \( u \) is wider than the others as shown in Figure 4.8. Also the amplitude of the first pulse is slightly greater than the other pulses. All other pulses have the same width as shown in Figure 4.8. This behaviour is reflected in the corresponding phase–plane graph displaying periodic nature of solutions as shown in Figure 4.8. As the value of \( T \) is lowered to \(-0.0003\), quasi-periodic dynamics develops as shown in Figure 4.8. In this case also each pulse of \( u \) and \( v \) is slightly wider than the previous one. When the value of \( T \) is further lowered to \(-0.00051\), chaotic dynamics develops after approximately 38 weeks.

Case 1b

Figure 4.9 shows the outputs for Data 1 with response function (b) along with two initial conditions and different values of the prey-taxis \( T \).

In the case of initial condition (i), phase–plane graphs of both \( u \) and \( v \) with \( T = -0.0002, -0.00045 \) and \(-0.0006\) have been shown in Figure 4.9.

At \( T = -0.0002\), both \( u \) and \( v \) produce regular oscillations till 75 weeks. This is reflected in the corresponding phase–plane graph shown in Figure 4.9. In this case, the predator–prey dynamics produces limit cycle, thus, displays periodic nature of solutions. When the value of \( T \) is lowered to \(-0.00045\), each pulse of \( u \) and \( v \) becomes slightly wider than the previous one. This behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.9. As the value of \( T \) is further decreased to \(-0.0006\), chaotic dynamics develops after approximately 55 days.
In the case of initial condition (ii), phase–plane graphs of both $u$ and $v$ with $T = -0.0001, -0.00035$ and $-0.00052$ have been shown in Figure 4.9. At $T = -0.0001$, the first pulse of prey population density $u$ is wider than others as shown in Figure 4.9. Also the maximum amplitude of the first pulse is higher than that of others. All other pulses have the same width and this behaviour is reflected in the corresponding phase–plane graph displaying periodic nature of solutions as shown in Figure 4.9. As the value of $T$ is lowered from $-0.0001$ to $-0.00035$, quasi-periodic dynamics develops as shown in Figure 4.9. In this case also each pulse of $u$ and $v$ is slightly wider than the previous one. When the value of $T$ is further lowered to $-0.00052$, chaotic dynamics develops after 42 days.

**Case 1c**

Figure 4.10 shows the outputs for Data 1 with response function (c) along with two initial conditions and different values of prey-taxis $T$.

In the case of initial condition (i), phase–plane graphs of both $u$ and $v$ with $T = -0.001, -0.006$ and $-0.015$ have been shown in Figure 4.10. At $T = -0.001$, both $u$ and $v$ produce oscillations till 12 weeks. After that, both densities show steady values of 90 and 5.5 respectively till 75 weeks. This behaviour
Table 4.2: Characteristics of equilibria with prey-taxis for response functions (a), (b) with Data 1 and initial conditions (i), (ii)

<table>
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<th>Resp. Func.</th>
<th>Point of Equilibrium</th>
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<th>In. Cond.-ition</th>
<th>T</th>
<th>p(k^2)</th>
<th>q(k^2)</th>
<th>r(k^2)</th>
<th>p(k^2)</th>
<th>Stable/Unstable</th>
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<td>Periodic</td>
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<td>-ive</td>
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<td>Chaotic</td>
</tr>
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</table>

is reflected in the corresponding phase-plane graph shown in Figure 4.10. In this case, the dynamics of the predator–prey system is a stable spiral. When the value of $T$ is lowered to $-0.006$, steady behaviours of $u$ and $v$ after 12 weeks are disturbed and this behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.10. As the value of $T$ is
Figure 4.10: Phase–plane graphs for Data 1 with response function (c).

further decreased to $-0.015$, chaotic dynamics develops after approximately 30 weeks. See Appendix for further detail.

In the case of initial condition (ii), phase–plane graphs of both $u$ and $v$ with $T = -0.0008$, $-0.003$ and $-0.012$ have been shown in Figure 4.10.

At $T = -0.0008$, both $u$ and $v$ produce oscillations till 20 weeks. After that, both densities show steady values of 90 and 6 respectively till 75 weeks. This behaviour is reflected in the corresponding phase–plane graph shown in Figure 4.10. When the value of $T$ is lowered to $-0.003$, steady behaviours of $u$ and $v$ after 20 weeks are disturbed and this behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.10. As the value of $T$ is further decreased to $-0.012$, chaotic dynamics develops after approximately 10 weeks. At $T = -0.012$, the maximum value of $u$ becomes 100, the carrying capacity of prey. See Appendix for further detail.

Case 2a

Figure 4.11 shows the outputs for Data 2 with response function (a) along with two initial conditions and different values of the prey-taxis $T$.

In the case of initial condition (i), phase–plane graphs of both prey popula-
Figure 4.11: Phase-plane graphs for Data 2 with response function (a).

Table 4.3: Characteristics of equilibria with prey-taxis for response function (c) with Data 1 and initial conditions (i), (ii)

<table>
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<th>Point of Equilibrium</th>
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<th>q(k²)</th>
<th>r(k²)</th>
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<tr>
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</tr>
</tbody>
</table>
tion density $u$ and predator population density $v$ with $T = -0.0002$, $-0.0005$ and $-0.00065$ have been shown in Figure 4.11.

At $T = -0.0002$, both $u$ and predator population density $v$ produce regular oscillations till 75 weeks. This is reflected in the corresponding phase–plane graph shown in Figure 4.11. In this case, the predator–prey dynamics produces limit cycle, thus, displays periodic nature of solutions. When the value of $T$ is lowered to $-0.0005$, each pulse of $u$ and $v$ becomes slightly wider than the previous one. This behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.11. As the value of $T$ is further decreased to $-0.00065$, chaotic dynamics develops after approximately 60 days.

In the case of initial condition (ii), phase–plane graphs of both $u$ and $v$ with $T = -0.0001$, $-0.0004$ and $-0.0006$ have been shown in Figure 4.11.

At $T = -0.0001$, both $u$ and $v$ produce regular oscillations till 75 weeks. The first pulse of prey population density $u$ is wider than others as shown in Figure 4.11. Also the maximum amplitude of the first pulse is higher than that of others. All other pulses have the same width. This behaviour is reflected in the corresponding phase–plane graph displaying periodic nature of solutions as shown in Figure 4.11. As the value of $T$ is lowered from $-0.0001$ to $-0.0004$, quasi-periodic dynamics develops as shown in Figure 4.11. When the value of $T$ is further lowered to $-0.0006$, chaotic dynamics develops after approximately 38 days.

**Case 2b**

Figure 4.12 shows the outputs for Data 2 with response function (b) along with two initial conditions and different values of the prey-taxis $T$.

In the case of initial condition (i), phase–plane graphs of both $u$ and $v$ with $T = -0.00025$, $-0.00045$ and $-0.00065$ have been shown in Figure 4.12.

At $T = -0.00025$, both $u$ and $v$ produce regular oscillations till 75 weeks. This is reflected in the corresponding phase–plane graph shown in Figure 4.12. In this case, the predator–prey dynamics produces limit cycle, thus, displays periodic nature of solutions. When the value of $T$ is lowered to $-0.00045$, each pulse of $u$ and $v$ becomes slightly wider. This behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.12.
As the value of $T$ is further decreased to $-0.00065$, chaotic dynamics develops after approximately 55 days.

In the case of initial condition (ii), phase–plane graphs of both $u$ and $v$ with $T = -0.00008, -0.00045$ and $-0.00057$ have been shown in Figure 4.12.

At $T = -0.00008$, the first pulse of $u$ is wider than others as shown in Figure 4.12. Also the maximum amplitude of the first pulse is higher than that of others. All other pulses have the same width as shown in Figure 4.12. This behaviour is reflected in the corresponding phase–plane graph displaying periodic nature of solutions as shown in Figure 4.12. As the value of $T$ is lowered from $-0.00008$ to $-0.00045$, quasi-periodic dynamics develops as shown in Figure 4.12. When the value of $T$ is further lowered to $-0.00057$, chaotic dynamics develops after approximately 38 days.

**Case 2c**

Figure 4.13 shows the outputs for Data 2 with response function (c) along with two initial conditions and different values of the prey-taxis $T$.

In the case of initial condition (i), phase–plane graphs of both $u$ and $v$ with $T = -0.001, -0.006$ and $-0.02$ have been shown in Figure 4.13.
Table 4.4: Characteristics of equilibria with prey-taxis for response functions (a),
(b) with Data 2 and initial conditions (i), (ii)

<table>
<thead>
<tr>
<th>Resp. Func.</th>
<th>Point of Equilibrium</th>
<th>(n)</th>
<th>In. Cond.-ition</th>
<th>(T)</th>
<th>(p(k^2))</th>
<th>(q(k^2))</th>
<th>(r(k^2))</th>
<th>(p(k^2))</th>
<th>(q(k^2))</th>
<th>(-r(k^2))</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>(19.6, 4.49, 0)</td>
<td>2</td>
<td>(i)</td>
<td>-0.0002</td>
<td>0.079</td>
<td>0.372</td>
<td>0.019</td>
<td>0.0104</td>
<td>Stable</td>
<td>Periodic</td>
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<td></td>
<td></td>
<td></td>
<td>-0.0005</td>
<td>0.079</td>
<td>0.372</td>
<td>0.047</td>
<td>-0.018</td>
<td>Unstable</td>
<td>Quasi – periodic</td>
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<td></td>
<td></td>
<td>-0.0006</td>
<td>0.079</td>
<td>0.372</td>
<td>0.061</td>
<td>-0.032</td>
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<td>Chaotic</td>
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<td></td>
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<tr>
<td>(ii)</td>
<td>(20.03, 4.57, 0)</td>
<td>2</td>
<td>(i)</td>
<td>-0.0001</td>
<td>0.079</td>
<td>0.372</td>
<td>0.009</td>
<td>0.0204</td>
<td>Stable</td>
<td>Periodic</td>
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<td>-0.0004</td>
<td>0.079</td>
<td>0.372</td>
<td>0.0373</td>
<td>-0.008</td>
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<td>Quasi – periodic</td>
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<td></td>
<td>-0.0006</td>
<td>0.079</td>
<td>0.372</td>
<td>0.056</td>
<td>-0.027</td>
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<td>Chaotic</td>
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<tr>
<td>(b)</td>
<td>(20.03, 4.57, 0)</td>
<td>2</td>
<td>(i)</td>
<td>-0.00025</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.0234</td>
<td>0.0134</td>
<td>Stable</td>
<td>Periodic</td>
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<td></td>
<td>-0.00045</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.0422</td>
<td>-0.005</td>
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<td>Quasi – periodic</td>
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<td></td>
<td>-0.00065</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.061</td>
<td>-0.024</td>
<td>Unstable</td>
<td>Chaotic</td>
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<td>(ii)</td>
<td>(20.03, 4.57, 0)</td>
<td>2</td>
<td>(i)</td>
<td>-0.00008</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.0075</td>
<td>0.0293</td>
<td>Stable</td>
<td>Periodic</td>
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<td></td>
<td>-0.00045</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.0422</td>
<td>-0.0053</td>
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<td></td>
<td></td>
<td>-0.00057</td>
<td>0.1012</td>
<td>0.364</td>
<td>0.0535</td>
<td>-0.0167</td>
<td>Unstable</td>
<td>Chaotic</td>
<td></td>
</tr>
</tbody>
</table>

At \(T = -0.001\), both \(u\) and \(v\) produce oscillations till 15 weeks. After that,
both densities show steady values of 90 and 6 respectively till 75 weeks. This
behaviour is reflected in the corresponding phase–plane graph shown in Figure 4.13.
In this case, the predator–prey dynamics produces spiral. When the value of \(T\) is
lowered to \(-0.006\), steady behaviours of \(u\) and \(v\) after 15 weeks are disturbed. This
behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.13. As the value of $T$ is further decreased to $-0.02$, chaotic dynamics develops after approximately 30 weeks.

In the case of initial condition (ii), phase–plane graphs of both $u$ and $v$ with $T = -0.0008, -0.0041$ and $-0.015$ have been shown in Figure 4.13.

At $T = -0.0008$, both $u$ and $v$ produce oscillations till 25 weeks. After that, both densities show steady values of 90 and 6 respectively till 75 weeks. This behaviour is reflected in the corresponding phase–plane graph shown in Figure 4.13. When the value of $T$ is lowered to $-0.0041$, steady behaviours of $u$ and $v$ after 20 weeks are disturbed. This behaviour is reflected in the corresponding phase–plane graph displaying quasi-periodic nature of solutions as shown in Figure 4.13. As the value of $T$ is further decreased to $-0.015$, chaotic dynamics develops after approximately 10 weeks. See Appendix for further detail.

The corresponding time-dependent graphs for all the cases considered in this section have been given in Appendix for clarification.
Table 4.5: Characteristics of equilibria with prey-taxis for response function (c) with Data 2 and initial conditions (i), (ii)

<table>
<thead>
<tr>
<th>Point of Equilibrium</th>
<th>n</th>
<th>In. Cond.</th>
<th>$T$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>(70.92,5.88,0)</td>
<td>4</td>
<td>(i)</td>
<td>−0.001</td>
<td>1.672</td>
<td>0.441</td>
<td>0.308</td>
<td>0.4295</td>
<td>Stable</td>
<td></td>
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<td></td>
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<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>Periodic</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>−0.006</td>
<td>1.672</td>
<td>0.441</td>
<td>1.846</td>
<td>−1.109</td>
<td>Unstable</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>−ive</td>
<td>Quasi–periodic</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>−0.02</td>
<td>1.672</td>
<td>0.441</td>
<td>1.538</td>
<td>−5.416</td>
<td>Unstable</td>
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<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>−ive</td>
<td>Chaotic</td>
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<tr>
<td></td>
<td>(ii)</td>
<td></td>
<td>−0.0008</td>
<td>1.672</td>
<td>0.441</td>
<td>0.246</td>
<td>0.491</td>
<td>Stable</td>
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<td>+ive</td>
<td>+ive</td>
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<td>+ive</td>
<td>Periodic</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>−0.0041</td>
<td>1.672</td>
<td>0.441</td>
<td>1.261</td>
<td>−0.524</td>
<td>Unstable</td>
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<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>−ive</td>
<td>Quasi–periodic</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>−0.015</td>
<td>1.672</td>
<td>0.441</td>
<td>4.615</td>
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<td>Unstable</td>
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<td>+ive</td>
<td>−ive</td>
<td>Chaotic</td>
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</tbody>
</table>

4.8 Discussion and conclusion

In this chapter, Lotka–Volterra logistic predator–prey-taxis equations (4.1)–(4.3) with $P. persimilis$ as the predator and $T. urticae$ as the prey have been considered along with three response functions, two data sets and two initial conditions.

First of all, characteristics of equilibria without prey-taxis and diffusion have been obtained as shown in Table 4.1. Both response functions (a) and (b) have unstable points of equilibria while response function (c) has a stable point of equilibrium as shown in Table 4.1.

Using Routh–Hurwitz conditions described in section 4.5, limits of prey-taxis $T$ have been obtained corresponding to each data set and response function for which the predator–prey dynamics is periodic, quasi-periodic or chaotic. Based on limits of $T$, results have further been verified numerically in section 4.7.

It has been seen that response function (a) with the same data set and different initial conditions (i) and (ii) produces different form of predator–prey dynamics as shown in Figures 4.8 and 4.11. Similar situations arise with response functions (b)
and (c) as can be seen in Figures 4.9, 4.12, 4.10 and 4.13.

This fact is further established with the appearance of similar graphs for a particular initial condition as shown in Figures 4.8, 4.9, 4.11 and 4.12. However, there is an exception in the case of response function (c) as shown in Figures 4.10 and 4.13. Thus it can be said that initial conditions play an important role to produce different forms of predator-prey dynamics.

It has been observed that in the case of response function (c), for a low value of prey-taxis, the nature of solution is spiral as shown in Figures 4.10 and 4.13 whereas in the cases of both response functions (a) and (b), solutions produce limit cycles as shown in Figures 4.8, 4.9, 4.11 and 4.12 respectively. This may be because, in the absence of prey-taxis, response function (c) has a stable point of equilibrium and the nature of the solution is spiral as shown in Table 4.1. Thus response functions have an effect on the nature of predator-prey dynamics.

It has been shown that with the inclusion of prey-taxis in a predator-prey system, it is possible to achieve three different states of equilibrium – periodic, quasi-periodic and chaotic whereas without prey-taxis only a particular state of equilibrium can be achieved. Thus it is concluded that prey-taxis has an important role in the equilibrium state of a predator-prey system. It can change the state of equilibrium from periodic to quasi-periodic or chaotic depending upon the sensitivity of predators to prey density.

In the next chapter formation of spatial patterns has been investigated with the introduction of both prey-taxis and diffusion in predator velocity in the predator-prey system.
Chapter 5

Spatial Patterns Generated by Prey-Taxis

5.1 Introduction

Spatial patterns in a predator–prey system can only be generated from spatiotemporal heterogeneity in the system. There are two different ways to introduce spatial structures and the formation of spatial patterns in a predator–prey system (Sapoukhina et al. [139]). The first is to describe space explicitly either by continuous or discrete coordinates. The second is where different kinds of heterogeneities can be included implicitly into the response function (Czárán [37], Sapoukhina et al. [139]). Response function dependent on both prey and predator can explain many spatial patterns observed in nature (Hassell and Varley [71], Hassell and May [69], Beddington [9], DeAngelis et al. [39]). Arditi and Ginzburg [3] have shown that spatial patterns generated by predators in a heterogeneous environment can only be explained by ratio-dependent response function. This was later confirmed by Poiggale et al. [133], Cosner et al. [35] and Arditi et al. [5] and also experimentally by Arditi and Saïah [4]. Even though this model explains real scenario, it fails to explain the spatial patterns on longer time-scale system (Sapoukhina et al. [139]).

Like predator interference and relative diffusion, there is also another factor called ‘prey-taxis' that can introduce instability in the system. This instability
leads to the formation of spatial patterns in the domain. In order to explain spatial patterns on longer time-scale, Sapoukhina et al. [139] have introduced prey-taxis in the existing predator–prey system as detailed in chapter 3. They have shown that spatial patchiness can be generated from an intrinsic source like prey-taxis. In their model, the spatial dynamics of the interacting populations show constantly moving density patches. This fits well with field observations as shown by Winder et al. [160]. Winder et al. [160] have found that the increase of ladybird (predator) activity is related positively to the degree of aphid (prey) clustering into patches, independent of the aphid abundance. According to Sapoukhina et al. [139], “predators respond to the heterogeneity of the prey density by accelerating toward the localities where prey are abundant, resulting in predator aggregation. When reaching a local maximum of prey concentration, predators decelerate because the prey gradient reverses. Predator aggregations lead to local prey extinctions, while patches with low predator densities play the role of partial refuges where prey densities grow. Then predators move actively to the newly formed prey clusters. In sum, this spatially explicit model is able to capture various kinds of heterogeneity that are liable to promote the persistence of predator–prey interactions (Hassell and Anderson [68]). Stability is known to be often bought at the expense of increased pest density (Briggs et al. [20]). For instance, a diffusion-limited mechanism, decreasing reproduction and predation rates because of limited individual mobility reduces the magnitude of oscillations of population densities, while the prey density tends to its carrying capacity (Cuddington and Yodzis [36]).”

Again according to Sapoukhina et al. [139] “the proposed model overcomes an existing controversy in the interpretation of the role of spatial activity of natural enemies in pest population depression and regulation. On the one hand, the model demonstrates that a natural enemy with a pronounced aggregated attack depresses the pest density to a very low level on which, furthermore, it can persist because of the emergence of a spatially heterogeneous regime. This confirms the major conclusion that aggregation is the key to stability and successful control (Hassell and May [69, 70], May [105]). On the other hand, Murdoch and Stewart-Oaten [114] had pointed out that the stabilizing effect of aggregation largely disappeared when
the natural enemy was allowed to redistribute within a generation. They concluded that aggregation is typically a destabilizing process. Also, studying the effect of habitat fragmentation on the stability of predator–prey interactions, Kareiva [79] emphasized that patchiness promoted aphid outbreaks because it interfered with the non random searching behavior of ladybird predators”.

The aim in this chapter is to investigate the formation of spatial patterns for longer time with the inclusion of prey-taxis and diffusion in predator velocity in the predator–prey system. In view of that, a particular value of prey-taxis $T$ is chosen from section 4.6 for which the predator–prey dynamics is quasi-periodic and the point of equilibrium is unstable. Using that value of $T$, bifurcation value of diffusion in predator velocity $d_3$ has been obtained. Next, with a value of $d_3$ and $T$, for which the point of equilibrium is unstable, the predator–prey-taxis equations have been solved numerically to determine the nature of spatial patterns. The entire study is based on two non-homogeneous initial conditions and three different response functions along with two data sets given in chapters 3 and 4 respectively.

### 5.2 Mathematical model

In one-dimensional form the predator–prey-taxis equations (Arditi et al. [5], Harrison [65], Sapoukhina et al. [139], Chakraborty et al. [30]) are written as:

\[
\frac{\partial u}{\partial t} = \rho (1 - \frac{u}{K}) u - e f(u, v) v + d_1 \frac{\partial^2 u}{\partial x^2}, \quad (5.1)
\]

\[
\frac{\partial v}{\partial t} = -\gamma v + \sigma f(u, v) v - \frac{\partial (v w)}{\partial x} + d_2 \frac{\partial^2 v}{\partial x^2}, \quad (5.2)
\]

\[
\frac{\partial w}{\partial t} = T \frac{\partial u}{\partial x} + d_3 \frac{\partial^2 w}{\partial x^2}, \quad (5.3)
\]

where all the symbols have their usual meanings as defined in chapter 3.

### 5.3 Response functions

The same response functions as used in chapter 3 have also been used here. Data 1 and Data 2 obtained in section 3.9 have been used here. The predator interference
parameter $\beta = 0.1$, carrying capacity parameter $K = 100$, specific prey growth rate parameter $\rho = 0.6$, diffusivity constant of prey and predator population densities $d_1 = 0.0000125$ and $d_2 = 0.02$ have not been changed throughout this study. Different non-zero values of the prey-taxis parameter $T$ and diffusivity constant of predator velocity $d_3$ have been used in order to investigate the formation of spatial patterns of both prey and predator population densities.

Hence the two data sets are:

(Data 1) $\phi = 19.409, \quad \gamma = 1.55, \quad \sigma = 3.0744, \quad e = 4.27,$

(Data 2) $\phi = 20.524, \quad \gamma = 1.60, \quad \sigma = 3.2756, \quad e = 4.31.$

Initial conditions (i) and (ii), already used in chapter 4, have also been used here. The numerical scheme of the operator splitting method and the boundary conditions of zero flux as used in chapter 3 have also been used here.

### 5.4 Stability of equilibria with prey-taxis and diffusion

Routh–Hurwitz stability conditions (4.7)–(4.9) have been re-written here as:

\[
p(k^2) > 0, \quad (5.4)
\]
\[
r(k^2) > 0, \quad (5.5)
\]
\[
p(k^2)q(k^2) - r(k^2) > 0. \quad (5.6)
\]

where

\[
p(k^2) = k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22}), \quad (5.7)
\]
\[
g(k^2) = k^4(d_1d_2 + d_2d_3 + d_3d_1) - c_1k^2 + c_2, \quad (5.8)
\]
\[
r(k^2) = k^2(d_1d_2d_3k^4 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3
\]
\[
+ a_{12}v^*T + a_{11}a_{22}d_3 - a_{22}d_1d_3k^2). \quad (5.9)
\]
Here $c_1$ and $c_2$ are given as

\[ c_1 = (a_{11}d_2 + a_{22}d_1 + a_{11}d_3 + a_{22}d_3), \quad (5.10) \]
\[ c_2 = (a_{11}a_{22} - a_{12}a_{21}). \quad (5.11) \]

Hence spatial patterns are generated if the equilibria are unstable and thus do not satisfy the above mentioned conditions (5.4)–(5.6).

### 5.4.1 Bifurcation value of diffusion in predator velocity, $d_3$

for a particular value of $T$

In order to achieve spatial patterns with prey-taxis $T$ and diffusivity in predator velocity $d_3$, the point of equilibrium has to be unstable. In view of that, following steps have been used:

**Step 1**: The predator–prey-taxis equations (5.1)–(5.3) have been solved without diffusion, advection and prey-taxis to obtain the point of equilibrium $(u^*, v^*, 0)$.

**Step 2**: The values of $u^*$ and $v^*$ are substituted in equation (3.20) to obtain values of $a_{11}, a_{12}, a_{21}$ and $a_{22}$ respectively.

**Step 3**: A particular value of $T$ has been chosen from section 4.6, for which the predator–prey dynamics is quasi-periodic and the point of equilibrium is unstable.

**Step 4**: With that value of $T$, the values of $v^*$ along with $a_{11}, a_{12}$ etc have been substituted in condition (5.6) to obtain the expressions in terms of $d_3$. Solution of this equation in terms of $d_3$ gives the bifurcation value of $d_3$ as detailed below.

For response functions (a) and (b), the first excited mode is 2 as shown in section 4.6 and thus the value of $n$ is assumed to be 2. Similarly, for response function (c), the values of $n$ is assumed to be 4. The final value of $d_3$ has been chosen for each response function after working through a number of numerical solutions in order to achieve distinct/prominent spatial patterns (Chakraborty et al. [29]).

**Case 1a**

In the case of response function (a) with Data 1, the predator–prey-taxis equations (5.1)–(5.3) have been solved without diffusion, advection and prey-taxis to obtain the point of equilibrium as $(u^*, v^*, 0) = (19.73, 4.41, 0)$. The values of
Figure 5.1: Bifurcation value of diffusivity in predator velocity $d_3$ for response function (a) with Data 1 and Data 2.

$u^*, v^*$ are substituted in equation (3.21) to obtain the values of $a_{11}, a_{12}$ etc. as $a_{11} = 0.124, a_{12} = -2.153, a_{21} = 0.172$ and $a_{22} = 0$. Substituting the values of $v^*$ along with $a_{11}$ etc and prey-taxis coefficient $T = -0.0003$, condition (5.6) can be expressed in terms of $d_3$ as

$$ p(k^2)q(k^2) - r(k^2) = 7.12303(-0.016704 + d_3)(0.0241131 + d_3) \triangleq m(d_3). $$

The graph has been drawn for $m(d_3)$, with $d_3$ as an unknown parameter, as shown in Figure 5.1. For an unstable point of equilibrium, $m(d_3) < 0$. Thus $m(d_3) = 0$ gives the bifurcation value of $d_3$. For $m(d_3) = 0, d_3 = 0.017$. The other value of $d_3$, being negative, is neglected. Thus for any value of $d_3$ lower than the bifurcation value 0.017, the point of equilibrium is unstable as shown in Table 5.1. In the next section 5.5, $T$ and $d_3$ have been chosen to be $-0.0003$ and 0.01 respectively for numerical simulations.

**Case 1b**

Again as specified in section 4.6, in the case of response function (b) with Data 1, the point of equilibrium is $(u^*, v^*, 0) = (20.19, 4.49, 0)$. The values of $a_{11}, a_{12}$ etc are obtained from equation (3.22) as $a_{11} = 0.1203, a_{12} = -2.1286, a_{21} = 0.1709$ and $a_{22} = -0.0174$. Substituting all these values with prey-taxis coefficient $T = -0.00035$, condition (5.6) can be expressed in terms of $d_3$ as

$$ p(k^2)q(k^2) - r(k^2) = 9.2177(-0.0068 + d_3)(0.0164 + d_3) \triangleq m(d_3). $$

The graph has been drawn for $m(d_3)$, with $d_3$ as an unknown parameter, as
Figure 5.2: Bifurcation value of diffusivity in predator velocity $d_3$ for response function (b) with Data 1 and Data 2.

Figure 5.3: Bifurcation value of diffusivity in predator velocity $d_3$ for response function (c) with Data 1 and Data 2.

shown in Figure 5.2. For $m(d_3) = 0, d_3 = 0.007$ as shown in Figure 5.2. The other value of $d_3$, being negative, is neglected. Thus for any value of $d_3$ lower than the bifurcation value 0.007, the point of equilibrium is unstable as shown in Table 5.1.

In the next section 5.5, $T$ and $d_3$ have been chosen to be $-0.00035$ and $0.001$ respectively for numerical simulations.

**Case 1c**

Again as specified in section 4.6, in the case of response function (c) with Data 1, the point of equilibrium is $(u^*, v^*, 0) = (71.97, 5.62, 0)$. The values of $a_{11}, a_{12}$ etc are obtained from equation (3.23) as $a_{11} = -0.299, a_{12} = -1.378, a_{21} = 0.026$ and $a_{22} = -0.558$. Substituting all these values with prey-taxis coefficient $T = -0.003$, condition (5.6) can be expressed in terms of $d_3$ as

$$p(k^2)q(k^2) - r(k^2) = 2567.35(-0.001735 + d_3)(0.0435 + d_3) \triangleq m(d_3).$$

The graph has been drawn for $m(d_3)$, with $d_3$ as an unknown parameter, as
shown in Figure 5.3. For \(m(d_3) = 0, d_3 = 0.0017\) as shown in Figure 5.3. Thus for any value of \(d_3\) lower than the bifurcation value 0.0017, the point of equilibrium is unstable as shown in Table 5.1. In the next section 5.5, \(T\) and \(d_3\) have been chosen to be \(-0.003\) and \(0.001\) respectively for numerical simulations.

**Case 2a**

Again as specified in section 4.6, in the case of response function (a) with Data 2, the point of equilibrium is \((u^*, v^*, 0) = (19.6, 4.49, 0)\). The values of \(a_{11}, a_{12}\) etc are \(a_{11} = 0.118, a_{12} = -2.105, a_{21} = 0.187\) and \(a_{22} = 0.0\). Substituting all these values with prey-taxis coefficient \(T = -0.0005\), condition (5.6) can be expressed in terms of \(d_3\) as

\[
p(k^2)q(k^2) - r(k^2) = 7.74055(-0.0431882 + d_3)(0.0512396 + d_3) \triangleq m(d_3).
\]

For \(m(d_3) = 0, d_3 = 0.043\) as shown in Figure 5.1. Thus for any value of \(d_3\) lower than the bifurcation value 0.043, the point of equilibrium is unstable as shown in Table 5.1. In the next section 5.5, \(T\) and \(d_3\) have been chosen to be \(-0.0005\) and 0.015 respectively for numerical simulations.

**Case 2b**

Again as specified in section 4.6, in the case of response function (b) with Data 2, the point of equilibrium is \((u^*, v^*, 0) = (20.03, 4.57, 0)\). The values of \(a_{11}, a_{12}\) etc are \(a_{11} = 0.114, a_{12} = -2.082, a_{21} = 0.186\) and \(a_{22} = -0.018\). Substituting all these values with \(T = -0.00045\), condition (5.6) can be expressed in terms of \(d_3\) as

\[
p(k^2)q(k^2) - r(k^2) = 9.85483(-0.0188628 + d_3)(0.0291135 + d_3) \triangleq m(d_3).
\]

For \(m(d_3) = 0, d_3 = 0.019\) as shown in Figure 5.2. Thus for any value of \(d_3\) lower than the bifurcation value 0.019, the point of equilibrium is unstable as shown in Table 5.1. In the next section 5.5, \(T\) and \(d_3\) have been chosen to be \(-0.00045\) and 0.015 respectively for numerical simulations.

**Case 2c**

Again as specified in section 4.6, in the case of response function (c) with Data 2, the point of equilibrium is \((u^*, v^*, 0) = (70.92, 5.88, 0)\). The values of \(a_{11}, a_{12}\) etc
Figure 5.4: Transient graphs for response function (a), Data 1, initial condition (i) at $t = 0$ and 200.

are $a_{11} = -0.29, a_{12} = -1.326, a_{21} = 0.0298$ and $a_{22} = -0.592$. Substituting all these values with $T = -0.0041$, condition (5.6) can be expressed in terms of $d_3$ as

$$p(k^2)q(k^2) - r(k^2) = 2606.76(-0.0043 + d_3)(0.0467 + d_3) = m(d_3).$$

For $m(d_3) = 0, d_3 = 0.0043$ as shown in Figure 5.3. Thus for any value of $d_3$ lower than the bifurcation value 0.0043, the point of equilibrium is unstable as shown in Table 5.1. In the next section 5.5, $T$ and $d_3$ have been chosen to be $-0.0041$ and 0.001 respectively for numerical simulations.

### 5.5 Numerical solutions

Lotka–Volterra logistic predator–prey–taxis equations (5.1)–(5.3) have been solved numerically for different values of $T$ and $d_3$ obtained in section 5.4 for Data 1, Data 2 and response functions (a)–(c). Transient graphs have been produced with each of the initial conditions (i) and (ii) for $t = 200$. 

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Table 5.1: Bifurcation value of diffusivity in predator velocity, $d_3$, for Data 1 and Data 2 with response functions (a)–(c)

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp. func.</th>
<th>$T$</th>
<th>$d_3$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>$p(k^2).q(k^2)$</th>
<th>$-r(k^2)$</th>
<th>Stable/Unstable</th>
</tr>
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<tr>
<td>1 (a)</td>
<td>$-0.0003$</td>
<td>0.018</td>
<td>0.251</td>
<td>0.358</td>
<td>0.033</td>
<td>0.0008</td>
<td>Stable</td>
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<td>0.016</td>
<td>0.231</td>
<td>0.357</td>
<td>0.083</td>
<td>0.0005</td>
<td>Unstable</td>
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<tr>
<td>(b)</td>
<td>$-0.00035$</td>
<td>0.008</td>
<td>0.174</td>
<td>0.346</td>
<td>0.06</td>
<td>0.0002</td>
<td>Stable</td>
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<td></td>
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<td>0.006</td>
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<td>0.344</td>
<td>0.053</td>
<td>0.0002</td>
<td>Unstable</td>
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<tr>
<td>(c)</td>
<td>$-0.003$</td>
<td>0.0018</td>
<td>1.72</td>
<td>0.556</td>
<td>0.949</td>
<td>0.007</td>
<td>Stable</td>
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<td>0.0016</td>
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<tr>
<td>2 (a)</td>
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<td>0.514</td>
<td>0.406</td>
<td>0.208</td>
<td>0.0007</td>
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<td>(b)</td>
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<td>0.114</td>
<td>0.0008</td>
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<td>0.018</td>
<td>0.279</td>
<td>0.382</td>
<td>0.1145</td>
<td>0.008</td>
<td>Unstable</td>
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<tr>
<td>(c)</td>
<td>$-0.0041$</td>
<td>0.0044</td>
<td>1.846</td>
<td>0.732</td>
<td>1.338</td>
<td>0.013</td>
<td>Stable</td>
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<td></td>
<td></td>
<td>0.0042</td>
<td>1.838</td>
<td>0.718</td>
<td>1.335</td>
<td>0.015</td>
<td>Unstable</td>
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</table>

**Case 1a**

In the case of response function (a) with Data 1 and initial condition (i), as shown in Figure 5.4, spatial patterns of both predator and prey population densities are achieved for $T = -0.0003$. For $d_3 = 0.0$ with $T = -0.0003$, prey population density $u$ shows symmetrical behaviour in the form aggregation around $u$ axis. The corresponding model has been referred to as model 1 in Table 5.2. For $d_3 = 0.01$
with $T = -0.0003$, aggregation of $u$ happens near the boundary of the domain as shown in Figure 5.4 and referred to as model 2 in Table 5.2. Also two distinct patches develop on both sides of $u$ axis and one around the middle of the domain. Predator population density $v$ shows unstable behaviour in this case.

In the case of response function (a) with Data 1 and initial condition (ii), as shown in Figure 5.5, spatial patterns of both predator and prey population densities are achieved for $T = -0.0003$. For $d_3 = 0.0$ with $T = -0.0003$, $u$ aggregates in the whole domain whereas $v$ has a tendency to aggregate more on the r.h.s. of $v$ axis. For $d_3 = 0.01$ with $T = -0.0003$, $u$ shows a tendency to aggregate in boundary of the domain as shown in Figure 5.5. Also a single patch develops in the domain ranging from $x = -0.7$ to $x = 0.6$ whereas $v$ shows unstable behaviour in this case.

It should be noted here that even though the values of $T$ and $d_3$ are the same for both initial conditions (i) and (ii), the graphs show quite different behaviour as shown in Figures 5.4 and 5.5 respectively.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.
The term ‘patch’ means the aggregation of individuals in a domain, with negligibly small population density near the edges and comparatively higher population density elsewhere. Thus a patch is a special type of aggregation. An aggregation is simply a cluster of individuals in a domain.

Case 1b

In the case of response function (b) with Data 1 and initial condition (i), as shown in Figure 5.6, spatial patterns of both predator and prey population densities are achieved for \( T = -0.00035 \). For \( d_3 = 0.0 \) with \( T = -0.00035 \), \( u \) shows a tendency to aggregate in the whole domain whereas \( v \) shows slightly unstable behaviour in this case. The corresponding model has been referred to as model 1 in Table 5.2. For \( d_3 = 0.001 \) with \( T = -0.00035 \), two interconnected patches develop on both sides of the \( u \) axis as shown in Figure 5.6 and referred to as model 2 in Table 5.2. Also \( v \) shows a tendency to aggregate in the entire domain in this case.

In the case of response function (b) with Data 1 and initial condition (ii), as shown in Figure 5.7, spatial patterns of predator and prey population densities are achieved for \( T = -0.00035 \). For \( d_3 = 0.0 \) with \( T = -0.00035 \), \( u \) aggregates

Figure 5.6: Transient graphs for response function (b), Data 1, initial condition (i) at \( t = 0 \) and 200.
in the entire domain and $v$ has a tendency to aggregate. For $d_3 = 0.01$ with $T = -0.00035$, $u$ shows a broad single patch ranging from $x = -0.9$ to $x = 0.8$ as shown in Figure 5.7. Also $v$ shows unstable behaviour near the boundary of the domain.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.

**Case 1c**

In the case of response function (c) with Data 1 and initial condition (i), as shown in Figure 5.8, spatial patterns of predator and prey population densities are achieved for $T = -0.003$. For $d_3 = 0.0$ with $T = -0.003$, both $u$ and $v$ show slightly unstable behaviour. The corresponding model has been referred to as model 1 in Table 5.2. For $d_3 = 0.001$ with $T = -0.003$, $u$ shows symmetrical distribution without any patch formation as shown in Figure 5.8 and referred to as model 2 in Table 5.2. In this case $v$ also shows symmetrical distribution around the middle of the domain without any patch formation.

In the case of response function (c) with Data 1 and initial condition (ii), as shown in Figure 5.9, spatial patterns of predator and prey population densities are
Figure 5.8: Transient graphs for response function (c), Data 1, initial condition (i) at $t = 0$ and 200. achieved for $T = -0.003$. For $d_3 = 0.0$ with $T = -0.003$, both $u$ and $v$ show unstable behaviour. For $d_3 = 0.001$ with $T = -0.003$, here is neither any patch formation nor aggregation of population densities as shown in Figure 5.9.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.

**Case 2a**

In the case of response function (a) with Data 2 and initial condition (i), as shown in Figure 5.10, spatial patterns of predator and prey population densities are achieved for $T = -0.0005$. For $d_3 = 0.0$ with $T = -0.0005$, both $u$ and $v$ show unstable behaviour. The corresponding model has been referred to as model 1 in Table 5.2. For $d_3 = 0.015$ with $T = -0.0005$, the aggregation of prey population density $u$ happens near the boundary of the domain as shown in Figure 5.10 and has been referred to as model 2 in Table 5.2. Also two distinct patches develop on both sides of $u$ axis and at the middle of the domain, there is no prey. In this case predator population density $v$ shows unstable behaviour.

In the case of response function (a) with Data 2 and initial condition (ii), as
Figure 5.9: Transient graphs for response function (c), Data 1, initial condition (ii) at $t = 0$ and 200.

shown in Figure 5.11, spatial patterns of predator and prey population densities are achieved for $T = -0.0005$. For $d_3 = 0.0$ with $T = -0.0005$, both $u$ and $v$ show prominent unstable behaviour. For $d_3 = 0.015$ with $T = -0.0005$, the aggregation of $u$ happens near the boundary of the domain as shown in Figure 5.11. Also a single patch develops in the domain ranging from $x = -0.9$ to $x = 0.7$. Predator population density $v$ shows unstable behaviour in this case.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.

Case 2b

In the case of response function (b) with Data 2 and initial condition (i), as shown in Figure 5.12, spatial patterns of predator and prey population densities are achieved for $T = -0.00045$. For $d_3 = 0.0$ with $T = -0.00045$, both $u$ and $v$ show unstable behaviour. The corresponding model for $T = -0.00045$ and $d_3 = 0.0$ has been referred to as model 1 in Table 5.2. For $d_3 = 0.015$ with $T = -0.00045$, the aggregation of prey population density $u$ happens near the boundary of the domain as shown in Figure 5.12 and has been referred to as model 2 in Table 5.2. Here two
interconnected patches develop on both sides of $u$ axis as shown in Figure 5.12. Also predator population density $v$ shows unstable behaviour in this case.

In the case of response function (b) with Data 2 and initial condition (ii), as shown in Figure 5.13, spatial patterns of predator and prey population densities are achieved for $T = -0.00045$. For $d_3 = 0.0$ with $T = -0.0005$, both $u$ and $v$ show unstable behaviour. For $d_3 = 0.015$ with $T = -0.00045$, a single patch of prey population density $u$ develops in the domain ranging from $x = -0.9$ to $x = 0.7$ as shown in Figure 5.13. Predator population density $v$ shows unstable behaviour in this case.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.

**Case 2c**

In the case of response function (c) with Data 2 and initial condition (i), as shown in Figure 5.14, spatial patterns of predator and prey population densities are achieved for $T = -0.0041$. For $d_3 = 0.0$ with $T = -0.0041$, both $u$ and $v$ show unstable behaviour. The corresponding model for $T = -0.0041$ and $d_3 = 0.0$
Figure 5.11: Transient graphs for response function (a), Data 2, initial condition (ii) at \( t = 0 \) and 200.

has been referred to as model 1 in Table 5.2. For \( d_3 = 0.001 \) with \( T = -0.0041 \), prey population density \( u \) shows symmetrical distribution around the middle of the domain without any patch formation as shown in Figure 5.14. The corresponding model for \( T = -0.0041 \) and \( d_3 = 0.001 \) has been referred to as model 2 in Table 5.2. Also predator population density \( v \) shows similar behaviour in this case.

In the case of response function (c) with Data 2 and initial condition (ii), as shown in Figure 5.15, spatial patterns of predator and prey population densities are achieved for \( T = -0.0041 \). For \( d_3 = 0.0 \) with \( T = -0.0041 \), both \( u \) and \( v \) show slightly unstable behaviour. For \( d_3 = 0.001 \) with \( T = -0.0041 \), there has been neither patch formation nor aggregation of population densities as shown in Figure 5.15.

Characteristics of the stability of equilibria for all the chosen models are shown in Table 5.2.
5.6 Discussion and conclusion

In order to achieve spatial patterns with prey-taxis and diffusion in predator velocity, first of all, the predator–prey-taxis equations (5.1)–(5.3) have been solved without prey-taxis and diffusion to obtain the point of equilibrium. As in chapter 4, here also two data sets, obtained in section 3.9, have been used along with three response functions and two nonhomogeneous initial conditions. The bifurcation value of diffusion in predator velocity $d_3$, as detailed in section 5.4.1, is determined with a particular value of prey-taxis $T$, obtained from section 4.6, for which the dynamics is quasi-periodic and the point of equilibrium is unstable. The reason for choosing the quasi-periodic dynamics is that if the point of equilibrium is unstable with prey-taxis, spatial patterns can be achieved in a longer time-scale. If the point of equilibrium is stable with prey-taxis and the predator–prey dynamics is periodic, it is not possible to obtain spatial patterns even for longer time. If the value of $T$ is chosen for which the point of equilibrium is unstable and the predator–prey dynamics is chaotic, spatial patterns over longer time-scale does not explain much.

In section 5.5, with particular values of $T$ and $d_3$, chosen in section 5.4.1, the
Figure 5.13: Transient graphs for response function (b), Data 2, initial condition (ii) at $t = 0$ and 200.

Predator–prey-taxis equations (5.1)–(5.3) have been solved numerically to investigate the formation of spatial patterns. Also, the stabilities of equilibria have been verified for all the cases using Routh–Hurwitz conditions as shown in Tables 5.1 and 5.2 respectively.

It has been seen that response function (a) with the same data set and different initial conditions (i) and (ii) show different form of predator–prey population densities as shown in Figures 5.4 and 5.5; 5.10 and 5.11. Similar situations arise with response functions (b) and (c) as can be seen in Figures 5.6 and 5.7; 5.8 and 5.9; 5.12 and 5.13; 5.14 and 5.15.

This fact has further been established with the appearance of similar graphs for a particular initial condition as shown in Figures 5.5, 5.7, 5.11, 5.13 and 5.15.

In the cases of response functions (a) and (b), the initial models without prey-taxis produce no specific spatial patterns as shown in Figures 5.4–5.7 and 5.10–5.13. However, inclusion of prey-taxis and diffusion in predator velocity produces spatial patterns in the form of aggregation or patch formation as shown in Figures 5.4–5.7 and 5.10–5.13. Also, it has been observed that patch formation occurs in the cases of
Figure 5.14: Transient graphs for response function (c), Data 2, initial condition (i) at $t = 0$ and 200.

response functions (a) and (b) with the introduction of diffusion in predator velocity $d_3$ in the predator–prey system as shown in Figures 5.4–5.7 and Figures 5.10–5.13.

Thus it can be said that in order to achieve spatial patterns with prey-taxis, response functions (a) and (b) are more suitable than response function (c). In the cases of response functions (a) and (b), spatial patterns can be achieved with negative values of prey-taxis that are not high in magnitude as given in Table 5.2. Here the negative sign indicates only the direction of movement of predator away from prey. But in the case of response function (c), spatial patterns are achieved with negative value of prey-taxis that has been very high in magnitude. That does not reflect the behaviour of *P. persimilis*.

Thus it is concluded that it has been possible to achieve spatial patterns with zero flux boundary conditions even in a smaller domain with suitable values of prey-taxis. Initial conditions and response functions play domineering roles in the pattern formation of prey population density.

In the next chapter formation of spatial patterns has been investigated in a predator–prey system with the introduction of diffusion–driven instability and in
Table 5.2: Characteristics of equilibria with prey-taxis and diffusion in predator velocity for Data 1 and Data 2 along with response functions (a) – (c)

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp Func.</th>
<th>Point of Equilibrium</th>
<th>Model</th>
<th>$d_3$</th>
<th>$T$</th>
<th>$p(k^2)$</th>
<th>$q(k^2)$</th>
<th>$r(k^2)$</th>
<th>$p(k^2) - r(k^2)$</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(19.73, 4.41, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.0003</td>
<td>0.073</td>
<td>0.346</td>
<td>0.028</td>
<td>−0.003</td>
<td>Unstable</td>
</tr>
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<td></td>
<td>+ive</td>
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<td>−ive</td>
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<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.01</td>
<td>−0.0003</td>
<td>0.172</td>
<td>0.353</td>
<td>0.062</td>
<td>−0.001</td>
<td>Unstable</td>
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<td></td>
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<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>−ive</td>
<td></td>
</tr>
<tr>
<td>(b)</td>
<td>(20.19, 4.49, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.0003</td>
<td>0.095</td>
<td>0.338</td>
<td>0.033</td>
<td>−0.0009</td>
<td>Unstable</td>
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<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.001</td>
<td>−0.00035</td>
<td>0.104</td>
<td>0.339</td>
<td>0.036</td>
<td>−0.0007</td>
<td>Unstable</td>
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<td>+ive</td>
<td>−ive</td>
<td></td>
</tr>
<tr>
<td>(c)</td>
<td>(71.97, 5.62, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.003</td>
<td>1.647</td>
<td>0.44</td>
<td>0.918</td>
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<td>Unstable</td>
<td></td>
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<td></td>
<td>2</td>
<td>0.001</td>
<td>−0.003</td>
<td>1.687</td>
<td>0.504</td>
<td>0.935</td>
<td>−0.085</td>
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<td>−ive</td>
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</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(19.6, 4.49, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.0005</td>
<td>0.079</td>
<td>0.371</td>
<td>0.047</td>
<td>−0.018</td>
<td>Unstable</td>
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<td></td>
<td></td>
<td>2</td>
<td>0.015</td>
<td>−0.0005</td>
<td>0.227</td>
<td>0.383</td>
<td>0.102</td>
<td>−0.015</td>
<td>Unstable</td>
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<td>−ive</td>
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</tr>
<tr>
<td>(b)</td>
<td>(20.03, 4.57, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.00045</td>
<td>0.101</td>
<td>0.364</td>
<td>0.042</td>
<td>−0.005</td>
<td>Unstable</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.015</td>
<td>−0.00045</td>
<td>0.249</td>
<td>0.379</td>
<td>0.096</td>
<td>−0.002</td>
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<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>−ive</td>
<td></td>
</tr>
<tr>
<td>(c)</td>
<td>(70.92, 5.88, 0)</td>
<td>1</td>
<td>0.0</td>
<td>−0.0041</td>
<td>1.672</td>
<td>0.441</td>
<td>1.261</td>
<td>−0.524</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>0.001</td>
<td>−0.0041</td>
<td>1.712</td>
<td>0.507</td>
<td>1.279</td>
<td>−0.411</td>
<td>Unstable</td>
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<td>+ive</td>
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<td>+ive</td>
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</tbody>
</table>

the absence of prey-taxis.
Figure 5.15: Transient graphs for response function (c), Data 2, initial condition (ii) at $t = 0$ and 200.
Chapter 6

Spatial Patterns Generated by Diffusion-Driven Instability

6.1 Introduction

Different spatial patterns, i.e., spatial inhomogeneity with certain regularity (excluding turbulent or chaotic phenomena), are found in a variety of physical sciences including biological sciences. According to Levin and Segel [95], “a natural way to approach the study of pattern generation is to investigate the fate of an initial small inhomogeneity in an otherwise uniform state. This approach is advantageous because in many cases it mimics the ‘ontogeny’ of pattern, and because, more generally, we may draw on the techniques of stability theory to provide a powerful method of estimating whether the small disturbance will evolve into a pattern”.

Patterns in reaction-diffusion systems form a natural starting point for many mathematicians because both diffusive movement and local ‘mass action’ can, to some extent, represent realistic ecological situations. Patterns that one can see, that is, morphological and geographical patterns are the most obvious examples (Levin and Segel [95]), Freedman and Shukla [50]).

A fundamental problem in developmental biology is to understand morphogenesis, the generation of form and pattern starting from a comparatively featureless initial state. Turing [152] proposed a reaction-diffusion theory of morphogenesis on the basis of well known laws of physical chemistry. He showed that under
certain conditions, uniform solutions were unstable to small perturbations, and he demonstrated by numerical analysis that stable non-uniform spatial patterns could result. Turing thus demonstrated that reaction-diffusion instabilities could, in theory, lead to pattern distribution of chemicals and therefore that distribution of chemical ‘morphogens’ might underlie the creation of biological patterns (Levin and Segel [95]).

Gierer and Meinhardt [57] developed a Turing-like idea without being aware of it. They proved that the key ingredient in the generation of diffusive patterns was the combination of short-range activation and long-range inhibition. They also showed that the gradient of morphogens, which many developmental biologists considered as underlying pattern generation, did not require pre-arranged sources and sinks; they could arise from instability. Above all, they used their general ideas in computer simulations that suggest solutions to many specific problems of developmental biology, in particular the control of head and foot regeneration in hydra (Levin and Segel [95]). As illustrated by the work of Murray [116] and Bard [8] on coat striping in zebras and other mammals, and of Hunding [75] on bipolar three-dimensional patterns, lively interest continues in reaction-diffusion explanations of developmental structure (Levin and Segel [95]).

A great amount of previous work has been done looking for biological mechanisms of pattern formation through diffusion-driven instabilities (Okubo and Levin [126]). The role of diffusion in a reaction-diffusion system is to accelerate the process. When diffusion is introduced in a predator–prey system, after certain time, both species attain uniform distributions in the domain. Thus it is said that diffusion acts as a stabilizer in a reaction-diffusion system (Murray [116]). But under certain conditions (Murray [116], Okubo and Levin [126], Alonso et al. [2]), diffusion can also destabilize the process and this can lead to a non-uniform distribution in a predator–prey system. This phenomenon of destabilization is known as diffusion-driven instability.

Segel and Jackson [142] were the first to show that the diffusion-driven instability advanced by Turing can appear in an ecological context. They analyzed a Lotka–Volterra ‘exploiter-victim’ system that incorporated two new features in re-
lation to previous predator–prey models: viz an autocatalytic effect on prey growth rate and density-dependent mortality of predators. The same model was suggested later as a possible explanation for the origins of planktonic patchiness (Levin and Segel [94]). As a generalization of Segel and Jackson’s model, Mimura and Murray [112] and Conway [34] considered other predator–prey models. Thus it can be said that density dependent predator mortality and autocatalytic prey growth are two necessary conditions (Alonso et al. [2]) to generate diffusion-driven instabilities.

Predator interference in the functional response is responsible for the auto-inhibitor effect of increased predator densities on the growth of predator populations. Thus, as random fluctuations increase local prey density over its equilibrium value, the prey population undergoes an accelerated growth. Simultaneously, the predator population also increases, but as predators diffuse faster than prey, they disperse away from the center of prey outbreaks. As a consequence, spatially uniform population distributions break down and two different spatial domains arise. In the center of the outbreaks the prey growth rate keeps positive. As a consequence, the prey population keeps increasing beyond predator control. Thereafter, the proportion of prey to predators in those central areas increases. By contrast, on the border of prey outbreaks, the proportion of prey to predators becomes lower and lower. According to Alonso et al. [2], “if relative diffusion ($d_2/d_1$) is large enough, prey growth rate will reach negative values there and the prey population will be driven by predators to a very low level in those regions. The final result is the formation of patches of high prey density surrounded by areas of low prey densities. Predators follow the same pattern, but, since they diffuse faster, their spatial distributions are smoother”.

In this chapter, the aim is to investigate the formation of spatial patterns over longer time-scale, in the absence of prey-taxis, in a predator–prey system. Patterns have been formed with the introduction of diffusion-driven instability. As mentioned earlier in chapter 2, diffusion-driven instability can only be achieved in a system, if the point of equilibrium is stable without diffusion but unstable with diffusion. In view of that, limits of predator interference $\beta$ have been obtained for which the point of equilibrium is stable without diffusion but unstable with
di®usion. Results have further been veri¯ed through numerical solutions using two
data sets, three response functions and two initial conditions as speci¯ed earlier in
chapters 4 and 5 respectively.

6.2 Mathematical model

In one-dimensional form the predator–prey equations (Arditi et al. [5], Harri-
son [65], Sapoukhina et al. [139], Chakraborty et al. [30]) are written as:

\[
\frac{\partial u}{\partial t} = \rho (1 - \frac{u}{K}) u - e f(u, v) v + d_1 \frac{\partial^2 u}{\partial x^2}, \quad (6.1)
\]

\[
\frac{\partial v}{\partial t} = -\gamma v + \sigma f(u, v) v + d_2 \frac{\partial^2 v}{\partial x^2}, \quad (6.2)
\]

where all the symbols have their usual meanings as de¯ned in chapter 3.

6.3 Response functions

The same response functions as used in chapter 3 have also been used here. Data 1
and Data 2 obtained in section 3.9 have been used here. The carrying capacity pa-
rameter \( K = 100 \), speci¯c prey growth rate parameter \( \rho = 0.6 \), diffusivity constant
of predator population density \( d_2 = 0.02 \) have not been changed throughout this
study. Di®erent values of predator interference \( \beta \) and the diffusivity constant of
prey population density \( d_1 \) have been used in order to investigate the formation of
spatial patterns generated through diffusion-driven instability in the predator–prey
population. Hence the two data sets have been reproduced here as:

(Data 1) \( \phi = 19.409, \; \gamma = 1.55, \; \sigma = 3.0744, \; e = 4.27 \),

(Data 2) \( \phi = 20.524, \; \gamma = 1.60, \; \sigma = 3.2756, \; e = 4.31 \).

Initial conditions (i) and (ii), already used in chapter 4, have also been used here.
The numerical scheme of operator splitting method and the boundary conditions
of zero ®ux as detailed in chapter 3 have also been used here.
6.4 Stability of equilibria with diffusion

As already shown in section 3.7, the predator–prey equations (6.1) and (6.2) have been linearised about the point of equilibrium \( E^* = (u^*, v^*) \) and thus take the form

\[
\frac{\partial U}{\partial t} = a_{11}U + a_{12}V + d_1 \frac{\partial^2 U}{\partial x^2},
\]

(6.3)

\[
\frac{\partial V}{\partial t} = a_{21}U + a_{22}V + d_2 \frac{\partial^2 V}{\partial x^2}.
\]

(6.4)

In order to examine the existence of linear stability, it is sufficient to assume solutions of equations (6.3) and (6.4) of the form (Okubo and Levin [126])

\[
U(x, t) = \sum_k \exp U_k(\lambda t + ikx),
\]

(6.5)

\[
V(x, t) = \sum_k \exp V_k(\lambda t + ikx),
\]

(6.6)

where \( \lambda \) and \( k \) are the frequency and wave number, respectively as described in chapters 3 and 4 respectively.

For a particular value of \( k \), the variational matrix \( M_4 \) for equations (6.3) and (6.4) is

\[
M_4 = \begin{pmatrix}
\lambda - a_{11} + k^2 d_1 & -a_{12} \\
a_{21} & a_{22} - d_2 k^2 - \lambda
\end{pmatrix}.
\]

Hence, the corresponding eigenvalues are

\[
\lambda = \frac{1}{2}(a_{11} + a_{22} - k^2(d_1 + d_2)) \pm \frac{1}{2}[(a_{11} + a_{22} - k^2(d_1 + d_2))^2 - 4((a_{11} - d_1 k^2)(a_{22} - d_2 k^2) - a_{12} a_{21})]^{1/2}.
\]

In the absence of diffusion, the eigenvalues are

\[
\lambda_{1,2} = \frac{1}{2}(a_{11} + a_{22}) \pm \frac{1}{2}[(a_{11} + a_{22})^2 - 4(a_{11} a_{22} - a_{12} a_{21})]^{1/2}.
\]

The point of equilibrium will be stable, if the real part of the eigenvalues are negative and the determinant of the corresponding matrix is positive.
This gives
\[ a_{11} + a_{22} < 0, \quad (6.7) \]
and \[ a_{11}a_{22} - a_{12}a_{21} > 0. \quad (6.8) \]

Similarly, in the presence of diffusion, the point of equilibrium will be stable, if
\[ a_{11} + a_{22} - k^2(d_1 + d_2) < 0, \quad (6.9) \]
\[ (a_{11} - d_1k^2)(a_{22} - d_2k^2) - a_{12}a_{21} > 0. \quad (6.10) \]

Diffusion-driven instability sets in when at least one of the conditions (6.9) or (6.10) is violated. It has been seen that the first condition (6.9) is not violated when inequality (6.7) is satisfied. Hence only the violation of the second condition (6.10) gives rise to diffusion-driven instability (Okubo and Levin [126]). Thus when inequality (6.10) is violated, it becomes
\[ (a_{11} - d_1k^2)(a_{22} - d_2k^2) - a_{12}a_{21} < 0, \]
\[ \Rightarrow d_1d_2k^4 - (d_1a_{22} + d_2a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21} < 0. \]

Let
\[ H(k^2) = d_1d_2k^4 - (d_1a_{22} + d_2a_{11})k^2 + a_{11}a_{22} - a_{12}a_{21}. \quad (6.11) \]

Differentiating \( H(k^2) \) on both sides w.r.t. \( k^2 \), it becomes
\[ \frac{\partial H}{\partial k^2} = 2d_1d_2k^2 - (d_1a_{22} + d_2a_{11}), \quad (6.12) \]
and
\[ \frac{\partial^2 H}{\partial k^4} = 2d_1d_2 > 0 \quad (6.13) \]
since both \( d_1 \) and \( d_2 \) are positive.

For \( H(k^2) \) to be maximum or minimum, \( \frac{\partial H}{\partial k^2} = 0 \).

Hence equation (6.12) gives
\[ 2d_1d_2k^2 - (d_1a_{22} + d_2a_{11}) = 0 \]
\[ \Rightarrow k^2 = (d_1a_{22} + d_2a_{11})/(2d_1d_2). \]
Thus $H(k^2)$ is minimum for $k^2 = (d_1 a_{22} + d_2 a_{11}) / (2d_1 d_2)$.

Substituting the value of $k^2$ in equation (6.11) and after simplification, it becomes

$$H(k^2) = a_{11} a_{22} - a_{12} a_{21} - (d_1 a_{22} + d_2 a_{11})^2 / 4d_1 d_2.$$  

Now diffusion-driven instability sets in when $H(k^2)$ is negative, that is, condition (6.10) is violated.

Hence,

$$a_{11} a_{22} - a_{12} a_{21} - (d_1 a_{22} + d_2 a_{11})^2 / 4d_1 d_2 < 0$$

gives

$$d_1 a_{22} + d_2 a_{11} > \left(2\sqrt{(a_{11} a_{22} - a_{12} a_{21})d_1 d_2}\right) > 0. \quad (6.14)$$

Equation (6.14) can be split as

$$f(d_1, d_2) = d_1 a_{22} + d_2 a_{11}, \quad (6.15)$$

$$g(d_1, d_2) = 2\sqrt{(a_{11} a_{22} - a_{12} a_{21})d_1 d_2}. \quad (6.16)$$

Thus for diffusion-driven instability of the point of equilibrium $(u^*, v^*)$ of a predator–prey system, one has

- a stable point of equilibrium $(u^*, v^*)$ satisfying

  $$a_{11} + a_{22} < 0, \quad (6.17)$$

  $$a_{11} a_{22} - a_{12} a_{21} > 0, \quad (6.18)$$

  and

- the values of diffusivity constants $d_1, d_2$ satisfying

  $$f(d_1, d_2) > g(d_1, d_2), \quad (6.19)$$

  $$g(d_1, d_2) > 0. \quad (6.20)$$
The aim is to first select a model with a stable point of equilibrium satisfying inequalities (6.17) and (6.18). Next the diffusivity constants $d_1$ and $d_2$ have been included in the predator–prey equations (6.1) and (6.2), to introduce diffusion-driven instability, satisfying inequalities (6.19) and (6.20), in the model otherwise with stable equilibria.

### 6.5 Limits of predator interference parameter $\beta$

Mutual interference of predator $\beta$ can affect the stability of a point of equilibrium in a predator–prey system (Alonso et al. [2]). In order to find the limits of $\beta$ for which diffusion-driven instability can be introduced in a predator–prey system, following steps have been used:

- **Step 1**: With $\beta$ as an unknown parameter, predator–prey equations (6.1) and (6.2) have been solved without diffusion to obtain the point of equilibrium $(u^*, v^*)$.
- **Step 2**: Values of $u^*$ and $v^*$ have been substituted in equation (3.20) to obtain the values of $a_{11}$, $a_{12}$, $a_{21}$ and $a_{22}$ respectively.
- **Step 3**: Values of $a_{11}$ etc are then substituted in inequalities (6.17) and (6.18) to obtain expressions in terms of $\beta$. Solution of these two inequalities gives the lower limit of $\beta$ for which the point of equilibrium is stable without diffusion.
- **Step 4**: Next, values of $a_{11}$ etc are substituted in inequalities (6.19) and (6.20) to obtain expressions in terms of $\beta$. Solution of these two inequalities gives the upper limit of $\beta$ for which the point of equilibrium is unstable with diffusion (Chakraborty et al. [29]).
- **Step 5**: Combining **Step 3** and **Step 4**, a limit of $\beta$ for which the point of equilibrium is unstable with diffusion but stable without diffusion is obtained.
- **Step 6**: In order to generate visible spatial patterns, the value of $\beta$ for numerical solution has been chosen for each response function through a number of numerical simulations.

Since response function (a) is not dependent on predator interference, varying the values of $\beta$ will not effect the stability of points of equilibrium. In view of this, response function (a) has not been considered in this chapter. Only response
functions (b) and (c) along with Data 1 and Data 2 have been used to obtain the values of $\beta$ responsible for diffusion-driven instability.

**Case 1b**

In the case of response function (b) with Data 1 and $\bar{\beta}$ as an unknown parameter, the predator–prey equations (6.1) and (6.2) have been solved without diffusion to obtain the point of equilibrium $(u^*, v^*)$ as

$$
u^* = \frac{-176.435 + 50\beta + 0.53A_2 + \beta(0.42 - 0.03A_2)}{\beta},$$

$$v^* = \frac{-1.87 + 0.03\beta^2 + 0.53A_2 + \beta(0.42 - 0.03A_2)}{\beta^2(0.016 - 0.0015 + 0.0015A_2)},$$

where $A_2 = \sqrt{12.4517 - 4.27186\beta + \beta^2}$.

**Lower limit of $\bar{\beta}$**

In order to determine the lower limit of $\beta$ for which the point of equilibrium is stable without diffusion, values of $u^*$ and $v^*$ have been substituted in equation (3.22) to obtain the values of $a_{11}, a_{12}, a_{21}$ and $a_{22}$. These values are then substituted in conditions (6.17) and (6.18) to obtain

$$a_{11} + a_{22} = [0.009 - 0.0026A_2 + \beta(-0.0085 + 0.0002A_2) + \beta^2(0.003 - 0.0004A_2) - 0.0004\beta^3] / [\beta(-0.038 + 0.011A_2 + 0.015\beta)^2] \triangleq M(\beta),$$

$$a_{11}a_{22} - a_{12}a_{21} = \{-0.3 + 0.074A_2 + \beta(0.33 - 0.08A_2) + \beta^2(0.18 + 0.03A_2) + \beta^3(0.05 - 0.008A_2) + \beta^4(-0.009 + 0.0008A_2) + 0.0008\beta^5\} / \{\beta(0.38 - 0.15\beta - 0.107A_2)^4\} \triangleq S(\beta).$$

The graphs have been drawn for $M(\beta)$ and $S(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.1. The point of equilibrium is stable without diffusion if $M(\beta) < 0$ and $S(\beta) > 0$. From Figure 6.1 it can be seen that $S(\beta) > 0$ for $\beta \geq 0$. Thus $M(\beta) = 0$ gives the bifurcation value of $\beta$ for which the point of equilibrium
becomes stable from unstable. For $M(\beta) = 0$, $\beta = 0.583193$. Other values of $\beta$, either being imaginary numbers or very small, have been neglected. Thus for any value of $\beta$ greater than the bifurcation value 0.583193, the point of equilibrium is stable without diffusion.

### Upper limit of $\beta$

In order to determine the upper limit of $\beta$ for which the point of equilibrium is unstable with diffusion, values of $a_{11}$ etc are then substituted in equations (6.15) and (6.16) to obtain

$$f(d_1, d_2) = \begin{cases} 1.81 - 0.51A_2 + \beta(-1.3 + 0.27A_2) + \beta^2(0.35 - 0.04A_2) - 0.04\beta^3 \\ \Delta G(\beta), \end{cases}$$

$$g(d_1, d_2) = 0.001\{[-0.62 + 0.18A_2 + (0.8 - 0.18A_2)\beta + (-0.042 + 0.08A_2)\beta^2 + (0.13 - 0.02A_2)\beta^3 + (-0.02 + 0.002A_2)\beta^4 + 0.002\beta^5] / [\beta(0.38 - 0.11A_2 + \beta(-0.43 + 0.1A_2) + \beta^2(0.2 - 0.04A_2) + \beta^3(-0.05 + 0.005A_2) + 0.005\beta^4)]\}^{1/2} \Delta P(\beta).$$

The graphs have been drawn for $G(\beta)$ and $P(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.1. According to conditions (6.19) and (6.20), the point of equilibrium is unstable with diffusion if $P(\beta) > 0$ and $G(\beta) > P(\beta)$. From Figure 6.1 it can be seen that $P(\beta) > 0$ for $\beta \geq 0$. Thus $G(\beta) = P(\beta)$ gives the bifurcation value of $\beta$ for which the point of equilibrium becomes stable (with
diffusion) from unstable (with diffusion). For $G(\beta) = P(\beta)$, $\beta = 1.8181$. Thus for any value of $\beta$ lower than the bifurcation value 1.8181, the point of equilibrium is unstable with diffusion.

Hence the condition for diffusion-driven instability holds for $0.583193 < \beta < 1.8181$. In the next section 6.6, $\beta$ has been chosen to be 0.85 for numerical solution.

**Case 1c**

In the case of response function (c) with Data 1 and $\beta$ as an unknown parameter, the predator–prey equations (6.1) and (6.2) have been solved without diffusion to obtain the point of equilibrium $(u^*, v^*)$ as

\[
\begin{align*}
u^* &= 26.8637 + \frac{-2.401 + 27.93\beta}{(-0.011\beta^2 + 0.386\beta^3 + 0.189B_2)^{1/3}} + \frac{0.49(-0.011\beta^2) + 0.386\beta^3 + 0.189B_2}{\beta^{1/3}}, \\
v^* &= \frac{5.8227 + 0.242u^* + 0.003(u^*)^2}{2.135 - 5.823\beta - 0.242\beta u^* + 0.003\beta(u^*)^2},
\end{align*}
\]

where $B_2 = \beta^{3/2} \sqrt{(0.99 - \beta)(0.003 - 0.109\beta + \beta^2)}$.

**Lower limit of $\beta$**

In order to determine the lower limit of $\beta$ for which the point of equilibrium is stable without diffusion, values of $u^*$ and $v^*$ have been substituted in equation (3.22) to obtain the values of $a_{11}, a_{12}, a_{21}$ and $a_{22}$. These values are then substituted in conditions (6.17) and (6.18) to obtain the values of $(a_{11} + a_{22})$ and $(a_{11}a_{22} - a_{12}a_{21})$ respectively. The expressions for $M(\beta)$ and $S(\beta)$, being too long, have not been produced here.

As in Case 1b, the graphs have been drawn for $M(\beta)$ and $S(\beta)$, with $\beta$ as
an unknown parameter, as shown in Figure 6.2. For $M(\bar{\beta}) = 0$, $\bar{\beta} = 0.015746$. Thus for any value of $\beta$ greater than the bifurcation value 0.015746, the point of equilibrium is stable without diffusion.

Upper limit of $\bar{\beta}$

In order to determine the upper limit of $\bar{\beta}$ for which the point of equilibrium is unstable with diffusion, values of $a_{11}$ etc are then substituted in equations (6.15) and (6.16) to obtain the values of $f(d_1, d_2)$ and $g(d_1, d_2)$ respectively. The expressions for $G(\bar{\beta})$ and $P(\bar{\beta})$, being too long, have not been produced here.

As in Case 1b, the graphs have been drawn for $G(\bar{\beta})$ and $P(\bar{\beta})$, with $\bar{\beta}$ as an unknown parameter, as shown in Figure 6.2. For $G(\bar{\beta}) = P(\bar{\beta})$, $\bar{\beta} = 0.047515$. Thus for any value of $\beta$ lower than the bifurcation value 0.047515, the point of equilibrium is unstable with diffusion.

Hence the condition for diffusion–driven instability holds for $0.015746 < \beta < 0.047515$. In the next section 6.6, $\bar{\beta}$ has been chosen to be 0.04 for numerical solution.

Case 2b

In the case of response function (b) and $\bar{\beta}$ as an unknown parameter, the predator–prey equations (6.1) and (6.2) have been solved without diffusion to obtain the point of equilibrium $(u^*, v^*)$ as

\[
\begin{align*}
u^* &= \frac{-183.728 + 50\beta + 50A_4}{\beta}, \\
v^* &= \frac{-5.0634 + 1.4A_4 + \beta(1.12 - 0.077A_4) + 0.777\beta^2}{\beta^2(0.04 - 0.004\beta + 0.004A_4)}
\end{align*}
\]

where $A_4 = \sqrt{13.5024 - 4.46856\beta + \beta^2}$.

Lower limit of $\bar{\beta}$

In order to determine the lower limit of $\beta$ for which the point of equilibrium is stable without diffusion, values of $u^*$ and $v^*$ have been substituted in equation (3.22) to obtain the values of $a_{11}$, $a_{12}$, $a_{21}$ and $a_{22}$. These values are then substituted in conditions (6.17) and (6.18) to obtain
Figure 6.3: Limits of $\beta$ for response function (b) with Data 2.

\[
\begin{align*}
\frac{a_{11} + a_{22}}{a_{11}a_{22} - a_{12}a_{21}} &= \{6.43 - 1.75A_4 + \beta(-5.97 + 1.33A_4) + \beta^2(1.96 - 0.27A_4) + \beta^3(-0.25 + 0.001A_4) - 0.001\beta^4\} \\
&\quad / [\beta(0.99 - 0.38\beta - 0.27A_4)^4] \triangleq M(\beta),
\end{align*}
\]

\[
\begin{align*}
\frac{a_{11}a_{22} - a_{12}a_{21}}{a_{11}a_{22} - a_{12}a_{21}} &= \{-1.38 + 3.77A_4 + \beta(16.8 - 3.94A_4) + \beta^2(-8.9 + 1.7A_4) + \beta^3(2.7 - 0.37A_4) + \beta^4(-0.44 + 0.035A_4) + 0.035\beta^5\} / [\beta(0.99 - 0.38\beta - 0.27A_4)^4] \triangleq S(\beta).
\end{align*}
\]

The graphs have been drawn for $M(\beta)$ and $S(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.3. For $M(\beta) = 0$, $\beta = 0.548411$. Thus for any value of $\beta$ greater than the bifurcation value 0.548411, the point of equilibrium is stable without diffusion.

**Upper limit of $\beta$**

In order to determine the upper limit of $\beta$ for which the point of equilibrium is unstable with diffusion, values of $a_{11}$ etc are then substituted in equations (6.15) and (6.16) to obtain

\[
\begin{align*}
\frac{f(d, d_2)}{f(d, d_2)} &= \{0.13 - 0.035A_4 + \beta(-0.087 + 0.02A_4) + \beta^2(0.023 - 0.002A_4 - 0.002\beta^3)\} \\
&\quad / [\beta(0.99 - 0.38\beta - 0.27A_4)^2] \triangleq G(\beta),
\end{align*}
\]
Figure 6.4: Limits of $\beta$ for response function (c) with Data 2.

$$g(d_1, d_2) = 0.001\left\{[-0.155 + 0.042A_4 + \beta(0.19 - 0.04A_4) + \beta^2(-0.101 + 0.02A_4) + \beta^3(0.03 - 0.004A_4) + \beta^4(-0.005 + 0.0004A_4) - 0.000043^5] / [\beta(0.086 - 0.023A_4 + \beta(-0.094 + 0.021A_4) + \beta^2(-0.009 + 0.0009A_4) + \beta^3(-0.009 + 0.0009A_4))\right\}^{1/2} \triangleq P(\beta).$$

The graphs have been drawn for $G(\beta)$ and $P(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.3. For $G(\beta) = P(\beta)$, $\beta = 1.79945$. Thus for any value of $\beta$ lower than the bifurcation value 1.79945, the point of equilibrium is unstable with diffusion.

Hence the condition for diffusion-driven instability holds for 0.548411 < $\beta$ < 1.79945. In the next section 6.6, $\beta$ has been chosen to be 0.9 for numerical solution.

**Case 2c**

In the case of response function (c) with Data 2 and $\beta$ as an unknown parameter, the predator–prey equations (6.1) and (6.2) have been solved without diffusion to obtain the point of equilibrium $(u^*, v^*)$ as

$$u^* = 26.492 + \frac{-6.597 + 74.65\beta}{(-0.198\beta^2 + 7.153\beta^3 + 3.72B_4)^{1/3}} + \frac{18.57(-0.198\beta^2 + 7.153\beta^3 + 3.72B_4)^{1/3}}{\beta},$$

$$v^* = \frac{15.393 + 0.596u^* - 0.0075(u^*)^2}{5.387 - 15.393\beta - 0.596\beta u^* + 0.0075\beta(u^*)^2},$$

where $B_4 = \beta^{3/2} \sqrt{(0.929 - \beta)(0.0035 - 0.112\beta + \beta^2)}$. 

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Lower limit of $\beta$

In order to determine the lower limit of $\beta$ for which the point of equilibrium is stable without diffusion, values of $u^*$ and $v^*$ have been substituted in equation (3.22) to obtain the values of $a_{11}$, $a_{12}$, $a_{21}$ and $a_{22}$. These values are then substituted in conditions (6.17) and (6.18) to obtain the values of $(a_{11} + a_{22})$ and $(a_{11}a_{22} - a_{12}a_{21})$ respectively. The expressions for $M(\beta)$ and $S(\beta)$, being too long, have not been produced here.

As in Case 1c, the graphs have been drawn for $M(\beta)$ and $S(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.4. For $M(\beta) = 0$, $\beta = 0.014516$. Thus for any value of $\beta$ greater than the bifurcation value 0.014516, the point of equilibrium is stable without diffusion.

Upper limit of $\beta$

In order to determine the upper limit of $\beta$ for which the point of equilibrium is unstable with diffusion, values of $a_{11}$ etc are then substituted in equations (6.15) and (6.16) to obtain the values of $f(d_1, d_2)$ and $g(d_1, d_2)$ respectively. The expressions for $G(\beta)$ and $P(\beta)$, being too long, have not been produced here.

As in Case 1c, the graphs have been drawn for $G(\beta)$ and $P(\beta)$, with $\beta$ as an unknown parameter, as shown in Figure 6.4. For $G(\beta) = P(\beta)$, $\beta = 0.04791$. Thus for any value of $\beta$ greater than the bifurcation value 0.04791, the point of equilibrium is unstable with diffusion.

Hence the condition for diffusion–driven instability holds for $0.014516 < \beta < 0.04791$. In the next section 6.6, $\bar{\beta}$ has been chosen to be 0.04 for numerical solution.

6.6 Numerical solutions

Lotka–Volterra logistic predator–prey equations (6.1) and (6.2) have been solved numerically using Data 1 and Data 2 obtained in section 3.9 along with response functions (b) and (c) defined in section 3.3 corresponding to each of the initial conditions (i) and (ii). In all the cases, transient graphs are given for $t = 0$ and 200.
Figure 6.5: Transient graphs for response function (b), Data 1, initial condition (i) at $t = 0$ and 200.

**Case 1b**

In the case of response function (b) with Data 1 and initial condition (i), diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.85$ as shown in Figure 6.5 and referred to as model 1 in Table 6.1. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.85$, prey population density $u$ shows a tendency to aggregate near the boundary of the domain as shown in Figure 6.5 and referred to as model 2 in Table 6.1. However, there is no patch formation in this case. Also predator population density $v$ shows unstable behaviour in this case.

Figure 6.6: Transient graphs for response function (b), Data 1, initial condition (ii) at $t = 0$ and 200.

In the case of response function (b) with Data 1 and initial condition (ii),
Figure 6.7: Transient graphs for response function (c), Data 1, initial condition (i) at $t = 0$ and 200.

Figure 6.8: Transient graphs for response function (c), Data 1, initial condition (ii) at $t = 0$ and 200.

diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.85$ as shown in Figure 6.6. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.85$, $u$ shows a single patch near $x = -1$ and a tendency to aggregate in the rest of the domain as shown in Figure 6.6. Also $v$ shows unstable behaviour in this case.

Characteristics of the stability of equilibria for the chosen models are shown in Table 6.1.

It should be noted here that even though the values of $\beta$ and $d_1$ are the same for both initial conditions (i) and (ii), the graphs show quite different behaviour as shown in Figures 6.5 and 6.6 respectively.
Case 1c

In the case of response function (c) with Data 1 and initial condition (i), diffusion-driven instability sets in the domain \([-1, 1]\) for \(\beta = 0.04\) as shown in Figure 6.7 and referred to as model 1 in Table 6.1. As the value of \(d_1\) is reduced from 0.0000125 to 0.00000125 with \(\beta = 0.04\), \(u\) shows a tendency to aggregate near the boundary of the domain as shown in Figure 6.7 and referred to as model 2 in Table 6.1. However, there is no patch formation in this case. Also \(v\) shows a tendency of unstable behaviour near the boundary of the domain.

In the case of response function (c) with Data 1 and initial condition (ii), diffusion-driven instability sets in the domain \([-1, 1]\) for \(\beta = 0.04\) as shown in Figure 6.8. As the value of \(d_1\) is reduced from 0.0000125 to 0.00000125 with \(\beta = 0.04\), \(u\) shows a single patch near the boundary and a tendency to aggregate in the rest of the domain as shown in Figure 6.8. Also \(v\) shows unstable behaviour in this case.

Characteristics of the stability of equilibria for the chosen models are given in Table 6.1.

Case 2b

In the case of response function (b) with Data 2 and initial condition (i),

<table>
<thead>
<tr>
<th>Resp. func.</th>
<th>Model</th>
<th>(\beta)</th>
<th>Point of Equilibrium</th>
<th>(d_1)</th>
<th>(a_{11})</th>
<th>(a_{11}a_{22})</th>
<th>(f(d_1,d_2))</th>
<th>(g(d_1,d_2))</th>
<th>Diffusively Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>(b)</td>
<td>1</td>
<td>0.85</td>
<td>(24.15,5.105)</td>
<td>0.0000125</td>
<td>-0.056</td>
<td>0.306</td>
<td>0.0017</td>
<td>0.00055</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.85</td>
<td>(24.15,5.105)</td>
<td>0.00000125</td>
<td>-0.056</td>
<td>0.306</td>
<td>0.0017</td>
<td>0.00017</td>
<td>Yes</td>
</tr>
<tr>
<td>(c)</td>
<td>1</td>
<td>0.04</td>
<td>(32.76,6.14)</td>
<td>0.0000125</td>
<td>-0.25</td>
<td>0.169</td>
<td>0.0011</td>
<td>0.0004</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.04</td>
<td>(32.76,6.14)</td>
<td>0.00000125</td>
<td>-0.25</td>
<td>0.169</td>
<td>0.0011</td>
<td>0.0001</td>
<td>Yes</td>
</tr>
</tbody>
</table>
Figure 6.9: Transient graphs for response function (b), Data 2, initial condition (i) at $t = 0$ and 200.

Figure 6.10: Transient graphs for response function (b), Data 2, initial condition (ii) at $t = 0$ and 200.

diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.9$ as shown in Figure 6.9 and referred to as model 1 in Table 6.2. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.9$, $u$ shows a tendency to aggregate near the boundary of the domain as shown in Figure 6.9 and referred to as model 2 in Table 6.2. However, there is no patch formation in this case. Also $v$ shows a tendency of unstable behaviour near the boundary of the domain.

In the case of response function (b) with Data 2 and initial condition (ii), diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.9$ as shown in Figure 6.10. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.9$,
$u$ shows a single patch near the boundary and a tendency to aggregate in the rest of the domain as shown in Figure 6.10. Also $v$ shows unstable behaviour in the entire domain.

Characteristics of the stability of equilibria for the chosen models are shown in Table 6.2.
Table 6.2: Diffusion-driven instability of equilibria for Data 2 and response functions (b) and (c)

<table>
<thead>
<tr>
<th>Resp. func.</th>
<th>Model</th>
<th>$\beta$</th>
<th>Point of Equilibrium</th>
<th>$d_1$</th>
<th>$a_{11}$ + $a_{22}$</th>
<th>$a_{11}a_{22}$</th>
<th>$f(d_1, d_2)$</th>
<th>$g(d_1, d_2)$</th>
<th>Diffusively Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>(b)</td>
<td>1</td>
<td>0.9</td>
<td>(24.07,5.21)</td>
<td>0.0000125</td>
<td>0.325</td>
<td>0.0016</td>
<td>0.00057</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.9</td>
<td>(24.07,5.21)</td>
<td>0.0000125</td>
<td>0.325</td>
<td>0.0015</td>
<td>0.00018</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>(c)</td>
<td>1</td>
<td>0.04</td>
<td>(32.07,6.21)</td>
<td>0.0000125</td>
<td>0.186</td>
<td>0.0011</td>
<td>0.0004</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.04</td>
<td>(32.07,6.21)</td>
<td>0.0000125</td>
<td>0.186</td>
<td>0.0011</td>
<td>0.0001</td>
<td>Yes</td>
<td></td>
</tr>
</tbody>
</table>

**Case 2c**

In the case of response function (c) with Data 2 and initial condition (i), diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.04$ as shown in Figure 6.11 and referred to as model 1 in Table 6.2. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.04$, $u$ shows a tendency to aggregate near the boundary of the domain as shown in Figure 6.11 and referred to as model 2 in Table 6.2. However, there is no patch formation in this case. Also $v$ shows a tendency of unstable behaviour near the boundary of the domain.

In the case of response function (c) with Data 2 and initial condition (ii), diffusion-driven instability sets in the domain $[-1, 1]$ for $\beta = 0.04$ as shown in Figure 6.12. As the value of $d_1$ is reduced from 0.0000125 to 0.00000125 with $\beta = 0.04$, $u$ shows a single patch near the boundary and a tendency to aggregate in the rest of the domain as shown in Figure 6.12. Also $v$ shows unstable behaviour in the entire domain.

Characteristics of the stability of equilibria for the chosen models are shown in Table 6.2.
6.7 Discussion and conclusion

In this chapter, formation of spatial patterns for *P. persimilis* and *T. urticae* has been achieved by varying only two parameters: predator interference $\beta$ and diffusivity of prey population density $d_1$. The predator–prey equations (6.1) and (6.2) with diffusion have been solved numerically for two different data sets corresponding to three response functions with two non-homogeneous initial conditions. Also stabilities of equilibria are established for all the cases using diffusion-driven instability criteria as shown in Tables 6.1 and 6.2. In the cases of response functions (b) and (c), it is possible to achieve diffusion-driven instability in the domain $x \in [-1, 1]$ with suitable values of predator interference $\beta$ as shown in Figures 6.5–6.12.

It has been seen that response function (b) with the same data set and different initial conditions (i) and (ii) show different form of spatial patterns as shown in Figures 6.5, 6.6 and Figures 6.9, 6.10. Similar situation arises with response function (c) as can be seen in Figures 6.7, 6.8 and Figures 6.11, 6.12. This shows that initial conditions play crucial roles in the formation of spatial patterns.

It is further confirmed when different data set with the same response function produce quite similar patterns for a particular initial condition as shown in Figures 6.5, 6.9; Figures 6.6, 6.10; Figures 6.8, 6.12.

Also initial condition (i) generally does not produce any patch irrespective of data set and response functions as shown in Figures 6.5, 6.9 and 6.11. However, there is an exception. In the case of response function (c) with initial condition (i) corresponding to Data 1, prey population density form spatial patches as can be seen in Figure 6.7. Data 1 and 2 with both response functions (b) and (c) corresponding to initial conditions (i) and (ii) generally produce aggregation of prey population density in all the cases as shown in Figures 6.5–6.12. However, there is an exception. In the case of response function (c) with initial condition (i) corresponding to Data 2 aggregation of prey population density is not achieved as shown in Figure 6.11.

Thus it can be said that to achieve spatial patterns with diffusion–driven instability, response function (c) is more suitable to achieve spatial patterns since for response function (c) the limits of predator interference parameter $\beta$ is quite low.
For an insect like two-spotted spider mite or its predator *P. persimilis*, the value of $\beta$ cannot be as high as 0.85 or 0.9 as shown in Tables 6.1 and 6.2 respectively.

It can be concluded that aggregation in prey population density is the main achievement in this chapter. There is no patch formation in prey population density and even, if there is any patch, it is quite narrow. The initial conditions play a domineering role in the pattern formation of prey population density. The formation of patches does not happen very quickly as the patchiness of prey population density $u$ happens from 200 weeks onwards.

In the next chapter formation of spatial patterns has been achieved with the presence of habitat edge inside a domain.
Chapter 7

Edge-Mediated Effects on the Formation of Spatial Patterns

7.1 Introduction

As already mentioned earlier in chapters 5 and 6, spatial patterns can only be generated from spatiotemporal heterogeneity in a predator–prey system. Like prey-taxis, predator interference or relative diffusion, presence of habitat edge inside a domain can also lead to the generation of spatial inhomogeneity in a system (Bider [13], Kareiva [79], Kareiva and Odell [80], Kareiva and Perry [81], Fagan et al. [43]). Fagan et al. [43] have defined edge “as an ecological feature that is hard to define verbally but often is immediately recognizable to observers in the field”. Thus an edge can be a boundary that separates two regions or habitats where two different species live separately. For example, on exposed intertidal shores along the northwest coast of America, the nearly continuous beds of mussel, Mytilus califarnianus, are interrupted by patches of both algae and sessile invertebrates (Sousa [149]). It is not necessary for an edge to be a sharp, step-wise boundary. It can also be a gradient-like boundary where the slope is very low. This kind of edge is frequently seen in nature. For example, changes in soil chemical content, humidity and noise levels can act as good ecological edges (Landsberg [93], Kapos [77], Ferris [45]).

Ecologists, in general, study pattern formation of species at or near habi-
tat edges. This is known as ‘edge effects’ (Odum [123], Kunin [92]). Recently there is a marked shift in interests among scientists from ‘edge effects’ to ‘edge-mediated effects’ where the focus is on the mechanism of the formation of edge-related spatial patterns rather than those patterns themselves (Kapos [77], Chen et al. [31], Saunders et al. [140], Aizen and Feinsinger [1], Kitchell et al. [86], Kareiva [79], Roland [134]). Fagan et al. [43] have studied different mechanisms of ‘edge-mediated effects’ where habitat edges have similar effects on different kinds of species interactions. Among these different mechanisms, the most widespread mechanism found in nature, is the one where edge acts as a barrier between two patches and restricts the movements of one species.

In nature, it has been seen that in many cases the presence of habitat edge influences predator–prey dynamics (Bider [13], Burkey [22], Kirkland et al. [85] Osunkoya [128], Sork [148]). Bowers and Dooley [18] have shown that during full moon periods, the mortality risk of mammalian seed predators living in Virginia old fields is increased near patch edges. During those times, the seed predators always have a tendency to move away from the patch edges and interact more inside the patches. This influences the spatial distribution of seeds in the domain. Kareiva and Odell [80] have studied predator–prey interactions between the ladybug beetle, *Coccinella septempunctata*, and the goldenrod aphid, *Uroleucon nigrotuberculatum*. In their ‘foraging-rule experiment’, aphids were distributed in patches with different uniform densities. Ladybugs were allowed to forage in rows of aphids. According to Kareiva and Odell [80], “eating time varied dramatically with prey density in a way that could be an important determinant of how many aphids a ladybug can eat in one day. In particular, as aphid density increases, ladybugs spent less time eating each aphid and apparently consume less and less of each aphid. When aphids are extremely dense, ladybugs seem to take just one big, juicy bite out of each aphid, before moving to the next victim”.

Many authors have compared ecological edges with cellular membranes or biological filters (Bider [13], Wegner and Merriam [157], Wiens et al. [159]). They have noted that some edges are impermeable and thus called ‘hard edges’ and some are permeable, like membranes, for certain species and known as ‘soft edges’. The
study in this chapter obviously considers only ‘soft edges’ and later mentioned simply as ‘edges’. In order to derive the boundary condition for the species, sensitive to the presence of an internal edge, Walsh [156], Cantrell and Cosner [23] have introduced skew Brownian motion at the edge. In skew Brownian motion it has been assumed that, when there is no boundary, individuals move according to ordinary diffusion. In the presence of a boundary, the probability that an individual will move into the region on one side of the boundary may be different than the probability it will move into the region on the other side. According to Cantrell and Cosner [23] “if the probability of crossing the boundary in either direction is 0.5, then the boundary is invisible to the population and the model for dispersal reduces to ordinary diffusion. If the probability of crossing the boundary in one direction is zero, the boundary acts as a perfectly reflecting barrier. If the probability of moving from the boundary into the region on one side is different from the probability of moving into the region on the other side then individuals display a preference for dispersing into one region rather than the other.” In most of the cases found in nature, the edge permeability is often asymmetric, i.e. the probability is neither 0 nor 0.5. For example, immigrants actively cross into patches but are quite hesitant to leave. According to Fagan et al. [43] “Such unidirectional edge filtering often results in intense, but short-lived, ‘supersaturation’ of remnant patches as animals flee recently modified matrix habitat for nearby remnants, only to have their densities decline below pre-isolation levels as resources are exhausted (Whitcomb et al. [158]).”

Nachman [117] has studied the spatial distributions of two-spotted spider mite *T. urticae* and their natural enemy, the phytoseiid predator *P. persimilis* on six full-grown cucumber plants. Initially both species have been distributed in patches and *P. persimilis* have a tendency to aggregate on leaves with abundant prey. According to Nachman [117] “the analysis clearly shows that the ability of the predators to search non-randomly increases their predation rate. On the other hand, the prey may gain if it adopts a more even distribution when its density is low and a more patchy distribution when density increases. Mutual interference between searching predators reduces the predation rate, but the effect is negligible.”
Azam et al. [6] have tested the hypothesis that habitat differences affect the migratory ability of the Chilean predatory mite, *P. persimilis*, a biological control agent of the two-spotted spider mite, *T. urticae*. To test their hypothesis the populations of the Chilean predatory mite have been established on potted bean plants in both remnant rainforest and adjacent open fields, and their migration has been monitored using sticky traps. Overall it has been found that prey populations on leaves are similar in both habitats, but those of predators are about 20% lower in rainforest. Based on the observation of Azam et al. [6], in this chapter the predator population density is chosen to be sensitive to an internal edge.

In this chapter, the aim is to investigate the edge-mediated effect on the formation of spatial patterns. If the system is unstable both with and without diffusion, it will no longer be able to support the outbreak of population densities (Ludwig et al. [102]). This will lead to inhomogeneity of population densities. Thus no spatial patterns will be generated over longer time-scale. In view of that, first of all, the stability of the points of equilibrium with diffusion has been examined as detailed in chapter 6. In order to determine the position of an internal edge, using the stability criteria, the minimum patch length is obtained. Based on the size of minimum patch length, the existing domain \([-1, 1]\) is increased to \([-2, 2]\). This domain has further been increased to \([-4, 4]\) in order to observe the effect of larger patch size on the formation of spatial patterns. Results have been verified numerically using different domain lengths with different values of predators’ sensitivity to the presence of an internal edge. Here also, Lotka–Volterra logistic predator prey equations without advection, as used in chapter 6, have been used along with three response functions, two non–homogeneous initial conditions and two data sets.

### 7.2 Mathematical model

Lotka–Volterra logistic predator–prey model with diffusion and without advection along with zero flux boundary conditions, as used in chapter 6, is also used here.

Hence the equations are rewritten here as:
\[
\frac{\partial u}{\partial t} = \rho (1 - \frac{u}{K}) u - v e f(u, v) + d_1 \frac{\partial^2 u}{\partial x^2}, \tag{7.1}
\]
\[
\frac{\partial v}{\partial t} = -\gamma v + v \sigma f(u, v) + d_2 \frac{\partial^2 v}{\partial x^2}, \tag{7.2}
\]
where all the symbols have their usual meanings as defined in chapter 3. The same three response functions, two data sets and two initial conditions, as used in chapters 3–6, are also used here.

This model represents predator–prey interactions in the entire domain. Since only one species is sensitive to the habitat, predator is chosen to be sensitive to the edge. Thus prey can move freely in the domain.

For the predator, the governing equation (Fagan et al. [43]) at the interface is:
\[
\alpha \frac{\partial v_1}{\partial x} = (1 - \alpha) \frac{\partial v_2}{\partial x}, \tag{7.3}
\]
where \( v_1 \) and \( v_2 \) are predator population densities in patch 1 and 2 respectively (Fagan et al. [43]). Here \( \alpha \) (0 < \( \alpha \) < 1) is the tendency of a predator to remain in the favourable patch or refuge. For example, when \( \alpha = 0.2 \), the left hand side patch is less favourable for the predator as compared to the right hand side one. If the value of \( \alpha \) is increased to 0.4, the left hand side becomes slightly less favourable than the right hand side one. For \( \alpha = 0.6 \), the left hand side patch is more favourable to the predator as compared to the right hand side one. If \( \alpha = 0.8 \), the left hand side patch is highly favourable to the predator as compared to the right hand side one. \( \alpha = 0.5 \) implies no bias at the habitat edge.

### 7.3 Stability of equilibria with diffusion

In this section, the stability of the points of equilibrium with diffusion are examined as detailed in section 6.4. First of all, the predator–prey equations (7.1) and (7.2) are linearised about the point of equilibrium \( E^* = (u^*, v^*) \) as shown in section 6.4.

Hence the linearised form of equations with diffusion are rewritten from section 6.4 as
\[(\lambda - a_{11} + k^2d_1)U - a_{12}V = 0, \quad (7.4)\]
\[a_{21}U + (a_{22} - d_2k^2 - \lambda)V = 0. \quad (7.5)\]

where \(a_{11}, a_{12}\) etc. are the elements of the Jacobian matrix \(J^*\) at the point of equilibrium as defined in equation (3.20).

The variational matrix \(M_4\) for equations (7.4) and (7.5) is also rewritten from section 6.4 as

\[M_4 = \begin{pmatrix}
\lambda - a_{11} + k^2d_1 & -a_{12} \\
2 & a_{21} & a_{22} - d_2k^2 - \lambda
\end{pmatrix}.\]

The corresponding eigenvalues are

\[
\lambda = \frac{1}{2}(a_{11} + a_{22} - k^2(d_1 + d_2)) \pm \frac{1}{2}[(a_{11} + a_{22} - k^2(d_1 + d_2))^2 - 4((a_{11} - d_1k^2)(a_{22} - d_2k^2) - a_{12}a_{21})^{1/2}].
\]

As already mentioned in section 6.4, the point of equilibrium is stable without diffusion if

\[a_{11} + a_{22} < 0, \quad (7.6)\]
\[\text{and} \quad a_{11}a_{22} - a_{12}a_{21} > 0. \quad (7.7)\]

Similarly, the point of equilibrium will be stable with diffusion if

\[a_{11} + a_{22} - k^2(d_1 + d_2) < 0, \quad (7.8)\]
\[(a_{11} - d_1k^2)(a_{22} - d_2k^2) - a_{12}a_{21} > 0. \quad (7.9)\]

Condition (7.9) can be written as

\[(a_{11} - d_1k^2)(a_{22} - d_2k^2) - a_{12}a_{21} > 0, \quad \Rightarrow H(k^2) > 0,
\]

where
\[ H(k^2) \triangleq d_1 d_2 k^4 - (d_1 a_{22} + d_2 a_{11}) k^2 + a_{11} a_{22} - a_{12} a_{21}. \] (7.10)

A system is stable with diffusion for \( H(k^2) > 0 \) and unstable (with diffusion) for \( H(k^2) < 0 \). Thus the bifurcation between spatially stable and unstable modes is when \( H(k^2) = 0 \). When this holds there is a critical wave number \( k_c \) which can be derived from equation (7.10) as

\[ k_c^2 = \frac{(d_1 a_{22} + d_2 a_{11})}{(2d_1 d_2)} \pm \frac{\sqrt{(d_1 a_{22} + d_2 a_{11})^2 - 4(a_{11} a_{22} - a_{12} a_{21}) d_1 d_2}}{(2d_1 d_2)}. \]

It gives

\[ k_1^2 = \frac{(d_1 a_{22} + d_2 a_{11})}{(2d_1 d_2)} + \frac{\sqrt{(d_1 a_{22} + d_2 a_{11})^2 - 4(a_{11} a_{22} - a_{12} a_{21}) d_1 d_2}}{(2d_1 d_2)}, \] (7.11)

\[ k_2^2 = \frac{(d_1 a_{22} + d_2 a_{11})}{(2d_1 d_2)} - \frac{\sqrt{(d_1 a_{22} + d_2 a_{11})^2 - 4(a_{11} a_{22} - a_{12} a_{21}) d_1 d_2}}{(2d_1 d_2)}. \] (7.12)

In the next section it has been shown that for any value of \( k \) satisfying \( k_2 < k < k_1 \), \( H(k^2) \) is negative, thus the system is unstable with diffusion. The system is, however, stable with diffusion for any value of \( k \) that satisfies the following condition:

\[ k < k_2 \text{ or } k > k_1. \] (7.13)

It is known that \( k = \frac{n \pi}{L} \) where \( n \) is the first mode of excitation and \( L \) is the length of the domain. Thus,

\[ L_1 = \frac{n \pi}{k_1}, \] (7.14)

\[ L_2 = \frac{n \pi}{k_2}, \] (7.15)

where \( L_1 \) and \( L_2 \) are the lengths of the domain for the chosen \( k_1 \) and \( k_2 \) respectively.
Combining conditions (7.9) and (7.13), one can obtain the conditions for a stable predator–prey system with diffusion as:

\[ H(k^2) > 0, \]
\[ \Rightarrow \text{either } k > k_1 \text{ or } k < k_2, \]
\[ \Rightarrow \text{either } L < L_1 \text{ or } L > L_2. \]  

(7.16)

7.4 Determination of minimum patch length

In this section, in order to determine the minimum patch length that can support the outbreak of predator population density, stability criteria of a predator–prey system as detailed in section 7.3, have been used. In view of that, following steps have been used:

**Step 1**: The predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium \((u^*, v^*)\).

**Step 2**: Values of \(u^*\) and \(v^*\) have been substituted in equation (3.20) to obtain the values of \(a_{11}, a_{12}\) etc.

**Step 3**: Values of \(a_{11}\) etc. are then substituted in conditions (7.6) and (7.7) to examine the stability of the point of equilibrium without diffusion. If condition (7.6) is not satisfied, the system is unstable. In this case, **Step 4** is followed. Otherwise, no further calculations are done.

**Step 4**: Values of \(a_{11}\) etc are substituted in equation (7.10) to obtain an expression in terms of \(k^2\). Solution of this equation in terms of \(k^2\) provides the limits of \(k\) for stable equilibrium.

**Step 5**: Values of \(k\) obtained from **Step 4**, are substituted in equations (7.14) and (7.15) to obtain expressions for \(L_1\) and \(L_2\) in terms of \(n\). Condition (7.16) provides the minimum patch length needed for spatial outbreak.

**Case 1a**

As already mentioned in section 4.6, in the case of response function (a) with Data 1, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as \((u^*, v^*) = (19.73, 4.41)\). The values of \(u^*, v^*\) are substituted in equation (3.21) to obtain the values of \(a_{11}, a_{12}\) etc. as
a_{11} = 0.124, a_{12} = -2.153, a_{21} = 0.172 and a_{22} = 0.0. Values of a_{11} etc. are then substituted in condition (7.6) to obtain (a_{11} + a_{22}) = 0.124. Since (a_{11} + a_{22}) is positive, the point of equilibrium is unstable without diffusion.

In order to determine the minimum patch length, values of a_{11} etc are further substituted in equation (7.10) to obtain

\[ H(k^2) = 0.370125 - 0.00248781k + 2.5 \times 10^{-7}k^2. \]

Graphs are drawn for \( H(k^2) \) with \( k^2 \) as an unknown parameter as shown in Figure 7.1. From the graph, it can be seen that for \( H(k^2) = 0 \), \( k_1^2 = 9800.18 \) and \( k_2^2 = 151.069 \). For any value of \( k^2 \) lying between 151.069 and 9800.18, \( H(k^2) \) is negative as shown in Figure 7.1. Hence, in order to achieve stable point of equilibrium with diffusion, i. e. \( H(k^2) > 0 \), either \( k^2 > 9800.18 \) or \( k^2 < 151.069 \), i.e. \( k > 98.9958 \) or \( k < 12.291 \). Substitution of the values of \( k_1 = 98.9958 \) and \( k_2 = 12.291 \) further in equations (7.14) and (7.15) gives \( L_1 = 0.0317346 \) and \( L_2 = 0.255601 \). In order to maintain consistency with chapters 4 and 5, the value of \( n \) is chosen to be 2. Hence \( L_1 = 0.0634692 \) and \( L_2 = 0.511202 \). Thus from equation (7.16), it can be said that spatial patterns will form if \( L < 0.0634692 \) or \( L > 0.511202 \).

**Case 1b**

As already mentioned in section 4.6, in the case of response function (b) with Data 1, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as \((u^*, v^*) = (20.19, 4.49)\). The values of \( a_{11}, a_{12} \) etc are obtained from equation (3.22) as \( a_{11} = 0.1203, a_{12} = -2.1286, a_{21} = 0.172 \), and \( a_{22} = 0.0 \). Values of \( a_{11} \) etc. are then substituted in condition (7.6) to obtain (\( a_{11} + a_{22} \)) = 0.124. Since (\( a_{11} + a_{22} \)) is positive, the point of equilibrium is unstable without diffusion.

In order to determine the minimum patch length, values of \( a_{11} \) etc are further substituted in equation (7.10) to obtain

\[ H(k^2) = 0.370125 - 0.00248781k + 2.5 \times 10^{-7}k^2. \]

Graphs are drawn for \( H(k^2) \) with \( k^2 \) as an unknown parameter as shown in Figure 7.1. From the graph, it can be seen that for \( H(k^2) = 0 \), \( k_1^2 = 9800.18 \) and \( k_2^2 = 151.069 \). For any value of \( k^2 \) lying between 151.069 and 9800.18, \( H(k^2) \) is negative as shown in Figure 7.1. Hence, in order to achieve stable point of equilibrium with diffusion, i. e. \( H(k^2) > 0 \), either \( k^2 > 9800.18 \) or \( k^2 < 151.069 \), i.e. \( k > 98.9958 \) or \( k < 12.291 \). Substitution of the values of \( k_1 = 98.9958 \) and \( k_2 = 12.291 \) further in equations (7.14) and (7.15) gives \( L_1 = 0.0317346 \) and \( L_2 = 0.255601 \). In order to maintain consistency with chapters 4 and 5, the value of \( n \) is chosen to be 2. Hence \( L_1 = 0.0634692 \) and \( L_2 = 0.511202 \). Thus from equation (7.16), it can be said that spatial patterns will form if \( L < 0.0634692 \) or \( L > 0.511202 \).
Figure 7.2: Determination of $H(k^2)$ for response function (b) with (i) Data 1 and (ii) Data 2.

0.1709 and $a_{22} = -0.0174$. Values of $a_{11}$ etc are substituted in condition (7.6) to obtain $(a_{11} + a_{22}) = 0.103$. Since $(a_{11} + a_{22})$ is positive, the point of equilibrium is unstable without diffusion.

In order to determine the minimum patch length, values of $a_{11}$ etc are further substituted in equation (7.10) to obtain

$$H(k^2) = 0.361801 - 0.00240516k + 2.5 \times 10^{-7}k^2.$$  

Graphs are drawn for $H(k^2)$ with $k^2$ as an unknown parameter as shown in Figure 7.2. From the graph, it can be seen that for $H(k^2) = 0$, $k_1^2 = 9467.8$ and $k_2^2 = 152.855$. For any value of $k^2$ lying between 152.855 and 9467.8, $H(k^2)$ is negative as shown in Figure 7.2. Hence, in order to achieve stable point of equilibrium with diffusion either $k^2 > 9467.8$ or $k^2 < 152.855$, i.e. $k > 97.3026$ or $k < 12.3635$. Substitution of the values of $k_1 = 97.3026$ and $k_2 = 12.3635$ in equations (7.14) and (7.15) gives $L_1 = 0.0322868 \, n$ and $L_2 = 0.254103 \, n$. In order to maintain consistency with chapters 4 and 5, the value of $n$ is chosen to be 2. Hence $L_1 = 0.0645736$ and $L_2 = 0.508206$. Thus from condition (7.16), it can be said that spatial patterns will form if $L < 0.0645736$ or $L > 0.508206$.

**Case 1c**

As already mentioned in section 4.6, in the case of response function (c) with Data 1, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as $(u^*, v^*) = (71.97, 5.62)$. The values of $u^*, v^*$ are substituted in equation (3.21) to obtain the values of $a_{11}, a_{12}$ etc. as $a_{11} = -0.299, a_{12} = -1.378, a_{21} = 0.026$ and $a_{22} = -0.558$. Values of $a_{11}$ etc. are
then substituted in condition (7.6) to obtain \((a_{11} + a_{22}) = -0.587\). Since \((a_{11} + a_{22})\) is negative, the point of equilibrium is stable without diffusion. Hence no further calculations are done.

**Case 2a**

As already mentioned in section 4.6, in the case of response function (a) with Data 2, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as \((u^*, v^*) = (19.6, 4.49)\). The values of \(a_{11}, a_{12}\) etc. are \(a_{11} = 0.118, a_{12} = -2.105, a_{21} = 0.187\) and \(a_{22} = 0.0\). Values of \(a_{11}\) etc are substituted in condition (7.6) to obtain \((a_{11} + a_{22}) = 0.118\). Since \((a_{11} + a_{22})\) is positive, the point of equilibrium is unstable without diffusion.

In order to determine the minimum patch length, values of \(a_{11}\) etc are further substituted in equation (7.10) to obtain

\[
H(k^2) = 0.394837 - 0.00236102k + 2.5 \times 10^{-7}k^2.
\]

Graphs are drawn for \(H(k^2)\) with \(k^2\) as an unknown parameter as shown in Figure 7.1. From the graph, it can be seen that for \(H(k^2) = 0\), \(k_1^2 = 9273.78\) and \(k_2^2 = 170.302\). For any value of \(k^2\) lying between 170.302 and 9273.78, \(H(k^2)\) is negative as shown in Figure 7.2. Hence, in order to achieve stable point of equilibrium with diffusion either \(k^2 > 9273.78\) or \(k^2 < 170.302\), i.e. \(k > 96.3005\) or \(k < 13.05\). Substitution of the values of \(k_1 = 96.3005\) and \(k_2 = 13.05\) in equations (7.14) and (7.15) gives \(L_1 = 0.0326228\) \(n\) and \(L_2 = 0.240735\) \(n\). As in Case 1a, the value of \(n\) is chosen to be 2. Hence \(L_1 = 0.0652456\) and \(L_2 = 0.48147\). Thus from condition (7.16), it can be said that spatial patterns will form if \(L < 0.0652456\) or \(L > 0.48147\).

**Case 2b**

As already mentioned in section 4.6, in the case of response function (b) with Data 2, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as \((u^*, v^*) = (20.03, 4.57)\). The values of \(a_{11}, a_{12}\) etc are \(a_{11} = 0.114, a_{12} = -2.082, a_{21} = 0.186\) and \(a_{22} = -0.018\). Values of \(a_{11}\) etc are substituted in condition (7.6) to obtain \((a_{11} + a_{22}) = 0.096\). Since \((a_{11} + a_{22})\) is positive, the point of equilibrium is unstable without diffusion.
In order to determine the minimum patch length, values of $a_{11}$ etc are further substituted in equation (7.10) to obtain

$$H(k^2) = 0.386291 - 0.00228293k + 2.5 \times 10^{-7}k^2.$$  

Graphs are drawn for $H(k^2)$ with $k^2$ as an unknown parameter as shown in Figure 7.2. From the graph, it can be seen that for $H(k^2) = 0$, $k_1^2 = 8959.24$ and $k_2^2 = 172.466$. For any value of $k^2$ lying between $172.466$ and $8959.24$, $H(k^2)$ is negative as shown in Figure 7.2. Hence, in order to achieve stable point of equilibrium with diffusion either $k^2 > 8959.24$ or $k^2 < 172.466$, i.e. $k > 94.6533$ or $k < 13.1326$. Substitution of the values of $k_1 = 94.6533$ and $k_2 = 13.1326$ in equations (7.14) and (7.15) gives $L_1 = 0.0331905$ and $L_2 = 0.23922$. As in Cases 1a and 1b, the value of $n$ is chosen to be 2. Hence $L_1 = 0.0666381$ and $L_2 = 0.47844$. Thus from condition (7.16), it can be said that spatial patterns will form if $L < 0.0666381$ or $L > 0.47844$.

**Case 2c**

As already mentioned in section 4.6, in the case of response function (c) with Data 2, the predator–prey equations (7.1) and (7.2) have been solved without diffusion to obtain the point of equilibrium as $(u^*, v^*) = (70.92, 5.88)$. The values of $a_{11}, a_{12}$ etc are $a_{11} = -0.29, a_{12} = -1.326, a_{21} = 0.0298$ and $a_{22} = -0.592$. Values of $a_{11}$ etc are substituted in condition (7.6) to obtain $(a_{11} + a_{22}) = -0.882$. Since $(a_{11} + a_{22})$ is negative, the point of equilibrium is stable without diffusion. Hence no further calculations are done.

The point of equilibrium for all models considered are shown in Table 7.1. The value of $L_1$ being very small for all the cases is neglected. So, the length of the domain is chosen to be greater than $L_2$. From Table 7.1 it can be seen that the maximum value of $L_2$ is 0.511 which occurs for response function (a) with Data 1 (Case 1a). This value of $L_2$ is chosen as the minimum domain length for numerical solutions. If any other value of $L_2$ is chosen instead of 0.511, for example, 0.48, spatial patterns will only be generated for response functions (a) and (b) with Data 2 (Cases 2a and 2b) while no spatial patterns will form for response functions (a) and (b) with Data 1 (Cases 1a and 1b).
Table 7.1: Minimum domain length for Data 1, Data 2 and response functions (a)–(c)

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp. func.</th>
<th>Point of Equilibrium</th>
<th>$a_{11} + a_{22}$</th>
<th>$a_{11}a_{22} - a_{12}a_{21}$</th>
<th>Stable/Unstable</th>
<th>$k_1$</th>
<th>$k_2$</th>
<th>Mode</th>
<th>$L_1$ (rounded values)</th>
<th>$L_2$ (rounded values)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(19.73, 4.41)</td>
<td>0.124 (+ive)</td>
<td>0.3701 (+ive)</td>
<td>Unstable</td>
<td>98.99</td>
<td>12.29</td>
<td>2</td>
<td>0.063</td>
<td>0.511</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.19, 4.49)</td>
<td>0.103 (+ive)</td>
<td>0.362 (+ive)</td>
<td>Unstable</td>
<td>97.30</td>
<td>12.36</td>
<td>2</td>
<td>0.064</td>
<td>0.508</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(71.97, 5.62)</td>
<td>-0.857 (-ive)</td>
<td>0.202 (+ive)</td>
<td>Stable</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(19.6, 4.49)</td>
<td>0.118 (+ive)</td>
<td>0.395 (+ive)</td>
<td>Unstable</td>
<td>96.3</td>
<td>13.05</td>
<td>2</td>
<td>0.065</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.03, 4.56)</td>
<td>0.096 (+ive)</td>
<td>0.386 (+ive)</td>
<td>Unstable</td>
<td>94.65</td>
<td>13.13</td>
<td>2</td>
<td>0.067</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(70.92, 5.88)</td>
<td>-0.882 (-ive)</td>
<td>0.211 (+ive)</td>
<td>Stable</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

When there is no habitat edge in the domain, that is, there is a single patch, both prey and predator can move freely. When there is an edge, the entire domain is divided in two patches where one of the species (in this case predator) is sensitive to the edge. Let the concept of domain be re-interpreted where it is equivalent to patch length. Thus the patch length should always be greater than 0.511.

In the domain $[-1, 1]$, if the edge is introduced at $x = -0.5$, then the length of left-hand side patch is 0.5 which is less than the minimum patch length. In order to have the desired patch length the domain is increased to $[-2, 2]$ from $[-1, 1]$.

### 7.5 Edge-mediated effect in the domain $[-2, 2]$

In this section, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) without advection are solved numerically for different values of $\alpha$ along with equation (7.3) in the domain $[-2, 2]$. In each case, Data 1 and Data 2 are used along with response functions (a)–(c) with each of the initial conditions (i) and (ii). In
Figure 7.3: Transient graphs for response function (a), Data 1, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.2.

In this subsection, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) are solved numerically for $\alpha = 0.2$ along with equation (7.3) in the domain $[-2, 2]$.

Case 1a

In the case of response function (a) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.3. In the absence of any habitat edge, the prey population density $u$ shows almost uniform distributions at $t = 100$ in the entire domain $[-2, 2]$. The predator population density $v$ is very
Figure 7.4: Transient graphs for response function (a), Data 1, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.2.

low, approximately equal to 0.5, in the entire domain $[-2, 2]$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.3, refuge dynamics of $u$ develops in the domain $[-2, -1)$ with a value 100, equivalent to its carrying capacity. The term ‘refuge dynamics’ in a two-species system implies the presence of only one species and the complete absence of the other. There is no coexistence of the two species in that specific domain.

There is, however, a sharp decrease in $u$ in the domain $(-1, -0.6)$. In the remaining part of the domain, $u$ decreases slowly towards 68 at $x = 2$. On the other hand $v$ has a peak at $x = -0.8$ with a value 1.

When the habitat edge is shifted to the middle of the domain, that is, at $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.3, the refuge dynamics of $u$ disappears. Instead both $u$ and $v$ show similar behaviour as that of no habitat edge.
In the case of response function (a) with Data 1 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.4. In the absence of any habitat edge, both the prey and predator population densities show fluctuations at $t = 100$ in the entire domain $[-2, 2]$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.4, $u$ has a refuge, like initial condition (i), in the domain $[-2, -1)$ with a value 100, equivalent to its carrying capacity. After a quite sharp decrease in the domain $(-1, -0.7)$, it has another peak at $x = 1.2$ with a value 20. Here $v$ has two peaks, at $x = -0.4$ and $x = 1$ respectively.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.4, the refuge dynamics of $u$ disappears. The value of $u$ remains constant in the domain $[-2, 0]$ with a value 50. Also two peaks of $u$ develops at $x = 0.1$ and 1 respectively. In this case $v$ also remains constant in the domain $[-2, 0]$ with a value 20. However, there is a sharp decrease in its value in the domain $[0, 1)$.

**Case 1b**

In the case of response function (b) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.5. In the absence of any habitat edge, $u$ shows nearly uniform distributions at $t = 100$ in the entire domain $[-2, 2]$. On the other hand, $v$ has its peak at $x = 0$ with a value 15. From $x = 0$, there is a slow decrease in the value of $v$ towards the boundaries.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.5, $u$ has a refuge in the domain $[-2, -1)$ with a value 100, equivalent to its carrying capacity. There is, however, a sharp decrease in prey population density $u$ in the domain $(-1.2, -0.8)$. In the remaining part of the domain, $u$ decreases slowly towards 5 at $x = 2$. Here $v$ has its maximum value approximately equal to 9 at $x = 1$. It also has another peak at $x = -0.8$. There is, however, a sharp decrease in the value of $v$ in the domain $(-1.1, -0.8)$.

When the habitat edge is shifted to the middle of the domain, that is, at $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.5, the refuge dynamics of $u$ disappears. Instead both $u$ and $v$ show similar behaviour as that of no habitat edge.

In the case of response function (b) with Data 1 and initial condition (ii), the
Figure 7.5: Transient graphs for response function (b), Data 1, initial condition (i) at \( t = 0 \) and 100 with \( \alpha \) as 0.2.

Initial model with no habitat edge is shown in Figure 7.6. Unlike initial condition (i), in the absence of any habitat edge, both the prey and predator population densities show fluctuations at \( t = 100 \) in the entire domain \([-2, 2]\).

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.2 \), as shown in Figure 7.6, \( u \) has a refuge, like initial condition (i), in the domain \([-2, -1]\) with a value 100, equivalent to its carrying capacity. It has another peak at \( x = 1.2 \). On the other hand \( v \) has a peak at \( x = -0.8 \).

When the habitat edge is shifted to \( x = 0 \) with \( \alpha = 0.2 \), as shown in Figure 7.6, the refuge dynamics of \( u \) disappears. Instead \( u \) moves to the right–hand side of the domain with a peak at \( x = 1 \). Here \( v \) also moves to the right–hand side of the domain with a peak only at \( x = 0.9 \). Both \( u \) and \( v \) have low but stable values in the domain \([-2, -1]\).
Figure 7.6: Transient graphs for response function (b), Data 1, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.2.

**Case 2a**

In the case of response function (a) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.7. In the absence of any habitat edge, both the prey and predators show almost uniform density distributions at $t = 100$ in the entire domain $[-2, 2]$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.7, no refuge dynamics develops for $u$ in the domain $[-2, -1)$. However it remains constant with an approximate value of 80. There is a sharp decrease in $u$ in the domain $(-1, -0.7)$. In the remaining part of the domain, the value of $u$ increases slowly to 60 at $x = 2$. On the other hand $v$ has two peaks at $x = -0.8$ and at $x = 0.5$ respectively. However, the value of $v$ remains constant in the domain $[-2, -1]$ with a value 10.
Figure 7.7: Transient graphs for response function (a), Data 2, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.2.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.7, both $u$ and $v$ show almost uniform distributions, as that of no habitat edge, in the entire domain $[-2, 2]$.

In the case of response function (a) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.8. In the absence of any habitat edge, both the prey and predator population densities show fluctuations at $t = 100$ in the entire domain $[-2, 2]$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.8, $u$ has a refuge in the domain $[-2, -1)$ with a value 100, equivalent to its carrying capacity. There is a sharp decrease in $u$ in the domain $[-1, 1]$. It has, however, a small peak with a value 30 at $x = 1.1$. In this case $v$ has a peak with a value 1 at $x = -0.9$. 
Figure 7.8: Transient graphs for response function (a), Data 2, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.2.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.8, the refuge dynamics of $u$ disappears. Instead $u$ moves to the right-hand side of the domain with a peak at $x = 1$. Predator population density $v$ also moves to the right-hand side of the domain with a peak only at $x = 0.9$. Both $u$ and $v$ have very low but constant values in the domain $[-2, -1]$. Here also predators forage in the entire domain.

Case 2b

In the case of response function (b) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.9. In the absence of any habitat edge, both the prey and predators show almost uniform density distributions at $t = 100$ in the entire domain $[-2, 2]$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Fig-
Figure 7.9: Transient graphs for response function (b), Data 2, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.2.

In Figure 7.9, no refuge dynamics develops for $u$ in the domain $[-2, -1)$. However it remains constant in the domain $[-2, -1)$ with an approximate value of 80. There is a sharp decrease in $u$ in the domain $(-1, -0.7)$. In the remaining part of the domain, the value of $u$ remains almost constant to 20 at $x = 2$. Predator population density $v$ remains constant in the domain $[-2, -1]$ with a value 10. It decreases slowly to 0 at $x = 0$.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.9, both $u$ and $v$ show almost uniform distributions, as that of no habitat edge, in the entire domain $[-2, 2]$.

In the case of response function (b) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.10. Unlike initial condition (i), in the absence of any habitat edge, both the prey and predator population...
Figure 7.10: Transient graphs for response function (b), Data 2, initial condition (ii) at \( t = 0 \) and 100 with \( \alpha \) as 0.2.

densities show fluctuations at \( t = 100 \) in the entire domain \([-2, 2]\).

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.2 \), as shown in Figure 7.10, prey population density \( u \) has a refuge, in the domain \([-2, -1]\) with a value 100. It has another peak at \( x = 1.3 \). Predator population density \( v \) has two peaks at \( x = -0.8 \) and at \( x = 1.3 \).

When the habitat edge is shifted to \( x = 0 \) with \( \alpha = 0.2 \), as shown in Figure 7.10, the refuge dynamics of \( u \) disappears. Instead the value of \( u \) remains constant in the domain \([-2, 0]\) with a value 68. It has another peak at \( x = 1.2 \). Predator population density \( v \) has two peaks at \( x = 0.3 \) and at \( x = 1 \) respectively.
Figure 7.11: Transient graphs for response function (a), Data 1, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.6.

### 7.5.2 Edge-mediated effect for $\alpha = 0.6$

In this subsection, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) are solved numerically for $\alpha$ as 0.6 along with equation (7.3) in the domain $[-2, 2]$.

Since response function (c) has stable point of equilibrium for all data sets, spatial dynamics of both prey and predator show similar behaviour for both $\alpha = 0.2$ and 0.6. Thus the corresponding graphs for response function (c) with $\alpha = 0.6$ are not reproduced here.

**Case 1a**

In the case of response function (a) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.11.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.11, both the prey and predator population densities show similar behaviour.
Figure 7.12: Transient graphs for response function (a), Data 1, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.6.

As that of with $\alpha = 0.2$, shown in Figure 7.3.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.11, both $u, v$ forage in the entire domain and have symmetrical distributions on both sides of $x = 0$. At $x = 0$, the value of $u$ is approximately equal to 5 and that of $v$ is approximately equal to 1. Also $u$ has two flattened peaks at $x = -1$ and at $x = 1$ respectively.

In the case of response function (a) with Data 1 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.12.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.12, both the prey and predator population densities show similar behaviour as that of with $\alpha = 0.2$, shown in Figure 7.4.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.12,
prey population density $u$ has two peaks at $x = 0$ and at $x = 1.1$ respectively. There is a sharp decrease in the value of $u$ in the domain $(-0.2, 0]$. From $x = -0.2$, the value of $u$ decreases slowly to 5 at $x = -2$. On the other hand, predator population density $v$ has three peaks at $x = -0.2$, at $x = 0.2$ and at $x = 1$ respectively.

**Case 1b**

In the case of response function (b) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.13.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.13, both the prey and predator population densities show similar behaviour as that of with $\alpha = 0.2$ given in Figure 7.5.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.13, both $u, v$ forage in the entire domain $[-2, 2]$. Here, both $u, v$ have symmetrical
Figure 7.14: Transient graphs for response function (b), Data 1, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.6.

distributions on both sides of $x = 0$. At $x = 0$, the value of $u$ is maximum, approximately equal to 85. From $x = 0$, the value of $u$ decreases towards the boundaries. In the case of $v$, at $x = 0$, its value is minimum, approximately equal to 2.5. It has two peaks at $x = -1$ and at $x = 1$ respectively with a value 18.

In the case of response function (b) with Data 1 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.14.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.14, both the prey and predator population densities show similar behaviour as that of with $\alpha = 0.2$ given in Figure 7.6.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.14, $u$ has a peak at around $x = 0$. On the other hand, predator population density $v$ has one peak at around $x = -0.2$. 
Figure 7.15: Transient graphs for response function (a), Data 2, initial condition (i) at \( t = 0 \) and 100 with \( \alpha \) as 0.6.

**Case 2a**

In the case of response function (a) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.15.

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.6 \), as shown in Figure 7.15, both the prey and predator population densities show different behaviour as that of with \( \alpha = 0.2 \), shown in Figure 7.7. In this case, both prey and predator forage in the entire domain \([-2, 2]\) as shown in Figure 7.15. Prey population density \( u \) has a maximum value approximately equal to 64 at \( x = 2 \). From that point, the value of \( u \) decreases slowly to 5 at \( x = 0 \). In the remaining part of the domain, the value of \( u \) remains constant. On the other hand, predator population density \( v \) has its maximum value 25 at \( x = 0.5 \). From this point, the value of \( v \) decreases slowly to 0.5 at \( x = -2 \) and to 15 at \( x = 2 \) respectively.
Figure 7.16: Transient graphs for response function (a), Data 2, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.6.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.15, here also, both prey and predator forage in the entire domain. In this case, both $u$ and $v$ have symmetrical distributions on both sides of $x = 0$. Prey population density $u$ has a minimum value approximately equal to 12 at $x = 0$. From this point, the value of $u$ increases to 65 at the boundaries. Predator population density $v$ has a minimum value approximately equal to 0.1 at $x = 0$. It has two peaks with a value 15 at $x = -1$ and 1 respectively. From this point, the value of $v$ decreases to 3.5 at the boundaries.

In the case of response function (a) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.16.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.16, both the prey and predator population densities show similar behaviour.
Figure 7.17: Transient graphs for response function (b), Data 2, initial condition (i) at \( t = 0 \) and 100 with \( \alpha \) as 0.6.

as that of with \( \alpha = 0.2 \), shown in Figure 7.8.

When the habitat edge is shifted to \( x = 0 \) with \( \alpha = 0.6 \), as shown in Figure 7.16, \( u \) has two peaks at \( x = 0 \) and at \( x = 1 \) respectively. There is a sharp increase in the value of \( u \) in the domain \((-0.8, 0]\). From \( x = -0.8 \), the value of \( u \) decreases slowly to 25 at \( x = -2 \). On the other hand, predator population density \( v \) has its peak at \( x = -0.2 \). From \( x = -0.2 \), the value of \( v \) decreases slowly to 0.1 at \( x = -2 \). On the other side, the value of \( v \) decreases slowly to 0 at \( x = 1.5 \).

**Case 2b**

In the case of response function (b) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.17.

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.6 \), as shown in Figure 7.17, both the prey and predator population densities show different behaviour
as that of with $\alpha = 0.2$, shown in Figure 7.9. In this case, both prey and predator forage in the entire domain $[-2, 2]$. The values of both $u$ and $v$ are almost constant in the domain $(-0.3, 2]$ and $[-2, -1)$ respectively.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.17, here also, both prey and predator forage in the entire domain $[-2, 2]$. In this case, both $u, v$ have symmetrical distributions on both sides of $x = 0$. At $x = 0$, the value of $u$ is approximately equal to 50. From this point, the value of $u$ sharply decreases to 6 at $x = -0.2$ and $x = 0.2$ respectively. From these points, the value of $u$ increases to 40 at the boundaries. On the other hand, at $x = 0$, the value of $v$ is 15. From this point, the value of $v$ decreases slowly to 2.5 at $x = -0.5$ and $x = 0.5$ respectively. From these points, the value of $v$ increases to 13 at the boundaries.
In the case of response function (b) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.18.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.6$, as shown in Figure 7.18, both the prey and predator population densities show similar behaviour as that of with $\alpha = 0.2$, shown in Figure 7.10.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.6$, as shown in Figure 7.18, prey population density $u$ has its peak with a value 70 at $x = 1$. From this point, the value of $u$ decreases slowly to 5 at $x = 0$. From $x = 0$, it increases slowly to 35 at $x = -2$. Also from, $x = 1$, there is a sharp decrease in the value of $u$ to 0 in the domain $[1, 1.5)$. On the other hand, predator population density $v$ has its peak at $x = -0.5$. from this point, it decreases slowly to 0.1 at $x = -2$ and to 0 at $x = 1.5$.

7.6 Edge-mediated effect in the domain $[-4, 4]$

In this section, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) are solved numerically for different values of $\alpha$ along with equation (7.3) in the domain $[-4, 4]$ with a view to observe the effect of increased domain / patch size on spatial patterns. Like the previous subsection, here also Data 1 and Data 2 are used along with response functions (a) and (b) with each of the initial conditions (i) and (ii). In each model, three different situations are considered – no habitat edge, edge at $x = -1$ and edge at $x = 0$. In all the cases, transient graphs are given for $t = 0$ and 100.

7.6.1 Edge-mediated effect for $\alpha = 0.2$

In this subsection, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) are solved numerically for $\alpha$ as 0.2 along with the equation (7.3) in the domain $[-4, 4]$.

Case 1a

In the case of response function (a) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.19. In the absence of any
Figure 7.19: Transient graphs for response function (a), Data 1, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.2.

habitat edge, prey population density $u$ has three peaks - at $x = -3, 0$ and 3 respectively. Predator population density $v$ has only a peak at $x = 0$.

When the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.19, $u$ has a refuge in the domain $(-3, -1)$ with a value 100, equivalent to its carrying capacity. Then it decreases slowly to 2 at $x = 1$. In the rest of the domain, it shows the similar behaviour as that of no habitat edge. On the other hand, $v$ has its peak at $x = 0$ with a value 21. From this point, it increases to 0 at $x = -1$ and 3.2 respectively.

As the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.19, both $u$ and $v$ show similar pattern as that of no habitat edge.

In the case of response function (a) with Data 1 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.20. In the absence of any
hAmong habitat edge, prey population density $u$ has two peaks at $x = 0.2$ and $1$ respectively. Predator population density $v$ has two peaks at $x = -4$ and $1$ respectively.

When the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.20, $u$ has a refuge the domain $[-4, -1]$ with a value $100$, equivalent to its carrying capacity. It has another peak at $x = 1$. On the other hand, $v$ has two peaks at $x = -1$ and $1$ respectively.

As the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.20, refuge dynamics of $u$ disappears. Instead the value of $u$ increases slowly in the domain $[-4, 0]$. It has another peak at $x = 1$. In the case of predator, the value of $v$ is slowly decreased in the domain $(-4, 0]$. From $x = 0$, there is a sharp decrease in the value of $v$ to $0$ at $x = 1.4$.
Case 1b

In the case of response function (b) with Data 1 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.21. In the absence of any habitat edge, both prey and predator population densities have symmetrical distributions around \( x = 0 \) at \( t = 100 \). Prey population density \( u \) has two peaks, at \( x = -3 \) and 3 respectively. On the other hand, predator population density \( v \) has two peaks at \( x = -2.8 \) and 2.8 respectively. In between these two peaks, the value of \( v \) is very low, approximately equal to 0.5.

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.2 \), as shown in Figure 7.21, prey population density \( u \) has a refuge in the domain \((-3, -1)\) with a value 100, equivalent to its carrying capacity. There is a sharp decrease in the value of \( u \) in the domain \((-1, -0.5)\). In the rest of the domain, \( u \) shows the similar
behaviour as that of no habitat edge. On the other hand, predator population density \( v \) has two peaks at \( x = -0.8 \) and 2.8 respectively. At \( x = 2.8 \), the value of \( v \) is maximum, approximately equal to 2.5.

When the habitat edge is shifted to \( x = 0 \) with \( \alpha = 0.2 \), as shown in Figure 7.21, both \( u \) and \( v \) show similar behaviour as that of no habitat edge.

In the case of response function (b) with Data 1 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.22. In the absence of any habitat edge, prey population density \( u \) has two peaks at \( x = -1.8 \) and 1.1 respectively. Predator population density \( v \) also has two peaks at \( x = -1 \) and 1 respectively.

As the habitat edge is introduced at \( x = -1 \) with \( \alpha = 0.2 \), as shown in Figure 7.22, prey population density \( u \) has a refuge in the domain \([-4, -1)\) with a
Figure 7.23: Transient graphs for response function (a), Data 2, initial condition (i) at \( t = 0 \) and 100 with \( \alpha \) as 0.2.

value 100, equivalent to its carrying capacity. It has another peak at \( x = 1 \). There is a sharp decrease in the value of \( u \) in the domain \((-1, -0.5)\) and \((1, 1.5)\). Predator population density \( v \) has its peak at \( x = 1 \). There is a sharp decrease in the value of \( v \) in the domain \((-1, -0.5)\) and \((1, 1.8)\).

When the habitat edge is shifted to \( x = 0 \) with \( \alpha = 0.2 \), as shown in Figure 7.22, both \( u \) and \( v \) remains almost constant in the domain \([-4, 0]\). Also \( u \) has a peak with a value 75 at \( x = 1 \). On the other hand, \( v \) has its peak at \( x = 1 \), and then decreases slowly towards 0 at \( x = 1.5 \).

**Case 2a**

In the case of response function (a) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.23. In the absence of any habitat edge, both prey and predator population densities have symmetrical
Figure 7.24: Transient graphs for response function (a), Data 2, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.2.

distributions around $x = 0$ at $t = 100$. Prey population density $u$ has two peaks, at $x = -3$ and 3 respectively. On the other hand, predator population density $v$ has two peaks at $x = -2.8$ and 2.8 respectively. In between these two peaks, the value of $v$ is very low, approximately equal to 0.5.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.23, $u$ remains almost constant in the domain $(-3, -1)$ with a value 100, equivalent to its carrying capacity. There is a sharp decrease in the value of $u$ in the domain $(-1, -0.5)$. In the rest of the domain, $u$ shows the similar behaviour as that of no habitat edge. On the other hand, predator population density $v$ has two peaks at $x = -1$ and 2.8 respectively. At $x = -1$, the value of $v$ is maximum, approximately equal to 2.5.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.23,
both $u$ and $v$ show similar behaviour as that of no habitat edge.

In the case of response function (a) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.24. In the absence of any habitat edge, prey population density $u$ has two peaks at $x = -1.5$ and 1.2 respectively. Predator population density $v$ also has two peaks at $x = -0.4$ and 1 respectively.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.24, prey population density $u$ has a refuge in the domain $[-4, -1)$ with a value 100, equivalent to its carrying capacity. It has another peak at $x = 1$. There is a sharp decrease in the value of $u$ in the domain $(-1, -0.5)$ and $(1, 1.4)$. Predator population density $v$ has its peak at $x = 1$. There is a sharp decrease in the value of $v$ in the domain $(-1, -0.8)$ and $(1, 1.7)$.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.24, both $u$ and $v$ remains almost constant in the domain $[-4, 0]$. Also $u$ has a peak with a value 75 at $x = 1$. On the other hand, $v$ has a peak with a value 8 at $x = 0.9$ and then decreases slowly towards 0 at $x = 1.5$.

Case 2b

In the case of response function (b) with Data 2 and initial condition (i), the initial model with no habitat edge is shown in Figure 7.25. In the absence of any habitat edge, both prey and predator population densities have symmetrical distributions around $x = 0$ at $t = 100$.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.25, $u$ remains almost constant in the domain $(-3, -2)$ with a value 100, equivalent to its carrying capacity. In the remain part of the domain, $u$ has two peaks at $x = 1$ and at $x = 3$ respectively. On the other hand, predator population density $v$ has two peaks at $x = 1.8$ and at $x = 3$ respectively.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.25, both $u$ and $v$ show similar behaviour as that of no habitat edge.

In the case of response function (b) with Data 2 and initial condition (ii), the initial model with no habitat edge is shown in Figure 7.26. In the absence of any habitat edge, prey population density $u$ has two peaks at $x = -3$ and at $x = 1$
Figure 7.25: Transient graphs for response function (b), Data 2, initial condition (i) at $t = 0$ and 100 with $\alpha$ as 0.2.

respectively. Predator population density $v$ also has two peaks at $x = -2.5$ and at $x = 1$ respectively.

As the habitat edge is introduced at $x = -1$ with $\alpha = 0.2$, as shown in Figure 7.26, prey population density $u$ has a refuge in the domain $[-4, -1)$ with a value 100, equivalent to its carrying capacity. It has another peak at $x = 1$. Predator population density $v$ has two peaks at $x = -1.8$ and at $x = 1$ respectively.

When the habitat edge is shifted to $x = 0$ with $\alpha = 0.2$, as shown in Figure 7.26, $u$ has two peaks at $x = 0$ and at $x = 1.1$. The value of $u$ tends to be 40 at $x = -4$. Predator population density $v$ has two peaks at $x = 0.5$ and at $x = 1.1$ respectively.
7.7 Discussion and conclusion

In this chapter, formation of spatial patterns for *P. persimilis* and *T. urticae* has been achieved with the introduction of an internal edge in the domain. First of all, Lotka–Volterra logistic predator–prey equations (7.1) and (7.2) have been solved to obtain the point of equilibrium. Next, stability of the point of equilibrium with diffusion has been examined using variational matrix criterion. Based on this result, minimum patch length for spatial patterns has been obtained and the domain length is increased to [−2, 2] from [−1, 1]. Since response function (c) has a stable point of equilibrium, it is not considered further to study pattern formation.

Predator–prey equations (7.1) and (7.2) along with equation (7.3) have been solved numerically to study spatial patterns and how these patterns are affected by the position of an internal edge including the tendency of predators to remain in a

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Figure 7.26: Transient graphs for response function (b), Data 2, initial condition (ii) at $t = 0$ and 100 with $\alpha$ as 0.2.
favourable patch. Both response functions (a) and (b) along with Data 1, Data 2 have been studied with internal edges at $x = -1$ and $x = 0$ for $\alpha = 0.2$ and $0.6$ in the domains $[-2, 2]$ and $[-4, 4]$ respectively. In all the cases results are shown for both initial conditions (i) and (ii).

It has been observed that for $\alpha = 0.2$, with the habitat edge at $x = -1$, in general prey population density takes a refuge in $[-2, -1]$ for both response functions (a) and (b) along with Data 1, Data 2 and initial conditions (i), (ii) as shown in Figures 7.3–7.10. However, there are exceptions in the cases of response functions (a) and (b) along with Data 2 and initial condition (i) as shown in Figures 7.7 and 7.9 respectively. When the habitat edge is shifted to $x = 0$, i.e. patch lengths are the same, in the case of initial condition (i) with response functions (a) and (b) along with Data 1 and Data 2, both prey and predator populations show similar behaviour (uniform or near uniform or symmetrical density distributions) as that of no habitat edge in the domain $[-2, 2]$ as shown in Figures 7.3, 7.5, 7.7 and 7.9. This shows that initial conditions play crucial roles in the formation of spatial patterns.

When the value of $\alpha$ is increased to 0.6 from 0.2, with the habitat edge at $x = -1$, prey population density takes a refuge in $[-2, -1]$ for both response functions (a) and (b) along with Data 1, Data 2 and initial condition (ii) as shown in Figures 7.12, 7.14, 7.16 and 7.18. With $\alpha = 0.6$ and the habitat edge at $x = 0$, in the case of initial condition (i) with response functions (a) and (b) along with Data 1 and Data 2, both prey and predator populations density show symmetrical distributions around $x = 0$. In comparison to the case of $\alpha = 0.2$, their behaviours are different from that of no habitat edge as shown in Figures 7.11, 7.13, 7.15 and 7.17. Thus the tendency of a predator to remain in a favourable patch plays significant role in the spatial distribution of both prey and predator population density.

In order to examine the effect of the size of a patch on the pattern formation, further investigation is done in section 7.6. In the case of initial condition (i) with $\alpha = 0.2$, in comparison to domain $[-2, 2]$ with domain $[-4, 4]$, with no habitat edge, prey population density produces peaks on both sides of domain $[-4, 4]$ as shown in Figures 7.19, 7.21, 7.23 and 7.25. On the other hand, in the domain $[-2, 2]$ the
prey population has simply spread without any peak in the domain \([-2, 2]\) as shown in Figures 7.3, 7.5, 7.7, 7.9 and 7.11. With habitat edge at \(x = -1\), concentration for the prey population has simply extended to \((-3, -1)\). With the habitat edge at \(x = 0\), prey population has again produced peaks on the both sides of domain \([-4, 4]\).

In case of initial condition (ii) in comparison to domain \([-2, 2]\) with domain \([-4, 4]\), with no habitat edge, prey population stay on the left of domain \([-4, 4]\), as shown in Figures 7.20, 7.22, 7.24 and 7.26. However in the domain \([-2, 2]\) it moves to the right of domain \([-2, 2]\) as shown in Figures 7.6, 7.8 and 7.10. With habitat edge at \(x = -1\), refuge situation for the prey population has simply extended to \([-4, -1]\) from \([-2, -1]\). With the habitat edge at \(x = 0\), there is no major impact of the increased domain size \([-4, 4]\), on the pattern formation as compared to the patterns produced in domain \([-2, 2]\).

\(\alpha = 0.6\) has not produced much difference in the pattern formation. Thus graphs for \(\alpha = 0.6\) in the domain \([-4, 4]\) have not been produced here.

In this chapter various aspects of spatial patterns generated with the introduction of an internal edge in a domain have been considered. It is concluded that the length of a patch in a domain is very crucial to achieve spatial patterns such as refuge of prey populations. This behavior of prey populations can help to achieve biological control of insects in a predator-prey system.

In the next chapter biological control of two-spotted spider mite has been achieved with the introduction of prey-taxis in the predator–prey system.
Chapter 8

Effect of Prey-taxis on Biological Control

8.1 Introduction

There has been much interest in the control of pests by a natural enemy. It has been shown by Bigger [14], Flaherty and Huffaker [46], Ghabbour [56], Huffaker and Kennett [74], and others that pesticides may cause more problems than they cure by killing off a greater percentage of the enemies than of the pests, or, as Bigger [14] has remarked, by shifting the system away from its equilibrium (Freedman [49]). Theoretical ecologists have been able to identify the methods or processes where it is possible that predator is able to maintain temporal and spatial variability of prey density low enough to avoid outbreaks above the economic threshold. One of the primary process is nonrandom search, that is, the tendency of predators to aggregate where prey are abundant, can bring stability in the system (Hassell and May [69, 70], Hassell [67], Free et al. [51], May [105], Chesson and Murdoch [32]). High searching efficiency, low handling time and directed movement of predator towards the prey, that is, prey-taxis are key points of successful biological control (Sapoukhina et al. [139]).

*P. persimilis* is an well known biological control agent of two-spotted spider mite. The ability of this predator to control two-spotted spider mites has been demonstrated on many plants, including cucumber (Gould [58, 59]), tomato (French
et al. [52]), ornamental ivy (Gould and Light [60]), rose (Simmonds [145], Boys and Burbutis [19]), lima bean (Force [48]), dahlia (Harris [64]) and strawberry (Laing and Huffaker [97]). Although these studies were conducted under greenhouse conditions (or in growth chambers), there is evidence that *P. persimilis* can be an effective natural enemy in commercial strawberry plantings (McMurtry et al. [110]) and on ornamental plants in commercial interior plantings (Lindquist [98]).

According to Biobest [15] “For a successful biological control it is important to detect the pest presence on time and to act immediately. As a spider mite population grows faster in summer and it is then more difficult to keep pace with it, it is advised to control them early in the season as soon as the first spider mites wake up from hibernation. After detecting the first spider mite hot spots, *P. persimilis* is released as soon as possible. Depending on the crop and the circumstances, an overall introduction of 3 - 6 *P. persimilis*/m² is advised. On and around the infested plants approximately 20 predatory mites/m² are released. In order to be sure to obtain a biological balance early in the season, some growers prefer the Pre-
*Phytoseiulus*-System. This consists of one tube of *P. persimilis* mites and two tubes of spider mites. On one plant two doses of spider mites are released on two different spots. In one of both introduction spots, one dose of *P. persimilis* is added. The predatory mites first exterminate the first spider mite colony, and then go looking for other spider mite colonies. Thanks to this early balance spider mite hot spots are kept down as from their emergence. In normal conditions *P. persimilis* is able to protect the crop from spider mites for the rest of the cropping season. However, at dry and warm weather problems can still appear. Experience has shown that in this case, the control activity of *P. persimilis* can be supported by creating high relative humidity by spraying water with high pressure and through a fine nozzle.”

The main aim of biological control is in general, first, to lower the prey population density and then to maintain it below economic threshold for longer time by adding suitable predator in the system. The efficiency of any biological control model is determined by the ratio “between the equilibrium population size of the pest in the presence and in the absence of the natural enemy” (Beddington et al. [9], Sapoukhina et al. [139]). From different field data Beddington et al. [9] have
observed that, in many successful cases of biological control, this ratio does not exceed 2.5% (Sapoukhina et al. [139]). Any mathematical model for a predator–prey system must show stable dynamics at such low prey density. According to Sapoukhina et al. [139] “pest extinctions or fluctuations that do not exceed the economic threshold all or most of the time are compatible with satisfactory control (Murdoch et al. [115]).”

Based on these observations, the main aim in this study is to lower the prey population density below its economic threshold, i.e. the ratio does not exceed 2.5% of the carrying capacity, and to maintain it for longer time. Since carrying capacity of two-spotted spider mite is 100, for successful biological control, the prey population should not exceed 2.5 at all or most of the time. In this chapter, a theoretical study to predict a low level of population densities is done through the development of interactions between prey *T. urticae* and predator *P. persimilis* populations. Data 1 and Data 2 have been used here as the chosen set of parameters with response functions (a), (b) and (c). Among all other parameters only two of these parameters, $\phi$ and $\gamma$ (Kozlova et al. [90]), have been varied to obtain the desired model with low population density. Any variations in these parameters $\phi$ and $\gamma$ reflect respectively the changes in searching effectiveness and mortality rate of the predator. The possibility of such changes in values of $\phi$ and $\gamma$ are discussed, for example, by McCauley et al. [108], Workman and Martin [161], Drukker et al. [41] and Garms et al. [54].

### 8.2 Mathematical model

In one-dimensional form the predator–prey-taxis equations (Arditi et al. [5], Harrison [65], Sapoukhina et al. [139], Chakraborty et al. [30]) are rewritten as:

\[
\frac{\partial u}{\partial t} = \rho(1 - \frac{u}{K})u - vef(u,v) + d_1 \frac{\partial^2 u}{\partial x^2}, \tag{8.1}
\]

\[
\frac{\partial v}{\partial t} = -\gamma v + v\sigma f(u,v) - \frac{\partial(vw)}{\partial x} + d_2 \frac{\partial^2 v}{\partial x^2}, \tag{8.2}
\]

\[
\frac{\partial w}{\partial t} = T \frac{\partial u}{\partial x} + d_3 \frac{\partial^2 w}{\partial x^2}, \tag{8.3}
\]
where all the symbols have their usual meanings as defined in chapter 3.

8.3 Response functions

The same response functions as used in chapter 3 have also been used here. The data sets 1 and 2 obtained in section 3.9 have been used here. The predator interference parameter \( \beta = 0.1 \), carrying capacity parameter \( K = 100 \), specific prey growth rate parameter \( \rho = 0.6 \), diffusivity constants \( d_1 = 0.0000125 \), \( d_2 = 0.02 \) and \( d_3 = 0.0 \) have not been changed throughout this study. Different values of prey-taxis coefficient \( T \) have been chosen in order to observe its effect on the periodicity of the predator-prey dynamics.

Hence the two data sets are:

\[
\text{(Data 1)} \quad \phi = 19.409, \quad \gamma = 1.55, \quad \sigma = 3.0744, \quad e = 4.27,
\]
\[
\text{(Data 2)} \quad \phi = 20.524, \quad \gamma = 1.60, \quad \sigma = 3.2756, \quad e = 4.31.
\]

Initial condition (i), already used in chapter 3, has also been used here. The numerical scheme of operator splitting method and the boundary conditions of zero flux as used in chapter 3 have also been used here.

8.4 Stability of equilibria without diffusion and prey-taxis

As already mentioned in section 6.4, the point of equilibrium will be stable, if the real parts of the eigenvalues of the variational matrix \( M_4 \) are negative and the determinant of the matrix is positive.

Hence equations (6.7) and (6.8) are reproduced here as:

\[
a_{11} + a_{22} < 0, \quad (8.4)
\]
\[
\text{and} \quad a_{11}a_{22} - a_{12}a_{21} > 0, \quad (8.5)
\]
where \(a_{11}, a_{12}\) etc are the elements of the variational matrix \(J^*\) defined in equation (3.20).

### 8.5 Stability of equilibria with diffusion and prey-taxis

In order to examine the stability of equilibria with prey-taxis, Routh–Hurwitz’s conditions, as detailed in section 4.5, have been used here. Hence the conditions are rewritten as:

\[
\begin{align*}
 p(k^2) &> 0, \quad (8.6) \\
 r(k^2) &> 0, \quad (8.7) \\
 p(k^2)q(k^2) - r(k^2) &> 0, \quad (8.8)
\end{align*}
\]

where

\[
\begin{align*}
 p(k^2) &= k^2(d_1 + d_2 + d_3) - (a_{11} + a_{22}), \quad (8.9) \\
 q(k^2) &= k^4(d_1d_2 + d_2d_3 + d_3d_1) - c_1k^2 + c_2, \quad (8.10) \\
 r(k^2) &= k^2(d_1d_2d_3k^3 - a_{11}d_2d_3k^2 - a_{12}a_{21}d_3 \\
 &\quad + a_{12}v^*T + a_{11}a_{22}d_3 - a_{22}d_1d_3k^2). \quad (8.11)
\end{align*}
\]

Here \(c_1\) and \(c_2\) are given as

\[
\begin{align*}
 c_3 &= d_2d_3 + d_1d_3 + d_1d_2, \\
 c_4 &= a_{22}d_3 + a_{11}d_3 + a_{22}d_1 + a_{11}d_2.
\end{align*}
\]

### 8.6 Estimation of parameters for biological control with prey-taxis

For successful low level of population densities of both prey and predator, the parameters \(\phi\) and \(\gamma\) have been estimated along with the variation of prey-taxis.
in such a way that the condition of the economic threshold is satisfied. In the presence of prey-taxis the predators always go for the place where the prey density is maximum. As soon as prey density starts decreasing, predators move to a place of higher prey density leaving behind some prey to grow and reproduce. Thus the prey population density below the economic threshold can be achieved only in a heterogeneous domain. Both predator and prey can survive for a longer time without any immigration of prey.

For successful biological control in space over longer time-scale, the point of equilibrium needs to be stable both with and without prey-taxis. In view of this, the following steps have been used (Chakraborty et al. [28]):

**Step 1**: Limit on predator mortality rate $\gamma$ is obtained for which $u^* \leq 0.025K$ as well as $2u^* \leq v^* \leq 5u^*$. In this study, carrying capacity parameter $K$ is chosen to be 100. This gives $u^* \leq 2.5$.

**Step 2**: Limit on parameter $\gamma$ is further investigated for which the point of equilibrium is stable and $u^* \leq 2.5$, $2u^* \leq v^* \leq 5u^*$. If there exists such a value of $\gamma$, **Step 4** is followed. Otherwise, we proceed to **Step 3**.

**Step 3**: Here a value of parameter $\gamma$ is considered for which both $u^* \leq 2.5$ and $2u^* \leq v^* \leq 5u^*$ are satisfied but the point of equilibrium is unstable. In order to obtain a stable point of equilibrium, bifurcation value of half-saturation $\phi$ is obtained. Here a value of $\phi$ is chosen for which the point of equilibrium is stable. Next **Step 5** is followed.

**Step 4**: With the new value of $\gamma$, obtained in **Step 3**, limit on prey-taxis coefficient $T$ is also obtained for which the point of equilibrium becomes stable from unstable.

**Step 5**: With those new values of $\gamma$ and $\phi$, obtained in **Step 3**, limit on prey-taxis coefficient $T$ is obtained for which the point of equilibrium becomes stable from unstable (Chakraborty et al. [28]).

### 8.6.1 Stability of equilibria without prey-taxis

**Case 1a**

In this case, response function (a) is considered with Data 1. With $\gamma$ as an unknown parameter, the point of equilibrium $(u^*, v^*)$ is expressed as a solution of
equations (8.1) and (8.2), in the absence of diffusion and advection, as

\[
\begin{align*}
    u^* &= \frac{97.045\gamma}{15372 - 5000\gamma}, \\
    v^* &= \frac{6.44 - 2.503\gamma}{(1.5 - 0.5\gamma)^2}.
\end{align*}
\]

Substitution of \( u^* = 2.5 \) gives \( \gamma = 0.350815 \). Thus any value of \( u^* \leq 2.5 \) will give \( \gamma \leq 0.350815 \).

In order to maintain difference between prey and predator population densities in the entire domain, \( 2u^* \leq v^* \leq 5u^* \) has been chosen.

This gives

\[
\begin{align*}
    v^* - 2u^* &= \frac{9.7(-3.12 + \gamma)(-0.213 + \gamma)}{(1.5 - 0.5\gamma)^2} \triangleq f(\gamma) \text{ and} \\
    5u^* - v^* &= \frac{24.2(-3.09 + \gamma)(-0.086 + \gamma)}{(1.5 - 0.5\gamma)^2} \triangleq h(\gamma).
\end{align*}
\]

A graph has been drawn for \( f(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.1. From the graph, it can be seen that for any value of \( \gamma \) lower than 0.213, \( f(\gamma) \) is positive.

\[
\begin{align*}
    f(\gamma) &> 0 \implies v^* - 2u^* > 0 \\
    &\implies v^* > 2u^* \text{ for } \gamma < 0.213.
\end{align*}
\]

Similarly a graph has been drawn for \( h(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.1. From the graph, it can be seen that for any value of \( \gamma \) greater than 0.0859, \( h(\gamma) \) is positive.

\[
\begin{align*}
    h(\gamma) &> 0 \implies 5u^* - v^* > 0 \\
    &\implies 5u^* > v^* \text{ for } \gamma > 0.0859.
\end{align*}
\]

Hence it can be said that for \( 0.0859 \leq \gamma \leq 0.213 \), both \( u^* \leq 2.5 \) and \( 2u^* \leq v^* \leq 5u^* \) hold true.
Also the point of equilibrium is stable if condition (8.4) is satisfied. The values of \( u^* \) and \( v^* \) are substituted in equation (3.21) to obtain the values of \( a_{11}, a_{12}, a_{21} \) and \( a_{22} \) in terms of \( \gamma \). The values of \( a_{11} \) etc are then substituted in condition (8.4) to obtain

\[
a_{11} + a_{22} = \frac{0.12\gamma(-2.075 + \gamma)}{-1.5 + 0.5\gamma} \triangleq g(\gamma).
\]

A graph has been drawn for \( g(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.2. From the graph, it can be seen that \( g(\gamma) \) is negative for \( \gamma > 2.075 \).

\[
g(\gamma) \quad < \quad 0
\]

\[
\Rightarrow a_{11} + a_{22} \quad < \quad 0 \quad \text{for} \quad \gamma > 2.075.
\]

Therefore the condition of stability holds for \( \gamma > 2.075 \). There is no value of \( \gamma \) satisfying both \( 0.0859 \leq \gamma \leq 0.213 \) and \( g(\gamma) < 0 \). With a view to choose a value of \( \gamma \) in the interval \( 0.0859 \leq \gamma \leq 0.213 \), the value of \( \gamma \) is chosen to be 0.2. The point of equilibrium for this value of \( \gamma \) is unstable.
Figure 8.3: Bifurcation value of $\phi$ for response function (a) with Data 1 and 2.

With $\phi$ as an unknown parameter, the point of equilibrium $(u^*, v^*)$ has been expressed as a solution of equations (8.1) and (8.2) for $\gamma = 0.2$, in the absence of diffusion and advection, as

$$u^* = 0.0695797\phi,$$

$$v^* = 0.1503(1 - 0.0007\phi)\phi.$$

Thus in term of $\phi$, condition (8.4) can be written as

$$a_{11} + a_{22} = 0.039 - 0.000445\phi \triangleq M(\phi).$$

A graph has been drawn for $M(\phi)$ with $\phi$ as an unknown parameter as shown in Figure 8.3. From the graph, it can be seen that $M(\phi)$ is negative for $\phi > 87.784$. Thus for any value of $\phi > 87.784$, the point of equilibrium is stable.

Now $\phi = 88.784$ is chosen which is slightly higher than the bifurcation value 87.784. With $\phi = 88.784$ and $\gamma = 0.2$, the point of equilibrium is stable without prey-taxis.

The characteristics of equilibria for all the cases are given in Table 8.1.

The high value of $\phi = 88.784$ is close to the carrying capacity 100, and thus is not realistic. The half-saturation parameter $\phi$ can be described as $\phi = e/e_1$ where $e_1$ is the searching effectiveness of the prey by the predator. The value of $e_1$ depends on the kind of host plants used. Here the range of $e_1$ is chosen from 0.21 to 0.62, which is in the middle range of $0 < e_1 < 1$ (Kozlova et al. [89]). Thus the range of $\phi$ should be $6.95 < \phi < 21$. Hence this case is not considered for further biological control.
Case 1b

In the case of response function (b) with Data 1, with \( \gamma \) as an unknown parameter, the point of equilibrium has been obtained, as a solution of equations (8.1) and (8.2), as

\[
\begin{align*}
    u^* &= -3508.33 + 1157.41\gamma + 1157.41A_1, \\
    v^* &= \frac{74.693 - 8.04\gamma^2 + 24.64A_1 + \gamma(48.87 - 8.04A_1)}{(0.001 + 0.0035\gamma + 0.0035A_1)},
\end{align*}
\]

where \( A_1 = \sqrt{9.1882 - 6.0289\gamma + \gamma^2} \).

Substitution of \( u^* = 2.5 \) gives \( \gamma = 0.346008 \). Thus any value of \( u^* \leq 2.5 \) will give \( \gamma \leq 0.346008 \).

As in Case 1a,

\[
\begin{align*}
    v^* - 2u^* &= \frac{74.693 - 9.64\gamma^2 + 24.64A_1 + \gamma(53.72 - 9.64A_1)}{0.001 + 0.0035\gamma + 0.0035A_1} \triangleq f(\gamma), \\
    5u^* - v^* &= \frac{74.693 - 12.06\gamma^2 - 24.64A_1 + \gamma(12.06A_1 - 60.99)}{0.001 + 0.0035\gamma + 0.0035A_1} \triangleq h(\gamma).
\end{align*}
\]

As in Case 1a, a graph has been drawn for \( f(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.4. From the graph, it can be seen that for any value of \( \gamma \) lower than 0.213, \( f(\gamma) \) is positive.

Similarly a graph has been drawn for \( h(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.4. From the graph, it can be seen that for any value of \( \gamma \) greater than 0.0859109, \( h(\gamma) \) is positive.

Hence it can be said that for 0.0859109 \( \leq \gamma \leq 0.213 \), both \( u^* \leq 2.5 \) and \( 2u^* \leq v^* \leq 5u^* \) hold true.

Next the values of \( u^* \) and \( v^* \) are substituted in equation (3.22) to obtain the values of \( a_{11}, a_{12}, a_{21} \) and \( a_{22} \) in terms of \( \gamma \). The values of \( a_{11} \) etc are then substituted in condition (8.4) to obtain

\[
\begin{align*}
a_{11} + a_{22} &= \left[ \gamma^2(2.1965 - 0.483A_1) + \gamma^3(-0.722 + 0.079A_1) + 0.079\gamma^4 + \gamma(-2.2 + 0.736A_1) \right]/[-0.745 + 0.247A_1 + (0.247)^2\gamma] \\
&\triangleq g(\gamma).
\end{align*}
\]
As in Case 1a, a graph has been drawn for $g(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.5. From the graph, it can be seen that $g(\gamma)$ is negative for $\gamma > 2.0137$. Therefore the condition of stability holds for $\gamma > 2.0137$. There is no value of $\gamma$ satisfying both $0.0859109 \leq \gamma \leq 0.213$ and $g(\gamma) < 0$. With a view to choose a value of $\gamma$ in the interval $0.0859109 \leq \gamma \leq 0.213$, the value of $\gamma$ is chosen to be 0.2. The point of equilibrium for this value of $\gamma$ is unstable.

Next, the point of equilibrium $(u^*, v^*)$ is expressed as a solution of equations (8.1) and (8.2) for $\gamma = 0.2$, in terms of $\phi$ as

$$u^* = -3276.852 + 21.52A_2,$$

$$v^* = \frac{-654.096 + 4.29A_2 + \phi(0.0874 + 0.000645A_2) - \phi(0.07 - 0.000021\phi - 0.00046A_2)^2}{0.0112 + 0.00006A_2},$$

where $A_2 = \sqrt{23193.6 + \phi}$.

Next, in terms of $\phi$, condition (8.4) has been expressed as

$$a_{11} + a_{22} = \frac{0.408 - 0.0027A_2 - 0.0001\phi}{(0.07 - 0.000021\phi - 0.00046A_2)^2} \triangleq M(\phi).$$

A graph has been drawn for $M(\phi)$ with $\phi$ as an unknown parameter as shown in

Figure 8.4: Graphs of (i) $f(\gamma)$ and (ii) $h(\gamma)$ for response function (b) with Data 1.

Figure 8.5: Bifurcation value of $\gamma$ for response function (b) with Data 1 and 2.
Figure 8.6: Bifurcation value of $\phi$ for response function (b) with Data 1 and 2.

Figure 8.6. From the graph, it can be seen that $M(\phi)$ is negative for $\phi > 80.6637$. Thus for any value of $\phi > 80.6637$, the point of equilibrium is stable.

Now $\phi = 81.6637$ is chosen which is slightly higher than the bifurcation value 80.6637. With $\phi = 81.6637$ and $\gamma = 0.2$, the point of equilibrium is stable without prey-taxis.

The characteristics of equilibria for all the cases are given in Table 8.1.

As in Case 1a, here also the value of $\phi = 81.6637$ is close to the carrying capacity 100, and thus is not realistic. Hence this case also is not considered for further biological control.

**Case 1c**

In the case of response function (c) with Data 1, with $\gamma$ as an unknown parameter, the point of equilibrium has been obtained in the same way as in Cases 1a and 1b. Substitution of $u^* = 2.5$ gives $\gamma = 0.24551$. Thus any value of $u^* \leq 2.5$ will give $\gamma \leq 0.24551$.

As in previous cases, here also expressions for $f(\gamma)$ and $h(\gamma)$ are obtained. These expressions being too long, have not been produced here.

As in Case 1b, a graph has been drawn for $f(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.7. For any value of $\gamma$ lower than 0.2115, $f(\gamma)$ is positive. Similarly a graph has been drawn for $h(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.7. For any value of $\gamma$ higher than 0.085723, $h(\gamma)$ is positive as shown in Figure 8.7.

Hence it can be said that for $0.085723 \leq \gamma \leq 0.2115$, both $u^* \leq 2.5$ and $2u^* \leq v^* \leq 5u^*$ hold true.

As in Case 1b, a graph has been drawn for $g(\gamma)$ with $\gamma$ as an unknown parameter.
as shown in Figure 8.8. From the graph it can be seen that for $0 < \gamma < 3.22163$, $g(\gamma)$ is negative, i.e. the point of equilibrium is stable. The expression for $g(\gamma)$, being too long, has not been produced here.

Next $\gamma = 0.19$ is chosen which is slightly lower than 0.2115. For this value of $\gamma$, the point of equilibrium is stable and satisfies the conditions $2u^* \leq v^* \leq 5u^*$ and $u^* \leq 2.5$.

The characteristics of equilibria for all the cases are given in Table 8.1.

**Case 2a**

In the case of response function (a) with Data 2, the point of equilibrium $(u^*, v^*)$ is expressed as a solution of equations (8.1) and (8.2), in terms of $\gamma$ as

$$u^* = \frac{51310\gamma}{8189 - 2500\gamma},$$

$$v^* = \frac{1.916 - 0.70499\gamma}{(0.82 - 0.25\gamma)^2}.$$

Substitution of $u^* = 2.5$ gives $\gamma = 0.355672$. Thus any value of $u^* \leq 2.5$ will give $\gamma \leq 0.355672$. 

---

Figure 8.7: Graphs of (i) $f(\gamma)$ and (ii) $h(\gamma)$ for response function (c) with Data 1.

Figure 8.8: Bifurcation value of $\gamma$ for response function (c) with Data 1 and 2.
As in Case 1a,

\[
v^* - 2u^* = \frac{2.56(-3.326 + \gamma)(-0.225 + \gamma)}{(0.82 - 0.25\gamma)^2} \triangleq f(\gamma),
\]

\[
5u^* - v^* = -\frac{6.42(-3.29 + \gamma)(-0.09 + \gamma)}{(0.82 - 0.25\gamma)^2} \triangleq h(\gamma).
\]

A graph has been drawn for \( f(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.9. From the graph it can be seen that \( f(\gamma) \) is positive for any value of \( \gamma \) lower than 0.225.

A graph has also been drawn for \( h(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.9. From the graph it can be seen that \( h(\gamma) \) is positive for any value of \( \gamma \) greater than 0.0906671.

Hence for \( 0.0906671 \leq \gamma \leq 0.225 \), both \( u^* \leq 2.5 \) and \( 2u^* \leq v^* \leq 5u^* \) hold true.

The values of \( u^* \) and \( v^* \) are substituted in equation (3.21) to express condition (8.4) in term of \( \gamma \) as

\[
a_{11} + a_{22} = \frac{0.052\gamma(-2.16 + \gamma)}{-0.82 + 0.25\gamma} \triangleq g(\gamma).
\]

As in previous cases, a graph has been drawn for \( g(\gamma) \) with \( \gamma \) as an unknown parameter as shown in Figure 8.2. From the graph it can be seen that \( g(\gamma) \) is negative for \( \gamma > 2.16 \).

Next \( \gamma = 0.215 \) is chosen which is slightly lower than 0.225. For this value of \( \gamma \), the point of equilibrium is unstable and satisfies the condition \( 2u^* \leq v^* \leq 5u^* \). The aim is now to obtain the bifurcation value of \( \phi \) for which the point of equilibrium becomes stable from unstable.
With \( \phi \) as an unknown parameter, the point of equilibrium \((u^*, v^*)\) is expressed as a solution of equations (8.1) and (8.2) for \( \gamma = 0.215 \), in the absence of diffusion and advection, as

\[
\begin{align*}
u^* &= 0.0702\phi, \\
v^* &= 0.149(1 - 0.0007\phi)\phi.
\end{align*}
\]

Thus in term of \( \phi \), condition (8.4) can be written as

\[
a_{11} + a_{22} = 0.0394 - 0.00045\phi \triangleq M(\phi),
\]

As in the previous cases, here also a graph has been drawn for \( M(\phi) \) with \( \phi \) as an unknown parameter as shown in Figure 8.3. From the graph it can be seen that for \( \phi > 87.6812 \), \( M(\phi) \) is negative. Thus for any value of \( \phi > 87.6812 \), the point of equilibrium is stable.

Now \( \phi = 89.6812 \) is chosen which is slightly higher than the bifurcation value 89.6812. With \( \phi = 89.6812 \) and \( \gamma = 0.215 \), the point of equilibrium is stable without prey-taxis.

The characteristics of equilibria for all the cases are given in Table 8.1.

As in Case 1a, here also the value of \( \phi = 89.6812 \) is close to the carrying capacity 100, and thus is not realistic. Hence this case also is not considered for further biological control.

**Case 2b**

In the case of response function (b) with Data 2, the point of equilibrium \((u^*, v^*)\) is expressed as a solution of equations (8.1) and (8.2) in terms of \( \gamma \) as

\[
\begin{align*}
u^* &= -3541.67 + 1096.49\gamma + 1096.49B_1, \\
v^* &= \frac{-19.03 - 1.803\gamma^2 + 5.89B_1 + \gamma(11.68 - 1.8B_1)}{(0.00027 + 0.00008\gamma + 0.00008B_1)},
\end{align*}
\]

where \( B_1 = \sqrt{10.4329 - 6.4226\gamma + \gamma^2} \).

Substitution of \( u^* = 2.5 \) gives \( \gamma = 0.350845 \). Thus any value of \( u^* \leq 2.5 \) will give \( \gamma \leq 0.350845 \).

As in Case 1a,
Figure 8.10: Graphs of (i) $f(\gamma)$ and (ii) $h(\gamma)$ for response function (b) with Data 2.

$$v^* - 2u^* = \frac{-19.03 - 2.16\gamma^2 + 5.89B_1 + \gamma(11.68 - 1.8B_1)}{(0.00027 + 0.00008\gamma + 0.00008B_1)} \triangleq f(\gamma),$$

$$5u^* - v^* = \frac{19.03 + 2.705\gamma^2 - 5.89B_1 + \gamma(2.705B_1 - 14.58)}{(0.00027 + 0.00008\gamma + 0.00008B_1)} \triangleq h(\gamma).$$

A graph has been drawn for $f(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.10. From the graph it can be seen that $f(\gamma)$ is positive for $\gamma < 0.224505$.

Similarly, a graph has also been drawn for $h(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.10. From the graph it can be seen that $h(\gamma)$ is positive for $\gamma > 0.0906595$.

Hence for $0.0906595 \leq \gamma \leq 0.224505$, both $u^* \leq 2.5$ and $2u^* \leq v^* \leq 5u^*$ hold true.

Next the values of $u^*, v^*$ are substituted in equation (3.22) to express condition (8.4) in terms of $\gamma$ as

$$a_{11} + a_{22} = [-3.07 - 0.95B_1 + \gamma(-1.97 + 0.32B_1) + \gamma^2(0.073 + 0.076B_1) + \gamma^3(0.16 - 0.026B_1 - 0.026\gamma^4)/[-0.19 + 0.06B_1 + 0.06\gamma)]^2$$

$$\triangleq g(\gamma).$$

A graph has been drawn for $g(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.5. From the graph it can be seen that $g(\gamma)$ is negative for $\gamma > 2.09032$.

Therefore the condition of stability holds for $\gamma > 2.09032$.

Next $\gamma = 0.214$ is chosen which is slightly lower than 0.224505. For this value of $\gamma$, the point of equilibrium is unstable and satisfies the condition $2u^* \leq v^* \leq 5u^*$. 

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As in Case 1a, with $\phi$ as an unknown parameter, the point of equilibrium $(u^*, v^*)$ is expressed as a solution of equations (8.1) and (8.2) for $\gamma = 0.214$, in the absence of diffusion and advection, as

\[
\begin{align*}
    u^* &= -3307.02 + 21.6633B_2, \\
    v^* &= \frac{-666.103 + 4.36B_2 + \phi(0.088 - 0.00065B_2)}{0.011 + 0.00006B_2},
\end{align*}
\]

where $B_2 = \sqrt{23303.7 + \phi}$.

Thus in term of $\phi$, condition (8.4) can be written as

\[
a_{11} + a_{22} = \frac{0.43 - 0.003B_2 - 0.0001\phi}{(0.07 - 0.0002\phi - 0.005B_2)^2} \leq M(\phi).
\]

For $\phi > 80.3027$, $M(\phi)$ is negative, as shown in Figure 8.6. Thus for any value of $\phi > 80.3027$, the point of equilibrium is stable.

Now $\phi = 81.3027$ is chosen which is slightly higher than the bifurcation value 80.3027. With $\phi = 81.3027$ and $\gamma = 0.214$, the point of equilibrium is stable without prey-taxis.

The characteristics of equilibria for all the cases are given in Table 8.1.

As in Case 1a, here also the value of $\phi = 81.3027$ is close to the carrying capacity 100, and thus is not realistic. Hence this case also is not considered for further biological control.

**Case 2c**

In the case of response function (c) with Data 2, the point of equilibrium $(u^*, v^*)$ is obtained in the same way as in the earlier cases.

Substitution of $u^* = 2.5$ gives $\gamma = 0.24452$. Thus any value of $u^* \leq 2.5$ will give $\gamma \leq 0.24452$.

As in previous cases, here also expressions for $f(\gamma)$ and $h(\gamma)$ are obtained. These expressions being too long, have not been produced here.

As in earlier cases, a graph has been drawn for $f(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.11. From the graph it can be seen that $f(\gamma)$ is positive for $\gamma < 0.22288$. 

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Similarly a graph has also been drawn for $h(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.11. From the graph it can be seen that $h(\gamma)$ is positive for $\gamma > 0.0904374$.

Hence for $0.0904374 \leq \gamma \leq 0.22288$, both $u^* \leq 2.5$ and $2u^* \leq v^* \leq 5u^*$ hold true.

As in Case 1c, here also the expression for $g(\gamma)$, being too long, has not been produced. A graph has been drawn for $g(\gamma)$ with $\gamma$ as an unknown parameter as shown in Figure 8.8. From the graphs it can be seen that for $0 < \gamma < 3.22163$, $g(\gamma)$ is negative. Next $\gamma = 0.19$ is chosen which is lower than 0.22288. For this value of $\gamma$, the point of equilibrium is stable and satisfies the condition $2u^* \leq v^* \leq 5u^*$.

The characteristics of equilibria for all the cases are given in Table 8.1.

### 8.6.2 Stability of equilibria with prey-taxis

In order to examine the existence of stable periodic solution with prey-taxis, values of predator mortality parameter $\gamma$ and half-saturation parameter of prey $\phi$, as shown in Table 8.1, have been used corresponding to Data 1 and Data 2 along with response function (c).

**Case 1c**

In the case of response function (c) with Data 1, the values of $\gamma$ and $\phi$ are chosen to be 0.19 and 19.409 respectively, as given in Table 8.1, for the point of equilibrium $(u^*, v^*, 0) = (1.86, 4.15, 0)$. Substitution of the values of $u^*$ and $v^*$ in equation (3.23) gives $a_{11} = 0.0403$, $a_{12} = -0.186$, $a_{21} = 0.387$ and $a_{22} = -0.056$. 
Table 8.1: Characteristics of equilibria without prey-taxis

<table>
<thead>
<tr>
<th>Data</th>
<th>Response function</th>
<th>Point of Equilibrium</th>
<th>$\gamma$</th>
<th>$\phi$</th>
<th>Eigenvalues</th>
<th>Nature of equilibrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(a)</td>
<td>(19.73, 4.41)</td>
<td>1.55</td>
<td>19.409</td>
<td>0.062±0.605i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.35, 2.88)</td>
<td>0.2</td>
<td>19.409</td>
<td>0.015±0.332i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6.18, 12.52)</td>
<td>0.2</td>
<td>88.784</td>
<td>-0.0002±0.324i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.19,4.49)</td>
<td>1.55</td>
<td>19.409</td>
<td>0.051±0.6i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.37,2.92)</td>
<td>0.2</td>
<td>19.409</td>
<td>0.014±0.33i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(5.76,11.73)</td>
<td>0.2</td>
<td>81.6637</td>
<td>-0.0002±0.323i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(71.97,5.62)</td>
<td>1.55</td>
<td>19.409</td>
<td>-0.43±0.14i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.86,4.15)</td>
<td>0.19</td>
<td>19.409</td>
<td>-0.008±0.26i</td>
<td>stable</td>
</tr>
<tr>
<td>2</td>
<td>(a)</td>
<td>(19.6,4.49)</td>
<td>1.6</td>
<td>20.524</td>
<td>0.06±0.63i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.44,3.01)</td>
<td>0.215</td>
<td>20.524</td>
<td>0.015±0.34i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6.3,12.52)</td>
<td>0.215</td>
<td>89.6812</td>
<td>-0.0004±0.34i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td>(b)</td>
<td>(20.03,4.56)</td>
<td>1.6</td>
<td>20.524</td>
<td>0.048±0.62i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.45,3.06)</td>
<td>0.214</td>
<td>20.524</td>
<td>0.013±0.34i</td>
<td>unstable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(5.76,11.57)</td>
<td>0.214</td>
<td>81.3027</td>
<td>-0.0002±0.33i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td>(c)</td>
<td>(70.92,5.88)</td>
<td>1.6</td>
<td>20.524</td>
<td>-0.44±0.13i</td>
<td>stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.87,4.41)</td>
<td>0.19</td>
<td>20.524</td>
<td>-0.01±0.26i</td>
<td>stable</td>
</tr>
</tbody>
</table>

Substituting known values of $a_{11}$ etc with $k = n\pi/2$, and $T$ as an unknown parameter in condition (8.11), it has been seen that

$$p(k^2)q(k^2) - r(k^2) = 0.001076 - 0.000098n^4 + 7.5155 \times 10^{-8}n^6 + n^2(0.003421 + 1.90975T) \triangleq s_2(T),$$

where $n = 1, 2, 3, 4$ and 5. Graphs of $s_2(T)$ are drawn with $T$ as an unknown parameter as shown in Figure 8.12.

From Figure 8.12, it can be seen that for $n = 1$, the value of $s_2(T)$ becomes 0 for $T = -0.00230347$. For any value of $T$ higher than $-0.00230347$, $s_2(T)$ is positive. Thus bifurcation value of $T$ for $n = 1$ is $-0.00230347$. Similarly, for $n = 2, 3, 4$ and 5, bifurcation values of $T$ are $-0.00172726$, $-0.00139452$, $-0.00101416$ and $-0.000553335$ respectively. The bifurcation value of $T$ closest
Figure 8.12: Bifurcation value of $T$ for response function (c) with Data 1 and 2.

to zero is $-0.000553335$ which occurs for $n = 5$. Thus $n = 5$ is the first excited mode and the corresponding bifurcation value of $T$ is $-0.000553335$. Characteristics of the stability of the point of equilibrium for this value of $T$ is shown in Table 8.2.

For numerical simulations, the value of $T$ is chosen to be $-0.0003$, higher than the bifurcation value $-0.000553335$, for which the point of equilibrium is stable with prey-taxis.

**Case 2c**

In the case of response function (c) with Data 2, the values of $\gamma$ and $\phi$ are chosen to be 0.19 and 20.524 respectively, as given in Table 8.1, for the point of equilibrium $(u^*, v^*, 0) = (1.87, 4.41, 0)$. As in earlier cases, the values of $a_{11}, a_{12}$ etc are obtained from equation (3.23) as $a_{11} = 0.038, a_{12} = -0.17, a_{21} = 0.41$ and $a_{22} = -0.058$.

Substituting all these values in condition (8.11) with $k = n\pi/2$ and $T$ as an unknown parameter, it has been seen that

$$p(k^2)q(k^2) - r(k^2) = 0.00139 - 0.000092n^4 + 7.5155 \times 10^{-8}n^6 + n^2(0.003367 + 1.88717T) \triangleq s_2(T),$$

where $n = 1, 2, 3, 4$ and 5. Graphs of $s_2(T)$ are drawn with $T$ as an unknown parameter as shown in Figure 8.12.

From Figure 8.12, it can be seen that for $n = 1$, the value of $s_2(T)$ becomes 0 for $T = -0.00247135$. For any value of $T$ higher than $-0.00247135$, $s_2(T)$ is positive. Thus bifurcation value of $T$ for $n = 1$ is $-0.00247135$. Similarly, for $n =$
Table 8.2: Characteristic of equilibria with prey-taxis for response function (c)

<table>
<thead>
<tr>
<th>Data</th>
<th>Resp. func.</th>
<th>Point of Equilibrium</th>
<th>Mode (n)</th>
<th>T</th>
<th>p(k²)</th>
<th>q(k²)</th>
<th>r(k²)</th>
<th>p(k²)/q(k²)</th>
<th>Stable/Unstable</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(c)</td>
<td>(1.86,4.15,0)</td>
<td>5</td>
<td>-0.0005</td>
<td>1.24986</td>
<td>0.02114</td>
<td>0.0234</td>
<td>0.003</td>
<td>Stable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.0006</td>
<td>1.24986</td>
<td>0.02114</td>
<td>0.02865</td>
<td>-0.0022</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>-ive</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>(c)</td>
<td>(1.87, 4.46, 0)</td>
<td>5</td>
<td>-0.0006</td>
<td>1.25462</td>
<td>0.0231</td>
<td>0.0283</td>
<td>0.00066</td>
<td>Stable</td>
</tr>
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<td>+ive</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.00065</td>
<td>1.25462</td>
<td>0.0231</td>
<td>0.0307</td>
<td>-0.0017</td>
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<td></td>
<td></td>
<td>+ive</td>
<td>+ive</td>
<td>+ive</td>
<td>-ive</td>
<td></td>
</tr>
</tbody>
</table>

2, 3, 4 and 5, bifurcation values of $T$ are $-0.00177284$, $-0.00142831$, $-0.00105669$ and $-0.000614085$ respectively. Here also $n = 5$ is the first excited mode and the corresponding bifurcation value of $T$ is $-0.000614085$. Characteristics of the stability of the point of equilibrium for this value of $T$ is shown in Table 8.2.

For numerical simulations, the value of $T$ is chosen to be $-0.0003$, higher than the bifurcation value $-0.000614085$, for which the point of equilibrium is stable with prey-taxis.

### 8.7 Numerical solutions

Here, the predator–prey-taxis equations (8.1)–(8.3) have been solved numerically for $t = 75$ weeks with response function (c), Data 1 and Data 2 along with values of $\gamma$, $\phi$ and prey-taxis $T$ obtained in sections 8.6.1 and 8.6.2 respectively.

In order to achieve biological control the initial conditions need to be modified in such a way so that initially the value of predator population density $v_0$ is at least twice than that of prey $u_0$ through out the domain. In addition, the value of $u_0$ should not exceed the economic threshold value 2.5 in the entire domain. The reason is that biological control is only successful when there is no or negligible damage on the host plant. This is only possible if predator is added at the very
beginning of plant infestation. Thus the existing initial condition is modified to:

\[ u_0 = 2 \exp(-x^2), \quad -1 \leq x \leq 1, \]
\[ v_0 = 6 \exp(-x^2), \quad -1 \leq x \leq 1, \]
\[ w_0 = 0, \quad -1 \leq x \leq 1, \]

and shown in Figure 8.13.

Figure 8.14: Transient graphs of prey and predator population densities for response function (c) with Data 1 at \( t = 0, 5, 10, ..., 70, 75 \) weeks.

**Case 1c**

In the case of response function (c) with Data 1, using \( \gamma = 0.19 \) and \( T = -0.0003 \), the transient graphs for prey population density \( u \) and predator population density \( v \) are shown in Figure 8.14. From the graphs, it is evident that for most of the time prey population density \( u \) is below 2.5 in the entire domain. Also it can be seen that \( u \) shows a tendency to aggregate near the boundary of the domain whereas in the case of \( v \), there is no aggregation in population density. In order to study distributions of \( u \) and \( v \) further, time-dependent graphs of both \( u \) and \( v \) are obtained at \( x = 0.5 \) as shown in Figure 8.15. It is seen that both \( u \) and \( v \) produce stable spiral (damped oscillations) till 75 weeks.
Figure 8.15: Predator–prey solutions for Data 1 with response function (c) and the corresponding phase–plane graph.

Figure 8.16: Transient graphs of prey and predator population densities for response function (c) with Data 2 at $t = 0, 5, 10, ..., 70, 75$ weeks.

**Case 2c**

In the case of response function (c) with Data 2, using $\gamma = 0.19$ and $T = -0.0003$, the transient graphs for prey population density $u$ and predator population density $v$ are shown in Figure 8.16. From the graphs, it is evident that for most of the time prey population density $u$ is below 2.5 in the entire domain. Also it can be seen that $u$ shows a tendency to aggregate near the boundary of the domain whereas in the case of $v$, there is no aggregation in population density. In order to study distributions of $u$ and $v$ further, time–dependent graphs of both $u$ and $v$ are obtained at $x = 0.5$ as shown in Figure 8.17. It is seen that both $u$ and $v$ produce stable spiral (damped oscillations) till 75 weeks.

**8.8 Discussion**

In this chapter, Lotka–Volterra logistic predator–prey-taxis equations (8.1)–(8.3) with $P. \text{persimilis}$ as the predator and $T. \text{urticae}$ as the prey are considered along with three response functions, two data sets and a set of non–homogeneous initial
conditions. The aim is to observe the effect of prey-taxis on biological control of prey population.

Using the newly estimated data set, obtained in section 3.9, biological control of two-spotted spider mite population is achieved with the help of non-random search i.e. prey-taxis. In order to lower the pest population density below economic threshold throughout the domain even for a longer time, certain measures are chosen as detailed in section 8.6. In this case, the economic threshold value of pest population is chosen to be 2.5 (Beddington et al. [10], Sapoukhina et al. [139]). Based on this observation, values of predator mortality rate parameter $\gamma$ and half-saturation parameter $\phi$ are varied to achieve successful low level of population densities of both prey and predator. First, a value of $\gamma$ is chosen for which the equilibrium value of prey population density $u^*$ is less than 2.5 and that of predator population density $v^*$ is at least twice than that of $u^*$ throughout the domain. The maximum value of $v^*$ should not exceed five times than that of $u^*$. The relation between $u^*$ and $v^*$ i.e. $2u^* \leq v^* \leq 5u^*$ is obtained through numerical simulations. Since it is necessary for the mathematical model to have a stable dynamics, the stability of the point of equilibrium is determined for a value of $\gamma$. In the case of response function (c), there is a common value of $\gamma$ satisfying the conditions related to the values of $u^*$, $v^*$ for which the population dynamics is stable. On the other hand, in the case of response functions (a) and (b), there is no such value of $\gamma$ satisfying all these three conditions. In that case, stability of population dynamics is achieved with the help of $\phi$. Using these newly obtained values of either $\gamma$ or both $\phi$ and $\gamma$, the bifurcation value of prey-taxis for stable dynamics is obtained.
as shown in section 8.6.2. For biological control of prey population density with prey-taxis, the values of parameter $T$ is chosen to be higher than the bifurcation values for which the point of equilibrium provides stable periodic solution.

In order to achieve biological control with prey-taxis, in the case of response function (a) with Data 1, the newly obtained values of $\phi$ and $\gamma$ are 88.784 and 0.2 respectively. As described in 8.6.1, half-saturation parameter $\phi$ is inversely proportional to the searching effectiveness parameter $e_1$. Thus a high value of $\phi$ like 88.784 indicates extremely low searching effectiveness of predator. For a successful biological control, this situation is unlikely to happen in nature. Similar situations occur with response function (a), Data 2 and response function (b) with both Data 1 and 2. Thus response functions (a) and (b) are not considered for further study. On the other hand, response function (c) proves to be the most suitable response function to achieve biological control of two-spotted spider mite. In this case, for Data 1, biological control can be achieved with the values of $\phi$ and $\gamma$ as 19.409 and 0.2 respectively. This value of $\phi$ is quite reasonable for biological control, since, in this case, the value of searching effectiveness $e_1$ is $e_1 = e/\phi = 4.27/19.409 = 0.22$.

For Data 2, biological control is possible with $\phi = 20.524$ and $\gamma = 0.21$. In this case, the value of searching effectiveness $e_1$ is $e_1 = e/\phi = 4.31/20.524 = 0.21$.

It is also seen that initial conditions play a crucial role to achieve biological control of prey population. In view of that initial conditions, mentioned in section 3.4, are modified to incorporate the followings:

(i) initially both prey and predator densities should be heterogeneous in the given domain.

(ii) initially prey population density should not exceed 2.5 (2.5% of economic threshold) in the entire domain.

(iii) initially predator population density should be at least twice than that of prey in the entire domain.
8.9 Conclusion

In this mathematical modelling it has been shown that biological control of prey population can be achieved without reintroducing predators from outside. It has been achieved through lowering the mortality of predator population and with an improved non–random searching efficiency (prey-taxis) of predator population. These two factors can be taken care with better environmental conditions in a glass house experiment. Thus prey-taxis is one of the important factors considered in this model which helped in improving the mobility of predator population within the spatial domain. The initial conditions in this model also contributed immensely to maintain prey population below economic threshold.
Chapter 9

Conclusion

The entire study in this thesis is based on the interactions of two-spotted spider mite *Tetranychus urticae* and its predacious mite *Phytoseiulus persimilis*. First of all, the parameters involved in this predator–prey system have been estimated in chapter 3 with the inclusion of prey-taxis in the system. Two data sets and three different response functions have been selected. The parameters have been estimated on the basis of minimization of errors as well as graphical comparisons to the field data.

In chapter 4 limits of prey-taxis have been used to obtain periodic, quasi-periodic and chaotic solutions with Data 1 and response functions (a), (b) and (c). Similar limits have been obtained with Data 2 and response functions (a) and (b). Response function (c) has not been taken into account for periodic or quasi-periodic behaviour of the predator-prey system since the nature of the point of equilibrium without prey-taxis and diffusion is always stable, steady state. With prey-taxis, only chaotic behaviour is displayed by the predator-prey system with response function (c). All these results have been verified numerically as shown in Figures 4.8–4.13. It has been shown that with the inclusion of prey-taxis in the predator–prey equations, it is possible to obtain three stages of equilibrium such as periodic, quasi-periodic and chaotic in a predator–prey system. It shows that the degree of predator sensitivity to prey density can alter the state of equilibrium in a predator–prey system. Predators find prey through odour emitted from leaves infected by two-spotted spider mites. Thus it is possible to change the direction of
movement of predator using different types of wind flow like still air, a stimulus-free air flow, an air flow with odours from uninfested leaves and an air flow with odours from infested leaves.

The limits of prey-taxis for which the predator–prey system produces quasi-periodic solutions have been used in chapter 5 to investigate the formation of spatial patterns with the variation of diffusion in predator velocity $d_3$. Transient graphs have been drawn for the numerical solutions of predator–prey-taxis equations for all data sets and response functions. It has been observed that response functions (a) and (b) are more suitable to produce spatial patterns in the form of patches of prey population density. In the case of response function (c) there is no such spatial pattern formation. It has also been observed that initial conditions play an important role in the formation of spatial patterns.

In chapter 6 the formation of spatial patterns have been investigated with the introduction of diffusion-driven instability in the predator–prey system. Here the predator–prey system is considered without prey-taxis and diffusion in predator velocity $d_3$. Predator interference produces instability among the prey population, thus leading to spatial patterns. Thus in the predator–prey equations, parameter $\beta$ introduces instability through predator interference in the system. First of all, limits of predator interference parameter $\beta$ for which the point of equilibrium becomes unstable have been established. Only response functions involving $\beta$ have been taken into consideration. Thus response functions (b) and (c) have only been used along with Data 1 and Data 2 to investigate the formation of spatial patterns. Spatial patterns in the form of aggregation have been produced. There is, however, no patch formation as happened in the case of spatial patterns with prey-taxis and diffusion in predator velocity. It has also been shown again here that initial conditions play an important role in the formation of spatial patterns.

In both chapters 5 and 6 it has been shown that spatial patterns can be developed even in a small domain with zero flux boundary conditions if either prey-taxis or diffusion-driven instability are considered in the existing predator–prey system.

In chapter 7 effects of habitat edge for predators on the formation of spatial patterns have been studied. Here the whole domain has been divided into two
patches and the flow of predators at the interface is governed by the equation

$$\alpha \frac{\partial v_1}{\partial x} = (1 - \alpha) \frac{\partial v_2}{\partial x}$$

where $v_1, v_2$ are predator population densities in patch 1 and 2 respectively, $\alpha$ is the tendency of predator to remain in a habitat. Prey population is, however, free to move unrestricted in the whole domain. First of all, investigation on the size of a domain, where spatial patterns can occur, has been performed. Domain length greater than $L_2$, for which spatial patterns can occur, corresponding to each of the two response functions (a) and (b) for Data 1 and Data 2 are given in Table 7.1. In view of that, the domain has been chosen as $[-2, 2]$. First of all, investigation has been done with $\alpha = 0.2$. It has been observed that in the domain $[-2, -1]$, prey population goes into refuge and the refuge situation disappears as soon as the length of the domain is increased to $[-2, 0]$. With $\alpha = 0.6$, the predator has greater tendency to remain in the left-hand domain $[-2, -1]$ or $[-2, 0]$. In order to observe the effect of length of a patch on the formation of spatial patterns, domain $[-4, 4]$ has been chosen as an extended domain from $[-2, 2]$.

It has been observed that a larger domain has resulted in producing different spatial patterns with the increase in the value of $\alpha$ from 0.2 to 0.6. In a smaller domain, it makes no difference in the nature of spatial patterns formation even with an increased value of $\alpha$. Physically it can be interpreted as predators having more space to forage in a larger domain as compared to a smaller domain. This leads to different forms of spatial patterns in a large size domain.

In chapter 8, biological control of prey population density by its natural predators has been investigated. It has been shown that it is possible to achieve by introducing predators when the prey population density is less than 2.5% of carrying capacity. Also predator population density should be at least twice that of the prey in the entire domain. This way biological control of prey population density in the entire domain can be achieved without adding any predators from outside again.

In this thesis Routh–Hurwitz stability criteria have been used as a powerful tool
to study:

- the effect of prey-taxis on the nature of predator-prey dynamics in a predator–prey system.
- the formation of spatial patterns generated in a predator–prey system with the inclusion of prey-taxis.
- the effect of prey-taxis on biological control of two-spotted spider mites.

Also variational matrix criteria, in the absence of prey-taxis, have been used to study:

- the formation of spatial patterns in a predator–prey system generated by diffusion-driven instability.
- the formation of spatial patterns in a predator–prey system with diffusion through edge-mediated effects.

The possible further research is to setup a glass house experiment to study:

- various stages of equilibria in a predator–prey system with prey-taxis by altering the degree of sensitivity of predators to prey population density.
- biological control of two-spotted spider mites using the technique developed in this thesis.

The entire mathematical study in this thesis can further be extended to two-dimensions. Also edge-mediated effects can be studied with the inclusion of buffer zone in a two-dimensional predator-prey system.
Bibliography


[59] Gould, H. J., Preliminary studies of an integrated control programme for cucumber pests and an evaluation of methods of introducing *Phytoseiulus*


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Appendix

Figure 1: Time-dependent graphs for Data 1 with response function (a).
Figure 2: Time-dependent graphs for Data 1 with response function (b).

Figure 3: Time-dependent graphs for Data 1 with response function (c).
Figure 4: Time-dependent graphs for Data 2 with response function (a).

Figure 5: Time-dependent graphs for Data 2 with response function (b).
Figure 6: Time-dependent graphs for Data 2 with response function (c).
List of Publications

The following papers have been published/submitted in support of and during this work:


★ Aspriha Chakraborty and Manmohan Singh, Edge-mediated effect on the formation of spatial patterns, (in preparation).

The following conference paper has been presented in support of and during this work: