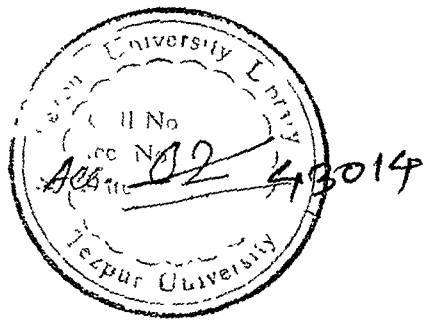


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MATHEMATICAL MODELLING AND STABILITY ANALYSIS OF SOME ECOLOGICAL PROBLEMS

*A Thesis Submitted
in Partial Fulfillment of the Requirements
For the degree of*

DOCTOR OF PHILOSOPHY

by
BARNALI DAS



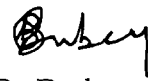
to the

**DEPARTMENT OF MATHEMATICAL SCIENCES
SCHOOL OF SCIENCE AND TECHNOLOGY
TEZPUR UNIVERSITY
MAY, 1999**

*Dedicated to
My
Mother Smt. Mukul Das
and
Father Sri Tirtha Das*

CERTIFICATE

This is to certify that the matter embodied in the thesis entitled "*MATHEMATICAL MODELLING AND STABILITY ANALYSIS OF SOME ECOLOGICAL PROBLEMS*" by Ms. Barnali Das for the award of degree of Doctor of Philosophy of Tezpur University is a record of bonafied research work carried out by her under my supervision and guidance. The results embodied in this thesis have not been submitted to any other University or Institute for the award of any degree or diploma.



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CHAPTER I

GENERAL INTRODUCTION

1.0 INTRODUCTION

The Biosphere is an important zone for biological activities which are mainly responsible for changes in ecology and environment on this planet. The wide-spread depletion of the world's biological resources is one of the most serious and challenging problems which mankind faces today. The fast growth of population causes a gradual reductions in per capita land, water availability and other resources. The manmade projects responsible for ecological and environmental degradation are mainly caused by faster industrial growth taken up for the socio-economic improvement of the people. As these developmental projects are essential, the study of environmental planning and management is necessary to maintain sustainable growth.

Natural and anthropogenic global changes are associated with sustainable ecological disturbances. The Banni Grasslands located in Katch, Gujrat, support the traditional grazers of this region. Though this area is a saline desert, after the rains it turns into a lush grassland. However, this ecosystem is now endangered due to uncontrolled grazing practices, shifting from cattle to sheep and goat, and the growth of foreign plant species.

The depletion of grass biomass due to their over exploitation by ungulates present in the grassland and cattle migrating from plains into the grassland during the period of scant rainfall and draught in the region is a major cause of concern to mankind because it not only destroys the grassland but also creates soil erosion problems in the

region. It may be noted that the development of fertile topsoil and forestry biomass are closely interlinked so much with each other that the severe depletion of either brings about the destruction of the other. In fact the depletion of fertile top soil causes lesser biomass production on the one hand while the depletion of forestry biomass would cause a shortage of rainfall, a decrease in soft water table, draught etc. on the other. These in turn would enhance soil erosions and thus decreasing the level of fertile topsoil. This cycle may, therefore transform the forested zone into a grassland, eventually converting it into a wasteland under excessive pressure due to grazing etc. (Frevert et al. (1962), Whyte (1964), Ghosh and Lohani (1972), Smith (1972), Moy-Meir (1976), Das (1977), Zachar (1982), Brown and Wolf (1984), Khoshoo (1986), Misra (1987)).

It is well known that the resource carrying capacity of our planet is limited. Therefore the growth and development in various sectors of the economy caused by a rapid pace of industrialization, a rising population and an increasing energy requirement have stressed our environment to such an extent that if concrete steps are not taken soon to control this menace, many undesirable effects would occur leading to disastrous consequences for mankind (Frevert et al. (1962), Smith (1972), Anon (1977a, b), Das (1977), Brown (1981), Gadgil et al. (1983), Larson et al. (1983), Brown and Wolf (1984), Haigh (1984), Repetto and Holmes (1983), Gadgil (1985), Waring and Schiessinger (1985), Khoshoo (1986), Munn and Fedorov (1986), Shukla et al. (1981, 1989), Quli (1992), Quli and Siddiqui (1997)).

The rich natural diversity of the Himalayas has sustained life in the entire Indo-gangetic region. Due to over exploitation of its resources, the Himalayan region is being rapidly degraded, with direct

ecological threat to life in the entire area. The Doon Valley in the northern part of Uttar Pradesh in India is also an example where the main reasons for the depletion of forestry resources and threat to ecological stability are given below (Munn and Fedorov, (1986)):

1. limestone quarrying, industrialization and associated pollution,
2. growth of human population,
3. growth of Livestock population.

The rapid rate of shrinkage of per capita forest area in Bihar, to an extent of 0.03ha, demands an urgent appraisal of various human impacts (Anon, (1995)). There are other ecologically unstable regions around the world such as the uplands of western Amazonia, the Atlantic Coast of Brazil, the Madagascar Islands, the Malaysian rain forest zones etc., (Wilson (1989)).

Biodiversity, the combination of species, genetic and ecological diversity (World Conservation Monitoring Centre (1992)) is currently one of the issues most frequently addressed in both scientific and mass media. Along with diversity, stability and complexity, resilience is a difficult ecological parameter to measure. It can be defined as the capacity to return to functional processes and interactions existing prior to disturbances (Pimm (1991), Shrader Frechelte and Mecoy (1993)). For centuries, biologists have been interested in the diversity of life forms and their evolution and extinction. The role of biological diversity in the functioning of different ecosystems have also been investigated for several decades. However, the convention on biological diversity adopted at the RIO Earth Summit in June 1992, has led to a resurgence of interest in the subject of biodiversity and its various human dimensions (Heywood and Watson (1995)).

The environmental crisis which society faces today can be controlled:

- * by restoring the productivity of the ecosystems and by conserving genetic resources and diversity,
- * by affecting better land use,
- * by insisting and assessing the environmental impact of developmental projects to ensure harmonization of environment with development,
- * by incorporating environmental safeguards and beneficial analysis for development of industrial projects,
- * by promoting environmental education awareness among people.

Keeping the above in view in the present thesis we develop some mathematical models of ecosystems, taking into account birth, death and interaction rates, habitat-size, species migration (diffusion), species-competition and the surrounding environment, (LaSalle and Lefschetz (1961), Smith (1972), Denn (1975), Okubo (1980), Rao (1981), Hallam and Levin (1986), Kormondy (1986), Munn and Fedorov (1986), Freedman (1987), Edelstein-Keshet (1988) etc.).

1.1 OBJECTIVES OF THE THESIS

The main objective of this thesis is to study problems of survival of species subject to ecological stability. Specifically the following three types of problems are studied in the thesis using mathematical models.

1. Depletion of grass biomass and its conservation,
2. Survival of diffusive species dependent on some resource in industrial environments.
3. Interaction among species in a diffusive system.

In the following we outline the relevant literature so that the

research work carried out in the thesis related to the above mentioned problems may be seen in its proper perspective.

1.1.1 EFFECTS OF DIFFUSION

Due to environmental factors and other related effects the tendency of any species living in a given habitat is to migrate to better suited regions for its survival and existence. In general, the movement of the species arises due to certain factors such as overcrowding, climate, predator-prey relationships, refuge and fugitive strategies and more importantly due to resource limitations in the given habitat, (Rosen (1974,75), Verma (1980), Grundy (1983)).

A determination of the effects of adding diffusion to ecological models is of biological interest in recent years. The first successful attempt to study the migration of species mathematically is due to Skellam (1951) using the concept of random dispersal. Since then, several investigators studied the effects of dispersion on local and global stability of an interacting species system by considering Lotka - Volterra and other types of prey-predator and competition models, (Comins and Blatt (1974), Murray (1975), Haderer and Rothe (1975), Jorne (1975, 1977), Chow and Tam (1976), Jorne and Carmi (1977), Caisson (1978), Fife (1979), Hallam (1979), Mimura and Kawasaki (1980), Cohen and Murray (1981), Leung (1981), Hastings (1982), Nallaswamy and Shukla (1982), Bergerud et al. (1984), Cosner and Laser (1984), Anderson and Arthur (1985), Bergerud and Page (1987), Freedman (1987), Cantrell and Cosner (1987, 1989), Freedman and Krisztin (1992), Freedman and Wu (1992), Angulo and Linares (1995)) etc.

Some workers have also studied the coexistence, persistence and extinction in single species and Lotka-Volterra reaction-diffusion

models, (Gopalsamy (1977), Allen (1983a, 1983b, 1987) as well as the global stability in generalized Lotka-Volterra models with diffusion (Takeuchi (1986a), and the references therein).

In general, a diffusion process in an ecosystem tends to give rise to a uniform density of population in the habitat. As a consequence, it may be expected that diffusion, when it occurs, plays a general role of increasing stability in a system of mixed populations and resources. However, there is an important exception, known as "diffusion induced instability" or "diffusive instability". This exception might not be a rare event especially in a prey-predator system, (see Levin (1976), Casten and Holland (1978), Wollkind et al. (1991), Timm and Okubo (1992), Chattopadhyay et al. (1996), Raychaudhury et al. (1996)). In models with reservoir-type boundary conditions proposed by Gopalsamy (1977), boundedness of the domain is necessary for the coexistence of competing species, in which the system is unstable without diffusion. Moreover, in Levin's (1876) model, boundedness of the domain and non linearity are requisite for the coexistence of competing species. For unequal but constant dispersion coefficients of the two species, it has been shown that for competition models, diffusion may increase the stability of an equilibrium state (at least non decreasing) but in the case of a prey-predator model, diffusion instability may occur, (Mimura and Nishida (1978), Chattopadhyay et al. (1996), Raychaudhury et al. (1996)).

1.1.2 DEPLETION OF GRASS BIOMASS AND ITS CONSERVATION

The depletion of grass biomass in a grassland due to grazing by ungulates present in the grassland have been studied by several researchers (Whyte (1964), Noy-Meir (1975, 1976, 1978), Gadgil et al.

(1983), MOA (1984), Gadgil (1985), Khoshoo (1986), Munn and Fedorov (1986)), but very little effort has been made to study the degradation of grass biomass by making suitable mathematical models. Noy-Meir (1975, 1976, 1978) was probably the first who has proposed a mathematical model for grazing of grasslands in terms of herbage growth and animal consumption rates. He has also studied the stability of grazing systems by using the concept of a prey-predator model. It may be noted here that in the study of Noy-Meir and his co-workers, the effects of migrating cattle populations from outside into the grassland has not been considered. Keeping this in view, Agarwal et al. (1993) studied the effect of a grazing of a forested grassland and its conservation. They considered the migration rates of cattle populations as a constant. They also considered the growth and death rates as either linear or bilinear which need not be necessarily true.

Keeping the above in mind, in chapter II, we propose and analyze a mathematical model to study the depletion of grass biomass due to overgrazing by animal populations. A model to conserve the grass biomass is also presented.

1.1.3 SURVIVAL OF SPECIES DEPENDENT ON RESOURCES IN INDUSTRIAL ENVIRONMENTS

As pointed out earlier, deforestation has caused migration and even extinction of certain animal species (at least locally) (Munn and Fedorov (1986), Shukla et al. (1989), (1996)). The Doon Valley in India is such an example where depletion of forest biomass has changed the overall ecological structure of the Valley (Munn and Fedorov (1986)). Several investigations have been conducted to study the effects of industrialization and population on resources using

mathematical models. Shukla et al. (1989, 1996) proposed some models to study the effect of industrialization and population on resource depletion and have shown that if the pressure of industrialization and population increase without control, the resource may not last long. However, if appropriate measures for conservation are taken, the resource can be maintained at a desired level even under the sustained pressure of industrialization and population. But little attention has been paid to study the effect on resource dependent biological species with diffusion using mathematical models (Rothe (1976), Hastings (1978b), Shukla and Shukla (1987), Freedman and Shukla (1989), Shukla et al. (1996)).

Keeping in mind of the above literature survey, in chapter III of this thesis a mathematical model in terms of nonlinear differential equation is proposed and analyzed in order to study the survival of species dependent on a resource under industrialization pressure in a given region and with diffusion. A model to conserve the resource biomass and to control the undesired level of industrialization pressure is also suggested.

1.1.4 INTERACTIONS AMONG THE SPECIES

Ecology is the science that deals with the relationship between living organisms and also between them and the physical environment. Within the framework of a given habitat. Ecology refers to the fact that various organisms share the same geographical space with man. An organism lives in a state of dynamic equilibrium with the environment. As the environment is in a constant state of flux, the organism has to make internal adjustment, failing which extinction of the species may result (Hardin (1960), Rosenzweig and MacArthur (1963), Paine (1966),

Connell (1970), Parrish and Saita (1970), Cramer and May (1972), Porter (1972, 1974), Goh (1976), Hsu et al. (1977), Harada and Fukao (1978), Hastings (1978a), Harrison (1979), Hsu and Hubbell (1979), Cushing (1980), Hsu (1981a, 1981b), Cosner and Laser (1984), Conway and Smoller (1985), Freedman et al. (1986), Harrison (1986), Kirlinger (1986, 1988), Cantrell and Cosner (1987), Gard (1987), Jenson (1987), Freedman (1979, 1989), Mukherjee and Roy (1990), Sarkar et al. (1991), Mitra et al. (1992), Bonan (1993), Bergman and Greenberge (1994), Sikder and Roy (1994a,b), Dubey (1997)).

As the species do not exist alone in nature it is of more biological significance to study the behavior of each population in a system of two or more species with and without diffusion in the given habitat (see the references above and in section 1.1.1). Keeping this in mind the following types of problems in the forthcoming chapters are discussed.

In Chapter IV of this thesis, a mathematical model based on the dynamics of a Gause-type model with diffusion is proposed and analyzed. In that model we consider a resource based ecological model where two predators are competing for a limited prey with interference in a diffusive system.

Chapter V of this thesis is devoted to study the effect of predation on two competing prey species with diffusion.

Chapter VI of this thesis is focused on modelling and analyzing a system of two predators competing for two resource prey species with diffusion.

In Chapter VII of this thesis, a general mathematical model for a predator-prey interaction with self and cross diffusion is proposed and analyzed.

In Chapter VIII of this thesis, a general model for two competing species with self and cross diffusion is proposed and analyzed.

1.2 MATHEMATICAL TECHNIQUES USED IN THE THESIS

In the deterministic analysis of evolution and stability of the systems described above, many mathematical approaches have been adopted. In the present thesis only the following approaches have been utilized.

1.2.1 THE METHOD OF CHARACTERISTIC ROOTS

The conclusions regarding asymptotic stability of the systems very much lie in the eigenvalues of the variational matrices, i.e. a Jacobian matrices of first order derivatives of interaction functions. As this Jacobian is determined by the Taylor expansion of the interaction functions about an equilibrium and neglecting nonlinear higher order terms, this method studies only the local stability of systems in vicinities of equilibria. Being a straightforward method, based purely on the signs of the real parts of the eigenvalues, the Routh-Hurwitz criteria (Sanchetz (1968) and Gershgorin's theorem (Lancaster and Tismanetsky (1985)) are very useful in order to study the local stability of a wide range of systems in homogeneous environments.

1.2.2 LIAPUNOV'S DIRECT METHOD

The physical validity of this method is contained in the fact that the stability of the system depends on the energy of the system which is a function of system variables. Liapunov's direct method consists in finding out such an energy function termed a Liapunov function which need not be unique. The major role in this process is played by positive or negative definite functions which can be

obtained in general by trial and error of some particular functions of state variables, and in some cases with a planned procedure. The two basic theorems on stability can be found in La Salle and Lefschetz (1961).

The stability analysis in conjunction with a suitable Liapunov function has its two salient features, namely it is a direct method, and second is that this procedure provides a realistic study of the stability of multispecies systems.

1.3 SUMMARY OF THE THESIS

In Chapter I, a general introduction with relevant literature is presented to provide a necessary background required for the forthcoming chapters.

In Chapter II, a mathematical model is proposed and analyzed in order to study the depletion of grass biomass due to overgrazing by animal populations

This model is analyzed using the stability theory of differential equations. It is shown that under certain conditions the density of the grass biomass settles down to its equilibrium level which decreases as the density of the animal populations increase. Further, this level may tend to zero if the density of the animal populations increase to a sufficiently high level.

A model to conserve the grass biomass is also suggested. By analyzing the conservation model it is shown that grass biomass can be maintained at an appropriate level by adopting suitable efforts.

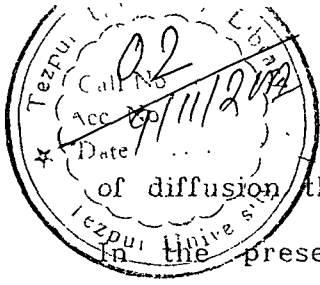
In Chapter III, we attempt to investigate the survival of wildlife species dependent on a resource biomass in an industrial environment with diffusion. The species is assumed to be partially or

wholly dependent or just predated on the resource biomass. The dynamics of the wildlife species, the resource biomass and the industrialization pressure are assumed to be governed by a system of autonomous logistic-type differential equations. When there is no diffusion it is shown that increasing industrialization may lead to a decrease in the density of the resource biomass and consequently the survival of the species will be threatened, but diffusive migration may prevent extinction of the species.

A model to conserve forestry biomass by irrigation, fencing programs, etc. and to control the undesired level of industrialization by some mechanical processes is also proposed. It is noted that if suitable efforts are made to conserve the resource biomass and to control the undesired level of industrialization pressure, the resource biomass can be maintained at a desired level and thus the survival of wildlife species living in the habitat may be ensured.

By analyzing the diffusion models, it is shown that global stability is more plausible in diffusion system than in the case of no diffusion. For a given habitat, it is shown that the unstable steady state of a system without diffusion can be made stable by increasing the diffusion coefficients to sufficiently large values.

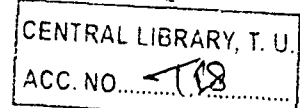
In Chapter IV, a Gause-type mathematical model is proposed and analyzed to study the growth and survival of two predator species competing for a single limited prey in a diffusive system. The growth rates of the interacting populations are assumed to be nonlinear. It is shown that the intraspecific interference coefficients of the competing predators play a crucial role in stabilizing the interior equilibrium of the system. If the intraspecific interference coefficients of the competing predators are zero, then in the absence



the interior equilibrium of the system becomes unstable. In the presence of diffusion it is shown that if the interior equilibrium of the system is asymptotically stable in the absence of diffusion, then it remains stable under diffusion. Further by increasing the diffusion coefficients to sufficiently large values, an unstable interior equilibrium can be stabilized.

In Chapter V, a Gause-type mathematical model is considered in order to investigate the effect of predation on two competing prey species in a diffusive system. It is assumed that the predator species is influenced by the damage effect caused by crowding from the members of its own populations. In the absence of diffusion criteria for local stability, instability and global stability have been obtained. In the absence of diffusion it is found that the global stability of the interior equilibrium depends upon the interspecific interference coefficients of the two competing prey species. If the interspecific interference is too high then it may lead the system to instability. However, diffusion, when it occurs, plays a general role of increasing stability in the system. It is shown that sufficiently rapid diffusion by the prey species may stabilize an otherwise unstable equilibrium.

In Chapter VI, a mathematical model is presented to study a system of two-predator species competing for two-resource prey species with diffusion. It is assumed that the dynamics of the prey species follow generalized logistic equations and the dynamics of the predator species are governed by general functional responses. In the absence of diffusion, it is noted that global stability behavior of the interior equilibrium depends on the intraspecific interference coefficients of the predator species. It is also noted that global stability of the interior equilibrium depends on the specific growth



rates of the prey species. It is shown that increasing the diffusion coefficients of both predator and/or prey species to sufficiently large values stabilizes an otherwise unstable interior equilibrium.

In Chapter VII, a Gause-type predator-prey interacting model with self as well as cross-diffusion is considered and the stability conditions in different environmental consequences are investigated.

The model is analyzed in three different cases. In the first case it is shown that if the predator species tend to diffuse in the direction of higher concentration of the prey species, and the prey species moves along its own concentration gradient, then the interior equilibrium state is locally asymptotically stable. It is also noted that when the critical wave length is too small, that the predator species tend to diffuse in the direction of lower concentration of prey species, and the prey species moves along its own concentration gradient, then this leads to local instability of the equilibrium state. In this case it is shown that the unstable equilibrium of the system becomes stable under certain parametric conditions. In the second case, it is shown that if the prey species tend to diffuse in the direction of lower concentration of the predator species, and the predator species moves along its own concentration gradient, then the equilibrium state is locally asymptotically stable. But this equilibrium becomes unstable if the critical wave length is very small. In such a case the prey species tend to diffuse in the direction of higher concentration of the predator species, and the predator species moves along its own concentration gradient. In the third case, it is shown that if the prey species tend to diffuse in the direction of lower concentration of the predator species, and the predator species tend to diffuse in the direction of higher

concentration of the prey species, then the equilibrium state remains stable. Further, it is found that if the equilibrium state of the system with no diffusion is globally stable, then the corresponding uniform steady state of the system with diffusion remains globally stable under a certain condition. It is also shown that if the equilibrium state of the system with no diffusion is unstable, then the corresponding uniform steady state of the system with diffusion can be made stable by increasing the self-diffusion coefficients to sufficiently large values.

In Chapter VIII, a nonlinear mathematical model is proposed and analyzed in order to study the behavior of two competing species with self and cross diffusion. It is assumed that the growth rate and carrying capacity of each competing species decreases as the density of the competitive species increases. In the absence of diffusion it is shown that the two competing species settle down to their respective equilibrium levels under certain conditions, whose magnitudes are lower than their respective density independent carrying capacities. It is noted that the density of either competitor decreases and the density of each species may tend to zero if the equilibrium density of the other species increases beyond a threshold value. In the presence of self-diffusion and in the absence of cross-diffusion it is found that the stability of the system increases and the otherwise unstable equilibrium becomes stable. In the presence of self and cross-diffusion it is noted that if the second competitor tends to diffuse in the direction of higher concentration of the first competitor, and the first competitor moves along its own concentration gradient, then the interior equilibrium, which is stable in the absence of diffusion, remains locally asymptotically stable. It is

further noted that if the critical wave length is sufficiently small, the second competitor tends to diffuse in the direction of lower concentration of the first competitor, and the first competitor moves along its own concentration gradient, then the interior equilibrium, which is stable in the absence of diffusion, becomes unstable. It is shown that the equilibrium may be stable or unstable depending upon the density of the competitors, their self and cross-diffusion coefficients and the critical wave lengths of the system. It is shown that if the equilibrium of the system without self and cross-diffusion is globally asymptotically stable, then the uniform steady state of the system with self-diffusion remains globally asymptotically stable. It is also noted that if the equilibrium is unstable in the absence of diffusion, then it can be made stable under certain conditions in the presence of self and cross-diffusion.

It is hoped that the research carried out in the present thesis, will provide a basis for better study of ecology of India and also will be a very fruitful step towards socio-economic sustainable development.

CHAPTER II

MODELS FOR THE DEPLETION OF A FORESTED GRASSLAND RESOURCE BY ANIMAL POPULATIONS

2.0 INTRODUCTION

One of the important problems in mathematical ecology is the study of depletion of resources by populations dependent upon such resources. The depletion of forested grassland resources (grass) due to its overexploitation by ungulates present in the grassland and by cattle migrating from the plains into the grassland during periods of scant rainfall and drought in the region is a major cause of concern because it not only destroys the grassland but also creates a soil erosion problem in the region. In general the forested grassland is depleted due to overgrazing by cattle populations and by various human activities such as its use for the expansion of agricultural land, its clearance for resettlement, colonization and industrialization, the cutting of trees for fuel fodder, etc., leading to a considerable loss of grass biomass on which the survival of cattle populations is dependent.

In recent decades some mathematical models have been proposed to study the problems of grass biomass grazing by animal populations, (Noy-Meir (1975, 1976, 1978), Noy-Meir et al. (1989)). In models of Noy-Meir and his coworkers, the grazing of grasslands is considered in terms of herbage growth and animal consumption rates but the migration of cattle populations from the plains into the grasslands is not taken

into account. Taking this aspect into consideration, Agarwal et al. (1993) proposed and analysed a mathematical model to study the effect of grazing of forested grasslands and their conservation by assuming the migration rate of the cattle population is a constant. In the study of Agarwal et al. (1993) the growth and the death rates appear either linear or bilinear which need not be the case. Therefore in this chapter a general non-linear model for grazing of forested grasslands is proposed by considering biomass density-dependent growth and death rate functions. A model to conserve the grass biomass is also proposed and analysed.

2.1 MATHEMATICAL MODEL

We consider a forested grassland consisting of a simple closed region R with smooth boundary ∂R where its resource biomass (grass) is being continuously depleted due to overgrazing by cattle populations. We assume that the dynamics of the grass biomass density follows a general logistic-type equation and the dynamics of the cumulative density of cattle populations is governed by a predator-prey type equation. Thus, the dynamics of the system can be governed by the following system of autonomous differential equations:

$$\begin{aligned} \frac{dG}{dt} &= r(N)G - \frac{r_0 G^2}{K} , \\ \frac{dN}{dt} &= Q(G) - p(G)N , \\ G(0) &\geq 0, N(0) \geq 0. \end{aligned} \tag{2.1}$$

Here $G(t)$ is the density of the grass biomass and $N(t)$ the cumulative density of cattle populations at time $t \geq 0$.

In model (2.1), $r(N)$ denotes the specific growth rate of the grass biomass which satisfies

$$r(0) = r_0 > 0, r'(N) < 0 \text{ for } N > 0,$$

and there exists a $\bar{N} > 0$ such that $r(\bar{N}) = 0$. (2.2)

This shows that the specific growth rate of grass biomass decreases as the density of the cattle populations increase and it may tend to zero if the density of the cattle populations become too high (i.e. at $N = \bar{N}$).

The function $Q(G)$ is net birth minus death rate of the cattle population and it increases as G increases, and hence we assume

$$Q(0) = Q_0 > 0, Q'(G) > 0 \text{ for } G > 0,$$

and $\lim_{G \rightarrow \infty} Q(G) = Q_\infty < \infty$. (2.3)

The function $p(G)$ may be thought of as the removal rate of the cattle population and it satisfies

$$p(0) = p_0 > 0, p'(G) < 0 \text{ for } G > 0. \quad (2.4)$$

The constant K in the first equation of model (2.1) is the carrying capacity of the forested grassland corresponding to the grass biomass.

Remark: It may be noted here that if we take

$$r(N) = r_0 - r_1 N, \quad Q(G) = Q_0, \quad p(G) = p_0 - p_1 G$$

where the parameters r_0, r_1, Q_0, p_0, p_1 are positive constants, then model (2.1) reduces to that of Agarwal et al. (1993).

Stability analysis of model (2.1)

Model (2.1) has two nonnegative equilibria, namely $E_0(0, Q_0/p_0)$ and $E^*(G^*, N^*)$, where G^* and N^* are the positive solutions of the following algebraic equations

$$G = K r(N)/r_0, \quad (2.5a)$$

$$N = Q(G)/p(G). \quad (2.5b)$$

It can easily be verified that the equilibrium E^* exists if and only if

$$Q_0 < p_0 \bar{N}. \quad (2.6)$$

By computing the variational matrices corresponding to each equilibrium, we note that E_0 is a saddle point whose unstable manifold is locally in the N direction and whose stable manifold is locally in the G direction.

In the following theorem we prove that E^* is locally asymptotically stable in the G - N plane.

Theorem 2.1.1: The equilibrium $E^*(G^*, N^*)$ of model (2.1) is locally asymptotically stable in the G - N plane.

Proof: The variational matrix corresponding to E^* is given by

$$M^* = \begin{bmatrix} -\frac{r}{K} G^* & r'(N^*)G^* \\ Q'(G^*) - N^*p'(G^*) & -p(G^*) \end{bmatrix}$$

Now the characteristic equation of M^* is

$$\lambda^2 + a_1 \lambda + a_2 = 0,$$

where

$$a_1 = \frac{r}{K} G^* + p(G^*) > 0,$$

$$a_2 = \frac{r}{K} G^* p(G^*) - r'(N^*) Q'(G^*) G^* + r'(N^*) p'(G^*) G^* N^* > 0.$$

By the Routh-Hurwitz criteria we note that all eigenvalues of M^* have negative real parts, and hence the theorem follows.

Now in order to investigate the global stability behavior of the interior equilibrium E^* , we first state the following lemma which establishes a region of attraction for system (2.1). The proof of this lemma is similar to Hsu (1978) and hence is omitted.

Lemma 2.1.1: The set

$$\Omega_1 = \{(G, N): 0 \leq G \leq K, 0 \leq N \leq N_k, N_k = Q(K)/p(K)\}$$

attracts all solutions initiating in the interior of the positive quadrant.

The following theorem gives criteria under which E^* is globally asymptotically stable.

Theorem 2.1.2: In addition to assumptions (2.2) - (2.4), let $r(N)$, $Q(G)$ and $p(G)$ satisfy in Ω_1

$$0 \leq -r'(N) \leq \rho_1, \quad 0 \leq Q'(G) \leq \rho_2, \quad 0 \leq -p'(G) \leq \rho_3 \quad (2.7)$$

for some positive constants ρ_1, ρ_2, ρ_3 . If the following inequality holds

$$[\rho_1 + \rho_2 + N_k \rho_3]^2 < r_0 p(G^*)/K \quad (2.8)$$

then E^* is globally asymptotically stable with respect to all solutions initiating in the interior of the positive quadrant.

Proof: We consider the following positive definite function about E^* ,

$$V(G, N) = G - G^* - G^* \ln(G/G^*) + \frac{1}{2} (N - N^*)^2. \quad (2.9)$$

Differentiating V with respect to t along solutions of (2.1), we get after some algebraic manipulations that

$$\begin{aligned} \dot{V} = & -\frac{r_0}{K} (G - G^*)^2 - p(G^*)(N - N^*)^2 \\ & + (\eta_1(N) + \eta_2(G) + N \eta_3(G))(G - G^*)(N - N^*), \end{aligned} \quad (2.10)$$

where

$$\eta_1(N) = \begin{cases} \frac{r(N) - r(N^*)}{N - N^*}, & N \neq N^* \\ r'(N^*), & N = N^* \end{cases},$$

$$\eta_2(G) = \begin{cases} \frac{Q(G) - Q(G^*)}{G - G^*}, & G \neq G^* \\ Q'(G^*), & G = G^* \end{cases},$$

$$\eta_3(G) = \begin{cases} \frac{p(G) - p(G^*)}{G - G^*}, & G \neq G^* \\ p'(G^*), & G = G^* \end{cases}.$$

We note from (2.7) and the mean value theorem that

$$|\eta_1(N)| \leq \rho_1, \quad |\eta_2(G)| \leq \rho_2, \quad |\eta_3(G)| \leq \rho_3. \quad (2.11)$$

Now \dot{V} can further be written as the sum of the quadratics,

$$V = -a_{11}(G - G^*)^2 + a_{12}(G - G^*)(N - N^*) - a_{22}(N - N^*)^2, \quad (2.12a)$$

where

$$a_{11} = \frac{r_0}{K}, \quad a_{22} = p(G^*), \quad a_{12} = \eta_1(N) + \eta_2(G) + N\eta_3(G). \quad (2.12b)$$

A sufficient condition for \dot{V} to be negative definite is that the following inequality holds

$$a_{12}^2 < 4a_{11}a_{22}. \quad (2.13)$$

Since (2.8) \Rightarrow (2.13) we conclude that V is a Liapunov function (Lasalle and Lefschetz (1961), Rao (1981)) with respect to E^* whose domain contains the region Ω_1 , proving the theorem.

2.2 CONSERVATION MODEL

To conserve the grass biomass, which is being depleted due to overgrazing by cattle population, some efforts such as irrigation, plantation, fencing, use of fertilizers, etc. must be adopted so that the grass biomass can be maintained at the desired level. Let $F(t)$ be the density of effort applied to conserve the grass biomass with $F(t)$ assumed to be proportional to the variance of the grass biomass from its carrying capacity K . Then the dynamics of the system can be written as

$$\begin{aligned} \frac{dG}{dt} &= r(N)G - \frac{r_0 G^2}{K} + r_1 F + r_2 GF, \\ \frac{dN}{dt} &= Q(G) - p(G)N, \end{aligned} \quad (2.14)$$

$$\frac{dF}{dt} = \mu_1 \left(1 - \frac{G}{K}\right) - \mu_0 F,$$

$$G(0) \geq 0, \quad N(0) \geq 0, \quad F(0) \geq 0.$$

Here $\mu_1 > 0$ is the growth rate coefficient of the effort applied and $\mu_0 > 0$ is its natural depreciation rate coefficient due to various factors such as human or financial. $r_1 > 0$ the growth rate coefficient of the grass biomass due to effort as in the case of fencing, $r_2 > 0$

is the growth rate coefficient of gras biomass due to its intraction with effort as in the case of irrigation, use of fertilizers etc. The interpretations of the other parameters and functions in model (2.14) are the same as in model (2.1).

Stability analysis of model (2.14)

It is easy to check that system (2.14) has only one interior equilibrium $\tilde{E}(\tilde{G}, \tilde{N}, \tilde{F})$, where \tilde{G} , \tilde{N} and \tilde{F} are the positive solutions of the following algebraic equations

$$r_0 G = K \left[r(f(G)) + \frac{\mu_1}{\mu_0} \left(\frac{r_1}{G} + r_2 \right) \left(1 - \frac{G}{K} \right) \right], \quad (2.15a)$$

$$N = \frac{Q(G)}{P(G)} = f(G), \quad (\text{say}) \quad (2.15b)$$

$$F = \frac{\mu_1}{\mu_0} \left(1 - \frac{G}{K} \right). \quad (2.15c)$$

It may be noted here that for \tilde{F} to be positive, we must have

$$\tilde{G} < K. \quad (2.16)$$

It can easily be verified that the first equation of (2.15) has a unique positive solution \tilde{G} in the interval $0 < \tilde{G} < K$, provided the inequality (2.6) holds. Then \tilde{N} and \tilde{F} can be computed from Eq.(2.15b) and (2.15c) respectively. Thus the interior equilibrium \tilde{E} exists under conditions (2.6) and (2.16).

In the following theorem we show that \tilde{E} is locally asymptotically stable. The proof of this theorem follows from the Routh-Hurwitz Criteria and hence is omitted.

Theorem 2.2.1: The equilibrium \tilde{E} is locally asymptotically stable in the G-N-F plane.

In the following lemma we show that all solutions are bounded. The proof of this lemma is similar to Lemma 2.1.1 and hence is omitted.

Lemma 2.2.1: The set

$$\Omega_2 = \{(G, N, F): 0 \leq G \leq G_c, 0 \leq N \leq N_c, 0 \leq F \leq \mu_1/\mu_0\}$$

is a region of attraction for all solutions initiating in the interior of the positive orthant, where

$$G_c = \frac{K}{2r_0} \left(r_0 + \frac{r_2 \mu_1}{\mu_0} \right) \left[1 + \left\{ 1 + \frac{4r_0 r_1 \mu_1}{\mu_0 K} \left/ \left(r_0 + \frac{r_2 \mu_1}{\mu_0} \right)^2 \right\}^{1/2} \right], \quad N_c = \frac{Q(G_c)}{p(G_c)}.$$

It may be noted here that the attracting set Ω_2 is larger than the set Ω_1 in Lemma 2.1.1 as expected.

In the following theorem we are able to write down sufficient conditions for \tilde{E} to be globally asymptotically stable.

Theorem 2.2.2: In addition to assumptions (2.2) - (2.4), let $r(N)$, $Q(G)$ and $p(G)$ satisfy in Ω_2

$$0 \leq -r'(N) \leq \tilde{\rho}_1, \quad 0 \leq Q'(G) \leq \tilde{\rho}_2, \quad 0 \leq -p'(G) \leq \tilde{\rho}_3 \quad (2.17)$$

for some positive constants $\tilde{\rho}_1, \tilde{\rho}_2, \tilde{\rho}_3$. If the following inequality holds

$$[\tilde{\rho}_1 + \tilde{\rho}_2 + N_c \tilde{\rho}_3]^2 < r_0 p(\tilde{G})/K, \quad (2.18)$$

then \tilde{E} is globally asymptotically stable with respect to all solutions initiating in the interior of the positive orthant.

Proof: We consider the following Liapunov function about \tilde{E} ,

$$V_1(G, N, F) = G - \tilde{G} - \tilde{G} \ln(G/\tilde{G}) + \frac{1}{2} (N - \tilde{N})^2 + \frac{K}{2\mu_1 \tilde{G}} (r_1 + r_2 \tilde{G})(F - \tilde{F})^2. \quad (2.19)$$

Differentiating V_1 with respect to t along the solutions of model (2.14), it can be seen that \dot{V}_1 is negative definite under condition (2.18), proving the theorem.

2.3 SIMULATION ANALYSIS

In this section we present a simulated analysis to explain the applicability of the result by choosing the following particular form of the functions in models (2.1) and (2.14):

$$r(N) = r_0 - r_{10} N, \quad Q(G) = Q_0 + Q_1 G, \quad p(G) = p_0 - p_1 G, \quad (2.20)$$

where all coefficients are positive.

Now we choose the following values of parameters in model (2.1) and in Eq.(2.20):

$$r_0 = 5.5, \quad r_{10} = 0.1, \quad K = 130.0 \\ Q_0 = 2.5, \quad Q_1 = 0.3, \quad p_0 = 6.8, \quad p_1 = 0.01. \quad (2.21)$$

Example 1. Using Eq. (2.20) and the above set of parameters given in (2.21) it can be checked that condition (2.6) for the existence of E^* is satisfied, and E^* is given by

$$G^* \simeq 114.583, \quad N^* \simeq 6.52172. \quad (2.22)$$

It can further be verified that condition (2.8) is also satisfied, which shows that E^* is globally asymptotically stable.

Example 2. To show the effect of conservation of grass biomass, we choose again the same set of functions as given in Eq.(2.20) and the same set of parameters as given in Eq. (2.21). In addition to these, we choose the following values of parameters in model (2.14).

$$r_1 = 2.5, r_2 = 1.5, \mu_0 = 0.1, \mu_1 = 3.0. \quad (2.23)$$

It can be seen that conditions (2.6) and (2.16) for the existence of \tilde{E} are satisfied, and \tilde{E} is given by

$$\tilde{G} \approx 128.1124, \tilde{N} \approx 7.41704, \tilde{F} \approx 0.4356. \quad (2.24)$$

It can also be checked that all eigenvalues of the variational matrix evaluated at \tilde{E} have negative real parts. This shows that \tilde{E} is locally asymptotically stable

Again in Theorem 2.2.2 it can be verified that condition (2.18) is satisfied, showing the global stability character of \tilde{E} .

Comparing the values from Eq.(2.22) and (2.24) we note that the equilibrium levels of \tilde{G} and \tilde{N} are considerably higher than their previous values showing the effect of conservation.

2.4 SUMMARY

In this chapter, a nonlinear mathematical model has been proposed and analysed in order to study the depletion of grass biomass in a forested grassland due to overgrazing by animal populations.

The model has been analysed using stability theory of differential equations. It has been shown that under certain conditions the density of the grass biomass settles down to its equilibrium level which decreases as the density of the animal populations increase. Further, this level may tend to zero if the

density of the animal populations increase to a critical level $N = \bar{N}$.

A model to conserve the grass biomass has also been proposed. By analysing the conservation model, it has been shown that the grass biomass can be maintained at an appropriate level by adopting suitable efforts. Thus, the grass biomass may remain sustainable for a long period even under continued grazing by animal populations.

CHAPTER III

MODELS WITH DIFFUSION FOR THE SURVIVAL OF SPECIES DEPENDENT ON A RESOURCE IN INDUSTRIAL ENVIRONMENTS

3.0 INTRODUCTION

The depletion of forest biomass due to the rapid pace of industrialization pressure and increase in population has become a serious problem for industrialized countries (Kormondy (1986), Munn and Fedorov (1986), Shukla et al. (1989, 1996)). Deforestation has led to many undesirable ecological and environmental consequences, such as top soil erosion, shortage of rainfall, lowering the water table, undesirable climatic change and formation of wasteland, apart from the obvious economic one (Kormondy (1986), Munn and Fedorov (1986)). Deforestation has also caused migration and even extinction of certain animal species (at least locally) (Munn and Fedorov (1986), Shukla et al. (1989)). The Doon Valley in India is such an example where the depletion of forest biomass has changed the overall ecological structure of the valley (Munn and Fedorov (1986)). Man-made projects such as the expansion of agricultural land for food production, growth of mining and wood based industries, development of housing complexes, timber trade and cutting of trees for fuel and fodder etc. are responsible for the ecological degradation of the valley (Munn and Fedorov (1986), Shukla et al. (1989, 1996)). Therefore the various developmental projects leading to industrialization, though essentially required for the benefit of human beings, must be undertaken by keeping in mind the scientific methods of environmental planning and management for maintaining ecological balance. In recent

years, some investigations have been made to study the effects of industrialization pressure on resource biomass (Shukla et al. (1989, 1996)), but little attention has been paid to study such effects on resource dependent biological species with diffusion using mathematical models (Rothe (1976), Hastings (1978b), Shukla and Shukla (1987), Freedman and Shukla (1989), Shukla et al. (1996)). In this chapter, therefore, a mathematical model in the form of nonlinear differential equations with diffusion, in order to study the survival of species dependent on resource in industrial environment, is proposed and analyzed. The effect of conservation of the resource biomass density and control of the undesired level of industrialization pressure is also incorporated into the model.

3.1 MATHEMATICAL MODEL

We consider a forest habitat assumed to consist of a simple closed region R with smooth boundary ∂R . We assume that the density of the wildlife species, resource biomass and industrialization pressure are governed by generalized logistic-type equations (Freedman (1987), Quaddus (1985)). Following (Freedman and Shukla (1989), Hastings (1978), Shukla et al. (1989), Shukla and Shukla (1987)), the model governing the system can be written by means of the following system of autonomous differential equations,

$$\begin{aligned}\frac{\partial N}{\partial t} &= r(B)N - \frac{r_0 N^2}{K_1(B,I)} + D_1 \nabla^2 N, \\ \frac{\partial B}{\partial t} &= Bg(B,K) - \alpha I p(B) - \beta N q(B) + D_2 \nabla^2 B, \\ \frac{\partial I}{\partial t} &= I f(I,L) + \alpha_1 I p(B) + D_3 \nabla^2 I.\end{aligned}\tag{3.1}$$

Here $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the Laplace diffusion operator and $N(t,x,y)$, $B(t,x,y)$, $I(t,x,y)$ are the densities of wildlife species, resource biomass and industrialization pressure, respectively, at coordinate $(x,y) \in R$ and time $t \geq 0$.

We impose the following initial and boundary conditions on system (3.1):

$$\begin{aligned} N(x,y,0) &= \phi(x,y) \geq 0, \\ B(x,y,0) &= \psi(x,y) \geq 0, \\ I(x,y,0) &= \xi(x,y) \geq 0, \\ \frac{\partial N}{\partial n} &= \frac{\partial B}{\partial n} = \frac{\partial I}{\partial n} = 0, \end{aligned} \quad (3.2)$$

where n is the unit outward normal to the region ∂R . The above boundary conditions imply that no external input is imposed from outside.

In model (3.1) the function $r(B)$ is the specific growth rate coefficient of the wildlife species and it increases as biomass density increases. The function $r(B)$ may satisfy the following three types of conditions,

$$1. r(0) > 0, r'(B) > 0 \text{ for } B \geq 0 \quad (3.3a)$$

i.e resource biomass is an alternate food for the wildlife species. Here the wildlife species depends partially on the resource biomass density.

$$2. r(0) = 0, r'(B) > 0 \text{ for } B \geq 0 \quad (3.3b)$$

i.e the 'wildlife species wholly depends upon the resource biomass density,

$$3. r(0) < 0, r(B_a) = 0 \text{ for some } B_a > 0, r'(B) > 0 \text{ for } B \geq 0 \quad (3.3c)$$

i.e the wildlife species act as a predator on the resource biomass density.

The function $K_1(B,I)$ is the carrying capacity of the forest habitat for wildlife species which increases as the density of the forest biomass increases and decreases as the industrialization pressure increases. Hence, we assume,

$$K_1(0,0) = K_{10} > 0, \frac{\partial K_1(B,I)}{\partial B} > 0, \frac{\partial K_1(B,I)}{\partial I} < 0 \text{ for } B \geq 0, I \geq 0, \quad (3.4)$$

where K_{10} is the carrying capacity independent of B and I .

The function $g(B,K)$ is the specific growth rate of forest biomass. For small density, the forest will grow in the absence of wildlife and industrialization pressure. However there is a carrying capacity K beyond which the forest resource will decline. Thus we assume,

$$g(0,0) = g_0 > 0, \frac{\partial g(B,K)}{\partial B} < 0, \frac{\partial g(B,K)}{\partial K} > 0 \text{ and } g(K,K) = 0. \quad (3.5)$$

The function $f(I,L)$ is the specific growth rate of industrialization pressure and it satisfies

$$f(0,0) = f_0 > 0, \frac{\partial f(I,L)}{\partial I} < 0, \frac{\partial f(I,L)}{\partial L} > 0, \text{ and } f(L,L) = 0, \quad (3.6)$$

where L is the carrying capacity for the industrialization pressure.

The functions $p(B)$ and $q(B)$ are functional responses corresponding to industrialization pressure and wildlife species respectively. Since the functional response $p(B)$ increases with the increase of forest resource biomass density, we assume,

$$p(0) = 0, p'(B) > 0 \text{ for } B \geq 0 \text{ and } \lim_{B \rightarrow \infty} p(B) = p_\infty < \infty. \quad (3.7)$$

The function $q(B)$ has similar properties as $p(B)$, so therefore we have

$$q(0) = 0, q'(B) > 0 \text{ for } B \geq 0, \lim_{B \rightarrow \infty} q(B) = q_{\infty} < \infty. \quad (3.8)$$

Also in model (3.1), D_1, D_2, D_3 are the diffusion coefficients in R for the wildlife species, the resource biomass and the industrialization pressure, respectively. The positive constants α and β are depletion rate coefficients of the forest biomass due to the industrialization and wildlife respectively and α_1 is the growth rate coefficient of the industrialization due to forest biomass.

3.2 THE MODEL WITHOUT DIFFUSION

In the case of no diffusion ($D_1 = D_2 = D_3 = 0$), model (3.1)-(3.2) takes the form

$$\begin{aligned} \dot{N} &= r(B)N - \frac{r_0 N^2}{K_1(B, I)}, \\ \dot{B} &= Bg(B, K) - \alpha I p(B) - \beta N q(B), \\ \dot{I} &= I f(I, L) + \alpha_1 I p(B), \end{aligned} \quad (3.9)$$

$$N(0) = \phi_0 > 0, B(0) = \psi_0 > 0, I(0) = \xi_0 > 0$$

where $\frac{d}{dt} \equiv \frac{d}{dt}$; $N(x, y, t) = N(t)$, $B(x, y, t) = B(t)$, $I(x, y, t) = I(t)$.

Stability analysis of model (3.9):

We first analyze model (3.9) when the wildlife species of density $N(t)$ depends partially on the resource biomass $B(t)$. In such a case the resource biomass may be considered as an alternate resource for the species. In this case the function $r(B)$ satisfies the condition (3.3a) and we take $r(0) = r_0 > 0$.

Existence of equilibria

Setting $\frac{dx}{dt} (x=N, B, I) = 0$ in equations (3.9), and on solving these equations we get eight equilibria, namely $E_{10}(0, 0, 0)$, $E_{11}(0, K, 0)$,

$E_{12}(0, 0, L)$, $E_{13}(K_{10}, 0, 0)$, $E_{14}(K_1(0, L), 0, L)$, $E_{15}(\bar{N}, \bar{B}, 0)$,
 $E_{16}(0, \tilde{B}, \tilde{I})$, $E_{17}^*(N^*, B^*, I^*)$. The equilibria $E_{10} - E_{14}$ obviously exist,
and we shall show the existence of other equilibria in the following.

Existence of $E_{15}(\bar{N}, \bar{B}, 0)$: Here \bar{N} and \bar{B} are the positive solutions of
the following equations

$$N = \frac{r(B)K_1(B,0)}{r_0} \quad (3.10a)$$

$$N = \frac{Bg(B,K)}{\beta q(B)}. \quad (3.10b)$$

From (3.10a) we note that

$$\lim_{B \rightarrow 0} N = K_{10} > 0, \quad (3.10c)$$

$$\frac{dN}{dB} = \frac{1}{r_0} \left\{ r'(B)K_1(B,0) + r(B) \frac{\partial K_1(B,0)}{\partial B} \right\} > 0. \quad (3.10d)$$

This shows that N is an increasing function of B starting from K_{10} .

From (3.10b) we note that

$$\text{when } B \rightarrow K, \quad N \rightarrow 0, \quad (3.10e)$$

$$\text{when } B \rightarrow 0, \quad N \rightarrow \frac{g(0,K)}{\beta q'(0)}, \quad (3.10f)$$

$$\frac{dN}{dB} = \frac{1}{\beta q(B)} \left\{ g(B,K) + B \frac{\partial g(B,K)}{\partial B} \right\} - \frac{Bg(B,K)q'(B)}{\beta q^2(B)} \quad (3.10g)$$

$$\lim_{B \rightarrow K} \frac{dN}{dB} = \frac{K}{\beta q(K)} \frac{\partial g(K,K)}{\partial B} < 0. \quad (3.10h)$$

From (3.10g) we note that $\frac{dN}{dB}$ may be positive or negative depending upon the values of the functions $g(B,K)$ and $q(B)$. However, it is negative in the neighborhood of the point $B = K$. Further, $\frac{dN}{dB}$ is negative provided

$$\frac{1}{g(B,K)} \frac{\partial g(B,K)}{\partial B} < \frac{Bq'(B) - q(B)}{Bq(B)}. \quad (3.10i)$$

Thus the two isoclines (3.10a) and (3.10b) intersect at a unique point (\bar{N}, \bar{B}) under the condition

$$K_{10} < \frac{g(0,K)}{\beta q'(0)}. \quad (3.10j)$$

Hence the equilibrium $E_{15}(\bar{N}, \bar{B}, 0)$ exists provided (3.10i) and (3.10j) hold.

Existence of $E_{16}(0, \tilde{B}, \tilde{I})$: Here \tilde{B} and \tilde{I} are the positive solutions of the system of algebraic equations:

$$I = \frac{Bg(B,K)}{\alpha p(B)}, \quad (3.11a)$$

$$f(I,L) = -\alpha_1 p(B). \quad (3.11b)$$

As in the existence of E_{15} , it can be seen that the equilibrium E_{16} exists, provided the following conditions hold:

$$\frac{1}{g(B,K)} \frac{\partial g(B,K)}{\partial B} < \frac{Bp'(B) - p(B)}{Bp(B)} \quad (3.11c)$$

$$\text{and } L < \frac{g(0,K)}{\alpha p'(0)}. \quad (3.11d)$$

Remark 1: For $p(B) = B$, $q(B) = B$ conditions (3.10i) and (3.11c) are satisfied automatically.

Existence of $E_{17}^(N^*, B^*, I^*)$:* Here N^* , B^* and I^* are the positive solutions of the following algebraic equations

$$N = \frac{r(B)K_1(B,I)}{r_0}, \quad (3.12a)$$

$$I = \frac{1}{\alpha r_0 p(B)} [r_0 Bg(B,K) - \beta q(B)r(B)K_1(B,I)], \quad (3.12b)$$

$$f(I,L) = -\alpha_1 p(B). \quad (3.12c)$$

From (3.12a) it is clear that N increases as B increases or as I decreases.

From (3.12b) we note the following:

$$\text{when } B \rightarrow 0, I \rightarrow I_c^* \text{ where } I_c^* = \frac{1}{\alpha p'(0)} [g(0,K) - \beta q'(0)K_1(0,I_c^*)], \quad (3.12d)$$

when $B \rightarrow K, I \rightarrow I_k^*$ where I_k^* is a zero of

$$F(I) = \alpha r_0 I p(K) + \beta q(K)r(K)K_1(K,I). \quad (3.12e)$$

We also have

$$\begin{aligned} \left[1 + \frac{\beta q(B)r(B)}{\alpha r_0 p(B)} \frac{\partial K_1(B,I)}{\partial I} \right] \frac{dI}{dB} &= \frac{g(B,K)}{\alpha p^2(B)} [p(B) - Bp'(B)] \\ &+ \frac{\beta r(B)K_1(B,I)}{\alpha r_0 p^2(B)} [p'(B)q(B) - p(B)q'(B)] \\ &+ \frac{1}{r_0 \alpha p(B)} \left[r_0 B \frac{\partial g(B,K)}{\partial B} - \beta q(B)r'(B)K_1(B,I) \right. \\ &\left. - \beta q(B)r(B) \frac{\partial K_1(B,I)}{\partial B} \right]. \end{aligned} \quad (3.12f)$$

Now $\frac{dI}{dB} < 0$ if either

(i) the right hand side of (3.12f) is negative and the coefficient of $\frac{dI}{dB}$ in the left hand side is positive (3.12g)

or

(ii) the right hand side of (3.12f) is positive and the coefficient of $\frac{dI}{dB}$ in the left hand side is negative. (3.12h)

The interpretation of the isocline (3.12c) is the same as that of (3.11b).

Thus from the above analysis it is clear that the isoclines (3.12b) and (3.12c) intersect at a unique point (B^*, I^*) if $I_c^* > L$ and

either (3.12g) or (3.12h) hold.

Knowing the values of B^* and I^* , the values of N^* can then be computed from (3.12a).

Stability of equilibria

The local stability of the equilibria can be studied from variational matrices (Freedman (1987)) corresponding to each equilibrium. By computing the variational matrices corresponding to each equilibrium we note the following obvious results

1. $E_{10}(0, 0, 0)$ has an unstable manifold lying in the N-B-I space.
2. $E_{11}(0, K, 0)$ is a saddle point whose unstable manifold is locally in the N-I plane and stable manifold is locally along the B-direction.
3. $E_{12}(0, 0, L)$ is a saddle point whose unstable manifold is locally in the N-B plane and stable manifold is locally along the I-direction, provided condition (3.11d) holds.
4. $E_{13}(K_{10}, 0, 0)$ is a saddle point whose unstable manifold is locally along the N-direction provided condition (3.10j) holds.
5. $E_{14}(K_1(0,L), 0, L)$ is a saddle point whose stable manifold is locally in the N-I plane and whose unstable manifold is locally along the B-direction, provided

$$g(0,K) - \alpha L p'(0) - \beta K_1(0,L) q'(0) > 0.$$

6. $E_{15}(\bar{N}, \bar{B}, 0)$ has an unstable manifold locally along the I-direction and has a stable manifold locally in the N-B plane, provided

$$g(\bar{B},K) + \bar{B} \frac{\partial g(\bar{B},K)}{\partial \bar{B}} - \beta \bar{N} q'(\bar{B}) < 0.$$

7. $E_{16}(0, \tilde{B}, \tilde{I})$ has an unstable manifold locally along the N-direction and a has stable manifold locally in the B-I plane if

$$g(\tilde{B},K) + \tilde{B} \frac{\partial g(\tilde{B},K)}{\partial \tilde{B}} - \alpha \tilde{I} q'(\tilde{B}) < 0.$$

In general there is no obvious remark to be made about whether E_{17}^* is locally asymptotically stable. In the following theorem we shall give sufficient conditions for E_{17}^* to be locally asymptotically stable.

Theorem 3.2.1: In addition to assumptions (3.3a), (3.4)-(3.8), if the following inequalities hold

$$G^* = g(B^*, K) + B^* \frac{\partial g(B^*, K)}{\partial B} - \alpha I^* p'(B^*) - \beta N^* q'(B^*) < 0, \quad (3.13a)$$

$$\left[r'(B^*) + \frac{r_0 N^*}{K_1^2(B^*, I^*)} \frac{\partial K_1(B^*, I^*)}{\partial B} - \frac{\beta q(B^*)}{B^*} \right]^2 < - \frac{r_0}{K_1(B^*, I^*)} \left[\frac{G^*}{B^*} \right], \quad (3.13b)$$

$$\left[\frac{\alpha p(B^*)}{B^*} + \alpha_1 p'(B^*) \right]^2 < \left[\frac{G^*}{B^*} \right] \left[\frac{\partial f(I^*, L)}{\partial I} \right], \quad (3.13c)$$

$$\left[\frac{r_0 N^*}{K_1^2(B^*, I^*)} \frac{\partial K_1(B^*, I^*)}{\partial I} \right]^2 < - \frac{r_0}{K_1(B^*, I^*)} \frac{\partial f(I^*, L)}{\partial I}, \quad (3.13d)$$

then E_{17}^* is locally asymptotically stable.

Proof: Linearizing system (3.9) by substituting

$$N = N^* + n, \quad B = B^* + b, \quad I = I^* + i$$

and using the following positive definite function about E_{17}^*

$$U(n, b, i) = \frac{1}{2} \left[\frac{n^2}{N^*} + \frac{b^2}{B^*} + \frac{i^2}{I^*} \right], \quad (3.14)$$

it can be seen that the time derivative of U along the solutions of (3.9) is negative definite under conditions (3.13), proving the theorem.

In the following theorem we will find conditions which guarantee

that E_{17}^* is globally asymptotically stable. We first state that the following lemma which establishes a region of attraction for system (3.9). The proof of this lemma is easy and hence is omitted.

Lemma 3.2.1: The set

$$\Omega_1 = \{(N, B, I) : 0 \leq N \leq N_k, 0 \leq B \leq K, 0 \leq I \leq L_k\}$$

is a region of attraction for all solutions initiating in the nonnegative orthant, where

$$N_k = r(K)K_1(K, 0)/r_0, \quad L_k = L \left\{ 1 + \frac{\alpha_1 p(K)}{f(0, L)} \right\}.$$

Theorem 3.2.2: In addition to assumptions (3.3a), (3.4) - (3.8), let $p(B)$, $q(B)$, $g(B, K)$, $f(I, L)$ and $K_1(B, I)$ satisfy the following conditions

$$0 \leq r'(B) \leq r_m, \quad p_0 \leq p'(B) \leq p_1, \quad p_2 \leq \frac{p(B)}{B} \leq p_3, \quad p_4 \leq \frac{d}{dB} \left(\frac{p(B)}{B} \right) \leq p_5,$$

$$q_0 \leq \frac{q(B)}{B} \leq q_1, \quad q_2 \leq \frac{d}{dB} \left(\frac{q(B)}{B} \right) \leq q_3, \quad K_m \leq K_1(B, I) \leq K_1(K, 0),$$

$$\rho_0 \leq -\frac{\partial g(B, K)}{\partial B} \leq \rho, \quad 0 \leq \frac{\partial K_1(B, I)}{\partial B} \leq \rho_1, \quad 0 \leq -\frac{\partial K_1(B, I)}{\partial I} \leq \rho_2,$$

$$\rho_3 \leq -\frac{\partial f(I, L)}{\partial I} \leq \rho_4, \tag{3.15}$$

in Ω_1 for some positive constants $r_m, p_0, p_1, p_2, p_3, p_4, p_5, q_0, q_1, q_2, q_3, K_m, \rho, \rho_0, \rho_1, \rho_2, \rho_3, \rho_4$.

If the following inequalities hold

$$\left[r_m + \frac{r_0 N_k \rho_1}{K_m^2} + \beta q_1 \right]^2 < \frac{r_0}{K_1(B^*, I^*)} \left[\rho_0 + \alpha I^* p_4 + \beta N^* q_2 \right], \tag{3.15a}$$

$$\left[\alpha_1 p_1 + \alpha p_3 \right]^2 < \rho_3 \left[\rho_0 + \alpha I^* p_4 + \beta N^* q_2 \right], \tag{3.15b}$$

$$\left[\frac{r_0 N_k \rho_2}{K_m^2} \right]^2 < \frac{r_0}{K_1(B^*, I^*)} \rho_3, \tag{3.15c}$$

then E_{17}^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

Proof: We consider the following positive definite function about E_{17}^*

$$V(N,B,I) = (N - N^* - N^* \ln(N/N^*)) + (B - B^* - B^* \ln(B/B^*)) \\ + (I - I^* - I^* \ln(I/I^*)). \quad (3.16)$$

Differentiating V with respect to t along the solutions of (3.9) we get

$$\dot{V} = \left(-\frac{r_0}{K_1(B^*, I^*)} \right) (N - N^*)^2 - (\alpha I^* \nu_1(B) + \beta N^* \nu_2(B) + \lambda_1(B)) (B - B^*)^2 \\ - \lambda_2(I)(I - I^*)^2 + (\eta_1(B) - r_0 N \xi_1(B, I) - \beta q(B)/B) (N - N^*)(B - B^*) \\ + (\alpha_1 \eta_2(B) - \alpha p(B)/B) (B - B^*)(I - I^*) - r_0 N \xi_2(B^*, I)(N - N^*)(I - I^*) \quad (3.16a)$$

where

$$\eta_1(B) = \begin{cases} \frac{r(B) - r(B^*)}{B - B^*}, & B \neq B^* \\ r'(B^*), & B = B^* \end{cases},$$

$$\eta_2(B) = \begin{cases} \frac{p(B) - p(B^*)}{B - B^*}, & B \neq B^* \\ p'(B^*), & B = B^* \end{cases},$$

$$\nu_1(B) = \begin{cases} \left[\frac{p(B)}{B} - \frac{p(B^*)}{B^*} \right] / (B - B^*), & B \neq B^* \\ \frac{d}{dB} \left(\frac{p(B)}{B} \right)_{B=B^*}, & B = B^* \end{cases},$$

$$\nu_2(B) = \begin{cases} \left[\frac{q(B)}{B} - \frac{q(B^*)}{B^*} \right] / (B - B^*), & B \neq B^* \\ \frac{d}{dB} \left(\frac{q(B)}{B} \right)_{B=B^*}, & B = B^* \end{cases},$$

$$\lambda_1(B) = \begin{cases} - \left[\frac{g(B, K) - g(B^*, K)}{B - B^*} \right], & B \neq B^* \\ - \frac{\partial}{\partial B} \left(g(B^*, K) \right), & B = B^* \end{cases},$$

$$\lambda_2(I) = \begin{cases} - \left[\frac{f(I, L) - f(I^*, L)}{I - I^*} \right], & I \neq I^* \\ - \frac{\partial}{\partial I} \left(f(I^*, L) \right), & I = I^* \end{cases},$$

$$\xi_1(B, I) = \begin{cases} \left[\frac{1}{K_1(B, I)} - \frac{1}{K_1(B^*, I)} \right] / (B - B^*), & B \neq B^* \\ \frac{-1}{K_1^2(B^*, I)} \frac{\partial}{\partial B} \left(K_1(B^*, I) \right), & B = B^* \end{cases},$$

$$\xi_2(B^*, I) = \begin{cases} \left[\frac{1}{K_1(B^*, I)} - \frac{1}{K_1(B^*, I^*)} \right] / (I - I^*), & I \neq I^* \\ \frac{-1}{K_1^2(B^*, I^*)} \frac{\partial}{\partial I} \left(K_1(B^*, I^*) \right), & I = I^* \end{cases}.$$

We note from (3.14) and the mean value theorem that

$$\begin{aligned} |\eta_1(B)| &\leq r_m, \quad p_0 \leq |\eta_2(B)| \leq p_1, \quad p_4 \leq |\nu_1(B)| \leq p_5, \\ q_2 &\leq |\nu_2(B)| \leq q_3, \quad \rho_0 \leq |\lambda_1(B)| \leq \rho, \quad \rho_3 \leq |\lambda_2(I)| \leq \rho_4, \\ |\xi_1(B, I)| &\leq \rho_1 / K_m^2, \quad |\xi_2(B, I)| \leq \rho_2 / K_m^2. \end{aligned} \quad (3.16b)$$

Now \dot{V} can further be written as the sum of the quadratics,

$$\begin{aligned}\dot{V} = & -\frac{1}{2} a_{11}(N - N^*)^2 + a_{12}(N - N^*)(B - B^*) - \frac{1}{2} a_{22}(B - B^*)^2 \\ & - \frac{1}{2} a_{22}(B - B^*)^2 + a_{23}(B - B^*)(I - I^*) - \frac{1}{2} a_{33}(I - I^*)^2 \\ & - \frac{1}{2} a_{33}(I - I^*)^2 + a_{31}(I - I^*)(N - N^*) - \frac{1}{2} a_{11}(N - N^*)^2\end{aligned}$$

where

$$a_{11} = \frac{r_0}{K_1(B^*, I^*)}, \quad a_{12} = \eta_1(B) - r_0 N \xi_1(B, I) - \beta q(B)/B,$$

$$a_{22} = \alpha I^* \nu_1(B) + \beta N^* \nu_2(B) + \lambda_1(B), \quad a_{23} = \alpha_1 \eta_2(B) - \alpha p(B)/B,$$

$$a_{33} = \lambda_2(I), \quad a_{31} = -r_0 N \xi_2(B^*, I).$$

Sufficient conditions for \dot{V} to be negative definite are that the following inequalities hold

$$a_{12}^2 < a_{11} a_{22}, \quad (3.17a)$$

$$a_{23}^2 < a_{22} a_{33}, \quad (3.17b)$$

$$a_{31}^2 < a_{33} a_{11}. \quad (3.17c)$$

Since (3.15a) \Rightarrow (3.17a), (3.15b) \Rightarrow (3.17b), (3.15c) \Rightarrow (3.17c), we conclude that \dot{V} is a Liapunov function (Lasalle and Lefschetz (1961), Rao (1981)) with respect to E_{17}^* whose domain contains the region Ω_1 , thus proving the theorem.

Remark 2. If the function $r(B)$ satisfies condition (3.3b), then model (3.9) can be analyzed in a similar fashion as described earlier. For example, it can be seen that there are six equilibria, namely $E_{20}(0,0,0)$, $E_{21}(0,K,0)$, $E_{22}(0,0,L)$, $E_{23}(\bar{N}, \bar{B}, 0)$, $E_{24}(0, \bar{B}, \bar{I})$, $E_{25}^*(N^*, B^*, I^*)$. It can be also checked that E_{23} exists if (3.10i)

holds. E_{24} exists, if (3.3c) and (3.3d) hold. E_{25}^* exists, if in addition to conditions (3.12g) or (3.12h), $g(0,K) > \alpha Lp'(0)$ holds. The stability behaviors of the equilibria are similar to the case described earlier.

Remark 3. If the function $r(B)$ satisfies condition (3.3c), then it can be seen that there are six equilibria, namely $E_{30}(0,0,0)$, $E_{31}(0,K,0)$, $E_{32}(0,0,L)$, $E_{33}(\bar{N},\bar{B},0)$, $E_{34}(0,\tilde{B},\tilde{I})$, $E_{35}(N^*,B^*,I^*)$. It can be checked that E_{33} exists if in addition to (3.10i), $B_a \leq K$ holds, where B_a is defined in (3.3c). E_{34} exists under conditions (3.11c) and (3.11d). E_{35}^* exists if in addition to conditions (3.12g) or (3.12h), the following inequality holds

$$r_0 g(0,K) - \beta q(0)r(0)K_1(0,I_c^*) > \alpha r_0 Lp'(0).$$

The stability behavior of the equilibria can be studied in a similar fashion as in the case when the wildlife species partially depends on the resource.

3.3 THE MODEL WITH DIFFUSION

In this section we analyze model (3.1) only for the case when $r(0) > 0$. A similar analysis can be carried out for the case when $r(0) = 0$ and $r(0) < 0$. The steady state solutions are obtained by solving the system of equations given below,

$$\begin{aligned} r(B)N + \frac{r_0 N^2}{K_1(B,I)} + D_1 \nabla^2 N &= 0, \\ Bg(B,K) - \alpha Ip(B) - \beta Nq(B) + D_2 \nabla^2 B &= 0, \\ If(I,L) + \alpha_1 Ip(B) + D_3 \nabla^2 I &= 0, \\ \frac{\partial N(x,y)}{\partial n} = \frac{\partial B(x,y)}{\partial n} = \frac{\partial I(x,y)}{\partial n} &= 0; \quad (x,y) \in \partial R. \end{aligned} \tag{3.18}$$

We observe that $N = N^*$, $B = B^*$, $I = I^*$ of E_{17}^* also satisfy (3.18) and is the uniform steady state for system (3.1).

We wish to show that if E_{17}^* is asymptotically stable for system (3.9), then the corresponding steady state is also asymptotically stable for system (3.1)-(3.2).

Now we prove it by considering the following Liapunov function

$$W(N(t), B(t), I(t)) = \iint_R V(N(t,x,y), B(t,x,y), I(t,x,y)) \, dA$$

where $V(N,B,I)$ is defined in (3.16).

$$\begin{aligned} \text{Thus } \dot{W}(N,B,I) &= \iint_R \left(\frac{\partial V}{\partial N} \frac{\partial N}{\partial t} + \frac{\partial V}{\partial B} \frac{\partial B}{\partial t} + \frac{\partial V}{\partial I} \frac{\partial I}{\partial t} \right) \, dA \\ &= I_1 + I_2, \end{aligned} \quad (3.19)$$

$$\text{where } I_1 = \iint_R \dot{V}(N,B,I) \, dA, \quad (3.19a)$$

$$I_2 = \iint_R \left(D_1 \frac{\partial V}{\partial N} \nabla^2 N + D_2 \frac{\partial V}{\partial B} \nabla^2 B + D_3 \frac{\partial V}{\partial I} \nabla^2 I \right) \, dA. \quad (3.19b)$$

We assume that \dot{V} does not change its sign in the region R . Then I_1 has the same sign as \dot{V} . Thus if $\dot{V} \leq 0$, then $I_1 \leq 0$.

Also we have the following conditions,

$$1. \left. \frac{\partial V}{\partial N} \right|_{\partial R} = \left. \frac{\partial V}{\partial B} \right|_{\partial R} = \left. \frac{\partial V}{\partial I} \right|_{\partial R} = 0 \text{ for all points of } R.$$

$$2. \frac{\partial^2 V}{\partial N \partial B} = \frac{\partial^2 V}{\partial B \partial I} = \frac{\partial^2 V}{\partial I \partial N} = 0,$$

$$3. \frac{\partial^2 V}{\partial N^2} > 0, \quad \frac{\partial^2 V}{\partial B^2} > 0, \quad \frac{\partial^2 V}{\partial I^2} > 0.$$

Again, using Green's first identity we have

$$\iint_R \frac{\partial V}{\partial N} \nabla^2 N \, dA = \int_{\partial R} \frac{\partial V}{\partial N} \frac{\partial N}{\partial n} \, ds - \iint_R \left[\nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N \right] \, dA$$

where s is the arc length of ∂R .

$$\text{Also} \quad \nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N = \frac{\partial^2 V}{\partial N^2} \left[\left(\frac{\partial N}{\partial x} \right)^2 + \left(\frac{\partial N}{\partial y} \right)^2 \right].$$

Using boundary condition (3.2) we get,

$$\iint_R \left(\frac{\partial V}{\partial N} \nabla^2 N \right) \, dA = - \iint_R \frac{\partial^2 V}{\partial N^2} \left[\left(\frac{\partial N}{\partial x} \right)^2 + \left(\frac{\partial N}{\partial y} \right)^2 \right] \, dA \leq 0.$$

Thus

$$\begin{aligned} I_2 = - \iint_R \left[D_1 \frac{\partial^2 V}{\partial N^2} \left\{ \left(\frac{\partial N}{\partial x} \right)^2 + \left(\frac{\partial N}{\partial y} \right)^2 \right\} + D_2 \frac{\partial^2 V}{\partial B^2} \left\{ \left(\frac{\partial B}{\partial x} \right)^2 + \left(\frac{\partial B}{\partial y} \right)^2 \right\} \right. \\ \left. + D_3 \frac{\partial^2 V}{\partial I^2} \left\{ \left(\frac{\partial I}{\partial x} \right)^2 + \left(\frac{\partial I}{\partial y} \right)^2 \right\} \right] \, dA \leq 0. \end{aligned} \quad (3.19c)$$

Hence $\dot{W} = I_1 + I_2 \leq 0$.

Thus if $E_{17}^*(N^*, B^*, I^*)$ is globally asymptotically stable for system (3.9), then the corresponding uniform steady state is also globally asymptotically stable for system (3.1)-(3.2). Further we note that even if $\dot{V} > 0$ (i.e., if $I_1 > 0$), by increasing D_1 , D_2 , D_3 sufficiently large, \dot{W} can be made negative.

We shall illustrate the above results for a rectangular habitat R , where R is given by

$$R = \{ (x, y): 0 \leq x \leq a, 0 \leq y \leq b \}.$$

In this case, we note from (3.19c) that I_2 can be written as

$$\begin{aligned}
I_2 \leq & - \int_0^b \int_0^a \left[\frac{D_1 N^*}{N_k^2} \left\{ \left(\frac{\partial(N - N^*)}{\partial x} \right)^2 + \left(\frac{\partial(N - N^*)}{\partial y} \right)^2 \right\} \right. \\
& + \frac{D_2 B^*}{K^2} \left\{ \left(\frac{\partial(B - B^*)}{\partial x} \right)^2 + \left(\frac{\partial(B - B^*)}{\partial y} \right)^2 \right\} \\
& \left. + \frac{D_3 I^*}{L_k^2} \left\{ \left(\frac{\partial(I - I^*)}{\partial x} \right)^2 + \left(\frac{\partial(I - I^*)}{\partial y} \right)^2 \right\} \right] dx dy. \quad (3.20a)
\end{aligned}$$

Letting $z = x/a$ we get

$$\int_0^b \int_0^a \left(\frac{\partial(N - N^*)}{\partial x} \right)^2 dx dy = \frac{1}{a} \int_0^b \int_0^1 \left(\frac{\partial(N - N^*)}{\partial z} \right)^2 dz dy. \quad (3.20b)$$

Now utilizing the known inequality (see Denn (1975), p. 225)

$$\int_0^1 \left(\frac{\partial x}{\partial u} \right)^2 du \geq \pi^2 \int_0^1 x^2 du,$$

in (3.20b), we get

$$\begin{aligned}
\int_0^b \int_0^a \left(\frac{\partial(N - N^*)}{\partial x} \right)^2 dx dy & \geq \frac{\pi^2}{a} \int_0^b \int_0^1 (N - N^*)^2 dz dy \\
& = \frac{\pi^2}{a^2} \iint_R (N - N^*)^2 dA. \quad (3.20c)
\end{aligned}$$

Similarly

$$\int_0^b \int_0^a \left(\frac{\partial(N - N^*)}{\partial y} \right)^2 dx dy \geq \frac{\pi^2}{b^2} \iint_R (N - N^*)^2 dA. \text{ etc.,} \quad (3.20d)$$

Using (3.20c-d) in (3.20a), we obtain

$$\begin{aligned}
I_2 \leq & - \left[\frac{(a^2 + b^2)\pi^2 N^*}{a^2 b^2 N_k^2} D_1 \iint_R (N - N^*)^2 dA \right. \\
& + \frac{(a^2 + b^2)\pi^2 B^*}{a^2 b^2 K^2} D_2 \iint_R (B - B^*)^2 dA \\
& \left. + \frac{(a^2 + b^2)\pi^2 I^*}{a^2 b^2 L_k^2} D_3 \iint_R (I - I^*)^2 dA \right].
\end{aligned}$$

Thus \dot{W} can be written as

$$\dot{W} \leq \iint_R \dot{V} \, dA - \iint_R \left[\frac{(a^2 + b^2)\pi^2 N^*}{a^2 b^2 N_K^2} D_1 (N - N^*)^2 + \frac{(a^2 + b^2)\pi^2 B^*}{a^2 b^2 K^2} D_2 (B - B^*)^2 + \frac{(a^2 + b^2)\pi^2 I^*}{a^2 b^2 L_K^2} D_3 (I - I^*)^2 \right] dA. \quad (3.20e)$$

Substituting the value of \dot{V} from (3.16a) into (3.20e) we note that sufficient conditions for \dot{W} to be negative definite are that the following inequalities hold:

$$a_{12}^2 < \left(a_{11} + \frac{(a^2 + b^2)\pi^2 N^*}{a^2 b^2 N_K^2} D_1 \right) \left(a_{22} + \frac{(a^2 + b^2)\pi^2 B^*}{a^2 b^2 K^2} D_2 \right) \quad (3.21a)$$

$$a_{23}^2 < \left(a_{22} + \frac{(a^2 + b^2)\pi^2 B^*}{a^2 b^2 K^2} D_2 \right) \left(a_{33} + \frac{(a^2 + b^2)\pi^2 I^*}{a^2 b^2 L_K^2} D_3 \right) \quad (3.21b)$$

$$a_{31}^2 < \left(a_{33} + \frac{(a^2 + b^2)\pi^2 I^*}{a^2 b^2 L_K^2} D_3 \right) \left(a_{11} + \frac{(a^2 + b^2)\pi^2 N^*}{a^2 b^2 N_K^2} D_1 \right) \quad (3.21c)$$

where the a_{ij} have the same meanings as in (3.17)

From (3.20e) we observe that if \dot{V} is negative definite, then so is \dot{W} . This is also clear as (3.17a) \Rightarrow (3.21a), (3.17b) \Rightarrow (3.21b), (3.17c) \Rightarrow (3.21c). It may be also be noted that even if \dot{V} is positive definite and if inequalities (3.21a-c) are satisfied, then \dot{W} will be negative definite. Further, inequalities (3.21a-c) may be satisfied by increasing diffusion coefficients D_i ($i = 1,2,3$) to sufficiently large values.

This implies that for a rectangular habitat an unstable steady state of the system with no diffusion can be made stable by increasing diffusion coefficients to sufficiently large values.

In other words we say that the unstable steady state of the system without diffusion can be made stable by increasing the diffusion coefficients.

3.4 CONSERVATION MODEL

Conservation of environment and ecology to sustain life and at the same time to ensure progress has become the challenge of the day. In the previous section it was noted that the density of the resource biomass may vanish due to uncontrolled industrialization pressure and consequently the survival of the species living in that habitat may be threatened. Keeping this in mind, we propose a model to conserve the forestry biomass and to control the undesired level of industrialization pressure. Let $F_1(t)$ be the density of the effort applied to conserve the resource biomass by afforestation, irrigation, fencing, etc., and let $F_2(t)$ be the density of effort applied to control the undesired level of industrialization pressure. It is assumed that F_1 is proportional to the variance of the biomass from its carrying capacity, and F_2 is proportional to the undesired level of the industrialization pressure. The system may then be governed by the following autonomous differential equations:

$$\begin{aligned}
 \frac{\partial N}{\partial t} &= r(B)N - \frac{r_0 N^2}{K_1(B,I)} + D_1 \nabla^2 N, \\
 \frac{\partial B}{\partial t} &= Bg(B,K) - \alpha Ip(B) - \beta Nq(B) + \theta_1 F_1 + D_2 \nabla^2 B, \\
 \frac{\partial I}{\partial t} &= If(I,L) + \alpha_1 Ip(B) - \theta_2 F_2 I + D_3 \nabla^2 I, \\
 \frac{\partial F_1}{\partial t} &= s_1 \left(1 - \frac{B}{K} \right) - \gamma_1 F_1, \\
 \frac{\partial F_2}{\partial t} &= s_2 (I - I_c)H(I - I_c) - \gamma_2 F_2.
 \end{aligned} \tag{3.22a}$$

The initial and boundary conditions are as follows:

$$\begin{aligned}
 N(x,y,0) &= \phi(x,y) \geq 0, \quad B(x,y,0) = \psi(x,y) \geq 0, \\
 I(x,y,0) &= \xi(x,y) \geq 0, \quad F_1(x,y,0) = \chi(x,y) \geq 0, \\
 F_2(x,y,0) &= \zeta(x,y) \geq 0,
 \end{aligned}$$

$$\frac{\partial N}{\partial n} = \frac{\partial B}{\partial n} = \frac{\partial I}{\partial n} = \frac{\partial F_1}{\partial n} = \frac{\partial F_2}{\partial n} = 0; \quad t > 0, \text{ where } n \text{ is the}$$
outward unit normal to the region ∂R . (3.22b)

In model (3.22), the constants $s_1 > 0$, $s_2 > 0$ are the growth rate coefficients of $F_1(t)$ and $F_2(t)$ respectively and $\gamma_1 > 0$, $\gamma_2 > 0$ are their respective depreciation rate coefficients, θ_1 is the growth rate coefficient of $B(t)$ due to the effort $F_1(t)$ and θ_2 is the depletion rate coefficient of $I(t)$ due to the effort $F_2(t)$. Also I_c is the critical value of I which is assumed to be harmless to the resource biomass. The function $H(I - I_c)$ is the unit step function which takes into account the case when $I \leq I_c$. It may be noted that in the unusual circumstance, even in the face of industrialization the forest biomass exceeds its carrying capacity, then $(\partial F_1 / \partial t)$ will be negative, giving a decrease in the reforestation effort. Other parameters and functions in model (3.22) are the same as in model (3.1).

3.5 THE CONSERVATION MODEL WITHOUT DIFFUSION

In the case of no diffusion, we take $D_1 = D_2 = D_3 = 0$ in (3.22). It can be checked that there are two equilibria, viz, $E(0, B, I, F_1, F_2)$ and $\hat{E}(\hat{N}, \hat{B}, \hat{I}, \hat{F}_1, \hat{F}_2)$. We shall establish the existence of the equilibrium \hat{E} only and the existence of E will then follow from the existence of \hat{E} .

Existence of \hat{E} : We note that $\hat{N}, \hat{B}, \hat{I}, \hat{F}_1, \hat{F}_2$ are the positive solutions of the following algebraic equations

$$N = r(B)K_1(B, I)/r_0, \quad (3.23a)$$

$$Bg(B, K) = \alpha_1 p(B) + \beta r(B)q(B)K_1(B, I)/r_0 - \frac{\theta_1 s_1}{\gamma_1} \left(1 - \frac{B}{K}\right), \quad (3.23b)$$

$$f(I, L) = -\alpha_1 p(B) + \frac{\theta_2 s_2}{\gamma_2} (I - I_c)H(I - I_c), \quad (3.23c)$$

$$F_1 = \frac{s_1}{\gamma_1} \left(1 - \frac{B}{K} \right), \quad (3.23d)$$

$$F_2 = \frac{s_2}{\gamma_2} (I - I_c) H(I - I_c). \quad (3.23e)$$

From (3.23b) we get,

$$\text{when } B \rightarrow 0, \text{ then } I \rightarrow \infty, \quad (3.24a)$$

when $B \rightarrow K$, then $I \rightarrow I_K$ where I_K is a zero of

$$F(I) = r_0 \alpha I p(K) + \beta q(K) r(K) K_1(K, I). \quad (3.24b)$$

We also have

$$\begin{aligned} \left[1 + \frac{\beta q(B) r(B)}{\alpha r_0 p(B)} \frac{\partial K_1(B, I)}{\partial I} \right] \frac{dI}{dB} &= \frac{1}{\gamma_1 r_0 p^2(B)} \left[r_0 \left(\gamma_1 g(B, K) - \frac{\theta_1 s_1}{K} \right) \right. \\ &\times (p(B) - B p'(B)) + \beta \gamma_1 r(B) K_1(B, I) (p'(B) q(B) - p(B) q'(B)) \\ &- r_0 \theta_1 s_1 p'(B) + \gamma_1 r_0 B p(B) \frac{\partial g(B, K)}{\partial B} - \beta \gamma_1 q(B) r'(B) K_1(B, I) \\ &\left. - \beta \gamma_1 q(B) r(B) \frac{\partial K_1(B, I)}{\partial B} \right]. \quad (3.24c) \end{aligned}$$

We note that $\frac{dI}{dB} < 0$, when either

(i) the right hand side of (3.24c) is negative and the coefficient of $\frac{dI}{dB}$ in the left hand side is positive, (3.24d)

or

(ii) the right hand side of (3.24c) is positive and the coefficient of $\frac{dI}{dB}$ in the left hand side is negative. (3.24e)

From (3.23c) we note that

$$\text{when } B \rightarrow 0, \text{ then } I \rightarrow I_0, \quad (3.25a)$$

where I_0 is given by

$$I_0 = \frac{\gamma_2}{\theta_2 s_2} f(I_0, L) + I_c. \quad (3.25b)$$

We also have

$$\left(1 - \frac{\gamma_2}{\theta_2 s_2} \frac{\partial f(I, L)}{\partial I} \right) \frac{dI}{dB} = \frac{\gamma_2 \alpha_1}{\theta_2 s_2} p'(B), \quad (3.25c)$$

which shows that $\frac{dI}{dB} > 0$.

Thus from the above analysis, we note that the two isoclines (3.23b) and (3.23c) intersect at a unique point (\hat{B}, \hat{I}) under the conditions (3.24d) or (3.24e).

Knowing the values of \hat{B} and \hat{I} , the values of \hat{N} , \hat{F}_1 , \hat{F}_2 can be computed from (3.23a), (3.23d), (3.23e) respectively.

By computing the variational matrix corresponding to equilibrium \hat{E} it can be checked that \hat{E} is a unstable point.

In the following theorem we find the conditions for \hat{E} to be locally asymptotically stable.

Theorem 3.5.1: Let the following inequalities hold:

$$\hat{G} = g(\hat{B}, K) + \frac{\hat{B} \partial g(\hat{B}, K)}{\partial B} - \alpha \hat{I} p'(\hat{B}) - \beta \hat{N} q'(\hat{B}) < 0, \quad (3.26a)$$

$$\left[r(\hat{B}) + \frac{r_0 \hat{N}}{K_1^2(\hat{B}, \hat{I})} \frac{\partial K_1(\hat{B}, \hat{I})}{\partial B} - \frac{\beta q(\hat{B})}{\hat{B}} \right]^2 < - \frac{r_0}{K_1(\hat{B}, \hat{I})} \left(\frac{\hat{G}}{\hat{B}} \right), \quad (3.26b)$$

$$\left[- \frac{\alpha p(\hat{B})}{\hat{B}} + \alpha_1 p'(\hat{B}) \right]^2 < \left(\frac{\hat{G}}{\hat{B}} \right) \left(\frac{\partial f(\hat{I}, L)}{\partial I} \right), \quad (3.26c)$$

$$\left[\frac{r_0 \hat{N}}{K_1^2(\hat{B}, \hat{I})} \frac{\partial K_1(\hat{B}, \hat{I})}{\partial I} \right]^2 < - \frac{r_0}{K_1(\hat{B}, \hat{I})} \frac{\partial f(\hat{I}, L)}{\partial I}, \quad (3.26d)$$

then \hat{E} is locally asymptotically stable.

Proof : Linearizing system (3.22) with $D_1 = D_2 = D_3 = 0$ by substituting

$$N = \hat{N} + n, B = \hat{B} + b, I = \hat{I} + i, F_1 = \hat{F}_1 + f_1, F_2 = \hat{F}_2 + f_2$$

and using the Liapunov function

$$U_1(n, b, i, f_1, f_2) = \frac{1}{2} \left[\frac{n^2}{N} + \frac{b^2}{B} + \frac{i^2}{I} + \frac{K\theta_1 f_1^2}{2s_1 B} + \frac{\theta_2 f_2^2}{2s_2} \right], \quad (3.27)$$

it can be checked that the derivative of U_1 with respect to t is negative definite under conditions (3.26). This proves the theorem.

We now show that \hat{E} may also be globally asymptotically stable. For this we need the following lemma, which establishes a region of attraction for system (3.22), whose proof is easy and hence is omitted.

Lemma 3.5.1: The set

$$\Omega_2 = \left\{ (N, B, I, F_1, F_2) : 0 \leq N \leq N_m, 0 \leq B \leq B_m, 0 \leq I \leq L_m, \right. \\ \left. 0 \leq F_1 \leq \frac{s_1}{\gamma_1}, 0 \leq F_2 \leq \frac{s_2}{\gamma_2} L_m \right\},$$

attracts all solutions initiating in the interior of the positive orthant, where

$$N_m = \frac{r(B_m)K_1(B_m, 0)}{r_0}, \quad B_m = \frac{K}{2} \left[1 + \left(1 + \frac{4\theta_1 s_1}{\gamma_1 K g(0, K)} \right)^{1/2} \right], \\ L_m = L \left(1 + \frac{\alpha_1 p(B_m)}{f(0, L)} \right).$$

Theorem 3.5.2: In addition to assumptions (3.3a), (3.4) - (3.8) let $r(B)$, $p(B)$, $q(B)$, $g(B, K)$, $f(I, L)$ and $K_1(B, I)$ satisfy the following conditions

$$\begin{aligned}
0 \leq r'(B) \leq \hat{r}_m, \quad \hat{p}_0 \leq p'(B) \leq \hat{p}_1, \quad \hat{p}_2 \leq \frac{p(B)}{B} \leq \hat{p}_3, \quad \hat{p}_4 \leq \frac{d}{dB} \left(\frac{p(B)}{B} \right) \leq \hat{p}_5, \\
\hat{q}_0 \leq \frac{q(B)}{B} \leq \hat{q}_1, \quad \hat{q}_2 \leq \frac{d}{dB} \left(\frac{q(B)}{B} \right) \leq \hat{q}_3, \quad \hat{K}_m \leq K_1(B, I) \leq \hat{K}_1(B_m, 0), \\
\hat{\rho}_0 \leq -\frac{\partial g(B, K)}{\partial B} \leq \hat{\rho}, \quad 0 \leq \frac{\partial K_1(B, I)}{\partial B} \leq \hat{\rho}_1, \quad 0 \leq -\frac{\partial K_1(B, I)}{\partial I} \leq \hat{\rho}_2, \\
\hat{\rho}_3 \leq -\frac{\partial f(I, L)}{\partial I} \leq \hat{\rho}_4
\end{aligned} \tag{3.28}$$

in Ω_2 for some positive constants $\hat{r}_m, \hat{p}_0, \hat{p}_1, \hat{p}_2, \hat{p}_3, \hat{p}_4, \hat{p}_5, \hat{q}_0, \hat{q}_1, \hat{q}_2, \hat{q}_3, \hat{K}_m, \hat{\rho}_0, \hat{\rho}, \hat{\rho}_1, \hat{\rho}_2, \hat{\rho}_3, \hat{\rho}_4$. If the following inequalities hold

$$\left[\hat{r}_m + \frac{r_0 N_m \hat{\rho}_1}{\hat{K}_m^2} + \beta \hat{q}_1 \right]^2 < \frac{r_0}{\hat{K}_1(B, I)} \left[\alpha \hat{I} \hat{p}_4 + \beta \hat{N} \hat{q}_2 + \hat{\rho}_0 \right], \tag{3.29a}$$

$$\left[\alpha \hat{p}_1 + \alpha \hat{p}_3 \right]^2 < \left[\alpha \hat{I} \hat{p}_4 + \beta \hat{N} \hat{q}_2 + \hat{\rho}_0 \right] \hat{\rho}_3, \tag{3.29b}$$

$$\left[\frac{r_0 N_m \hat{\rho}_2}{\hat{K}_m^2} \right]^2 < \hat{\rho}_3 \frac{r_0}{\hat{K}_1(B, I)}. \tag{3.29c}$$

Then \hat{E} is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

Proof: Taking the following positive definite function about \hat{E}

$$\begin{aligned}
V_1(\hat{N}, \hat{B}, \hat{I}, \hat{F}_1, \hat{F}_2) = & (N - \hat{N} - \hat{N} \ln(N/\hat{N})) + (B - \hat{B} - \hat{B} \ln(B/\hat{B})) \\
& + (I - \hat{I} - \hat{I} \ln(I/\hat{I})) + \frac{K\theta_1}{2Bs_1} (F_1 - \hat{F}_1)^2 + \frac{\theta_2}{2s_2} (F_2 - \hat{F}_2)^2, \tag{3.30}
\end{aligned}$$

it can be checked that the derivative of V_1 with respect to t along solutions of (3.22) is negative definite under conditions (3.29), proving the theorem.

3.6 THE CONSERVATION MODEL WITH DIFFUSION

We now consider model (5.1) with $D_1 > 0$, $D_2 > 0$, $D_3 > 0$.

We shall show in the following theorem that the uniform steady state $N(x,y,t) = \hat{N}$, $B(x,y,t) = \hat{B}$, $I(x,y,t) = \hat{I}$, $F_1(x,y,t) = \hat{F}_1$, $F_2(x,y,t) = \hat{F}_2$ of system (3.22a)-(3.22b) may be globally asymptotically stable.

Theorem 3.6.1: If the equilibrium \hat{E} of system (3.22) without diffusion is globally asymptotically stable, then the corresponding positive uniform steady state of system (3.22) is also globally asymptotically stable with respect to all solutions such that $\phi(x,y) > 0$, $\psi(x,y) > 0$, $\xi(x,y) > 0$, $\chi(x,y) > 0$, $\zeta(x,y) > 0$, $(x,y) \in R$.

Proof: Considering the following positive definite function,

$$W_1 = \iint_R V_1(N, B, I, F_1, F_2) dA \quad (3.31)$$

it can be verified under an analysis similar to section 3.3 that \dot{W}_1 is negative definite if \dot{V}_1 is negative definite, where V_1 is defined in (3.30). This completes the proof.

By comparing \dot{V} with \dot{W} , and \dot{V}_1 with \dot{W}_1 , we note that there is an extra negative term in \dot{W} and \dot{W}_1 . This shows that the global stability is more plausible in diffusive system than in the case of no diffusion.

3.7 SIMULATION ANALYSIS

In this section we present a simulation analysis to explain the applicability of the results by choosing the following particular form of the functions in model (3.9) and (3.20).

$$r(B) = r_0 + r_1 B,$$

$$K_1(B,I) = K_{10} + K_{11} B - K_{12} I,$$

$$g(B, K) = r_B \left(1 - \frac{B}{K}\right), \quad (3.32)$$

$$f(I, L) = r_I \left(1 - \frac{I}{L}\right),$$

$$p(B) = q(B) = B,$$

where all coefficients are positive.

Now we choose the following values of the parameters in model (3.9) and Eq. (3.32):

$$\begin{aligned} r_0 &= 10.5, r_1 = 0.02, K_{10} = 25.0, K_{11} = 0.05, \\ K_{12} &= 0.01, r_B = 5.0, K = 35.0, \alpha = 0.04, \\ \beta &= 0.06, r_1 = 8.0, L = 15.0, \alpha_1 = 0.03. \end{aligned} \quad (3.33)$$

With the above set of values of the parameters in model (3.9), we show the effect of industrialization on N and B in the following examples

Example 1. Using Eq. (3.32) and the above set of parameters given in (3.33) it can be checked that conditions (3.12g), and $I_c^* > L$ for the existence E_{17}^* are satisfied, and E_{17}^* is given by

$$N^* = 26.79435, B^* = 19.24329, I^* = 16.08244. \quad (3.34)$$

It can be verified that conditions (3.13) in Theorem 3.2.1 are satisfied. This shows that E_{17}^* is locally asymptotically stable.

By choosing $K_m = 10.0$ in Theorem 3.2.2 it can also be seen that conditions (3.15) are satisfied, which shows that E_{17}^* is globally asymptotically stable.

Example 2. to show the effect of afforestation and control of industrialization pressure we choose again the same set of functions as given in Eq. (3.32) and the same set of parameters as given in Eq. (3.33) with the following additional values of parameters for model

(3.22) without diffusion.

$$\begin{aligned}\theta_1 &= 3.0, \theta_2 = 1.5, s_1 = 4.5, s_2 = 4.0, \\ \gamma_1 &= 0.1, \gamma_2 = 0.2, I_c = 1.0.\end{aligned}\tag{3.35}$$

It can be seen that conditions for existence of \hat{E} are satisfied, and \hat{E} is given by

$$\begin{aligned}\hat{N} &= 27.92672, \hat{B} = 28.58464, \hat{I} = 1.27263, \\ \hat{F}_1 &= 8.24832, \hat{F}_2 = 5.45254.\end{aligned}\tag{3.36}$$

It can also be checked that conditions (3.26) in Theorem 3.5.1 are satisfied, which shows that \hat{E} is locally asymptotically stable.

Again choosing $\hat{K}_m = 10.0$ in Theorem 3.5.2, it can be verified that conditions (3.29) are satisfied. This shows that \hat{E} is globally asymptotically stable.

Comparing Eq. (3.34) and Eq.(3.36) we note that the equilibrium levels of wildlife species and resource biomass increase whereas the equilibrium level of industrialization pressure decreases due to the conservation effort.

3.8 SUMMARY

This chapter is an attempt to investigate the survival of wildlife species dependent on resource in an industrial environment with diffusion. The species is assumed to be partially or wholly dependent or just predated on the resource biomass. The dynamics of the wildlife species, the resource biomass and the industrialization pressure are assumed to be governed by autonomous logistic-type differential equations. The model has been analyzed using the stability theory of differential equations. In absence of diffusion, criteria for local and global stability for positive equilibria are obtained. It has been concluded that increasing industrialization may

lead to a decrease in the density of the resource biomass and consequently the survival of the species may be threatened in absence of diffusion, but diffusive migration may prevent extinction of the species.

A model to conserve the forestry biomass by afforestation, irrigation, fencing programs etc. and to control the undesired level of industrialization is also proposed. It has been noted here that if suitable efforts are made to conserve the resource biomass and to control the undesired level of industrialization pressure, the resource biomass can be maintained at a desired level and thus the survival of wildlife species living in the habitat may be ensured.

By analyzing the diffusion models, it has been shown that the stability is more plausible in a diffusive system than the case of no diffusion. For a given habitat, it has been pointed out that the unstable steady state of a system without diffusion can be made stable by increasing the diffusion coefficients. Since forest diffusion is too slow, when forest habitat is under industrialization pressure, a forestry regeneration program is needed to prevent extinction of species.

CHAPTER IV

A MODEL FOR TWO INTERACTING PREDATORS COMPETING FOR A PREY SPECIES WITH DIFFUSION

4.0 INTRODUCTION

The existence of interacting populations using mathematical models have been of great interest in the past few decades and have been investigated by several researchers (May (1976), Goh (1976,78), Kazarinoff and van den Driessche (1978), Hsu (1978; 1981a,b), Albrecht et al. (1974), Harrison (1979), Freedman and Waltman (1984), Gopalsamy (1986), Dubey (1997)). The study of two predator species competing for a single prey has occupied an important place in the ecological literature (Harrison (1979), Hsu (1981a), Freedman and Waltman (1984), Mitra et al. (1992)). In particular, Hsu (1981a) proposed and analyzed a mathematical model with two predator species exploiting a single limited prey. He found that when the interspecific interference coefficient is small, the winner in purely exploitation competition out competes its rival successfully. However, if the interference is large enough, then the competitive outcome depends upon the initial population of the predator species. In this study, the effect of intraspecific interference has not been investigated. Freedman and Waltman (1984) considered three level food webs - two competing predators feeding on a single prey and a single predator feeding on two competing prey populations. They derived persistence criteria for the system. Gopalsamy (1986) established a model of two consumer species and one resource species, and obtained sufficient conditions for the three species system to converge as $t \rightarrow \infty$ to an equilibrium.

Mitra et al. (1992) studied the permanent coexistence and global stability of a simple Lotka-Volterra-type mathematical model of a living resource supporting two competing predators. They showed that the permanent coexistence of the system depends on the threshold of the ratio between the coefficients of numerical responses of the two consumers. Dubey (1997) proposed and analyzed a mathematical model in which two species utilize a common resource and one of the species is itself an alternative resource for the other.

Keeping in mind the above, in this chapter we develop a mathematical model of a three dimensional system in order to study the interaction of two predators competing for a limited prey. We consider the growth rates of the prey and predator species as nonlinear with crowding effects. In our model the effect of diffusion on the stability of the system is also considered. Some investigations (Rothe (1976), Jorne (1977), Jorne and Carmi (1977), Nallaswamy and Shukla (1982), Freedman et al. (1989)) have been made to study the dispersal of prey and predator through diffusion. In the absence of diffusion, our model generalizes the results of Hsu (1981a) and Mitra et al. (1992). In the presence of diffusion our results agree with those in Hastings (1978b), Shukla and Shukla (1987), Shukla and Verma (1981), Shukla et al. (1989), Freedman and Shukla (1989). By constructing a suitable Liapunov function (La Salle and Lefschetz (1961)) we investigate the local and global behavior of the uniform steady state of the system.

4.1 MATHEMATICAL MODEL

Consider an ecosystem where we wish to model the interaction of two predators competing for a limited prey with diffusion. The predator species compete not only by predating on the population of

the shared prey but also by interfering with its rival and with themselves. We consider the interference coefficients to be α_{ij} measuring the damage effect of predator species j on predator species i , and γ_i measuring the damage effect from its own species. Then the dynamics of the system can be written as

$$\begin{aligned}\frac{\partial N}{\partial t} &= Ng(N, K) - b_1 x_1 p_1(N) - b_2 x_2 p_2(N) + D \nabla^2 N, \\ \frac{\partial x_1}{\partial t} &= x_1 (\beta_1 p_1(N) - \delta_1 - \gamma_1 x_1 - \alpha_{21} x_2) + d_1 \nabla^2 x_1, \\ \frac{\partial x_2}{\partial t} &= x_2 (\beta_2 p_2(N) - \delta_2 - \gamma_2 x_2 - \alpha_{12} x_1) + d_2 \nabla^2 x_2.\end{aligned}\quad (4.1)$$

We impose the following boundary and initial conditions on system (4.1).

$$\begin{aligned}N(0, u, v) &= \phi(u, v) \geq 0, \quad x_i(0, u, v) = \psi_i(u, v) \geq 0, \\ \frac{\partial N}{\partial n} &= \frac{\partial x_i}{\partial n} = 0, \quad i = 1, 2,\end{aligned}\quad (4.2)$$

where n is the unit outward normal to the region ∂R . ϕ and ψ_i ($i=1,2$) are smooth initial functions. R is a simply connected domain in the u - v plane with piecewise smooth boundary ∂R .

In model (4.1), $\nabla^2 \equiv \frac{\partial^2}{\partial u^2} + \frac{\partial^2}{\partial v^2}$ is the Laplacian diffusion operator and $N(t, u, v)$, $x_i(t, u, v)$ ($i=1,2$) are the population densities of the prey species and the i^{th} predator species respectively, at time $t \geq 0$ and coordinates $(u, v) \in R$.

The function $g(N, K)$ is the specific growth rate of the prey species. It increases as the carrying capacity K of the prey species increases and decreases as the density of the prey increases. Hence we assume

$$g(0,0) > 0, \quad \frac{\partial g(N,K)}{\partial N} < 0, \quad \frac{\partial g(N,K)}{\partial K} > 0, \quad (4.3)$$

and there exists an $x = K$ such that $g(K, K) = 0$.

The function $p_i(N)$ is the functional response of the i^{th} predator and it satisfies

$$p_i(0) = 0, p_i'(N) > 0, \text{ for } N \geq 0, i=1,2. \quad (4.4)$$

D, d_1, d_2 are the diffusion coefficients of $N(t), x_1(t), x_2(t)$ in R respectively. b_i is the feeding rate per predator (predator species i) per unit prey consumed, β_i is the birth rate per predator (predator species i) per unit prey consumed, δ_i is the death rate of the predator species i .

Remark 1: It may be pointed out here that if we take

$$\gamma_1 = \gamma_2 = D = d_1 = d_2 = 0, g(N,K) = r(1 - \frac{N}{K}), p_1(N) = N = p_2(N),$$

where r is a positive constant, then model (4.1) reduces to that of Hsu (1981a).

4.2 THE MODEL WITHOUT DIFFUSION

We consider the model without diffusion (i.e., $D = d_1 = d_2 = 0$) as follows

$$\begin{aligned} \dot{N} &= Ng(N,K) - b_1 x_1 p_1(N) - b_2 x_2 p_2(N), \\ \dot{x}_1 &= x_1 (\beta_1 p_1(N) - \delta_1 - \gamma_1 x_1 - \alpha_{21} x_2), \\ \dot{x}_2 &= x_2 (\beta_2 p_2(N) - \delta_2 - \gamma_2 x_2 - \alpha_{12} x_1), \\ N(0) &\geq 0, x_i(0) \geq 0 \quad (i = 1,2). \end{aligned} \quad (4.5)$$

Before analysis we state one important lemma as follows, the proof of which directly follows from system (4.5).

Lemma 4.2.1: A necessary condition for either predator species x_i to survive is

$$\beta_i p_i(K) > \delta_i, \quad i=1,2.$$

Existence of equilibria

Setting $\frac{dZ}{dt} = 0$ ($Z = N, x_1, x_2$) and solving (4.5) we get the following possible non-negative equilibria, namely, $E_0(0, 0, 0)$, $E_1(K, 0, 0)$, $E_2(\bar{N}, \bar{x}_1, 0)$, $E_3(\tilde{N}, 0, \tilde{x}_2)$, $E^*(N^*, x_1^*, x_2^*)$. The equilibria E_0 and E_1 clearly exist. We shall show the existence of the other equilibria as follows.

Existence of $E_2(\bar{N}, \bar{x}_1, 0)$

Here \bar{N} and \bar{x}_1 are the positive solutions of the following equations:

$$x_1 = \frac{Ng(N,K)}{b_1 p_1(N)}, \quad (4.6a)$$

$$\delta_1 + \gamma_1 x_1 = \beta_1 p_1(N). \quad (4.6b)$$

From (4.6a) we note the following

$$\text{when } N \rightarrow K, x_1 \rightarrow 0, \quad (4.7a)$$

$$\text{when } N \rightarrow 0, x_1 \rightarrow \frac{g(0,K)}{b_1 p_1'(0)} > 0, \quad (4.7b)$$

$$\frac{dx_1}{dN} = \frac{1}{b_1 p_1^2(N)} \left[g(N,K)(p_1(N) - Np_1'(N)) + Np_1(N) \frac{\partial g(N,K)}{\partial N} \right], \quad (4.7c)$$

$$\lim_{N \rightarrow K} \frac{dx_1}{dN} = \frac{K}{b_1 p_1(K)} \left[\frac{\partial g(K,K)}{\partial N} \right] < 0. \quad (4.7d)$$

From (4.7c) we note that $\frac{dx_1}{dN}$ may be positive or negative. However, it is negative in the neighborhood of the point $N = K$.

Further, $\frac{dx_1}{dN}$ is negative provided

$$\frac{1}{g(N,K)} \frac{\partial g(N,K)}{\partial N} < \frac{Np_1'(N) - p_1(N)}{Np_1(N)}. \quad (4.7e)$$

From (4.6b) we note the following

$$\text{when } N \rightarrow K, \text{ then } x_1 \rightarrow \frac{1}{\gamma_1} (\beta_1 p_1(K) - \delta_1) > 0, \quad (4.8a)$$

$$\text{when } N \rightarrow 0, \text{ then } x_1 \rightarrow -\frac{\delta_1}{\gamma_1} < 0, \quad (4.8b)$$

$$\frac{dx_1}{dN} = \frac{\beta_1 p'_1(N)}{\gamma_1} > 0. \quad (4.8c)$$

From the above analysis we note that the two isoclines (4.6a) and (4.6b) intersect at a unique point (\bar{N}, \bar{x}_1) under condition (4.7e). Thus E_2 exists if condition (4.7e) holds. This implies that if inequality (4.7e) is satisfied, then the prey species survives with the first predator, whereas the second predator is driven to extinction.

Remark 2: If $p_1(N) = N$, then condition (4.7e) is automatically satisfied.

Existence of $E_3(\tilde{N}, 0, \tilde{x}_2)$

Here \tilde{N} and \tilde{x}_2 are the positive solutions of the following equations:

$$x_2 = \frac{Ng(N,K)}{b_2 p_2(N)}, \quad (4.9a)$$

$$\delta_2 + \gamma_2 x_2 = \beta_2 p_2(N). \quad (4.9b)$$

As in the existence of E_2 , one can see that the equilibrium E_3 exists if the following inequality holds at E_3 ,

$$\frac{1}{g(N,K)} \frac{\partial g(N,K)}{\partial N} < \frac{Np'_2(N) - p_2(N)}{Np_2(N)}. \quad (4.9c)$$

Thus, if condition (4.9c) holds, then the prey species survives along with its second predator, whereas the first predator dies out.

Existence of $E(N, x_1, x_2)$

Here N^* , x_1^* and x_2^* are the positive solutions of the following algebraic equations:

$$Ng(N,K) - b_1 x_1 p_1(N) - b_2 x_2 p_2(N) = 0, \quad (4.10a)$$

$$\beta_1 p_1(N) - \delta_1 - \gamma_1 x_1 - \alpha_{21} x_2 = 0, \quad (4.10b)$$

$$\beta_2 p_2(N) - \delta_2 - \gamma_2 x_2 - \alpha_{12} x_1 = 0. \quad (4.10c)$$

Solving (4.10a) and (4.10b), we get

$$x_1 = \frac{\mu_1}{\mu_2}, \quad (4.11a)$$

$$x_2 = \frac{\mu_3}{\mu_2}, \quad (4.11b)$$

where $\mu_1 = b_2 p_2(N)(\beta_1 p_1(N) - \delta_1) - \alpha_{21} Ng(N,K),$ (4.12a)

$$\mu_2 = \gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N), \quad (4.12b)$$

$$\mu_3 = \gamma_1 Ng(N,K) - b_1 p_1(N)(\beta_1 p_1(N) - \delta_1). \quad (4.12c)$$

We note that $x_1 > 0$ if either

$$(i). \mu_1 > 0, \mu_2 > 0, \quad (4.13a)$$

$$\text{or (ii). } \mu_1 < 0, \mu_2 < 0 \text{ hold.} \quad (4.13b)$$

Similarly, $x_2 > 0$ if either

$$(i). \mu_3 > 0, \mu_2 > 0, \quad (4.14a)$$

$$\text{or (ii). } \mu_3 < 0, \mu_2 < 0 \text{ hold.} \quad (4.14b)$$

Substituting (4.11a) and (4.11b) into (4.10c) and taking

$$F(N) = \frac{1}{\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N)} \left[(\gamma_1 b_2 p_2(N) - \alpha_{21} b_1 p_1(N))(\beta_2 p_2(N) - \delta_2) - (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) Ng(N,K) + (\beta_1 p_1(N) - \delta_1)(\gamma_2 b_1 p_1(N) - \alpha_{12} b_2 p_2(N)) \right], \quad (4.15)$$

we note that

$$F(0) = \frac{1}{\gamma_1 b_2 p_2'(0) - \alpha_{21} b_1 p_1'(0)} \left[(\gamma_1 b_2 p_2'(0) - \alpha_{21} b_1 p_1'(0))(-\delta_2) - (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) g(0, K) + (\gamma_2 b_1 p_1'(0) - \alpha_{12} b_2 p_2'(0))(-\delta_1) \right], \quad (4.16a)$$

$$F(K) = \frac{1}{\gamma_1 b_2 p_2'(K) - \alpha_{21} b_1 p_1'(K)} \left[(\gamma_1 b_2 p_2'(K) - \alpha_{21} b_1 p_1'(K))(\beta_2 p_2(K) - \delta_2) + (\gamma_2 b_1 p_1'(K) - \alpha_{12} b_2 p_2'(K))(\beta_1 p_1(K) - \delta_1) \right]. \quad (4.16b)$$

$$F'(N) = \beta_2 p_2'(N) + \frac{\gamma_1 b_2 p_2'(N) - \alpha_{21} b_1 p_1'(N)}{(\gamma_1 b_2 p_2'(N) - \alpha_{21} b_1 p_1'(N))^2} \left[(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) N g(N, K) - (\gamma_2 b_1 p_1'(N) - \alpha_{12} b_2 p_2'(N))(\beta_1 p_1(N) - \delta_1) \right] - \frac{1}{\gamma_1 b_2 p_2'(N) - \alpha_{21} b_1 p_1'(N)} \left[(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) (g(N, K) + N \frac{\partial g(N, K)}{\partial N}) - (\beta_1 p_1(N) - \delta_1)(\gamma_2 b_1 p_1'(N) - \alpha_{12} b_2 p_2'(N)) - \beta_1 p_1'(N)(\gamma_2 b_1 p_1'(N) - \alpha_{12} b_2 p_2'(N)) \right]. \quad (4.16c)$$

From (4.16) we note that $F(0)$, $F(K)$ and $F'(N)$ may be positive or negative. However, there exists a positive unique solution $N = N^*$ of (4.15) in the interval $0 < N^* < K$ such that $F(N^*) = 0$, if the following inequalities hold:

$$F(0) < 0, F(K) > 0, F'(N) > 0. \quad (4.17)$$

Knowing the value of N^* , then x_1^* and x_2^* can be computed from (4.11a) and (4.11b) respectively. Thus the interior equilibrium E^* exists if (4.13), (4.14) and (4.17) hold.

Stability of equilibria

The local stability of the equilibria can be studied by computing variational matrices (Freedman (1987)) corresponding to each

equilibrium. From these matrices we note the following results:

1. $E_0(0, 0, 0)$ is a saddle point whose unstable manifold is locally in the N direction and stable manifold is locally in the x_1 - x_2 plane.
2. From Lemma 3.1, we note that if $\delta_1 > \beta_1 p_1(K)$, then no predator will survive. In such a case $E_1(K, 0, 0)$ is locally asymptotically stable. If $\delta_1 < \beta_1 p_1(K)$, then both predators will survive and $E_1(K, 0, 0)$ will be a saddle point with stable manifold locally in the N -direction and with unstable manifold locally in the x_1 - x_2 plane.
3. $E_2(\bar{N}, \bar{x}_1, 0)$ is locally asymptotically stable if

$$\beta_2 p_2(\bar{N}) - \delta_2 - \alpha_{12} \bar{x}_1 < 0 \text{ and } \bar{H} = g(\bar{N}, K) + \bar{N} \frac{\partial g(\bar{N}, K)}{\partial N} - b_1 \bar{x}_1 p_1'(\bar{N}) < 0.$$

4. $E_3(\tilde{N}, 0, \tilde{x}_2)$ is locally asymptotically stable if

$$\beta_1 p_1(\tilde{N}) - \delta_1 - \alpha_{21} \tilde{x}_2 < 0 \text{ and } \tilde{H} = g(\tilde{N}, K) + \tilde{N} \frac{\partial g(\tilde{N}, K)}{\partial N} - b_1 \tilde{x}_1 p_1'(\tilde{N}) < 0.$$

In the following theorems we are able to write down conditions for local stability and instability of E^* . The proofs of these theorems follow from the Routh-Hurwitz criteria, and hence we omit them.

We first write out the following notations:

$$A_1 = -H^* + \gamma_1 x_1^* + \gamma_2 x_2^*, \quad (4.18a)$$

$$A_2 = -H^*(\gamma_1 x_1^* + \gamma_2 x_2^*) + (\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) x_1^* x_2^* + b_1 \beta_1 x_1^* p_1(N^*) p_1'(N^*) \\ + b_2 \beta_2 x_2^* p_2(N^*) p_2'(N^*), \quad (4.18b)$$

$$A_3 = -(\gamma_1 \gamma_2 - \alpha_{12} \alpha_{21}) H^* x_1^* x_2^* + \beta_2 p_2'(N^*) x_1^* x_2^* (\gamma_1 b_2 p_2(N^*) - \alpha_{21} b_1 p_1(N^*)) \\ + \beta_1 p_1'(N^*) x_1^* x_2^* (\gamma_2 b_1 p_1(N^*) - \alpha_{12} b_2 p_2(N^*)), \quad (4.18c)$$

$$H^* = g(N^*, K) + N^* \frac{\partial g(N^*, K)}{\partial N} - b_1 x_1^* p_1'(N^*) - b_2 x_2^* p_2'(N^*). \quad (4.18d)$$

Theorem 4.2.1: Let the following inequalities hold

$$A_i > 0 \quad (i=1,2,3) \text{ and } A_1 A_2 - A_3 > 0. \quad (4.19)$$

Then E^* is locally asymptotically stable.

Theorem 4.2.2: Let $\gamma_1 = \gamma_2 = 0$. Then E^* is unstable.

It may be pointed out here that the result of Theorem 4.2.2 agrees with Hsu (1981a).

In the following theorem we show that E^* may be globally asymptotically stable. We first state the following lemma which establishes a region of attraction for system (4.5). The proof of this lemma is easy and hence is omitted.

Lemma 4.2.2: The set

$$\Omega = \{(N, x_1, x_2): 0 \leq N \leq K, 0 \leq x_1 \leq \frac{1}{\gamma_1} (\beta_1 p_1(K) - \delta_1), i=1,2\}$$

is a region of attraction for all solutions initiating in the positive orthant.

Theorem 4.2.3: In addition to assumptions (4.3)-(4.5), let $g(N,K)$, and $p(N)$ satisfy the following conditions in Ω :

$$G_m \leq - \frac{\partial g(N,K)}{\partial N} \leq G_M, \quad \rho_i \leq p'_i(N) \leq \rho_{i+2}, \quad i = 1,2 \quad (4.20)$$

for some positive constants $G_m, G_M, \rho_i, \rho_{i+2}$. ($i=1,2$).

If the following inequality holds

$$(c_2 \alpha_{12} + c_1 \alpha_{21})^2 < c_1 c_2 \gamma_1 \gamma_2 \quad (4.21)$$

where

$$c_1 = \frac{b_1 p_1(N^*)}{\beta_1 \rho_3 N^*}, \quad c_2 = \frac{b_2 p_2(N^*)}{\beta_1 \rho_3 N^*}, \quad (4.22)$$

then E^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

Proof: We consider the following positive definite function about E^* ,

$$V(N, x_1, x_2) = N - N^* - N^* \ln(N/N^*) + c_1(x_1 - x_1^* - x_1^* \ln(x_1/x_1^*)) \\ + c_2(x_2 - x_2^* - x_2^* \ln(x_2/x_2^*)). \quad (4.23)$$

Differentiating V with respect to t along the solutions of (4.5) we get after some algebraic manipulations

$$\dot{V} \leq -\lambda(N)(N - N^*)^2 - c_1 \gamma_1 (x_1 - x_1^*)^2 - c_2 \gamma_2 (x_2 - x_2^*)^2 \\ + (c_1 \beta_1 \mu_1(N) - b_1 p_1(N^*/N^*)) (N - N^*)(x_1 - x_1^*) \\ + (c_2 \beta_2 \mu_2(N) - b_2 p_2(N^*/N^*)) (N - N^*)(x_2 - x_2^*) \\ + (c_2 \alpha_{12} + c_1 \alpha_{21}) (x_1 - x_1^*)(x_2 - x_2^*), \quad (4.24)$$

where

$$\lambda(N) = \begin{cases} - \left[\frac{g(N, K)^* - g(N, K)}{N - N^*} \right], & N \neq N^* \\ - \frac{\partial g(N, K)}{\partial N}, & N = N^* \end{cases},$$

$$\mu_i(N) = \begin{cases} \frac{p_i(N) - p_i(N^*)}{N - N^*}, & N \neq N^* \\ p_i'(N), & N = N^*. \end{cases}$$

From (4.20) and the mean value theorem we note that,

$$G_m \leq |\lambda(N)| \leq G_M, \quad \rho_i \leq |\mu_i(N)| \leq \rho_{i+2}, \quad i=1,2.$$

Now \dot{V} can further be written as the sum of quadratics,

$$\dot{V} \leq -\frac{1}{2} a_{11} (N - N^*)^2 + a_{12} (N - N^*)(x_1 - x_1^*) - \frac{1}{2} a_{22} (x_1 - x_1^*)^2 \\ - \frac{1}{2} a_{22} (x_1 - x_1^*)^2 + a_{23} (x_1 - x_1^*)(x_2 - x_2^*) - \frac{1}{2} a_{33} (x_2 - x_2^*)^2 \\ - \frac{1}{2} a_{33} (x_2 - x_2^*)^2 + a_{31} (x_1 - x_1^*)(N - N^*) - \frac{1}{2} a_{11} (N - N^*)^2, \quad (4.25)$$

where

$$\begin{aligned} a_{11} &= \lambda(N), \quad a_{22} = c_1 \gamma_1, \quad a_{33} = c_2 \gamma_2, \\ a_{12} &= c_1 \beta_1 \mu_1(N) - b_1 p_1(N^*)/N^*, \\ a_{23} &= (c_2 \alpha_{12} + c_1 \alpha_{21}), \\ a_{31} &= c_2 \beta_2 \mu_2(N) - b_2 p_2(N^*)/N^*. \end{aligned}$$

Sufficient conditions for \dot{V} to be negative definite are that the following inequalities hold

$$a_{12}^2 < a_{11} a_{22}, \quad (4.26a)$$

$$a_{23}^2 < a_{22} a_{33}, \quad (4.26b)$$

$$a_{31}^2 < a_{33} a_{11}. \quad (4.26c)$$

By choosing c_1 and c_2 as defined in (4.22) we note that conditions (4.26a) and (4.26c) are automatically satisfied. Further, (4.21) (4.26b). Thus, we conclude that \dot{V} is a Liapunov function with respect to E^* , whose domain contains the region Ω , proving the theorem.

4.3 THE MODEL WITH DIFFUSION

In this section we consider the complete model (4.1)-(4.2). We note that $N = N^*$, $x_1 = x_1^*$, $x_2 = x_2^*$ is the uniform steady state for system (4.1)-(4.2). We wish to show that if E^* is asymptotically stable for system (4.5), then the corresponding uniform steady state is also asymptotically stable for system (4.1)-(4.2). Further, we will also show that by increasing the diffusion coefficients to sufficiently large values an unstable equilibrium state can be stabilized. Now we prove this by considering the following Liapunov function

$$W(N(t), x_1(t), x_2(t)) = \iint_R V(N(u,v,t), x_1(u,v,t), x_2(u,v,t)) \, dA, \quad (4.27)$$

where V is defined in Eq. (4.23).

Now the time derivative of W along the solutions of (4.1)-(4.2) is given by,

$$\begin{aligned} \dot{W}(N(t), x_1(t), x_2(t)) &= \iint_R \left(\frac{\partial V}{\partial N} \frac{\partial N}{\partial t} + \frac{\partial V}{\partial x_1} \frac{\partial x_1}{\partial t} + \frac{\partial V}{\partial x_2} \frac{\partial x_2}{\partial t} \right) dA \\ &= I_1 + I_2, \end{aligned} \quad (4.28)$$

$$\text{where} \quad I_1 = \iint_R \dot{V}(N(u, v, t), x_1(u, v, t), x_2(u, v, t)) dA \quad (4.29)$$

$$I_2 = \iint_R \left(D \frac{\partial V}{\partial N} \nabla^2 N + d_1 \frac{\partial V}{\partial x_1} \nabla^2 x_1 + d_2 \frac{\partial V}{\partial x_2} \nabla^2 x_2 \right) dA. \quad (4.30)$$

We first assume that \dot{V} does not change its sign in R . We now note the following properties of V , namely

$$1. \left. \frac{\partial V}{\partial N} \right|_{\partial R} = \left. \frac{\partial V}{\partial x_i} \right|_{\partial R} = 0 \text{ for all points of } R \ (i=1,2), \quad (4.31)$$

$$2. \frac{\partial^2 V}{\partial N \partial x_i} = \frac{\partial^2 V}{\partial x_i \partial x_j} = \frac{\partial^2 V}{\partial x_j \partial N} = 0, \quad (4.32)$$

$$3. \frac{\partial^2 V}{\partial N^2} > 0, \quad \frac{\partial^2 V}{\partial x_i^2} > 0 \ (i=1,2). \quad (4.33)$$

From Green's first identity, we have

$$\begin{aligned} \iint_R \frac{\partial V}{\partial N} \nabla^2 N dA &= \int_{\partial R} \frac{\partial V}{\partial N} \frac{\partial N}{\partial n} ds - \iint_R \left[\nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N \right] dA \\ &= - \iint_R \left[\nabla \left(\frac{\partial V}{\partial N} \right) \cdot \nabla N \right] dA, \text{ using (4.2)}. \end{aligned} \quad (4.34)$$

$$\text{But we have } \nabla \left(\frac{\partial V}{\partial N} \right) = \frac{\partial^2 V}{\partial N^2} \frac{\partial N}{\partial u} \hat{i} + \frac{\partial^2 V}{\partial N^2} \frac{\partial N}{\partial v} \hat{j}.$$

Hence (4.34) reduces to

$$\iint_R \frac{\partial V}{\partial N} \nabla^2 N dA = - \iint_R \frac{\partial^2 V}{\partial N^2} \left[\left(\frac{\partial N}{\partial u} \right)^2 + \left(\frac{\partial N}{\partial v} \right)^2 \right] dA \leq 0.$$

Similarly we get

$$\iint_R \frac{\partial V}{\partial x_1} \nabla^2 x_1 \, dA = - \iint_R \frac{\partial^2 V}{\partial x_1^2} \left[\left(\frac{\partial x_1}{\partial u} \right)^2 + \left(\frac{\partial x_1}{\partial v} \right)^2 \right] dA \leq 0. \quad (4.35)$$

This implies that $I_2 \leq 0$, $i=1,2$. Thus from (4.28) we get

$$\begin{aligned} \dot{W}(N(t), x_1(t), x_2(t)) &\leq \iint_R \dot{V}(N(u,v,t), x_1(u,v,t), x_2(u,v,t)) \, dA \\ &\quad - \frac{DN^*}{K^2} \iint_R \left[\left(\frac{\partial N}{\partial u} \right)^2 + \left(\frac{\partial N}{\partial v} \right)^2 \right] dA \\ &\quad - \sum_{i=1,2} \frac{d_1 x_1^* \gamma_i^2}{(\beta_1 p_1(K) - \delta_1)^2} \iint_R \left[\left(\frac{\partial x_1}{\partial u} \right)^2 + \left(\frac{\partial x_1}{\partial v} \right)^2 \right] dA. \end{aligned} \quad (4.36)$$

From (4.36) we note that if \dot{V} is negative definite, then \dot{W} is also negative definite. This shows that if the equilibrium E^* of the model without diffusion is globally stable, then the corresponding uniform steady state E^* of the initial boundary value problems (4.1)-(4.2) is also globally stable. Further, we also note that if \dot{V} is positive definite, then by increasing D , d_1 , d_2 to sufficiently large values, \dot{W} can be made negative definite. This implies that if the positive equilibrium E^* of the model with no diffusion is unstable, then the corresponding uniform steady state of the model with diffusion can be made stable by increasing diffusion coefficients to sufficiently large values.

If we consider the region R to be a rectangular habitat given by

$$R = \{ (u,v): 0 \leq u \leq a, 0 \leq v \leq b \},$$

then under an analysis similar to chapter III, \dot{W} can be estimated by,

$$\begin{aligned} \dot{W} &\leq \iint_R \dot{V} \, dA - \left[\frac{(a^2 + b^2)\pi^2}{a^2 b^2} \left(\frac{DN^*}{K^2} (N - N^*)^2 + \frac{c_1 d_1 x_1^* \gamma_1^2}{(\beta_1 p_1(K) - \delta_1)^2} (x_1 - x_1^*)^2 \right. \right. \\ &\quad \left. \left. + \frac{c_2 d_2 x_2^* \gamma_2^2}{(\beta_2 p_2(K) - \delta_2)^2} (x_2 - x_2^*)^2 \right) \right] dA. \end{aligned} \quad (4.37)$$

This shows that if the interior equilibrium E^* of model (4.5) is globally asymptotically stable, then the uniform steady state of the initial boundary value problems (4.1)-(4.2) is also globally asymptotically stable. We further note that, even if (4.26) is not satisfied, then by increasing diffusion coefficients D, d_1, d_2 to sufficiently large values, \dot{W} can be made negative definite. Thus an unstable equilibrium can be made stable by increasing diffusion coefficients appropriately.

Remark 3: From Theorem 4.2.2, we note that if $\gamma_1 = 0 = \gamma_2$, then the interior equilibrium E^* of model (4.5) is unstable. Then from (4.36) and (4.37) we note that, sufficiently rapid diffusion by the prey species will stabilize the unstable equilibrium E^* .

4.4 SIMULATION ANALYSIS

In this section a numerical example is presented to check the feasibility of the results discussed above. We take the following particular form of the functions $g(N,K)$ and $p_1(N), p_2(N)$ in model (4.5):

$$g(N,K) = r(1-N/K), p_1(N) = N = p_2(N). \quad (4.38)$$

We choose the following values of the various parameters in model (4.5) and in Eq. (4.38),

$$r = 35.0, b_1 = 2.0, b_2 = 1.8, K = 60.0,$$

$$\beta_1 = 1.0, \delta_1 = 1.5, \gamma_1 = 5.0, \alpha_{21} = 1.5,$$

$$\beta_2 = 1.05, \delta_2 = 0.6, \gamma_2 = 3.5, \alpha_{12} = 1.8.$$

With the above set of values of parameters, it can be seen that the conditions (4.13), (4.14) and (4.18) for the existence of the interior equilibrium E^* are satisfied, and E^* is given by

$$N = 28.20468, x_1 = 3.37458, x_2 = 6.55450.$$

It can also be checked that conditions (4.19) in Theorem 4.2.1 are satisfied. This shows that E^* is locally asymptotically stable.

It can also be verified that condition (4.21) in Theorem 4.2.3 is satisfied which shows that E^* is globally asymptotically stable.

4.5 SUMMARY

In this chapter, a mathematical model has been considered in order to study the growth and survival of two predator species competing for a single limited prey in a diffusive system. The growth rates of the interacting populations are assumed to be nonlinear and the dynamics of the system is of Gause-type. In the absence of diffusion, criteria for local stability, instability and global stability have been obtained. In the absence of diffusion it has been shown that the intraspecific interference coefficients of the competing predators play a crucial role in stabilizing the interior equilibrium of the system. If the intraspecific interference coefficients of the competing predators are zero, then the interior equilibrium becomes unstable. In the case of diffusion it has been shown that if the interior equilibrium E^* of model (4.5) is asymptotically stable, then the uniform steady state E^* of system (4.1)-(4.2) must be asymptotically stable. It has also been noted that when the interior equilibrium E^* of model (4.5) is unstable, then the uniform steady state E^* of system (4.1)-(4.2) can be made stable by increasing diffusion coefficients appropriately under certain conditions. Thus it has been concluded that the solutions of the model with diffusion approach to its equilibrium faster than the case of no diffusion.

CHAPTER V

A MODEL FOR THE EFFECT OF PREDATION ON TWO COMPETING PREY SPECIES WITH DIFFUSION

5.0 INTRODUCTION

One of the important problems in mathematical ecology is to study the effect of predation on competing prey species (Parrish and Salla (1970), Kazarinoff and van den Driessche (1978), Tansky (1978), Harrison (1979), Cheng et al. (1981), Brauer and Soudack (1981), Hsu (1981b) etc.). In particular, Kazarinoff and van den Driessche (1978) proposed a predator-prey model which incorporates competition among prey with a general functional response. They obtained criteria for the stability of small amplitude periodic solutions of the system. Tansky (1978) studied the interaction of two prey and one predator which has the switching property of predation. Harrison (1979) studied the global stability of predator-prey interactions using Liapunov functions and showed that conclusions do not depend exclusively on the specific function chosen by the modeler, but also on their general properties. Conell (1979) discussed the role of predators in preventing competitive exclusion in the rain forest and the intertidal zone. Cheng et al. (1981) proposed a general model for predator-prey interactions with predator functional responses and derived some conditions to ensure the global stability of the system. Brauer and Soudack (1981) investigated the qualitative effects of constant rate stocking of either or both species in a predator-prey system. Hsu (1981b) discussed the effect of predation on the two competing prey species and observed that the outcomes depend

critically on the prey species's capability of invading the complementary sub community formed by predator species and other prey. The competitive-exclusion principle (Hardin (1960)) states that two competing species can coexist only if they exploit their environment differently. Hsu (1981b) showed that competing prey species can coexist even with exactly identical resource requirements if each prey species has invasion potential for the complementary predator-prey sub community. Liou and Cheng (1988) proposed a general model for predator-prey interaction and studied the global stability of the system. In most of the above studies the effect of diffusion has not been considered, though such investigations are important from the point of size of the habitat (McMurtrie (1978), Freedman and Shukla (1989), Freedman et. al (1989)).

Keeping the above in mind, in this chapter our main purpose is to discuss the effect of predation on two competing prey species in which the predator species is also influenced by the damage effect from its own species. Further we also consider the effect of diffusion on the stability of the uniform steady state of the system. By constructing a suitable Liapunov function, the local and global behavior of the uniform steady state are investigated. In the absence of diffusion our model is more general than that of Hsu (1981b), and in presence of diffusion, our results agree with those in Hastings (1978), Shukla and Verma (1981), Shukla and Shukla (1987), Bergerud et al. (1984), Shukla et al. (1989), Freedman and Shukla (1989).

5.1 MATHEMATICAL MODEL

Consider an ecosystem where we wish to model the interaction of a predator with two competing prey species in a diffusive system. Using

a Gause model, the dynamics of the system can be governed by the following differential equations, (Hsu (1981b)):

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= N_1 g_1(N_1, K_1) - b_{13} x p_1(N_1) - \alpha_{12} N_1 N_2 + D_1 \nabla^2 N_1, \\ \frac{\partial N_2}{\partial t} &= N_2 g_2(N_2, K_2) - b_{23} x p_2(N_2) - \alpha_{21} N_1 N_2 + D_2 \nabla^2 N_2, \\ \frac{\partial x}{\partial t} &= x(\beta_{31} p_1(N_1) + \beta_{32} p_2(N_2) - \delta - \gamma x) + D \nabla^2 x.\end{aligned}\quad (5.1)$$

We impose the following initial and boundary conditions on system (5.1)

$$\begin{aligned}N_i(0, u, v) &= \phi_i(u, v) \geq 0, \quad x(0, u, v) = \psi(u, v) \geq 0, \quad (i=1,2) \\ \frac{\partial N_1}{\partial n} &= \frac{\partial N_2}{\partial n} = \frac{\partial x}{\partial n} = 0,\end{aligned}\quad (5.2)$$

where n is the unit outward normal to the region ∂R . ϕ_i and ψ ($i=1,2$) are the smooth initial functions. R is a simply connected domain in the u - v plane with piecewise smooth boundary ∂R .

In model (5.1), $\nabla^2 \equiv \frac{\partial^2}{\partial u^2} + \frac{\partial^2}{\partial v^2}$ is the Laplacian diffusion operator and $N_i(t, u, v)$, $x(t, u, v)$ ($i=1,2$) are the population density of i^{th} prey species and predator species respectively, at time $t \geq 0$ and coordinates $(u, v) \in R$.

The function $g_i(N_i, K_i)$ is the specific growth rate of the i^{th} prey species. It increases as the carrying capacity K_i of the prey species increases and decreases as the density of the prey species increases. Hence we assume

$$g_i(0,0) > 0, \quad \frac{\partial g_i(N_i, K_i)}{\partial N_i} < 0, \quad \frac{\partial g_i(N_i, K_i)}{\partial K_i} > 0, \quad (5.3)$$

and there exists $N_i = K_i$ such that $g_i(K_i, K_i) = 0$, $i = 1, 2$.

The function $p_i(N_i)$ is the predator functional response on the i^{th} prey species and it satisfies

$$p_i(0) = 0, p_i'(N_i) > 0, \text{ for } N_i \geq 0, (i=1,2). \quad (5.4)$$

D_1, D_2, D are the diffusion coefficients in R for N_1, N_2, x respectively. b_{i3} is the feeding rate per predator (prey species i) per unit prey consumed. α_{12}, α_{21} are the interspecific interference coefficients of prey species N_1 and N_2 respectively, β_{3i} is the birth rate per predator per unit prey (prey species i) consumed. δ is the death rate and γ is the intraspecific interference coefficient of the predator species.

Remark 1: If we take the following particular form of functions in model (5.1)

$$\begin{aligned} g_1(N_1, K_1) &= r_1(1 - N_1/K_1), \quad g_2(N_2, K_2) = r_2(1 - N_2/K_2), \\ p_1(N_1) &= N_1, \quad p_2(N_2) = N_2, \quad D_1 = D_2 = D = \gamma = 0 \end{aligned} \quad (5.5)$$

then model (5.1) reduces to the model in Hsu (1981b).

5.2 THE MODEL WITHOUT DIFFUSION

In this section we consider the model without diffusion. In such a case model (5.1) reduces to

$$\begin{aligned} \dot{N}_1 &= N_1 g_1(N_1, K_1) - b_{13} x p_1(N_1) - \alpha_{12} N_1 N_2, \\ \dot{N}_2 &= N_2 g_2(N_2, K_2) - b_{23} x p_2(N_2) - \alpha_{21} N_1 N_2, \\ \dot{x} &= x(\beta_{31} p_1(N_1) + \beta_{32} p_2(N_2) - \delta - \gamma x), \end{aligned} \quad (5.6)$$

$$N_i(0) \geq 0, x(0) \geq 0 \quad (i = 1,2).$$

Setting $\frac{dZ}{dt} = 0$ ($Z = N_1, N_2, x$) and solving (5.6) we get the

following nonnegative equilibria, namely $E_0(0, 0, 0)$, $E_1(K_1, 0, 0)$, $E_2(0, K_2, 0)$, $E_3(\bar{N}_1, \bar{N}_2, 0)$, $E_4(\check{N}_1, 0, \tilde{x})$, $E_5(0, \hat{N}_2, \hat{x})$, $E^*(N_1^*, N_2^*, x^*)$.

The equilibria E_0 , E_1 and E_2 obviously exist. We shall show the existence of other equilibria as follows.

Existence of $E_3(\bar{N}_1, \bar{N}_2, 0)$

Here \bar{N}_1 and \bar{N}_2 are the positive solutions of the following equations:

$$\alpha_{12} N_2 = g_1(N_1, K_1), \quad (5.7a)$$

$$\alpha_{21} N_1 = g_2(N_2, K_2). \quad (5.7b)$$

From (5.7a) we note that

$$\text{when } N_1 \rightarrow K_1, \quad N_2 \rightarrow 0, \quad (5.8a)$$

$$\text{when } N_1 \rightarrow 0, \quad N_2 \rightarrow \frac{g_1(0, K_1)}{\alpha_{12}}. \quad (5.8b)$$

$$\text{Also } \frac{dN_2}{dN_1} = \frac{1}{\alpha_{12}} \frac{\partial g_1(N_1, K_1)}{\partial N_1} < 0. \quad (5.8c)$$

From (5.7b) we note that

$$\text{when } N_2 \rightarrow K_2, \quad N_1 \rightarrow 0, \quad (5.9a)$$

$$\text{when } N_2 \rightarrow 0, \quad N_1 \rightarrow \frac{g_2(0, K_2)}{\alpha_{21}}, \quad (5.9b)$$

$$\text{also } \frac{dN_1}{dN_2} = \frac{1}{\alpha_{21}} \frac{\partial g_2(N_2, K_2)}{\partial N_2} < 0. \quad (5.10)$$

The above analysis shows that the two isoclines (5.7a) and (5.7b) intersect at a unique point (\bar{N}_1, \bar{N}_2) if

$$\text{either } K_1 < \frac{g_2(0, K_2)}{\alpha_{21}} \text{ and } K_2 < \frac{g_1(0, K_1)}{\alpha_{12}} \quad (5.11a)$$

$$\text{or } K_1 > \frac{g_2(0, K_2)}{\alpha_{21}} \text{ and } K_2 > \frac{g_1(0, K_1)}{\alpha_{12}} \quad (5.11b)$$

hold.

Existence of $E_4(N_1, 0, x)$

Here \tilde{N}_1 and \tilde{x} are the positive solutions of following equations:

$$x = \frac{N_1 g_1(N_1, K_1)}{b_{13} p_1(N_1)}, \quad (5.12a)$$

$$\gamma x + \delta = \beta_{31} p_1(N_1). \quad (5.12b)$$

From (5.12a) we note that

$$\text{when } N_1 \rightarrow K_1, \quad x \rightarrow 0, \quad (5.13a)$$

$$\text{when } N_1 \rightarrow 0, \quad x \rightarrow \frac{g_1(0, K_1)}{b_{13} p_1'(0)} > 0, \quad (5.13b)$$

$$\frac{dx}{dN_1} = \frac{1}{b_{13} p_1^2(N_1)} \left[g_1(N_1, K_1) (p_1(N_1) - N_1 p_1'(N_1)) + N_1 p_1(N_1) \frac{\partial g_1(N_1, K_1)}{\partial N_1} \right], \quad (5.14a)$$

$$\lim_{N_1 \rightarrow K_1} \frac{dx}{dN_1} = \frac{K_1}{b_{13} p_1(K_1)} \frac{\partial g_1(K_1, K_1)}{\partial N_1} < 0. \quad (5.14b)$$

From (5.14a) we note that $\frac{dx}{dN_1}$ may be positive or negative.

However, it is negative in the neighborhood of the point $N_1 = K_1$.

Further, $\frac{dx}{dN_1}$ is negative provided

$$\frac{1}{g_1(N_1, K_1)} \frac{\partial g_1(N_1, K_1)}{\partial N_1} < \frac{N_1 p_1'(N_1) - p_1(N_1)}{N_1 p_1(N_1)}. \quad (5.15)$$

From (5.12b) we note that

$$\text{when } N_1 \rightarrow K_1, \quad x \rightarrow \frac{1}{\gamma} (\beta_{31} p_1(K_1) - \delta) > 0 \text{ for } \beta_{31} p_1(K_1) > \delta, \quad (5.16a)$$

$$\text{when } N_1 \rightarrow 0, x \rightarrow -\frac{\delta}{\gamma} < 0, \quad (5.16b)$$

$$\frac{dx}{dN_1} = \frac{\beta_{31} p'_1(N_1)}{\gamma} > 0. \quad (5.17)$$

Thus the two isoclines (5.12a) and (5.12b) intersect at a unique point (\tilde{N}_1, \tilde{x}) if in addition to condition (5.15), the inequality

$$\beta_{31} p_1(K_1) > \delta \quad (5.18)$$

holds.

This shows that the equilibrium E_4 exists under the conditions (5.15) and (5.18).

Remark 2: If $p_1(N_1) = N_1$, then (5.15) is automatically satisfied.

Existence of $E_5(0, \hat{N}_2, \hat{x})$

Here we note that \hat{N}_2 and \hat{x} are the positive solutions of

$$x = \frac{N_2 g_2(N_2, K_2)}{b_{23} p_2(N_2)}, \quad (5.19a)$$

$$\delta + \gamma x = \beta_{32} p_2(N_2). \quad (5.19b)$$

Similar to the existence of E_4 , one can check that the equilibrium $E_5(0, \hat{N}_2, \hat{x})$ exists if

$$\frac{1}{g_2(N_2, K_2)} \frac{\partial g_2(N_2, K_2)}{\partial N_2} < \frac{N_2 p'_2(N_2) - p_2(N_2)}{N_2 p_2(N_2)}, \quad (5.20a)$$

$$\beta_{32} p_2(K_2) > \delta \quad (5.20b)$$

hold.

Existence of $E^(N_1^*, N_2^*, x^*)$*

Here N_1^* , N_2^* and x^* are the positive solutions of the following algebraic equations,

$$\alpha_{12}N_2 = g_1(N_1, K_1) - b_{13}xp_1(N_1)/N_1, \quad (5.21a)$$

$$\alpha_{21}N_1 = g_2(N_2, K_2) - b_{23}xp_2(N_2)/N_2, \quad (5.21b)$$

$$x = \frac{1}{\gamma} \left[\beta_{31}p_1(N_1) + \beta_{32}p_2(N_2) - \delta \right] = f(N_1, N_2), \text{ (say)}. \quad (5.21c)$$

From (5.21a) we note the following

when $N_2 \rightarrow 0$, $N_1 \rightarrow N_{a1}$ where N_{a1} is a solution of

$$N_1 g_1(N_1, K_1) - b_{13} f(N_1, 0) p_1(N_1) / N_1 = 0.$$

Taking

$$h_1(N_1) = [N_1 g_1(N_1, K_1) - b_{13} f(N_1, 0) p_1(N_1)] / N_1, \quad (5.22)$$

we note that

$$h_1(0) = g_1(0, K_1) + \delta b_{13} p_1'(0) / \gamma > 0, \quad (5.23a)$$

$$h_1(K_1) = -b_{13} (\beta_{31} p_1(K_1) - \delta) p_1(K_1) / \gamma K_1 < 0, \quad (5.23b)$$

if the inequality (5.18) holds.

Thus, N_{a1} is a positive unique solution of (5.22) in the interval $0 < N_{a1} < K_1$ if

$$\begin{aligned} \frac{dh_1(N_1)}{dN_1} &= \frac{\partial g_1(N_1, K_1)}{\partial N_1} - \frac{b_{13} p_1(N_1) \beta_{31} p_1'(N_1)}{\gamma N_1} \\ &\quad - b_{13} f(N_1, 0) (N_1 p_1'(N_1) - p_1(N_1)) / \gamma N_1^2 < 0. \end{aligned} \quad (5.24)$$

Again from (5.21a) we note that

when $N_1 \rightarrow 0$, $N_2 \rightarrow N_{a2}$ where N_{a2} is a solution of

$$\alpha_{12} \gamma N_2 + (\beta_{32} p_2(N_2) - \delta) b_{13} p_1'(0) - \gamma g_1(0, K_1) = 0.$$

Taking

$$h_2(N_2) = \alpha_{12} \gamma N_2 + b_{13} p_1'(0) (\beta_{32} p_2(N_2) - \delta) - \gamma g_1(0, K_1) \quad (5.25)$$

we see that

$$h_2(0) = -b_{13}p_1'(0)\delta - \gamma g_1(0, K_1) < 0, \tag{5.26a}$$

$$h_2(K_2) = [\alpha_{12}K_2 - g_1(0, K_1)]\gamma + b_{13}p_1'(0)(\beta_{32}p_2(K_2) - \delta) > 0, \tag{5.26b}$$

if

$$\alpha_{12}K_2 > g_1(0, K_1) \tag{5.27}$$

and inequality (5.20b) holds.

We also have,
$$\frac{dh_2(N_2)}{dN_2} = \alpha_{12}\gamma + b_{13}p_1'(0)\beta_{32}p_2'(N_2) > 0. \tag{5.28}$$

Thus N_{a2} is a positive unique solution of (5.25) in the interval

$0 < N_{a2} < K_2$ if (5.20b) and (5.27) hold.

Again from (5.21a), we have

$$\frac{dN_2}{dN_1} < 0 \text{ if } X_1 < 0 \tag{5.29a}$$

where

$$X_1 = \frac{\partial g_1(N_1, K_1)}{\partial N_1} - b_{13}f(N_1, N_2)(N_1 p_1'(N_1) - p_1(N_1))/N_1^2 - b_{13}\beta_{31}p_1(N_1)p_1'(N_1)/(N_1\gamma). \tag{5.29b}$$

The isocline (5.21b) can be analyzed in a similar fashion. It may be seen that this isocline passes through the points $(N_{b1}, 0)$ and $(0, N_{b2})$, where $0 < N_{b1} < K_1$ and $0 < N_{b2} < K_2$, and it has negative slope if in addition to assumptions (5.18) and (5.20b) the following conditions hold:

$$\alpha_{21}K_1 > g_2(0, K_2), \tag{5.30a}$$

$$\frac{\partial g_2(N_2, K_2)}{\partial N_2} - \frac{b_{23} p_2(N_2) \beta_{32} p_2'(N_2)}{\gamma N_2} - b_{23} f(0, N_2) (N_2 p_2'(N_2) - p_2(N_2)) / \gamma N_2^2 < 0, \quad (5.30b)$$

$$x_2 = \frac{\partial g_2(N_2, K_2)}{\partial N_2} - b_{23} f(N_1, N_2) (N_2 p_2'(N_2) - p_2(N_2)) / N_2^2 - b_{23} \beta_{32} p_2(N_2) p_2'(N_2) / (N_2 \gamma) < 0. \quad (5.30c)$$

From the above analysis it is clear that the two isoclines (5.21a) and (5.21b) intersect at a unique point (N_1^*, N_2^*) if in addition to assumptions (5.18), (5.20b), (5.27), (5.29a) and (5.30), any one of the following inequalities hold:

$$1. N_{a1} > N_{b2} \text{ and } N_{a1} < N_{b1}, \quad (5.31a)$$

$$2. N_{a1} < N_{b1} \text{ and } N_{a2} > N_{b2}. \quad (5.31b)$$

Knowing the values of N_1^* and N_2^* we can compute the value of x^* from (5.21c). We note that for x^* to be positive must have

$$\beta_{31} p_1(N_1^*) + \beta_{32} p_2(N_2^*) - \delta > 0. \quad (5.31c)$$

This completes the existence of E^* .

Stability of equilibria

The local stability of the equilibria can be studied from variational matrices corresponding to each equilibrium. By computing the variational matrices corresponding to each equilibrium we note the following results:

1. $E_0(0,0,0)$ is a saddle point whose stable manifold is locally in the x direction and unstable manifold is locally in the $N_1 - N_2$ plane.

2. $E_1(K_1, 0, 0)$ is locally asymptotically stable if

$$K_1 > g_2(0, K_2)/\alpha_{21} \text{ and } \beta_{31} p_1(K_1) < \delta \quad (5.32)$$

hold. If the inequalities in Eq. (5.32) are reversed, then E_1 is a saddle point with stable manifold locally in the N_1 direction and with unstable manifold locally in the N_2 -x plane.

3. $E_2(0, K_2, 0)$ is locally asymptotically stable if

$$K_2 > g_1(0, K_1)/\alpha_{12} \text{ and } \beta_{32} p_2(K_2) < \delta \quad (5.33)$$

hold. If inequalities in Eq. (5.33) are reversed, then it is a saddle point with stable manifold locally in the N_2 direction and with unstable manifold locally in the N_1 -x plane.

4. $E_3(N_1, N_2, 0)$ is locally asymptotically stable if

$$\begin{aligned} \beta_{31} p_1(\bar{N}_1) + \beta_{32} p_2(\bar{N}_2) - \delta &< 0, \\ -(\bar{H}_1 + \bar{H}_2) &> 0, \\ \text{and } \bar{H}_1 \bar{H}_2 - \alpha_{12} \alpha_{21} \bar{N}_1 \bar{N}_2 &> 0, \end{aligned}$$

where

$$\bar{H}_1 = g_1(\bar{N}_1, K_1) + \bar{N}_1 \frac{\partial g_1(\bar{N}_1, K_1)}{\partial \bar{N}_1} - \alpha_{12} \bar{N}_2, \quad (5.34a)$$

and

$$\bar{H}_2 = g_2(\bar{N}_2, K_2) + \bar{N}_2 \frac{\partial g_2(\bar{N}_2, K_2)}{\partial \bar{N}_2} - \alpha_{21} \bar{N}_1 \quad (5.34b)$$

hold. Otherwise it is an unstable equilibrium.

5. $E_4(\hat{N}_1, 0, \hat{x})$ is locally asymptotically stable if

$$\hat{H}_1 = g_1(N_1, K_1) + \hat{N}_1 \frac{\partial g_1(\hat{N}_1, K_1)}{\partial \hat{N}_1} - b_{13} \hat{x} p_1'(\hat{N}_1) < 0, \quad (5.35a)$$

$$\hat{H}_2 = g_2(0, K_2) - b_{23} \hat{x} p_2'(0) - \alpha_{21} \hat{N}_1 < 0 \quad (5.35b)$$

hold. Otherwise it is an unstable equilibrium.

6. $E_5(0, \tilde{N}_2, \tilde{x})$ is locally asymptotically stable if

$$\tilde{H}_1 = g_1(0, K_1) - b_{13} p_1'(0) \tilde{x} - \alpha_{12} \tilde{N}_2 < 0, \quad (5.36a)$$

$$\tilde{H}_2 = g_2(N_2, K_2) + N_2 \frac{\partial g_2(N_2, K_2)}{\partial N_2} - b_{23} \tilde{x} p_2'(N_2) < 0 \quad (5.36b)$$

hold. Otherwise it is unstable point.

In the following theorem we are able to write down conditions for local stability of E^* . The proof of the theorem follows from the Routh-Hurwitz criteria, and hence we omit it. We first write the following notations:

$$A_1 = - (H_1^* + H_2^*) + \gamma x^*, \quad (5.37a)$$

$$\begin{aligned} A_2 = & H_1^* H_2^* - (H_1^* + H_2^*) \gamma x^* - \alpha_{12} \alpha_{21} N_1^* N_2^* \\ & + b_{23} \beta_{32} x^* p_2(N_2^*) p_2'(N_2^*) \\ & + b_{13} \beta_{31} x^* p_1(N_1^*) p_1'(N_1^*), \end{aligned} \quad (5.37b)$$

$$\begin{aligned} A_3 = & (H_1^* H_2^* - \alpha_{12} \alpha_{21} N_1^* N_2^*) \gamma x^* \\ & - b_{23} x^* p_2(N_2^*) (\alpha_{32} H_1^* p_2'(N_2^*) + \alpha_{12} \beta_{31} N_1^* p_1'(N_1^*)) \\ & - b_{13} x^* p_1(N_1^*) (\beta_{31} H_2^* p_1'(N_1^*) + \alpha_{21} \beta_{32} N_2^* p_2'(N_2^*)), \end{aligned} \quad (5.37c)$$

$$H_1^* = g_1(N_1^*, K_1) + N_1^* \frac{\partial g_1(N_1^*, K_1)}{\partial N_1} - b_{13} x^* p_1'(N_1^*) - \alpha_{12} N_2^*, \quad (5.38a)$$

$$H_2^* = g_2(N_2^*, K_2) + N_2^* \frac{\partial g_2(N_2^*, K_2)}{\partial N_2} - b_{23} x^* p_2'(N_2^*) - \alpha_{21} N_1^*. \quad (5.38b)$$

Now we can state the following results.

Theorem 5.2.1: Let the following inequalities hold

$$A_1 > 0, \text{ and } A_1 A_2 > A_3, \quad i = 1, 2, 3. \quad (5.39)$$

Then $E^*(N_1^*, N_2^*, x^*)$ is locally asymptotically stable.

It may be noted here that if any one of the inequalities in Eq. (5.39) is not satisfied, then E^* is unstable.

In the following theorem we shall show that E^* is globally asymptotically stable. We first state the following lemma which establishes a region of attraction for system (5.5). The proof of the lemma is easy and hence is omitted.

Lemma 5.2.1: The set

$$\Omega_1 = \{ (N_1, N_2, x) : 0 \leq N_1 \leq K_1, 0 \leq N_2 \leq K_2, \\ 0 \leq x \leq \frac{1}{\gamma} (\beta_{31} p_1(K_1) + \beta_{32} p_2(K_2) - \delta) \}$$

is a region of attraction for all solutions initiating in the positive orthant.

Theorem 5.2.2: In addition to assumptions (5.3) and (5.4), let $g_i(N_i, K_i)$, $p_i(N_i)$ satisfy the following conditions in Ω

$$G_{mi} \leq - \frac{\partial g_i(N_i, K_i)}{\partial N_i} \leq G_{Mi}, \quad \rho_i \leq p_i'(N_i) \leq \rho_{i+2}, \quad (i=1,2) \quad (5.40)$$

for some positive constants G_{mi} , G_{Mi} , ρ_i , ρ_{i+2} , ($i=1,2$).

If the following inequality holds

$$(\alpha_{12} + \alpha_{21} c_1)^2 < c_1 G_{m1} G_{m2} \quad (5.41)$$

where $c_1 = \frac{c_2 \beta_{32} \rho_1}{b_{23} p_2(N_2^*)/N_2^*}$, $c_2 = \frac{b_{13} p_1(N_1^*)/N_1^*}{\beta_{31} \rho_3}$,

then E^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

Proof: We consider the following positive definite function about E^* ,

$$V(N_1(t), N_2(t), x(t)) = N_1 - N_1^* - N_1^* \ln(N_1/N_1^*) + c_1(N_2 - N_2^* - N_2^* \ln(N_2/N_2^*)) \\ + c_2(x - x^* - x^* \ln(x/x^*)). \quad (5.42)$$

Differentiating V with respect to t along the solution of (5.5) we get after some algebraic manipulations

$$\dot{V} \leq -\lambda_1(N_1)(N_1 - N_1^*)^2 - \lambda_2(N_2)c_1(N_2 - N_2^*)^2 - \gamma c_2(x - x^*)^2 \\ + (c_2\beta_{31}\xi_1(N_1) - b_{13}p_1(N_1^*/N_1^*)(N_1 - N_1^*)(x - x^*)) \\ + (c_2\beta_{32}\xi_2(N_2) - c_1b_{23}p_2(N_2^*/N_2^*)(N_2 - N_2^*)(x - x^*)) \\ + (\alpha_{12} + c_1\alpha_{21})(N_1 - N_1^*)(N_2 - N_2^*), \quad (5.43)$$

where

$$\lambda_1(N_1) = \begin{cases} - \left[\frac{g_1(N_1, K_1) - g_1(N_1, K_1^*)}{N_1 - N_1^*} \right], & N_1 \neq N_1^* \\ - \frac{\partial g_1(N_1^*, K_1)}{\partial N_1}, & N_1 = N_1^* \end{cases},$$

$$\xi_1(N_1) = \begin{cases} \frac{p_1(N_1) - p_1(N_1^*)}{N_1 - N_1^*}, & N_1 \neq N_1^* \\ p_1'(N_1^*), & N_1 = N_1^* \end{cases}.$$

From (5.40) and the mean value theorem we note that,

$$G_{m_1} \leq |\lambda_1(N_1)| \leq G_{M_1}, \quad \rho_1 \leq |\xi_1(N_1)| \leq \rho_{1+2}; \quad i=1,2. \quad (5.44)$$

Now \dot{V} can further be written as the sum of quadratics,

$$\dot{V} \leq -\frac{1}{2} m_{11}(N_1 - N_1^*)^2 + m_{12}(N_1 - N_1^*)(N_2 - N_2^*) - \frac{1}{2} m_{22}(N_2 - N_2^*)^2 \\ - \frac{1}{2} m_{22}(N_2 - N_2^*)^2 + m_{23}(N_2 - N_2^*)(x - x^*) - \frac{1}{2} m_{33}(x - x^*)^2 \\ - \frac{1}{2} m_{33}(x - x^*)^2 + m_{31}(x - x^*)(N_1 - N_1^*) - \frac{1}{2} m_{11}(N_1 - N_1^*)^2,$$

$$\text{where } m_{11} = \lambda_1(N_1), \quad (5.45a)$$

$$m_{22} = c_1 \lambda_2(N_2), \quad (5.45b)$$

$$m_{33} = c_2 \gamma, \quad (5.45c)$$

$$m_{12} = (\alpha_{12} + c_1 \alpha_{21}), \quad (5.45d)$$

$$m_{23} = c_2 \beta_{32} \xi_2(N_2) - c_1 b_{23} p_2(N_2^*)/N_2^*, \quad (5.45e)$$

$$m_{31} = c_2 \beta_{31} \xi_1(N_1) - b_{13} p_1(N_1^*)/N_1^*. \quad (5.45f)$$

Sufficient conditions for \dot{V} to be negative definite are that the following inequalities hold

$$m_{12}^2 < m_{11} m_{22}, \quad (5.46a)$$

$$m_{23}^2 < a_{22} a_{33}, \quad (5.46b)$$

$$m_{31}^2 < m_{33} m_{11}. \quad (5.46c)$$

We note that in Eq. (5.41) the values of c_1 and c_2 are such that conditions (5.46b) and (5.46c) are automatically satisfied. Further (5.41) \Rightarrow (5.46d), we conclude that \dot{V} is a Liapunov function with respect to E^* whose domain contains region Ω_1 , proving the theorem.

5.3 THE MODEL WITH DIFFUSION

In this section we consider the complete model (5.1) together with initial and boundary conditions (5.2). We observe that $N_1 = N_1^*$, $N_2 = N_2^*$, $x = x^*$ is the uniform steady state for system (5.1)-(5.2). We state the main results of this section in the form of the following theorem.

Theorem 5.3.1: If the interior equilibrium E^* is asymptotically stable for system (5.6) then the corresponding uniform steady state is also asymptotically stable for system (5.1)-(5.2).

Proof: Let us consider the following Liapunov function

$$W(N_1(t), N_2(t), x(t)) = \iint_R V(N_1(u, v, t), N_2(u, v, t), x(u, v, t)) \, dA \quad (5.48)$$

where V is defined by Eq. (5.42).

Now the time derivative of W along the solutions of model (5.1)-(5.2) is given by

$$\begin{aligned} \dot{W}(N_1(t), N_2(t), x(t)) &= \iint_R \left(\frac{\partial V}{\partial N_1} \frac{\partial N_1}{\partial t} + \frac{\partial V}{\partial N_2} \frac{\partial N_2}{\partial t} + \frac{\partial V}{\partial x} \frac{\partial x}{\partial t} \right) \, dA \\ &= I_1 + I_2, \end{aligned} \quad (5.49)$$

$$\text{where } I_1 = \iint_R \dot{V}(N_1(u, v, t), N_2(x, y, t), x(u, v, t)) \, dA, \quad (5.50)$$

$$I_2 = \iint_R \left(D_{11} \frac{\partial V}{\partial N_1} \nabla^2 N_1 + D_{22} \frac{\partial V}{\partial N_2} \nabla^2 N_2 + D_{xx} \frac{\partial V}{\partial x} \nabla^2 x \right) \, dA. \quad (5.51)$$

We first assume that \dot{V} does not change its sign in R .

We now note the following properties of V , namely

$$1. \left. \frac{\partial V}{\partial N_i} \right|_{\partial R} = \left. \frac{\partial V}{\partial x} \right|_{\partial R} = 0 \text{ for all points of } R \ (i=1,2), \quad (5.52)$$

$$2. \frac{\partial^2 V}{\partial N_1 \partial N_2} = \frac{\partial^2 V}{\partial N_2 \partial x} = \frac{\partial^2 V}{\partial x \partial N_1} = 0, \quad (5.53)$$

$$3. \frac{\partial^2 V}{\partial N_i^2} > 0, \frac{\partial^2 V}{\partial x^2} > 0 \ (i=1,2). \quad (5.54)$$

Now under an analysis similar to chapter III, it can be checked that

$$\iint_R \frac{\partial V}{\partial N_i} \nabla^2 N_i \, dA = - \iint_R \frac{\partial^2 V}{\partial N_i^2} \left[\left(\frac{\partial N_i}{\partial u} \right)^2 + \left(\frac{\partial N_i}{\partial v} \right)^2 \right] \, dA \leq 0, \ (i = 1,2). \quad (5.55)$$

and

$$\iint_R \frac{\partial V}{\partial x} \nabla^2 x \, dA = - \iint_R \frac{\partial^2 V}{\partial x^2} \left[\left(\frac{\partial x}{\partial u} \right)^2 + \left(\frac{\partial x}{\partial v} \right)^2 \right] \, dA \leq 0, \ (i = 1,2) \quad (5.56)$$

This shows that $I_2 \leq 0$.

Thus from (5.49), \dot{W} can be estimated as

$$\begin{aligned} \dot{W}(N_1(t), N_2(t), x(t)) &\leq \iint_R \dot{V}(N_1(u, v, t), N_2(u, v, t), x(u, v, t)) \, dA \\ &- \frac{D_1 N_1^*}{K_1^2} \iint_R \left[\left(\frac{\partial N_1}{\partial u} \right)^2 + \left(\frac{\partial N_1}{\partial v} \right)^2 \right] dA - \frac{D_2 N_2^*}{K_2^2} \iint_R \left[\left(\frac{\partial N_2}{\partial u} \right)^2 + \left(\frac{\partial N_2}{\partial v} \right)^2 \right] dA \\ &- \frac{Dx^* \gamma^2}{(\beta_{31} p_1(K_1) + \beta_{32} p_2(K_2) - \delta)^2} \iint_R \left[\left(\frac{\partial x}{\partial u} \right)^2 + \left(\frac{\partial x}{\partial v} \right)^2 \right] dA. \end{aligned} \quad (5.57)$$

From (5.57) we note that if $\dot{V} \leq 0$, then $\dot{W} \leq 0$. This implies that if E^* is asymptotically stable for system (5.6), then the uniform steady state E^* of system (5.1)-(5.2) is also asymptotically stable, and hence the theorem follows.

If we consider the region R to be a rectangular habitat given by

$$R = \{ (u, v): 0 \leq u \leq a, 0 \leq v \leq b \} \quad (5.58)$$

then under an analysis similar to chapter III, \dot{W} can be estimated as

$$\begin{aligned} \dot{W} &\leq \iint_0^R \dot{V} \, dA - \frac{(a^2 + b^2)\pi^2}{a^2 b^2} \iint_0^R \left[\frac{D_1 N_1^*}{K_1^2} (N_1 - N_1^*)^2 + \frac{D_2 N_2^*}{K_2^2} (N_2 - N_2^*)^2 \right. \\ &\quad \left. \frac{Dx^* \gamma^2}{\beta_{31} p_1(K_1) + \beta_{32} p_2(K_2) - \delta)^2} (x - x^*)^2 \right] dA. \end{aligned} \quad (5.59)$$

This shows that if the interior equilibrium E^* of model (5.6) is globally asymptotically stable, then the uniform steady state of the initial boundary value problem (5.1)-(5.2) is also globally asymptotically stable. We further note that, even if \dot{V} is positive definite, i.e. E^* is unstable in the absence of diffusion, then by increasing the diffusion coefficients to sufficiently large values, \dot{W}

can be made negative definite. This implies that by increasing the diffusion coefficients to sufficiently large values, an unstable equilibrium can be made stable.

5.4 SIMULATION ANALYSIS

In this section a numerical example is presented to demonstrate the feasibility of the results discussed above. We take the particular form of the functions as defined by Eq. (5.5) for model (5.6).

We choose the following values of parameters in model (5.6) and in Eq. (5.5),

$$\begin{aligned} r_1 &= 3.56, K_1 = 12.0, b_{13} = 0.10, \alpha_{12} = 0.12, \\ r_2 &= 7.50, K_2 = 10.0, b_{23} = 0.2, \alpha_{21} = 0.4, \\ \beta_{31} &= 4.6, \beta_{32} = 5.5, \delta = 1.0, \gamma = 2.0. \end{aligned} \quad (5.60)$$

With the above set of values of parameters, it can be seen that conditions for the existence of the interior equilibrium E^* are satisfied. Our numerical computation shows that E^* is given by

$$N_1^* = 4.90183, N_2^* = 2.60347, x^* = 17.93375.$$

It can be checked that conditions (5.39) in Theorem 5.2.1 are satisfied. This shows that E^* is locally asymptotically stable.

It can also be verified that condition (5.41) in Theorem 5.2.3 is satisfied which shows that E^* is globally asymptotically stable.

5.4 SUMMARY

In this chapter, a Gause type mathematical model has been considered to study the effect of predation on two competing prey species in a diffusive system. We discussed here the effect of predation on two competing prey species, in which the predator species

is influenced by the damage effect caused by crowding from the members of its own population in a diffusive system. In the absence of diffusion, criteria for local stability, instability and global stability have been obtained. In the absence of diffusion it has been shown that the global stability of the interior equilibrium E^* depends upon the interspecific interference of the two competing prey species. If the interspecific interference of the two competing prey species is too high then the system may lead to instability.

By analyzing the complete model with diffusion (5.1)-(5.2), it has been shown that if the interior equilibrium E^* of model (5.5) is asymptotically stable, then the uniform steady state of system (5.1)-(5.2) is asymptotically stable with diffusion. It has also been shown that sufficiently rapid diffusion by the prey species may stabilize an otherwise unstable equilibrium.

CHAPTER VI

A MODEL FOR TWO PREDATORS COMPETING FOR TWO PREY SPECIES WITH DIFFUSION

6.0 INTRODUCTION

It is well known that species may not coexist always in their habitat under certain conditions. Therefore it is of biological significance to investigate the existence of each population in a system of two or more interacting species. In recent years a growing interest has been shown by several researchers to determine the criteria for coexistence and persistence (MacArthur (1972), Gopalsamy (1977), Hsu and Hubbell (1979), Verma (1980), Rai et al. (1983), Freedman and Waltman (1984), Sikder and Roy (1994a), Dubey (1997) etc.). MacArthur (1972) studied the Volterra classical model of two species competition and obtained some conditions for existence involving competition coefficients and carrying capacities from his two consumer two resource model. However he didn't completely determine analytically under what conditions will either, one, or both predator species and one or both prey species survive. Hsu and Hubbell (1979) proposed and analyzed MacArthur's model with more general parameters and concluded that the two-predator, two-prey system catastrophically collapses to a one-predator, two prey system or even to one-predator, one-prey system. They considered and analysed the behavior of a model of two species competing exploitatively for two prey species. They showed that each prey species grows logistically in the absence of predation, and the predator species consume the prey according to a linear functional response. It has been also shown that

if n predator species are competing for a single prey species which grows logistically, and if the predators consume prey according to a linear functional response then only one predator species will survive in the end. In the above investigation, the effect of diffusion has not been considered though it does play an important role in stabilizing the system (Cosner and Laser (1984), Bergerud and Page (1987), Cantrell and Cosner (1987,89), Freedman and Shukla (1989), Shukla et. al (1989), etc.).

In this chapter, therefore, we propose a mathematical model to study the effect of two competing predators on two prey species. Our model is the generalization of the Hsu & Hubbel model (1979). In the present model we take the specific growth rates and the functional responses of the species as nonlinear functions by incorporating the effect of diffusion on the stability of the system.

6.1 MATHEMATICAL MODEL

Consider an ecosystem where two predators are feeding on two prey species. We assume that the dynamics of the prey species are governed by generalized logistic equations and the growth rates of the predators are governed by general functional responses. If $N_i(t)$ and $x_i(t)$ ($i=1,2$) are the population densities of the i^{th} prey and predator species respectively at time $t \geq 0$, then the dynamics of the system with diffusion can be written as

$$\begin{aligned} \frac{\partial N_1}{\partial t} &= N_1 g_1(N_1, K_1) - b_{11} x_1 p_1(N_1) - b_{21} x_2 p_2(N_1) + D_1 \nabla^2 N_1, \\ \frac{\partial N_2}{\partial t} &= N_2 g_2(N_2, K_2) - b_{12} x_1 q_1(N_2) - b_{22} x_2 q_2(N_2) + D_2 \nabla^2 N_2, \\ \frac{\partial x_1}{\partial t} &= x_1 (\beta_{11} p_1(N_1) + \beta_{12} q_1(N_2) - \delta_1 - \gamma_1 x_1) + d_1 \nabla^2 x_1, \\ \frac{\partial x_2}{\partial t} &= x_2 (\beta_{21} p_2(N_1) + \beta_{22} q_2(N_2) - \delta_2 - \gamma_2 x_2) + d_2 \nabla^2 x_2. \end{aligned} \quad (6.1a)$$

We impose the following boundary and initial conditions on system

(6.1)

$$N_i(0, u, v) = \phi_i(u, v) \geq 0, \quad x_i(0, u, v) = \psi_i(u, v) \geq 0,$$

$$\frac{\partial N_i}{\partial n} = \frac{\partial x_i}{\partial n} = 0, \quad i = 1, 2, \quad (6.1b)$$

where n is the unit outward normal to the region ∂R . ϕ_i and ψ_i ($i=1,2$) are the smooth initial functions. R is a simply connected domain in the u - v plane with piecewise smooth boundary ∂R .

In model (6.1), $\nabla^2 \equiv \frac{\partial^2}{\partial u^2} + \frac{\partial^2}{\partial v^2}$ is the Laplacian diffusion operator.

The function $g_i(N_i, K_i)$ is the specific growth rate of the i^{th} prey species. It increases as the carrying capacity K_i of the prey species increases and decreases as the density of the prey species increases. Hence we assume

$$g_i(0,0) > 0, \quad \frac{\partial g_i(N_i, K_i)}{\partial N_i} < 0, \quad \frac{\partial g_i(N_i, K_i)}{\partial K_i} > 0,$$

and there exists $N_i = K_i$ such that $g_i(K_i, K_i) = 0$. (6.2)

The function $p_i(N_1)$ is the i^{th} predator functional response on the prey species of density N_1 and it satisfies the following properties

$$p_i(0) = 0, \quad p_i'(N_1) > 0, \quad \text{for } N_1 \geq 0, \quad i=1,2. \quad (6.3)$$

The function $q_i(N_2)$ has similar properties as $p_i(N_1)$ and it satisfies,

$$q_i(0) = 0, \quad q_i'(N_2) > 0 \quad \text{for } N_2 \geq 0, \quad i = 1,2. \quad (6.4)$$

D_i , d_i are the diffusion coefficients of the i^{th} prey and predator species in R , respectively. b_{ij} is the feeding rate per predator (predator species i) per unit prey (prey species j) consumed,

β_{ij} is the birth rate per predator (predator species i) per unit prey (prey species j) consumed, δ_i is the death rate and γ_i is the intraspecific interference coefficient of i^{th} predator species respectively.

Remark 1: It may be pointed out that if we take

$$\begin{aligned} D_1 = D_2 = d_1 = d_2 = 0, \quad \gamma_1 = \gamma_2 = 0, \\ p_1(N_1) = N_1 = p_2(N_1), \quad q_1(N_2) = q_2(N_2) = N_2 \\ g_1(N_1, K_1) = r_1(1 - N_1/K_1), \quad g_2(N_2, K_2) = r_2(1 - N_2/K_2), \end{aligned} \quad (6.5)$$

where r_1 and r_2 are positive constants, then model (6.1) reduces to Hsu and Hubbell's model (1979).

6.2 THE MODEL WITHOUT DIFFUSION

We consider the model without diffusion (i.e., $D_i = d_i = 0$) as follows:

$$\begin{aligned} \dot{N}_1 &= N_1 g_1(N_1, K_1) - b_{11} x_1 p_1(N_1) - b_{21} x_2 p_2(N_2), \\ \dot{N}_2 &= N_2 g_2(N_2, K_2) - b_{12} x_1 q_1(N_2) - b_{22} x_2 q_2(N_2), \\ \dot{x}_1 &= x_1 (\beta_{11} p_1(N_1) + \beta_{12} q_1(N_2) - \delta_1 - \gamma_1 x_1), \\ \dot{x}_2 &= x_2 (\beta_{21} p_2(N_1) + \beta_{22} q_2(N_2) - \delta_2 - \gamma_2 x_2), \\ N_i(0) &\geq 0, \quad x_i(0) \geq 0, \quad i = 1, 2. \end{aligned} \quad (6.6)$$

Setting $\frac{dZ}{dt} = 0$ ($Z = N_1, N_2, x_1, x_2$) and solving (6.6) we get the following possible nonnegative equilibria, namely $E_0(0, 0, 0, 0)$, $E_1(K_1, 0, 0, 0)$, $E_2(0, K_2, 0, 0)$, $E_3(K_1, K_2, 0, 0)$, $E_4(\bar{N}_1, 0, \bar{x}_1, 0)$, $E_5(\bar{N}_1, 0, 0, \bar{x}_2)$, $E_6(0, \hat{N}_2, \hat{x}_1, 0)$, $E_7(0, \hat{N}_2, 0, \hat{x}_2)$, $E_8(\tilde{N}_1, \tilde{N}_2, \tilde{x}_1, 0)$, $E_9(\tilde{N}_1, \tilde{N}_2, 0, \tilde{x}_2)$, $E_{10}(N_{11}, 0, x_{11}, x_{21})$, $E_{11}(0, N_{22}, x_{12}, x_{22})$, $E^*(N_1^*, N_2^*, x_1^*, x_2^*)$.

The equilibria $E_0 - E_3$ clearly exist. We shall show the existence of other equilibria as follows.

Here \bar{N}_1 and \bar{x}_1 are the positive solutions of the following equations:

$$x_1 = \frac{N_1 g_1(N_1, K_1)}{b_{11} p_1(N_1)}, \quad (6.7a)$$

$$\gamma_1 x_1 + \delta_1 = \beta_{11} p_1(N_1). \quad (6.7b)$$

It can be checked that the two isoclines (6.7a) and (6.7b) intersect at a unique point (\bar{N}_1, \bar{x}_1) if the following inequalities hold:

$$\frac{1}{g_1(N_1, K_1)} \frac{\partial g_1(N_1, K_1)}{\partial N_1} < \frac{N_1 p_1'(N_1) - p_1(N_1)}{N_1 p_1(N_1)}, \quad (6.8a)$$

$$\beta_{11} p_1(K_1) > \delta_1. \quad (6.8b)$$

This implies that if inequalities (6.8a) and (6.8b) hold, then the prey species of density N_1 and the predator species of density x_1 survive while the other prey and predator species die out.

Existence of $E_5 (\bar{N}_1, 0, 0, \bar{x}_2)$

Here \bar{N}_1 and \bar{x}_2 are the positive solutions of the following equations:

$$x_2 = \frac{N_1 g_1(N_1, K_1)}{b_{21} p_2(N_1)}, \quad (6.9a)$$

$$\gamma_2 x_2 + \delta_2 = \beta_{21} p_2(N_1). \quad (6.9b)$$

It can be checked that the two isoclines (6.9a) and (6.9b) intersect at a unique point (\bar{N}_1, \bar{x}_2) if the following inequalities hold:

$$\frac{1}{g_1(N_1, K_1)} \frac{\partial g_1(N_1, K_1)}{\partial N_1} < \frac{N_1 p_2'(N_1) - p_2(N_1)}{N_1 p_2(N_1)}, \quad (6.10a)$$

$$\beta_{21} p_2(K_1) > \delta_2. \quad (6.10b)$$

This shows that the prey species of density N_1 and the predator

of density x_2 survive if inequalities (6.10a) and (6.10b) are satisfied.

Existence of $E_6(0, \hat{N}_2, \hat{x}_1, 0)$

Here \hat{N}_2 and \hat{x}_1 are the positive solutions of the following equations:

$$x_1 = \frac{N_2 g_2(N_2, K_2)}{b_{12} q_1(N_2)}, \quad (6.11a)$$

$$y_1 x_1 + \delta_1 = \beta_{12} q_2(N_2). \quad (6.11b)$$

It can be checked that the two isoclines (6.11a) and (6.11b) intersect at a unique point (\hat{N}_2, \hat{x}_1) if the following inequalities hold:

$$\frac{1}{g_2(N_2, K_2)} \frac{\partial g_2(N_2, K_2)}{\partial N_2} < \frac{N_2 (q_1(N_2) - q_1(N_2))}{N_2 q_1(N_2)}, \quad (6.12a)$$

$$\beta_{12} q_1(K_2) > \delta_1. \quad (6.12b)$$

This implies that if the inequalities (6.12a) and (6.12b) hold then the prey species of density N_2 and the predator species of density x_1 survive while the other prey and predator species die.

Existence of $E_7(0, \tilde{N}_2, 0, \tilde{x}_2)$

Here \tilde{N}_2 and \tilde{x}_2 are the positive solutions of the following equations:

$$x_2 = \frac{N_2 g_2(N_2, K_2)}{b_{22} q_2(N_2)}, \quad (6.13a)$$

$$y_2 x_2 + \delta_2 = \beta_{22} q_2(N_2). \quad (6.13b)$$

It can be checked that the two isoclines (6.13a) and (6.13b) intersect at a unique point $(\tilde{N}_2, \tilde{x}_2)$ if the following inequalities hold:

$$\frac{1}{g_2(N_2, K_2)} \frac{\partial g_2(N_2, K_2)}{\partial N_2} < \frac{N_2 q_2'(N_2) - q_2(N_2)}{N_2 q_2(N_2)}, \quad (6.14a)$$

$$\beta_{22} q_2(K_2) > \delta_2. \quad (6.14b)$$

This implies that if inequalities (6.14a) and (6.14b) hold, then the prey species of density N_2 and the predator species x_2 survive while the other prey and predator die out.

Existence of $E_8(\tilde{N}_1, \tilde{N}_2, \tilde{x}_1, 0)$

Here \tilde{N}_1 , \tilde{N}_2 and \tilde{x}_1 are the positive solutions of the following equations:

$$g_1(N_1, K_1) - x_1 b_{11} p_1(N_1)/N_1 = 0, \quad (6.15a)$$

$$g_2(N_2, K_2) - x_1 b_{12} q_1(N_2)/N_2 = 0, \quad (6.15b)$$

$$x_1 = f_1(N_1, N_2), \quad (6.15c)$$

where $f_1(N_1, N_2) = (\beta_{11} p_1(N_1) + \beta_{12} q_1(N_2) - \delta_1)/\gamma_1$.

It can be checked that isocline (6.15a) passes through the points $(\tilde{N}_{1a}, 0)$ and $(0, \tilde{N}_{2a})$ if the following inequalities hold:

$$1. \beta_{11} p_1(K_1) - \delta_1 > 0, \quad (6.16a)$$

$$2. g_1(0, K_1) - b_{11} p_1'(0)(\beta_{12} q_1(K_2) - \delta_1)/\gamma_1 < 0, \quad (6.16b)$$

$$3. \frac{d\tilde{h}_1(N_1)}{dN_1} < 0, \quad (6.16c)$$

where $\tilde{h}_1(N_1) = g_1(N_1, K_1) - b_{11} p_1(N_1) f_1(N_1, 0)/N_1$.

Here \tilde{N}_{1a} and \tilde{N}_{2a} are the positive solutions of

$$g_1(N_1, K_1) - b_{11} p_1(N_1) f_1(N_1, 0)/N_1 = 0,$$

$$g_1(0, K_1) - b_{11} f_1(0, N_2) p_1'(0) = 0,$$

where $0 < \tilde{N}_{1a} < K_1$, $0 < \tilde{N}_{2a} < K_1$,

It can also be seen that isocline (6.15a) has a negative slope if the following inequality holds

$$\frac{\partial g_1(N_1, K_1)}{\partial N_1} - \frac{b_{11}}{N_1^2} \left[\beta_{11} N_1 p_1(N_1) p_1'(N_1) / \gamma_1 + f_1(N_1, N_2) (N_1 p_1'(N_1) - p_1(N_1)) \right] < 0. \quad (6.16d)$$

Similarly isocline (6.15b) passes through the points $(\tilde{N}_{1b}, 0)$ and $(0, \tilde{N}_{2b})$ if the following inequalities hold:

$$1. \beta_{12} q_1(K_2) - \delta_1 > 0, \quad (6.17a)$$

$$2. g_2(0, K_2) - b_{12} q_1'(0) (\beta_{11} p_1(K_1) - \delta_1) / \gamma_1 < 0, \quad (6.17b)$$

$$3. \frac{d\tilde{h}_2(N_2)}{dN_2} < 0, \quad (6.17c)$$

where $\tilde{h}_2(N_2) = g_2(N_2, K_2) - b_{12} q_1(N_2) f_1(0, N_2) / N_2$.

Here \tilde{N}_{1b} and \tilde{N}_{2b} are the positive solutions of

$$g_2(0, K_2) - b_{12} q_1'(0) f_1(N_1, 0) = 0,$$

$$g_2(N_2, K_2) - b_{12} q_1(N_2) f_1(0, N_2) / N_2 = 0,$$

$$\text{where } 0 < \tilde{N}_{1b} < K_2, 0 < \tilde{N}_{2b} < K_2.$$

Further, isocline (8.15b) has negative slope if the following inequality holds

$$\frac{\partial g_2(N_2, K_2)}{\partial N_2} - \frac{b_{12}}{N_2^2} \left[\beta_{12} N_2 q_1(N_1) q_1'(N_2) / \gamma_1 + f_1(N_1, N_2) (N_2 q_1'(N_2) - q_1(N_2)) \right] < 0. \quad (6.17d)$$

Thus, the two isoclines (6.15a) and (6.15b) intersect at a unique point $(\tilde{N}_1, \tilde{N}_2)$ if any one of the following holds:

$$1. \tilde{N}_{2b} > \tilde{N}_{2a} \text{ and } \tilde{N}_{1b} < \tilde{N}_{1a}, \quad (6.18a)$$

$$2. \tilde{N}_{1b} > \tilde{N}_{1a} \text{ and } \tilde{N}_{2b} < \tilde{N}_{2a}. \quad (6.18b)$$

Knowing the values of \tilde{N}_1, \tilde{N}_2 we can compute \tilde{x}_1 from (6.15c). It may be noted that for \tilde{x}_1 to be positive we must have

$$\beta_{11}p_1(\tilde{N}_1) + \beta_{12}q_1(\tilde{N}_2) - \delta_1 > 0. \quad (6.19)$$

Thus we conclude that the equilibrium E_g exists if conditions (6.16a)-(6.16d), (6.17a)-(6.17d) and either (6.18a) or (6.18b) hold.

Existence of $E_g(\tilde{N}_1, \tilde{N}_2, 0, \tilde{x}_2)$

Here \tilde{N}_1, \tilde{N}_2 and \tilde{x}_1 are the positive solutions of the following equations:

$$g_1(N_1, K_1) - x_2 b_{21} p_2(N_1)/N_1 = 0, \quad (6.20a)$$

$$g_2(N_2, K_2) - x_2 b_{22} q_2(N_2)/N_2 = 0, \quad (6.20b)$$

$$x_2 = f_2(N_1, N_2), \quad (6.20c)$$

where $f_2(N_1, N_2) = (\beta_{21}p_2(N_1) + \beta_{22}q_2(N_2) - \delta_2)/\gamma_2$.

It can be checked that the isocline (6.20a) passes through the points $(\tilde{N}_{1a}, 0)$ and $(0, \tilde{N}_{2a})$ if the following inequalities hold:

$$1. \beta_{21}p_2(K_1) - \delta_2 > 0, \quad (6.21a)$$

$$2. g_1(0, K_1) - b_{21}p_2'(0)(\beta_{22}q_2(K_2) - \delta_2)/\gamma_2 < 0, \quad (6.21b)$$

$$3. \frac{d\tilde{I}_1(N_1)}{dN_1} < 0, \quad (6.21c)$$

where $\tilde{I}_1(N_1) = g_1(N_1, K_1) - b_{21}p_2(N_1)f_2(N_1, 0)/N_2$.

Here \tilde{N}_{1a} and \tilde{N}_{2a} are the positive solutions of

$$g_1(N_1, K_1) - b_{21} p_2(N_1) f_2(N_1, 0) / N_2 = 0,$$

$$g_1(0, K_1) - b_{12} p_2'(0) f_2(0, N_2) = 0,$$

$$\text{where } 0 < \tilde{N}_{1a} < K_1, 0 < \tilde{N}_{2a} < K_1.$$

Further, the isocline (6.20a) has a negative slope if the following inequality holds:

$$\frac{\partial g_1(N_1, K_1)}{\partial N_1} - \frac{b_{21}}{N_1^2} \left[\beta_{21} N_1 p_2(N_1) p_2'(N_1) \gamma_2 + f_2(N_1, N_2) (N_1 p_2'(N_1) - p_2(N_1)) \right] < 0. \quad (6.21d)$$

Similarly the isocline (6.20b) passes through the points $(\tilde{N}_{1b}, 0)$ and $(0, \tilde{N}_{2b})$ if the following inequalities hold:

$$1. \beta_{22} q_2(K_2) - \delta_2 > 0, \quad (6.22a)$$

$$2. g_2(0, K_2) - b_{22} q_2'(0) (\beta_{21} p_2(K_1) - \delta_2) / \gamma_2 < 0, \quad (6.22b)$$

$$3. \frac{d\tilde{I}_2(N_2)}{dN_2} < 0, \quad (6.22c)$$

where $\tilde{I}_2(N_2) = g_2(N_2, K_2) - b_{22} q_2(N_2) f_2(0, N_2) / N_2$.

Here \tilde{N}_{1b} and \tilde{N}_{2b} are the positive solutions of

$$g_2(0, K_2) - b_{22} q_2'(0) f_2(N_1, 0) = 0,$$

$$g_2(N_2, K_2) - b_{22} q_2(N_2) f_2(0, N_2) / N_2 = 0,$$

$$\text{where } 0 < \tilde{N}_{1b} < K_2, 0 < \tilde{N}_{2b} < K_2.$$

It can also be checked that the isocline (8.20b) has negative slope if the following hold

$$\frac{\partial g_2(N_2, K_2)}{\partial N_2} - \frac{b_{22}}{N_2^2} \left[\beta_{22} N_2 q_2(N_2) q_2'(N_2) / \gamma_2 + f_2(N_1, N_2) (N_2 q_2'(N_2) - q_2(N_2)) \right] < 0. \quad (6.22d)$$

Thus, the two isoclines (6.20a) and (6.20b) intersect at a unique solution $(\tilde{N}_1, \tilde{N}_2)$, if any one of the following inequality holds

$$1. \tilde{N}_{2b} > \tilde{N}_{2a} \text{ and } \tilde{N}_{1b} < \tilde{N}_{1a}, \quad (6.23a)$$

$$2. \tilde{N}_{1b} > \tilde{N}_{1a} \text{ and } \tilde{N}_{2b} < \tilde{N}_{2a}. \quad (6.23b)$$

Knowing the values of \tilde{N}_1, \tilde{N}_2 we can compute \tilde{x}_1 from (6.20c). It may be noted that for \tilde{x}_2 to be positive we must have

$$\beta_{21} p_2(\tilde{N}_1) + \beta_{22} q_2(\tilde{N}_2) - \delta_2 > 0. \quad (6.24)$$

Thus, we conclude that the equilibrium E_9 exists if conditions (6.21a)-(6.21d), (6.22a)-(6.22d) and either (6.23a) or (6.23b) hold.

Existence of $E_{10}(N_{11}, 0, x_{11}, x_{12})$

Here N_{11}, x_{11} and x_{12} are the positive solutions of the following equations:

$$g_1(N_1, K_1) - b_{11} x_{11} p_1(N_1) / N_1 - b_{12} x_{12} p_2(N_1) / N_1 = 0, \quad (6.25a)$$

$$x_{11} = (\beta_{11} p_1(N_1) - \delta_1) / \gamma_1, \quad (6.25b)$$

$$x_{12} = (\beta_{21} p_2(N_1) - \delta_2) / \gamma_2. \quad (6.25c)$$

It can be seen that the equilibrium E_{10} exists if the following inequalities hold:

$$1. \beta_{11} p_1(K_1) - \delta_1 > 0 \text{ and } \beta_{21} p_2(K_1) - \delta_2 > 0, \quad (6.26a)$$

$$\begin{aligned}
2. \frac{\partial g_1(N_1, K_1)}{\partial N_1} &= \frac{(N_1 p'_1(N_1) - p_1(N_1))}{N_1^2 \gamma_1} (\beta_{11} p_1(N_1) - \delta_1) b_{11} \\
&- \frac{(N_1 p'_2(N_1) - p_2(N_1))}{N_1^2 \gamma_2} (\beta_{21} p_2(N_1) - \delta_2) b_{12} \\
&- b_{11} \beta_{11} p_1(N_1) p'_1(N_1) / N_1 \gamma_1 - b_{12} \beta_{21} p_2(N_1) p'_2(N_1) / N_1 \gamma_2 < 0. \quad (6.26b)
\end{aligned}$$

It may be noted that for x_{11} and x_{12} to be positive we must have respectively

$$\beta_{11} p_1(N_{11}) - \delta_1 > 0, \quad (6.27a)$$

$$\beta_{21} p_2(N_{11}) - \delta_2 > 0. \quad (6.27b)$$

Existence of $E_{11}(0, N_{22}, x_{21}, x_{22})$

Here N_{22} , x_{21} and x_{22} are the positive solutions of the following equations:

$$g_2(N_2, K_2) - b_{12} x_1 q_1(N_2) / N_2 - b_{22} x_2 q_2(N_2) / N_2 = 0, \quad (6.28a)$$

$$x_1 = (\beta_{12} q_1(N_2) - \delta_1) / \gamma_1, \quad (6.28b)$$

$$x_2 = (\beta_{22} q_2(N_2) - \delta_2) / \gamma_2. \quad (6.28c)$$

It can be seen that the equilibrium E_{11} exists if the following inequalities hold:

$$1. \beta_{12} q_1(K_2) - \delta_1 > 0 \text{ and } \beta_{22} q_2(K_2) - \delta_2 > 0, \quad (6.29a)$$

$$\begin{aligned}
2. \frac{\partial g_2(N_2, K_2)}{\partial N_2} &= \frac{(N_2 q'_1(N_2) - q_1(N_2))}{N_2^2} (\beta_{12} q_1(N_2) - \delta_1) b_{12} \\
&- \frac{(N_2 q'_2(N_2) - q_2(N_2))}{N_2^2} (\beta_{22} q_2(N_2) - \delta_2) b_{22} \\
&- b_{12} \beta_{12} q_1(N_2) q'_1(N_2) / N_2 \gamma_1 - b_{22} \beta_{22} q_2(N_2) q'_2(N_2) / N_2 \gamma_2 < 0. \quad (6.29b)
\end{aligned}$$

It may be noted here that for x_{21} and x_{22} to be positive we must have respectively

$$\beta_{21}q_1(N_{22}) - \delta_1 > 0, \quad (6.30a)$$

$$\beta_{22}q_2(N_{22}) - \delta_2 > 0. \quad (6.30b)$$

Existence of $E^(N_1^*, N_2^*, x_1^*, x_2^*)$*

Here $N_1^*, N_2^*, x_1^*, x_2^*$ are the positive solutions of the following algebraic equations

$$g_1(N_1, K_1) - b_{11}x_1p_1(N_1)/N_1 - b_{21}x_2p_2(N_1)/N_1 = 0, \quad (6.31a)$$

$$g_2(N_2, K_2) - b_{12}x_1q_1(N_2)/N_2 - b_{22}x_2q_2(N_2)/N_2 = 0, \quad (6.31b)$$

$$x_1 = f_1(N_1, N_2), \quad (6.31c)$$

$$x_2 = f_2(N_1, N_2). \quad (6.31d)$$

where $f_1(N_1, N_2) = (\beta_{11}p_1(N_1) + \beta_{12}q_1(N_2) - \delta_1)/\gamma_1$,

$f_2(N_1, N_2) = (\beta_{21}p_2(N_1) + \beta_{22}q_2(N_2) - \delta_2)/\gamma_2$.

From (6.31a) we note the following:

when $N_2 \rightarrow 0$, then $N_1 \rightarrow N_{1a}$, where N_{1a} is a positive solution of

$$g_1(N_1, K_1) - b_{11}p_1(N_1)f_1(N_1, 0)/N_1 - b_{21}p_2(N_1)f_2(N_2, 0)/N_1 = 0.$$

Taking

$$F_1(N_1) = g_1(N_1, K_1) - b_{11}p_1(N_1)(\beta_{11}p_1(N_1) - \delta_1)/\gamma_1 N_1 \\ - b_{21}p_2(N_1)(\beta_{21}p_2(N_1) - \delta_2)/\gamma_2 N_1, \quad (6.32a)$$

we note that

$$F_1(0) = g_1(0, K_1) + b_{11}p_1'(0)\delta_1/\gamma_1 + b_{21}p_2'(0)\delta_2/\gamma_2 > 0, \quad (6.32b)$$

$$F_1(K_1) = -b_{11}p_1(K_1)(\beta_{11}p_1(K_1) - \delta_1)/K_1\gamma_1 \\ - b_{21}p_2(K_1)(\beta_{21}p_2(K_1) - \delta_2)/K_1\gamma_2 < 0, \quad (6.32c)$$

$$\text{if } \beta_{i1} p_i(K_i) - \delta_i > 0, i=1,2. \quad (6.32d)$$

Thus, N_{1a} is a positive unique solution of (6.32a) in the interval

$$0 < N_{1a} < K_1 \text{ if}$$

$$\frac{dF_1(N_1)}{dN_1} = X < 0, \quad (6.32e)$$

where

$$\begin{aligned} X = \frac{\partial g_1(N_1, K_1)}{\partial N_1} &- b_{11} \beta_{11} p_1(N_1) p'_1(N_1) / N_1 \gamma_1 - b_{21} \beta_{21} p_2(N_1) p'_2(N_1) / \gamma_2 N_1 \\ &- b_{11} (N_1 p'_1(N_1) - p_1(N_1)) (\beta_{11} p_1(N_1) - \delta_1) / \gamma_1 N_1^2 \\ &- b_{21} (N_1 p'_2(N_1) - p_2(N_1)) (\beta_{21} p_2(N_1) - \delta_2) / \gamma_2 N_1^2. \end{aligned}$$

Thus, there exists a unique positive solution $N_1 = N_{1a}$ in the interval $0 < N_{1a} < K_1$ such that $F_1(N_{1a}) = 0$, if inequalities (6.32d) and (6.32e) are satisfied.

Again from (6.31a) we note that, when $N_1 \rightarrow 0$, $N_2 \rightarrow N_{2a}$ where N_{2a} is a positive solution of

$$g_1(0, K_1) - [b_{11} p'_1(0) (\beta_{12} q_1(N_2) - \delta_1) / \gamma_1 + b_{21} p'_2(0) (\beta_{22} q_2(N_2) - \delta_2) / \gamma_2] = 0.$$

Taking

$$\begin{aligned} F_2(N_2) = g_1(0, K_1) &- [b_{11} p'_1(0) (\beta_{12} q_1(N_2) - \delta_1) / \gamma_1 \\ &+ b_{21} p'_2(0) (\beta_{22} q_2(N_2) - \delta_2) / \gamma_2], \end{aligned} \quad (6.33a)$$

we note that,

$$F_2(0) = g_1(0, K_1) + b_{11} \delta_1 p'_1(0) / \gamma_1 + b_{21} p'_2(0) \delta_2 / \gamma_2 > 0, \quad (6.33b)$$

$$\begin{aligned} F_2(K_2) = g_1(0, K_1) &- [b_{11} p'_1(0) (\beta_{12} q_1(K_2) - \delta_1) / \gamma_1 \\ &+ b_{21} p'_2(0) (\beta_{22} q_2(K_2) - \delta_2) / \gamma_2], \end{aligned} \quad (6.33c)$$

$$\frac{dF_2(N_2)}{dN_2} = -b_{11} \beta_{12} p'_1(0) q'_1(N_2) / \gamma_1 - b_{21} \beta_{22} p'_2(0) q'_2(N_2) / \gamma_2 < 0. \quad (6.33d)$$

The above analysis shows that there exists a positive unique solution $N_2 = N_{2a}$ in the interval $0 < N_{2a} < K_2$ such that $F_2(N_{2a}) = 0$ if

$$F_2(K_2) < 0, \quad (6.33e)$$

where $F_2(K_2)$ is defined in Eq. (6.33c).

Also from (6.31a) we note that $\frac{dN_2}{dN_1} < 0$ if

$$\begin{aligned} \frac{\partial g_1(N_1, K_1)}{\partial N_1} &= b_{11} \beta_{11} p'_1(N_1)/N_1 \gamma_1 - b_{21} \beta_{21} p_2(N_1) p'_2(N_1)/N_1 \gamma_2 \\ &- b_{11} f_1(N_1, N_2)(N_1 p'_1(N_1) - p_1(N_1))/N_1^2 \\ &- b_{21} f_2(N_1, N_2)(N_1 p'_2(N_1) - p_2(N_1))/N_1^2 < 0. \end{aligned} \quad (6.33f)$$

The isocline (6.31b) can be analyzed in a similar way. It may be checked that there exist two unique solutions $(N_{1b}, 0)$ and $(0, N_{2b})$ in intervals $0 < N_{1b} < K_1$ and $0 < N_{2b} < K_2$ respectively if the following inequalities hold

$$1. \beta_{12} q_1(K_2) - \delta_1 > 0, \quad \beta_{22} q_2(K_2) - \delta_2 > 0, \quad (6.34a)$$

$$2. g_2(0, K_2) - b_{12} q'_1(0)(\beta_{11} p_1(K_1) - \delta_1) - b_{22} q'_2(0)(\beta_{21} p_2(K_1) - \delta_2) < 0, \quad (6.34b)$$

$$\begin{aligned} 3. \frac{\partial g_2(N_2, K_2)}{\partial N_2} &= b_{12} f_1(0, N_2)(N_2 q'_1(N_2) - q_1(N_2))/N_2^2 \\ &- b_{12} \beta_{12} q_1(N_2) q'_1(N_2)/N_2 \gamma_1 \\ &- b_{22} f_2(0, N_2)(N_2 q'_2(N_2) - q_2(N_2))/N_2^2 \\ &- b_{22} \beta_{22} q_2(N_2) q'_2(N_2)/N_2 \gamma_2 < 0. \end{aligned} \quad (6.34c)$$

From (6.31b) we also note that $\frac{dN_2}{dN_1} < 0$ if the following holds:

$$\begin{aligned}
 \frac{\partial g_2(N_2, K_2)}{\partial N_2} &= b_{12} f_1(N_1, N_2)(N_2 q_1'(N_2) - q_1(N_2))/N_2^2 \\
 &\quad - b_{12} \beta_{12} q_1(N_2) q_1'(N_2)/N_2 \gamma_1 \\
 &\quad - b_{22} f_2(N_1, N_2)(N_2 q_2'(N_2) - q_2(N_2))/N_2^2 \\
 &\quad - b_{22} \beta_{22} q_2(N_2) q_2'(N_2)/N_2 \gamma_2 < 0.
 \end{aligned} \tag{6.34d}$$

From the above analysis it is clear that the two isoclines (6.31a) and (6.31b) intersect at a unique point (N_1^*, N_2^*) if in addition to assumptions (6.32d), (6.32e), (6.33e), (6.33f), (6.34a-d), any one of the following inequities hold:

$$1. N_{2a} > N_{2b} \text{ and } N_{1a} < N_{1b}, \tag{6.35a}$$

$$2. N_{2a} < N_{2b} \text{ and } N_{1a} > N_{1b}. \tag{6.35b}$$

Knowing the values of N_1^*, N_2^* we can compute x_1^*, x_2^* from (6.31c) and (6.31d) respectively. It may be noted that for x_1^* and x_2^* to be positive we must have respectively

$$f_i(N_1^*, N_2^*) > 0, \quad i = 1, 2. \tag{6.36}$$

Stability of equilibria

The local stability of the equilibria can be studied from variational matrices corresponding to each equilibrium. By computing the variational matrices corresponding to each equilibrium we note the following results:

1. $E_0(0, 0, 0, 0)$ is a saddle point whose stable manifold is locally in the x_1 - x_2 plane and unstable manifold is locally in the N_1 - N_2 plane.
2. $E_1(K_1, 0, 0, 0)$ is a saddle point whose stable manifold is locally in the N_1 direction and whose unstable manifold is locally in the N_2 -direction. Further, E_1 has an unstable manifold in the x_1 - x_2 plane

if

$$\beta_{11} p_1(K_1) - \delta_1 > 0,$$

$$\beta_{21} p_2(K_1) - \delta_2 > 0.$$

3. $E_2(0, K_2, 0, 0)$ is a saddle point whose stable manifold is locally in the N_2 direction and whose unstable manifold is locally in the N_1 -direction. Further, E_2 has an unstable manifold in the x_1 - x_2 plane if

$$\beta_{12} q_2(K_2) - \delta_1 > 0,$$

$$\beta_{22} q_2(K_2) - \delta_2 > 0.$$

4. $E_3(K_1, K_2, 0, 0)$ is also a saddle point with stable manifold locally in the N_1 - N_2 plane and with unstable manifold locally in the x_1 - x_2 plane if the following hold

$$\beta_{i1} p_i(K_1) + \beta_{i2} q_i(K_2) - \delta_i > 0, \quad (6.37a)$$

$$K_i \frac{\partial g_i(N_i, K_i)}{\partial N_i} - b_{1i} p'_i(N_i) x_1 - b_{2i} x_2 p_i(N_i) < 0, \quad i = 1, 2. \quad (6.37b)$$

5. $E_4(\bar{N}_1, 0, \bar{x}_1, 0)$ is a saddle point with stable manifold locally in the N_1 - x_1 plane and with unstable manifold locally in the N_2 - x_2 plane if the following hold

$$g_1(\bar{N}_1, K_1) + \bar{N}_1 \frac{\partial g_1(\bar{N}_1, K_1)}{\partial \bar{N}_1} - b_{11} \bar{x}_1 p'_1(\bar{N}_1) < 0, \quad (6.38a)$$

$$g_2(0, K_2) - b_{12} q'_1(0) x_1 < 0, \quad (6.38b)$$

$$\beta_{21} p_2(\bar{N}_1) - \delta_2 > 0. \quad (6.38c)$$

6. $E_5(\bar{N}_1, 0, 0, \bar{x}_2)$ is a saddle point with stable manifold locally in the N_1 - x_2 plane and with unstable manifold locally in the N_2 - x_1 plane if the following hold

$$g_1(\bar{N}_1, K_1) + \bar{N}_1 \frac{\partial g_1(\bar{N}_1, K_1)}{\partial \bar{N}_1} - b_{21} \bar{x}_2 p'_2(\bar{N}_1) < 0, \quad (6.39a)$$

$$g_2(0, K_2) - b_{22} q'_2(0) \bar{x}_2 > 0, \quad (6.39b)$$

$$\beta_{11} p_1(\bar{N}_1) - \delta_1 > 0. \quad (6.39c)$$

7. $E_6(0, \hat{N}_2, \hat{x}_1, 0)$ is a saddle point with stable manifold locally in $N_2 - x_1$ plane and with unstable manifold in the $N_1 - x_2$ plane if the following hold

$$g_2(\hat{N}_2, K_2) + \hat{N}_2 \frac{\partial g_2(\hat{N}_2, K_2)}{\partial \hat{N}_2} - b_{12} \hat{x}_1 q'_1(\hat{N}_2) < 0, \quad (6.40a)$$

$$g_1(0, K_1) - b_{11} p'_1(0) \hat{x}_1 > 0, \quad (6.40b)$$

$$\beta_{22} q_2(\hat{N}_2) - \delta_2 > 0. \quad (6.40c)$$

8. $E_7(0, \check{N}_2, 0, \check{x}_2)$ is a saddle point with stable manifold locally in the $N_2 - x_1$ plane and with unstable manifold locally in the $N_1 - x_1$ plane if the following hold:

$$g_2(\check{N}_2, K_2) + \check{N}_2 \frac{\partial g_2(\check{N}_2, K_2)}{\partial \check{N}_2} - b_{22} \check{x}_2 q'_2(\check{N}_2) < 0, \quad (6.41a)$$

$$g_1(0, K_1) - b_{21} p'_2(0) \check{x}_2 > 0, \quad (6.41b)$$

$$\beta_{12} q_1(\check{N}_2) - \delta_1 > 0. \quad (6.41c)$$

9. $E_8(\check{N}_1, \check{N}_2, \check{x}_1, 0)$ is locally unstable in the x_2 direction if

$$\beta_{21} p_2(\check{N}_1) + \beta_{22} q_2(\check{N}_2) - \delta_2 > 0. \quad (6.42)$$

Using the Routh-Hurwitz criteria it can be seen that E_8 has a stable manifold locally in the $N_1 - N_2 - x_1$ space if the following inequalities hold:

$$a_1 > 0, a_3 > 0 \text{ and } a_1 a_2 > a_3, \quad (6.43)$$

where

$$\begin{aligned}
 a_1 &= -(\tilde{H}_1 + \tilde{H}_2) + \gamma_1 \tilde{x}_1, \\
 a_2 &= \tilde{H}_1 \tilde{H}_2 - (\tilde{H}_1 + \tilde{H}_2) \gamma_1 \tilde{x}_1 + b_{12} \beta_{12} \tilde{x}_1 q_1(\tilde{N}_2) q'_1(\tilde{N}_2) \\
 &\quad + b_{11} \beta_{11} \tilde{x}_1 p_1(\tilde{N}_1) p'_1(\tilde{N}_1), \\
 a_3 &= \tilde{H}_1 \tilde{H}_2 \gamma_1 \tilde{x}_1 - H_1 b_{12} \beta_{12} \tilde{x}_1 q_1(\tilde{N}_2) q'_1(\tilde{N}_2) - H_2 b_{11} \beta_{11} \tilde{x}_1 p_1(\tilde{N}_1) p'_1(\tilde{N}_1), \\
 \tilde{H}_1 &= g_1(\tilde{N}_1, K_1) + \tilde{N}_1 \frac{\partial g_1(\tilde{N}_1, K_1)}{\partial \tilde{N}_1} - b_{11} \tilde{x}_1 p'_1(\tilde{N}_1), \\
 \tilde{H}_2 &= g_2(\tilde{N}_2, K_2) + \tilde{N}_2 \frac{\partial g_2(\tilde{N}_2, K_2)}{\partial \tilde{N}_2} - b_{12} \tilde{x}_1 q'_1(\tilde{N}_2).
 \end{aligned}$$

It may be noted here that

$$\text{if } \tilde{H}_i < 0, \quad i=1,2, \text{ then } a_j > 0, \quad j=1,2,3. \quad (6.44)$$

10. $E_9(\tilde{N}_1, \tilde{N}_2, 0, \tilde{x}_2)$ is locally unstable in the x_1 -direction if

$$\beta_{11} p_1(\tilde{N}_1) + \beta_{12} q_1(\tilde{N}_2) - \delta_1 > 0. \quad (6.45a)$$

Using the Routh-Hurwitz criteria it can be seen that E_9 has a stable manifold in the $N_1 - N_2 - x_2$ space if the following inequalities hold:

$$a_{11} > 0, \quad a_{13} > 0, \quad a_{11} a_{12} > a_{13}, \quad (6.45b)$$

where

$$\begin{aligned}
 a_{11} &= -(\tilde{H}_1 + \tilde{H}_2) + \gamma_2 \tilde{x}_2, \\
 a_{12} &= \tilde{H}_1 \tilde{H}_2 - (\tilde{H}_1 + \tilde{H}_2) \gamma_2 \tilde{x}_2 + b_{22} \beta_{22} \tilde{x}_2 q_2(\tilde{N}_2) q'_2(\tilde{N}_2) + b_{21} \beta_{21} \tilde{x}_2 p_2(\tilde{N}_1) p'_2(\tilde{N}_1), \\
 a_{13} &= \tilde{H}_1 \tilde{H}_2 \gamma_2 \tilde{x}_2 + \tilde{H}_1 b_{22} \beta_{22} \tilde{x}_2 q_2(\tilde{N}_2) q'_2(\tilde{N}_2) - \tilde{H}_2 b_{21} \beta_{21} \tilde{x}_2 p_2(\tilde{N}_1) p'_2(\tilde{N}_1), \\
 \tilde{H}_1 &= g_1(\tilde{N}_1, K_1) + \tilde{N}_1 \frac{\partial g_1(\tilde{N}_1, K_1)}{\partial \tilde{N}_1} - b_{21} \tilde{x}_2 p'_2(\tilde{N}_1), \\
 \tilde{H}_2 &= g_2(\tilde{N}_2, K_2) + \tilde{N}_2 \frac{\partial g_2(\tilde{N}_2, K_2)}{\partial \tilde{N}_2} - b_{22} \tilde{x}_2 q'_2(\tilde{N}_2).
 \end{aligned}$$

It may be noted here that

$$a_{1j} > 0 \quad (j=1,2,3) \text{ if } H_1 < 0, \quad i = 1,2. \quad (6.45c)$$

11. $E_{10}(N_{11}, 0, x_{11}, x_{21})$ is locally asymptotically stable if the following inequalities hold:

$$H_{21} < 0, \quad a_{21} > 0, \quad a_{23} > 0 \text{ and } a_{21}a_{22} > a_{23}, \quad (6.46)$$

where $H_{21} = g_2(0, K_2) - b_{12}x_{11}q'_1(0) - b_{22}x_{21}q'_2(0)$,

$$a_{21} = -H_{11} + \gamma_1 x_{11} + \gamma_2 x_{21},$$

$$a_{22} = \gamma_1 \gamma_2 x_{11} x_{21} - \gamma_2 H_{11} (x_{11} + x_{21}) + b_{11} \beta_{11} x_{11} p'_1(N_{11}) p'_1(N_{11}) \\ + b_{21} \beta_{21} x_{21} p'_2(N_{11}) p'_2(N_{11}),$$

$$a_{23} = -H_{11} \gamma_1 \gamma_2 x_{11} x_{21} + b_{11} \beta_{11} \gamma_2 x_{11} x_{21} p'_1(N_{11}) p'_1(N_{11}) \\ + b_{21} \beta_{21} x_{11} x_{21} \gamma_1 p'_2(N_{11}) p'_2(N_{11}),$$

$$H_{11} = g_1(N_{11}, K_1) + N_{11} \frac{\partial g_1(N_{11}, K_1)}{\partial N_1} - b_{11} x_{11} p'_1(N_{11}) - b_{21} x_{21} p'_2(N_{11}).$$

It may be noted that if $H_{11} < 0$, then $a_{2j} > 0$, ($j = 1,2,3$).

Further, if $H_{21} > 0$, then E_{10} is locally unstable in the N_2 -direction.

12. $E_{11}(0, N_{22}, x_{12}, x_{22})$ is locally asymptotically stable if the following inequalities hold:

$$H_{12} < 0, \quad a_{31} > 0, \quad a_{33} > 0, \quad a_{31}a_{32} > a_{33}, \quad (6.47)$$

where $H_{12} = g_1(0, K_1) - b_{11}x_{12}p'_1(0) - b_{21}x_{22}p'_2(0)$, (6.48)

$$a_{31} = -H_{22} + \gamma_1 x_{12} + \gamma_2 x_{22},$$

$$a_{32} = \gamma_1 \gamma_2 x_{12} x_{22} - H_{22} (\gamma_1 x_{12} + \gamma_2 x_{22}) + b_{12} \beta_{12} x_{11} q_1(N_{22}) q'_1(N_{22}) \\ + b_{22} \beta_{22} x_{22} q_2(N_{22}) q'_2(N_{22}),$$

$$a_{33} = -H_{22} \gamma_1 \gamma_2 x_{12} x_{22} + b_{12} \beta_{12} \gamma_2 x_{12} x_{22} q_1(N_{22}) q'_1(N_{22}) \\ + b_{22} \beta_{22} x_{12} x_{22} q_2(N_{22}) q'_2(N_{22}),$$

$$H_{22} = g_2(N_{22}, K_2) + N_{22} \frac{\partial g_2(N_{22}, K_2)}{\partial N_2} - b_{12} x_{12} q'_1(N_{22}) - b_{22} x_{22} q'_2(N_{22}). \quad (6.49)$$

It may be noted that if $H_{22} < 0$, then $a_{3j} > 0$ ($j=1,2,3$). Further,

if $H_{12}^* > 0$, then E_{11}^* is locally unstable in the N_1 -direction.

In the following theorem we are able to find sufficient conditions for E^* to be locally asymptotically stable.

Theorem 6.2.1 In addition to assumptions (6.3)-(6.5), let the following inequalities hold:

$$H_2^* = g_2(N_2^*, K_2) + N_2^* \frac{\partial g_2(N_2^*, K_2)}{\partial N_2} - b_{12} x_1^* q_1'(N_2^*) - b_{22} x_2^* q_2'(N_2^*) < 0, \quad (6.50a)$$

$$\left(k_3 x_2^* \beta_{22} q_2'(N_2^*) + k_1 b_{22} q_2'(N_2^*) \right)^2 < -k_1 k_3 H_2^* \gamma_2, \quad (6.50b)$$

$$\text{where } k_1 = \frac{k_2 x_1 \beta_{12} q_1'(N_2^*)}{b_{12} q_1(N_2^*)}, \quad k_2 = \frac{b_{11} p_1(N_1^*)}{x_1^* \beta_{11} p_1'(N_1^*)}, \quad k_3 = \frac{b_{21} p_2(N_1^*)}{x_2^* \beta_{21} p_2'(N_1^*)}. \quad (6.50c)$$

Then E^* is locally asymptotically stable.

Proof : Linearizing system (6.6) by substituting

$$N_1 = N_1^* + n_1, \quad N_2 = N_2^* + n_2, \quad x_1 = x_1^* + X_1, \quad x_2 = x_2^* + X_2$$

and using the following Liapunov function

$$U(n_1, n_2, X_1, X_2) = \frac{1}{2} \left(n_1^2 + k_1 n_2^2 + k_2 X_1^2 + k_3 X_2^2 \right),$$

where the k_j 's ($j=1,2,3$) are defined in (6.50c), it can be checked that the time derivative of U along the solutions of system (6.6) under conditions (6.50a,b) is negative definite, proving the theorem.

In the following theorem we are able to write down conditions which guarantee that F^* is globally asymptotically stable. We first state the following lemma which establishes a region of attraction for system (6.6). The proof of the lemma is easy and hence is omitted.

Lemma 6.2.1: The set

$$\Omega = \{(N_1, N_2, x_1, x_2) : 0 \leq N_1 \leq K_1, 0 \leq x_i \leq L_i / \gamma_i, i = 1, 2\} \quad (6.51)$$

is a region of attraction for all solutions initiating in the interior of the positive orthant, where

$$L_i = \beta_{i1} p_i(K_1) + \beta_{i2} q_i(K_2) - \delta_i > 0. \quad (6.51a)$$

Theorem 6.2.2 In addition to assumptions (6.3)-(6.5), let $g_i(N_i, K_i)$, $p_i(N_1)$, $q_i(N_2)$ satisfy the following conditions in Ω

$$G_{mi} \leq - \frac{\partial g_i(N_i, K_i)}{\partial N_i} \leq G_{Mi}, \quad 0 \leq p'_i(N_1) \leq \rho_i, \quad 0 \leq q'_i(N_2) \leq \theta_i, \quad i=1,2 \quad (6.52)$$

for some positive constants G_{mi} , G_{Mi} , ρ_i , θ_i , ($i=1,2$). If the following inequality holds

$$\{c_3 \beta_{22} \theta_2 + c_1 b_{22} q_2(N_2^*)/N_2^*\}^2 < c_1 c_3 \gamma_2 G_{m2}, \quad (6.53a)$$

$$\text{where } c_1 = \frac{c_2 \beta_{12} \theta_1 N_2^*}{b_{12} q_1(N_2^*)}, \quad c_2 = \frac{b_{11} p_1(N_1^*)}{\beta_{11} \rho_1 N_1^*}, \quad c_3 = \frac{b_{21} p_2(N_1^*)}{\beta_{21} \rho_2 N_1^*}, \quad (6.53b)$$

then E^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

Proof: We consider the following positive definite function around E^* ,

$$\begin{aligned} V(N_1(t), N_2(t), x_1(t), x_2(t)) &= N_1^* - N_1 - N_1 \ln(N_1^*/N_1) \\ &+ c_1 (N_2 - N_2^* - N_2^* \ln(N_2/N_2^*)) + c_2 (x_1 - x_1^* - x_1^* \ln(x_1/x_1^*)) \\ &+ c_3 (x_2 - x_2^* - x_2^* \ln(x_2/x_2^*)). \end{aligned} \quad (6.54)$$

Differentiating V with respect to t along the solutions of (6.6) we get after some algebraic manipulation

$$\begin{aligned} \dot{V} &\leq -\lambda_1(N_1)(N_1 - N_1^*)^2 - c_1 \lambda_2(N_2)(N_2 - N_2^*)^2 - c_2 \gamma_1 (x_1 - x_1^*)^2 - c_3 \gamma_2 (x_2 - x_2^*)^2 \\ &+ (c_2 \beta_{11} \mu_1(N_1) - b_{11} p_1(N_1^*)/N_1^*) (N_1 - N_1^*)(x_1 - x_1^*) \\ &+ (c_3 \beta_{21} \mu_2(N_1) - b_{21} p_2(N_2^*)/N_2^*) (N_1 - N_1^*)(x_2 - x_2^*) \\ &+ (c_2 \beta_{12} \xi_1(N_2) - c_1 b_{12} q_1(N_2^*)/N_2^*) (N_2 - N_2^*)(x_1 - x_1^*) \\ &+ (c_3 \beta_{22} \xi_2(N_2) - c_1 b_{22} q_2(N_2^*)/N_2^*) (N_2 - N_2^*)(x_2 - x_2^*), \end{aligned} \quad (6.55a)$$

where

$$\lambda_i(N_i) = \begin{cases} - \left[\frac{g_i(N_i, K_i) - g_i(N_i^*, K_i)}{N_i - N_i^*} \right], & N_i \neq N_i^* \\ - \frac{\partial g_i(N_i, K_i)}{\partial N_i}, & N_i = N_i^* \end{cases},$$

$$\mu_i(N_1) = \begin{cases} \frac{p_i(N_1) - p_i(N_1^*)}{N_1 - N_1^*}, & N_1 \neq N_1^* \\ p_i'(N_1), & N_1 = N_1^* \end{cases},$$

$$\xi_i(N_2) = \begin{cases} \frac{q_i(N_2) - q_i(N_2^*)}{N_2 - N_2^*}, & N_2 \neq N_2^* \\ q_i'(N_2), & N_2 = N_2^* \end{cases}.$$

We note from (6.52a) and the mean value theorem that,

$$G_{mi} \leq |\lambda_i(N)| \leq G_{Mi}, \quad 0 \leq |\mu_i(N_1)| \leq \rho_i, \quad 0 \leq |\xi_i(N_2)| \leq \theta_i; \quad i = 1, 2. \quad (6.55b)$$

Now \dot{V} can further be written as the sum of quadratics,

$$\begin{aligned} \dot{V} \leq & -\frac{1}{2} a_{11} (N_1 - N_1^*)^2 + a_{12} (N_1 - N_1^*)(x_1 - x_1^*) - \frac{1}{2} a_{33} (x_1 - x_1^*)^2 \\ & - \frac{1}{2} a_{11} (N_1 - N_1^*)^2 + a_{14} (N_1 - N_1^*)(x_2 - x_2^*) - \frac{1}{2} a_{44} (x_2 - x_2^*)^2 \\ & - \frac{1}{2} a_{22} (N_2 - N_2^*)^2 + a_{23} (N_2 - N_2^*)(x_1 - x_1^*) - \frac{1}{2} a_{33} (x_1 - x_1^*)^2 \\ & - \frac{1}{2} a_{22} (N_2 - N_2^*)^2 + a_{24} (N_2 - N_2^*)(x_2 - x_2^*) - \frac{1}{2} a_{44} (x_2 - x_2^*)^2, \end{aligned} \quad (6.56)$$

$$\text{where } a_{11} = \lambda_1(N_1), \quad a_{22} = c_1 \lambda_2(N_2), \quad a_{33} = c_2 \gamma_1, \quad a_{44} = c_3 \gamma_2, \quad (6.57a)$$

$$a_{13} = c_2 \beta_{11} \mu_1(N_1) - b_{11} p_1(N_1^*)/N_1^*, \quad (6.57b)$$

$$a_{14} = c_3 \beta_{21} \mu_2(N_1) - b_{21} p_2(N_1^*)/N_1^*, \quad (6.57c)$$

$$a_{23} = c_2 \beta_{12} \xi_1(N_2) - c_1 b_{12} q_1(N_2^*)/N_2^*, \quad (6.57d)$$

$$a_{24} = c_3 \beta_{22} \xi_2(N_2) - c_1 b_{22} q_2(N_2^*)/N_2^*. \quad (6.57e)$$

Sufficient conditions for \dot{V} to be negative definite are that the following inequalities hold:

$$a_{13}^2 < a_{11} a_{33}, \quad (6.58a)$$

$$a_{14}^2 < a_{11} a_{44}, \quad (6.58b)$$

$$a_{23}^2 < a_{22} a_{33}, \quad (6.58c)$$

$$a_{24}^2 < a_{22} a_{44}. \quad (6.58d)$$

We note that in Eq. (6.53a) the values of c_1 , c_2 and c_3 are such that conditions (6.58a-c) are automatically satisfied. Further (6.53a) \Rightarrow (6.58d), we conclude that \dot{V} is a Liapunov function with respect to E^* whose domain contains the region Ω , proving the theorem.

The above analysis shows that both the prey and predator species settle down to their respective equilibrium levels under certain conditions. It has been noted that the interspecific interference coefficient of either predator species plays a crucial role in stabilizing the interior equilibrium.

6.3 THE MODEL WITH DIFFUSION

In this section we consider the complete model (6.1) together with initial and boundary conditions (6.2). We observe that $N_i = N_i^*$, $x_i = x_i^*$ ($i=1,2$) is the uniform steady state for system (6.1a)-(6.1b). We state the main results of this section in the form of the following theorem.

Theorem 6.3.1

(i) If E^* is asymptotically stable for system (6.6) then the corresponding steady state is also asymptotically stable for system (6.1)-(6.2).

(ii) If the equilibrium E^* of model (6.6) is unstable, then sufficiently rapid diffusion by the prey species N_1 and N_2 will stabilize the unstable equilibrium E^* .

Proof : Consider the following Liapunov function

$$W(N_1(t), N_2(t), x_1(t), x_2(t)) = \iint_R V(N_1(u, v, t), N_2(u, v, t), x_1(u, v, t), x_2(u, v, t)) \, dA, \quad (6.59)$$

where V is defined in Eq.(6.54).

Now the time derivative of W along the solutions of model (6.1a)-(6.1b) is given by

$$\begin{aligned} \dot{W}(N_1(t), N_2(t), x_1(t), x_2(t)) &= \iint_R \left(\frac{\partial V}{\partial N_1} \frac{\partial N_1}{\partial t} + \frac{\partial V}{\partial N_2} \frac{\partial N_2}{\partial t} + \frac{\partial V}{\partial x_1} \frac{\partial x_1}{\partial t} + \frac{\partial V}{\partial x_2} \frac{\partial x_2}{\partial t} \right) dA \\ &= I_1 + I_2, \end{aligned} \quad (6.60)$$

where

$$I_1 = \iint_R \dot{V}(N_1(u, v, t), N_2(u, v, t), x_1(u, v, t), x_2(u, v, t)) \, dA, \quad (6.61a)$$

$$I_2 = \iint_R \left(D_1 \frac{\partial V}{\partial N_1} \nabla^2 N_1 + D_2 \frac{\partial V}{\partial N_2} \nabla^2 N_2 + d_1 \frac{\partial V}{\partial x_1} \nabla^2 x_1 + d_2 \frac{\partial V}{\partial x_2} \nabla^2 x_2 \right) dA. \quad (6.61b)$$

Under an analysis similar to chapter III, \dot{W} can be estimated as

$$\begin{aligned} \dot{W}(N_1(t), N_2(t), x_1(t), x_2(t)) &\leq \iint_R \dot{V}(N_1(u, v, t), N_2(u, v, t), x_1(u, v, t), x_2(u, v, t)) \, dA \\ &\quad - \sum_{i=1,2} \left[\frac{D_i N_i^*}{K_i^2} \iint_R \left\{ \left(\frac{\partial N_i}{\partial u} \right)^2 + \left(\frac{\partial N_i}{\partial v} \right)^2 \right\} \right. \\ &\quad \left. + \frac{d_i x_i^* y_i^2}{(\beta_{i1} p_i(K_1) + \beta_{i2} q_i(K_2) - \delta_i)^2} \iint_R \left\{ \left(\frac{\partial x_i}{\partial u} \right)^2 + \left(\frac{\partial x_i}{\partial v} \right)^2 \right\} \right] dA. \end{aligned} \quad (6.62)$$

From (6.62) we note that if $\dot{V} \leq 0$, then $\dot{W} \leq 0$. This implies that if E^* is asymptotically stable for system (6.6), then the uniform steady state E^* of system (6.1a)-(6.1b) is also asymptotically stable. From (6.62) we also note that if \dot{V} is positive definite, then by increasing D_i , d_i ($i=1,2$), \dot{W} can be made negative definite. This shows that if the interior equilibrium E^* of model (6.6) is unstable, then by increasing D_i and d_i , ($i=1,2$) to sufficiently large values, the unstable equilibrium can be made stable. Hence the theorem follows.

If we consider the region R to be a rectangular habitat given by

$$R = \{(u,v): 0 \leq u \leq a, 0 \leq v \leq b\},$$

then under an analysis similar to chapter III, \dot{W} can be estimated as

$$\begin{aligned} \dot{W} \leq \iint_R \dot{V} \, dA - \iint_R \left[\frac{(a^2 + b^2)\pi^2}{a^2 b^2} \left(\frac{D_1 N_1^*}{K_1^2} (N_1 - N_1^*)^2 + \frac{D_2 N_2^*}{K_2^2} (N_2 - N_2^*)^2 \right. \right. \\ \left. \left. + \frac{d_1 x_1^* \gamma_1^2}{(\beta_{11} p_1(K_1) + \beta_{12} q_1(K_2) - \delta_1)^2} (x_1 - x_1^*)^2 \right. \right. \\ \left. \left. + \frac{d_2 x_2^* \gamma_2^2}{(\beta_{21} p_2(K_1) + \beta_{22} q_2(K_2) - \delta_2)^2} (x_2 - x_2^*)^2 \right) \right] dA. \quad (6.63) \end{aligned}$$

This shows that if the interior equilibrium E^* of model (6.6) is globally asymptotically stable, then the uniform steady state of the initial-boundary-value-problem (6.1a)-(6.1b) is also globally asymptotically stable. We further note that even if \dot{V} is positive definite, i.e. E^* is unstable in the absence of diffusion, then by increasing the diffusion coefficients to sufficiently large values \dot{W} can be made negative definite.

6.4 SIMULATION ANALYSIS

In this section a numerical example is presented to explain the applicability of the results discussed in section 6.2. we take the particular form of the functions as given in Eq.(6.5).

We choose the following values of parameters in model (6.1) and in Eq. (6.5):

$$\begin{aligned} r_1 &= 5.0, K_1 = 15.0, b_{11} = 0.1, b_{21} = 0.2, \\ r_2 &= 5.5, K_2 = 10.0, b_{12} = 0.2, b_{22} = 0.4, \\ \beta_{11} &= 2.5, \beta_{12} = 3.0, \delta_1 = 1.0, \gamma_1 = 1.5, \\ \beta_{21} &= 1.5, \beta_{22} = 2.5, \delta_2 = 1.0, \gamma_2 = 2.0. \end{aligned}$$

With the above set of values of parameters, it can be seen that the criteria for the existence of the interior equilibrium E^* are satisfied. Our numerical computation shows that E^* is given by

$$N_1^* = 7.40178, N_2^* = 0.79002, x_1^* = 13.2496, x_2^* = 6.03886.$$

It can be checked that conditions (6.50) in Theorem 6.2.1 are satisfied. This shows that E^* is locally asymptotically stable.

It can also be verified that condition (6.53a) in Theorem 6.2.2 is satisfied which shows that E^* is globally stable.

6.5 SUMMARY

In this chapter a mathematical model has been presented to study the effect of competition of two predator species for two resource prey in a diffusive system. It has been assumed that the dynamics of the prey species follow generalized logistic equations and the dynamics of predators species are governed by general functional responses. In the absence of diffusion, criteria for local stability, instability and global stability of the interior equilibrium of the system have been obtained. It has been noted that global behavior of the interior equilibrium depends on the intraspecific interference coefficient of both predator species. It has also been noted that global stability of the interior equilibrium depends on the specific growth rate of both of the prey species. It has also been shown that diffusion stabilizes the otherwise unstable equilibrium. It has been further noted that increasing diffusion coefficients of the predator and prey species to sufficiently large values, an unstable interior equilibrium can be stabilized.

CHAPTER VII

A PREDATOR-PREY INTERACTION MODEL WITH SELF AND CROSS-DIFFUSION

7.0 INTRODUCTION

In recent years there has been considerable interest to investigate the stability behavior of a system of interacting populations by taking into account the effect of self as well as cross-diffusion (Gurtin (1974), Jorne (1975), Freedman (1976), Gatto and Rinaldi (1977), Jorn and Carmi (1977), Hastings (1978b), Okubo (1980), Shukla and Verma (1981), Chattopadhyay et al. (1996)). In most of these studies, models for interacting populations are of Lotka-Volterra type, and the general interaction with functional response has not been studied. Although there has been some investigations of a general predator-prey system without diffusion where interesting stability criteria have been found depending on the nature of growth and the functional response (Rosenzweig and MacArthur (1963), Freedman (1976), Goh (1976), Hsu (1978)). In particular, Goh (1976) established sufficient conditions for global stability in a Lotka-Volterra model of two species interactions. Freedman (1976) explained the stability of the equilibrium of a two-dimensional mathematical model for predator-prey interactions by using a graphical method (Rosenzweig and MacArthur (1963)). Hsu (1978) proposed two criteria for global stability of the equilibrium of a predator-prey model to make the graphical method of Rosenzweig and MacArthur more significant. Gatto and Rinaldi (1977) studied the stability properties of the non-trivial equilibrium of a generalized Lotka-Volterra model using Liapunov's method. The global stability of two species is also

discussed in detail by some other researchers (Goh (1978), Hastings (1978), Kazarinoff and van den Driessche (1978) Harrison (1979), Cheng et al. (1981)). Hastings (1978) derived sufficient conditions for global stability in n -species Lotka-Volterra systems with diffusion. Freedman and Shukla (1989) extended the two dimensional predator-prey system to three dimensions by considering the influence of an additional resource term and investigated the effect of self-diffusion. Mimura and Murray (1978) showed that when the diffusion of prey is small compared with that of the predator, then stable heterogeneity can persist indefinitely. However, if the diffusion of both species is sufficiently large then there can be no spatial structure within a bounded region, the faster a species moves around the less chance it has of staying in a locality long enough to make its presence felt there. Recently, Takeuchi and Lu (1995) considered a diffusive competitive Lotka-Volterra model, and studied the permanence and global stability of the system. But in all these studies, little attention has been paid in studying the effect of cross-diffusion (Gurtin (1974), Jorne (1975), Shukla and Verma (1981), Pao (1995a,b), Chattopadhyay et al. (1996)). In particular, Gurtin (1974) investigated the effect of self and cross-diffusion in population dynamics and showed that the effect of cross-diffusion may give rise to the segregation of the two species. Shukla and Verma (1981) showed that the cross-diffusion of species may lead to stability depending upon the nature and the magnitudes of the self and cross-diffusion coefficients. Pao (1995a,b) studied the reaction diffusion equations with nonlocal boundary and initial conditions. Chattopadhyay et al. (1996) showed that the critical wave length is just sufficient to drive a system into local instability. Segal and

Jackson (1972) were the first to draw attention to this fact and they presented an example of a predator-prey interaction. Kuznetsov et al. (1994) presented a mathematical model of cross-diffusion type with two interacting components qualitatively describing spatial-temporal dynamics of a mixed-age mono-species forest. But the general predator-prey system with self and cross-diffusion has not been investigated. The prey species may tend to diffuse away from its exploiter and the predator may tend to move towards the lower concentration of the victims in search of easy catch in the absence of strong group defence by the latter. Thus, the diffusion of the prey may affect the growth of the predator and visa versa. The main purpose of this chapter is to examine the stability behavior of a modified Gause-type model of a predator-prey interacting system by taking into account self as well as cross-diffusion.

The model considered in this chapter reduces to Hsu (1978) in the absence of diffusion. Then we consider the effect of self and cross-diffusion on the predator-prey interaction. We also investigate the effect of critical wave length on the stability of two species. Following the construction of a suitable Liapunov function (La Salle and Lefschetz (1961)), the global behavior of the system is also examined.

7.1 MATHEMATICAL MODEL

In nature the tendency of the prey would be to keep away from predators and hence the escape velocity of the prey may be taken as proportional to the dispersive velocity of predators. Also, the tendency of predators would be to get closer to the prey and hence the chase velocity of predators may be considered to be proportional to the

dispersive velocity of the prey. Thus prey-predator model with self and cross-diffusion can be written as

$$\begin{aligned}\frac{\partial x}{\partial t} &= xg(x) - yp(x) + D_{11} \frac{\partial^2 x}{\partial u^2} + D_{12} \frac{\partial^2 y}{\partial u^2}, \\ \frac{\partial y}{\partial t} &= y(-q(x) + cp(x)) + D_{22} \frac{\partial^2 y}{\partial u^2} + D_{21} \frac{\partial^2 x}{\partial u^2}.\end{aligned}\quad (7.1)$$

Model (7.1) needs to be analyzed with the initial populations

$$x(u,0) > 0, y(u,0) > 0. \quad (7.2)$$

We also assume that no external input is imposed from outside.

Hence zero flux boundary conditions

$$\left. \frac{\partial x}{\partial u} \right|_{u=0,R} = \left. \frac{\partial y}{\partial u} \right|_{u=0,R} = 0 \quad (7.3)$$

are assumed.

In model (7.1), $x(u,t)$ and $y(u,t)$ represent the prey and predator population density respectively at time t .

The function $g(x)$ represents the specific growth rate of the prey in the absence of any predator and it satisfies

$$g(0) > 0, \text{ and } g'(x) \leq 0 \text{ for } x \geq 0,$$

and there exists a $K > 0$, called the carrying capacity of the environment, such that

$$g(K) = 0. \quad (7.4)$$

The function $p(x)$ is the predator response function for the predator with respect to that particular prey. We assume

$$p(0) = 0, p'(x) > 0 \text{ for } x \geq 0. \quad (7.5)$$

The death rate $q(x)$, which depends on the prey population, is assumed to satisfy

$$q(0) = q_0 > 0, q'(x) \leq 0 \text{ for } x \geq 0, \lim_{x \rightarrow \infty} q(x) = q_\infty > 0. \quad (7.6)$$

D_{11} , D_{22} are the self-diffusion coefficients and D_{12} , D_{21} are the cross-diffusion coefficients of prey and predator respectively in a

finite one-dimensional domain (u).

7.2 THE MODEL WITHOUT DIFFUSION

In this section we consider model (7.1) without diffusion (i.e. $D_{11} = D_{22} = D_{12} = D_{21} = 0$). In such a case the model reduces to

$$\begin{aligned}\dot{x} &= xg(x) - yp(x), \\ \dot{y} &= y(-q(x) + cp(x)), \\ x(0) &> 0, y(0) > 0.\end{aligned}\tag{7.7}$$

There are three equilibria, namely $E_0(0,0)$, $E_1(K,0)$ and $E^*(x^*,y^*)$. The last one exists (Hsu (1978)) and is in the first quadrant if there exists x^* with $0 < x^* < K$, such that

$$cp(x^*) = q(x^*).\tag{7.8a}$$

We then have

$$y^* = \frac{x^*g(x^*)}{p(x^*)}.\tag{7.8b}$$

By computing the variational matrices (Freedman (1987)) corresponding to E_0 and E_1 , it can be checked that E_0 is a saddle point with stable manifold locally in the y-direction and unstable manifold locally in the x-direction. E_1 is also a saddle point with stable manifold in the x-direction and unstable manifold locally in the y-direction. We state the following results from Hsu (1978).

Let

$$H(x^*) = x^*g'(x^*) + g(x^*) - y^*p'(x^*),\tag{7.9}$$

which is the trace of the variational matrix corresponding to $E^*(x^*,y^*)$, and

$$V(x,y) = \int_{x^*}^{x(u,t)} \left(\frac{-q(\xi) + cp(\xi)}{p(\xi)} \right) d\xi + y(u,t) - y^* - y^* \ln \frac{y(u,t)}{y^*},\tag{7.10}$$

which is our Liapunov function.

Theorem 7.2.1

(i) If $H(x^*) < 0$, then $E^*(x^*, y^*)$ is locally asymptotically stable.

(ii) If $H(x^*) > 0$, then $E^*(x^*, y^*)$ is unstable.

Lemma 7.2.1 The solutions of (7.7) are positive and bounded, and furthermore, there exists a $T \geq 0$ such that $x(t) < K$ for $t \geq T$.

Theorem 7.2.2 If $\left(\frac{xg(x)}{p(x)} - y^* \right) (x - x^*) \leq 0$, then $E^*(x^*, y^*)$ is globally asymptotically stable in the positive quadrant.

In the next section we shall investigate the effect of diffusion on the prey-predator model (7.1).

7.3 THE MODEL WITH DIFFUSION

In this section we consider the full model (7.1) together with initial and boundary conditions (7.2) and (7.3). As a consequence of initial-boundary conditions (7.2)-(7.3), $E^*(x^*, y^*)$ is a uniform steady state for this system.

We now investigate the stability conditions for system (7.1)-(7.3) in different environmental consequences and show that the critical wave length, which is given by $l = R/n\pi$, where R is the length of the system and $2\pi/n$ is the period, plays a crucial role for instability.

With the boundary conditions under consideration, we look for eigenfunctions of the form

$$\sum_{n=0}^{\infty} \begin{pmatrix} a_n \\ b_n \end{pmatrix} \exp(\lambda t) \cos\left(\frac{n\pi u}{R}\right), \quad (7.11a)$$

and thus for solutions, of the linearized system, of the form

$$\begin{pmatrix} A \\ B \end{pmatrix} \exp(\lambda t) \cos\left(\frac{n\pi u}{R}\right). \quad (7.11b)$$

Then the characteristic equation of the system is given by

$$\lambda^2 + \sigma_1 \lambda + \sigma_2 + a\rho_1 - b\rho_2 - \rho_1\rho_2 = 0, \quad (7.12)$$

where

$$\sigma_1 = -H(x^*) + (D_{11} + D_{22}) \frac{n^2 \pi^2}{R^2}, \quad (7.13a)$$

$$\sigma_2 = \left\{ -q'(x^*) + cp'(x^*) \right\} p(x^*) y^* + \left\{ -H(x^*) + D_{11} \frac{n^2 \pi^2}{R^2} \right\} D_{22} \frac{n^2 \pi^2}{R^2}, \quad (7.13b)$$

$$\rho_1 = \frac{n^2 \pi^2}{R^2} D_{12}', \quad (7.13c)$$

$$\rho_2 = \frac{n^2 \pi^2}{R^2} D_{21}', \quad (7.13d)$$

$$a = (-q'(x^*) + cp'(x^*)) y^* > 0, \quad (7.13e)$$

$$b = p(x) > 0. \quad (7.13f)$$

We note that if $H(x^*) < 0$, then $\sigma_1 > 0$ and $\sigma_2 > 0$. Thus from the Routh-Hurwitz criteria, the stability of the equilibrium E^* depends on the sign of

$$\sigma_2 + a\rho_1 - b\rho_2 - \rho_1\rho_2. \quad (7.14)$$

We shall discuss the following cases under the assumption that $H(x^*) < 0$.

Case I: $D_{12} = 0$ and $D_{21} \neq 0$.

Then $E^*(x^*, y^*)$ is locally stable if

$$\sigma_2 - bD_{21} n^2 \pi^2 / R^2 > 0,$$

$$\text{i.e. } R^2 / n^2 \pi^2 > bD_{21} / \sigma_2 \text{ for all } n \geq 0. \quad (7.15a)$$

We note that if $D_{21} < 0$, then (7.15a) is automatically satisfied.

This shows that if the predator species tends to diffuse in the direction of higher concentration of the prey species, and the prey species moves along its own concentration gradient, then the equilibrium E^* remains locally asymptotically stable. This situation is a usual phenomenon in nature.

If $D_{21} > 0$, E^* is unstable, there always exist values of n such that

$$R^2/n^2\pi^2 < bD_{21}/\sigma_2. \quad (7.15b)$$

This shows that when the critical wave length is too small that the predator species tends to diffuse in the direction of lower concentration of the prey species, and the prey species moves along its own concentration gradient, then the equilibrium state E^* becomes unstable. Such a case arises in nature where the predator prefers to avoid group defense by a large number of prey and chooses to catch its prey from a smaller group unable to sufficiently resist.

Remark 1: Let $H(x^*) > 0$. Then from Theorem 7.2.1, we note that the interior equilibrium $E^*(x^*, y^*)$ of model (7.7) is unstable. Then in case I (i.e. $D_{12} = 0$, $D_{21} \neq 0$), the unstable equilibrium E^* will be stable if the following inequalities hold:

$$\sigma_1 > 0, \quad (7.16a)$$

$$\sigma_2 - b\rho_2 > 0. \quad (7.16b)$$

It may be noted that if $D_{21} < 0$, then by increasing D_{11} to a large value, so that $-H(x^*) + D_{11} \frac{n^2\pi^2}{R^2} > 0$, inequalities (7.16a) and (7.16b) are satisfied.

Case II: $D_{12} \neq 0$ and $D_{21} = 0$.

Then $E^*(x^*, y^*)$ is locally stable if

$$(R^2/n^2\pi^2) + (aD_{12}/\sigma_2) > 0 \quad \text{for all } n \geq 0. \quad (7.17a)$$

We note that if $D_{12} > 0$, then (7.17a) is satisfied. This implies that if the prey species moves in the direction of lower concentration of the predator species, and the predator species moves along its own concentration gradient, then the equilibrium E^* remains locally asymptotically stable. This situation can be compared in nature where the prey moves towards the lower concentration of the predator in search of new food.

But $E^*(x^*, y^*)$ is unstable if $D_{12} < 0$, since there always exist values of n such that

$$R^2/n^2\pi^2 < -aD_{12}/\sigma_2. \quad (7.17b)$$

This shows that when the critical wave length is so small that the prey species moves towards the higher concentration of the predator species and the predator species moves along its own concentration gradient, then the equilibrium state which is stable without self and cross-diffusion becomes unstable. This situation can be compared in nature where the predator attracts the prey towards itself as a predation technique and the suicidal tendencies among the prey exist.

Remark 2: Let $H(x^*) > 0$. Then the interior equilibrium E^* of model (7.7) is unstable. In case II (i.e., $D_{12} \neq 0$, $D_{21} = 0$), the unstable equilibrium E^* becomes stable if the following inequalities hold:

$$\sigma_1 > 0, \quad (7.18a)$$

$$\sigma_2 + a\rho_1 > 0. \quad (7.18b)$$

We note that by increasing D_{11} to a large value so that

$D_{11} \frac{n^2 \pi^2}{R^2} - H(x^*) > 0$, and if $D_{12} > 0$, then inequalities (7.18a) and (7.18b) are satisfied.

Case III: $D_{12} \neq 0$ and $D_{21} \neq 0$.

In this case $E^*(x^*, y^*)$ is locally stable if

$$\sigma_2 + a\rho_1 - b\rho_2 - \rho_1\rho_2 > 0, \quad (7.19)$$

and unstable if the inequality is reversed in Eq. (7.19). We note that if $\rho_1 > 0$ and $\rho_2 < 0$ i.e., if $D_{12} > 0$ and $D_{21} < 0$, then condition (7.19) is automatically satisfied. This shows that if the prey species tends to diffuse in the direction of lower concentration of the predator species, and the predator species tends to diffuse in the direction of higher concentration of the prey species, then the stable equilibrium state without self and cross-diffusions remains stable. Such situations are common in nature for the survival of the prey-predator species.

Remark 3: Let $H(x^*) > 0$. Then the interior equilibrium E^* of model (7.7) is unstable. In case III (i.e., $D_{12} \neq 0$, $D_{21} \neq 0$) it may be seen that the unstable equilibrium E^* becomes stable if the following inequalities hold:

$$\sigma_1 > 0, \quad (7.20a)$$

$$\sigma_2 + a\rho_1 - b\rho_2 - \rho_1\rho_2 > 0. \quad (7.20b)$$

In particular, it may be noted that the above two inequalities are satisfied if $\rho_1 > 0$ (i.e., $D_{12} > 0$), $\rho_2 < 0$ (i.e., $D_{21} < 0$), and if D_{11} is increased to a large value so that

$$-H(x^*) + D_{11} \frac{n^2 \pi^2}{R^2} > 0.$$

In the following theorem we shall investigate the global

stability behavior of the interior equilibrium E^* . For this, we first write the following notations:

$$a_{11} = D_{11} \frac{q(x)p'(x) - p(x)q'(x)}{p(x)^2} > 0, \quad (7.21a)$$

$$a_{22} = D_{22} \frac{y^*}{y^2} > 0, \quad (7.21b)$$

$$a_{12} = -D_{12} \frac{q(x)p'(x) - p(x)q'(x)}{p(x)^2} - D_{21} \frac{y^*}{y^2}. \quad (7.21c)$$

Theorem 7.3.1: Let $D_{12} \neq 0$, $D_{21} \neq 0$. If the following conditions hold:

$$\left(\frac{xg(x)}{p(x)} - y^* \right) (x - x^*) < 0, \quad (7.22a)$$

$$a_{12}^2 < 4a_{11}a_{22}, \quad (7.22b)$$

then the uniform steady state E^* of the initial-boundary-value problem (7.1)-(7.2) is globally asymptotically stable with respect to all solutions initiating in the positive quadrant.

Proof: For the sake of notation, let $x(u,t) = x$ and $y(u,t) = y$. Now, using the positivity of x and y for $u \in [0,R]$ and $t \in [0,\infty)$, we define a functional

$$V_1(t) = \int_0^R V(x,y) du, \quad (7.23)$$

where V is defined in Eq.(7.10).

Taking the derivative of V_1 along the solutions of model (7.1), we obtain

$$\begin{aligned} \dot{V}_1 &= \int_0^R \dot{V}(x,y) du + D_{11} \int_0^R \frac{\partial V}{\partial x} \frac{\partial^2 x}{\partial u^2} du + D_{22} \int_0^R \frac{\partial V}{\partial y} \frac{\partial^2 y}{\partial u^2} du \\ &+ D_{12} \int_0^R \frac{\partial V}{\partial x} \frac{\partial^2 y}{\partial u^2} du + D_{21} \int_0^R \frac{\partial V}{\partial y} \frac{\partial^2 x}{\partial u^2} du. \end{aligned}$$

Using the boundary conditions we get

$$\begin{aligned}
 \dot{V}_1 &= \int_0^R \dot{V}(x,y) \, du - D_{11} \int_0^R \frac{q(x)p'(x) - p(x)q'(x)}{p(x)^2} \left(\frac{\partial x}{\partial u} \right)^2 \, du \\
 &\quad - D_{22} \int_0^R \left(\frac{y^*}{y^2} \right) \left(\frac{\partial y}{\partial u} \right)^2 \, du - D_{12} \int_0^R \frac{q(x)p'(x) - p(x)q'(x)}{p(x)^2} \left(\frac{\partial x}{\partial u} \right) \left(\frac{\partial y}{\partial u} \right) \, du \\
 &\quad - D_{21} \int_0^R \left(\frac{y^*}{y^2} \right) \left(\frac{\partial y}{\partial u} \right) \left(\frac{\partial x}{\partial u} \right) \, du. \\
 \dot{V}_1 &= \int_0^R \dot{V}(x,y) \, du + \int_0^R \left[-a_{11} \left(\frac{\partial x}{\partial u} \right)^2 + a_{12} \frac{\partial x}{\partial u} \frac{\partial y}{\partial u} - a_{22} \left(\frac{\partial y}{\partial u} \right)^2 \right] \, du,
 \end{aligned} \tag{7.24}$$

where a_{ij} are defined in (7.21).

From Eq.(7.24) we note that \dot{V}_1 is negative definite under conditions (7.22a-b), proving the theorem.

Remark 4: If $D_{12} = D_{21} = 0$, then we note that condition (7.22b) is automatically satisfied. This shows that if the equilibrium E^* of model (7.7) is globally asymptotically stable, then the uniform steady state E^* of the initial-boundary-value problem (7.1)-(7.2) is also globally asymptotically stable.

Remark 5: If $D_{12} \neq D_{21} \neq 0$, and if \dot{V} is positive definite, then from Eq. (7.24) we note that \dot{V}_1 can be made negative definite by increasing D_{11} and D_{22} to sufficiently large values. This implies that the unstable equilibrium E^* of model (7.1) can be made stable by increasing self diffusion coefficient to sufficiently large values.

7.4 SUMMARY

In this chapter we have considered a Gause-type predator-prey interacting model with self as well as cross-diffusion and investigated the stability conditions in different environmental consequences. We have analyzed the model by using stability theory of differential equations. Criteria for local stability, instability and global stability of an interior equilibrium are obtained. Criteria for global stability are also obtained by constructing a suitable Liapunov function.

By analyzing the initial-boundary value problems (7.1)-(7.3) it has been shown that in case I (i.e. $D_{12} = 0$, $D_{21} \neq 0$), if the predator species tend to diffuse in the direction of higher concentration of the prey species, and the prey species moves along its own concentration gradient, then the equilibrium state E^* is locally asymptotically stable. In this case it has also been noted that when the critical wave length is too small, that the predator species tends to diffuse in the direction of lower concentration of the prey species, and the prey species moves along its own concentration gradient, then it leads to local instability of the equilibrium state. In this case, it has been noted that the unstable equilibrium E^* of model (7.7) becomes stable if conditions (7.16a) and (7.16b) are satisfied. In case II (i.e. $D_{12} \neq 0$, $D_{21} = 0$), it has been shown that if the prey species tend to diffuse in the direction of lower concentration of the predator species, and the predator species moves along its own concentration gradient, then the equilibrium state E^* is locally asymptotically stable. But this equilibrium E^* becomes unstable if the critical wave length is very small. In such a case the prey species tend to diffuse in the direction of higher concentration

of the predator species. and the predator species moves along its own concentration gradient. In this case, it has also been noted that the unstable equilibrium E^* of model (7.7) becomes stable if conditions (7.18a) and (7.18b) are satisfied. In case III (i.e. $D_{12} \neq 0, D_{21} \neq 0$) it has been shown that if the prey species tend to diffuse in the direction of lower concentration of the predator species, and the predator species tend to diffuse in the direction of higher concentration of the prey species, then the equilibrium state remains stable. In this case it has been found that the unstable equilibrium E^* of model (7.7) becomes stable if the conditions (7.20a) and (7.20b) are satisfied. Further, it has been found that the uniform steady state E^* of the initial boundary value problems (7.1)-(7.2) is globally asymptotically stable under a certain condition. It has been shown that if the equilibrium state E^* of the system with no diffusion is globally stable, then the corresponding uniform steady state of the system with diffusion remains globally stable. It has also been shown that if the equilibrium state E^* of the system with no diffusion is unstable, then the corresponding uniform steady state of the system with diffusion can be made stable by increasing self-diffusion coefficients to sufficiently large values.

CHAPTER VIII

A MODEL FOR TWO COMPETING SPECIES WITH SELF AND CROSS-DIFFUSION

3.0 INTRODUCTION

In a real habitat each species has an inhibiting effect on the growth of the other due to competition for food, breeding sites, etc. The usual analysis of competition between two species goes back to Lotka (1925), Volterra (1927) and Gause (1934). Since then several investigations have been made to study conditions which must be satisfied if two competing species are to co-exist in the same habitat (Hardin (1960), Gopalsamy (1977, 86), Harada and Fukao (1978), Hsu et al. (1978, 1979, 1981a, 1995), Freedman (1979, 1987), Cushing (1980), Cheng et al. (1981), Cosner and Laser (1984), Cantrell et al. (1987), Mitra et al. (1992), Dubey (1997) etc.). It may be noted that the Lotka-Volterra model focuses on population interactions at a point in space ignoring movement, which means perfect mixing of the species in a given region, (Levin (1974, 1976, 1986), Okubo (1980)).

In general, the movement of the species in the habitat may arise due to certain factors such as overcrowding, anticlimate, predator chasing prey etc., but more importantly due to a resource limitation in the habitat, (Verma (1980)). In recent years, considerable interest has been paid in order to study the permanence and global stability of a competitive Lotka-Volterra diffusive system, but little attention has been paid in studying the effect of cross-diffusion (Jorne (1975), Hastings (1978), Gurtin (1974), Shukla and Verma (1981), Allen (1983a,b), Pao (1995a, b), Takeuchi and Lu (1995), Chattapadhyay et al. (1996), Raychaudhuri et al. (1996)). Keeping these in mind, this

chapter is devoted to develop and analyse a general nonlinear competition model for two species taking into account self as well as cross-diffusion. Criteria for local stability, global stability and instability are obtained in the absence of diffusion. By constructing a suitable Liapunov function, the global stability of the system is investigated.

3.1 MATHEMATICAL MODEL

We consider an ecosystem where we wish to develop a nonlinear competition model with self and cross-diffusion. In the model, it is assumed that the intrinsic growth and carrying capacity of each species decrease as the population density of the other increases. Then the dynamics of the system is governed by the following autonomous differential equations :

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= r_1(N_2)N_1 - \frac{r_{10}N_1^2}{K_1(N_2)} + D_{11} \frac{\partial^2 N_1}{\partial x^2} + D_{12} \frac{\partial^2 N_2}{\partial x^2}, \\ \frac{\partial N_2}{\partial t} &= r_2(N_1)N_2 - \frac{r_{20}N_2^2}{K_2(N_1)} + D_{22} \frac{\partial^2 N_2}{\partial x^2} + D_{21} \frac{\partial^2 N_1}{\partial x^2}.\end{aligned}\quad (8.1)$$

Model (8.1) needs to be analyzed with the initial populations

$$N_1(x, 0) > 0, N_2(x, 0) > 0. \quad (8.2)$$

We also assume that no external input is imposed from the outside. Hence zero flux boundary conditions

$$\left. \frac{\partial N_i}{\partial x} \right|_{x=0, R} = 0 \quad i = 1, 2 \quad (8.3)$$

are assumed.

In model (8.1), $N_1(x, t)$ and $N_2(x, t)$ represent the densities of two competing species at time $t \geq 0$.

The function $r_1(N_2)$ represents the specific growth rate of

the competing species of density N_1 , and it satisfies,

$$r_1(0) = r_{10} > 0, \quad \frac{\partial r_1(N_2)}{\partial N_2} < 0, \text{ for } N_2 \geq 0, \text{ and there exists } N_2 = \bar{N}_2$$

such that $r_1(\bar{N}_2) = 0$. (8.4)

This shows that the specific growth rate of the first competing species decreases as the density of the second competing species increases and it may tend to zero if the density of the second competitor reaches a critical level $N_2 = \bar{N}_2$.

The function $r_2(N_1)$ represents the specific growth rate of the species of density N_2 , and it also satisfies the following condition:

$$r_2(0) = r_{20} > 0, \quad \frac{\partial r_2(N_1)}{\partial N_1} < 0, \text{ for } N_1 \geq 0, \text{ and there exists } N_1 = \bar{N}_1$$

such that $r_2(\bar{N}_1) = 0$. (8.5)

This implies that the specific growth rate of the second competitor decreases as the density of the first competitor increases, and it may also tend to zero if the density of the first competitor reaches a critical level $N_1 = \bar{N}_1$.

The function $K_i(N_j)$ is the maximum density of the i^{th} competitor which the environment can support and it decreases as N_j increases. Hence we assume,

$$K_i(0) = K_{i0} > 0, \quad K'_i(N_j) < 0 \text{ for } N_j \geq 0, \quad i, j = 1, 2, \quad i \neq j. \quad (8.6)$$

D_{11} and D_{22} are the self-diffusion coefficients and D_{12} and D_{21} are the cross-diffusion coefficients of N_1 and N_2 species respectively in a finite one-dimensional domain (x) . D_{11} and D_{22} are assumed to be positive constants, whereas D_{12} and D_{21} may be positive, negative or zero.

In the next section we analyze the system without diffusion.

3.2 THE MODEL WITHOUT DIFFUSION

In this section we consider model (8.1)-(8.3) without diffusion (i.e. $D_{11} = D_{22} = D_{12} = D_{21} = 0$). In such a case the model reduces to

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 \left(r_1(N_2) - \frac{r_{10} N_1}{K_1(N_2)} \right), \\ \frac{dN_2}{dt} &= N_2 \left(r_2(N_1) - \frac{r_{20} N_2}{K_2(N_1)} \right), \\ N_i(0) &> 0, \quad i = 1, 2.\end{aligned}\tag{8.7}$$

It is easy to check that there are four nonnegative equilibria, namely, $E_0(0,0)$, $E_1(K_{10}, 0)$, $E_2(0, K_{20})$, $E^*(N_1^*, N_2^*)$. The equilibria E_0 , E_1 and E_2 clearly exist. We shall show the existence of E^* as follows.

Existence of $E^(N_1^*, N_2^*)$*

Here N_1^* and N_2^* are the positive solutions of the following algebraic equations:

$$N_1 = \frac{r_1(N_2) K_1(N_2)}{r_{10}},\tag{8.8a}$$

$$N_2 = \frac{r_2(N_1) K_2(N_1)}{r_{20}}.\tag{8.8b}$$

From (8.8a) we note the following :

$$\text{when } N_2 \rightarrow 0, \quad N_1 \rightarrow K_{10},\tag{8.9a}$$

$$\text{when } N_2 \rightarrow \bar{N}_2, \quad N_1 \rightarrow 0,\tag{8.9b}$$

$$\frac{dN_1}{dN_2} = \frac{1}{r_{10}} \left(r_1(N_2) K_1'(N_2) + K_1(N_2) r_1'(N_2) \right) < 0.\tag{8.10}$$

Further, from (8.8b) we note the following:

$$\text{when } N_1 \rightarrow 0, \quad N_2 \rightarrow K_{20},\tag{8.11a}$$

$$\text{when } N_1 \rightarrow \bar{N}_1, \quad N_2 \rightarrow 0,\tag{8.11b}$$

$$\frac{dN_2}{dN_1} = \frac{1}{r_{20}} \left(r_2(N_1) K_2'(N_1) + k_2(N_1) r_2'(N_1) \right) < 0. \quad (8.12)$$

From the above analysis we note that the two isoclines (8.8a) and (8.8b) intersect at a unique point $E^*(N_1^*, N_2^*)$ if any one of the following inequality hold:

$$(i) \bar{N}_1 > K_{10} \text{ and } \bar{N}_2 > K_{20}, \quad (8.13a)$$

$$(ii) \bar{N}_1 < K_{10} \text{ and } \bar{N}_2 < K_{20}. \quad (8.13b)$$

Stability of equilibra

The local stability of the equilibria can be studied from variational matrices corresponding to each equilibrium. By computing the variational matrices corresponding to each equilibrium we note the following results.

1. $E_0(0, 0)$ is unstable in the N_1 - N_2 plane.
2. $E_1(K_{10}, 0)$ is a saddle point whose stable manifold is locally along N_1 -direction and unstable manifold locally along the N_2 -direction.
3. $E_2(0, K_{20})$ is also a saddle point whose stable manifold is locally along the N_2 -direction and unstable manifold is locally along the N_1 -direction.
4. $E^*(N_1^*, N_2^*)$ is locally asymptotically stable if and only if the following inequality holds :

$$\frac{r_{10} r_{20} N_1^* N_2^*}{K_1(N_2^*) K_2(N_1^*)} - G_1^* G_2^* > 0, \quad (8.14)$$

where G_1^* and G_2^* are defined as follows:

$$G_1^* = N_1^* r_1'(N_2^*) + \frac{r_{10} N_1^*}{K_1^2(N_2^*)} K_1'(N_2^*) < 0, \quad (8.15a)$$

$$G_2^* = N_2^* r_2'(N_1^*) + \frac{r_{20} N_2^{*2}}{K_2^2(N_1^*)} K_2'(N_1^*) < 0. \quad (8.15b)$$

Now in order to investigate the global behavior of the interior equilibrium E^* , we first state the following lemma which establishes a region of attraction for system (8.7). The proof of this lemma is easy and hence we omit it.

Lemma 8.2.1 The set

$$\Omega = \left\{ (N_1^*, N_2^*) : 0 < N_1 \leq K_{10}, 0 < N_2 \leq K_{20} \right\}$$

attracts all solutions initiating in the positive quadrant.

The following theorem gives criteria under which E^* is globally asymptotically stable.

Theorem 8.2.1

In addition to assumptions (8.4)-(8.6), let $r_1(N_1)$, $r_2(N_2)$, $K_1(N_1)$, $K_2(N_2)$ satisfy

$$\begin{aligned} 0 \leq -r_1'(N_2) \leq \rho_1, \quad 0 \leq -r_2'(N_1) \leq \rho_2, \quad 0 \leq -K_1'(N_2) \leq \rho_3, \\ 0 \leq -K_2'(N_1) \leq \rho_4, \quad K_m \leq K_1(N_2) \leq K_{10}, \quad K_s \leq K_2(N_1) \leq K_{20} \end{aligned} \quad (8.16)$$

in Ω for some positive constants ρ_1 , ρ_2 , ρ_3 , ρ_4 , K_m , K_s . If the following inequality holds

$$\left(\rho_1 + \rho_2 + \frac{r_{10} \rho_3 K_{10}}{K_m^2} + \frac{r_{20} \rho_4 K_{20}}{K_s^2} \right)^2 < 4 \frac{r_{10} r_{20}}{K_1(N_2^*) K_2(N_1^*)}, \quad (8.17)$$

then E^* is globally asymptotically stable with respect to all solutions initiating in the positive quadrant.

Proof: We consider the following positive definite function about E^* ,

$$V(N_1, N_2) = N_1 - N_1^* - N_1^* \ln(N_1/N_1^*) + N_2 - N_2^* - N_2^* \ln(N_2/N_2^*). \quad (8.18)$$

Differentiating V with respect to t along the solutions of (8.7) we get

$$\begin{aligned} \dot{V} = & -\frac{r_{10}}{K_1(N_2)} (N_1 - N_1^*)^2 - \frac{r_{20}}{K_2(N_1)} (N_2 - N_2^*)^2 \\ & + \left(\lambda_1(N_2) + \lambda_2(N_1) - r_{10} N_1 \xi_1(N_2) - r_{20} N_2 \xi_2(N_1) \right) (N_1 - N_1^*)(N_2 - N_2^*), \end{aligned} \quad (8.19)$$

where

$$\lambda_1(N_2) = \begin{cases} \frac{r_1(N_2) - r_1(N_2^*)}{N_2 - N_2^*}, & N_2 \neq N_2^* \\ r_1'(N_2^*), & N_2 = N_2^* \end{cases},$$

$$\lambda_2(N_1) = \begin{cases} \frac{r_2(N_1) - r_2(N_1^*)}{N_1 - N_1^*}, & N_1 \neq N_1^* \\ r_2'(N_1^*), & N_1 = N_1^* \end{cases},$$

$$\xi_1(N_2) = \begin{cases} \left[\frac{1}{K_1(N_2)} - \frac{1}{K_1(N_2^*)} \right] / (N_2 - N_2^*), & N_2 \neq N_2^* \\ -\frac{K_1'(N_2^*)}{K_1^2(N_2^*)}, & N_2 = N_2^* \end{cases},$$

$$\xi_2(N_1) = \begin{cases} \left[\frac{1}{K_2(N_1)} - \frac{1}{K_2(N_1^*)} \right] / (N_1 - N_1^*), & N_1 \neq N_1^* \\ -\frac{K_2'(N_1^*)}{K_2^2(N_1^*)}, & N_1 = N_1^* \end{cases}.$$

From (8.16) and the mean value theorem we note that,

$$\begin{aligned} 0 \leq |\lambda_1(N_2)| \leq \rho_1, \quad 0 \leq |\lambda_2(N_1)| \leq \rho_2, \\ |\xi_1(N_2)| \leq \rho_3 / K_m^2, \quad |\xi_2(N_1)| \leq \rho_4 / K_s^2. \end{aligned}$$

Now \dot{V} can be written as the sum of quadratics,

$$\dot{V} = -a_{11}(N_1 - N_1^*)^2 - a_{22}(N_2 - N_2^*)^2 + a_{12}(N_1 - N_1^*)(N_2 - N_2^*), \quad (8.20)$$

where

$$a_{11} = \frac{r_{10}}{K_{10}}, \quad (8.21a)$$

$$a_{22} = \frac{r_{20}}{K_{20}}, \quad (8.21b)$$

$$a_{12} = \lambda_1(N_2) - \lambda_2(N_1) - r_{10}N_1\xi_1(N_2) - r_{20}N_2\xi_2(N_1). \quad (8.21c)$$

The sufficient condition for \dot{V} to be negative definite is that the following inequality holds.

$$a_{12}^2 < 4a_{11}a_{22} \quad (8.22)$$

Since (8.17) \Rightarrow (8.22), we conclude that V is a Liapunov function with respect to E^* whose domain contains the region Ω , proving the theorem.

The above theorem implies that in the absence of diffusion the two competing species coexist and settle down to their respective equilibrium levels under certain conditions whose magnitudes are lower than their respective density independent carrying capacities. Keeping in view of (8.18) it is further noted that the equilibrium level of each species decreases as the equilibrium level of the other increases and if the equilibrium level of one increases beyond a threshold value the other species may become extinct.

8.3 THE MODEL WITH DIFFUSION

In this section we consider the full model (8.1) together with initial and boundary conditions (8.2) and (8.3). As a consequence of initial-boundary conditions (8.2)-(8.3), $E^*(N_1^*, N_2^*)$ is a uniform

steady state for this system.

We now investigate the stability conditions for system (8.1)-(8.3) in different environmental consequences as follows.

With the boundary conditions under consideration, we look for an eigenfunction of the form

$$\begin{pmatrix} a \\ b \end{pmatrix} \exp(\lambda t) \cos\left(\frac{n\pi x}{R}\right). \quad (8.23)$$

Here $l = R/n\pi$ is the critical wave length,

R = length of the system,

and $\frac{2\pi}{n}$ = period of the cosine.

The characteristic equation of the system is given by

$$\lambda^2 + \sigma_1 \lambda + \{\sigma_2 + G_1^* \mu_2 + G_2^* \mu_1 - \mu_1 \mu_2\} = 0, \quad (8.24)$$

where

$$\sigma_1 = \frac{r_{10} N_1^*}{K_1(N_2^*)} + \frac{r_{20} N_2^*}{K_2(N_1^*)} + (D_{11} + D_{22}) \frac{n^2 \pi^2}{R^2} > 0,$$

$$\begin{aligned} \sigma_2 = & \frac{r_{10} r_{20} N_1^* N_2^*}{K_1(N_2^*) K_2(N_1^*)} - G_1^* G_2^* + \left(\frac{r_{10} N_1^*}{K_1(N_2^*)} + D_{11} \frac{n^2 \pi^2}{R^2} \right) D_{22} \frac{n^2 \pi^2}{R^2} \\ & + D_{11} \frac{r_{20} N_2^*}{K_2(N_1^*)} \frac{n^2 \pi^2}{R^2}, \end{aligned}$$

$$\mu_1 = \frac{n^2 \pi^2}{R^2} D_{12}'$$

$$\mu_2 = \frac{n^2 \pi^2}{R^2} D_{21}'$$

and G_1^*, G_2^* are given by (8.15).

Thus, from the Routh Hurwitz criteria the stability of the equilibrium E^* depends on the sign of

$$\sigma_2 + G_1^* \mu_2 + G_2^* \mu_1 - \mu_1 \mu_2. \quad (8.25)$$

Now we shall discuss the following cases under the assumption that in the absence of diffusion the interior equilibrium $E^*(N_1^*, N_2^*)$ is locally asymptotically stable, which implies that (8.14) is satisfied. In such a case $\sigma_2 > 0$.

Case I : $D_{12} = 0$ and $D_{21} \neq 0$.

Then E^* is locally stable if

$$\begin{aligned} \sigma_2 + G_1^* \mu_2 &> 0, \\ \text{i.e., } \sigma_2 + G_1^* D_{21} \frac{n^2 \pi^2}{R^2} &> 0, \text{ for all } n \geq 0. \end{aligned} \quad (8.26)$$

We note that if $D_{21} < 0$, then (8.26) is automatically satisfied. This shows that the N_2 -species tends to diffuse in the direction of higher concentration of the N_1 -species and the N_1 -species moves along its own concentration gradient, then the interior equilibrium E^* remains locally asymptotically stable. Further, E^* is unstable if $D_{21} > 0$, since there always exists values of n such that

$$\frac{R^2}{n^2 \pi^2} < - \frac{G_1^* D_{21}}{\sigma_2}. \quad (8.27)$$

This shows that when the critical wave length $(\frac{R}{n\pi})$ is too small that the competitor species N_2 tends to diffuse in the direction of lower concentration of the other competitor species N_1 and the N_1 -species moves along its own concentration gradient, then the equilibrium state E^* becomes unstable. Such a case arises in nature where one competitor species prefers to avoid group defense by a large number of other competitor species, and chooses to attack its competitor from a smaller group unable to sufficiently resist.

Similarly reverse cases will arise if $D_{12} \neq 0$ and $D_{21} = 0$.

Remark: Let the equilibrium $E^*(N_1^*, N_2^*)$ of model (8.7) is unstable. then condition (8.14) is not satisfied. This implies that σ_2 need not be positive. Then in case I (i.e. $D_{12} = 0, D_{21} \neq 0$) the unstable equilibrium E^* can be made locally stable if the following inequality holds:

$$\sigma_2 + G_1^* \frac{n^2 \pi^2}{R^2} D_{21} > 0, \text{ for all } n \geq 0. \quad (8.28)$$

As it is assumed in case I that inequality (8.14) is satisfied. Hence $\sigma_2 > 0$ and if $D_{21} < 0$, then inequality (8.26) is automatically satisfied. But in (8.28), σ_2 may not be positive and hence even if $D_{21} < 0$, inequality (8.28) may not be satisfied. It may further be noted that the inequality (8.28) may be satisfied by increasing D_{11} and D_{22} to sufficiently large values.

Case II : $D_{12} \neq 0$ and $D_{21} \neq 0$.

In this subcase E^* is locally stable if

$$\sigma_2 + G_1^* \mu_2 + G_2^* \mu_1 - \mu_1 \mu_2 > 0, \quad (8.29)$$

and unstable if the inequality is reversed.

Theorem 8.3.1

I. Let $D_{12} = D_{21} = 0$. Then the following results hold.

(a) If the time derivatives of V along the solutions of model (8.7) is negative definite (i.e. if the interior equilibrium E^* of model (8.7) is globally asymptotically stable), then the uniform steady state E^* of the initial boundary value problems (8.1)-(8.3) is also globally asymptotically stable.

(b) If the interior equilibrium E^* of model (8.7) is unstable, then by increasing the self diffusion coefficients D_{11} and D_{22} to sufficiently large values, the unstable equilibrium E^* can be made stable.

II. Let $D_{12} \neq 0$, $D_{21} \neq 0$. Let the time derivative of V along the solutions of model (8.7) be negative definite. If the following inequality holds

$$\left(D_{12} \frac{N_1^*}{N_1^2} + D_{21} \frac{N_2^*}{N_2^2} \right)^2 < 4 D_{11} D_{22} \frac{N_1^* N_2^*}{N_1^2 N_2^2}, \quad (8.30)$$

then the uniform steady state E^* of the initial boundary value problems (8.1)-(8.3) is globally asymptotically stable.

Proof : For the sake of notation, let

$$N_1(x, t) = N_1 \text{ and } N_2(x, t) = N_2.$$

Now using the positivity and boundedness N_1 and N_2 for $x \in [0, R]$ and $t \in [0, \infty)$, we define a functional

$$V_1(t) = \int_0^R V(N_1, N_2) dx,$$

where V is defined in Eq (8.18). Taking the derivative of V_1 along the solutions of model (8.1) and initial boundary conditions (8.2)-(8.3), we obtain

$$\begin{aligned} \dot{V}_1 = & \int_0^R \dot{V} dx + D_{11} \int_0^R \frac{\partial V}{\partial N_1} \frac{\partial^2 N_1}{\partial x^2} dx + D_{22} \int_0^R \frac{\partial V}{\partial N_2} \frac{\partial^2 N_2}{\partial x^2} dx \\ & + D_{12} \int_0^R \frac{\partial V}{\partial N_1} \frac{\partial^2 N_2}{\partial x^2} dx + D_{21} \int_0^R \frac{\partial V}{\partial N_2} \frac{\partial^2 N_1}{\partial x^2} dx. \end{aligned}$$

After a little algebraic manipulation \dot{V}_1 can be written as

$$\begin{aligned} \dot{V}_1 = & \int_0^R \dot{V} dx + \int_0^R \left[-D_{11} \left(\frac{N_1^*}{N_1^2} \right) \left(\frac{\partial N_1}{\partial x} \right)^2 + \left\{ -D_{12} \frac{N_1^*}{N_1^2} - D_{21} \frac{N_2^*}{N_2^2} \right\} \frac{\partial N_1}{\partial x} \frac{\partial N_2}{\partial x} \right. \\ & \left. - D_{22} \left(\frac{N_2^*}{N_2^2} \right) \left(\frac{\partial N_2}{\partial x} \right)^2 \right] dx. \end{aligned} \quad (8.31)$$

We note from Eq. (8.31) that if $D_{12} = D_{21} = 0$ and \dot{V} is negative definite, then \dot{V}_1 is also a negative definite function. If \dot{V} is positive definite then by increasing D_{11} and D_{22} to sufficiently large

values \dot{V}_1 can be made negative definite, hence the first part of the theorem follows.

When $D_{12} \neq 0$, $D_{21} \neq 0$, it may be noted that if \dot{V} is negative definite along solutions of (8.7), then \dot{V}_1 is also negative definite under condition (8.30), and hence the second part of the theorem follows.

8.4 SUMMARY

In this chapter, a nonlinear mathematical model has been proposed and analyzed to study the behavior of two competing species with self and cross-diffusion. It has been assumed that the growth rate and carrying capacity of each competing species decreases as the density of the other species increases. In the absence of diffusion it has been shown that the two competing species settles down to their respective equilibria levels under a certain condition, and their magnitudes are lower than their respective density independent carrying capacities. It has been noted that density of either competitor decreases and the density of each species may tend to zero if the equilibrium density of the other species increases beyond a threshold value. In the presence of self-diffusion and in the absence of cross diffusion it has been found that the stability of the system increases and the otherwise unstable equilibrium becomes stable. In the presence of self and cross-diffusion it has been noted that if the second competitor of density N_2 tends to diffuse in the direction of higher concentration of the first competitor of density N_1 , and the first competitor moves along its own concentration gradient ($D_{12} = 0$, $D_{21} < 0$), then the interior equilibrium E^* , which is stable in the absence of diffusion, remains locally asymptotically stable. It has

been further found that if the critical wave length $l = \frac{R}{n\pi}$ is too small that the second competitor of density N_2 tends to diffuse in the direction of lower concentration of the first competitor of density N_1 , and the first competitor moves along its own concentration gradient, ($D_{12} = 0, D_{21} > 0$) then the interior equilibrium, which is stable in the absence of diffusion, becomes unstable. Similar results have also been found in the case when $D_{12} \neq 0, D_{21} = 0$. When $D_{12} \neq 0, D_{21} \neq 0$, it has been shown that the equilibrium may be stable or unstable depending upon the density of the competitors, their self and cross-diffusion coefficients and the critical wave length of the system. It has been shown that if the equilibrium E^* of the system with self and cross-diffusion is globally asymptotically stable, then the uniform steady state E^* of the system with self-diffusion only remains globally asymptotically stable. It has also been found that if the equilibrium E^* is unstable in the absence of diffusion, then it can be made stable under certain conditions in the presence of self and cross-diffusion.

REFERENCES

- Agarwal M., Shukla A. and Pal V. N. (1993) Grazing of forested grassland and its conservation, *Ecol. Model.* 69: 57-62.
- Albrecht F., Gatzke H., Hadded A. and Wax N., (1974), The dynamics of two interacting populations, *J. Math. Anal. Appl.* 46: 658-670.
- Allen L. J. S., (1983a), Persistence and extinction in Lotka-Volterra reaction diffusion equations, *Math. Biosci.* 65: 1-12.
- Allen L. J. S., (1983b) Persistence and extinction in single-species reaction diffusion populations, *Bull. Math. Biol.* 45(2): 209-227.
- Allen L. J. S., (1987) Persistence, extinction and critical patch number for island populations, *J. Math. Biol.* 24: 617-625.
- Anderson N. and Arthurs A. M., (1985) Analytical boundary functions for diffusion problems with Michaelis-Menten kinetics, *Bull. Math. Biol.* 47(1), 145-153.
- Angulo J. and Linares F., (1995) Global existence of solutions of a nonlinear dispersive model, *J. Math. Anal. & Appl.* 195(3): 797-808.
- Anon (1977a) Deforestation and its Control, ICAR, New Delhi, P. 358.
- Anon (1977b) Desertification: Its Causes and Consequences, Penman Press Oxford.
- Anon (1995), Forestry Statistics, India FRI Publication, Dehradun, PP: 200.
- Bergerud A. T., Butler H. E. and Millar D. R. (1984) Antipredator tactics of calving caribou: dispersion in mountains, *Can. J. Zool.* 62: 1566-1575.
- Bergerud A. T. and Page R. E., (1987) Displacement and dispersion of parturient caribou at calving as antipredator tactics, *Can. J. Zool.* 65: 1597-1606.
- Bergman E. and Greenberg L. A., (1994) Competition between a Planktivore, a benthivore and a species with ontogenetic diet shifts, *Ecology*, 75(5) 1233-1245.
- Bonan G. B., (1993) Analysis of neighborhood competition among annual plants: Implications of a plant growth model, *Ecol. Model.* 65: 123-136.
- Brauer F. and Soudack, (1981) Constant rate stocking of predator-prey systems, *J. Math. Biol.* 11: 1-14.
- Brown L. R. (1981) World population growth and soil erosion and food security, *Science*, 214: 1087-1095.

- Brown, L. R. and Wolf E. C. (1984) Soil Erosion: Quiet Crises in the World Economy, World Watch Paper 60.
- Cantrell R. S. and Cosner C., (1987) On the steady state problem for the Volterra-Lotka competition model with diffusion, *Houston J. Math.* 13: 337-352.
- Cantrell R. S. and Cosner C., (1989) Diffusive logistic equations with indefinite weights: population models in disrupted environments, *Proc. Royal Soc. of Edinb.* 112A: 293-318.
- Caisson V. (1978) Global solution for a diffusive nonlinear deterministic epidemic model, *SIAM. J. Appl. Math.* 35: 274-284.
- Casten R. G., and Holland C. J., (1978) Instability results for reaction diffusion equations with Neumann Boundary conditions, *J. Differ. Equns.* 27: 266-273.
- Chattopadhyay J., Sarkar A. K. and Tapaswi P. K. (1996) Effect of cross-diffusion on a diffusive prey-predator system - A non linear analysis, *J. Biol. Sys.* 4(2): 159-169.
- Cheng K. S., Hsu S. B. and Lin S. S. (1981) Some results on global stability of a predator-prey system, *J. Math. Biol.* 12: 115-126.
- Chow P. L. and Tam W. C., (1976) Periodic and travelling wave solutions to Volterra-Lotka equations with diffusion, *Bull. Math. Biol.* 38: 643-658.
- Cohen D. S. and Murray J. D. (1981) A generalized diffusion model for growth and dispersal in a population, *J. Math. Biol.* 12: 237-249.
- Conway E. D. and Smoller J. A., (1986) Global analysis of a system of predator prey equations, *SIAM J. Appl. Math.* 46: 630-642.
- Comins H. N. and Blatt D. W. E., (1974) Prey predator models in spatially heterogeneous environment, *J. Theor. Biol.* 48: 75-83.
- Connell J. H., (1970) A predator-prey system in the marine intertidal region. I. *Balanus Glandula* and several predator species of *Thais*, *Ecol. Monogr.* 40: 49-78.
- Cosner C. and Laser A. C., (1984) Stable coexistence states in the Volterra-Lotka competition model with diffusion, *SIAM J. Appl. Math.* 44: 1112-1132.
- Cramer N. F. and May R. M., (1972), Interspecific competition, predation and species diversity: a comment, *J. Theoret. Biol.* 34: 289-293.
- Cushing J. M. (1980) Two species competition in a periodic environment, *J. Math. Biol.* 10: 385-400.
- Das D. C. (1977), Soil Conservation Practices and Erosion Control in India - a case study, *IAO Soil Bulletin*, 33 : 11 - 50.

Denn M. M. *Stability of Reaction and Transport Processes* (Prentice Hall, Englewood Cliffs, New Jersey, 1975).

Dubey B., (1997) A resource based competing model: effect of population, *Far east J. Appl. Math.* 1: 11-32.

Edelstein-Keshet, L., (1988) *Mathematical Models in Biology*, New York, Random House.

Fife, P. (1979) Mathematical aspects of reacting and diffusing systems, Lecture Notes in Biomathematics 28: Berlin, Springer-Verlag.

Freedman H. I., (1976) Graphical stability, enrichment, and pest control by a natural enemy, *Math. Biosci.* 31: 207-225.

Freedman H. I. (1979) Stability analysis of a predator prey system with mutual interference and density dependent death rates, *Bull Math. Biol.* 41:67-78.

Freedman H. I., *Deterministic Mathematical Models in Population Ecology* (HIFR Consulting Ltd., Edmonton 1987).

Freedman H. I. (1987) Single species migration in two habitats: Persistence and extinction. *Math. Model.* 8: 778-780.

Freedman H. I. (1989) Persistence and extinction in models of two-habitat migration, *Math. Comput. Model.* 12(1): 105-112.

Freedman H. I. and Krisztin T. (1992) Global stability in models of population dynamics with diffusion I. Patchy environments. *Proc. Royal Soc. of Edinb.* 122A: 69-84.

Freedman H. I. , Rai B. and Waltman P. (1986) Mathematical models of population interactions with dispersal II: Differential survival in a change of habitat, *J. Math. Anal. Appl.* 115(1).

Freedman H. I. and Shukla J. B., (1989) The effect of a predator resource on a diffusive predator prey system, *Nat. Res. Model.* 3: 359-383.

Freedman H. I., Shukla J. B. and Takeuchi Y. (1989) Population diffusion in a two patch environment, *Math Biosci.* 95: 111-123.

Freedman H. I. and Waltman P., (1984) Persistence in models of three interacting predator-prey populations, *Math. Biosci.* 68: 213-231.

Freedman H. I. and Wu J. (1992) Steady state analysis in a model for population diffusion a multi patch environment, *Nonlinear Analysis: Theory, Method and Application*, 18(6): 517-542.

Frevert R. K., Schwab G. O., Edminster T. W., Barnes K. K. (1962), *Soil and water conservation engineering* : John Wiley and Sons, INC, New York.

Gadgil M. (1985), Social restraint on resource utilization, *The Indian Experience*.

- Gadgil M., Prasad S. N., and Ali R. (1983) Forest management in India : A critical review, *Social Action*, 33 : 127 - 155.
- Gard T. C., (1987) Uniform persistence in multispecies population models, *Math. Biosci.* 12: 221-229.
- Gatto M. and Rinaldi S. (1977) Stability analysis of predator-prey models via the Liapunov method, *Bull. Math. Biol.* 39: 339-347.
- Gause G. F., *The Struggle for Existence*, Williams and Wilkins, Baltimore (1934).
- Ghosh R. C. and Lohani D. N., (1972) Plantation forestry - Its implication in Indian economy, *Proc. 7th world for Cong.* Buenos Aires, Argentina.
- Goh B. S. (1976) Global stability in two species interactions, *J. Math. Biol.* 3: 313-318.
- Goh B. S. (1978) Global stability in a class of prey-predator models, *Bull. Math. Biol.* 40: 525-533.
- Gopalsamy K., (1977) Competition, dispersion and coexistence, *Math. Biosci.* 33: 25-33.
- Gopalsamy K. (1986) Convergence in a resource based competition system. *Bull. Math. Biol.* 48: 681-699.
- Grundy R. E., (1983) Local similarity solutions for the initial value problem in nonlinear diffusion, *IMA J. App. Math.* 30: 209-214.
- Gurtin M. E. (1974) Some mathematical models for population dynamics that lead segregation, *Quart. J. Appl. Maths.* 32: 1-8.
- Hadeler K. P. and Rothe F. (1975) Travelling fronts in nonlinear diffusion equation, *J. Math. Biol.*, 2: 251-263.
- Haigh M. J. (1984) Deforestation and disasters in northern India, *Land Use Policy*, 187-198.
- Hallam T. G. (1979) A temporal study of diffusion effects on a population modelled by quadratic growth, *Nonl. Anal. Theo. Math. Appl.* 3: 123-133.
- Hallam T. G. and Levin S. A. (1986) *Mathematical Ecology, Biomathematics*, Vol. 17, Springer-Verlag.
- Harada K. and Fukao T., (1978) Coexistence of competing species over a linear habitat of finite length, *Math. Biosci.* 38: 279-291.
- Hardin G., (1960) The competitive exclusion principle, *Science* 131: 1292-1298.
- Harper J. L., (1964), *The role of predation in vegetational diversity: in Diversity and Stability in Ecological Systems* (G. M. Woodwell and H. H. Smith, Eds.), Brookhaven National Laboratory,

Upton, N. Y., 48-62.

Harrison G. W. (1979) Global stability of predator-prey interactions, *J. Math. Biol.* 8: 159-171.

Harrison G. W. (1986) Multiple stable equilibria in a predator-prey system, *Bull. Math. Biol.* 48(2): 137-148.

Hastings A. (1978) Global stability of two species systems, *J. Math. Biol.* 5: 399-403.

Hastings A. (1978a) Spatial heterogeneity and the stability of predator prey systems: Predator-mediated coexistence, *Theoret. Population Biol.* 14: 380-395.

Hastings A. (1978b) Global stability in Lotka-Volterra systems with diffusion, *J. Math. Biol.* 6: 163-168.

Hastings A. (1982) Dynamics of a single species in a spatially varying environment: The stabilizing role of high dispersal rates, *J. Math. Biol.* 16: 49-55.

Heywood V. H. and Watson R. T. (1995) Global biodiversity assesment, Cambridge University Press, Cambridge, U. K. 1140 pages.

Hsu S. B. (1978) On global stability of a predator prey system, *Math. Biosci.* 39: 1-10.

Hsu S. B. (1981a) On resource based ecological competetion model with interference *J. Math. Biol.* 12: 45-52.

Hsu S. B. (1981b) Predator - mediated coexistence and extinction, *Math. Biosci.* 54: 231-248.

Hsu S. B. and Hubbell (1979) Two predators competing for two prey-species: An analysis of MacArthur's model, *Math. Biosci.* 47: 143-171.

Hsu, S. B. Hubbell S. P. and Waltman P., (1977) A mathematical theory of single-nutrient competitions in continuous cultures of microorganism, *SIAM J. Appl. Math.* 32: 366-383.

Hsu S. B. and Huang T. W., (1995) Global stability for a class of predator-prey systems *SIAM J. Appl. Math.* 55: 763-783.

Jenson A. L. (1987) Simple model for exploitative and interference competition, *Ecol. Model.* 35:113-121.

Jorne J. (1975) Negative ionic cross diffusion coefficients in electrolytic solutions, *J. Theor. Biol.* 55: 529.

Jorne J. (1977) The diffusive Lotka-Volterra oscillatory system, *J. Theor. Biol.* 65: 133-139.

Jorne J. and Carmi S. (1977) Liapunov stability of the diffusive Lotka-Volterra equations, *Math. Biosci.* 37: 51-61.

- Kazarinoff N. D. and van den Driessche P. (1978) A model predator-prey system with functional response, *Math. Biosci.* 39: 125-134.
- Khoshoo T. N. (1986) Environmental properties in India and sustainable development. ISCA New Delhi.
- Kirlinger G., (1986) Permanence in Lotka-Volterra equations: linked prey-predator systems, *Math. Biosci.* 82: 165-191.
- Kirlinger G., (1988) Permanence of some ecological systems with several predator and one prey species, *J. Math. Biol.* 26: 217-232.
- Kormondy E. J., *Concept of Ecology*, (Prentice Hall, London 1986).
- Kuzentsov Yu. A., Antonovsky M. Ya., Biktashev V. N. and Aponina E. A., (1994) A cross-diffusion model of forest boundary dynamics, *J. Math. Biol.* 32: 219-232.
- La Salle J. and Lefschetz S. *Stability by Liapunov's Direct Method with Applications*, (Academic Press, New York, 1961).
- Lancaster P. L. and Tismanetski M. (1985) *The Theory of Matrices*, Second Ed., Academic Press, New York.
- Larson W. E., Pierce F. J. and Dondy R. H. (1983) The threat of soil erosion to long term crop production, *Science*, 219: 458-465.
- Leung A., (1981) Stabilities for equilibria of competing species reaction-diffusion equations with homogeneous Dirichlet condition, *Funkclalaj Ekvacioj*, 24: 201-210.
- Levin S. A. (1974) Dispersion and population interactions, *Am. Nat.* 108: 207-228.
- Levin S. A. (1976) Spatial patterning and the structure of ecological communities, *Lectures on Mathematical Ecology*, T. G. Hallam and S. A. Levin, eds. Springer, New York, 295-321.
- Levin S. A. (1986) Population model and community structure in heterogeneous environments, in mathematical ecology, T. G. Hallam and S. A. Levin eds., New York, 295-321.
- Liou L. P. and Cheng K. S., (1988) Global stability of a predator-prey system, *J. Math. Biol.* 25: 65-71.
- Lotka A. J. *Elements of Physical Biology*, Williams and Wilkins, Baltimore (1925).
- MacArthur M. A., *Geographical Ecology*, Harper and Row, (1972).
- MacArthur R. (1978) Persistence and stability of single species and prey-predator system in spatially heterogeneous environments, *J. Math. Biol.* 39: 11-51.
- May R. M. (1976) *Models for two interacting populations in Theoretical Ecology*, Principles and Applications (R. M. May ed.) London: Blackwell Scientific publications.

- McMurtrie R. (1978) Persistence and stability of single species and prey-predator system in spatially heterogeneous environments, *Math. Biosci.* 39:11-51.
- Mimura M. and Kawasaki K., (1980) Spatial segregation in competitive interaction diffusion equations, *J. Math. Biol.* 9: 49-64.
- Mimura M. and Murray J. D. (1978) On a diffusive prey-predator model which exhibits patchiness, *J. Theor. Biol.* 75:249-262.
- Mimura M. and Nishida T., (1978) On some semilinear parabolic systems related to the Lotka-Volterra ecological model, *Publ. RIMS Univ.* 14: 269-282.
- Misra O. P (1987) Environmental Effects on Ecosystems: A Contribution to Mathematical Ecology, Ph. D. Thesis, IIT, Kanpur (India).
- Mitra D., Mukharjee D., Roy A. B and Ray S., (1992) Permanent coexistence in a resource based competition system, *Ecol. model.* 60: 77-85.
- MOA, (1984), Report of the Task Force to study all aspects of grazing and fodder to evolve a National Grazing Policy, Ministry of Agriculture GOI, New Delhi.
- Mukherjee D. and Roy A. B., (1990) Uniform persistence and global stability of two prey-predator pairs linked by competition, *Math. Biosci.* 99:31-45.
- Munn R. E. and Fedorov V. *The Environmental Assessment*, (IIASA Project Report, Vol.1, International Institute for Applied Systems Analysis Laxenburg, Austria 1986).
- Murray J. D. (1975) Non-existence of a wave solution for the class of reaction-diffusion equations given by the Volterra interacting population equation with diffusion, *J. Theor. Biol.* 52: 459-469.
- Nallaswamy R. and Shukla J. B, (1982) Effects of dispersal on the stability of a prey-predator system with functional response, *Math. Biosci.* 60: 123-132.
- Noy-Meir I. (1975) Stability of grazing systems: An application of predator-prey graphs, *J. Ecol.* 63: 459-481.
- Noy-Meir I. (1976) Rotational grazing in a continuously growing pasture: A simple model. *Agriculture Systems.* 1: 87-112.
- Noy-Meir I. (1978) Stability in simple grazing models: effects of explicit functions, *J. Theor. Biol.* 71: 347-380.
- Noy-Meir I. Gutman M. and Kalpan Y. (1989) Response of Mediterranean grassland plants to grazing and protection, *J. Ecol.* 77: 290-310.
- Okubo A. *Diffusion and Ecological Problems: Mathematical Models*, Biomathematics, Vol. 10 (Springer, Berlin, 1980).

- Paine R. T., (1966) Food web complexity and species diversity, *Amer. Nat.* 100: 65-75.
- Pao C. V., (1995a) Reaction diffusion equations with nonlocal boundary and nonlocal initial conditions *J. Math. Anal. & Appl.* 195(3): 702-718.
- Pao C. V., (1995b) Dynamics of reaction diffusion equations with nonlocal boundary conditions, *Quart. Appl. Math.* 53: 173-186.
- Parrish. J. D and Salla S. B, (1970) Interspecific competition, predation and species diversity, *J. Theoret. Biol.* 27: 207-220.
- Pimm (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*, The University of Chicago Press, Chicago, 434 pages.
- Porter J. W, (1972) Predation by *Acanthaster* and its effect on coral species diversity, *Amer. Nature*, 106: 487-492.
- Porter J. W, (1974) Community structure of coral reefs on opposite sides of the isthmus of Panama, *Science*, 186: 543-545.
- Quaddus M. A. (1985) On applying logistic models in technological forecasting. *Socio-Econ. Plann. Sci.* 20: 201-206.
- Quli S.M.S (1992) Management for preserving natural biodiversity, In : Abs. Proc. Summer Institute on Breeding, Management and Disease Control of wild Animals, Sponsored by ICAR at BVC Patna (16th June - 5th July, 1992) P : 503 - 504.
- Quli S. M. S and Siddiqui M. H. (1997) Biodiversity conservation : status survey methodology, conservation strategies and restorative measures, Myforest (in press).
- Rai B., Freedman H. I. and Addicot J. F., (1983) Analysis of models of mutualism in predator-prey and competitive systems, *Math. Biosci.* 65: 13-50.
- Rao M. R. M. *Ordinary Differential Equations - Theory and Applications*, (Arnold, London, 1981).
- Raychaudhari S., Sinha D. K. and Chattopadhyay J. (1996), Effect of time varying cross-diffusively in a two species Lotka-Volterra competitive system. *Ecol. Model.* 92 : 55-64.
- Repetto R. and Holmes T. (1983) The role of population in resource depletion in developing countries, *Population and Development Review*, 9:609-632.
- Rosen G. (1974) Global theorem for species distributions governed by reaction-diffusion equations, *J. Chemical Physics*, Vol 61 (9), 3676-3679.
- Rosen G. (1975) Solutions to systems of nonlinear-diffusion equations, *Bull. Math. Biol.* 37: 277-289.

Rosenzweig M. L. and MacArthur R. H. (1963) Graphical representation and stability conditions of predator-prey interactions, *Amer. Nat.* 47: 209-223.

Rothe F. (1976) Convergence to the equilibrium state in the Volterra-Lotka diffusion equation, *J. Math. Biol.* 3: 319-324.

Rothe F., (1984) Global solution of reaction-diffusion systems, Lecture Notes in Math., 1972, Springer-Verlag Berlin Heidelberg New York, Tokyo.

Sanchez D. A. (1968) Ordinary differential equations and stability theory: An introduction, Freeman, San Fransisco,

Sarkar A. K., Mitra D., Ray S. and Roy A. B., (1991) Permanence and oscillatory co-existence of a detritus-based prey-predator model, *Ecol. Model.* 53: 147-156.

Segal L. A. and Jackson J. L. (1972) Dissipative structure: an explanation and an ecological example, *J. Theor. Biol.* 37: 354-359.

Shrader Frechelte K. S. and Macoy E. D. (1993) Methods in Ecology, Cambridge University Press, Cambridge. 328p.

Shukla J. B. and Dubey B. (1996) Effect of changing habitat on species: Application to Keoladeo National Park, India, *Ecol Model.* 36: 91-99.

Shukla J. B. and Dubey B. (1997) Modelling the depletion and conservation of forestry resource: effect of population and pollution, *J. Math. Biol.* 36: 71-94.

Shukla J. B., Dubey B., Freedman H.I. (1996) Effect of changing habitat on survival of species. *Ecol. Model.* 87: (1-3), 205-216.

Shukla J. B., Freedman H. I., Pal V. N., Mishra O. P., Agarwal M., Shukla A. (1989) Degradation and subsequent regeneration of a forestry resource: a mathematical model, *Ecol. Model.* 44: 219-229.

Shukla J. B. and Verma S. (1981) Effects of convective and dispersive interactions on the stability of two species, *Bull. Math. Biol.* 43: 593-610.

Shukla V. P. and Shukla J. B. (1987) Multispecies food webs with diffusion, *J. Math. Boil.* 13: 339-344.

Shukla V. P. Shukla J. B. and Das P. C. (1981) Environmental effects on the linear stability of a three species food chain model *Math. Biosci.* 57: 35-58.

Sikder A. and Roy A. B., (1994a) Persistence of a generalised Gause-type prey-predator pair linked by competition, *Math. Biosci.* 122: 1-32.

Sikder A. and Roy A. B., (1994b) Multiple cyclic sets connecting saddle points and limit cycle (s) of a four species system and its uniform persistence, *Math. Biosci.* 121: 141-154.

Skellam (1951) Random dispersal in theoretical populations, *Biometrika*, 38: 196-218.

Smith R. L. (1972), *The ecology of man: An ecosystem approach*, New York, Harper and Row.

Takeuchi Y., (1986a) Global stability in generalized Lotka-Volterra diffusion systems, *Bull. Math. Anal. & Appl.* 116(1).

Takeuchi Y. (1986b) Diffusion effect on stability of Lotka-Volterra models, *Bull. Math. Biol.* 48: 585-601.

Takeuchi Y. and Lu. Z. (1995) Permanence and global stability for competitive Lotka-Volterra systems, *Nonlin. Anal. Th. Meth & Applic.* 21: 91-104.

Tansky M., (1978) Switching effect in prey-predator systems. *J. Theor. Biol.* 70: 263-271.

Timm U. and Okubo A. (1992) Diffusion-driven instability in a predator-prey system with time varying diffusivity, *J. Math. Biol.* 30: 307-320.

Verma S. (1980) Effects of convective and dispersive migration on stability of interacting species system in heterogeneous habitats, (Ph. D thesis) IIT Kanpur.

Volterra V., (1927) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi, *Mem. R. Com. Talassogr. Ital*, 131:1-142.

Whyte R. O. (1964) *The Grassland and Fodder Resources of India*. ICAR, New Delhi.

Wilson E. O. (1989) Threats of biodiversity, In the *Scientific American Special Issue (Managing Planet Earth)*, September, 108-117, New York.

Wollkind D. J. Collings J. B. and Barba M. C. B. (1991) Diffusive instabilities in a one dimensional temperature dependent model system for a mite predator-prey interaction on fruit trees. Dispersal mortality and aggregative prey effects, *J. Math. Biol.* 38: 35-362.

Waring R. H. and Schiessinger W. H. (1985) *Forest ecosystem: concepts and management*, Academic Press, New York.

Zachar D. (1982), *Soil Erosion*, Elsevier Amsterdam, 540P.